



ELSEVIER

Forest Ecology and Management 139 (2000) 93–108

Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Effects of soil fertility and land-use on forest succession in Amazônia

Emilio F. Moran^{a,*}, Eduardo S. Brondizio^{a,2}, Joanna M. Tucker^{b,3},
Maria Clara da Silva-Forsberg^c, Stephen McCracken^a, Italo Falesi^d

^a*Anthropological Center for Training and Research on Global Environmental Change, Indiana University, Student Building 331, Bloomington, IN 47405, USA*

^b*Center for Latin American Studies, University of Arizona, Tucson, AZ 85721, USA*

^c*School of Public and Environmental Affairs, Indiana University, Student Building 331, Bloomington, IN 47405, USA*

^d*Centro de Pesquisa Agroflorestal da Amazônia Oriental/Empresa Brasileira de Pesquisa Agropecuária (CPATU/EMBRAPA), caixa postal 48, Belém, Pará 66 000, Brazil*

Received 22 March 1999; accepted 21 November 1999

Abstract

This paper examines the role of soil fertility and land-use history on the rates of forest successional regrowth in five regions of the Amazon Basin. Sites are located in the Bragantina Region, Tomé Açú Region, Altamira Region and Marajó Region of the State of Pará, Brazil and in a region of the Colombian Vaupés. Methods used included vegetation inventories of successional and mature forests, soil sampling, ethnographic assessment of land-use histories, and land cover classification based on multi-temporal Landsat Thematic Mapper digital satellite data. The paper examines inter-regional differences, intra-regional differences, and Basin-wide differences in rates of forest regrowth. Inter-regional differences are best explained by the differences between areas in soil fertility, whereas intra-regional differences are best explained by the differential impact of land-use history on forest recovery. Basin-wide differences in rates of succession can best be captured by differences in tree height, and secondarily by differences in basal area. In inter-regional comparisons we found that ultisols, oxisols, and spodosols present similar rates of regrowth, but considerably slower rates when compared to alfisols. During the first 5–10 years of regrowth, alfisol areas have average stand height 1 m higher, and this difference doubles after 15 years of regrowth. In intra-regional comparisons, using one region as an example, we found that land-use differences are most able to explain differences. Areas that had been in swidden agriculture grew back at a rate of 1.5 m per year, as compared with 0.45 m per year for areas that had experienced mechanized land preparation, and 0.62 m per year for areas that had been in pasture. In Basin-wide comparisons we have been able to discriminate three distinct stages of secondary succession using structural criteria, across both soil and land-use types with height as the most predictive criteria of overall structural development. By comparing our five sites' data with that of other investigators, the paper proposes Basin-wide patterns of regrowth for each of three structural stages of secondary succession that facilitate linking the field vegetation data to remotely-sensed data of land cover. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Amazonia; Succession; Land cover; Land-use; Remote sensing; Regional analysis; Inter-site comparisons; Deforestation

* Corresponding author. Tel.: +1-812-855-6181; fax: +1-812-855-3000

E-mail address: moran@indiana.edu (E.F. Moran).

¹ James H. Rudy Professor of Anthropology and Director.

² Assistant Professor of Anthropology and Assistant Director.

³ Graduate student.

1. Introduction

Interest in tropical secondary forest successional processes has steadily increased in the past decade (Uhl, 1987; Dantas, 1988; Saldarriaga et al., 1988; Brown et al., 1989; Nepstad et al., 1991; Moran et al., 1994, 1996; Montagnini and Mendelsohn, 1997; Tucker et al., 1998 to name but a few). Attention to succession, rather than deforestation, shifts the focus from aggregate examination of deforestation rates (INPE, 1988, 1989, 1998; Lean and Warrilow, 1989; Skole and Tucker, 1993) and climate change (Salati, 1985; Dickinson, 1987; Shukla et al., 1990; Gash et al., 1996) to the human use of the landscape. In other words, it shifts attention from land cover to land-use. Attention to both land-use and land cover are necessary to understand successional dynamics.

Succession studies bring attention to local-level and regional-level trajectories of land-use change (Brondízio et al., 1994, 1996) to differences in post-deforestation processes of forest regrowth (Mausel et al., 1993; Moran et al., 1994, 1996) and to the contribution of secondary forest regrowth to carbon sequestration (Dale et al., 1993; Randolph et al., 1996; IPCC, 1998). By focusing on land-use to understand successional processes, investigation shifts to things like agricultural use of deforested areas (Uhl et al., 1988; Nepstad et al., 1991), soil quality and its management (Tucker et al., 1998), and management practices such as managed fallows (Denevan and Padoch, 1985; Brondízio and Siqueira, 1997) that can extend the productivity of an area or speed up its restoration. While we must continue to monitor tropical deforestation and carbon emissions, it is very important that we also monitor the expansion of successional forests and the magnitudes of carbon sequestration that these forests are responsible for, and the rich biodiversity that these forests nurture. Successional forests provide important corridors for a variety of mature forest species, as well as a nursery for the return of the mature forest, and opportunities for a diverse array of pioneers.

In this study we explore two hypotheses. First, we hypothesize that secondary successional regrowth is largely a function of soil fertility and previous history of land-use. Other important factors, such as the size of the area cleared, neighboring vegetation, and climate factors such as drought, are not considered in this

paper. Second, we hypothesize that despite differences in regrowth rates that result from differences in soil fertility and land-use, it is possible to discriminate structural patterns in initial, intermediate, and advanced secondary succession across the Amazon Basin. In order to test these hypotheses, we sampled secondary vegetation of different ages and contrasting land-use histories across a gradient of soil fertility ranging from fertile to infertile soils.

2. Study areas

The five study areas in this study represent differences in soil fertility conditions and land-use in the Amazon region. *Altamira*⁴ in the Xingu Basin is characterized by patches of nutrient-rich alfisols and less fertile ultisols; Ponta de Pedras in *Marajó island* is located in a transitional environment composed of upland oxisols and floodplain alluvial soils; Igarapé-Açú in the *Bragantina* region is characterized by both nutrient-poor spodosols and oxisols; *Tomé-Açú* (south of Igarapé-Açú) represents a mosaic of oxisols and ultisols; and *Yapú* located at the Vaupés tributary of the Rio Negro Basin is composed of large patches of nutrient-poor spodosols intermixed with stretches of oxisols.

Land-use varies between these areas, but in most cases it can be characterized as variations of swidden cultivation, agroforestry, and pasture management. The site of *Altamira*, along the Transamazon highway began to be colonized by settlers in 1971, and has experienced high rates of deforestation and secondary succession associated with implementation of agropastoral projects (Moran, 1981; Smith, 1982; Moran et al., 1994, 1996). In contrast, the Ponta de Pedras, *Marajó* site has been historically occupied by Caboclo populations, mainly devoted to agroforestry activities in the floodplain and swidden agriculture in the uplands, although pasture and mechanized agriculture can be found in the upland oxisols (Brondízio et al., 1994, 1996; Brondízio, 1996). Land-use in the Igarapé-Açú, *Bragantina* region has gone through several phases, and today the dominant form is short-fallow swidden cultivation and pasture development, given the proximity of the Belém market for producers.

⁴ Bold italicized sites refer to the site names found in the figures.

**SECONDARY SUCCESSION IN AMAZÔNIA
A.C.T. RESEARCH SITES***

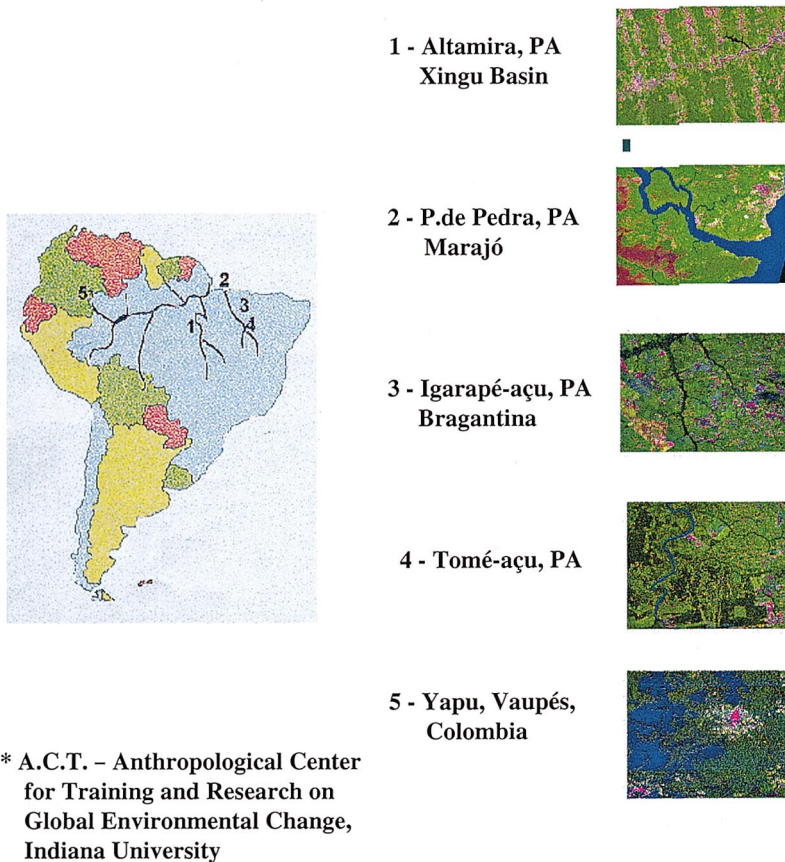


Fig. 1. Research sites discussed in this paper. Four of them are located in the eastern Amazon of Brazil, while one is located in the Colombian Vaupés, also known as the Northwest Amazon.

Cultivation of secondary growth areas has been common for decades, and islands of mature forest are rare (Penteado, 1967; EMBRAPA, 1980, 1992). The *Tomé-Açu* site has experienced the most intensive agriculture of our sites and is associated with monocrop production, followed by agroforestry development during the past two decades carried out by Japanese colonizers, and now by pasture formation (Falesi et al., 1964; Batistella and Moran, in preparation; Gradwohl and Greenberg, 1988; Subler and Uhl, 1990; Yamada, 1999). Finally, the Vaupés site at *Yapú* is populated by indigenous Amazonians who practice traditional long-fallow swidden cultivation based on

bitter manioc (Dufour, 1983; Castro et al., 2000). Each, however, has a very distinct landscape and land-cover pattern that reflects human uses in time and space (see Fig. 1).

3. Methods

Three data sets were used in this analysis: field inventories of successional and mature forest vegetation sites, ethnographic assessment of land-use history associated with fallows, and land cover classification using Landsat TM satellite images of the study areas.

Preparatory steps to image analysis began with georeferencing. This process made it possible to precisely associate study sites (e.g. a fallow stand) to the image by using a GPS device (Global Positioning System) when the image has been precisely overlaid on a coordinate system in a base map. Other important steps were image registration and atmospheric correction to balance spectral differences between dates. Both procedures are used when multitemporal image analysis is undertaken (see Mausel et al., 1993; Moran et al., 1994; Brondizio, 1996 for more details of methods used).

Our work began with preliminary analysis of satellite images to determine the spatial configuration and distribution of land-cover classes in the study area. During this stage, visual analysis and unsupervised classification were used. Rather than work with whole scenes, sub-areas were selected for detailed analysis in areas representing different kinds of land-use or of land cover. This is the first step towards linking regional scale analysis with micro-regional land-use patterns. These sub-areas make it possible to 'think' more locally while dealing simultaneously with what is a regional-scale data set, thus providing a preparatory step towards fieldwork. This step gave us an important component in choosing fieldwork strategies, such as which vegetation classes should be sampled and the distribution of samples within the study area.

Fieldwork used a bottom-up strategy that made our research a considerable departure from how other remote sensing studies commonly proceed. A fieldwork protocol was prepared based on a NASA fieldwork guide developed for MSS image analysis (Joyce, 1978). We prepared satellite image print-outs (at scales 1:25,000 or 1:30,000) with a 1 km grid overlay using a UTM coordinate system that allowed for the precise location of study sites while in the field and helped us interact with farmers and record their input or visual image interpretation of their area. Throughout the study area interviews were conducted with farmers in order to obtain land-use histories of sites that were potential candidates for vegetation and soil inventories. To reduce possible errors in locating study areas, we chose candidate sites for inventory that were relatively large to ensure precise location despite the degradation of accuracy resulting from Selective Availability (SA) (i.e. up to 100 m error introduced by the Defense Department in civilian receivers).

Upon arrival, a discussion with the farmer took place, followed by a visit to the secondary forest area of interest. During the interview we recorded the sequence of management steps applied in the sampling area. Data included the date the forest was cut, when it was burned and the quality of the burn, when it was planted, the crop yield, pasture age, and any repeated burnings since the time of abandonment. Information on the length of fallow is important to ensure inclusion of a range of lengths of fallow in the study and to examine the impact of land-use on floristic and structural attributes of fallow vegetation. Farmers' descriptions about land-use history were cross-checked with other information, such as that provided by comparison with Landsat TM multitemporal images. In order to verify the age of fallow and decrease the margin of error, a series of questions were asked that included the comparison between age of the farmers' offspring and the age of the field reported during the interview. For instance, a typical question was, 'How old was your oldest son when you planted that field?' Another useful example was the use of particular events (for instance, a presidential or state gubernatorial election) to gauge the age of the field. While visiting the area we verified the coherence between fallow age and vegetation structure, and additional questions concerning the land-use history of the site were posed. If the area was judged to be appropriate for sampling, we asked permission to have the team come at a convenient time to carry out the detailed soil/vegetation inventories.

3.1. Distribution of the research sites

For the purpose of site selection during fieldwork and further analysis of the impact of land-use history on regrowth, age classes were developed as a baseline. Sites were aggregated at 5-year intervals and preliminarily associated with structural classes. Initial secondary succession encompassed fallows of 0–5 years, intermediate secondary succession encompassed fallows of 5–10 years, and advanced secondary succession represented fallows above 10 years. One stage grades almost imperceptibly into another, thus creating periods that mix characteristics of both stages. For these reasons, sites in the middle of each class range were selected for sampling in order to understand unique and overlapping structural features. Age

classes will be dismissed later in the paper as an organizing principle of regrowth stages, although they will be used to study the impact of land-use history on fallow sites of the same age. As this paper will show, the structure and composition of successional forests is a product of land-use history and soil fertility, that makes age of lesser significance for discussing structure and process (also see Uhl et al., 1988).

3.2. Vegetation and soil inventory

The sampling strategy used was comparable across sites and regions. The same plot and subplot sizes were used at each site and region, allowing cross-comparison and integration at the level of plot, site, and region. Plots (10×15 m) and subplots (5×2 m) were randomly distributed, but nested inside each other to account for the detailed inventory of trees (DBH≥10 cm), saplings (DBH 2–10 cm), seedlings (DBH<2 cm), and herbaceous vegetation. In the plots, all the individual trees were identified, and measured for DBH, stem height (height of the first major branch), and total height. In the subplots, all individual saplings were identified and measured for diameter and total height, while all seedlings and herbaceous vegetation were identified and counted.

Species identification was carried out by experienced botanists in the field and doubtful identifications were checked at the herbarium of EMBRAPA in Belém, Pará. Botanical samples were collected from half of all species identified to ensure accuracy of taxonomic identification. Identification included family, genus and species, and common name when known. At each site sampled a complete soil profile was collected to one meter depth using a Dutch bipartite bucket auger. The sample was taken within one of the subplots, after having walked the entire plot to be sampled to ensure that the soils appeared to be relatively uniform in the plot. In a couple of cases when they were not, two samples were taken. Soil samples were analyzed at the CEPLAC and EMBRAPA soil laboratories in Belém for chemical and physical properties. Soil color was recorded using the Munsell soil color charts. Soil color was recorded during the same time of the day (i.e. between 4 and 5 p.m.) and on days with comparable cloud cover in order to avoid bias from change in light intensity between different sample descriptions.

All inventory and soil data were entered into a spreadsheet. A stand inventory table including absolute and relative frequency, density, dominance, basal area, importance value, and stem and total height was prepared for each of the inventoried sites.

Above-ground dry biomass was derived from inventory data using allometric equations from the literature. Two different biomass equations were used to differentiate between trees and saplings. Brown et al. (1989) equation was used to estimate tree biomass (DBH≥10 cm). Another equation from Uhl et al. (1988) was used to estimate sapling biomass (DBH 2–10). Brown et al. (1989) equation was selected due to its focus on estimating mature forest biomass. This equation was developed based on a large number of forest inventories from different areas of the tropics, focusing on adult trees and mature stands. Uhl et al. (1988) equation was developed from data collected from different stages of secondary succession sites in eastern Amazonia, derived mainly from sapling data. Uhl's generic species equation was selected due to its applicability to a wide range of species. One representative site of each vegetation type was selected for drawing a vegetation profile. Profile drawings were carried out in transects of 4×50 m. All individuals with DBH≥2 cm were identified, measured, and represented in the profile. Attention was paid to individual architecture, such as shape of trunk, branch distribution, canopy shape and intersection between different canopies. This vegetation profile was an important source of information about vegetation structure and stratification. Such information has been useful during image classification and interpreted in conjunction with inventory data (Brondizio, 1996; Tucker et al., 1998). Sampled areas were located on the satellite image, and its coordinates were obtained with a Magellan Nav 1000 Pro GPS receiver. In areas of closed canopy that obscure signal reception by the GPS device, ground control points were collected on the fringes of the vegetation and, when possible, at its corners.

A soil fertility index to summarize differences between regions was used (Alvim, 1974). The index uses pH, organic matter, phosphorus, potassium, calcium and magnesium, and aluminum (inverse value). The index was prepared for each depth (0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, and 80–100 cm) and an average index was prepared across depths.

The data were submitted to statistical analysis to provide a structural comparison between sites. One-way analysis of variance (ANOVA) was performed using Stata 1.0 software. Each inventoried site was subdivided into plots (10 plots at each site of intermediate secondary succession (hereafter SS2), 10 plots at advanced secondary succession sites (hereafter SS3), and five plots at each initial secondary successional site (hereafter SS1). This data arrangement increased the number of samples to be analyzed and facilitated the comparison of sites on the basis of standard deviation and variance. Early work using ANOVA to compare the significance of structural parameters to discriminate regrowth stages found that average height is the most significant indicator of structure (Brondizio, 1996). DBH and basal area were also tested. Both DBH and basal area gave poorer fit because they could not effectively discriminate between SS2 and SS3 stages (see Basin wide discussion later in this paper). For this reason, only average height was used to test for differences in rates of regrowth between and within sites. First, ANOVA ($p \geq 0.05$) was used to compare the five regions in terms of average height across age classes. This made it possible to reorganize age classes into structural classes. Second, ANOVA ($p \geq 0.05$) was repeated, but this time we controlled for soil fertility differences between sites. We used the soil fertility index as an indicator of regional-level fertility.

Using a similar statistical analysis, the data from the Marajó region was used to analyze the impact of land-use on regrowth. Land-use was divided into four categories of intensity: Abandoned pasture ($n=15$), swidden cultivation on abandoned mechanized field ($n=15$), traditional swidden cultivation ($n=30$), and no use (upland forest) ($n=20$). These classes represent four intensities of use: heavy (abandoned pasture), moderate (swidden cultivation on abandoned mechanized field), light (traditional swidden cultivation), and no use (upland forest).

4. Results and discussion

4.1. Inter-regional differences in rates of regrowth

Soil fertility proves to be a key element that helps to discriminate between rates of secondary succession in

inter-regional comparisons. This is especially true when land-use is considered as a variable affecting rates of regrowth. In nutrient-poor areas nutrient stocks are largely concentrated in the vegetation and in the organic horizon of the soil profile, rather than in the mineral soil itself. This is a process well described for the Rio Negro area (Jordan and Herrera, 1981) and frequently associated with physiological mechanisms developed by the vegetation to prevent the loss of the limited nutrients within the vegetation-soil complex. On the other hand, in nutrient-rich areas, such as Altamira's alfisols, nutrients in the mineral soil are more important and are also less concentrated in the biomass itself.

Nutrient cycles in these two types of regions present different degrees of susceptibility to anthropogenic impacts. In nutrient-poor areas, any loss of nutrients through leaching have serious consequences, particularly in very sandy soils such as the spodosols of the Vaupés and Rio Negro. Therefore, factors influencing the pace of ground cover and successional vegetation establishment, such as above-ground root sprouting, mycorrhizal interactions, and species colonization from neighboring vegetation, are crucial to avoid nutrient losses following disturbance. In nutrient-rich areas, factors affecting species colonization, such as area size, neighboring vegetation, and micro-climatic conditions are more likely to be limiting to succession establishment and development than soil chemical and physical conditions alone.

Differences in soil types need to be understood in terms of nutrient availability and other related factors such as pH, organic matter and cation exchange capacity, and by differences in soil texture (Moran and Brondizio, 1998). However, textural differences also need to consider parent material. This is especially true for differentiating alfisols and spodosols. Whereas both soil types are characterized by a clayish B-horizon and similar amounts of sand in the A-horizon, spodosols differ from alfisols due to a characteristic spodic horizon composed of hydromorphic clays. Oxisols and ultisols present small differences in fertility with the most notable difference being increasing clay content with depth in the ultisols (Sanchez, 1976).

Soil structure and texture of the study regions, as represented by percentage of fine sand, coarse sand, silt, and clay at five depths were analyzed. Coarse sand

and clay are the elements most able to provide discrimination across regions. Four major textural groups can be distinguished in the study regions. Altamira soils have low content of fine and coarse sand at all depths (averaging around 10%) and clay content above 45% at all depths. The Yapú region presents a similar textural pattern, but differs in the presence of a spodic-B horizon with low permeability and penetrability, often characterized as groundwater humic podzols (Sombroek, 1984). Marajó and Bragantina soils are rather similar in terms of sand and clay content at all depths. In both the cases, average fine and coarse sand content are above 25% and average clay content is below 20% at all depths. Tomé-Açú soils, although similar overall to Marajó and Bragantina, are distinct because of lower content of fine sand (below 25%) and higher clay content (between 30 and 40%) at all depths. Therefore, while the first two are typical examples of oxisols, Tomé-Açú presents a soil type closer to ultisols.

Differences in soil fertility are significant between the study regions. Altamira stands alone in terms of its high soil fertility, while differences are subtle among Marajó, Bragantina, Tomé-Açú, and Yapú, as shown in Fig. 2. Average pH above 5 in Altamira contrasts with pH below 5 in the other regions. A pH above 5.5 is viewed as necessary for most domesticated cultigens, except for a few like manioc, cowpeas, and sugarcane adapted to low pH conditions. However, within the last group, lower pH is found in Marajó and Yapú (below 4.4 in the first 20 cm) when compared to Bragantina and Tomé-Açú.

The combined analysis of aluminum and calcium/magnesium provides further criteria to distinguish between regions. Yapú has the highest aluminum concentrations and also the lowest concentrations of calcium and magnesium. This nutrient-poor pattern is reinforced by the low availability of phosphorus. High concentrations of aluminum impede root development and tend to limit absorption of other nutrients, especially of calcium and magnesium that are closely related to root growth and plant development (Lathwell and Grove, 1986). Phosphorus is considered the most limiting nutrient in Amazonia (Cochrane and Sanchez, 1982), frequently found only as a trace (below 1 ppm). Although phosphorus is low at all sites, Altamira presents larger amounts when compared to the other regions. Only traces of phosphorus

are present in Yapú and Marajó. No difference is found in the amount of organic matter between regions. The analysis of these elements reveals that soil fertility is significantly different between Altamira and the other regions, but similar overall for the other four regions. This similarity may be further brought out by looking at particular elements (e.g. pH and Al in Fig. 2).

Analysis of variance shows that soil fertility is a significant indicator of differences in secondary succession between regions ($\text{Adj } r^2=0.69$; $p \geq 0.05$) when average stand height is used as a parameter to measure the rate of regrowth. Differences in fertility result in faster regrowth in Altamira and differentiate it from the other regions. Similar regrowth rates between Marajó, Bragantina, Tomé-Açú, and Yapú are consistent with their similarity in soil endowments. These differences are illustrated in Fig. 3 where each site is compared to Altamira. Altamira is the only region presenting rates of regrowth above average. During the first 5 and 10 years, Altamira fallows are a meter higher when compared to the average fallow of all other regions. This difference increases by two-fold after 15 years of fallow. Such an increase may be related to the faster development of trees in relation to saplings in Altamira. Overall, Altamira has a lower understory density and a higher upper story, indicating a faster pace of tree development and forest structure. This pattern is reinforced by the differences in family diversity between Altamira and the other regions. Overall, family diversity in the understory is higher during the first 5 years, decreases during the following 10 years and increases again as vegetation reaches a mature forest-like structure. In the canopy, family diversity presents a progressive rate of increase as age proceeds. However, significant variations in this patterns can be perceived. Whereas Altamira has a lower understory diversity when compared to other regions (especially Bragantina), it has the highest diversity of tree families. The Bragantina region in particular presents a higher degree of understory family diversity. The Bragantina landscape is dominated by fallows and a land-use strategy that puts emphasis on short-fallow swidden cultivation. The higher diversity of the saplings and the herbaceous components in this region may be closely associated with the adaptation of a specific group of families and species to disturbance (Denich, 1991; Vieira et al., 1996).

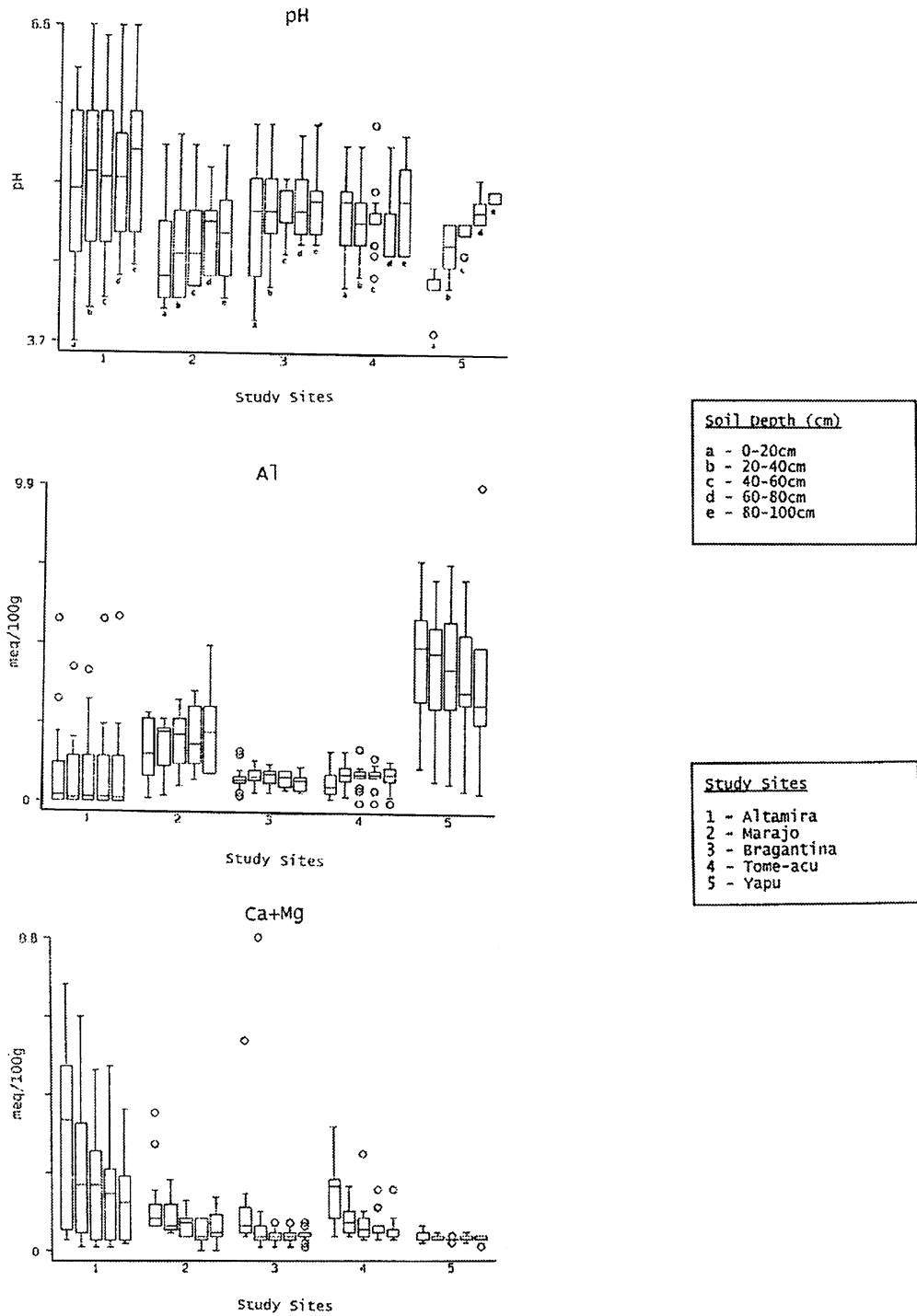


Fig. 2. Comparison of pH, Aluminum, Calcium and Magnesium at the five study regions. For each region (1, 2, 3, 4, 5) chemical status is presented at each 20 cm of depth (a — 0–20 cm depth; b — 20–40 cm; c — 40–60 cm; d — 60–80 cm; e — 80–100 cm). It is important to note that the less aluminium the better, whereas a higher pH, Calcium and Magnesium amount is preferable in these soils.

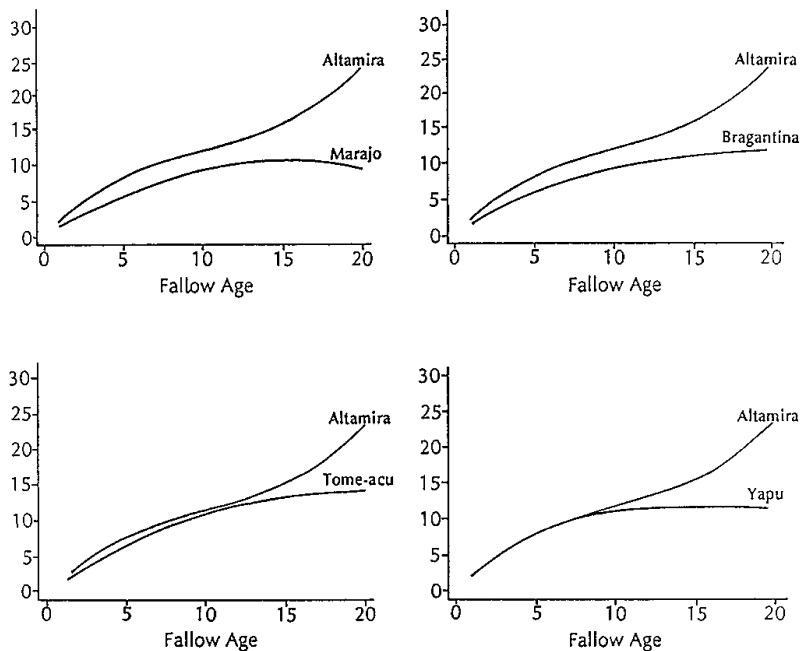


Fig. 3. The trajectory of increments in height in secondary succession. Altamira develops much faster than all other sites and the difference increases over time. This allows Altamira to develop an upper story canopy faster, which leads to a more forest-like appearance not only in the canopy but also in the relatively sparse understory. (Source: Moran and Brondizio, 1998, 108). Y-axis is height in meters. X-axis is age in years.

4.2. Basin-wide patterns of rates of regrowth

An important find of this study is the characterization of Basin-wide stages of regrowth based on the analysis of average stand height and basal area of the study sites. Fig. 4 provides a comparison of stand height data for our five study sites and for nine other study areas carried out by other investigators. The data from our sites is consistent with those of other locations, including some from Ecuador, Peru, and Venezuela that have comparable data (i.e. Uhl, 1980; Flores Paitan, 1987; Uhl et al., 1988; Saldarriaga et al., 1988; Dantas, 1989; Irvine, 1989; Denich, 1991; Salomão, 1994; Alves et al., 1997). The data on basal area from our sites is also consistent with those of these other study areas (see Fig. 5). Stand height proves to be a statistically significant discriminator of regrowth stages at this level. Although less significant, basal area can also be used to define structural stages of regrowth. Three structural stages of regrowth can be delimited based upon our inter-regional comparison: initial (SS1), intermediate (SS2), and advanced (SS3)

regrowth stages. Each of these stages can be broadly associated with age classes, but, more importantly, they have distinctive clustering that allows for Basin-wide comparisons (see Fig. 6).

Initial secondary succession (SS1) is associated with a period of establishment that includes herbaceous and woody species. Saplings are the main structural element in a SS1 landscape and represent the majority of the vegetation biomass. This stage ranges in average height from 2 to 6 m, depending on regional characteristics and land-use history. Most of individuals have height equal to or less than 2 m during the first two years, whereas individuals between 3 and 6 m start to contribute significantly after that. In terms of basal area, this stage presents a variation that ranges from 1 to 10 m²/ha. The vast majority of individuals at this stage have DBH ranging from 2 to 5 cm. In age terms, it encompasses the first 5 years of fallow.

Intermediate secondary succession (SS2) is characterized as a period of selection wherein the thinning of herbaceous and grass species, a rapid increase in sapling dominance, and small trees occurs. During this

REGROWTH STAGES BY STAND HEIGHT ACT RESEARCH SITES & LITERATURE DATA

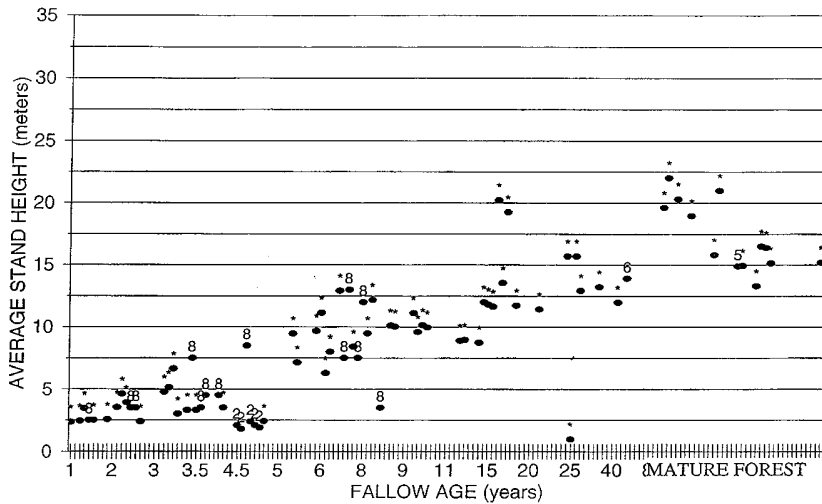


Fig. 4. Comparison of regrowth stages by relative stand height in our five study areas with seven other study areas researched by other investigators. Asterisk denotes our five study areas; 1 — the study by Dantas (1989); 2 — the study by Denich (1991, Bragantina); 3 — the study by Flores Paitan (1987, Peru); 4 — the study by Saldarriaga et al. (1988, Rio Negro, Venezuela); 5 — the study by Salomão, (1994, Bragantina); 6 — the study by Uhl (1980, San Carlos de Rio Negro, Venezuela); 8 — the study by Uhl et al. (1988, Paragominas, Brazil).

REGROWTH STAGES BY BASAL AREA (M²/HA) ACT RESEARCH SITES & LITERATURE DATA

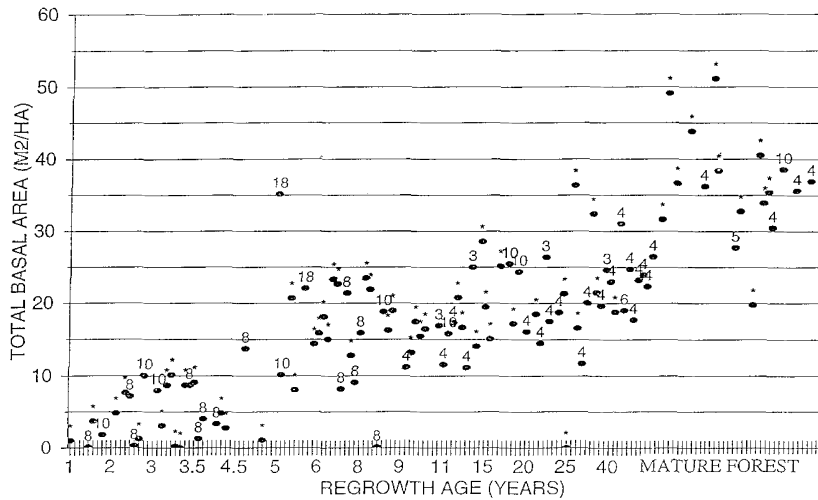


Fig. 5. Comparison of basal area in fallows of different ages in our five study areas and eight study areas researched by other investigators. Asterisks denote data from our five study areas; 1 — the study by Dantas (1989); 2 — the area studied by Denich (1991, Bragantina); 3 — the area studied by (Flores Paitan (1987, Peru); 4 — the area studied by Saldarriaga et al. (1988, Rio Negro, Venezuela); 5 — the area studied by Salomão (1994, Bragantina); 8 — the area studied by Uhl et al. (1988, Paragominas), 10 — the area studied by Alves et al. (1997, Rondônia) and 18 — the area studied by Irvine (1989, Ecuador).

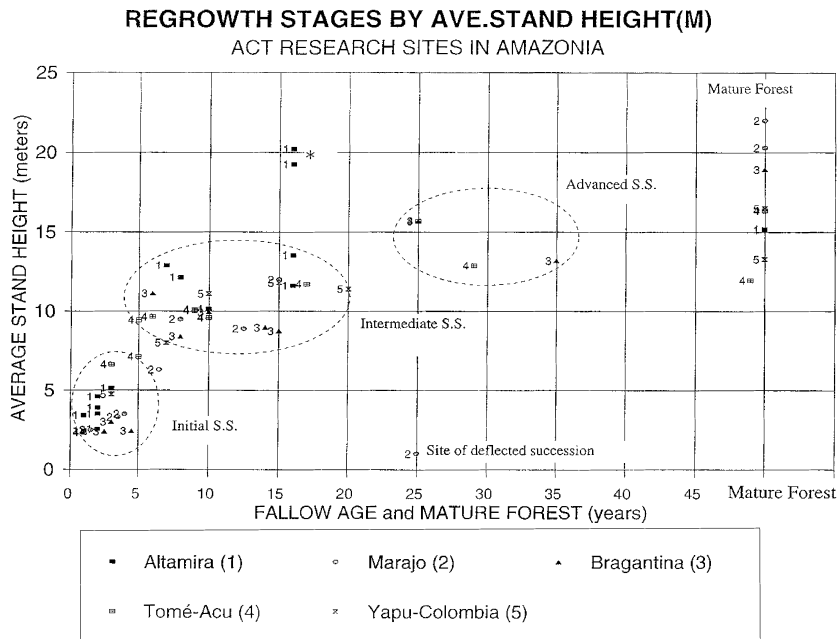


Fig. 6. Comparison of regrowth stages and average stand height in meters at our five study areas. The circles constitute our proposed range for initial, intermediate and advanced secondary growth along an average stand height criteria that seems to describe most Amazonian sites, despite soil fertility and land-use differences. A few outlier stands are present. (Source: Moran and Brondizio, 1998, 109).

stage, saplings are still a major contributor to total basal area and biomass, and young trees dominate canopy structure. It is at this stage that vegetation begins to differentiate canopy from understory individuals, but stratification is still subtle. The increase in shade during this stage is an important element in species selection. This stage (SS2) ranges in average height from 7 to 13 m. Overall, the majority of individuals have 4–9 m in height, while DBH is between 5 and 15 cm. A small number of individuals can reach a height ranging from 10 to 15 m. In terms of basal area, this stage ranges from 10 to 25 m²/ha. It encompasses fallows from 5 to 15 years.

Advanced secondary succession (SS3) is characterized by the subtle stratification between understory and canopy and by the decreasing contribution of saplings to total basal area and biomass. This stage (SS3) ranges in average height from 13 to 17 m, with a considerable number of individuals with only 6–13 m in height. Individuals with DBH from 10 to 15 cm are still of major importance at this stage, but a considerable number of larger individuals are present. Basal area has a similar range to the intermediate stage,

although sites with larger basal area are likely to occur at advanced age. One of the reasons for similar basal area is related to the process of species selection that occurs between SS2 and SS3. Fast growth trees that occupy SS2 (e.g. *Cecropia* spp.) and contribute to its basal area are replaced by forest tree species during SS3. Therefore, instead of a progressive increment in basal area from SS2 to SS3, there is a replacement of the species and individuals contributing to it. Since forest tree species tend to have a slower rate of diameter growth in relation to height development, increment in basal area tends to be slower during this stage. Thus, advanced secondary succession (SS3) can be termed a period of transition towards mature forest structure that includes the thinning of the understory and the dominance of tree species. In age terms, this stage encompasses fallows older than 15 years.

Mature forest vegetation varies widely within the Amazon Basin. Average height varies from less than 15 m to around 24 m. However, distinguishing between forest and advanced regrowth can be achieved by taking into account additional features that characterize mature forest vegetation. First,

species composition needs to be considered a discriminator of forest environment. Mature forest has higher canopy and understory diversity characterized by the presence of particular species not found elsewhere. Emergent trees with very large diameter are also distinctive. Most individuals have DBH above 30 cm and height greater than 15 m. Basal area in mature forest (upland) ranges from 25 to 50 m²/ha, therefore, providing a distinct structural difference from advanced regrowth.

In summary, establishment accounts for pioneer colonization of grass, vines, shrubs, and seedlings. This stage is followed by a selection that favors young trees and saplings. In turn, this second stage is followed by a transition in which large trees shade an understory composed of fewer saplings and a larger number of species with fewer individuals.

This model of regrowth stages (see Fig. 6) can be largely applied to the Amazon region. Land-use intensity, landscape diversity, and soil fertility variables speed up or slow down a vegetation's structural development, thus making comparison of major attributes such as height, DBH and basal area difficult if not impossible if one relies exclusively on age to describe secondary forest vegetation. For instance, dominance of grasses in abandoned pasture specifically controls the colonization by seedlings, whereas in an area of traditional swidden cultivation, a larger number of species is expected to enjoy more equal opportunity for colonization. The nature of this process is closely related to the future structure of intermediate and advanced stages of secondary vegetation. The faster establishment of tree species during initial and intermediate stages is likely to speed up regrowth towards an advanced structural stage, as we saw earlier for the Altamira site.

The proposed regrowth classes provide a useful baseline for remote sensing interpretation and for comparison between regions given the flexibility that it provides to investigators, and that it appears to hold across sites in Brazil, Ecuador, Venezuela and Peruvian Amazonia. It may also find applications in developing a model of regrowth and to unveil land-use strategies that are likely to improve the economic use of fallow vegetation (Brondizio, 1996; Brondizio and Siqueira, 1997; Moran et al., 2000). We have found creative use of abandoned fallows, as have others, wherein continued economic use of planted

and pioneer species increases the value of these areas to the human population. Fruit trees with a tall enough canopy to remain above the growing pioneer species for up to 10 years, fallow enrichment with valuable rapid growing native species such as mahogany, and the creation of agroforestry groves that combine native species with exotics are among the land-use strategies which mimic successional forest structure and function, while meeting immediate human needs.

4.3. Intra-regional differences in rates of regrowth and the impact of land-use history

The variation in land-use practices in the Marajó region provides an interesting example of the impact of land-use history on regrowth. Land-use strategies in the region encompass a mosaic of land-use types representative of Amazonia: traditional swidden cultivation, agroforestry, mechanized agriculture, and cattle ranching. These land-use types are analyzed here in relation to average stand height and biomass. Analysis of variance examining the relationship between age and regrowth structure (i.e. average stand height), shows that land-use type has a significant impact on regrowth. The analysis of average stand height indicates that fallows following traditional swidden cultivation increase in stand height by increments of 1.5 m/year, while fallows in areas of abandoned pasture and abandoned mechanized fields, increase 0.62 m and 0.45 m, respectively (see Fig. 7). However, this is not a linear increment. Height increments are larger during the first 8 years and tend to decrease after that.

The contribution of understory and canopy to total biomass is also a good indicator of overall changes characterizing vegetation development in relation to land-use impact. As succession proceeds, there is a progressive increase in the importance of canopy over understory vegetation. In other words, while for initial secondary succession the understory accounts for the majority of biomass at the site, at intermediate and advanced stages the importance of canopy individuals increases. There is a positive correlation between age and canopy biomass and a negative correlation between age and understory biomass. Overall, fallows following traditional swidden cultivation have higher total biomass in all the cases examined. Fallows

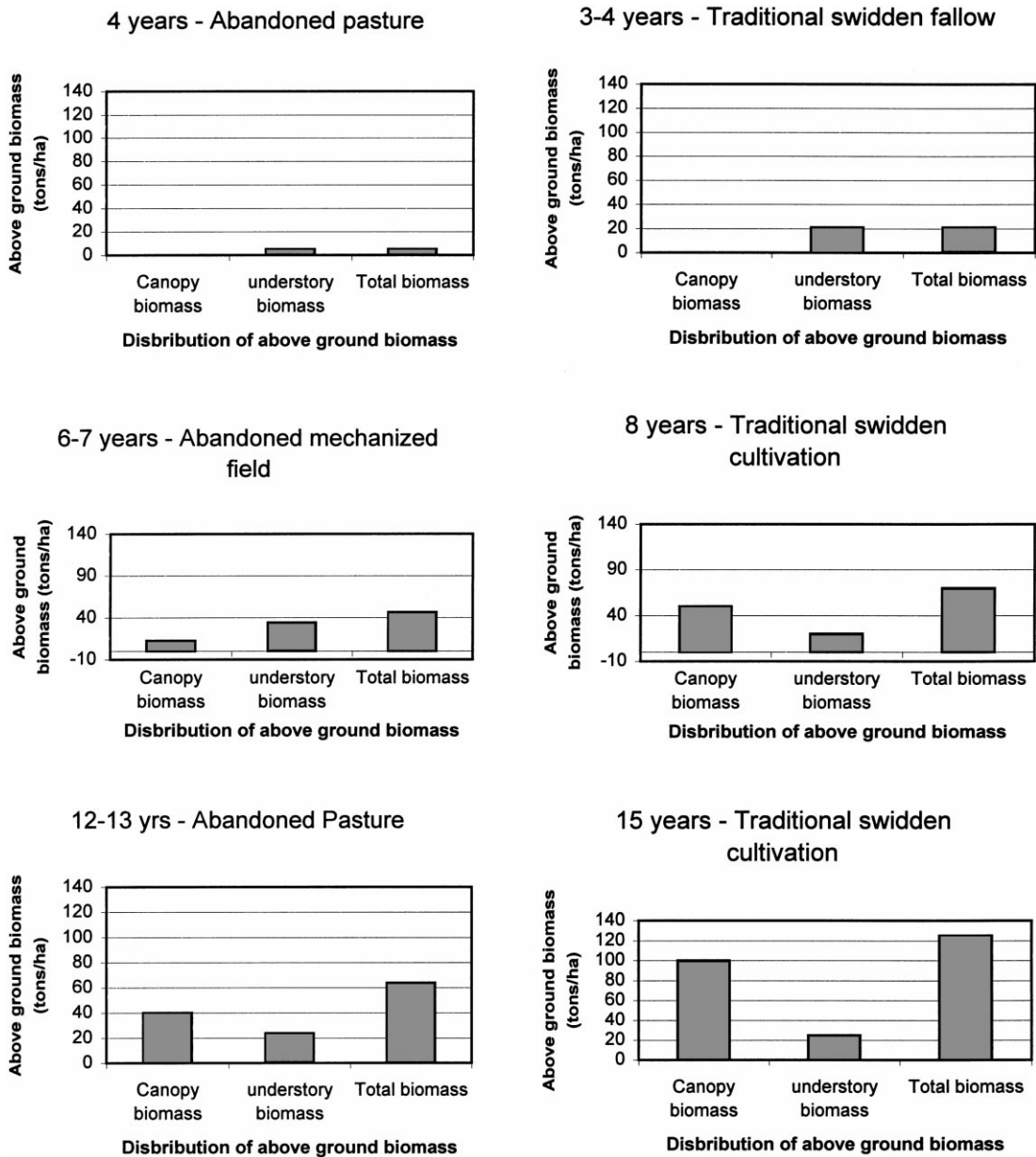


Fig. 7. Impact of previous land-use on above ground biomass (understory, canopy and total biomass), Ponta de Pedras, Pará State, Brazil. Traditional swidden fallow are compared to pasture and mechanized field uses.

following traditional swidden cultivation have a higher dominance of canopy biomass by the 8th year of fallow. Understory vegetation tends to be dominant for a longer time in sites more heavily used, indicative of slower pace tree development and a higher density

of saplings. The variations in the process of structural transition, evident in the interplay between saplings and trees in relation to height, density and biomass, reinforce the value of using land-use history as a variable in succession studies.

5. Conclusions

This study has sought to identify the responses of major variables at different levels of analysis for secondary successional processes in Amazonia. Whereas *soil fertility is particularly important in explaining inter-regional differences in rates of regrowth, land-use intensity and landscape diversity are more important in the intra-regional analysis.* Another contribution of this paper has been the development of a Basin-wide association between total height and regrowth stages that seems to apply to large-scale analysis of land-use and deforestation dynamics in Amazonia. If confirmed by further studies, this height-based shortcut to understanding structural pattern will assist with environmental monitoring of secondary vegetation and estimation of carbon sequestration by secondary forests. This will be particularly true when soon-to-be launched orbital satellites begin to provide a way to estimate with relative accuracy tree-height data (Janetos, pers. commun.).

Secondary succession has socioeconomic and ecological importance at local, regional, and global scales. Therefore, understanding the nature of regrowth processes requires the integration of a variety of methods nested at different scales in spatial and temporal terms. Remote sensing and GIS technologies offer important opportunities for vegetation ecologists in understanding the spatial and temporal dimensions of regrowth, such as those related to landscape diversity, area, and neighboring vegetation. Vegetation ecologists will increasingly pursue large-scale analysis made possible by remote sensing, while remote sensing analysts will be able to improve the fineness of land-use analysis by calibrating large-scale studies at a number of site-specific sites to grasp subtle and not so subtle variations in structure and species composition that have escaped them in the past. Social scientists have begun to contribute to a better understanding of the human dimensions of these processes as members of research groups that combine all three types of scientific communities (see Liverman et al., 1998). Together, vegetation ecologists, remote sensing analysis, and social scientists complement each others' questions, while developing interdisciplinary methods and research strategies to understand reforestation processes in Amazônia and elsewhere. This paper is an example of this blending of scientific traditions in

the interest of understanding land-use and land cover change in Amazonia. It is our hope that other scientists test our findings at their sites and contribute to a cumulative data set that makes comparison of secondary successional areas increasingly straight-forward.

Acknowledgements

This paper was originally presented at the symposium 'Ecological Processes in Lowland Tropical Secondary Forests' at the 1996 Annual meeting of the Ecological Society of America, Providence, Rhode Island. The authors wish to acknowledge the support of the National Science Foundation (grants 91-00526, 93-10049 and 95-21918) from the Geography and Regional Science and the Program on the Human Dimensions of Global Environmental Change; the Midwestern Regional Center of the National Institute of Global Environmental Change; and NICHD (through grant 9701386A) for support for these studies. The authors are thankful to NASA's Global Change Fellowship Program (NASA 3708-GC94-0096) that supported E.Brondízio's studies in Marajó island. The authors acknowledge the assistance of the late Lucival Rodrigues Marinho and Jair da Costa Freitas for their help with plant taxonomy and field research and to the Administration of EMBRAPA/CPATU in Belém for freeing them from other obligations to collaborate with us. We also thank Dr. Mario Dantas of EMBRAPA for his valuable assistance in the field and in developing an effective field methodology. The authors are thankful to other members of our research team not listed as authors: Fabio de Castro, Amy Gras, JoAnne Michael, Alissa Packer, Vonnice Peischl, J.C. Randolph, Bernadette Slusher, Cindy Sorrensen, Warren Wilson, and Masaki Yamada. Finally, we wish to acknowledge the support of the people of Altamira, Ponta de Pedras, Igarapé-Açú, Tome-Açú, and Yapú. Responsibility for the views expressed in this paper are the sole responsibility of the authors and do not reflect the views of the funding sources or collaborators.

References

- Alves, D.S., Soares, J.V., Amaral, S., Mello, E.K., Almeida, S.A.S., Silva, O.F., Silveira, A.M., 1997. Biomass of primary and

- secondary vegetation in Rondônia, Western Brazilian Amazônia. *Global Change Biol.* 3, 451–461.
- Alvim, P.T., 1974. Um novo sistema de representação gráfica da fertilidade de solos para cacau. *Cacau Atualidades* 11 (1), 2–6.
- Batistella, M., Moran, E., Land cover change in Tome-Acu: a regional analysis (1985–91), in preparation.
- Brondizio, E.S., 1996. Forest farmers: Human and landscape ecology of Caboclo populations in the Amazon estuary. Ph.D. Dissertation, Indiana University, Bloomington.
- Brondizio, E., Siqueira, A., 1997. From extractivists to forest farmers: changing concepts of Caboclo agroforestry in the Amazon estuary. *Res. Econ. Anthropol.* 18, 233–279.
- Brondizio, E.S., Moran, E.F., Mausel, P., Wu, Y., 1994. Land-use change in the Amazon estuary: patterns of Caboclo settlement and landscape management. *Human Ecol.* 22 (3), 249–278.
- Brondizio, E.S., Moran, E.F., Mausel, P., Wu, Y., 1996. Land cover in the Amazon estuary: linking of the thematic mapper with botanical and historical data. *Photogramm. Eng. Remote Sen.* 62 (8), 921–929.
- Brown, S., Gillespie, A.J.R., Lugo, A., 1989. Biomass estimation methods for tropical forests with applications to forest inventory data. *For. Sci.* 35 (4), 881–902.
- Castro, F., Silva-Forsberg, M.C., Wilson, W., Brondizio, E.S., Moran, E.F., 2000. The use of remotely-sensed data in rapid rural assessment. In: Moran, E.F. (Ed.), *Environmental Monitoring in Latin America: Bringing Space Science Down to Earth* (under review).
- Cochrane, T.T., Sanchez, P., 1982. Land resources, soils, and their management in the Amazon region. In: Hecht, S. (Ed.), *Amazonia: Agriculture and Land-use Research*. CIAT Cali, Col., pp. 137–209.
- Dale, V.H., O'Neill, R.V., Pedlowski, M., Southworth, F., 1993. Cause and effects of land-use change in central Rondônia, Brazil. *Photogramm. Eng. Remote Sen.* (6), 997–1005.
- Dantas, M., 1988. Studies on succession in cleared areas of Amazonian rain forest. Ph.D. Thesis: Oxford University, Oxford, UK.
- Denevan, W., Padoch, C., 1985. *Swidden fallow agroforestry*. New York Botanical Garden Monograph Series No. 5, New York.
- Denich, M., 1991. Estudo da Importancia de uma Vegetacao Secundaria Nova para o Incremento da Produtividade do Sistema de Producao na Amazônia Oriental. Embrapa/Cpatu: GTZ. Ph.D. Dissertation. 284pp.
- Dickinson, R.E. (Ed.), 1987. *The Geophysiology of Amazônia: Vegetation and Climate Interactions*. Wiley, New York.
- Dufour, D., 1983. Nutrition in the Northwest Amazon. In: Vickers, W., Hames, R. (Eds.), *Adaptive Responses of Native Amazonians*. Academic Press, New York, pp. 329–355.
- EMBRAPA, 1980. Consequencias da Exploracao Agropecuaria sobre as condicoes fisicas e quimicas dos solos das micro-regioes do nordeste paraense. Belem: Centro de Pesquisa Agropecuaria do Trópico úmido.
- EMBRAPA, 1992. Sistemas de Produção de Pequenos Produtores de Mandioca no Município de Bragança, Para. Belem: Centro de Pesquisa Agroflorestal da Amazônia Oriental.
- Falesi, I.C., dos Santos, W.H., Vieira, L.S., 1964. Os Solos da Colonia Agricola de Tomé-Acú. Belem: Centro de Pesquisa Agropecuaria do Trópico úmido. Boletím Técnico No. 44.
- Flores Paitan, S., 1987. Old managed fallows at Brillo Nuevo. In: Denevan, W., Padoch, C. (Eds.), *Swidden-Fallow Agroforestry in the Peruvian Amazon*, *Advances in Economic Botany*, Vol. 5, pp. 53–66.
- Gash, J.H.C., Nobre, C.A., Roberts, J.M., Victoria, R.L. (Eds.), 1996. *Amazonian Deforestation and Climate*. Wiley, London.
- Gradwohl, J., Greenberg, R., 1988. *Saving the Tropical Forests*. Island Press, New York.
- INPE. 1988. PRODES I (Projeto Desmatamento) São José dos Campos: Instituto Nacional de Pesquisas Espaciais.
- INPE. 1989. PRODES II (Projeto Desmatamento). São José dos Campos: Instituto Nacional de Pesquisas Espaciais.
- INPE. 1998. Desflorestamento, 1995–1997. São José dos Campos, SP: Instituto Nacional de Pesquisas Espaciais, 23pp.
- IPCC. 1998. The regional impacts of climate change: an assessment of vulnerability. A Special Report From The Intergovernmental Panel on Climate Change. Cambridge University Press, New York.
- Irvine, D., 1989. Succession management and resource distribution in an Amazonian rain forest. *Adv. Econ. Bot.* 7, 223–237.
- Jordan, C., Herrera, R., 1981. Tropical rain forests: are nutrients really critical? *Am. Natur.* 117, 167–180.
- Joyce, A.T., 1978. Procedures for gathering ground truth information for a supervised approach to a computer-implemented land cover classification of Landsat-acquired multispectral scanner data. NASA Ref. Publication 1015.
- Lathwell, D.J., Grove, T.L., 1986. Soil-plant relationship in the tropics. *Annu. Rev. Ecol. Syst.* 17, 1–16.
- Lean, J., Warrilow, D., 1989. Simulation of the regional climate impact of Amazonian deforestation. *Nature* 342, 411–412.
- Liverman, D., Moran, E.F., Rindfuss, R.R., Stern, P.C. (Eds.), 1998. *People and Pixels: Linking Remote Sensing and Social Science*. National Research Council. Washington, DC, 268pp.
- Mausel, P., Wu, Y., Li, Y., Moran, E.F., Brondizio, E.S., 1993. Spectral identification of successional stages following deforestation in the Amazon. *Geocarto Int.* 8, 61–72.
- Montagnini, F., Mendelsohn, R.O., 1997. Managing forest fallows: improving the economics of swidden agriculture. *Ambio* 26 (2), 118–123.
- Moran, E.F., 1981. *Developing the Amazon*. Indiana University Press, Bloomington.
- Moran, E.F., Brondizio, E.S., 1998. Land-use change after deforestation in Amazônia. In: Liverman, D., Moran, E.F., Rindfuss, R.R., Stern, P.C. (Eds.), *People and Pixels*. National Academy Press, Washington, DC, pp. 94–120.
- Moran, E.F., Brondizio, E., McCracken, S., 2000. Trajectories of land-use: soils, succession, and crop choice. In: Wood, C. et al (Eds.), *Patterns and Process of Land-use and Forest Change in the Amazon*. University of Florida Press, Gainesville.
- Moran, E.F., Brondizio, E.S., Mausel, P., Wu, Y., 1994. Integrating Amazonian vegetation, land-use and satellite data. *BioScience* 44 (5), 329–339.

- Moran, E.F., Packer, A., Brondizio, E.S., Tucker, J., 1996. Restoration of vegetation cover in the eastern Amazon. *Ecol. Econ.* 18, 41–54.
- Nepstad, D.C., Uhl, C., Serrão, E.A.S., 1991. Recuperation of a degraded Amazonian landscape. Forest recovery and agricultural restoration. *Ambio* 20 (6), 248–255.
- Penteado, A.R., 1967. Problemas de Colonização e de Uso da Terra na Região Bragantina do Estado do Pará. Two volumes. Universidade Federal do Pará, Belem.
- Randolph, J.C., Slusher, R.B., Moran, E.F., Brondizio, E.S., 1996. Primary production, litterfall, and decomposition in second growth forest in the Eastern Amazon. *Bull. Ecol. Soc. Am.* 77, 367.
- Salati, E., 1985. The climatology and hydrology of Amazônia. In: Prance, G., Lovejoy, T. (Eds.), *Key Environments: Amazônia*. Pergamon, London, pp. 18–48.
- Saldarriaga, J.G., West, D.C., Tharp, M.L., Uhl, C., 1988. Long-term chronosequence of forest succession in the Upper Rio Negro of Colombia and Venezuela. *J. Ecol.* 76, 938–958.
- Salomão, R.P., 1994. Estimativas de Biomassa e Avaliação do Estoque de Carbono da Vegetação de Florestas Primárias e Secundárias de Diversas Idades Capoeiras na Amazônia Oriental, Município de Peixe-Boi, Pará. Master's Thesis, Universidade Federal do Pará, Belem PA.
- Sanchez, P., 1976. *Properties and Management of Soils in the Tropics*. Wiley, New York.
- Shukla, J., Nobre, C., Sellers, P., 1990. Amazon deforestation and climate change. *Science* 247, 1322–1325.
- Skole, D., Tucker, C.J., 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260, 1905–1910.
- Smith, N.J.H., 1982. *Rainforest Corridors: The Transamazon Colonization Scheme*. University of California Press, Los Angeles.
- Subler, S., Uhl, C., 1990. Japanese agroforestry in Amazônia: a case study in Tome-Acu, Brazil. In: Anderson, A. (Ed.), *Alternatives to Deforestation*. Columbia University Press, New York, pp. 152–166.
- Tucker, J.M., Brondizio, E.S., Moran, E.F., 1998. Rates of forest regrowth in eastern Amazônia: a comparison of Altamira and Bragantina Regions, Pará State, Brazil. *Interciencia* 23 (2), 64–73.
- Uhl, C., 1980. *Studies of Forest, Agricultural, and Successional Environments in the upper Rio Negro region of the Amazon Basin*. Ph.D. Dissertation, Michigan State University.
- Uhl, C., 1987. Factors controlling succession following slash-and-burn agriculture in Amazônia. *J. Ecol.* 75, 377–407.
- Uhl, C., Buschbacher, R., Serrão, A.S., 1988. Abandoned pastures in eastern Amazônia. I. Patterns of plant succession. *J. Ecol.* 76, 663–681.
- Vieira, I.C.G., de Paiva Salomao, R., de Araujo Rosa, N., Nepstad, D.C., Roma, J.C., 1996. O renascimento da floresta no rastro da agricultura. *Ciencia Hoje* 20 (119), 38–44.
- Yamada, M., 1999. Japanese immigrant agroforestry in the Brazilian Amazon: a case study of sustainable rural development in the tropics. Ph.D. Dissertation, Department of Forestry, University of Florida, Gainesville.