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LINKING AMAZONIAN SECONDARY SUCCESSION FOREST GROWTH TO SOIL PROPERTIES

D. LU,[1]* E. MORAN[1,2] AND P. MAUSEL[3]

[1]*Center for the Study of Institutions, Population, and Environmental Change (CIPEC), Indiana University, Bloomington, USA*
[2]*Anthropological Center for Training and Research on Global Environmental Change (ACT), Indiana University, Bloomington, USA*
[3]*Department of Geography, Geology, and Anthropology Indiana State University, Terre Haute, USA*

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ABSTRACT

The Amazon Basin has suffered extensive deforestation in the past 30 years. Deforestation typically leads to changes in climate, biodiversity, hydrological cycle, and soil degradation. Vegetation succession plays an important role in soil restoration through accumulation of vegetation biomass and improved soil/plant interaction. However, relationships between succession and soil properties are not well known. For example, how does vegetation succession affect nutrient accumulation? Which soil factors are important in influencing vegetation growth? What is the best way to evaluate soil fertility in the Amazon basin? This paper focuses on the interrelationships between secondary succession and soil properties. Field soil sample data and vegetation inventory data were collected in two regions of Brazilian Amazonia (Altamira and Bragantina). Soil nutrients and texture were analyzed at successional forest sites. Multiple regression models were used to identify the important soil properties affecting vegetation growth, and a soil evaluation factor (SEF) was developed for evaluating soil fertility in Alfisols, Ultisols, and Oxisols, which differ in the ways they affect vegetation growth. For example, the upper 40 cm of soil is most important for vegetation growth in Alfisols, but in Ultisols and Oxisols deeper horizons significantly influence vegetation growth rates. Accumulation of vegetation biomass increased soil fertility and improved soil physical structure in Alfisols but did not completely compensate for the nutrient losses in Ultisols and Oxisols; however, it significantly reduced the rate of nutrient loss. Copyright © 2002 John Wiley & Sons, Ltd.

KEY WORDS: Amazonia; secondary succession; soil fertility; soil evaluation factor; above-ground biomass; multiple regression analysis

INTRODUCTION

The deforestation rate in the Amazon basin has risen during the past 30 years because of road building and logging (Moran *et al.*, 1994) and agropastoral expansion (Fearnside, 1987; Skole *et al.*, 1994). Deforestation typically leads to climate change (Shukla *et al.*, 1990; Houghton, 1991), losses of biological diversity (Skole and Tucker, 1993), alteration of the hydrologic cycle, increased soil erosion, and loss of productivity (Lavelle, 1987; Ross *et al.*, 1990). In tropical rainforests, most soils are infertile with a low content of nutrients, making nutrient cycling an important mechanism in maintaining the ecosystem. When the process is disturbed, nutrients can be rapidly lost (Jordan, 1989), and the greater the disturbance of a mature forest, the longer it will take to recover. An extreme situation is when disturbance produces intense degradation with no chance for recovery. In this case, the process may be followed by ecosystem degradation (loss of structural and functional integrity), environmental degradation (loss of populations or critical functions), biodiversity degradation (loss of genetic diversity), and agricultural degradation (loss of productivity) (Vieira *et al.*, 1993). When these extremes do not occur, succession starts the

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*Correspondence to: Dr D. Lu, Center for the Study of Institutions, Population, and Environmental Change (CIPEC), Indiana University, Bloomington, IN 47408, USA. E-mail: dlu@indiana.edu

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recovery of vegetation. Abandonment brings rapid transformation to a competitive environment that induces successional change (Kellman, 1980).

Succession generally refers to changes in species composition and abundance during or following the disturbance of a site. The process is dependent on four main sources of recovery: regeneration of remnant individuals, germination from the soil seedbank, sprouting from cut or crushed roots and stems, and seed dispersion and migration from other areas (Tucker *et al.*, 1998). In the Amazon, three central factors control succession: availability of regeneration mechanisms (e.g. sprouts, seeds buried in the soil, seeds dispersed from surrounding areas); availability of seed germination and seedling establishment in microhabitats (e.g. fruit trees and slash piles); and availability of nutrients, which may be affected by previous management (Uhl, 1987). Tree species diversity and biomass accumulation vary depending on time and intensity of land use before recovering. Different degrees of disturbance result in different rates of secondary regrowth (Uhl *et al.*, 1988). Successional vegetation appears to be better adapted than crop plants to the diminishing nutrient availability. Another important adaptation of successful successional species is their high dissemination capability and high sprouting capability after fire, both depending on disturbance intensity and duration (Vieira *et al.*, 1996).

Soil fertility and land-use history emerge as critical factors influencing the rate of forest regrowth (Tucker *et al.*, 1998). Uhl *et al.* (1982) found that the time of recovery depends on the intensity of land use following the removal of forest. Large, cleared patches, where seed sources are far away, may take hundreds of years to return to primary forest, and different regeneration patterns depend on land management following deforestation. In forests regenerated vigorously on sites that had only light use, the biomass accumulation rate was fast and tree species richness was high. Moderately grazed pastures also developed forest, but biomass accumulation and tree species richness were lower. Abandoned pastures subjected to heavy use had the least distinct patterns of succession (an eight-year-old site was dominated by grasses and forbs). Only where land has been used too intensively for long periods is reforestation uncertain. Thus, in the absence of fire, forests recover on abandoned sites, accumulating biomass and species at a rate that is inversely related to the intensity of use prior to abandonment (Nepstad *et al.*, 1991).

Increasing pressure from the human population's need for more timber, fuelwood, and agricultural lands has led to rapid deforestation rates in the Amazon basin. Inadequate management of deforested lands has also resulted in soil degradation. Thus, an increasing amount of soil fertility/quality is being lost because of poor management, reducing further the total available arable land. This in turn leads to more deforestation for food production, forming a vicious cycle of deforestation and soil degradation. Although high temperature and humidity in the tropical regions induce rapid rock weathering, the surface layers of soil are easily eroded and nutrients are lost rapidly if the forest is cleared. Vegetation plays an important role in providing and holding nutrients in the soil and maintaining soil structure (Lavelle, 1987; Moran *et al.*, 2000b). For example, vegetation protects the soil from rapid drying, compaction, and leaching by rain (Dos Santos, 1987). Vegetation cover affects soil temperature and moisture and forms a microenvironment suitable for vegetation growth. The presence of forest also modifies soil fertility through the interaction of vegetation biomass and soil. Vegetation roots extract nutrients released by the mineralization of the organic reserves and leached down from the surface, reducing the nutrient leaching (Lavelle, 1987). Vegetation also regulates the natural ecosystem, optimizes the release of nutrients or their accumulation in stable forms, and conserves the soil structure. Living roots have considerable impact on the soil organisms within the rhizosphere, and dead leaves and roots provide the energy and nutrients to the soil system (Lavelle, 1987). The vegetation roots' diffuse systems and associated mycorrhiza allow them to act as scavengers and collect small amounts of nutrients occurring over a wide area and a large soil volume (Bradshaw, 1999). Because of this scavenging, losses by leaching are substantially reduced once vegetation becomes established. Nutrients become concentrated in the plant and ultimately accumulate in the surface layers of the soil through litter-fall accumulation and decomposition. In this way plant growth leads to an improvement of available nutrient levels in the soil. A large proportion of nutrients, e.g. K, Ca, Mg, P, and N, is stored in the plant biomass, especially in the Oxisol and Ultisol sites.

Previous work has shown that successional forests play an important role in soil restoration through accumulation of biomass, build-up of litter and organic matter, and other beneficial soil/plant interactions (Moran *et al.*, 2000a,b; Moran *et al.*, in press). Soil fertility and physical structure, land use, and original vegetation cover are the most important aspects affecting vegetation regrowth in the Amazon basin (Tucker *et al.*, 1998; Moran *et al.*, 2000b). Meanwhile, other factors such as climate (e.g. temperature and precipitation), soil parent material, and time can also influence soil fertility (Buol *et al.*, 1989). However, for Amazon soils, it is not clear how different soil chemical and physical patterns change within different soil layers and between different successional stages, what soil patterns are the main factors in affecting vegetation growth, and how to evaluate soil fertility. Therefore, this paper addresses these questions through analyzing Alfisols, Ultisols, and Oxisols in Altamira and Bragantina in the eastern part of the Brazilian Amazon.

STUDY AREAS

The Altamira study area is located along the Transamazon Highway in the Brazilian state of Pará (Figure 1). The city of Altamira and the Xingu River form the eastern edge of the study area. In the 1950s an effort was made to attract colonists from northeast Brazil, mostly from Piauí, who came and settled along streams as far as 20 km from the city center. With the construction of the Transamazon Highway in 1970, this population and older Caboclo settlers from earlier rubber eras claimed land along the new highway and legalized their land claims (Moran, 1981). Early settlement was driven by geopolitical goals and political economic policies that transferred production of staples like rice, corn, and beans from southern Brazilian states to the Amazon region. The region has had a gradual shift to a more diverse set of land uses: pasture, cocoa, sugar cane, black pepper, and staple crops. Mahogany is beginning to be planted with cocoa groves as a diversification strategy and can be expected to benefit landowners who have the better soils in this area (Moran *et al.*, 2000b). Altamira has experienced high rates of deforestation and secondary succession associated with implementation of agropastoral projects since 1971. The dominant native types of vegetation are mature moist forest and liana forest. Nutrient-rich Alfisols, as well as

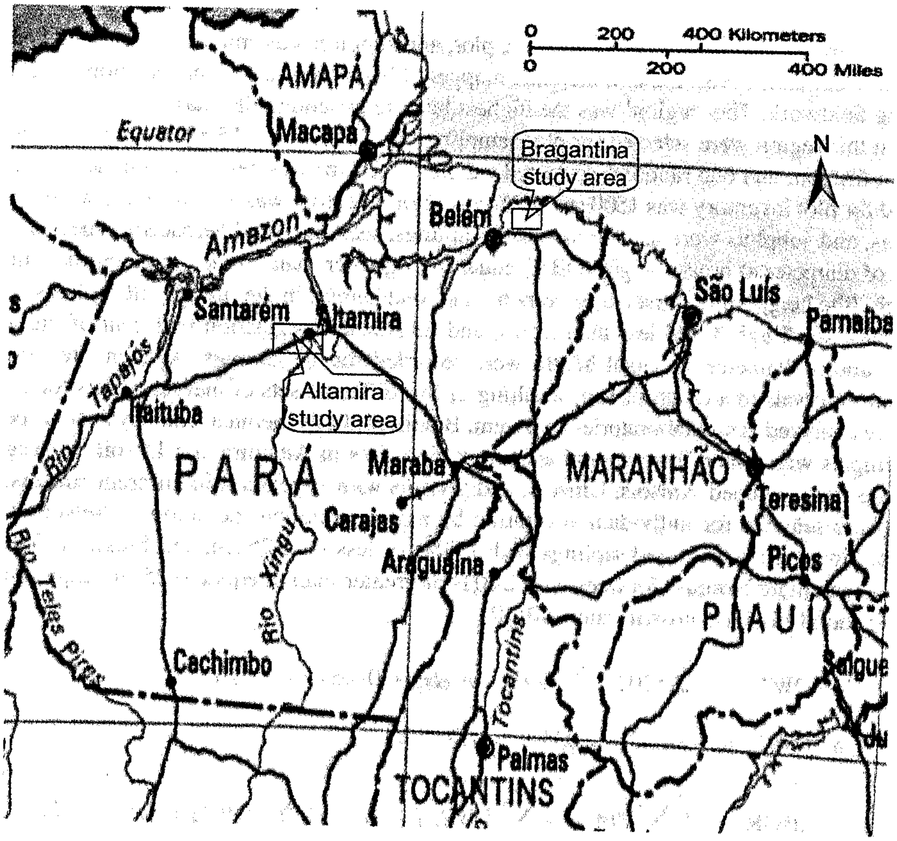

Figure 1. Location of the study areas.

nutrient-poor Ultisols and Oxisols can be found in this area. Annual rainfall is approximately 2000 mm and is concentrated from late October through early June. The average temperature is about 26°C.

The Bragantina study area is located within the municipality of Igarapé-Açú in the state of Pará (Figure 1). The vegetation in this region is mostly comprised of secondary growth forest (capoeira), flooded forest (igapó), and a few remaining areas of dense forest. At the beginning of the 20th century, almost one million hectares of dense, tropical rainforest covered the Bragantina region; however, less than 2 per cent of the original forests remained by 1960. The dense forest that once surrounded the town of Castanhal had an average height of 23 m. Heavy occupation of this region has eliminated almost all dense forests and transformed the landscape into a mosaic comprised of a variety of secondary vegetation (Tucker *et al.*, 1998). The main agricultural products are passion fruit (maracujá), manioc, oil palm, rice, corn, beans, and cotton. Other important crops are pepper, papaya, tobacco, melon, sugar cane, rubber, avocado, citrus, coconut, banana, cocoa, and mango. The Bragantina study area is dominated by nutrient-poor soils (i.e. Oxisols and Ultisols). Land use in this region has gone through several phases, and today the dominant form is short-fallow swidden cultivation and pasture development. Cultivation of secondary growth areas has been common for decades, and islands of mature forest are rare (Moran *et al.*, 2000b). The long settlement history, high human population density, repeated land clearing, including burning, over the past century in Bragantina has degraded the landscape. In Bragantina, annual rainfall ranges from 2200 mm to 2800 mm with annual variation as much as +/− 1000 mm from the mean. The average annual temperature of this region is 25–26°C, and the dry period extends from September through November.

METHODS

Data Collection and Analysis

A nested sampling strategy, organized by region, site, plot, and subplot, was employed to collect field data (CIPEC, 1998; Moran and Brondízio, 1998). Landsat thematic mapper (TM) images and global position system (GPS) devices were used during fieldwork. The 'region' was the highest level representing the study area that included all sample sites. The sites in this region were selected for plot sampling. Ten plots (10 × 15 m) in each site were allocated in a stratified random fashion, and one randomly selected subplot (5 × 2 m) was nested within each plot. So in each site the area sampled for plot inventory was 1500 m^2 and for subplot inventory was 100 m^2. Plots were designated for the inventory of trees, and subplots were used to inventory saplings, seedlings, and herbaceous species. In each plot, all individual trees of diameter at breast height (DBH) equal to or greater than 10 cm were identified and measured for DBH, stem height (the height of the first major branch), and total height. In the subplot, all saplings (DBH from 2 cm to less than 10 cm), seedlings (DBH less than 2 cm), and herbaceous vegetation (per cent of ground cover) were identified and counted; diameter and total height were recorded for all saplings. At each site, soil samples were collected at 20 cm intervals to a depth of 1 m, resulting in five different sets of measurements for each sample site. Soil samples were analyzed at soil laboratories in Belem, Brazil, for both chemical and physical properties. Data was recorded and samples were taken from 14 soil and vegetation sites in Altamira and 15 soil and vegetation sites in Bragantina. These sites included Alfisols, Ultisols, and Oxisols with vegetation in different successional stages.

Two models were selected for individual vegetation biomass estimation. Equation 1 (Nelson *et al.*, 1999) was used to calculate biomass for trees and saplings with DBHs of less than 25 cm, and Equation 2 (Overman *et al.*, 1994) was used to calculate biomass for trees with DBHs of greater than or equal to 25 cm. Equation 3 was used to calculate above-ground biomass growth rate (ABGR).

$$\ln\,(DW1) = -2{\cdot}5202 + 2{\cdot}1400 * \ln\,(D) + 0{\cdot}4644 * \ln\,(H) \tag{1}$$

$$\ln\,(DW2) = -3{\cdot}843 + 1{\cdot}035 * \ln\,(D^2 * H) \tag{2}$$

$$\mathrm{ABGR} = \left[\left(\sum_{i=1}^{m} DW1_i + \sum_{j=1}^{n} DW2_j\right)\Big/ AP + \left(\sum_{k=1}^{s} DW1_k\right)\Big/ AS\right]\Big/ T, \tag{3}$$

where D is DBH (cm); H is total height (m); $DW1$ is individual tree or sapling biomass (kg) when DBH is less than 25 cm; $DW2$ is the individual tree biomass when DBH is greater than or equal to 25 cm; m is the total number of trees in a site with DBH greater than or equal to 25 cm; n is the total number of trees in a site with DBH from 10 cm to less than 25 cm; and s is the total number of saplings with DBH from 2 cm to less than 10 cm in subplot areas sampled within a site. AP and AS are the total plot areas and total subplot areas in a site (in m^2), respectively, and T is the vegetation age in years. ABGR is expressed in $kg\,m^{-2}\,yr^{-1}$.

Soil Data Analysis

In humid tropical regions, high temperature and humidity lead to a rapid turnover of nutrients between vegetation, litter, and soil. Because of very low nutrient reserves and low cation exchange capacity in Oxisols and Ultisols, the nutrients in the natural ecosystems are largely within living or dead plant tissues (Buol *et al.*, 1989). Vegetation biomass accumulation has a critical role in maintaining soil fertility and soil physical structure. Some previous research has shown that vegetation biomass is closely related to nutrient accumulation or soil fertility (Lopes and Cox, 1977; Regina, 2000; Hartemink, 2001; Hunter, 2001; Johnson *et al.*, 2001; Lilienfein *et al.*, 2001). For instance, Hunter (2001) analyzed above-ground biomass and nutrient uptake of three tree species (*Eucalyptus camaldulensis*, *Eucalyptus grandis*, and *Dalbergia sissoo*) at three years of age in southern India. Johnson *et al.* (2001) compared carbon and nutrient concentrations and stocks in above-ground vegetation and soils between secondary forests and primary forest fragments in the Bragantina region, Brazil. Hartemink (2001) tested succession vegetation (23-month-old *Piper aduncum* and *Imperata cylindrica*) and nutrient accumulation relations in the humid lowlands of Papua New Guinea. Moran *et al.* (2000a,b) explored relationships between soil fertility and succession in the Amazon basin and concluded that soil fertility was particularly important in explaining interregional differences in rates of regrowth and that land use and landscape diversity were more important in intraregional analysis. Vegetation growth can significantly reduce soil erosion and nutrient leaching. Above-ground biomass is a factor that seems to respond to soil nutrient status. However, total standing vegetation biomass is not appropriate for comparative analysis between different sites because total above-ground biomass amount is related to vegetation age, in addition to soil fertility, land use, and topography. Average ABGR is more accurately associated with soil conditions in different sites. For example, nutrient-rich soil induces fast vegetation growth rate and rapid vegetation biomass accumulation. Nutrient-poor soil results in slow vegetation growth rate. Therefore, vegetation biomass growth rate was used to analyze soil conditions in this research and was selected as a dependent variable. Soil texture (e.g. clay, silt, fine sand, and coarse sand) and soil chemical components (e.g. Ca, Mg, Al, OM, N) were used as independent variables, and multiple regression models were developed to explore important soil factors that affect vegetation regrowth rate.

Soil Evaluation Methods

Because of the complexity of soil properties, it is difficult to find an appropriate method to evaluate soil conditions. Soil scientists have made great efforts to develop methods to assess soil conditions. For example, soil quality is a combination of the physical, chemical, and biological properties that contribute to soil function (Knoepp *et al.*, 2000). Scientists try to construct soil quality standards and guidelines to assess soil capacity to support sustainable development in forests (Knoepp *et al.*, 2000; Page-Dumrose *et al.*, 2000; Schoenholtz *et al.*, 2000). However, it is difficult to establish such a soil quality standard because of the diversity of soil properties, climate conditions in the ecosystem, appraisal techniques, and soil uses (Page-Dumrose *et al.*, 2000). For a homogeneous forest with similar vegetation ages, a site index is often used to evaluate the soil conditions, and the dominant tree height is used to model the site index. However, in a complex vegetation stand structure with abundant vegetation species and dissimilar vegetation ages, a site index or dominant tree height is not appropriate for evaluation of soil conditions in the moist tropical regions. To date, an effective method to evaluate soil fertility is still lacking in the humid tropical region. Moran and his colleagues (1998; 2000a,b, in press) used a soil fertility index (SFI) to explore the relationship between soil fertility and secondary succession rate and crop choice. They used Equation 4 to calculate SFI values.

$$\mathrm{SFI} = \mathrm{pH} + \mathrm{OM} + \mathrm{P} + \mathrm{K} + \mathrm{Ca} + \mathrm{Mg} - \mathrm{Al} \tag{4}$$

The drawback of Equation 4 is that the meaning of SFI is not very clear because different units are used in the SFI model. For example, the unit of Ca, Mg, K, and Al is Meq 100 g^{-1}, P is ppm, and OM is a per cent. Meanwhile, the pH value is a comprehensive factor that is strongly related to the amount of Ca, Mg, and Al. Usually, the soil chemical components Ca and Al have strongly negative relationships. High amounts of Ca and Mg that are associated with a low amount of Al lead to a high pH value, making soils alkaline. Conversely, lower amounts of Ca and Mg associated with a high amount of Al result in a low pH value, making soils acidic. So pH is not an independent value; it depends on the relative proportion of Ca, Mg, and Al in the soil. Neither a very high nor a very low pH value is suitable for good vegetation growth. In the humid tropical region, due to high temperature and humidity, nutrients are easily lost through soil erosion and leaching, leading to acidic soil. Therefore, a new model called a soil evaluation factor (SEF) is developed in this paper:

$$\mathrm{SEF} = [\mathrm{Ca} + \mathrm{Mg} + \mathrm{K} - \log(1 + \mathrm{Al})] * \mathrm{OM} + 5 \tag{5}$$

High amounts of Ca, Mg, and K are beneficial for vegetation growth, but high Al restricts vegetation growth. Soil organic matter is related to nutrient availability, soil structure, air and water infiltration, and water retention (Knoepp *et al.*, 2000). Soil physical structure is also related to nutrient conditions. A clay-rich soil structure can hold nutrients in the soil for a long time, but a coarse sand-rich soil structure permits nutrients to leach rapidly. SEF is a comprehensive factor that represents soil fertility. The unit of Ca, Mg, K, and Al is Meq 100 g^{-1}, OM is a per cent, and the SEF unit is also Meq 100 g^{-1}. The use of the constant 5 in this model avoids negative SEF values if there are high Al amounts in the soil. An SEF value with less than 5 indicates extremely poor soil fertility. Higher SEF indicates higher soil fertility; for example, the SEF of the surface Alfisol in advanced successional forest can reach 15. The SEF value is used to evaluate soil fertility in the different soil types and different successional stages in this paper.

RESULTS AND DISCUSSION

Soil Properties in the Soil Profile of Different Successional Stages

Table I provides soil nutrients and physical structures in different soil layers, covering different successional stages. The soil samples used are Alfisols in Altamira and Ultisols and Oxisols in Bragantina. Three to five soil samples were averaged for each soil layer based on different successional stages.

In Altamira, considering the soil properties at different depths of the soil profile but with the same successional stage, pH value increases with depth from the surface to 1 m but Ca, Mg, K, N, and OM decrease. The Al content in the initial secondary succession (SS1) increases with depth, but in the intermediate secondary succession (SS2) and advanced secondary succession (SS3) it decreases. Coarse sand content decreases with depth, but clay content increases. Silt and fine structures in SS1 change slightly and unstably with depth, but in SS2 and SS3 they decrease. Considering the same depth level in the soil profile but in different successional stages, pH value decreases from SS1 to SS2, then slightly increases from SS2 to SS3. Ca increases from SS1 to SS3 in the surface soil (0–20 cm). In the subsurface soil (from 20 to 100 cm), Ca increases from SS1 to SS2 but decreases from SS2 to SS3. Mg and N decrease from SS1 to SS2, then increase from SS2 to SS3. Al and OM increase from SS1 to SS2, then significantly decrease from SS2 to SS3. K changes only slightly in different successional stages. Coarse sand content increases from SS1 to SS2, then decreases from SS2 to SS3. Fine sand content decreases in the surface soil, but in the other layers of soil it increases from SS1 to SS3. Silt content increases, especially from SS2 to SS3. Clay content changes only slightly in the surface soil, but in the subsurface, clay content decreases from SS1 to SS3. Analyses of these data indicate that vegetation growth improved the soil physical structure through the vegetation root system.

In Bragantina, considering the same successional stages but different depths in soil profile, pH value increases from surface to 1 m depth but Ca, Mg, K, Al, N, and OM decrease. Coarse sand, fine sand, and silt content decrease with depth but clay content increases. This indicates that clay illuviates from surface to depth and makes the surface coarser (sandier). Considering the same soil depth layers in the soil profile but with different successional stages, pH value decreases from SS1 to SS2, then increases from SS2 to SS3. Ca and Mg decrease as vegetation

Table I. Comparison of soil properties in different succession stages

	Type	Depth	pH	Ca	Mg	K	Al	N	OM	Coarse	Fine	Silt	Clay
Altamira (Alfisols)	SS1	0–20	5·15	2·15	0·60	0·07	0·15	0·19	2·19	15	19	12	55
		20–40	5·40	1·00	0·50	0·03	0·15	0·15	1·44	10	12	14	65
		40–60	5·35	0·80	0·50	0·01	0·15	0·10	1·11	7	9	16	68
		60–80	5·45	0·70	0·45	0·02	0·20	0·10	0·80	8	11	11	70
		80–100	5·55	0·60	0·65	0·01	0·25	0·09	1·35	5	9	16	70
	SS2	0–20	4·60	2·20	0·55	0·07	1·15	0·19	3·49	14	14	17	56
		20–40	4·90	1·70	0·40	0·02	1·00	0·11	2·00	14	12	14	61
		40–60	4·95	1·75	0·15	0·02	0·85	0·09	1·37	12	11	15	63
		60–80	5·10	1·25	0·30	0·01	0·90	0·07	1·06	11	10	14	66
		80–100	5·25	1·30	0·00	0·01	0·75	0·06	0·84	10	11	14	66
	SS3	0–20	4·95	2·90	0·55	0·06	0·25	0·22	2·85	10	11	25	55
		20–40	4·90	1·00	0·70	0·04	0·25	0·16	1·59	8	9	21	63
		40–60	4·95	0·85	0·35	0·02	0·20	0·11	1·20	7	9	23	61
		60–80	5·00	0·70	0·45	0·01	0·15	0·10	0·95	7	9	19	65
		80–100	5·30	0·65	0·55	0·01	0·05	0·10	0·58	7	9	21	64
Bragantina (Oxisols and Ultisols)	SS1	0–20	5·16	0·76	0·34	0·02	0·48	0·05	1·55	39	37	14	10
		20–40	4·92	0·36	0·22	0·02	0·72	0·05	0·75	34	36	11	19
		40–60	4·98	0·28	0·20	0·01	0·72	0·04	0·82	32	32	14	22
		60–80	5·10	0·30	0·18	0·01	0·70	0·04	0·85	33	31	12	24
		80–100	5·06	0·32	0·18	0·01	0·68	0·03	1·03	32	34	10	24
	SS2	0–20	4·67	0·33	0·25	0·03	0·80	0·06	1·79	42	34	13	11
		20–40	4·75	0·25	0·15	0·03	0·83	0·04	1·40	40	30	13	17
		40–60	4·80	0·27	0·18	0·02	0·87	0·04	0·75	35	31	12	22
		60–80	4·92	0·28	0·16	0·02	0·82	0·04	0·47	32	33	12	23
		80–100	4·90	0·30	0·20	0·02	0·72	0·03	0·74	35	29	11	25
	SS3	0–20	4·93	0·47	0·23	0·03	0·70	0·06	1·53	48	31	12	9
		20–40	5·03	0·20	0·13	0·01	0·90	0·05	1·26	42	29	11	18
		40–60	5·03	0·13	0·07	0·01	0·70	0·04	0·95	41	28	11	20
		60–80	5·10	0·15	0·10	0·01	0·70	0·04	0·79	39	28	11	21
		80–100	5·27	0·13	0·10	0·01	0·43	0·04	0·86	38	29	11	22

Note: The unit for soil depth is cm; the unit for Ca, Mg, K, and Al is Meq $100\,g^{-1}$; the unit for N, OM, and soil structure (coarse, fine, silt, and clay) is per cent.

grows. K and Al increase from SS1 to SS2, then decrease from SS2 to SS3. N increases slightly as vegetation grows. OM increases from SS1 to SS2 then decreases from SS2 to SS3 in the upper 40 cm of surface soil, but OM decreases from SS1 to SS2, then increases from SS2 to SS3 in the 40–100 cm layers of the soil profile. Coarse sand content increases from SS1 to SS3 but fine sand, silt, and clay contents decrease. This indicates that clay content is still removed as vegetation grows, making the soil increase in coarse sand content.

Comparing soil properties between Altamira and Bragantina indicates that pH values of SS1 and SS2 are higher in Altamira than in Bragantina. Ca, Mg, K, N, and OM contents are much higher in Altamira than in Bragantina. Al content in SS1 and SS3 is lower in Altamira than in Bragantina, but Al in SS2 is the converse. The clay and silt contents are much higher in Altamira than in Bragantina, but the coarse and fine sand contents are the inverse. Overall, Altamira has much higher nutrient contents and higher clay content than Bragantina. Physical structure is related to nutrient content retention in the soil layers. Higher clay content associated with lower coarse sand content can hold more nutrients in the soil. Conversely, low clay content associated with high coarse sand content results in low nutrient retention in the soil.

Identification of Important Soil Factors Influencing Vegetation Growth

Table II provides the regression coefficient and significant variables identified from multiple regression models for each soil layer in Altamira and Bragantina. In Altamira, regression coefficients in the upper two soil layers

Table II. Relationships between soil properties and average yearly biomass growth rate

Study area	Depth	R	Significant variables
Altamira (Alfisols)	0–20	0·788*	N%, Silt, Clay, Fine, Mg, Al, OM%, K
	20–40	0·791*	OM%, Clay, Fine, Mg, N%, Al, Ca
	40–60	0·630	Fine, N%, Ca
	60–80	0·595	Fine, Ca
	80–100	0·588	No variables
Bragantina (Ultisols and Oxisols)	0–20	0·828*	Ca, Mg, Al, K
	20–40	0·798*	K, Fine, OM%
	40–60	0·689*	Al, OM%, Fine
	60–80	0·850*	Al, OM%, Fine, Ca
	80–100	0·882*	Al, N%, Fine, OM%

Note: *Indicates that regression coefficient is significant at 0·05 level.

(0–20 cm and 20–40 cm) are significant at the 0·05 level, but they are not significant in the other three layers. Soil nutrients and physical structures in the upper two layers are critical for the vegetation biomass accumulation rate. In the 40–80 cm layers, fine structure and Ca are important factors in influencing vegetation growth. Below a depth of 80 cm, soil texture and nutrients do not significantly affect vegetation biomass growth rate. In the Alfisols, the interaction between vegetation and soil seems to be more concentrated in the upper 80 cm. The abundance of nutrients, organic matter, and moisture in the topsoil may not require the deep rooting for good growth as noted by Nepstad *et al.* (1999) in particular areas where strong moisture deficiency occurs in sand-dominated profiles.

In Bragantina, regression coefficients in all five layers are significant at the 0·05 level, especially in the deeper soil at 60–100 cm, which emerge as strongly related to vegetation growth rate. Nutrients such as Ca, K, and Al and fine sand content are important factors in influencing vegetation growth rate in this nutrient-poor area; OM, especially in different layers, has significant influence on the vegetation biomass accumulation rate. Coarse sand content makes nutrients leach rapidly in Ultisols and Oxisols, resulting in very poor nutrient content in these soils. Deficiency of nutrients (e.g. Ca, Mg, K) and abundant Al restrict vegetation growth. Vegetation roots spread both horizontally and vertically in the soil profile to find nutrients and water.

The physical structure of Alfisols is very important to vegetation growth. In Ultisols and Oxisols, soil nutrients and organic matter have greater influence on vegetation growth. This proves that in nutrient-rich soils such as Altamira's Alfisols, nutrients tend to be less concentrated in the vegetation biomass itself and soil nutrient stocks are more important. But in nutrient-poor soils such as Bragantina's Oxisols and Ultisols, nutrient stocks are largely concentrated in the vegetation and in the organic matter.

Evaluation of Soil Condition

Previous analysis indicates that nutrient accumulation is related to physical structure. Ca, Mg, K, and OM have significant effects on biomass accumulation. Increasing these nutrients induces fast vegetation growth rate, but increasing Al content tends to restrict vegetation growth. The SEF value derived from soil chemical patterns provides a way to evaluate soil fertility conditions in different soil types or successional stages. Figure 2 illustrates SEF values in the soil profile under different successional stages in Altamira and Bragantina.

In Altamira, soil fertility of Alfisols decreases with depth, which is especially obvious in the upper 60 cm. SS3 and SS2 have significantly higher SEF values than SS1 in the surface layer. This indicates that vegetation growth contributes to rapidly increase soil fertility in the surface soil. SS2 has the highest SEF values and SS1 has the lowest in the layers between 20 cm and 80 cm. But in the 80–100 cm layer, SS1 has the highest SEF value. This indicates that soil nutrients leached down from surface to deep layers in the initial few years of vegetation regrowth. On the other hand, vegetation roots find it difficult to absorb the accumulated soil nutrients beyond a depth of 80 cm due to restriction posed by the heavy clay structure.

In Bragantina, SEF value decreases from 0–40 cm, then stays relatively low and stable in the layers between 40 cm and 100 cm. SS1 has the highest SEF and SS3 has the lowest in the surface layer; however, SEF values for all

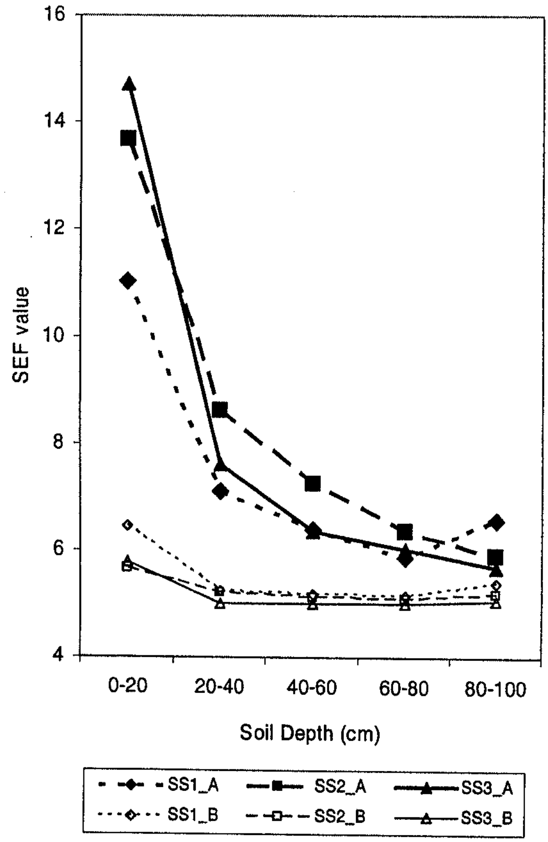

Figure 2. Comparison of SEF values of successional forests in Altamira (A) and Bragantina (B).

successional stages are very similar and stay at low values. At a depth of 80–100 cm, SEF values increase slightly. This indicates that high coarse sand content in Bragantina induces rapid nutrient leaching. In the surface layer, nutrient accumulation from vegetation growth cannot compensate for the nutrient loss, resulting in decreased SEF value. In the subsurface layers, SS1 and SS2 have similar SEF values, but SS3 has a lower SEF value because of the nutrient absorption of vegetation roots and nutrient leaching. Figure 2 indicates that Altamira has much higher SEF values than Bragantina and shows that Alfisols have higher soil fertility than Ultisols and Oxisols.

Figure 3 illustrates SEF dynamic change in the soil profiles of Altamira, covering Alfisols, Ultisols, and Oxisols. Analysis of Figure 3 confirms that Alfisols have much higher SEF values than Ultisols and Oxisols, and Oxisols have the lowest SEF value. The SEF value in Alfisols decreases with depth from surface to 80 cm and is stable from 80 cm to 100 cm. The SEF value in Ultisols decreases slightly from 0 cm to 40 cm and then is stable in the 40–100 cm layers. Again, the SEF value in Oxisols decreases slightly from 0 cm to 40 cm but increases to approximately its original value from 40 cm to 100 cm. This indicates that Alfisols concentrate more nutrients in the surface layers and that rapid vegetation biomass accumulation increases the soil fertility. Conversely, Ultisols and Oxisols concentrate their limited nutrients along the soil profile, and the slow vegetation biomass accumulation cannot compensate for the nutrient losses due to leaching.

Figure 4 illustrates the average ABGRs of different successional stages in Altamira and Bragantina. The rate increases as vegetation grows in Altamira, but it decreases with time in Bragantina. In Altamira, the sample data are from Alfisols, which have high-nutrient, rich clay and silt contents (clay and silt contents account for 80 per cent). This high soil fertility maintains the rapid vegetation growth. Conversely, Ultisols and Oxisols in Bragantina,

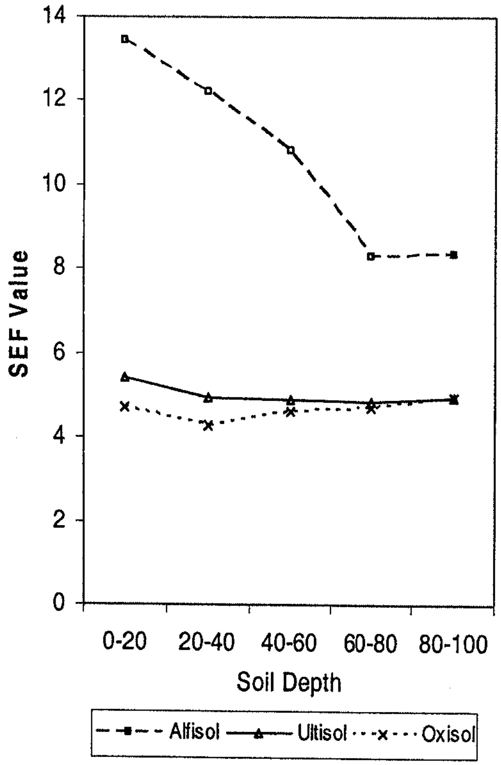

Figure 3. Comparison of SEF values of different soil types in Altamira.

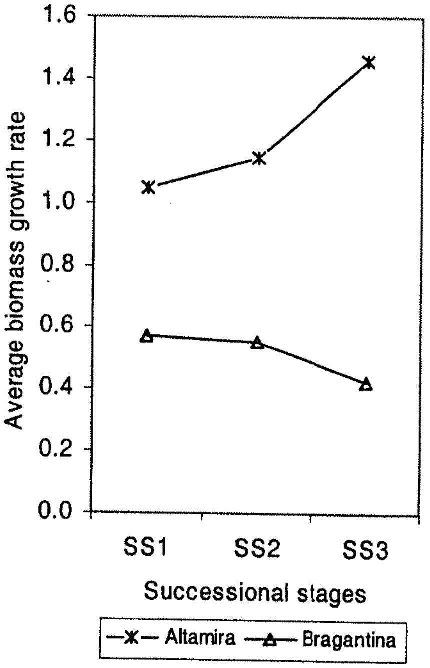

Figure 4. Comparison of average biomass growth rates (kg $m^{-2} y^{-1}$) in Altamira and Bragantina.

which have very low nutrients and sandy soil structure (coarse and fine sand accounts for at least 70 per cent), results in very slow vegetation growth rate, and the vegetation growth rate decreases with time, probably due to nutrient limitations.

DISCUSSION

When vegetation is cleared, dramatic changes occur in soil temperature and moisture creating a much larger diurnal range and becoming hotter and drier on average (Lavelle, 1987). Nutrients are lost rapidly through soil erosion and leaching, and the high water evaporation leads to soil drying quickly. Heavy rain and constantly high temperature tend to rapidly degrade soils when they are exposed. N, P, and K are lost in eroded soil when forest is completely cleared. Therefore, mechanisms and techniques must be sought to retain leaf litter and soil OM on site after tree removal. Such practices are especially important for maintaining soil fertility and for sustaining subsequent agricultural cultivation (Lavelle, 1987). The clay fraction and organic matter particles are especially important in storing nutrients in the soil layers. The amount of clay which a soil contains, together with its OM content, determines its ability to hold and exchange needed nutrient elements with plant roots.

Different land uses have significant influences on vegetation succession and soil nutrient conditions (Carpenter *et al.*, 2001; Giovannini *et al.*, 2001; Moran *et al.*, in press). For instance, good soil management can slow down soil erosion and nutrient loss and help maintain soil structure. In Alfisols, rich nutrients and good soil structure make succession proceed faster. Vegetation biomass also accumulates rapidly, forming good interrelations in the cycle of vegetation and soil. In Ultisols and Oxisols, poor nutrients and coarse sandy structure lead to poor soil fertility, and, if not managed properly, such soils will become floristically impoverished and succession will be difficult or require many years for recuperation. Recognition of nutrients and physical structure constraints allows the development of proper management strategies for alleviating soil degradation. So careful land-use planning and soil management are needed in order to achieve sustained production with a minimum of soil degradation (Lavelle, 1987).

Vegetation biomass accumulation, land use, topography, soil types, and climate interact with each other and influence vegetation growth and soil properties. Recognition of the relationship between vegetation regrowth and soil nutrient accumulation is important in order to find a better way to use soil resources and restore degraded landscape. Misuse of soil resources can result in disastrous soil degradation and make vegetation restoration difficult. In order to promote the vegetation biomass accumulation rate in poor nutrient soils, adding organic matter and/or artificial fertilizers to improve the soil structure and nutrient conditions is necessary. Better management of deforested areas and selection of proper land uses are critical to slow down nutrient losses and to keep the soil productive.

CONCLUSION

Our research indicates that soil nutrients such as Ca, Mg, K, and N decrease with depth in the soil studied. Clay-rich Alfisols hold more nutrients in the soil and support fast vegetation growth compared to Ultisols and Oxisols. Coarse and fine sand contents in Ultisols and Oxisols lead to fast nutrient losses and low soil fertility, resulting in slow vegetation biomass accumulation. This accumulation increases soil fertility, especially in the surface layer of Alfisols, but does not completely compensate for nutrient losses in Ultisols and Oxisols. The soil nutrients and structure in the upper 80 cm of Alfisol soil significantly influence the vegetation biomass accumulation rate; however, in Ultisols and Oxisols, the nutrients in deeper soil layers remain important for vegetation growth because of low nutrient levels in the top layer. The clay-rich Alfisols restrict the deep spread of vegetation roots, but the coarse-sand Ultisols and Oxisols allow vegetation roots to spread deeply for extraction of nutrients and water if not impeded by Al saturation. Thus, vegetation is especially important in reducing nutrient losses in poorly structured soils. The soil evaluation factor developed in this paper allows comparative analyses of soil fertility among sites of different successional growth to evaluate soil conditions and vegetation growth. Recognition of soil nutrient conditions is very important to help landowners select appropriate soil management methods to maintain sustainable utility of soils.

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