FOREST SUCCESSION AFTER SHIFTING CULTIVATION IN EASTERN AMAZONIA

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By

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I hereby declare that this thesis has been composed by myself and except where otherwise stated the work contained herein is my own.

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In memory of my dear father and Dr. João Murça Pires

With love and gratitude to Nazo, Murilo and my family

ABSTRACT

Succession following shifting cultivation was studied in secondary forests (5 to 40 years old) and a primary forest in Bragantina region, Pará, Brazil. Secondary forests covered 62% of the study area (89 km^2) and crops and pasture 18%. Soil analyses showed an increase in pH, exchangeable calcium, magnesium and potassium and a decrease of organic matter and exchangeable aluminium, immediately after burning. Organic matter and extractable phosphorus increased with forest age, exchangeable aluminium and potassium were the same in both secondary and primary forests and exchangeable calcium and magnesium remained higher in the secondary forests. The highest densities of individuals and the least basal area and height were found in the younger secondary forests. The number of woody species (≥ 5 cm dbh) 250-m^2 plot ranged from 8 to 17 in the secondary forests and 17 to 27 in the primary forest. Ordination and classification of floristic data suggested four successional communities. The forests regenerated readily and studies showed: the largest seed bank (0-5 cm) in the 5-years-old forest (1190 ± 284 seeds m^{-2}) and a decrease with age to 137 ± 19 seeds m^{-2} in the primary forest; the highest seed rain in the 5-years-old forest (883 ± 230 seeds m^{-2}) and least in the primary forest (220 ± 80); 46% of the smaller plants (≥ 1 m tall, < 5 cm dbh) were seedlings and 54% were sprouts in the 5-years-old forest but in the 10-years and 20-years-old forests, seedlings (81%) predominated; adult plants (≥ 5 cm dbh) in 5 to 20-years-old plots regenerated mainly from sprouts. Even after about 90 years of shifting cultivation the region has the potential for forest regeneration and the soil nutrients are able to recover to values similar to those in the primary forest. This raises the hope that, if a land use plan for Bragantina could be implemented, then it would be successful.

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CHAPTER 1

BACKGROUND AND OBJECTIVES

Introduction

Tropical forests are being degraded and destroyed at high rates at a time when the knowledge of these forests is still rudimentary. In eastern Amazônia (Pará and Amapá states), increasing population densities and land use pressures have been responsible for a high rate of deforestation. Historically, the Bragantina region, in this part of Amazônia has had over a century a high exploitation by shifting cultivators. The region, is now less intensively farmed than formerly, as explained in Chapter 2 and there is much secondary forest at a range of successional stages of recovery. The secondary forests are representative of ecosystems where human intervention has been important and provide an opportunity to study succession.

Theoretical considerations about succession

The classic theory was developed in North America during the first two decades of this century. Clements' (1916) view of succession was of an orderly and predictable process in which vegetation converged towards a climax, a condition of stability and equilibrium. He recognized primary and secondary successions. Primary succession was defined as vegetation development on a newly formed substratum which contained no previous vegetation, no seed bank, and no organic matter. Secondary succession is the replacement of pre-existing vegetation, following a disturbance where a developed soil and seed or seedling bank are present from the previous vegetation. Gleason (1927) viewed communities as resulting from the fortuitous overlap of distributions of species with similar environmental tolerances. He emphasized the importance of stochastic processes in succession. Egler (1954) stressed the importance in secondary succession of the species composition at the time of disturbance (initial floristic composition model) through buried seeds, and vegetative perennating organs. He suggested that distinct phases of dominance occur because of differences in the growth rates of different groups of plants in the sequence: annual herbs, perennial herbs, short-lived woody plants, long-lived woody plants. Margalef (1963) and Odum (1969) summarized a number of successional trends in community and ecosystem attributes (e.g. biomass, diversity) and they believed that there was a tendency of ecosystems to develop in complexity with more trophic levels and greater diversity of species and life-forms. Horn (1976) suggested that patchy disturbance could lead to the situation where any species could, if propagules were present, invade an opening resulting from the death of any other species. He suggested that some of the local diversity of tropical forests could be due to this mechanism. Connell & Slatyer (1977) summarized species interactions during succession into three processes: facilitation, inhibition and tolerance. Each of these processes is composed of several mechanisms that often act together. Facilitation describes a situation in which one or more species helps the establishment, growth or development of another species. Inhibition is the prevention of plant maturation or growth, or the prevention of plant establishment, by existing plants. Tolerance describes the situation where one or more species neither inhibits nor helps other species during the succession. In the new theory of succession (Grime 1979; Finegan 1984), two concepts can be recognized: " a progressive alteration in the structure and species composition of the vegetation" and "the directional change with time of the species composition and vegetation physiognomy of a single species".

In tropical forests, succession has been explained according to Clements' concepts and based on Egler's initial floristic composition model. Theoretically, all the species participating in a succession become established at or very shortly after initiation and with sufficient time after disturbance, a disturbed site develops the structure, function, and complexity of mature forest (Odum 1969; Finegan 1984). The first successional studies in the tropics were based on descriptions of changes in floristic composition and structure in early stages of species colonization (Budowski 1965; Gomez-Pompa 1971) and only recently have some contributors emphasized forest dynamics (Whitmore 1978; Ewel 1979; Uhl *et al.* 1982a). The major progress in understanding the patterns of succession in the tropics came from the chronosequence studies of Purata (1986), Saldarriaga *et al.* (1988), and Uhl *et al.* (1988) among others. It is generally accepted that species of late successional and mature forests do not colonize clearings until there is already a well established pioneer vegetation, dominated by fast-growing pioneer trees (Gomez-Pompa & Vasquez-Yanes 1981; Whitmore 1983).

Some authors (Pickett 1976) have emphasized that an understanding of succession requires an understanding of the life histories of species. For example Gomez-Pompa & Vasquez-Yanes (1981) and Whitmore (1983) list some of the life history properties of secondary species in tropical lowland forests, including short life cycles, high growth rates, high reproductive resource allocations, continuous and early seed production, small seed size, long seed viability, and chemical protection against herbivory. The importance of life history properties was undertaken by Noble & Slatyer (1980) who termed such properties "vital attributes" that come to play at specific times or under specific conditions following a disturbance. In reality, there is a multiplicity of interacting mechanisms that operates during succession, including, among others, differential seed rain and propagule availability and other factors resulting from life history differences, competition, herbivory and changes in environmental factors. A site may be colonized by a species through recruitment from seeds or vegetative propagules. These are fundamentally different processes. Thus, establishment from seed is a two-step process: dispersal and germination. Vegetative propagation, on the other hand, is a one-step process. It establishes a population from the moment a vegetative propagule arrives at a site as part of the actual flora. One way to examine dispersal is to start at the sites receiving seeds rather than at the seed source. In this kind of study, seed traps are used to determine what seeds are reaching the site (i.e. the local seed rain). Seed rain studies have shown that seasonal and annual seed inputs into an area vary greatly, both qualitatively and quantitatively. Burial of seeds by soil after dispersal often improves the seed's chances of survival and germination, but only if they are not buried too deep. Seeds that do not get covered are more likely to be eaten and may lose viability sooner. Seeds that do not germinate immediately after dispersal enter and remain in the seed bank (the pool of viable seeds in the soil at a given time) until they finally germinate, lose viability or are eaten (Fenner 1985). Vegetative propagation is an important mechanism for the persistence of species in sites subjected to periodic disturbances, particularly fire (Noble & Slatyer 1980). Many species are able to sprout from below-ground organs after fire has killed their above-ground parts.

General aspects of shifting cultivation

In its traditional form, shifting cultivation commonly involves a short period of cultivation on cleared and burnt forest land followed by an extended period of forest fallow (Seavoy 1973; Clarke, 1976; Eden 1987). Under this type of agriculture the small farmers transform the original vegetation into a mosaic of agricultural lands and fallows. It is recognized that slash and burn techniques release nutrients from the biomass which acts as a nutrient pool which can be released as "fertilizer" when burned. Abandonment of individual fields is usually seen as a response to declining crop productivity associated with either nutrient loss or weed competition (Scott 1977).

The traditional system of shifting-cultivation has sustained the human population for centuries in the Amazon region. It has been practised by Indian tribes and *caboclos*, and more recently by the large contingent of peasant migrants from many parts of Brazil. In eastern Amazônia, this agricultural system is responsible for 80% of the regional production of basic food (such as beans, maize, manioc and rice) (Burger & Kitamura 1987). Managing the fallow is important to maintain favorable soil conditions, and includes controlling the ratio of the cropping to the fallow periods, and managing the composition of the successional community (Kleinman *et al.* 1995). A decline in the fallow period and disturbance through grazing and burning almost always leads to declining crop yields and the invasion of grass and herbaceous vegetation (Scott 1987).

In a broad sense, slash-and-burn agriculture is one of the few truly sustainable agroecosystems in the world because crop yields can be maintained without inputs of non-renewable fossil energy, including fertilizers and pesticides (Kidd & Pimentel 1992) and like all agricultural systems, shifting cultivation can be mismanaged and result in serious environmental degradation.

Patterns of plant succession after shifting cultivation

In slash and burn agriculture, when a forest is converted to cultivated land, not only is its original vegetation destroyed, but the site is subject to fire, the introduction of crop species, weeding, hoeing, and other disturbances to the soil when the crops are harvested (Toky & Ramakrishnan 1983a). Recovery from agricultural use is affected by the nature of such practices as type of clearing (mechanical vs. manual), type of cultivation (permanent vs. intermittent), the last crop, and the size of the cultivated area (Purata 1986). Other important variables that affect the succession and hence site recovery and possibilities of re-cultivation are: the history of the site (Whitmore 1983), the fire intensity (Uhl *et al.* 1982b), the length of cropping periods, regrowth age, the proximity and extent of the remnant forest (Purata 1986). Land use practices such as pastures, that eliminate the sources of tree shoots and seeds from the soil impede forest regrowth because of the numerous barriers to tree seed dispersal, tree seed survival and tree seedling survival (Nepstad *et al.* 1996b). The time required to regrow a forest on a deforested area depends on how the forest is removed, the type of land use following removal, the size of clearings, the distance to primary forest and the length of land use (Uhl *et al.* 1982b).

In general, the early secondary succession following tropical slash-and-burn agriculture is dominated by grasses, forbs and successional trees and shrubs (Ewel 1979; Uhl *et al.* 1982a; Stromgaard 1986; Purata 1986) and the reasons for their dominance on newly abandoned farm sites are the presence of many seeds in the seed bank or easily dispersed seeds or both (Uhl *et al.* 1982a; Swaine & Hall 1983), or resistance to fire (Stromgaard 1986). Swaine & Hall (1983) showed that the early stages of succession can be invaded by many species simultaneously but only long-lived species persist in the mature community. The structural characteristics of secondary forests are: high total stem density with short trees with small diameters; low basal area and wood volume; and high leaf area indices (Brown & Lugo 1990). These characteristics change with age and Saldarriaga *et al.* (1988) estimated that about 190 years are needed by a previously cultivated site to reach primary forest basal area and biomass values.

Nutrients under secondary succession

Under shifting cultivation, essential nutrients build up temporarily. However changes occur in the physio-chemical characteristics of the soil because of increased insolation and subsequent changes in soil moisture and atmospheric humidity (Ramakrishnan & Toky 1981). The fallow period allows some improvement of soil structure, prevention of erosion, protection of organic and inorganic crumbs against disintegration, recycling of nutrients, and prevention of leaching (Newton 1960).

The amounts of soil nutrients available are not the only factor affecting their uptake by vegetation (Uhl 1987). Many of the early regrowth species have efficient nutrient uptake mechanisms (Vitousek 1984) and after a few years a high proportion of the total nutrient pool has been immobilized in the plants and the soil nutrient levels are similar to those in primary forest (Uhl & Jordan 1984). These species appear to be able to mobilize phosphorus which is not available to crops (Saldarriaga 1987). The rapid growth of the native vegetation which immobilizes nutrients in the plant tissue and prevents losses (Tergas & Poppenoe 1971; Williams-Linera 1983) may restore the soil nutrients. The rate and degree of fertility restoration appear to depend on the development of vegetation and particularly on tree regeneration (Aweto 1981b). In Nigeria, six years after cultivation, the soil nutrient concentrations were still less than those in the primary forest soils (Adedeji 1984) but by the end of the tenth year the top soil organic matter concentration was similar to that under primary forest (Aweto 1981b). There is a strong positive relationship between topsoil nutrient and organic matter status and tree size and vegetation cover (Aweto 1981c). The implication of this relationship is that secondary forest is efficient in restoring soil nutrients during the succession.

Research objectives

To study forest succession following shifting cultivation, secondary forests of 5-years, 10-years, 20-years and 40-years-old and a lowland evergreen rain forest (*terra firme*) were chosen within an area of 89 km^2 in the Bragantina region, Pará. The following objectives were considered:

1. Quantify recent land use and successional stages of forests;
2. Evaluate the changes in soil characteristics and vegetation structure, composition and diversity in five forest age-classes;
3. Examine the regeneration mechanisms of species in successional forests.

The thesis begins with a description of the Bragantina region (Chapter 2) and the recent changes in land use (Chapter 3). Chapter 4 describes the research sites. Chapter 5 documents the soils and evaluates the successional changes. Chapters 6 and 7 describe changes in the floristics and structure of the forest in each forest age-class and Chapter 8 provides information on plant regeneration mechanisms, analyzing seed bank, seed rain, and regeneration from seedlings and sprouts. Chapter 9 gives the conclusion.

Importance of the research objectives

According to Gomez-Pompa *et al.* 1972 the rain forest regeneration mechanisms are best-adapted to tree fall gaps, and not well-adapted to larger disturbances resulting from agricultural activities and the tendency is towards an accumulation of degraded areas in the tropics. Research carried out in northern and eastern Amazônia showed that regeneration is rapid following small-scale disturbances such as treefalls gaps and shifting cultivation because nutrient losses are small and because there are efficient regeneration mechanisms (Uhl *et al.* 1982a; Uhl & Jordan 1984; Saldarriaga *et al.* 1988). However other severe (such as bulldozer clearing of the forest) or prolonged (such as conversion of forests to pastures) disturbances, can prevent recovery by eliminating nutrient stocks and the mechanisms of regeneration (Uhl *et al.* 1982b; Uhl *et al.* 1988; Buschbacher *et al.* 1988; Nepstad *et al.* 1996b). The pattern and mechanisms of recovery after repeated use of land under shifting cultivation (such is the case in the Bragantina region, which has about 90 years under this land use) is poorly known and this research provides an integrated description of succession, evaluating soil and vegetation changes and the mechanisms of species regeneration, following agricultural abandonment in the Bragantina region, eastern Amazônia, where almost all the primary forest was removed and shifting cultivation has been practised over secondary forests at least eight cycles of slash, burn, and fallow.

CHAPTER 2

THE BRAGANTINA REGION

Location

The Bragantina region (or zone) is located east of Belém in the state of Pará, Brazil between 0^0 45' and 1^0 39' S and 46^0 16' and 48^0 15' W (Fig. 1). Initially the Bragantina zone referred to all the area that was influenced economically by the Belém-Bragança railway along its 228 km route. Today FIBGE (1990, 1993) recognizes the *Mesorregião Bragantina,* comprising 13 counties and extending for 11,182 km^2 and the *Microrregião Bragantina* defined as the area covered by 11 counties, within an area of 8,703 km^2, and corresponds to 0.69% of the total area (1,253.164 km^2) of Pará state (FIBGE 1990, 1993). Here I am concerned with *Microrregião Bragantina*. The region has a gentle relief, with elevations of not more than 50 m, but is well drained by many rivers that flow to the Atlantic Ocean.

Climate

The climate corresponds to the "Am" type in the Köppen classification (Bastos 1972), with temperatures never below 18 $^\circ$ C and with a relatively long dry period. According to Diniz (1986) the mean annual temperature is constant, ranging from about 25-26^0 C and the average bright sunlight is 2,200-2,400 h year^{-1}. The minimum and maximum temperatures range from 20-22° C and

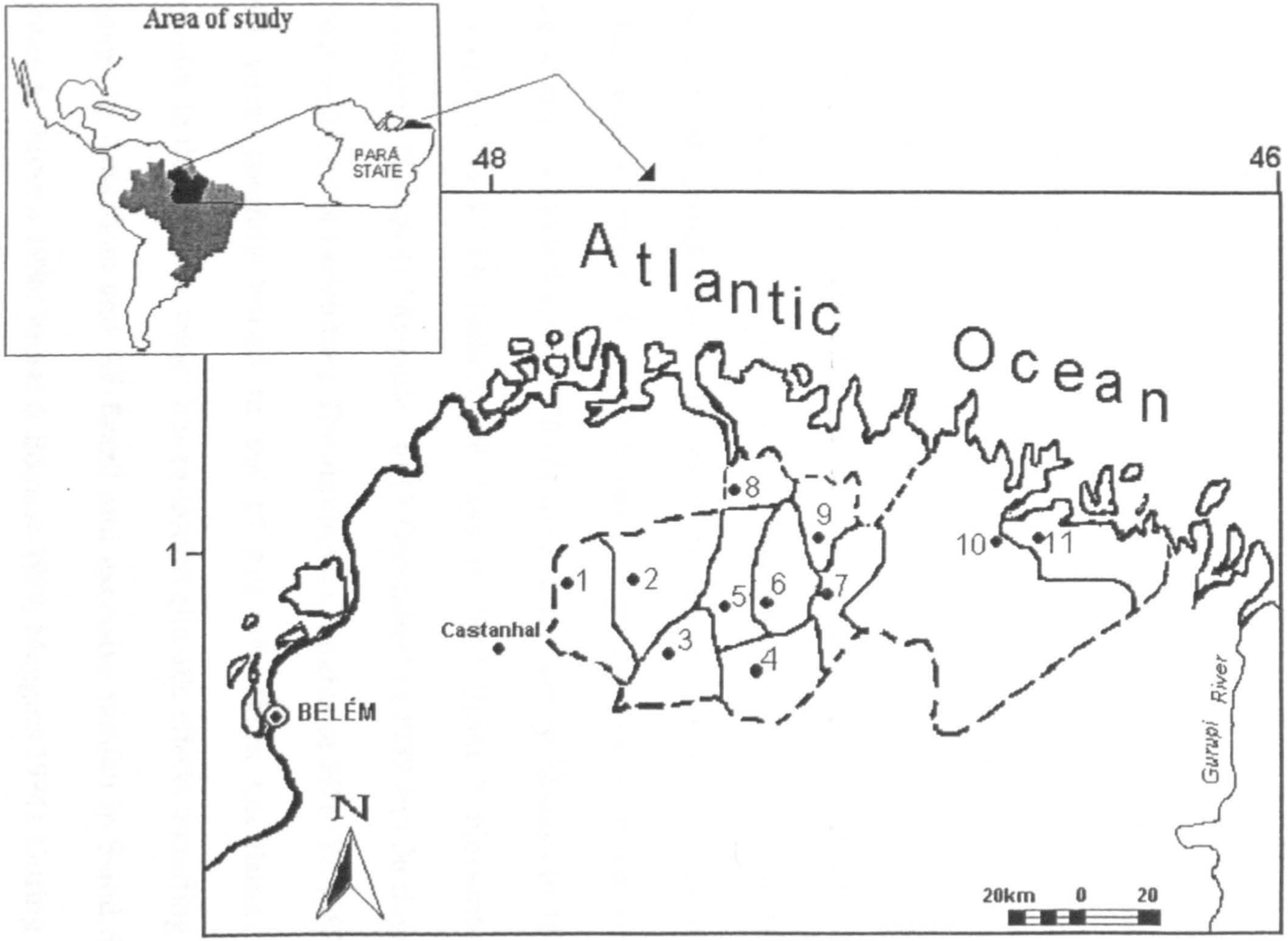

Figure 1. Location of the Bragantina region (*Microrregião Bragantina*), Pará, Brazil. Inside the bold pecked line are the counties: 1. São Francisco do Pará; 2. Igarapé-Açu; 3. Santa Maria do Pará; 4. Bonito; 5. Nova Timboteua; 6. Peixe-Boi; 7. Capanema; 8. Santarém Novo; 9. Primavera; 10. Bragança and 11. Augusto Correa. The internal boundaries of the counties are outlined with continuous lines.

29-32 °C (EMBRAPA-CPATU 1969-1993, measured at two meteorological stations at Belém and Castanhal (Fig. 1).

Rainfall data for April 1966 to April 1995 were obtained for a meteorological station at Departamento Nacional de Águas e Energia Elétrica - DNAEE, Brazil, located in Capanema county (01° 11' 00" S, 47° 10' 10" W) about 10 km E from the study sites (Fig. 1). There is a well marked dry season from September to November (usually less than 100 mm rainfall in these months). In general the wettest month is March and the driest is November (Fig. 2). The mean rainfall from April 1966 to April 1995 was 2144 mm in the rainy season and 140 mm in the dry season. There is a large variation in rainfall among the years (Fig. 3). From 1967 to 1994, the lowest precipitation occurred in 1983 (1656 mm) and 1992 (1687 mm) and the highest precipitation was in 1973, 1975, 1985 and 1986 (ranging from 3133 to 3346 mm). The longest consecutive period of days without rain (< 0.2 mm) during this period was recorded between 29 August and 21 December of 1976 (74 days) followed by 52 days in 1977 (from 25 October to 15 December), 49 days in 1982 (from 8 November to 26 December), 45 days (1 November to 15 December) in 1983 and 36 days in 1992 (9 November to 14 December). The abnormal droughts of 1976/77, 1982/83 and 1992 were possibly linked to the El Niño/Southern Oscillation (ENSO) episodes in those years, which has profound climatic effects including unusual dryness in Amazônia and NE-Brazil and excessive rainfall in S-and SE-Brazil (Nobre & Oliveira 1986; Vetter & Botosso 1989; Meggers 1994). During the field

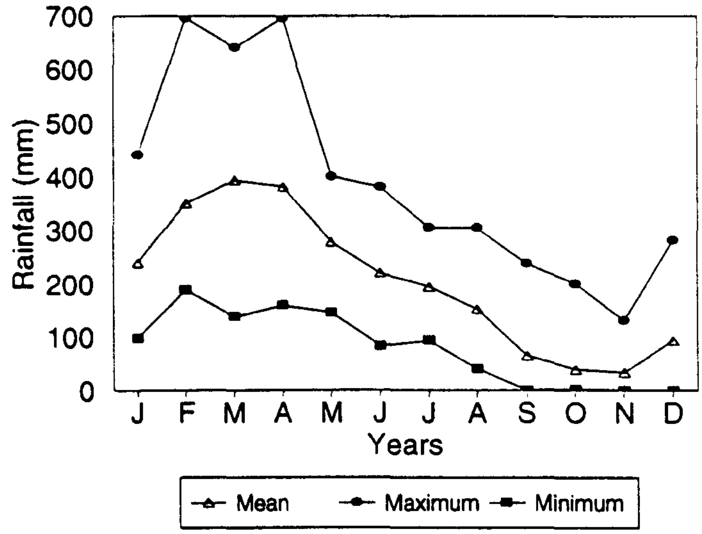

Figure 2. Mean, maximum and minimum monthly precipitation on Capanema county, Bragantina region, Pará (see Fig. 1) from April 1966 to April 1995 (Data from DNAEE unpublished).

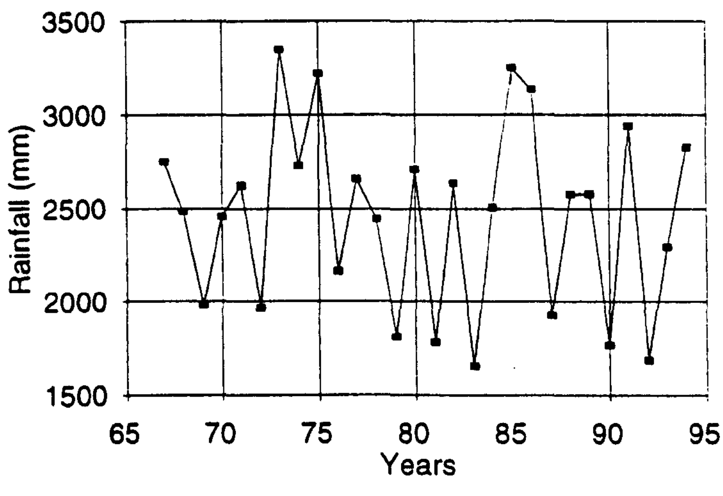

Figure 3. Total annual precipitation on Capanema county, Bragantina region, Pará (from 1967 to 1994) (Data from DNAEE unpublished).

study, the mean annual rainfall (1992-1994) was 2270 mm of which about half fell between 1 January and 30 April.

Geology and soils

The majority of the sediments in Brazilian Amazon was formed during the Tertiary period and was derived from the Brazilian and Guiana shields (Bigarella & Ferreira 1985). In the Bragantina region the Tertiary period is represented by the Barreiras sediments which lie stratigraphically above the Pirabas Formation (Francisco *et al.* 1971). The analysis of these Barreiras sediments suggests that their deposition took place in an alluvial flat system, possibly influenced by marine processes (Rossetti *et al.* 1990). They include sandy and silty-clayey deposits (Bigarella & Ferreira 1985). The Pirabas Formation was formed by marine successions and is a sandy clay limestone (very rich in fossil fauna) which originated in the Early Miocene (Ackermann 1964). Paleontological evidence indicates that the final phase of the Pirabas Formation and the begining of Barreiras deposition were contemporary, and can therefore be included in the same depositional model (Goes *et al.* 1990). According to the descriptions of Ackermann (1964) this Formation underlies part of the area of this study between Nova Timboteua and Capanema counties (Fig. 1). Today the Pirabas Formation is worked for cement in Capanema county.

The most important soils in the Bragantina region are Oxisols and Ultisols (USDA 1975) (*latossolo amarelo* and *podzolico vermelho-amarelo,* according to the Brazilian classification (EMBRAPA 1981) (Vieira *et al.* 1967; IPEAN 1975;

Falesi *et al.* 1980; Denich 1991). Oxisols are well drained and Ultisols have good to poor drainage. The extent of Oxisols and Ultisols is far from fully agreed. For Oxisols, estimates vary from 9.6% (IPEAN 1975) to 78.6% (Vieira *et al.* 1967) of the total area of Bragantina region.

Vegetation

The potential vegetation of the Bragantina region is classified as Tropical Lowland Evergreen Rain Forest (*sensu* Whitmore 1984), and according to Ducke & Black (1953) and Prance (1977) is included in the Atlantic coast region of Amazônia. The practical classification of vegetation in Bragantina is based primarily on the relief, and two principal types of vegetation are recognized (Pires 1973): dry land forest (*terra firme*) and the inundated forests (*igapó;* which are a type of Freshwater Swamp Forest in the classification of Whitmore (1984), formed by flooding with black and clear water rivers without sediments. Littoral grasslands, characterized by a cover of creeping grasses and shallow soil and frequent lakes (Pires & Prance 1985) and mangroves occur over small areas. However, the natural vegetation has been replaced by man-made vegetation during this century (Lima 1954; Egler 1961; Ackermann 1966). Even in 1950, the secondary forests covered 27.5% of the total area of the holdings, which represented 10 times more than the land devoted to annual crops and 180 times than the land devoted to perennial crops (Penteado 1967). By 1986, little remained of the primary forests; at least 90% of the forest cover in every county had been altered (CSRA-SUDAM 1988). Much of the land cleared in Bragantina is now secondary forest which remains in early stages of forest succession owing to intensive agricultural use (Denich 1986b; 1991). In Peixe-Boi county, which had most of the sites studied in this thesis, the predominant vegetation (46% of the county area) is secondary forest. Primary forest covered 16% of Peixe-Boi. Of this, 4,400 ha was *igapó* and 2,800 ha was *terra firme*. Of the *terra firme* forest 1,000 ha (2% of the area of Peixe-Boi county occurs in fragments greater than 100 ha (Fig. 4) (I.C.G. Vieira *et al.* unpublished).

Colonization and agricultural development

At the beginning of the rubber boom in Amazônia, during the 1870s, an agricultural colonization project was planned by the government of Pará for the Bragantina region and migrants from Europe (mainly Spanish, Portuguese, and French) and from the northeastern part of Brazil were brought in to become farmers (Egler 1961; Penteado 1967). Around 1915 after the great drought in the state of Ceará, in the northeastern part of Brazil, some 30,000 migrants came to Bragantina on their own initiative (Sioli 1973). Land holdings of 25 ha were distributed by the government and supplied by the Belém-Bragança railway (228 km). Owing to the large market for agricultural produce in Belém, the Bragantina region was quickly occupied: in 1950, 37% of the total inhabitants of Pará state lived in Bragantina (Ackermann 1966) which produced one fourth of the rice, beans, cassava and maize in Pará. The farming system was based on forest clearance and burning (shifting cultivation) but crop yields fell rapidly due to declining fertility and weed invasion (Penteado 1967). Individual fields were then abandoned, reverting to secondary forest or *capoeiras*. The main factors cited as having contributed to the failure of early planned colonization

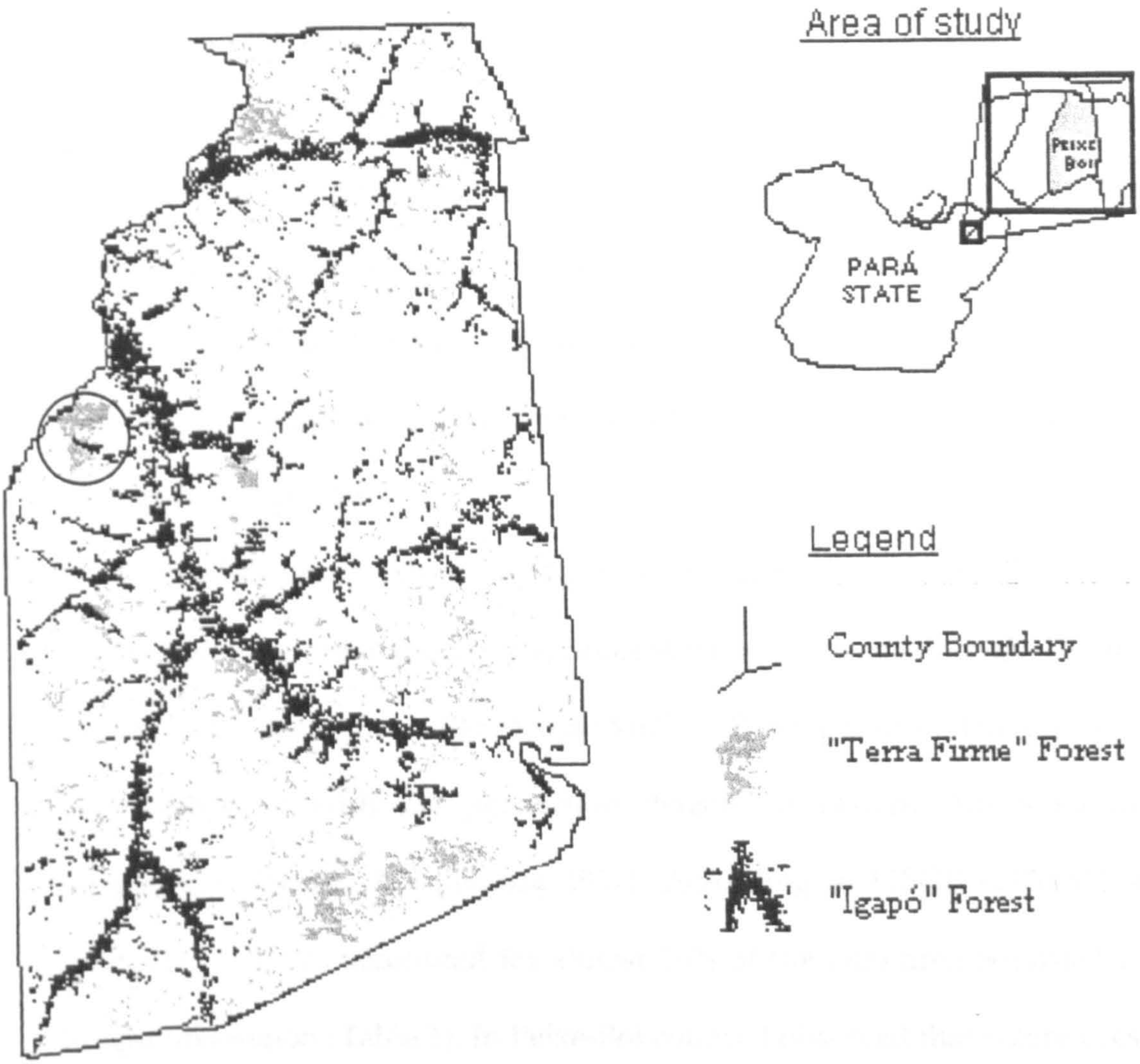

Figure 4. Map of distribution of remnant primary forests (*terra firme* and *igapó*) in Peixe-Boi county, Bragantina region, Pará. The circled area in the diagram at the extreme left shows the primary forest of *fazenda Monte Verde*.

in the Bragantina region were: the limited agricultural experience of most of the original settlers (Camargo 1948), insufficient official support, inadequate administration of the settlements (Egler 1961), archaic and rudimentary cultivation techniques employed (Penteado 1967), and local environmental conditions (Eden 1990). With the construction of the Belém-Brasília highway in 1960 and the incorporation of new areas in the agricultural frontier in eastern Amazônia, Bragantina became less important within the regional agricultural context. The Belém-Bragança railway was closed in 1966 and the farmers of the region stop receiving government incentives and subsidies for agriculture (Valverde & Dias 1967).

The most recent statistics of population demography from FIBGE (1985), showed that the population in the Bragantina region was still high. From 1970 to 1985 it increased from 20.8 people km^{-2} to 35 people km^{-2}. These values are high compared with the population density in eastern Amazônia of 2.6 people/km^2 (Burger & Kitamura 1987). According to FIBGE (1970-85) small holdings (< 50 ha) accounted for almost 50% of the total area occupied in the Bragantina region (Table 1). In Peixe-Boi county I observed that recent pressure for land and lack of capital to improve their agriculture has led many small farmers to sell their lands, establish themselves in villages and rent a small piece of land to subsistence cultivation. Since 1970 Bragantina has been occupied by land holders who bought small holdings and turned them to cattle ranching or commercial agriculture (e.g. black pepper, oil palm, papaya, rubber). There was an increase of almost 84,000 ha in the area of larger holdings (> 200 ha) from 1970 to 1985 (Table 1). In this period the area occupied

Table 1. Number of holdings and area occupied by them (ha) in the Bragantina region, Pará.

Classes of area (ha)	1970 no. holdings	1970 area	1985 no. holdings	1985 area
less than 10	7446	25904	12621	34424
10 - < 50	8551	218047	8596	228145
50 - < 100	1160	81480	1004	74195
100 - < 200	407	55940	377	52738
200 - < 500	87	25553	164	48375
500 - < 2000	21	18280	59	56618
2000 - < 5000	1	4427	8	22214
> 5000	1	6500	1	14999
Total	17674	436135	22830	531708

Source: FIBGE 1970, 1985.

Table 2. Changes of land use in the Bragantina region, Pará, 1970-1985.

	Total area (ha) 1970	Total area (ha) 1985	Rate of annual increase (1970-85)
Annual crop	33754	48398	2.43%
Perennial crop	3550	13813	9.48%
Pasture	22921	106831	10.81%

Source: FIBGE 1970, 1985.

by annual crops increased only 2.4% per year while perennial crops and pastures increased almost 10% annually (Table 2).

In the Bragantina region the agriculture is practised under secondary forests which have had at least eight cycles of shifting cultivation. The shifting cultivators grow annual crops, mainly manioc (*Manihot sculenta* Crantz.) and maize (*Zea mays* L.) for one or two years and then fallow the land for three to five years before re-cultivation. Burning occurs once a year in late October-early November near the end of the dry season. In this system maize is planted in the December or January after burning, and manioc is planted close to the harvest of the corn, a few months later in April-May. Depending on the individual farmer and amount of weed growth, some weeding may take place during each cropping. The yields from farmers' fields are generally low, ranging from 7-10 t ha^{-1} of fresh tubers of cassava and 6.5 t ha^{-1} of fresh corn (FIBGE 1984). These values are two to three times lower than the productivity of these crops in the new agricultural frontiers in Amazônia such as in Rondônia state or south of Pará state, where the farmers practise shifting cultivation after burning the primary forest.

CHAPTER 3

LAND USE AND FOREST SUCCESSION

Introduction

The monitoring and analysis of changes in vegetation cover of Amazônia has focused on total removal of forest (INPE 1992; Fearnside 1993). However many deforested areas are in stages of regrowth with a partial recovery of forest structure and function (Uhl *et al.* 1988; Nepstad *et al.* 1996a). Because of the significance of secondary forests for the global earth-atmosphere energy and carbon budgets (Brown & Lugo 1990) a number of studies using remote sensing data were made to quantify secondary forests in Amazônia (Lucas *et al.* 1993; Mausel *et al.* 1993; Moran *et al.* 1994; Alves & Skole 1996; Steininger 1996) but few of them looked at land use changes and succession. In this chapter, I report an analysis by remote sensing and Geographic Information System (GIS), of a subsite (i.e. a subsample of the whole scene of 185 x 185 km^2) of the Landsat Thematic Mapper (TM) of 1984 and 1991 that covers 89 km^2 of the Bragantina region, to determine the trends in land cover and to evaluate the process of successional dynamics in this landscape.

Methods

Two Landsat TM images taken on 27 July 1984 and 16 August 1991 were acquired from INPE (Instituto Nacional de Pesquisas Espaciais, Brazil). The images were processed at the GIS Laboratory of the Instituto de Pesquisas Ambientais da Amazônia (IPAM) in Belém, Brazil, using the program IDRISI 4.1 (Eastman, 1992). First a geometric rectification of the images was conducted using points collected in the field with GPS (Global Positioning System) that permitted accurate location of control points for geocorrection. The atmospheric rectification of the images was not necessary since none showed distortion or deformation. The study site (8.05 km x 11.1 km) was selected from the whole image. A complete analysis for the entire scene of the Landsat image, comprising the counties of Nova-Timboteua, Peixe-Boi and Capanema, will be developed elsewhere.

During 1991 many field expeditions were made to evaluate the types of land use and their characteristics. The features of interest included primary forest, three age classes of secondary forests (young , 1-10 years; intermediate, 10-20 years; and old, >20 years), lakes and rivers, grasslands, crops and pastures. A floristic inventory was made of the forests (Chapter 6). The current (1991) knowledge about the studied subsite was used as the ground-truth for the remote sensing approach and is described in chapter 4. The training sites (i.e. sampled areas of known land use) were located using GPS. Spectral signatures of these features were developed by IDRISI for the 1991 image, and the classification technique used was Supervised Maximum Likelihood Classification (IDRISI 1992). Classification of the 1984 image was developed using historical data from 28 holdings of 25 ha each *(lotes)*, all belonging to Mr. Mario Sato (of PA 394 highway km 31, Nova Timboteua, Pará) who knew his land well and could describe the use of each holding in 1984 and in 1991. His descriptions could be used to test the accuracy of the results of the classification for the 1991 TM image.

Results

The classification of the 1984 and 1991 images of the Bragantina subsite (about 8,900 ha, including part of Peixe-Boi and Nova Timboteua counties) defined 13 land cover classes, including 3-6% unclassified (Table 3 and Figs 5 and 6). After more than one century of agriculture, only 15% of the landscape was covered by primary forest. The fragmentation of Bragantina's forests has not lead to isolated patches but mainly to riverine corridors. The increase (189 ha) in primary forest from 1984 to 1991 is a result of recognizing this type of forest in 1991 among land cover that was unclassified in 1984 (Table 3; Fig. 6). The most common vegetation cover was secondary forest in both years (5,504 ha in 1984 and 5,457 ha in 1991). The intermediate age and old secondary forests, were dominant in 1984 (2,125 ha and 2,264 ha respectively) but in 1991 the area with old secondary forest increased by about 300 ha and intermediate secondary forest diminished by almost 630 ha. Pastures and agriculture were each 8-9% of the total area analyzed on both dates.

The classified images of 1984 and 1991 were overlaid using the program IDRISI 4.1 and the successional dynamics in this subsite between these years were analyzed. Forty-eight percent (2,600 ha) of the secondary forests did not change class and were considered stable. The remaining 52% (2,860 ha) of the secondary forest area (Figs 5 and 6), was divided into *successional* and *farmed*.

Table 3. Area and percentage of each land cover class in a Supervised Maximum Likelihood Classification (IDRISI 1992) of a Bragantina subsite located within the counties of Peixe-Boi and Nova Timboteua, using two dates (1984 and 1991) for Landsat TM data.

Land cover classes	1984 Area (ha)	1984 %	1991 Area (ha)	1991 %
1. Primary Forest	1,142.0	13.0	1,331.0	15.0
2. Old secondary forest	2,264.0	25.0	2,554.0	29.0
3. Intermediate secondary forest	2,125.0	24.0	1,493.0	17.0
4. Young secondary forest	1,115.0	12.0	1,409.0	16.0
5. Degraded pasture	480.0	5.0	413.0	5.0
6. Managed pasture	377.0	5.0	411.0	4.0
7. Perennial crops	386.0	4.0	439.0	5.0
8. Annual crops	352.0	4.0	362.0	4.0
9. Rivers and lakes	66.0	0.7	57.0	0.6
10. Grasslands	108.0	1.0	22.0	0.2
11. Cloud	9.0	0.1	68.0	0.7
12. Shadow	20.0	0.2	91.0	1.0
13. Unclassified	491.0	6.0	287.0	3.0

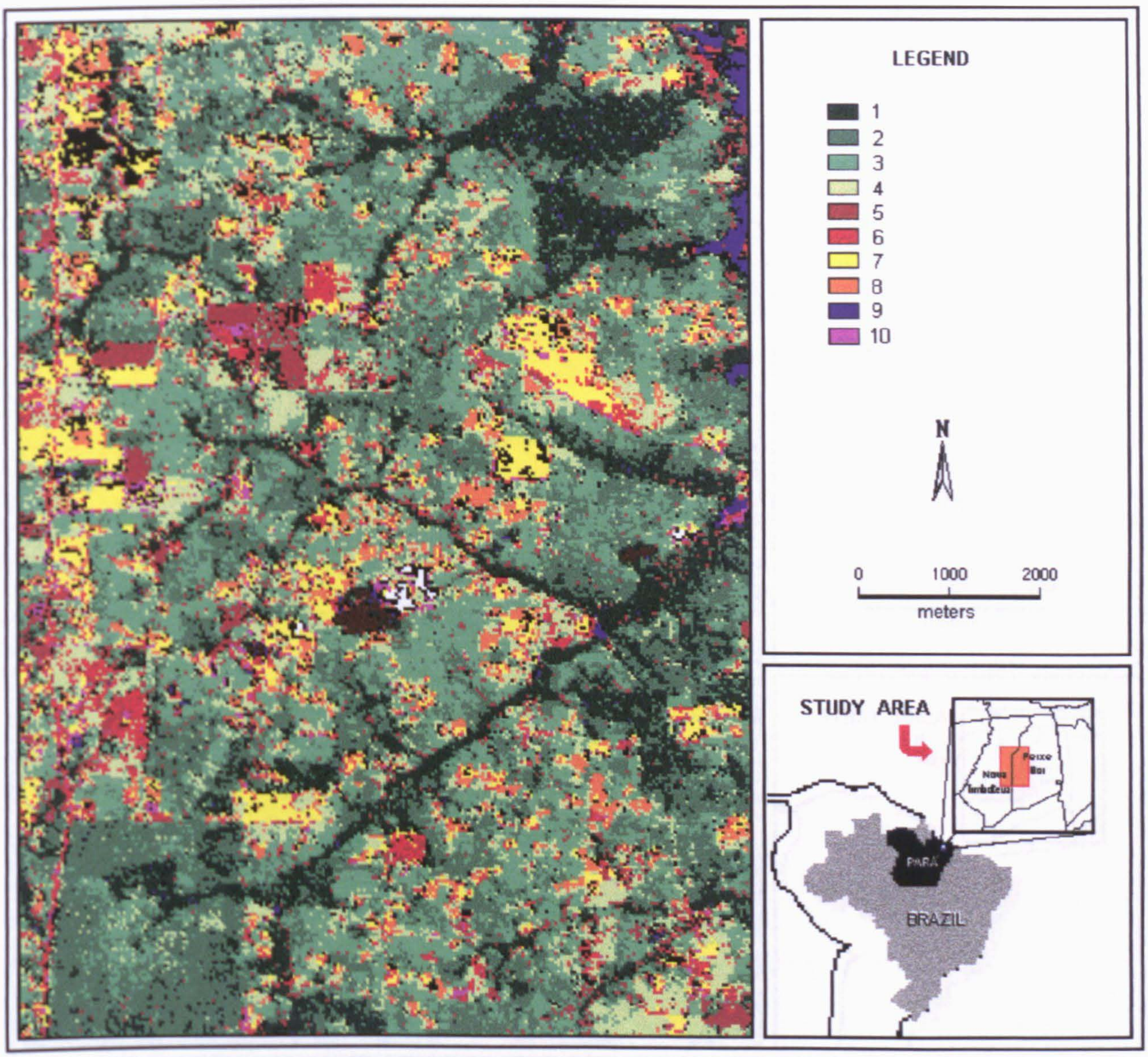

Figure 5. Supervised Maximum Likelihood Classification (IDRISI 1992) of a Bragantina subsite located within the counties of Peixe-Boi and Nova Timboteua, Pará, using Landsat TM data (July 1984). Legend: 1. Primary forest; 2. Old secondary forest; 3. Intermediate secondary forest; 4. Young secondary forest; 5. Degraded pasture; 6. Managed pasture; 7. Perennial crops; 8. Annual crops; 9. Rivers and lakes; 10. Grasslands. Cloud is represented by lack of colour, shadow by dark brown and unclassified by black.

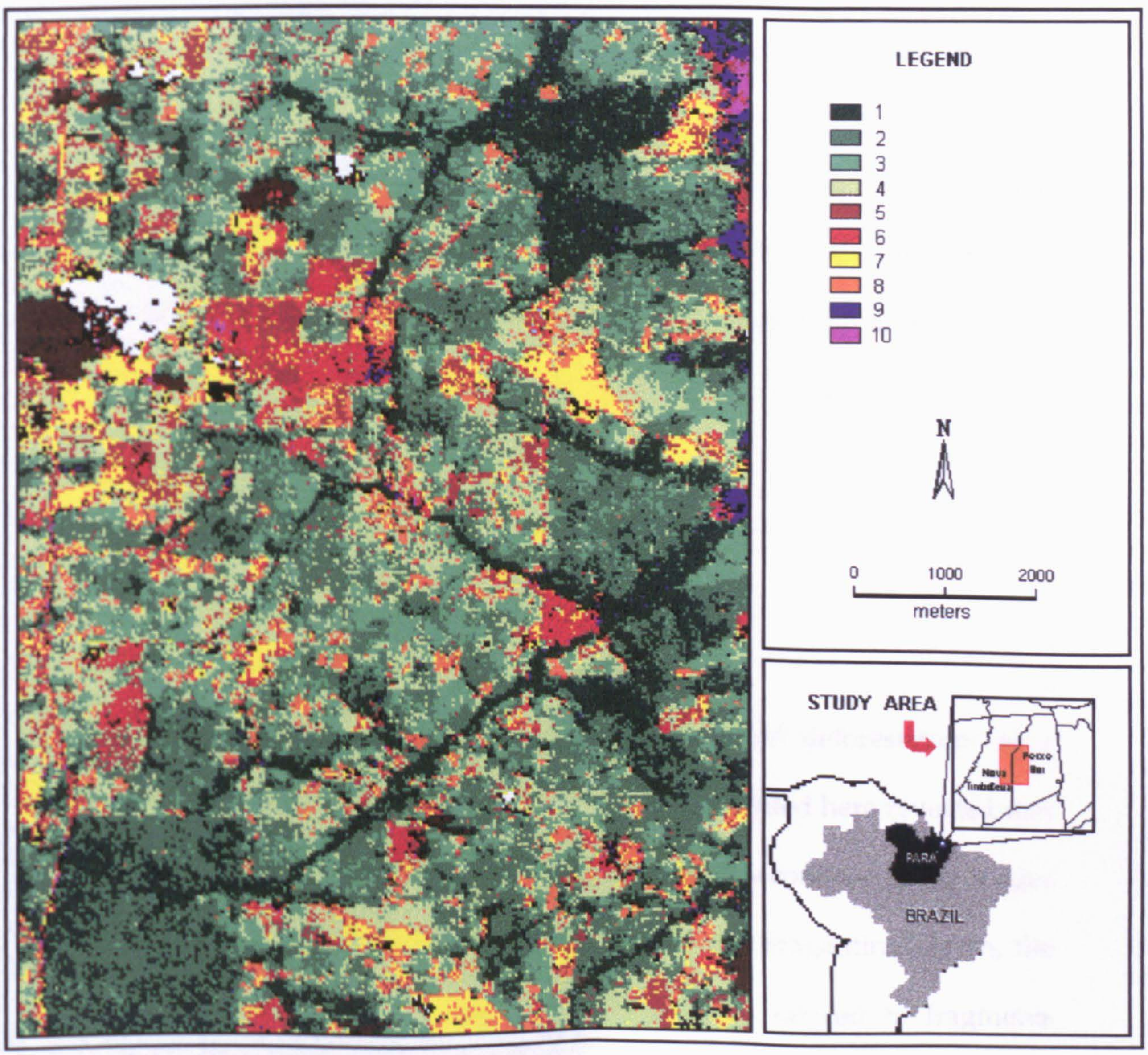

Figure 6. Supervised Maximum Likelihood Classification (IDRISI 1992) of a Bragantina subsite located within the counties of Peixe-Boi and Nova Timboteua, Pará, using Landsat TM data (August 1991). Legend: 1. Primary forest; 2. Old secondary forest; 3. Intermediate secondary forest; 4. Young secondary forest; 5. Degraded pasture; 6. Managed pasture; 7. Perennial crops; 8. Annual crops; 9. Rivers and lakes; 10. Grasslands. Cloud is represented by lack of colour, shadow by dark brown and unclassified by black.

Successional is defined as those cases where the earlier stages such as young secondary forest go (with little disturbances) to later ones. In contrast, *farmed* refers to those forests which were felled and the land cultivated. In the study site, there was a clear trend of increasing the successional area, as 32% (1,741 ha) of the secondary forests proceeded to more advanced stages while 20% (1,119 ha) re-entered a shifting cultivation cycle or were converted to pasture.

The overall accuracy of this study was 82%. In the 28 25-ha plots examined, the classification was found to be correct for 23 of them. Five were misclassified because of a confusion of degraded pastures with secondary forest. This is surprising but probably results from these weeded-infested pastures having the same spectral response as young secondary forest.

Discussion

The Bragantina region is characterized as an "old deforestation" area (INPE 1992; Skole & Tucker 1993), but the analysis presented here revealed that 15% is covered by primary forest, and a further 62% by secondary forest of ages up to at least 40 years. As agriculture spread over the Bragantina region, the large area occupied with evergreen rain forest was reduced to fragments ranging in size from a few hundred hectares to areas containing only few remaining trees (Fig. 4). The general trend of this study was that the remnant primary forests were not cut for land use. In similar studies made in 25-years-old frontiers in Amazônia (Altamira county, Pará and Rondônia state) it was shown that a large portion of the primary forest was remaining, but that abandonment was an important practise with secondary vegetation as an important source of land for clearing (Moran *et al.* 1994; Alves & Skole 1996).

In 1991 46% of the area was covered by secondary forests older than 10 years (Table 3) but in Igarapé-Açu county Denich (1991) indicated that much of the secondary forests were in the early stages owing to the intensive agriculture. In the study site, 20% of secondary forest was converted to agriculture or pasture between 1984 and 1991. Although much of the study site is still under secondary forests but few of them are on small farms. Owners of large holdings acquired more land than can be farmed in the short term, and they leave large areas of secondary forests. The owner with 28 holdings, for example, had in 1991, 46% of his land under secondary forests in spite of the development of permanent agriculture. Many of the pastures in the region were established after 1970, after the fungal disease *Fusarium* devastated the black pepper plantation but many of the newly created pastures were degraded due to inadequate management and invasion by weeds. Light-used pastures in eastern Amazônia, can sustain forest regrowth on abandonment of lightly used cattle pastures (Uhl *et al.* 1988). However, in recent years, bulldozers and fertilizers and new species of grasses have been employed to improve degraded pastures and this has prevented the return of the forest (Uhl *et al.* 1988; Mattos & Uhl 1994).

In conclusion, about 90 years of human impact on Bragantina has resulted in a mosaic of lowland forest fragments, secondary forests of different ages, cultivated lands, and pastures. From 1984-91 there were important changes in the use of secondary forests, most of which were undisturbed during this period.

Few of them were converted to agricultural fields or pastures between 1984 and 1991. Until recently Bragantina has been known for its agricultural landscape but it now is well wooded and has a relatively high tree biomass.

CHAPTER 4

SITE AND PLOT SELECTION

The study sites

The study sites are located in the counties of Peixe-Boi and Nova Timboteua, Bragantina Region, eastern Amazônia (Fig. 1).

The primary forest

In a search for a sample of primary forest, I traveled throughout the whole Bragantina Region, and finally found a remnant of about 200 ha, protected by its owner and surrounded by secondary forests and grasslands. This forest fragment, which represents 20% of the dry land (*terra firme*) forests larger than 100 ha in Peixe-Boi county is one of the foci of this study, as it provides the best record of the original vegetation. It is located at *fazenda Monte Verde* (Fig. 4) and is Lowland Evergreen Rain Forest (*sensu* Whitmore 1984), with a canopy 30-40 m tall. Two tree species (*Manilkara amazonica* and *Lecythis lurida*) were selective logged about 50 years ago, but at a low intensity which caused little damage and allowed both species to regenerate well.

The secondary forests

Limitation of time and the impossibility that the plots could be studied for a long time, made me use a "static" approach (*sensu* Austin 1977) to study plots of different ages. This method has been used in the tropics by many researchers (Kellman 1970; Purata 1986; Young *et al.* 1987; Saldarriaga *et al.* 1988; Uhl *et al.* 1988).

Shifting cultivation began in the west of the Bragantina near Belém in 1877 (Ackermann 1966). It apparently spread eastwards and by 1903 included the sites described in this thesis (Egler 1961). It is impossible to date the first forest clearance at each individual site studied but it can be estimated as about 90 years ago. Thirty-one sites were selected for intensive studies, after interviewing local residents. The sites were ascertained as having only grown annual crops, never sprayed with herbicides or fertilized, and of a size large enough for vegetation survey plots. All selected sites had been used intensively over at least eight cycles of shifting cultivation. The sites were selected to represent the following age classes of secondary forest: 4 to 5 years (N=10), 10 to 12 years (N=10), 20 to 23 years (N=10) and 40 to 45 years (N=1). These age classes are hence referred to as 5, 10, 20 and 40 years. The secondary forests of 5, 10 and 20 years were located within a radius of 3 km of the *Monte Verde* primary forest. The 40-years-old secondary forest was located about 10 km S from the *Monte Verde* primary forest which was an agricultural colony with 650 *lotes* of 25-ha each given to small farmers to cultivate. As has been the case with many colonies in Bragantina, this one failed and the farmers left it. Since about 1950 this area has been preserved by the Brazilian Army.

Plot size was based on Denich (1986a) who found that plots of 50 m^2 were suitable, based on a species-area curve, for a vegetation survey of young secondary forests in Bragantina. However, larger plots were used (250 m^2) because old forests were included in my study. It should be noted that the small farmers of the Bragantina region cultivate very small patches (ranging from about 0.01-1 ha) depending on the available labour.

Pseudo-replications

Owing to the difficulty of finding secondary forests of 40-years-old and primary forests in different sites in the Bragantina, the optimum design of replicated plots of these forests in different sites was not possible. The chosen design of these two forests, involving replicate plots in just one site of each, is open to criticisms of "pseudo-replication" (Hurlbert 1984), but was the only practicable design in the circumstances.

CHAPTER 5

THE SOILS

Introduction

The fallowing of land before re-cultivation is a common practice of shifting cultivators. Changes in the nutrient stock in the soil owing to the burning and utilization by crops must occur in such systems and a knowledge of the soil is essential to understand the way in which the fertility is restored during the secondary-forest period. This chapter examines the changes in some physical and chemical properties of the soils as the forest ages.

Methods

Soil pits

A soil pit of 1.5 m was dug close to transect 2 of the primary forest and close to one plot in each age class of secondary forest (5, 10, 20 and 40-years-old). The soil profile descriptions were made using the Munsell colour chart (Munsell 1954) and an EMBRAPA manual (1979). Soil samples were collected from each horizon to measure the particle-size composition in January 1994.

Soil sampling and analyzing

Soil pH, soil organic matter, and soil nutrient concentrations were measured in ten soil samples collected at random in five of the sites of 10 and

20-years-old secondary forests (chosen based on the availability of them for such studies since the farmers used the fallows for cropping) and of five sites of recently (within 7 days) burned areas (formerly a 5-years old secondary forest). The samples were taken to a depth of 0-5 cm, 5-10 and 10-20 cm in each of the sites (total of 50 samples/forest age-class/depth). For the 40-years secondary forest and the primary forest, the soil samples were collected at random along the same transects used for the vegetation survey (Chapter 6), so that for each depth there were 50 samples for each of these forest age-classes. The samples were air-dried and sieved through a 2-mm mesh. Bulk density was measured at ten points in each of the secondary forest sites and at fifty points along the transects of the primary forest. Bulk density was measured using a bottomless metal cylinder 4 cm high and 6 cm diameter, inserted into the soil to depths of 0-5 and 5-10 cm and the soil excavated, weighed in the field and then ovendried at 105 °C before reweighing in the laboratory.

Soil analyses were carried out by the Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC, Brazil) soil laboratory. pH was determined using a 1:2.5 soil:water suspension using a pH meter and a glass electrode. Organic matter was determined by the Walkley-Black method (1934). The percentage of carbon was obtained by dividing the concentration of organic matter by 1.724. Phosphorus and potassium were extracted by 0.0125 M sulphuric acid and 0.05 M hydrochloric acid solution (1:10). Phosphorus was measured colorimetrically by the molybdate-ascorbic acid method described by Murphy & Riley (1962) using a Bausch & Lomb spectronic 20 spectrophotometer. Potassium was analyzed using flame photometry. Calcium with magnesium, and aluminium were extracted by 1 M potassium chloride solution. Calcium + magnesium were analyzed by titration with 0.025 M EDTA-Na solution and determined separately using murexide indicator (ammonium purpurate). Aluminium was determined by titration with 0.025 M sodium hidhroxide solution using bromothymol indicator. Total acidity (H^+ + Al^{3+}) was measured for three samples of soil for each forest age-class and depth by titration after leaching 3-g of subsamples with five 20-ml portions of 1 M potassium chloride solution. Another titration with 10 ml of 2.5 mM sodium hydroxide solution using phenolphthalein as indicator, was made to estimate total acidity. Cation exchange capacity (CEC) was calculated from the sum of total exchangeable cations plus total acidity.

Particle-size composition was measured using the pipette method for three 30-g soil samples taken randomly from the ten samples used for the chemical analysis described above for each site of the recently burned areas and 10 and 20 years-old secondary forests. Thus there was a total of 15 soil samples for each depth for each forest age-class. For the 40 years-old secondary forest and primary forest sites the particle-size composition was measured in 15 soil samples randomly selected from the fifty samples used for the chemical analysis.

Values of nutrient concentrations were converted to kg ha^{-1} based on the bulk density measurements of 0-5 cm and 5-10 cm samples separately, to calculate nutrient stocks in the upper 10 cm of soil.

Statistical analysis

For each depth (0-5, 5-10 and 10-20 cm) log transformed data from soils of 10-years-old, 20-years-old and recently burned areas, which have the same sample size (five replicate sites; 10 soil samples/site) were analyzed by a two-way nested analysis of variance with factor A (forest age-classes) considered as fixed, and factor B (replicate sites) as random (Zar 1996). I did not use the 40-years-old and the primary forest in this analysis because only one site of each was sampled. A Tukey test was used to compare the means of nutrient concentrations among the five forest age-classes, including the primary forest and 40-years-old secondary forests (for which only one site was sampled but which had the same number (50) of soil samples for each depth).

Results

Soil pits

A description of each soil pit is given in Table 4. The soils were classified as Oxisols (USDA 1975) or *latossolo amarelo* in the Brazilian classification (EMBRAPA 1981). The particle-size composition from each horizon of the pits is shown in Table 5. The soils were mostly sandy, especially in the secondary forests which had 64-86% of sand and 8-23% of clay in the first two horizons. The deepest horizons had a heavier texture ranging from 55-71% of sand and 22-31% of clay. The primary forest had 61-72% of sand in the surface horizon and 55% at 130-160 cm depth.

Table 4. Soil profile descriptions from pits near one plot of each forest age-class (5-years, 10-years, 20-years and 40-years-old secondary forest and primary forest) in the Bragantina region, Pará.

Depth (cm)	5-years-old secondary forest
0 - 21	A horizon. Sand, 10 YR 3/2 (very dark grayish brown), very weak small to medium granular structure, friable peds, many roots, good porosity with a clear boundary.
21 - 39	AB horizon. Sandy loam, 10 YR 3/6 (dark yellowish brown), weak fine to medium granular and sub-angular blocky structure, friable peds, many roots, good porosity, diffuse boundary.
39 - 60	BA horizon. Sandy clay loam, 10 YR 4/4 (dark yellowish brown), very weak fine sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
60 - 78	B_1 horizon. Sandy clay loam, 7.5 YR 4/6 (strong brown), weak fine to medium sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
78 - 109	B_2 horizon. Sandy clay loam, 7.5 YR 5/6 (strong brown), weak fine to medium sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
109 - 159	B_3 horizon. Sandy clay loam, 7.5 YR 5/6 (strong brown). weak fine to medium sub-angular blocky structure, friable peds, common roots, good porosity.

Depth (cm)	10-years-old secondary forest
0 - 22	A horizon. Loamy sand, 10 YR 3/2 (very dark grayish brown), weak , small to medium granular structure, friable peds, many roots, presence of charcoal, good porosity with a clear boundary.
22 - 49	AB horizon. Sandy loam, 10 YR 4/4 (dark yellowish brown), weak fine to medium granular blocky structure, friable peds, many roots, good porosity, diffuse boundary.
49 - 69	BA horizon. Sandy clay loam, 10 YR 4/4 (dark yellowish brown), very weak fine sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
69 - 97	B_1 horizon. Sandy clay loam, 7.5 YR 5/6 (strong brown), weak fine to medium sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
97 - 138+	B_2 horizon. Sandy clay loam, 7.5 YR 5/6 (strong brown), weak fine sub-angular blocky structure, friable peds, common roots, good porosity.

Depth (cm)	20-years-old secondary forest
0 - 14	A horizon. Loamy sand, YR 3/2 (very dark grayish brown), weak small to medium granular structure, friable peds, many roots, presence of charcoal, good porosity with a clear boundary.
14 - 30	AB horizon. Sandy loam, 10 YR 4/2 (dark grayish brown), weak fine to medium granular and sub-angular blocky structure, friable peds, many roots, good porosity, diffuse boundary.
30 - 49	BA horizon. Sandy clay loam, 10 YR 4/4 (dark yellowish brown), very weak fine sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.

49 - 74	B_1 horizon. Sandy clay loam, 10 YR 5/6 (yellowish brown), very weak fine sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
74 - 110	B_2 horizon. Sandy clay loam, 10 YR 6/6 (brownish yellow), weak fine sub-angular blocky structure, friable peds, few roots, good porosity, diffuse boundary.
110 - 160	B_3 horizon. Sandy clay loam, 10 YR 6/6 (brownish yellow), weak fine sub-angular blocky structure, friable peds, fewroots, good porosity.

Depth (cm)	**40-years-old secondary forest**
0 - 15	A horizon. Loamy sand, YR 3/3 wet (dark brown), weak small to medium granular structure, friable peds, many roots, presence of charcoal, good porosity with a clear boundary.
15 - 28	AB horizon. Sandy clay loam, 10 YR 5/4 (yellowish brown), very weak fine granular and sub-angular blocky structure, friable peds, many roots, good porosity, diffuse boundary.
28 - 48	BA horizon. Sandy clay loam, 10 YR 5/6 (yellowish brown), very weak fine sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
48 - 73	B_1 horizon. Sandy clay loam, 10 YR 6/6 (brownish yellow), very weak fine sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
73 - 103	B_2 horizon. Sandy clay loam, 10 YR 6/6 (brownish yellow), weak sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
103 - 153	B_3 horizon. Sandy clay loam, 10 YR 6/6 (brownish yellow), weak sub-angular blocky structure, friable peds, common roots, good porosity.

Depth (cm)	**Primary forest**
0 - 19	A horizon. Sandy loam, YR 3/2 (very dark grayish brown), weak small granular structure, friable peds, many roots, good porosity with a clear boundary.
19 - 42	AB horizon. Sandy loam, 10 YR 3/6 (dark yellowish brown), weak fine sub-angular blocky structure, friable peds, many roots, good porosity, diffuse boundary.
42 - 69	BA horizon. Sandy clay loam, 10 YR 3/6 (dark yellowish brown), weak fine sub-angular blocky structure, friable peds, many roots, good porosity, diffuse boundary.
69 - 100	B_1 horizon. Sandy clay loam, 10 YR 3/6 (dark yellowish brown), weak medium sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
100 - 130	B_2 horizon. Sandy clay loam, 10 YR 5/6 (yellowish brown), weak medium sub-angular blocky structure, friable peds, common roots, good porosity, diffuse boundary.
130 - 150	B_3 horizon. Sandy clay loam, 10 YR 5/6 (strong brown), weak medium sub-angular blocky structure, friable peds, common roots, good porosity.

Table 5. Particle size composition from each soil horizon depth from a pit dug close to one site of each forest age-class in the Bragantina region, Pará.

Horizon depth (cm)	Particle-size fraction (%)			
	Clay (< 0.002 mm)	Silt (< 0.05 - 0.002 m)	Fine sand (< 0.2 - 0.05 mm)	Coarse sand (< 2 - 0.2 mm)
5-years-old				
0-21	8	6	18	68
21-39	18	11	24	47
39-60	29	11	20	40
60-78	35	10	18	37
78-109	30	11	19	40
109-159	31	12	18	39
10-years-old				
0-22	9	11	25	55
22-49	19	17	22	42
49-69	27	3	21	49
69-97	25	9	20	46
97-138	26	11	18	45
20-years-old				
0-14	9	8	18	65
14-30	15	12	24	49
30-49	22	8	22	48
49-74	24	9	19	48
74-110	24	8	23	45
110-160	22	7	20	51
40-years-old				
0-15	8	10	18	64
15-28	23	11	21	45
28-48	27	12	21	40
48-73	28	11	19	42
73-103	29	8	18	45
103-153	28	10	20	42
Primary forest				
0-19	15	13	18	54
19-42	22	17	20	41
42-69	30	14	19	37
69-100	31	13	17	39
100-130	29	11	17	43
130-160	29	16	19	36

Soil chemical analysis

Soil chemical, particle-size composition, and bulk density for the 0-5 cm, 5-10 cm and 10-20 cm samples are shown in Tables 6, 7 and 8. The difference of the nutrient concentrations among replicate sites of burned areas ($p < 0.01$ for all variables) could be a consequence of the different intensities of burning. However variation among replicate sites of secondary forests of the same age (10 or 20-years-old) was large relatively to the range of nutrient concentrations observed ($p < 0.01$ for all except for aluminium). Burning was found to bring about an increase of 1-2 units of soil pH and pH was higher in the soil of the successional forests than in the primary forest ($p<0.01$). There was a considerable change in soil organic matter with burning. Most of the surface soils (0-5 cm) of the secondary forests had 1.5-2% organic matter. In the 20-years-old forest, the organic matter was almost the same as that of the primary forest. The apparent decrease after 40 years may be a result of "pseudo-replication". The mean concentration of organic matter in the lowest soil depths (5-10 and 10-20 cm) is lower than in the topsoil (0-5 cm). Exchangeable potassium, calcium and magnesium increased with burning and then decreased significantly ($p < 0.01$) with the age of the secondary forests to the primary forest values except for magnesium which remained significantly ($p < 0.01$) higher than in the primary forest (Tables 6 to 8). Aluminium decreased after burning and increased with the age of the secondary forests. There was a marked increase of extractable phosphorus in the topsoil after burning. The secondary forests showed an increase of extractable phosphorus until the twentieth year, after which there was a small decline in the 40-years-

Table 6. Means (and ranges) of soil (0-5 cm depth) chemical properties, bulk density (n=50 samples/habitat) and particle size composition (n=15 samples/habitat) from recently burned areas, 10-years, 20-years and 40-years-old secondary forests and a primary forest in the Bragantina region, Pará. The mean values followed by different letters in the rows are significantly different according to the Tukey test, $p < 0.01$. n.d. = no data.

	Burned Area	10-years forest	20-years forest	40-years forest	Primary forest
$pH_{(H2O)}$	6.18 a	4.53 b	4.5 b	4.45 b	4.15 c
	(5.4-6.7)	(4.1-4.9)	(3.9-5.5)	(4-5.1)	(3.6-4.9)
Organic matter (%)	1.61 a	1.97 b	2.04 bc	1.53 a	2.44 c
	(0.67-2.81)	(1.08-2.67)	(1.22-3.43)	(0.75-2.81)	(1.15-4.51)
C (%)	0.94 a	1.14 b	1.19 bc	0.89 a	1.42 c
	(0.39-1.63)	(0.63-1.55)	(0.71-1.99)	(0.44-1.63)	(0.67-2.62)
P extractable ($\mu g\ g^{-1}$)	7.08 a	2.72 b	3.52 c	2.98 bc	4.42 d
	(2-16)	(1-5)	(2-6)	(2-6)	(2-7)
Exchangeable cations (meq 100 g^{-1})					
K	0.15 a	0.03 b	0.03 b	0.02 c	0.03 b
	(0.03-0.45)	(0.02-0.06)	(0.01-0.09)	(0.01-0.03)	(0.02-0.06)
Ca	2.15 a	1.05 b	1.07 b	0.99 b	0.93 b
	(0.8-3.3)	(0.4-1.6)	(0.4-2.8)	(0.4-2.2)	(0.3-3.4)
Mg	0.86 a	0.5 b	0.5 b	0.53 b	0.22 c
	(0.3-1.7)	(0.3-0.7)	(0.2-1.1)	(0.2-1.2)	(0.1-0.5)
Al	0.01 a	0.79 b	0.82 b	0.52 c	0.83 b
	(0-0.2)	(0.3-1.3)	(0.4-1.3)	(0.1-1.1)	(0-1.8)
Total acidity	2.57	4.37	7.23	4.03	5.00
($H^{+} + Al^{3+}$)	(1.6-4.1)	(3.0-5.6)	(5.5-8.4)	(3.5-4.6)	(3.5-5.9)
CEC (meq 100 g^{-1})	5.26a	5.95a	8.83a	5.65a	6.27a
	(3.54 -7.76)	(4.04 -7.75)	(8.0 -9.54)	(4.92 -6.72)	(4.22-7.64)
Bulk density (g cm^{-3})	1.35 a	1.24 b	1.28 b	n.d.	1.24 b
	(1.14-1.51)	(0.95-1.37)	(1.11-1.43)		(1.11-1.38)
Particle size (%)					
Clay	4 a	9 bc	8 abc	7 ab	11 c
	(1-8)	(4-13)	(4-13)	(4-18)	(4-21)
Silt	7 a	14 b	7 a	5 a	8 a
	(2-13)	(7-26)	(3-13)	(2-9)	(5-12)
Fine sand	15 a	28 b	26 b	17 a	29 b
	(3-28)	(20-36)	(18-42)	(10-24)	(19-39)
Coarse sand	74 a	49 b	59 b	71 a	52 b
	(58-93)	(36-64)	(33-72)	(59-82)	(33-68)

Table 7. Means (and ranges) of soil (5-10 cm depth) of soil chemical properties, bulk density (n=50 samples/habitat) and particle size composition (n=15 samples/habitat) from recently burned areas, 10-years, 20-years and 40-years-old secondary forests and a primary forest in the Bragantina region, Pará. The mean values followed by different letters in the row are significantly different according to the Tukey test, $p < 0.01$. n.d. = no data.

	Burned area	10-years forest	20-years forest	40-years forest	Primary forest
$pH_{(H2O)}$	5.67 a (4.7-6.8)	4.56 b (4-5.1.)	4.46 bc (4.1-4.9)	4.35 c (4-5)	4.18 d (3.8-5.3)
Organic matter (%)	1.5 a (0.3-4.9)	1.7 b (1.04-2.33)	1.7 b (1.12-2.81)	1.43 a (0.6-3.67)	1.98 b (1.27-3.32)
C (%)	0.87 a (0.18-2.89)	0.99 b (0.60-1.35)	1.01 b (0.65-1.76)	0.83 a (0.35-2.13)	1.15 b (0.74-1.93)
P extractable ($\mu g\ g^{-1}$)	2.9 a (1-9)	1.76 bc (1-4)	2.2 ab (1-4)	1.58 c (1-3)	2.24 a (1-4)
Exchangeable cations (meq 100 g^{-1})					
K	0.05 a (0.02-0.19)	0.02 b (0.01-0.04)	0.02 b (0.01-0.04)	0.02 b (0.01-0.03)	0.02 b (0.02-0.04)
Ca	1.37 a (0.5-3.7)	0.71 b (0.2-1.3)	0.49 cd (0.3-0.9)	0.54 bc (0.3-1.3)	0.4 d (0.2-1.2)
Mg	0.41 a (0.2-1)	0.38 ab (0.1-0.7)	0.34 ab (0.2-0.7)	0.32 b (0.7-0.7)	0.13 c (0-0.3)
Al	0.14 a (0-0.8)	0.9 b (0.5-1.5)	1.15 b (0.5-1.6)	0.89 b (0.3-1.4)	1.12 b (0.5-1.6)
Total acidity ($H^{+} + Al^{3+}$)	3.27 (1.6-4.5)	5.20 (4.1-6.1)	7.20 (6.1-7.8)	4.20 (3.7-4.6)	6.77 (5.7-7.9)
CEC (meq 100 g^{-1})	5.93a (2.73-9.27)	6.47a (5.64-7.34)	7.93a (6.72-8.74)	5.18a (4.70 -5.52)	7.39 a (6.22-8.32)
Bulk density ($g\ cm^{-3}$)	1.39 a (1.26-1.55)	1.34 b (1.00-1.42)	1.34 ab (1.25-1.48)	n.d.	1.32 b (1.14-1.48)
Particle size (%)					
Clay	7 a (1-15)	10 a (7-13)	10 a (6-14)	8 a (5-13)	15 b (9-23)
Silt	8 a (1-17)	15 b (8-29)	9 a (5-13)	7 a (4-10)	9 a (6-13)
Fine sand	18 a (6-28)	30 b (24-37)	27 bc (19-42)	21 ac (10-32)	27 bc (19-35)
Coarse sand	67 a (43-90)	45 b (33-60)	54 bc (33-65)	64 ac (53-77)	49 b (34-63)

Table 8. Means (and ranges) of soil (10-20 cm depth) chemical properties (n=50 samples/habitat) and particle size composition (n=15 samples/habitat) from recently burned areas, 10-years, 20-years and 40-years-old secondary forests and a primary forest in the Bragantina region, Pará. The mean values followed by different letters in the row are significantly different according to the Tukey test, $p < 0.01$.

	Burned Area	10-years forest	20-years forest	40-years forest	Primary forest
$pH_{(H2O)}$	5.58 a	4.59 b	4.6 b	4.5 b	4.2 c
	(4.7-7)	(4.0-5.0)	(4.3.5)	(4-4.9)	(3.9-4.5)
Organic matter (%)	1.42 ab	1.59 bc	1.58 bc	1.23 a	1.74 c
	(0.46-3.29)	(1.01-2.0)	(1.05-2.36)	(0.62-2.39)	(1.08-2.44)
C (%)	0.83 ab	0.93 bc	0.92 bc	0.72 a	1.01 c
	(0.27-1.91)	(0.58-1.32)	(0.61-1.37)	(0.36-1.39)	(0.63-1.42)
P extractable ($\mu g\ g^{-1}$)	2.34 a	1.64 bc	1.78 ab	1.3 c	1.79 ab
	(1-6)	(1-4)	(1-4)	(1-2)	(1-3)
Exchangeable cations (meq 100 g^{-1})					
K	0.06 a	0.02 b	0.02 c	0.02 cd	0.02 bd
	(0.02-0.16)	(0.01-0.04)	(0.01-0.06)	(0.01-0.03)	(0.01-0.04)
Ca	1.15 a	0.7 b	0.63 bc	0.47 c	0.36 d
	(0.5-2.2)	(0.2-1.1)	(0.2-2)	(0.2-0.9)	(0.2-0.8)
Mg	0.49 a	0.39 b	0.37 ab	0.25 c	0.14 d
	(0.2-1.5)	(0.1-0.8)	(0.2-0.9)	(0.1-0.6)	(0.1-0.5)
Al	0.15 a	0.76 b	1.1 cd	0.9 bc	1.14 d
	(0-0.5)	(0.5-1.3)	(0.4-1.6)	(0.1-1.5)	(0.8-1.9)
Total acidity	2.57	4.10	4.67	4.80	7.00
($H^{+} + Al^{3+}$)	(1.6-3.3)	(3.7-4.9)	(4.1-5.0)	(4.2-5.5)	(6.3-8.2)
CEC (meq 100 g^{-1})	4.23a	5.08ab	5.38ab	5.42ab	7.46 b
	(2.53-5.61)	(4.42-6.22)	(4.51-6.03)	(4.92 -6.02)	(6.73-8.73)
Particle size (%)					
Clay	9 a	12 b	12 ab	12 b	17 c
	(3-15)	(10-16)	(8-15)	(9-16)	(10-25)
Silt	8 ab	15 c	10 abc	7 a	12 bc
	(4-15)	(9-27)	(7-14)	(3-9)	(7-19)
Fine sand	20 a	29 b	27 b	20 a	30 b
	(7-29)	(20-34)	(21-39)	(15-26)	(17-41)
Coarse sand	63 a	44 b	51 bc	61 a	41 b
	(44-86)	(33-60)	(36-61)	(51-71)	(23-62)

old secondary forest. The primary forest had a significantly ($p < 0.01$) higher than extractable phosphorus concentration than all the secondary forests. The mean values of CEC were similar ($P<0.01$) among all forest age-classes in the first two depths (0-5 cm and 5-10 cm) (Tables 6 and 7). However, at 10-20 cm the CEC's of the burned area were significantly lower than primary forest ($p<0.01$) (Table 8). The surface (0-5 cm) bulk density of the primary forest soils was lower than in the deeper layer (5-10 cm). For the secondary forest sites the bulk density of both layers showed higher values then those observed in the primary forest but they were not statistically different from each other ($p>0.05$) (Tables 6 and 7). The mean bulk density was higher after burning (1.35 g cm^{-3} for 0-5 cm and 1.39 g cm^{-3} for 5-10 cm). The three soil depths analyzed for the secondary forests showed a large amount of coarse sand. The 40-years-old secondary forest was more sandy than the other forest age-classes and the primary forest had a little more clay in the 5-10 cm layer than the secondary forests (Tables 6 to 8).

Nutrient stocks in the soil

In the burned area the stocks in the top 10 cm of the soil are two or three times greater than in the secondary and primary forests, except for aluminium and organic matter (Fig. 7). Organic matter and extractable phosphorus stocks increased in the order: 10-years-old secondary forest > 20-years-old secondary forest > primary forest (Fig. 7). Potassium stocks remained the same in all forest age classes (around 10 kg ha^{-1}) while in the burned areas they reached almost

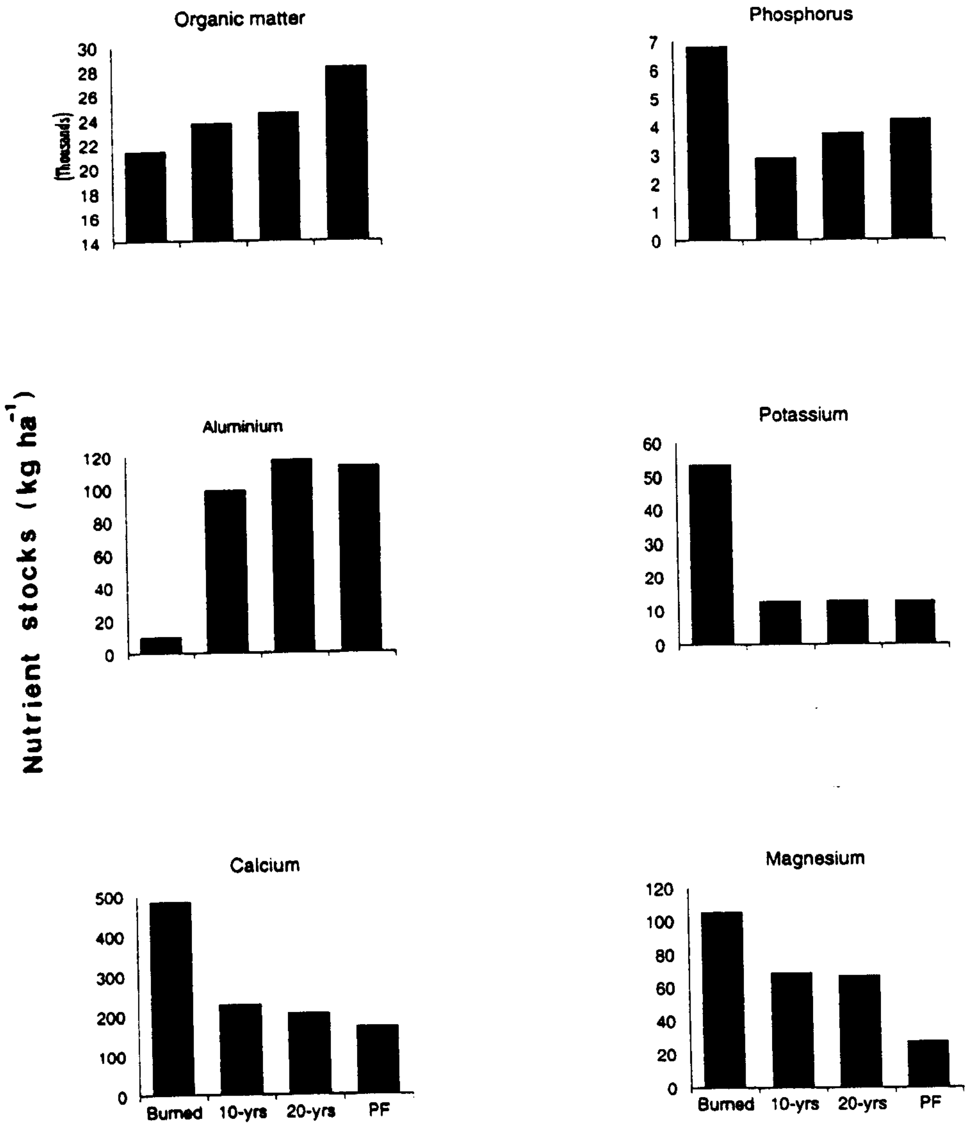

Figure 7. Stocks of soil organic matter and chemical elements (kg ha^{-1}) in soil (0-10 cm) of recently burned areas and three forest age-classes in the Bragantina region, Pará, Brazil.

50 kg ha^{-1}. The stocks of calcium and magnesium were greater in the secondary than in the primary forest.

Discussion

The results obtained for the 40-years-old secondary forest may be less comparable because it is 10 km from the primary forest and 7-10 km from the 10 and 20-years-old secondary forests and may have soils on a somewhat different parent material. I will restrict the discussion to the burned areas, 10 and 20-years-old secondary forests and the primary forest where I can more certainly say that the major differences found can be attributed to land use effect.

The physical properties of the soil remain almost intact when shifting cultivation is practised (Nortcliff & Dias 1988; Gerold 1994). In this study, I found that the bulk density for all soils was above 1 g cm^{-3} (Tables 6 to 8) and that there was no difference of bulk density between secondary and primary forests. Uhl & Jordan (1984) reported similar bulk densities of soils under a 5-years-old secondary forest and a primary forest. Martins *et al.* (1991) also found that bulk density of a primary forest and a 3-years-old secondary forest in eastern Amazônia were similar, but the values were lower than the values found in this study.

Most previous studies in primary Amazonian rain forests have been shown that the soils have low concentrations of nutrients (Eden 1974; Uhl & Jordan 1984; Jordan 1985; Thompson *et al.* 1992). However low nutrient concentrations can be compensated by high turnover rates of litter (Klinge 1977; Jordan 1989). The surface soils (0-5 cm) of the primary forest studied here are low in clay and similar to other soils under *terra firme* forests (Table 9). Some nutrients such as extractable phosphorus and calcium are amongst the highest values reported for soils of Amazonian *terra firme* forests (Table 9) while exchangeable potassium and magnesium are amongst the lowest values reported. The soil pH (4.2) of the primary forest studied is a little less than the soils under three other forests (4.3-4.9) in eastern Pará (Table 8) and is in the same range as most of the *terra firme* forests in Amazônia.

After burning, biomass nutrients become partially available to crops. The most noteworthy effects of burning (Tables 6 to 8) in this study were the increase in soil pH, the loss of organic matter, a reduced amount of exchangeable aluminium and an increase in calcium, magnesium and potassium (Tables 6 to 8) all of which are typical for shifting cultivation systems (Roder *et al.* 1993). Burning brings about a temporary increase (Brinkmann & Nascimento 1973) in available nutrients but crop productivity often decreases after 2 or 3 years, and the area has to be left under fallow for several years. The data indicate that as secondary forests age there is a significant increase in soil carbon (Tables 6 to 8 and Fig. 7). Martins *et al.* (1990, 1991) reported that the surface organic matter in recently burned areas in eastern Amazônia was much less than in primary forest, but in a 3-years-old secondary forest the total soil carbon was about 80% of that in the primary forest. They suggested that such a recovery was due to an increase of mesofaunal activity, which seems to be a characteristic of soils under secondary forests. Studies by Aweto (1981b) also

Table 9. The pH_{H_2O}, organic carbon, extractable phosphorus, exchangeable potassium, calcium and magnesium, CEC, clay and sand concentrations in the surface layers of some Amazonian soils under lowland evergreen rain forest (*terra firme*). n.d. = no data.

Location	Depth (cm)	Type of soil	pH (H_2O)	C (%)	P extractable ($\mu g\ g^{-1}$)	K	Ca ($meq\ kg^{-1}$)	Mg	CEC	Clay (%)	Sand (%)	Reference
Eastern Pará, Brazil (Peixe-Boi)	0-5	Oxisol	4.2	1.4	4.4	0.3	9.3	2.2	6.3.	11	81	this study
	5-10	Oxisol	4.2	1.2	2.2	0.2	4.0	1.3	7.4.	15	76	this study
Eastern Pará, Brazil (Paragominas)	0-15	Oxisol	4.9	2.0	3.4	0.9	13.9	6.4	n.d.	n.d.	n.de	Buschbacher *et al.* (1988)
	0-15	Oxisol	4.4	1.6	5.4	0.7	4.4	3.7	n.d.	n.d.	n.d	Buschbacher *et al.* (1988)
Eastern Pará, (Capitão-Poço)	0-20	Oxisol	4.3	2.0	n.d.	1.9	12.3	5.7	3.1	n.d.	n.d	Martins & Cerri (1986)
Manaus, Brazil	0-20	Oxisol	4.4	n.d.	1.8	0.7	0.9	n.d.	n.d.	n.d.	n.d	Correa & Reichardt (1989)
San Carlos, Venezuela	0-10	Oxisol	3.2	1.8	n.d.	0.4	0.3	0.3	n.d.	n.d.	n.d	Uhl & Jordan (1984)
Venezuela	0-10	n.d.	4.2	1.4	n.d.	0.3	2.0	0.6	7.4	17	77	Eden (1974)
Maracá, Roraima	0-10	Podzol	4.9	0.5	5.1	0.7	2.3	1.8	8.5	12	76	Thompson *et al.* (1992)
Jari, Amapá, Brazil	0-5	Ferralic arenosol	n.d.	n.d.	3.0	0.6	0.9	3.9	n.d.	n.d.	n.d	Jordan & Russel (1989)
Roraima, Brazil	0-10	Ultisol	4.6	1.6	3.6	1.1	8.1	8.6	3.1	n.d.	n.d.	Eden *et al.* (1991)
Amazonas, Brazil	0-3	Podzol	4.4	n.d.	n.d.	0.7	0.5	0.3	9.4	n.d.	n.d.	Stark (1970)

showed that the organic matter concentration of secondary forest soils tended to increase. These results were attributed to the greater vegetation cover and litter production. Also Ewel (1976) pointed out that the contribution by litterfall and decomposition to organic matter and nutrients in the upper soil appears to account for a large part of the restoration of fertility.

One of the main benefits of shifting cultivation is the fallow accumulation of nutrients which become available to subsequent crops. In this study, extractable phosphorus increased slightly in older secondary forests. Exchangeable cations followed a similar trend to the extractable phosphorus with a slight increase in the older secondary forests (Tables 6 to 8). Similar observations have been made by researchers elsewhere (Nigeria, Aweto 1981b; India, Mishra & Ramakrishnan 1983b; Toky & Ramakrishnan 1983b, Ramakrishnan 1989). However these authors, found a decline caused by transfer to growing vegetation in element concentrations in the soils during the first years and a return of elements (by litterfall and decomposition) after about 10-years. Uhl & Jordan (1984) showed that soil pH, organic matter and nutrients were remarkably similar in the primary forest and in a 5-years-old secondary forests after shifting cultivation in Venezuela. They found that there was a higher concentration of nutrients in the leaves of the secondary vegetation and that these species had the ability to take up nutrients rapidly when primary forest was cut and burned. Other studies addressing the change in soil nutrient stocks in successional forest after pasture in tropical countries have also reported that the stocks increase with the age (Buschbacher *et al.* 1988; Correa & Reichardt 1989; Reiners *et al.* 1994). However, as Buschbacher *et al.*

(1988) pointed out, other factors than soil nutrients are important for forest recovery.

The stocks of total organic carbon and exchangeable phosphorus in the Bragantina forests are within the recorded values for tropical rain forests (Uhl & Jordan 1984; Martins *et al.* 1990; Thompson *et al.* 1992). However the stock of exchangeable potassium (10 kg ha^{-1}) was low and that of calcium (150 kg ha^{-1}) was high compared with the values found by Uhl & Jordan (1984) in Venezuela or Thompson *et al.* (1992) on Maracá Island, Brazil. Probably such high values of calcium in the soils of the primary forest are due to the influence of the Pirabas Formation, which is rich in limestone, and underlies part of the study area between Nova Timboteua and Capanema counties (Ackermann 1964). Denich (1991) found that 5-years-old secondary forests in the Bragantina region had 7 kg ha^{-1} of extractable phosphorus, 47 kg ha^{-1} of exchangeable potassium, 405 kg ha^{-1} of exchangeable calcium and 62 kg ha^{-1} of exchangeable magnesium in the top 30 cm of soil. These values indicated that in this ecosystem 23% to 50% of the stock of these nutrients are in the soil. The data underestimated the total soil stock since they refer to extractable or exchangeable nutrient quantities however.

In my study it was found that as a result of cutting and burning the vegetation, the total amount of nutrients in the top 10 cm of soil increases (Fig. 7). It is important to observe that the burning was made in a 5-years-old secondary forest after at least eight previous cycles of utilization and that the burned biomass gave a high nutrient input to the soil. Nutrient input to the soil continued over the fallow, and the stock of potassium in the secondary forests remained the same the stock in the primary forest and the stocks of calcium, and magnesium in the 20-years-old secondary forest remained above the stock in the primary forest (Fig. 7). The low values observed in the stock of calcium and magnesium in the primary forest soils may be attributed to nutrient immobilization in the woody vegetation (Furch & Klinge 1989; Klinge 1977). Medina & Cuevas (1989) showed that the accumulation of potassium, calcium and magnesium in the biomass of *terra firme* forests was higher than the amount of soil exchangeable cations. However the stock of nutrients in the soil and vegetation together was higher in the primary forest than in the secondary forests (Uhl & Jordan 1984).

Since the soil nutrients in secondary forests more than 10 years are similar to those in the primary forest it seems that after about 90 years of shifting cultivation in the Bragantina region the soils are still in relatively good condition.

CHAPTER 6

FLORISTICS AND STRUCTURE (FOR WOODY PLANTS $\geq$ 5 CM DBH) IN PRIMARY AND SECONDARY FORESTS OF AGE-CLASSES 5 - 40 YEARS.

Introduction

One of the possible consequences of shifting cultivation is the reduction in numbers or even local extinction of primary forest animal and plant species and the development of secondary forests which are not well known ecologically (Gomez-Pompa 1971). In view of this, the elucidation of the secondary succession on lands abandoned after known periods of shifting cultivation is important. Bragantina provides an important opportunity to study the response of Amazonian vegetation to such disturbance. This chapter examines the vegetation of secondary forests of a range of ages and of a primary forest and analyzes the successional changes.

Methods

Floristic inventories

The secondary forests

A floristic inventory was made between October 1991 and June 1992 in ten secondary forest sites in each age-class of 5, 10, 20 years. One site of 40-years-old secondary forest was inventoried in January 1994. The sites were located within the counties of Peixe-Boi and Nova Timboteua (Fig. 1).

The diameter at breast height (130 cm) and the height of all woody individuals (dbh ≥5 cm) was measured in one 5 m x 50 m plot (0.025 ha) set up at random in each of the ten sites in each of the 5, 10 and 20-years-old secondary forests. The total sampled area for each of age-class was 0.25 ha. In the 40-years-old secondary forest I established randomly eight subplots of 10 m x 25 m (total sampled 0.20 ha) inside an area of 1 ha randomly chosen for botanical studies (see Chapter 7) in which I identified and measured the dbh and estimated the total height of all woody plants ≥ 5 cm dbh. A profile diagram of all trees over 5 cm dbh was made for one plot in each age class using a 5 m wide x 10 m transect. The identification of the species was made by technicians of Museu Paraense Emilio Goeldi (MPEG), Belém, with the assistance of the botanist Dr. João Murça Pires and confirmed in the Herbarium of MPEG. Ninety-two percent of the plants were identified to species level in each case and only one species was not identified to at least family level.

The primary forest

In the 200-ha primary forest of *fazenda Monte Verde*, Peixe-Boi county (Fig. 4) three 1-ha plots were marked randomly for botanical inventories (see chapter 7). Inside each 1-ha plots I randomly located eight subplots of 10 x 25 m in which I identified and measured the dbh and total height of all woody plants (trees and lianas) ≥ 5 cm dbh (area sampled = 0.6 ha). If the tree branched below the level of the dbh measurement (1.3 m), then each stem was measured separately if it exceeded 10 cm dbh the multiple-stemmed trees were only recorded as single individuals. For trees with buttresses and prop roots reaching more than 1.3 m the diameters were measured at 20 cm above the protuberance. The procedures made for the identification of the species were described above. Ninety-six percent of the plants were identified to species level.

Data analysis

The phytosociological analysis was made by using the software FITOPAC 2, of Dr. George Shepherd, University of Campinas, São Paulo, Brazil. The relative density and dominance of species and families were calculated according to Mueller-Dombois & Ellenberg (1974). The cover value index (CVI) was calculated by summing the relative values of density and dominance. The similarity between the secondary forests was evaluated through the Similarity index of Sørensen (Brower & Zar 1984). Species diversity was calculated using two indices: the Simpson's diversity index (Ds) and the Shannon-Wiener diversity index (H') (Brower & Zar 1984). Both indices were an estimate of diversity based on the proportional abundance of species, taking into account the species-richness and the proportion of individuals among species. However, the Shannon index is more sensitive to an alteration in the dominance of the species (Peet 1974). A measure of evenness (J) was calculated as the ratio of observed diversity (H') to maximum diversity (H_{max}) (Brower & Zar 1984). Species-area curves were made for the ten 250-m^2 plots of the secondary forests and for the eight 250-m^2 plots of each transect of the primary forest and 40-years-old secondary forest.

A one-way ANOVA of log transformed data was used to compare structural features (density, basal area, and mean height) and species richness among the forests and a Tukey test was used for comparisons of plot means (Zar 1996).

Ordination and classification of species and plots

The floristic data (density) of each 250 m^2 were organized in a matrix. The species with less than five individuals in all plots combined were excluded from the data set which then consisted of 100 species. Detrended correspondence analysis (DCA) (Hill & Gauch 1980) was made using the CANOCO program version 3.0 (ter Braak 1988; Kent & Coker 1996). The floristic data were classified by Two-way indicator species analysis (TWINSPAN, Hill 1979). TWINSPAN is a divisive hierarchical method which uses pseudospecies (the presence of a species at different "cut-levels" of abundance) to make the classification. In this study, pseudospecies cut-levels of 0, 2, 5, 10 and 20 were used and all pseudospecies were given equal weight. The "cut-levels" in this case refer to the following numbers of individuals: 0, no individuals present; 2, 2-4 individuals; 5, 5-9; 10, 10-19; 20, ≥ 20.

Results

A species list with the species names, authorities and families of each forest age-class is given in Appendix 1.

The 5-years-old secondary forest

A total of 274 individuals representing 24 families, 33 genera and 41 species were sampled. The number of individuals recorded per 250-m^2 plot ranged from

11 to 57 and the number of species ranged from 3 to 12 (Table 10). The total basal area in the ten plots was 1.057 m^2 with a range of 0.0271 m^2 to 0.1012 m^2 between plots (Table 10). The maximum tree height was 13 m and the maximum dbh was 19 cm. The mean tree height in the plots ranged from 6.5 m to 8 m and the mean dbh from 5.6 cm to 7.7 cm (Table 10). In all the 5-years-old secondary forest plots together, 91% of the recorded individuals were between 5 and 10 m high (Fig. 8) and 95% of the recorded plants had a dbh between 5 and 10 cm (Fig. 9).

The most dominant species were *Vismia guianensis, Croton matourensis, Cecropia palmata, Inga edulis* and *Banara guianensis* (Table 11). The less abundant *Tapirira guianensis* had individual trees with a higher basal area than *Banara guianensis*. The families that showed the highest CVI's were Clusiaceae, Mimosaceae, Euphorbiaceae, Moraceae, Flacourtiaceae and Anacardiaceae, comprising 76.6% of the total sampled individuals and 39% of the total number of species (Table 12). The highest basal areas 2500 m^{-2} were: Clusiaceae (0.18 m^2), Mimosaceae (0.15 m^2), Euphorbiaceae (0.15 m^2) and Moraceae (0.13 m^2). Sixteen families were represented by only a single species, including the abundant Clusiaceae and Moraceae, represented here by *Vismia guianensis* and *Cecropia palmata*.

The 10-years- old secondary forest

The total density was 446 individuals and included 23 families, 49 genera and 61 species. The number of individuals recorded in each 250-m^2 plot ranged from 27 to 62 and the number of species ranged from 12 to 16 (Table 10). The total basal area in the ten plots was 2.709 m^2 (range: 0.1405 m^2 to 0.4323 m^2 between

Table 10. Number of individuals (N), number of species (Sp), total basal area (BA), mean height, and mean dbh for each 250-m^2 plot in the 5, 10, 20 and 40-years-old secondary forests in the Bragantina region, Pará. Plots are ranked by basal area.

5-years-old secondary forest

Plot	N	Sp	BA (m^2)	Mean height (m)	Mean dbh (cm)
7	57	11	0.25	8.5	7.1
10	41	12	0.22	8.8	7.7
8	39	8	0.17	8.5	7.3
4	32	8	0.10	7.3	6.3
5	30	12	0.09	7.0	6.2
6	21	6	0.06	7.2	5.9
2	20	5	0.05	6.5	5.8
1	11	7	0.05	7.0	7.3
9	12	8	0.03	6.2	5.7
3	11	3	0.03	6.7	5.6

10-years-old secondary forest

Plot	N	Sp	BA (m^2)	Mean height (m)	Mean dbh (cm)
13	27	12	0.43	12.4	12.4
19	53	12	0.34	11.5	8.5
20	56	12	0.33	11.6	8.1
15	47	13	0.31	9.1	8.4
14	57	12	0.28	8.3	7.6
17	62	13	0.25	7.9	7.0
12	42	16	0.23	8.5	7.8
16	43	14	0.23	10.7	7.8
11	31	14	0.16	9.4	7.6
18	28	14	0.14	9.3	7.3

20-years-old secondary forest

Plot	N	Sp	BA (m^2)	Mean height (m)	Mean dbh (cm)
21	45	18	0.68	11.8	12.0
29	50	23	0.51	11.2	9.5
24	42	19	0.46	11.5	10.1
25	21	12	0.44	12.6	13.3
22	47	16	0.41	12.1	9.6
26	26	17	0.41	12.0	12.4
27	36	20	0.38	10.5	10.0
23	49	17	0.35	10.8	8.8
30	36	15	0.28	10.2	8.4
28	36	14	0.26	10.8	9.0

40-years-old secondary forest

Plots	N	Sp	BA (m^2)	Mean height (m)	Mean dbh (cm)
31	34	15	0.47	12.2	11.7
33	20	12	0.47	12.0	15.1
34	28	14	0.40	10.9	11.6
38	45	18	0.37	8.6	8.8
32	34	18	0.33	9.8	9.7
36	54	22	0.28	9.6	7.7
35	46	20	0.27	8.8	8.1
38	58	18	0.26	8.3	7.2

Table 11. The 15 most abundant species of woody plants ≥ 5 cm dbh occurring in ten 250-m^2 plots in the 5, 10 and 20-years-old secondary forests and in eight 250-m^2 plots in the 40-years-old secondary forest in the Bragantina region, Pará, with number of individuals (N), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Species are ranked by CVI.

Species	N	RD (%)	BA (m^2)	RDo (%)	CVI
5-years-old secondary forest					
Vismia guianensis	56	20.44	0.18	16.86	37.30
Croton matourensis	32	11.68	0.15	14.23	25.91
Cecropia palmata	27	9.85	0.13	12.26	22.11
Banara guianensis	29	10.58	0.07	6.92	17.51
Inga edulis	20	7.30	0.07	6.61	13.91
Tapirira guianensis	13	4.74	0.08	7.31	12.06
Saccoglotis guianensis	12	4.38	0.05	5.11	9.49
Inga ingoides	11	4.01	0.03	2.95	6.96
Maximiliana maripa	2	0.73	0.06	5.36	6.09
Spondias mombim	6	2.19	0.03	2.74	4.93
Inga velutina	7	2.55	0.02	2.23	4.79
Trattinickia rhoifolia	4	1.46	0.01	1.41	2.87
Cordia scabrifolia	4	1.46	0.01	1.17	2.63
Rollinia exsucca	4	1.46	0.01	1.11	2.57
Cassia fastuosa	4	1.46	0.01	0.96	2.42
10-years-old secondary forest					
Vismia guianensis	75	16.82	0.43	15.77	32.58
Lacistema pubescens	86	19.28	0.28	10.48	29.77
Rollinia exsucca	41	9.19	0.16	6.04	15.24
Zanthoxylum rhoifolium	33	7.40	0.16	5.90	13.30
Inga nitida	23	5.16	0.15	5.45	10.60
Inga thibaudiana	26	5.83	0.13	4.65	10.48
Tapirira guianensis	9	2.02	0.15	5.40	7.42
Casearia grandiflora	16	3..59	0.08	3.16	6.75
Stryphnodendron pulcherrimum	4	0.90	0.16	5.78	6.68
Maximiliana maripa	4	0.90	0.14	5.35	6.25
Croton matourensis	7	1.57	0.11	4.19	5.76
Sapium lanceolatum	7	1.57	0.11	4.13	5.70
Inga rubiginosa	9	2.02	0.07	2.61	4.63
Caryocar villosum	4	0.90	0.06	2.32	3.21
Cordia sp.	6	1.35	0.02	0.85	2.20
20-years-old secondary forest					
Croton matourensis	26	6.70	0.84	20.03	26.73
Lacistema pubescens	47	12.11	0.19	4.48	16.59
Inga thibaudiana	32	8.25	0.21	5.16	13.40
Stryphnodendron guianense	11	2.84	0.41	9.84	12.67
Cordia scabrifolia	17	4.38	0.20	4.70	9.08
Vismia guianensis	20	5.15	0.14	3.30	8.45
Tapirira guianensis	8	2.06	0.25	6.07	8.13
Rollinia exsucca	18	4.64	0.13	3.17	7.81
Inga edulis	12	3.09	0.13	3.04	6.13
Inga alba	5	1.29	0.20	4.83	6.12
Sapium lanceolatum	6	1.55	0.17	4.16	5.70
Inga ingoides	8	2.06	0.10	2.51	4.57
Zanthoxylum rhoifolium	8	2.06	0.07	1.80	3.86
Jacaranda copaia	2	0.52	0.12	2.96	3.47
Himatanthus sucuuba	6	1.55	0.08	1.86	3.40
40-years-old secondary forest					
Croton matourensis	17	5.33	0.68	23.53	28.86
Lacistema pubescens	43	13.48	0.15	5.15	18.63
Tapirira guianensis	12	3.76	0.41	14.45	18.21
Guatteria poeppigiana	27	8.46	0.14	5.09	13.55
Rollinia exsucca	21	6.58	0.10	3.46	10.05
Lecythis lurida	21	6.58	0.10	3.45	10.03
Inga edulis	8	2.51	0.12	4.05	6.56
Zanthoxylum regnellianum	7	2.19	0.07	2.59	4.78
Lecythis pisonis	9	2.82	0.05	1.70	4.52
Vismia guianensis	8	2.51	0.05	1.87	4.38
Maquira guianensis	9	2.82	0.04	1.44	4.26
Matayba guianensis	8	2.51	0.04	1.40	3.90
Margaritaria nobilis	6	1.88	0.05	1.87	3.75
Cordia scabrida	5	1.57	0.06	2.16	3.72
Thyrsodium paraense	8	2.51	0.03	1.09	3.60

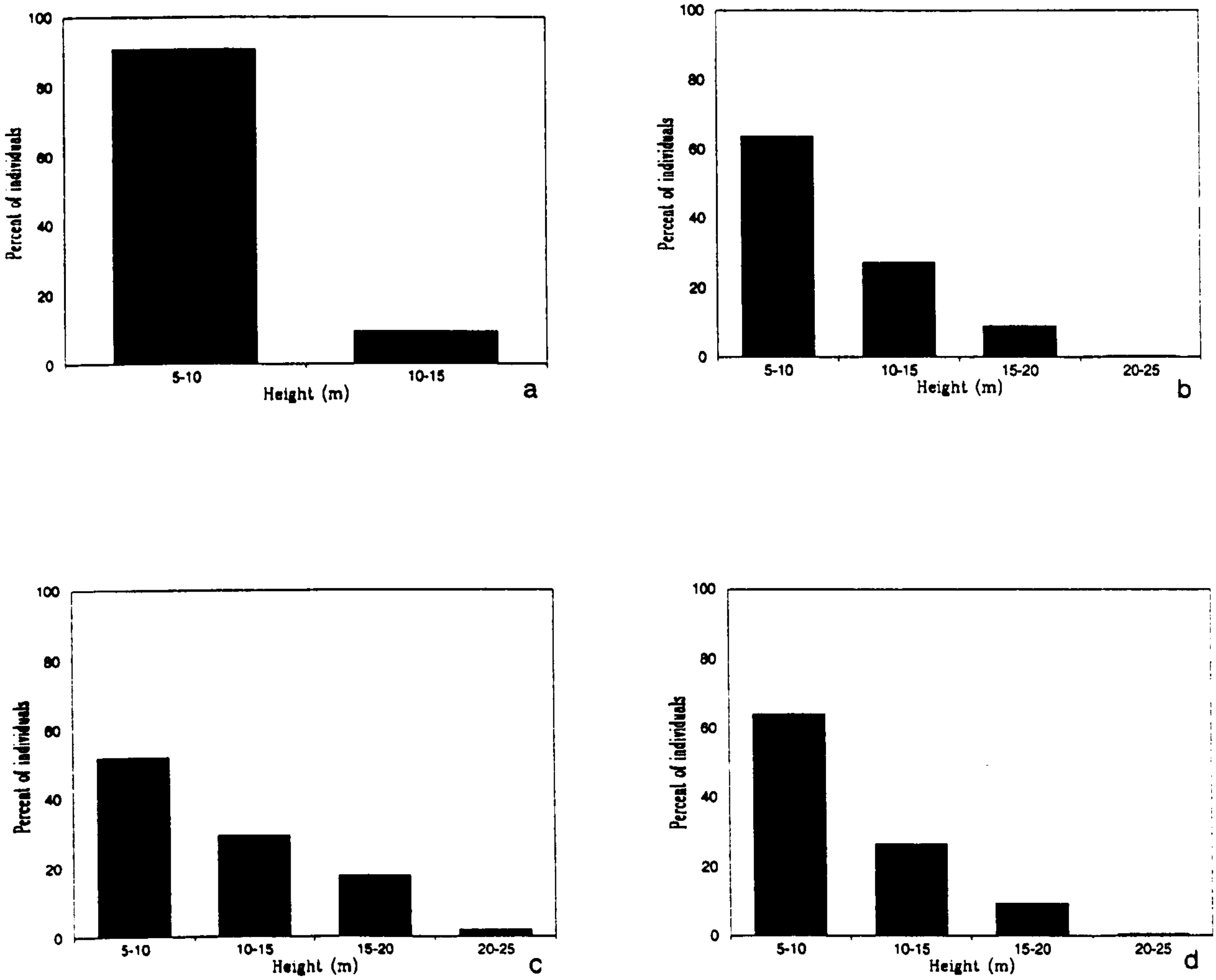

Figure 8. Distribution by height for individuals ≥ 5 cm dbh in ten 250-m^2 plots of (a) 5-years, (b) 10-years and (c) 20-years-old secondary forests and in eight 250-m^2 plots in (d) 40-years-old secondary forest in the Bragantina region, Pará.

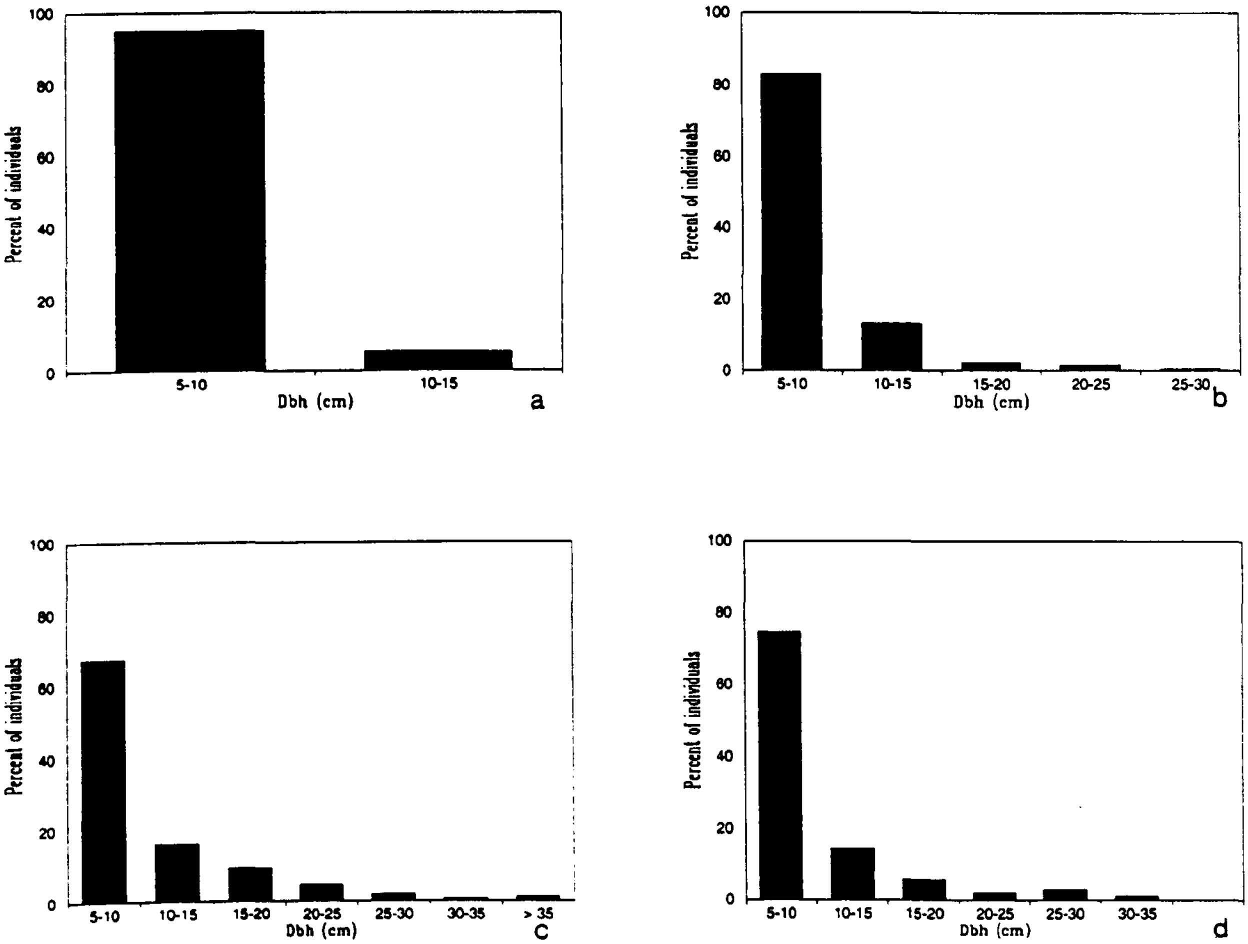

Figure 9. Distribution by dbh for individuals ≥ 5 cm dbh in ten 250-m^2 plots of (a) 5-years, (b) 10-years and (c) 20-years-old secondary forests and in eight 250-m^2 plots in (d) 40-years-old secondary forest in the Bragantina region, Pará.

Table 12. The15 most abundant families of woody plants ≥ 5 cm dbh occurring in ten 250-m² plots in the 5, 10 and 20-years-old secondary forests and in eight 250-m² plots in the 40-years-old secondary forest in the Bragantina region, Pará, with number of individuals (N), number of species (Sp), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Families are ranked by CVI.

Family	N	Sp	RD (%)	BA (m²)	RDo (%)	CVI
5-years-old secondary forest						
Clusiaceae	56	1	20.44	0.18	16.86	37.30
Mimosaceae	45	8	16.42	0.15	14.63	31.05
Euphorbiaceae	33	2	12.04	0.15	14.46	26.51
Moraceae	27	1	9.85	0.13	12.26	22.11
Flacourtiaceae	30	2	10.95	0.07	7.12	18.06
Anacardiaceae	19	2	6.93	0.11	10.06	16.99
Humiriaceae	12	1	4.38	0.05	5.11	9.49
Palmae	2	1	0.73	0.06	5.36	6.09
Annonaceae	9	4	3.28	0.03	2.63	5.91
Caesalpiniaceae	7	3	2.55	0.02	1.64	4.19
Burseraceae	4	1	1.46	0.01	1.41	2.87
Boraginaceae	4	1	1.46	0.01	1.17	2.63
Lacistemaceae	4	2	1.46	0.01	0.85	2.31
Rutaceae	3	1	1.09	0.01	0.82	1.92
Fabaceae	3	1	1.09	0.01	0.76	1.85
10- years-old secondary forest						
Mimosaceae	71	8	15.92	0.59	21.73	37.65
Clusiaceae	75	1	16.82	0.43	15.77	32.58
Lacistemaceae	86	1	19.28	0.28	10.48	29.77
Annonaceae	48	5	10.76	0.25	9.07	19.84
Euphorbiaceae	23	5	5.16	0.25	9.42	14.57
Rutaceae	33	1	7.40	0.16	5.90	13.30
Flacourtiaceae	33	6	7.40	0.15	5.47	12.87
Anacardiaceae	11	2	2.47	0.15	5.56	8.03
Palmae	6	2	1.35	0.15	5.49	6.84
Moraceae	9	5	2.02	0.06	2.27	4.28
Boraginaceae	11	3	2.47	0.04	1.38	3.84
Lecythidaceae	10	4	2.24	0.03	1.26	3.50
Sapindaceae	9	5	2.02	0.03	1.25	3.27
Caryocaraceae	4	1	0.90	0.06	2.32	3.21
Fabaceae	4	2	0.90	0.02	0.63	1.53
20-years-old secondary forest						
Mimosaceae	78	10	20.10	1.12	26.93	47.03
Euphorbiaceae	38	4	9.79	1.05	25.06	34.86
Lacistemaceae	47	1	12.11	0.19	4.48	16.59
Lecythidaceae	28	6	7.22	0.10	2.31	9.52
Annonaceae	21	4	5.41	0.16	3.82	9.23
Anacardiaceae	11	2	2.84	0.26	6.35	9.19
Boraginaceae	17	1	4.38	0.20	4.70	9.08
Clusiaceae	20	1	5.15	0.14	3.30	8.45
Myrtaceae	16	7	4.12	0.07	1.67	5.79
Moraceae	13	5	3.35	0.09	2.26	5.61
Flacourtiaceae	15	5	3.87	0.06	1.43	5.30
Sapindaceae	15	3	3.87	0.06	1.37	5.24
Apocynaceae	8	2	2.06	0.08	1.97	4.03
Caesalpiniaceae	12	4	3.09	0.04	0.86	3.95
Rutaceae	8	1	2.06	0.07	1.80	3.86
40-years-old secondary forest						
Euphorbiaceae	33	6	10.34	0.79	27.74	38.08
Annonaceae	48	2	15.05	0.24	8.56	23.60
Anacardiaceae	20	2	6.27	0.44	15.54	21.81
Lacistemaceae	44	2	13.79	0.15	5.22	19.01
Lecythidaceae	38	5	11.91	0.17	5.94	17.85
Mimosaceae	26	6	8.15	0.22	7.77	15.92
Sapindaceae	15	3	4.70	0.07	2.42	7.12
Caesalpiniaceae	10	4	3.13	0.10	3.55	6.69
Palmae	5	2	1.57	0.09	3.28	4.85
Clusiaceae	9	2	2.82	0.06	1.97	4.79
Rutaceae	7	1	2.19	0.07	2.59	4.78
Moraceae	9	1	2.82	0.04	1.44	4.26
Flacourtiaceae	8	4	2.51	0.04	1.35	3.85
Boraginaceae	5	1	1.57	0.06	2.16	3.72
Nyctaginaceae	6	1	1.88	0.03	0.96	2.84

plots). The maximum tree height was 22 m and the maximum dbh was 27.3 cm. The mean tree height in the plots ranged from 8.3 m to 12.4 m and the mean dbh from 7.3 cm to 12.4 cm (Table 10). In all the 10-years-old plots together, 64% of the recorded plants were between 5 and 10 m height, and 27% were between 10 and 15 m. Only 9% of the plants recorded were trees > 15 m tall (Fig. 8). Three species have individuals higher than 20 m (*Xylopia aromatica, Sapium lanceolatum* and *Tapirira guianensis*). The majority of plants (83%) had a dbh between 5-10 cm, followed by 13% with a dbh between 10 and 15 cm (Fig. 9). Only two individuals had a dbh between 25-30 cm and both were of the species *Stryphnodendron pulcherrimum.*

The species *Vismia guianensis, Lacistema pubescens, Rollinia exsucca, Zanthoxylum rhoifolium, Inga nitida and Inga thibaudiana* had the highest CVI's (Table 11). These species together accounted for 63.67% of the total number of individuals sampled and also had the highest basal area. However *Tapirira guianensis* and *Maximiliana maripa* were less abundant and had a relatively high basal area. The most dominant families were Mimosaceae, Clusiaceae, Lacistemaceae, Annonaceae, Euphorbiaceae, Rutaceae and Flacourtiaceae, which accounted for 82.73% of the total individuals and 44.26% of the total number of species (Table 12). The highest basal areas 2500 m^{-2} were: Mimosaceae (0.59 m^2), Clusiaceae (0.43 m^2), Lacistemaceae (0.28 m^2) and Annonaceae (0.25 m^2). Ten families were represented by only a single species.

The 20-years-old secondary forest

The total number of individuals was 388, representing 31 families, 61 genera and 81 species (Appendix 1). The number of individuals recorded per 250-m^2 plot ranged from 21 to 50 and the number of species ranged from 12 to 23 (Table 10). The total basal area for all plots was 4.179 m^2 (range: 0.2598 m^2 to 0.6854 m^2 between plots). The maximum tree height was 25 m and the maximum dbh was 39.3 cm. The mean tree height in the plots ranged from 10.2 m to 12.6 m and the mean dbh from 8.4 to 13.3 cm (Table 10). Fifty-one percent of the recorded plants were between 5-10 m height, 29% between 10-15 m and almost 20% were trees > 15 m height (Fig. 8). The species with individuals higher than 20 m were *Bauhinia guianensis, Croton matourensis, Inga alba* and *Sapium lanceolatum*. The majority of plants (67%) had a dbh between 5 and 10 cm, followed by 16% with dbh between 10 and 15 cm (Fig 9). Six individuals had a dbh greater than 30 cm (*Croton matourensis* (3), *Jacaranda copaia, Tapirira guianensis, Stryphnodendron guianensis*).

The species *Croton matourensis, Lacistema pubescens, Inga thibaudiana, Stryphnodendron guianense, Cordia scabrifolia, Vismia guianensis* and *Tapirira guianensis* were the most dominant (Table 11), and accounted for 41.49% of the total number of individuals sampled. Individual trees of *Inga alba* and *Sapium lanceolatum* were less abundant but had a high basal area. The most dominant families were Mimosaceae, Euphorbiaceae, Lacistemaceae, Lecythidaceae, Annonaceae, Anacardiaceae, Boraginaceae and Clusiaceae which accounted for 67% of the total sampled individuals and 35% of the total number of species (Table 12). The highest basal areas 2500 m^{-2} were: Mimosaceae (1.12 m^2), Euphorbiaceae (1.05 m^2), Anacardiaceae (0.26 m^2) and Boraginaceae (0.19 m^2). Sixteen families were represented by a single species.

The 40-years-old secondary forest

The total number of individuals was 319, belonging to 30 families, 49 genera and 62 species (Appendix 1). The number of individuals recorded per 250 m^2 plot ranged from 20 to 58 and the number of species ranged from 12 to 22 (Table 10). The total basal area for all plots was 2.867 m^2 (range: 0.2654 m^2 to 0.4711 m^2 between plots). The maximum tree height was 21 m and the maximum dbh was 32.9 cm. The mean tree height in the plots ranged from 8.3 m to 12.2 m and the mean dbh from 7.2 to 15.1 cm (Table 10). Sixty-four percent of the recorded plants were distributed between 5-10 m height, 25% were between 10-15 m and only 10% of the plants recorded were trees > 15 m height (Fig. 8). The majority of plants (75%) had a dbh between 5 and 10 cm, followed by 14% with a dbh between 10 and 15 cm (Fig. 9). Only three individuals had a dbh greater than 30 cm (*Hymenaea parvifolia, Maximiliana maripa* and *Croton matourensis*).

The species *Croton matourensis, Lacistema pubescens, Tapirira guianensis, Guatteria poeppigiana, Rollinia exsucca, Lecythis lurida* and *Inga edulis* were the most dominant, having the highest CVI (Table 11) and accounting for 47% of the total number of individuals sampled. The most dominant families were Euphorbiaceae, Annonaceae, Anacardiaceae, Lacistemaceae, Lecythidaceae and Mimosaceae, comprising 65% of the total sampled individuals and 37% of the total number of species (Table 11). The highest basal areas 2000 m^{-2} were achieved by Euphorbiaceae (0.79 m^2), Anacardiaceae (0.44 m^2), Annonaceae

(0.24 m^2) and Mimosaceae (0.22 m^2). Fourteen families were represented by only a single species (Table 12).

The primary forest

The total number of individuals sampled was 718, belonging to 47 families, 121 genera and 200 species (Appendix 2). The number of individuals recorded per 250-m^2 plot ranged from 16 to 50 and the number of species ranged from 13 to 32 (Table 13). The total basal area for all plots was 15.26 m^2 (range: 0.34 m^2 to 1.71 m^2 between plots). The maximum height was 39 m and the maximum dbh was 120.5 cm. Forty-five to 57% of the recorded individuals were distributed in the first height class (5-10 m) and from 0.4 to 1.6% of the plants recorded were large trees > 30 m height (Fig. 10). The majority of plants (range: 50% to 68% between transects) were between 5-10 cm dbh and the distribution of the rest extended along at least six classes more (Fig. 11). From 4% to 5.4% of the individuals had a dbh greater than 35 cm.

The species *Eschweilera coriacea* and *Lecythis idatimon* were the most dominant, having the highest CVI's among the plants ≥ 5 cm dbh sampled in the primary forest (Table 14) and accounting for 12% of the total number of individuals sampled. Only two individuals of *Dipteryx odorata* were responsible for its high dominance. Eighty-one species (40.5% of the total) had only one individual. The most dominant families were Lecythidaceae, Mimosaceae, Caesalpiniaceae, Burseraceae, Euphorbiaceae and Sapotaceae comprising 48% of the total sampled individuals and 32% of the total number of species in the plots of the primary forest. The highest basal areas for the three replicate 2000-m^2 plots were:

Table 13. Number of individuals (N), number of species (Sp), total basal area (BA), and mean height for eight 250-m^2 plots in each transect (PF1, PF2 and PF3) of the primary forest in the Bragantina region, Pará. Plots are ranked by basal area.

Plots/ Transects	N	Sp	BA (m^2)	Mean height (m)
PF1				
40	21	14	1.71	14.3
39	26	21	0.85	14.0
44	22	16	0.69	12.5
45	29	20	0.61	12.2
46	20	14	0.45	11.9
42	16	13	0.43	11.6
43	24	17	0.41	11.4
41	27	18	0.39	10.0
PF2				
49	27	21	1.22	12.5
53	41	32	0.85	11.9
48	40	30	0.58	11.3
50	50	30	0.53	10.7
52	39	28	0.50	11.5
54	30	24	0.45	12.5
47	33	30	0.43	9.5
51	41	24	0.38	9.6
PF3				
58	24	13	1.01	14.6
60	24	18	0.93	13.1
62	32	23	0.78	10.3
61	31	18	0.54	11.8
56	33	29	0.42	10.1
59	24	19	0.37	10.9
55	32	22	0.35	10.6
57	32	23	0.34	10.5

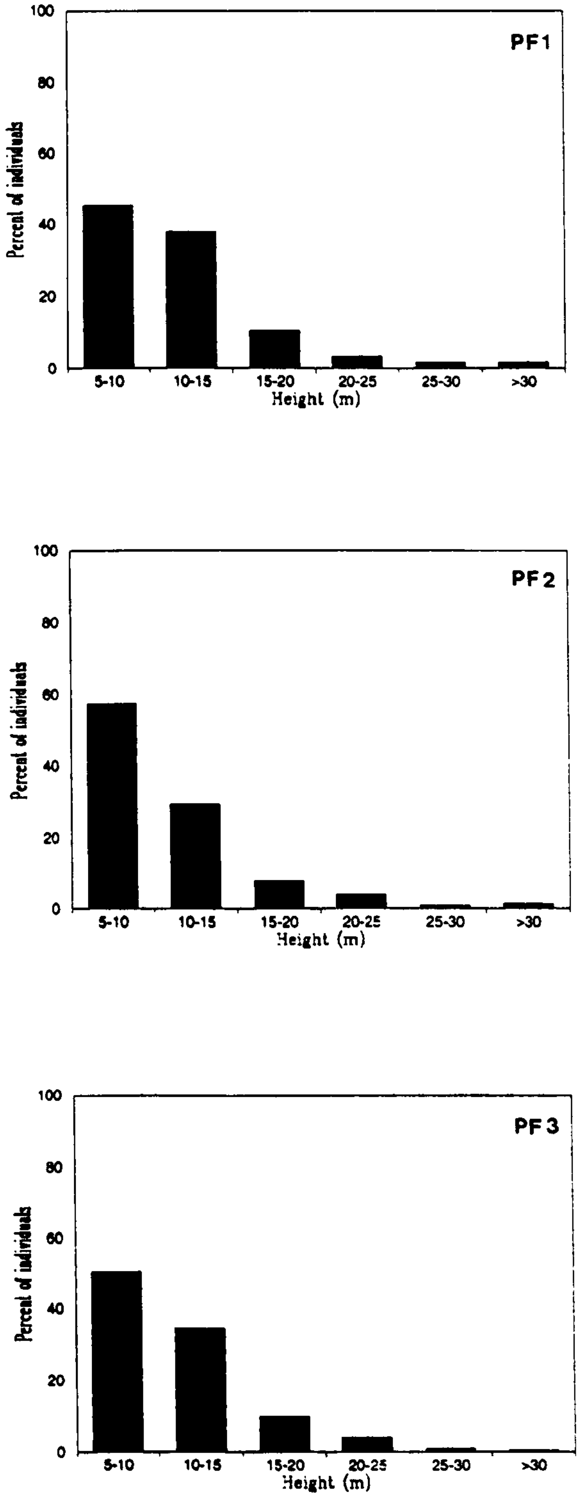

Figure 10. Distribution by height for individuals ≥ 5 cm dbh in eight 250-m^2 plots in a primary forest in the Bragantina region, Pará. PF1, PF2 and PF3 are the sampled transects.

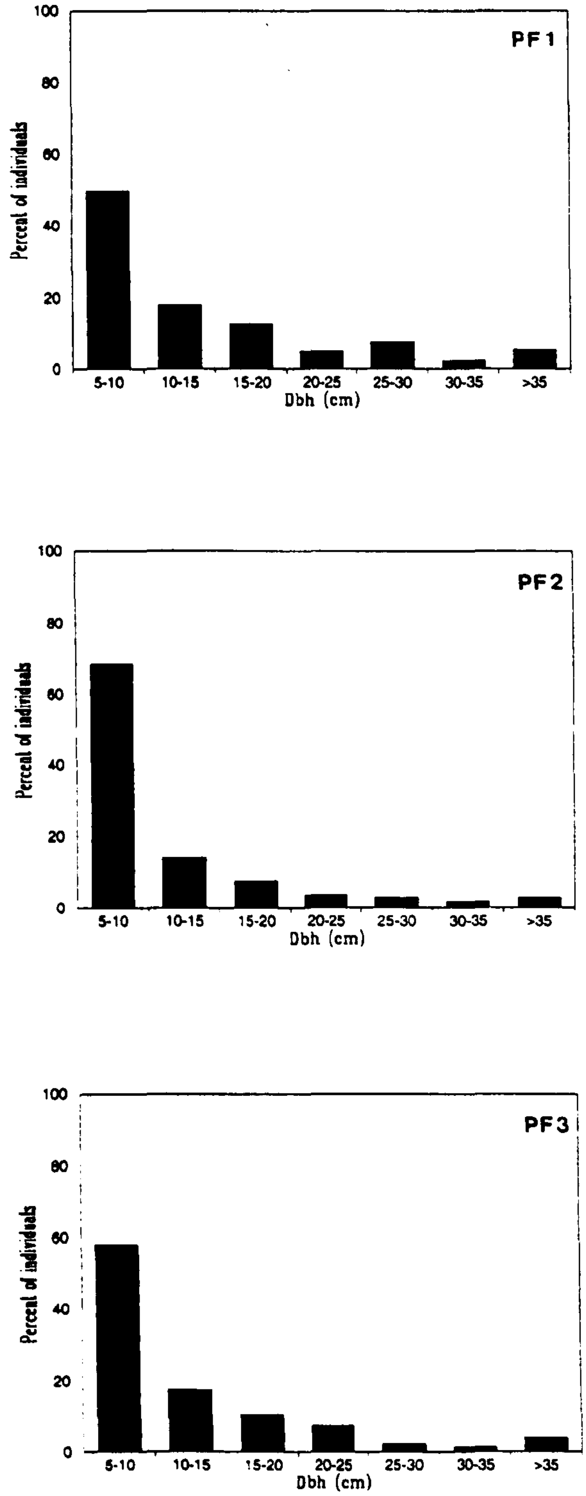

Figure 11. Distribution by dbh for individuals ≥ 5 cm dbh in eight 250-m² plots in a primary forest in the Bragantina region, Pará. PF1, PF2 and PF3 are the sampled transects.

Table 14. The 30 most abundant species of woody plants ≥ 5 cm dbh occurring in three replicates 0.2-ha plots in a primary forest in the Bragantina region, Pará, with number of individuals (N), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Species are ranked by CVI.

Species	N	RD (%)	BA(m^2)	RDo (%)	CVI
Eschweilera coriacea	57	7.94	1.9157	12.56	20.50
Lecythis idatimon	28	3.90	0.7197	4.72	8.62
Dipteryx odorata	2	0.28	1.1429	7.49	7.77
Gustavia augusta	45	6.27	0.1782	1.17	7.44
Goupia glabra	5	0.70	0.5581	3.66	4.35
Newtonia suaveolens	3	0.42	0.5994	3.93	4.35
Mabea aff. *speciosa*	16	2.23	0.2987	1.96	4.19
Tachigalia alba	8	1.11	0.4655	3.05	4.17
Tapirira guianensis	7	0.97	0.4473	2.93	3.91
Newtonia psilostachya	3	0.42	0.4497	2.95	3.37
Virola michelii	16	2.23	0.1631	1.07	3.30
Inga alba	2	0.28	0.4611	3.02	3.30
Apuleia leiocarpa	2	0.28	0.3667	2.40	2.68
Erisma uncinatum	2	0.28	0.3629	2.38	2.66
Micropholis guianensis	5	0.70	0.2940	1.93	2.62
Protium pilosum	16	2.23	0.0581	0.38	2.61
Trichilia micrantha	11	1.53	0.1501	0.98	2.52
Poraqueiba guianensis	10	1.39	0.1586	1.04	2.43
Nectandra aff. *globosa*	9	1.25	0.1729	1.13	2.39
Aparisthmium cordatum	14	1.95	0.0667	0.44	2.39
Sterculia pruriens	14	1.95	0.0497	0.33	2.28
Geissospermum sericeum	10	1.39	0.0805	0.53	1.92
Protium decandrum	8	1.11	0.1210	0.79	1.91
Protium trifoliolatum	11	1.53	0.0562	0.37	1.90
Neea sp.	6	0.84	0.1618	1.06	1.90
Carapa guianensis	1	0.14	0.2552	1.67	1.81
Protium sagotianum	5	0.70	0.1652	1.08	1.78
Sterculia cf. *pilosa*	1	0.14	0.2489	1.63	1.77
Pouteria echinocarpa	1	0.14	0.2463	1.61	1.75
Lecythis lurida	8	1.11	0.0938	0.61	1.73

Lecythidaceae (3.17 m^2), Mimosaceae (1.66 m^2), Fabaceae (1.16 m^2) and Caesalpiniaceae (1.10 m^2). Thirteen families were represented by only a single species (Table 15).

Change through time

The profile diagrams (Fig. 12) show the typical sequence of structural development. The density of trees (≥ 5 cm dbh) was low in the 5-years-old secondary forests but increased for 10-years and 20-years-old secondary forests. There was a little change in density but a large increase in height between 10 and 20-years-old secondary forests, and in the 40-years-old secondary forest some large trees reached 25 m high.

The ANOVA showed that there was a significant difference between the forest age-class for density ($F= 4.92$, $df= 6$; $p<0.01$), number of species ($F= 27.19$; $df=6$; $p<0.001$), basal area ($F= 33.46$; $df=6$; $p<0.001$) and mean height ($F=33.46$; $df= 6$; $p<0.001$). The highest densities of individuals per 250-m^2 plot (≥ 5 cm dbh) were found in the secondary forests older than 5 years, however Tukey tests showed that the mean tree densities (≥ 5 cm dbh) of plots in the transects PF1 and PF3 of the primary forest were not significant from those of the 5-years-old secondary forest (Table 16). The mean basal area per 250-m^2 plot of 5-years-old secondary forest (0.10 m^2) was the lowest value found and significantly different ($p<0.05$) from the other forests. The mean basal area of the older secondary forests (≥ 10 years) were significantly different ($p<0.05$) from the primary forests, except from transect PF3. The lowest mean height was found in the 5-years-old forest (7.4 m) and was

Table 15. The 30 most abundant families of woody plants ≥ 5 cm dbh occurring in three replicates 0.2-ha plots in a primary forest in the Bragantina region, Pará, with number of individuals (N), number of species (Sp), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Families are ranked by CVI.

Family	N	Sp	RD (%)	BA (m^2)	RDo (%)	CVI
Lecythidaceae	152	9	21.17	3.1739	20.81	41.97
Mimosaceae	20	11	2.79	1.6560	10.86	13.64
Caesalpiniaceae	36	13	5.01	1.0956	7.18	12.20
Burseraceae	53	9	7.38	0.5474	3.59	10.97
Euphorbiaceae	49	8	6.82	0.6168	4.04	10.87
Sapotaceae	32	14	4.46	0.9027	5.92	10.37
Fabaceae	8	5	1.11	1.1607	7.61	8.72
Meliaceae	25	7	3.48	0.6026	3.95	7.43
Sterculiaceae	25	4	3.48	0.3529	2.31	5.80
Moraceae	29	16	4.04	0.2628	1.72	5.76
Myrtaceae	32	15	4.46	0.1895	1.24	5.70
Anacardiaceae	15	3	2.09	0.5346	3.50	5.59
Chrysobalanaceae	23	8	3.20	0.3290	2.16	5.36
Celastraceae	7	2	0.97	0.6283	4.12	5.09
Apocynaceae	25	6	3.48	0.1884	1.24	4.72
Lauraceae	17	4	2.37	0.2788	1.83	4.20
Sapindaceae	17	7	2.37	0.2651	1.74	4.11
Vochysiaceae	5	4	0.70	0.4521	2.96	3.66
Myristicaceae	18	2	2.51	0.1685	1.10	3.61
Melastomataceae	14	6	1.95	0.2196	1.44	3.39
Icacinaceae	13	2	1.81	0.1849	1.21	3.02
Tiliaceae	5	2	0.70	0.2500	1.64	2.34
Violaceae	14	3	1.95	0.0506	0.33	2.28
Olacaceae	11	2	1.53	0.0645	0.42	1.95
Nyctaginaceae	6	1	0.84	0.1618	1.06	1.90
Annonaceae	8	3	1.11	0.1084	0.71	1.82
Combretaceae	3	3	0.42	0.2043	1.34	1.76
Elaeocarpaceae	7	3	0.97	0.0671	0.44	1.41
Quiinaceae	8	1	1.11	0.0436	0.29	1.40
Caryocaraceae	5	2	0.70	0.0890	0.58	1.28

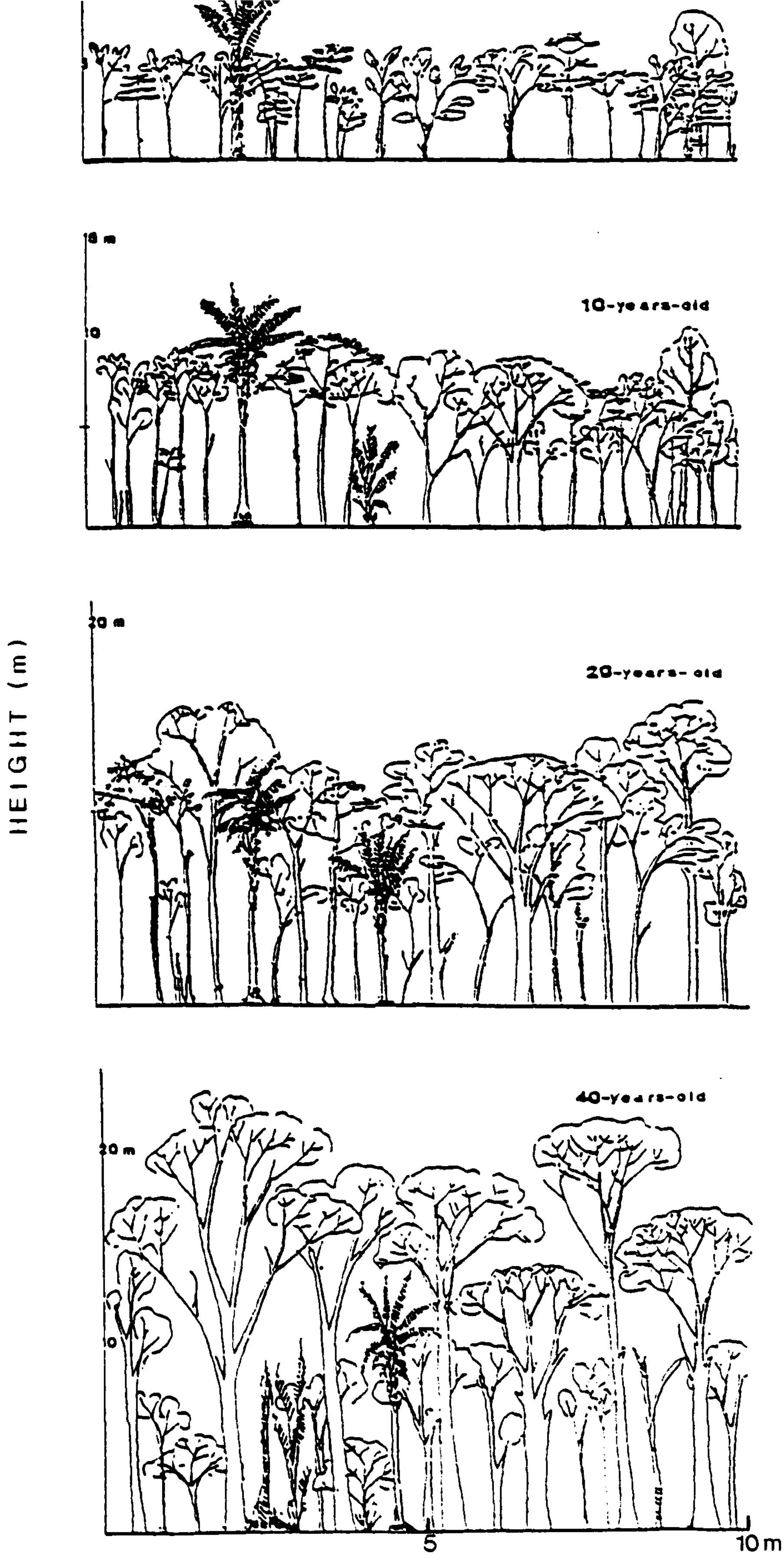

Figure 12. Profile diagrams (5 m wide x 10 m) representing the plants ≥ 5 cm dbh in the 5, 10, 20 and 40-years-old secondary forests in the Bragantina region, Pará.

Table 16. Structural characteristics (density, basal area, and height) of woody plants (≥ 5 cm dbh) in five forest age-classes in the Bragantina region, Pará. Values are means ± SE of ten 250-m^2 plots (n=10, except for 40-years-old secondary forest and primary forest which had eight 250-m^2 plots).

Forest age-classes	Density (ha)	Basal Area ($m^2 ha^{-1}$)	Height (m)
5-years-old	27.4 ± 4.82 a	0.10 ± 0.02 a	7.4 ± 0.29 a
10-years-old	44.6 ± 4.00 b	0.27 ± 0.03 b	9.9 ± 0.50 b
20-years-old	38.8 ± 3.07 b	0.42 ± 0.04 b	11.3 ± 0.25 bc
40-years old	39.9 ± 4.62 b	0.36 ± 0.03 b	10.0 ± 0.54 b
Primary forest			
PF1	23.1 ± 1.49 a	0.69±0.16 c	14.7 ± 0.90 d
PF2	37.6 ± 2.59 b	0.62 ± 0.10 c	11.2 ± 0.74 bc
PF3	29.0 ± 1.48 ab	0.59 ± 0.10 bc	12.8 ± 0.97 c

Table 17. Species richness, diversity and evenness of woody plants (≥ 5 cm dbh) in five forest age-classes in the Bragantina region, Pará.

Forest age-classes	Mean number of species 250-m^{-2} plot	Number of total species	Simpson index of diversity (Ds)	Shannon index of diversity (H')	Evenness (J)
5-years-old	8.0 ± 0.94 a	41	0.91	2.89	0.77
10-years-old	13.2 ± 0.42 b	61	0.91	3.07	0.75
20-years-old	17.1 ± 0.99 c	81	0.96	3.73	0.85
40-years-old	17.1 ± 1.16 c	62	0.96	3.52	0.85
Primary forest					
PF1	16.6 ± 1.03 c	84	0.97	3.92	0.88
PF2	27.4 ± 1.38 d	130	0.98	4.43	0.89
PF3	20.6 ± 1.68 cd	96	0.97	4.10	0.88

significantly different from the other forests. The highest mean height was for transect PF1 (14.7 m) and was significantly ($p < 0.05$) from the other forests.

The mean number of species per 250-m^2 plot was 8 in 5-years, 13 in 10-years and 17 in each 20-years-old, 40-years-old and transect PF1 of the primary forest and these values were significantly different (Tukey test, $p<0.05$). The highest mean number of species per plot was found in transects PF2 and PF3 of the primary forest and the values were significantly different from the rest. The total number of species was found to be lower in the secondary forests than in primary forest (Table 17). From the 5-years-old to 20-years-old forest the total number of species in the sample plots ranged from 41 to 81. The 40-years-old forest showed the same number of species as 10-years-old forest (Table 17). The total number of species in the primary forest ranged from 84 to 130 (Table 17). Considering each plot of 250 m^2, we can see from Fig. 13 that the species-area curve is steeper in older forests. The number of primary tree species (in common with the primary forest) gradually increased with the age of the secondary forest (Table 17), except for the 40-years-old forest which had the same number of primary tree species as the 10-years-old forest, but was far from reaching the number of species found in the primary forest.

The Shannon index of diversity (H') showed an increase from 5-years-old to primary forest, ranging from 2.89 to 3.73 for the secondary forests and from 3.92 to 4.43 for the primary forest transects (Table 17). The Simpson's diversity index was lower for the 5 and 10-years-old forests (0.91) and higher for 20 and 40-years-old forests (0.96) and for the primary forest (range: 0.97 to 0.98) (Table 17), indicating higher species dominance in younger forests and a reduction through the primary

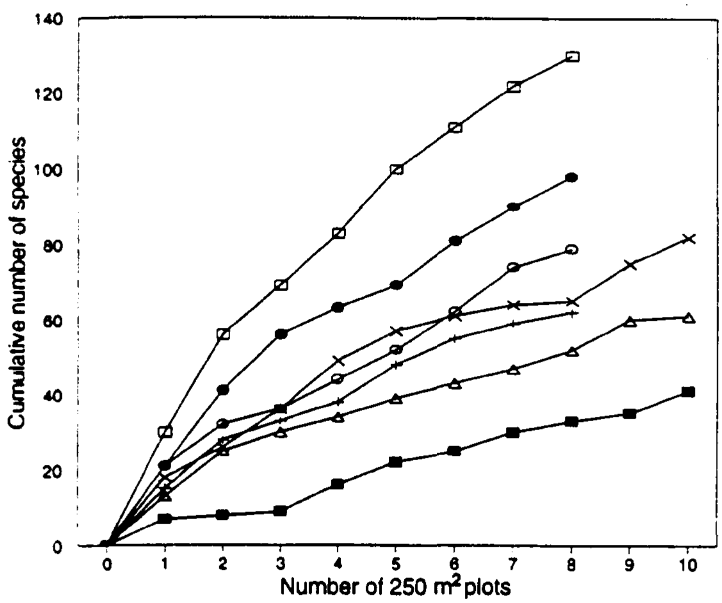

Figure 13. The cumulative number of species per each 250 m^2 for woody plants (≥ 5 cm dbh) in 5-years (■), 10-years (△), 20-years (x), and 40-years-old (+) secondary forests and in a primary forest (plots on transects PF1 o; PF2 □; PF3 ●) in the Bragantina region, Pará.

forest. The ratio, J, of H' and H_{max} (Brower & Zar 1984) indicated a relatively high degree of species evenness (Table 17).

The forest age-classes showed low similarity in species composition, with values of the Sørensen index less than 0.5 (Table 18), except between 5 and 10 years, which had a similarity of 0.51. In general, there was higher similarity among the secondary forests than between secondary forests and primary forest and the index increased between secondary forests of close ages (Table 18). The highest mean floristic similarity between secondary forests and primary forest was 0.27 (between 20-years and transect PF2 of primary forest). It means that a site, which today sustains a 20-years-old secondary forest, has a low rate of recovery of primary forest species. An attempt to calculate the number of years required for a secondary forest plot to become as floristically similar to a primary forest plot as another primary forest plot, was made. The mean Sorensen's index of similarity between the secondary forests and the primary forest plots was fitted to a linear regression (where Y= Sorensen's index and X= age in years), but the regression (Y= 0.136 + 0.0019 X) was statistically significant only at the 5% level (r^2= 0.33, p< 0.5, n= 4). By solving for X with this regression coefficient, where Y is equal to 0.47 (the highest index between two pairs of primary forests), the time required for a successional forest to attain close floristic similarity with primary forest was calculated as 168 years. However, one must take into account the limitations of doing such estimate with the low r^2 (0.33) in the regression.

Table 18. Similarity index of Sørensen among sampled areas (0.25 ha each for the 5-20-years-old forests and 0.20 ha for the 40-years-old forest and transects PF1, PF2 and PF3 of the primary forest) of five forest age-classes of Bragantina region, Pará.

	5-years-old	10-years-old	20-years-old	40-years-old	PF2	PF3
10-years-old	**0.51**					
20-years-old	**0.41**	**0.48**				
40-years-old	**0.39**	**0.42**	**0.41**			
PF1	**0.08**	**0.15**	**0.23**	**0.18**	**0.42**	**0.47**
PF2	**0.11**	**0.21**	**0.27**	**0.25**		**0.41**
PF3	**0.13**	**0.15**	**0.19**	**0.15**		

Ordination of species and plots

The DCA ordination of plots and species based on floristic data (Figs 14 and 15) showed an eigenvalue of 0.8204 for axis 1 and an eigenvalue of 0.4721 for axis 2. These values were higher than the eigenvalues for the third (0.3555) and fourth (0.2607) axis. It means that the relative contribution of these first two axes in explaining the total variation in the data was higher than the other two. DCA ordination suggested two distinct groups of forests. The secondary forests were clustered in the left side of axis 1 of the ordination while the primary forest plots were on the right (Fig. 14). Within the group of secondary forests there was a temporal ordination of the plots and species along axis 1. Plots and species were arranged along axis 1 according to a gradient from 5 to 40-years-old secondary forests. However there is a greater variation among the 5 and 40-years-old plots than of the 10-years and 20-years old plots. Some plots of 5 and 40-years-old were more floristically similar to the 10-years and 20-years-old secondary forests since in the ordination they were located closest to them. Many factors may have contributed to this pattern such as: the location of the plots, the number of species that was left (not cut or burned) by the farmers, the number of previous shifting cultivation cycles, the extent of weeding, the intensity of burning and possibly a mistake in the plot aging. Also one site of 40-years-old secondary forest was analyzed while for the other secondary forests there were 10 different sites. Within the primary forest group there is a gradient along axis 1 that could be explained by past disturbance by fire that took place in the *fazenda Monte Verde* primary forest more than fifty years ago during a drought (Mr. Marcelo Costa personal communication). This event should produce differences in the structure of the

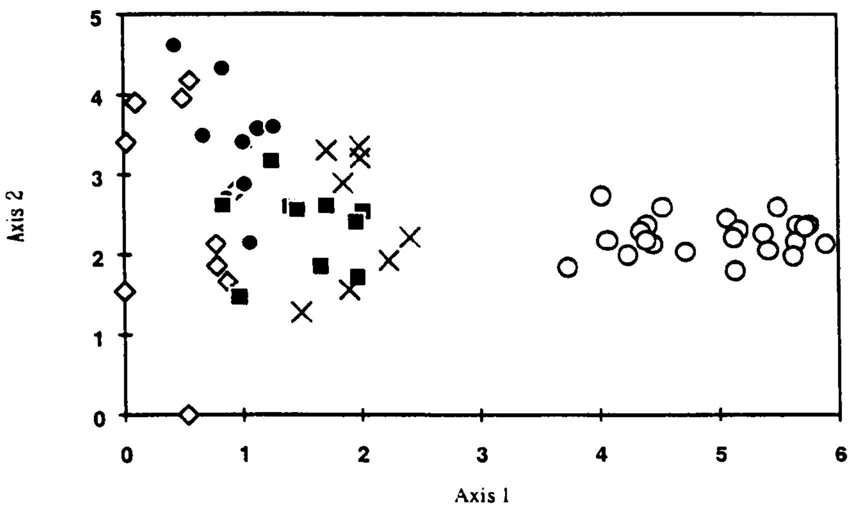

Figure 14. DCA ordination of all 250-m^2 plots of 5, 10, 20 and 40 years-old secondary forests and a primary forest in the Bragantina region, Pará, based on floristic data (≥ 5 cm dbh). Symbols: ◊ 5-years-old, ● 10-years-old, ■ 20-years-old, X 40-years-old secondary forests, and o primary forest.

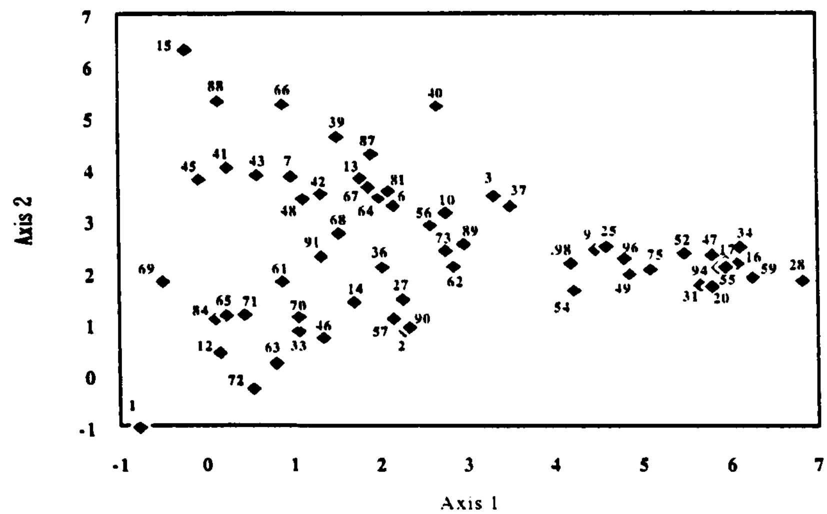

Figure 15. DCA ordination of the 20 most abundant species in each of the forest-age classes (plants ≥ 5 cm dbh) in the Bragantina region, Pará, based on floristic data. See Appendix 3 for the names of species.

forest and may help to explain the differences observed within the transects of the primary forest. DCA axis 2 suggests a vertical gradient among the secondary forests but it remains unexplained.

Classification of species and plots

The TWINSPAN classification of species and plots based on floristic data resulted in a sorted two-way table of the original data matrix (Table 19). Four major groups were obtained. The first division (eigenvalue of 0.757; indicator species *Escheweilera coriacea, Lacistema pubescens, Vismia guianensis and Rollinia exsucca*) separated completely the 38 plots of secondary forests from the 24 plots of primary forest. A second division towards the left of the hierarchy (eigenvalue of 0.394; indicator species: *Cecropia palmata, Inga thibaudiana, Lacistema pubescens, Vismia guianensis and Zanthoxylum rhoifolium*) resulted in two groups (I and II). Two borderlines occurred in this division: borderline negative (plot 18) and borderline positive (plot 27) and one misclassified negative (plot 9). The first group was formed mainly from 5-years-old plots with some plots of 10 and 20-years-old. Amongst the preferential species were: *Banara guianensis, Cecropia palmata, Croton matourensis, Inga edulis* and *Vismia guianensis*. The second group was formed mainly of 20-years-old and 40-years-old plots but with some 10-years-old plots. Amongst the preferential species were *Casearia decandra, Inga thibaudiana, Lacistema pubescens, Lecythis lurida, Guatteria poeppigiana, Gustavia augusta,* and *Stryphnodendron guianensis*. Non-preferential species, i.e. species that occurred in both groups were *Croton matourensis, Cordia scabrifolia, Inga edulis, Rollinia exsucca, Tapirira guianensis* and *Vismia guianensis*. The third division towards the right (eigenvalue of 0.480;

Table 19. Twinspan classification of plots and species based on floristic data (plants > 5 cm dbh of 5 10, 20 and 40-years-old secondary forests and primary forest in the Bragantina region, Para. In the columns of the sixty-two plots (1-10, 5-years-old; 11-20, 10-years-old; 21-30, 20-years-old; 31-38, 40-years-old secondary forest; 39-46 transect PF1; 47-54, transect PF2 and 55-62 transect PF3 of the primary forest).'-' means no occurrence of the species in the plots and the values 1 to 5 refers to the cut-levels classes of pseudospecies. See appendix 3 for the names of species.

```
                                              Plots
      Species    1    12      11221111112233333333222223454555553444555566444446
No. Code         01236904578925121346783456781234567890938041259135678901024672

 21 Trat  rho    -------21------------1--------11-------1-----------1----------  000
 40 Dipt  odo    -12---2-----------------------------1-------------------1---1-  000
 62 Inga  alb    -------1-----1-1-----------------112------------------1---1---  000
  1 Spon  mom    ----------3---------------------------------------------------  0010
  4 Anno  pal    2------1--------1--------------------1------------------------  0010
 15 Cord  sp.    -----22-------------------------------------------------------  0010
 33 Crot  mat    4------331222232-1-----3---13-32----32------------------------  0010
 39 Sapi  lan    -----22-------2--------------1---2-1--------------------------  0010
 41 Bana  gui    22333----2--1--------11--12----------------------1------------  0010
 45 Vism  gui    22322443341224-41142323-2112------1---------------------------  0010
 46 Sacc  gui    4-------------------------------------------------------------  0010
 66 Inga  nit    -1---23-1--1-2--2--3-------------------------1----------------  0010
 69 Inga  vel    2---2-------2-1--11-------------------------------------------  0010
 72 Cecr  pal    ----1--1134-2-11------2-----------1----------------1----------  0010
 79 Myrc  spl    --------------12--------------------2-------------------------  0010
 84 Maxi  mar    2-----------1----2------------1-------------------------------  0010
 88 Zant  rho    ----244--1--2122-------------------12-------------------------  0010
  2 Tapi  gui    ------2--42---2211---2---1-2--23--2----11----2--1-1--1--------  0011
 12 Jaca  cop    ----------1-1-------1-----------1-1---------------------------  0011
 14 Cord  sca    --------2--12-22-----------------322---1----------------------  0011
 22 Bauh  gui    ---------------1------1--1------1---1-------------------------  0011
 50 Nect  cus    --------1-------------------1-1--11---------------------------  0011
 63 Inga  edu    ---------43-1-22------------3-----22--------------------------  0011
 65 Inga  ing    -------32-----------------------211112------------------------  0011
  7 Roll  exs    -11--13--2--3213213232222332----1-2-12------------------------  0100
 13 Cord  scb    -------------------------2---1--------------------------------  0100
 32 Crot  caj    --------------------------------211---------------------------  0100
 35 Mabe  ang    1-----1--------------21-----1---------------------------------  0100
 36 Marg  nob    -------------------------111-12-------------------------------  0100
 42 Case  dec    ----------------2-112--1-1-1-------3--------------------------  0100
 43 Case  gra    ------1-1-------2-12323--1-------1----------------------------  0100
 44 Lind  lat    ----------------2---1---------------1-------------------------  0100
 48 Laci  pub    -------2----33-23344524334332112-12343------------------------  0100
 61 Abar  coc    -----------------2------------------2-------------------------  0100
 64 Inga  het    ------------------------22----1-------------------------------  0100
 68 Inga  thi    -----------122-122323-13--221---213323--------------------1-1-  0100
 70 Stry  gui    --------1--------------2-1------3-1--1------------------------  0100
 71 Stry  pul    ---------1-------2---1----------------------------------------  0100
 81 Neea  sp3    ------------------------112--2--------------------------------  0100
 86 Cous  ova    ------------------2------------2------------------------------  0100
 87 Zant  reg    ------------------------122-----------------------------------  0100
 91 Mata  sp.    ------------------------------------32------------------------  0100
  6 Guat  poe    1--------------------21-13432--------------11-----------------  0101
 56 Lecy  lur    --1---1----1--1--111-12132321-12-11-1222-11-1----------1------  0101
 57 Lecy  pis    -------------------2--------22-1-------1----------------------  0101
 67 Inga  rub    ------------------32---211-----1---1----1---------------------  0101
 73 Maqu  gui    ------------------1-2--2--1113------1---1-----------------1--1  0101
  3 Thyr  par    ------2----------------22121-2-----------2--2------------1----  0110
 10 Hima  suc    --------------------1-3-2--------------1-11-----------------1-  0110
 24 Bauh  mac    ------------------------1---212----------2--------------------  0110
 27 Cary  vil    -----------------2----------------------1---------------------  0110
 30 Lica  oct    -------------------------1--1-----1--2-1---1------------------  0110
 89 Cupa  scr    --------------------1-12-2---211---2-----11-----1-----------1-  0110
 90 Mata  gui    ---------2--------------1---22---------2----------------------  0110
 23 Bauh  jar    --------------2-------------------12-1--11---1----------------  0111
 51 Cour  gui    -----1--------2-------------------21---1-1-------1----1-------  100
 53 Esch  ped    1----2------------------1------------1----2---1-1-------------  100
 11 Lacm  acu    -----------------------11--------1---------1----1------------1  101
 37 Pogo  sch    ----------------1---------3----2------1---1-2---------------1-  101
 83 Astr  mum    ------------1---1--------21-----------1--1--------1---------1-  101
 54 Gust  aug    --------------3---------2--1--11-11---22341332--11--------2-11  1100
 92 Tali  ret    -----------------------1------------1--2-2--------------------  1100
  9 Geis  ser    ---------------------------------------111222-----------------  1101
 25 Tach  alb    ----------------------------------------2-2-11----1---------1-  1101
 26 Tach  pan    ---------------------------------------1--12------------------  1101
 49 Nect  glo    --------------------------------------11---2-2-1--1-----------  1101
 77 Caly   sp    --------------------------------------1-11------------------2-  1101
 78 Euge  pat    ------------------------------------1--2---11-----------------  1101
 80 Neea  spl    --------------------------------------12-1------1--1----------  1101
 82 Heis  acu    -----------------------2--------------1-121--------1--1------1  1101
 85 Lacu  cre    -----------------------------------------3---1-----1-1--------  1101
 93 Fran  sag    --------------------------------------2---1------------1----1-  1101
 95 Sand  egr    ----------------------------------------2---1-1--1------------  1101
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 96 Ster  pru   --------------------------------------22--1211---11-----1----1  1101
 97 Theo  spe   ------------------------------------------1212----1------2----  1101
 99 Amph  sur   ---------------------------------------2---------------1----11  1101
  8 Ambe  aci   -------------------2-----------------------2----1---1--1------  1110
 19 Prot  ten   -----------------------------------------1---2---2---1--------  1110
 74 Pour  acu   -------------------------------------------11--------2----1---  1110
 75 Viro  mic   --------------------------------------2----221-2-111-1-------1  1110
 98 Apei  bur   -----------------------1---------1------1----------------12---  1110
  5 Fusa  lon   ----------------------------------------------1-----11------11  1111
 16 Prot  dec   --------------------------------------1------111------2----1--  1111
 17 Prot  pil   -------------------------------------------21--12-1221--------  1111
 18 Prot  sag   ----------------------------------------------11------21------  1111
 20 Prot  tri   -------------------------------------------2--12---1----1--11-  1111
 28 Goup  gla   -----------------------------------------------1----12-------1  1111
 29 Lica  can   -----------------------------------------1----1--1------1--21-  1111
 31 Apar  cor   --------------------------------------------------12-1------23  1111
 34 Mabe  spe   ---------------------------------------------1-22-2---212-----  1111
 38 Sapi  poe   --------------------------1------------------------2--------11  1111
 47 Pora  gui   -----------------------------------------------12-1-12-11-1---  1111
 52 Esch  cor   ---------------------------2--------1---11---22223213223222112  1111
 55 Lecy  ida   ----------------------------------------2---1-2122-21113-112--  1111
 58 Mour  bra   ----------------------------------------------1------1-1-----2  1111
 59 Tric  mic   ---------------------------------------1-------2-1-111-2-----1  1111
 60 Tric  sch   -----------------------------------------1-------------21--111  1111
 76 Caly  mac   -------------------------------------------------1------11112-  1111
 94 Micr  gui   ----------------------------------------------1-1--1-----1---1  1111
100 Rino  neg   -------------------------------------------------2-----2-----1  1111

                00000000000000000000000000000000000000111111111111111111111111
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                01111001111111110000000000001111000011001110   00000000001111
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indicator species: *Gustavia augusta, Geissospermum sericeum, Escheweilera coriacea, Lecythis lurida, Poraqueiba guianensis, Lecythis idatimon* and *Sterculia pruriens*) divides the primary forest in two groups (III and IV). The third group was formed mainly by seven plots of transect PF2 and one from transect PF3 while all the plots of transect PF1 and most of the plots of transect PF3 were in the fourth group. Amongst the preferentials of group III were: *Apeiba burchelii, Geissospermum sericeum, Gustavia augusta, Nectandra cuspidata, Sterculia pruriens,* and *Tachigalia alba.* The fourth group was dominated by primary forest species such as *Aparisthimium cordatum, Escheweilera coriacea, Poraqueiba guianensis,* and *Trichilia micrantha.*

The relationships between ordination and classification of the plots are shown in Fig. 16. In general, the plots were distributed in a chronosequence, although plots 18 and 27 were borderline. Kent & Coker (1996) pointed out that such cases frequently happen in a complex data set. The diagram illustrates the four different ecological species groups recognized along the time sequence (Fig. 17).

Discussion

Numerous studies of succession after shifting cultivation have been carried out (Kellman 1970; Golley *et al.* 1976; Hall & Okali 1979; Aweto 1981a; Ewel *et al.* 1983; Mitza & Hladick 1989) but in Amazônia these studies have mostly restricted to the north (Uhl *et al.* 1981; Uhl *et al.* 1982a; Uhl & Jordan 1984; Saldarriaga *et al.* 1988). Owing to the large variation in the features of shifting cultivation, the secondary forest vegetation is variable and comparison is difficult. The lack of

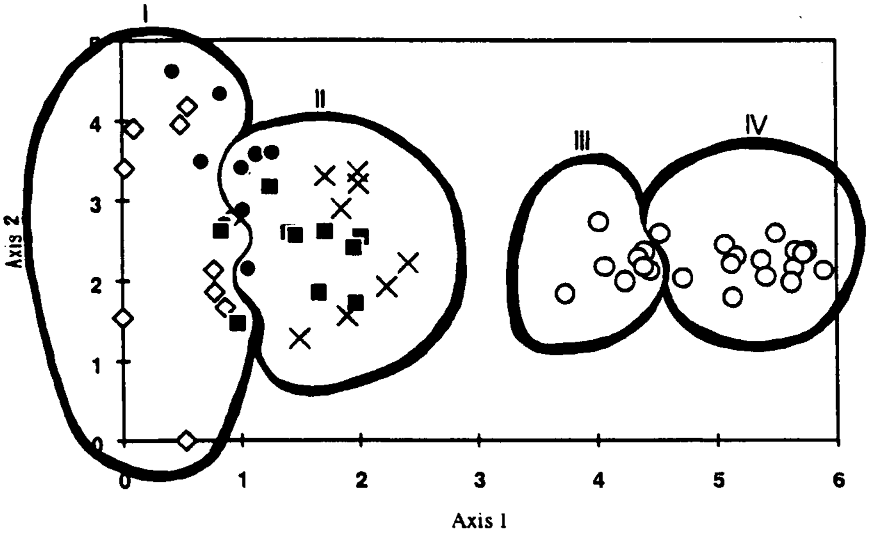

Figure 16. DCA ordination of all 250 m^2-plots (the same as Fig. 14) of 5, 10, 20 and 40-years-old secondary forests and a primary forest in the Bragantina region, Pará, with TWINSPAN groups (I, II, III and IV) inside the circles. Symbols: ◊ 5-years- old, ● 10-years-old, ■ 20-years-old, x 40-years-old secondary forests and o primary forest.

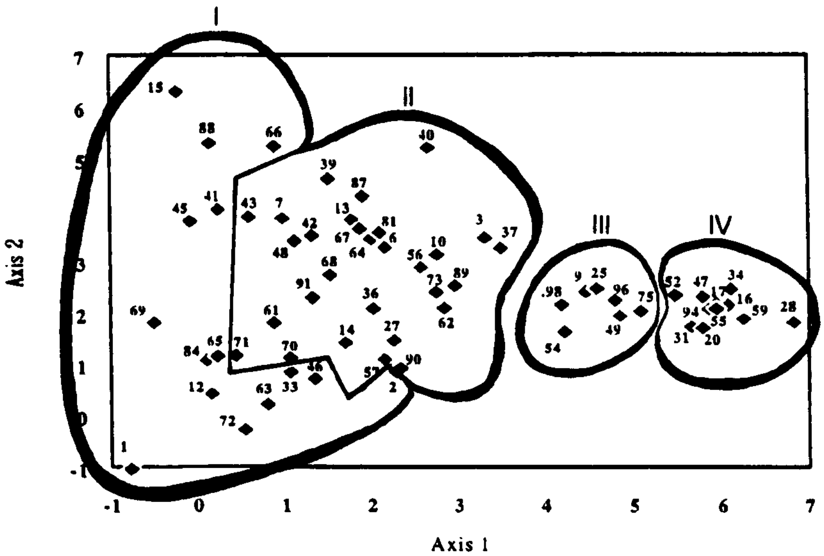

Figure 17. DCA ordination of the 20 most abundant species (the same as Fig. 15 in each of the forest-age classes in the Bragantina region, Pará, with TWINSPAN groups (I, II, III and IV) inside the circles. See Appendix 3 for the names of species.

uniformity of floristic inventories in such vegetation (e.g. different sizes of sampled areas, minimal dbh, ages of secondary forest) also contributes to the problems of comparison.

In Bragantina, species richness ranged from 41 to 81 for woody plants ($\geq$ 5 cm) 0.25 ha^{-1} in each age-class of secondary forest. These values were low compared with values for primary forest plots (84-130 0.20 ha^{-1}). Denich (1991) and Nunez (1995) working in a 4-5-years-old secondary forest of Igarapé-Açu, in the Bragantina region, found 183 species in 150 m^2 sampled (including trees, shrubs, vines and forbs) and 73 species (plants higher than 30 cm) in 50 m^2, while in San Carlos, Venezuela, Uhl & Jordan (1984) found 56 tree species ($\geq$ 2 m tall) and 15 species ($\geq$ 10 cm dbh) in 900 m^2 of a secondary forest of the same age. Studies in other tropical areas showed an enormous range of species richness in secondary forests up to 10-years-old. When the inventory includes only woody plants ($\geq$ 1 cm dbh) the range is from 23 to 62, while with inventories of total vascular plants, the number of species ranges from 75 to more than 300 (Kellman 1970; Golley *et al.* 1976; Hall & Okali 1979; Aweto 1981a; Ewel *et al.* 1983; Purata 1986; Saldarriaga *et al.* 1988; Mitza & Hladick 1989; Kapelle *et al.* 1995). The species richness of plants with dbh $\geq$ 5 cm dbh was low in the young Bragantina secondary forests and increased significantly in older ones (Table 17). The 5-20 years-old study sites were selected at distances from 1 to 3 km from the *Monte Verde* primary forest, while the only site of 40-years-old-forest available was almost 10 km from the primary forest. This spatial separation must have contributed to some of the differences observed between the 40-years-old site and the others. The Bragantina secondary forests showed similarities to those described from elsewhere in that the younger successional stages were often dominated by a few species and the species number increased gradually as the succession proceeded (Denslow 1980; Aweto 1981a; Mishra & Ramakrishnan 1983a; Uhl & Jordan 1984; Saldarriaga *et al.* 1988).

Calculated values of Simpson's diversity index of the forests studied here (0.91 to 0.96 to secondary forests and 0.97 to 0.98 to the primary forest) were close to those reported by Saldarriaga *et al.* (1988) (0.85 for 10-years and 0.97 to 80-years-old forests) and to the values of 0.92 reported by Knight (1975) for a 30-years-old forest. Values of this index indicated that dominance is higher for 5-years and 10-years-old forest. The values of the Shannon-Wiener index (Table 17) for the secondary forests (2.89 to 3.73) suggested that the distribution of individuals among species has a high degree of species evenness by the twentieth years.

The structure of the Bragantina's forests is characterized by a large number of individuals (40% to 100%) in the first 5-10 cm dbh size-class (Figs 9 and 10) and may reflect the slow rate of growth of the species in such forests. A similar stem distribution by dbh was observed in San Carlos, Venezuela (Saldarriaga *et al.* 1988). These authors suggested that the large number of small individuals in all stages of succession is a result of species strategies for survival in a dynamic ecosystem that is caused by a low soil nutrient availability. The mean values of 10.87 m^2 ha^{-1} and 16.72 m^2 ha^{-1} for the basal area of plants $\geq$ 5 cm dbh in the 10-years and 20-years-old Bragantina forests are similar to those reported by Saldarriaga *et al.* (1988) for other stands of the same age in northern Amazônia (10.19 m^2 ha^{-1} for 9-14-years-old secondary forests and 13.63 m^2 ha^{-1} for 20-years-old secondary forests for trees $\geq$ 5 cm dbh). The above-ground biomass ($\geq$ 5 cm dbh) of the same plots of 5, 10 and 20-years-old studied here was estimated by Salomão (1994) using alometric equations proposed by Uhl *et al.* (1988), and the values of 13, 44, and 81 t ha^{-1}, respectively, were found. Such values were lower than the ones reported by Denich (1991) and Nunez (1995) for 5-years-old secondary forests (19.9 t ha^{-1} in both studies). These two authors considered all plants (forbs, shrubs, vines and trees) in 50 m^2 and used destructive methods to estimate the biomass.

All the main species found in the present study have been listed by other authors (Uhl *et al.* 1988; Denich 1991; Nunez 1995) as components of the secondary forests of eastern Amazônia. Not only the floristic composition but also the relative importance of the species varied with the age of the secondary forest (Table 11). Of the 41 species present in the 5-years-old forest, 26 were still present at 10 years and 20 species present at 5- and 10-years were still there at 20 years (Appendix 1). These species represented 74% of the basal area at 5 years and 63% at 20 years. Certain primary forest trees such as *Andira retusa, Apeiba burchelii, Batesia floribunda, Eschweilera coriacea, Eugenia patrisii, Gustavia augusta, Heisteria acuminata, Lacmellea aculeata, Licania octandra, Nectandra cuspidata, Quiina paraensis, Talisia retusa* and *Terminalia amazonica* were restricted to the 20-years or 40-years-old forests. They were always present with a low density (≤ 3 individuals in the 0.25 ha sampled), except for *Gustavia augusta* which was more abundant. At 10 years the plots were characterized by woody pioneer species such as, *Casearia decandra, Casearia grandifolia, Inga nitida, Inga rubiginosa, Lindackeria latifolia, Lecythis lurida, Mabea angustifolia, Maquira guianensis* and 51% of the woody pioneer species were also found at 5-years. Some of these trees were present in the young secondary forest because the stumps were left by the farmers. The importance of species such as *Banara guianensis, Inga edulis, Lacistema pubescens, Vismia guianensis,* in younger secondary forests of Bragantina has been reported by Denich (1991). The failure of *Vismia guianensis* and other successional species to retain dominance in later stages (10 to 40 years) is possibly because they are poor competitors for light (J.M. Pires personal communication). Many of the common Bragantina successional species were dispersed by animals or have the capacity of sprouting after cutting and burning. The mechanisms involved in the establishment of the species in secondary forests will be analyzed in Chapter 8.

Both ordination and classification recognized a successional pattern. A series of sixty-two plots were divided in four successional phases and the species were ordered according to the recovery gradient in DCA axis 1 (Figs 16 and 17). Group I is characterized by the species that have the highest CVI in the 5-years and 10-years-old secondary forests such as *Vismia guianensis, Croton matourensis, Cecropia palmata, Banara guianensis, Inga edulis, Tapirira guianensis, Zanthoxylum rhoifolium*. These species were mainly medium pioneer species (according to the classification of Swaine & Whitmore 1988) and reached 5-25 m tall in the secondary forests (Table 20). Amongst the species of group II there were some medium and large pioneer species with a high CVI in the 20 and 40-years-old secondary forest such as *Casearia grandifolia, Lacistema pubescens, Lecythis lurida, Rollinia exsucca* and *Stryphnodendron guianense*. Surprisingly the plots and species in the primary forest were also divided into two groups (III and IV) along the DCA axis 1. Although the primary phase can form a larger portion of the forest, disturbance on a relatively small scale occurs through the death and falling of individual trees, to form gaps. Also, more than fifty years ago some trees of *Manilkara amazonica* and *Lecythis lurida* were selectively cut for fence posts and at about the same time fire occurred in part

Table 20 The commonest species in the four TWINSPAN groups, their ecological class (*sensu* Swaine & Whitmore 1988), and their height and dbh in the Bragantina secondary and primary forests. Where more than one individual occurs the range of values is given for height and dbh. n.o. means not recorded in the sample plots.

Species	Ecological class	Height (m)		Dbh (cm)	
		Secondary forests	Primary forest	Secondary forests	Primary forest
I Group					
Banara guianensis	small pioneer	5-10	9	5-7.5	7.1
Cecropia palmata	medium pioneer	9-16	10	9.1-15.9	7.3
Croton matourensis	large pioneer	8-23	14-26	9.7-20.4	12-64
Dipteryx odorata	large pioneer	8-15	38	5-7	120
Inga edulis	medium pioneer	9-20	n.o.	6.8-16.9	n.o.
Inga nitida	medium pioneer	6-18	12	5-15	18.4
Inga velutina	small pioneer	7-18	< 8	6-9.3	< 5
Jacaranda copaia	large pioneer	7-20	25-37	5-39	18-65
Lecythis lurida	medium pioneer	6-12	8-22	5-8.7	10-52
Sapium lanceolatum	medium pioneer	17-22	< 30	16-23	<5
Tapirira guianensis	large pioneer	5-25	4.7-25	6-36	10-50
Trattinickia rhoifolia	large pioneer	10	10.7-29	9.5	13-83
Vismia guianensis	medium pioneer	5-16	n.o.	5-18	n.o.
Zanthoxylum rhoifolium	medium pioneer	6-18	n.o.	5.1-16	n.o.
II Group					
Casearia decandra	medium pioneer	7-13	15	5-10.9	21
Cordia scabrifolia	large pioneer	3-20	11-18	6-22	14-16
Cupania scrobiculata	medium pioneer	6-8	7.8-13	5-8.3	5-8.5
Inga thibaudiana	medium pioneer	3-20	11-14.5	6.7-16.5	10-21
Inga rubiginosa	medium pioneer	6.5-17	9-17.5	6-16	9-17
Lacistema pubescens	medium pioneer	2-15	n.o.	5-12.5	n.o.
Lindackeria latifolia	small pioneer	6-8	< 8	5-8.6	< 5
Mabea angustifolia	small pioneer	6-9	n.o.	5-5.2	n.o.
Stryphnodendron guianense	medium pioneer	4-19	n.o.	8.5-35	n.o.
Rollinia exsucca	medium pioneer	5-17	n.o.	5-15.8	n.o.
III Group					
Couratari guianensis	medium mature	5.5-10	17-17.5	6.5-13	11-21
Gustavia augusta	medium mature	5-7.5	4.5-11	5.3-7	10-15
Nectandra cuspidata	small pioneer	5-8	< 8	6.4-8.5	< 5
Sterculia pruriens	medium mature	n.o.	12	n.o	9
Tachigalia alba	large mature	n.o.	35	n.o	43
Eschweilera coriacea	large mature	7-9	21	7-7.6	41
IV Group					
Lecythis idatimon	large mature	n.o.	30	n.o.	40
Goupia glabra	large pioneer	n.o.	21	n.o.	73
Protium trifoliolatum	large mature	n.o.	10	n.o.	12
Trichilia micrantha	large mature	n.o.	17	n.o.	37

of the forest having spread from agricultural burns during a very dry weather. These disturbances are probably responsible for the high density, species richness and diversity in the plots of transect PF2 (TWINSPAN group III). Some of the species in this group such as *Apeiba burchelii, Gustavia augusta, Nectandra cuspidata, Sterculia pruriens* and *Tachigalia alba* also occurred in secondary forests and in Figs 16 and 17 it can be seen that group III is close to the secondary forest groups I and II. From the three models of species replacement proposed by Connel & Slatyer (1977) (facilitation, tolerance and inhibition models), the tolerance model seems to be more applicable in Bragantina, since primary forest species become established in the abandoned secondary forests without completely eliminating the pioneer species that arrived earlier. This model was also reported in other successional studies in Amazônia (Uhl & Jordan 1984; Uhl *et al.* 1981). The facilitation model may occur in earlier stages of succession as was demonstrated by Vieira *et al.* (1994) and Nepstad *et al.* (1996b) in abandoned pastures of eastern Amazônia and Guevara *et al.* (1986) in Mexico.

The rate of floristic recovery is slow. Roughly a period of 168 years are required for an abandoned farm to recover the tree species composition of primary forest. Other researchers (Riswan *et al.* 1985; Saldarriaga *et al.* 1988) estimate that a period of 100-200 years is needed for areas disturbed by shifting cultivation in Indonesia and Venezuela to attain the basal area of primary forest, and Kapelle *et. al.* (1995) estimated that at least 65 years are needed to reestablish a terrestrial vascular flora similar to that of a primary forest in Costa Rica.

This study reveals the potential for forest regeneration after about 90 years of shifting cultivation. However, the structure, floristic composition and dominance of woody species of the secondary forests is different from the primary forest. Regrowth age alone does not give a complete explanation of community development (Purata 1986 and Uhl *et al.* 1988) and a study of many more sites with a broad range of land use histories is necessary to ensure firm conclusions about secondary succession in the Bragantina region.

CHAPTER 7

FLORISTICS AND STRUCTURE (FOR WOODY PLANTS ≥ 10 CM DBH) IN PRIMARY AND 40-YEARS-OLD SECONDARY FORESTS.

Introduction

Chapter 6 was concerned with woody plants (≥ 5 cm dbh) which were sampled from 250-m^2 plots. This chapter deals with woody plants (≥ 10 cm dbh) sampled from the 1-ha plots which were located only in the 40-years-old secondary forest and primary forest. Larger plots could not be set up in the younger forests because the fragments were too small.

In 1988 there were an estimated 16,000 km^2 of forest remnants (isolated primary forests surrounded by modified habitat) in Amazônia (Skole & Tucker 1993). About 15% of the landscape of the Bragantina region has recently been discovered to be remnant forest (I.C.G. Vieira *et al.* unpublished), mostly concentrated along streams on sites where agriculture is impossible. Old secondary forests (≥ 20 years) account for 23% of the region. The remnant forests play an important role in preventing the spread of fire across the landscape and in maintaining hundreds of species of plants and animals (D.C. Nepstad *et al.* 1996a). Because most of the studies of succession in tropical forests have focused on the early stages there is a gap in understanding secondary succession in the longer term (Knight 1975; Finegan 1996). In this chapter I examine longer-term succession by comparing the main floristic and structural features of the primary forest remnant (*terra firme*) and the 40-years-old secondary forest.

Methods

Floristic inventory

The primary forest

A inventory of the 200-ha primary forest at *fazenda Monte Verde* (Fig. 4) was made in May 1991 for all woody plants (≥10 cm dbh) in three 10 m x 1000 m randomly located transects (subdivided into forty subplots of 10 m x 25 m each). The dbh and height were measured. The procedures used for tress with multiple-stem, buttresses and prop roots were described in Chapter 6. The identification of the species was made by technicians of MPEG as described in the Chapter 6.

The 40-years-old secondary forest

The 40-years-old secondary forest was inventoried in January 1994 from two random transects of 20 m x 250 m (subdivided into twenty subplots of 10 m x 25 m each), using the methods described for the primary forest. The transects were shorter than those in the primary forest because the forest extent was narrower.

Data analysis

The phytosociological analysis was made by using the software FITOPAC 2 (Chapter 6). Species diversity was calculated using Simpson's diversity index (Ds) and the Shannon-Wiener diversity index (H') (Brower & Zar 1984). Species-area curves were made for each 1-ha transect of the primary forest and for two 0.5 ha transects combined for the 40-years-old forest.

Results

The primary forest

There were 1346 trees and lianas in the 3 ha, representing 52 families, 146 genera and 233 species (Appendix 4). Mean values for the three 1-ha transects were: density 449 ha^{-1} (range: 413 to 493), genera 98 (range 92 to 108) and families 44 (range 43 to 46) (Table 21). The mean basal area was 24.7 m^2 ha^{-1} and ranged from 23 to 27 $m^2 ha^{-1}$ (Table 21). The height and dbh distribution of the 1346 individuals are shown in Figs 18 and 19. The majority of individuals (93% of the total) ranged in height from 5 m to 25 m (Fig. 18). Ninety-nine individuals (7% of the total) exceeded 25 m and three were higher than 40 m (*Aspidosperma desmanthum, Parinari rodolphii and Vochysia vismiifolia*). The majority of species (64.5%) had a dbh between 10 and 20 cm, 20% had a dbh between 20 and 30 cm and only 0.52% (seven individuals) had a dbh greater than 90 cm (*Couratari multiflora, Dipteryx odorata, Goupia glabra, Newtonia psilostachya, Parinari rodolphii, Vochysia vismiifolia* (2)) (Fig. 19).

The species-area curves for the three primary forest transects were similar in shape (Fig. 20). However the total number of species increased by 58% with the addition of the second transect to the first and only 20% with the adition of the third transect, showing that the curve was flattening off at 3 ha. The mean number of species ≥ 10 cm dbh per ha in the primary forest was 137 (range 126-156)

Table 21. Mean (with range in parentheses) number of individuals (≥ 10 cm dbh), number of species, number of families, diversity index and basal area for three 1-ha plots in a primary forest and 1-ha (two 0.5-ha plots combined) in a 40-years-old secondary forest in the Bragantina region, Pará.

	Primary forest	40-years-old forest
Number of individuals ha^{-1}	448.7 (413 - 493)	493
Number of species ha^{-1}	137.0 (126 - 156)	66
Number of genera ha^{-1}	98 (92 - 108)	56
Number of families	44 (46 - 45)	31
Shannon-Wiener diversity index	4.44*	3.33
Simpson's diversity index	0.98*	0.93
Basal area (m^2 ha^{-1})	24.7 (23 - 27)	12.7

*Calculated for 3-ha plots combined.

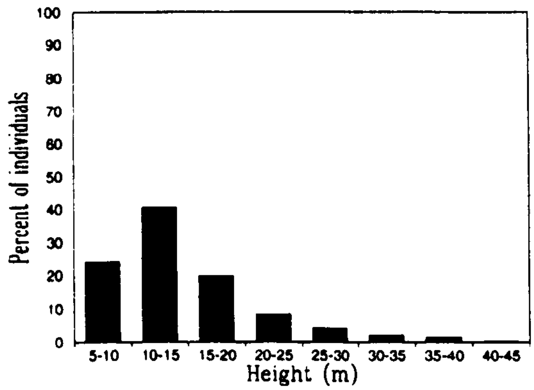

Figure 18. Distribution by height for individuals ≥ 10 cm dbh in 3-ha (three 1-ha plots combined) in a primary forest of Bragantina region, Pará.

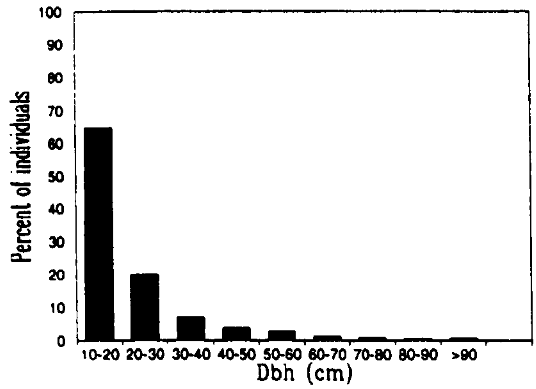

Figure 19. Distribution by dbh for individuals ≥ 10 cm dbh in 3 ha (three 1-ha plots combined) in a primary forest of Bragantina region, Pará.

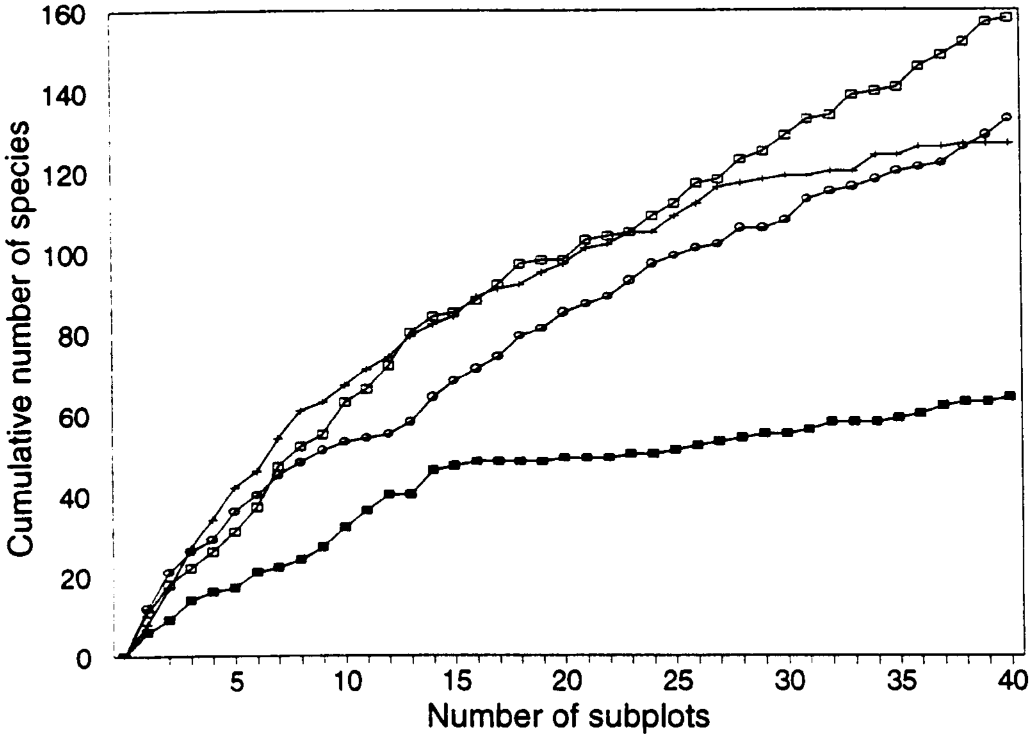

Figure 20. The cumulative number of species and area for plants (trees and lianas) ≥ 10 cm dbh in three 1-ha plots in a primary forest (o PF1; □ PF2; + PF3) and in 1-ha (two 0.5-ha plots combined) in a 40-years-old secondary forest (■) in the Bragantina region, Pará.

(Table 21). Simpson's diversity index calculated for the 3 ha was 0.98 and Shannon's index was 4.44. Thirty-four percent of the species were represented by only one individual.

The thirty most abundant species represented 48% of the total individuals sampled (Table 22). The species *Eschweilera coriacea, Lecythis idatimon, Newtonia psilostachya* and *Mabea* cf. *speciosa* were the most abundant (Table 22). *Virola michelii* was less abundant but it had 20 large trees with a high total basal area (3.4619 m^2). The families that showed the highest CVI were the Lecythidaceae (41.35), Mimosaceae (17.51), Caesalpiniaceae (11.57), Sapotaceae (10.04), Euphorbiaceae (9.24) and Moraceae (7.75) (Table 23).

The 40-years-old secondary forest

A total of 493 plants (all trees) ≥10 cm dbh were sampled in the two 0.5-ha transects of the 40-years-old secondary forest, representing 31 families, 56 genera and 66 species (Appendix 5 and Table 21). Figs 21 and 22 show the distribution of individuals in height and dbh classes. The majority (83.77%) of the 493 individuals ranged in height from 10 to 20 m, and the maximum height was 25 m, reached by a *Croton matourensis*. A large number of individuals (76.47% of the total) had a dbh between 10-20 cm and only five trees of *Tapirira guianensis* (1% of the total) had a dbh greater than 40 cm.

The thirty species with the highest CVI comprised 89.6% of the total individuals sampled (Table 24), and *Croton matourensis, Tapirira guianensis, Rollinia exsucca* and *Margaritaria nobilis* were the most abundant. The Simpson's diversity index value was 0.93 and Shannon-Wiener index 3.3. The most abundant families

Table 22. The 30 most abundant species of plants (trees and lianas) ≥ 10 cm dbh occurring in 3-ha (three 1-ha plots combined) in a primary forest in the Bragantina region, Pará, with number of individuals (N), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Species are ranked by CVI.

Species	N	RD (%)	BA (m^2)	RDo (%)	CVI
Eschweilera coriacea	124	9.21	5.30	5.87	15.08
Lecythis idatimon	96	7.13	3.97	5.36	12.49
Newtonia psilostachya	15	1.11	3.78	5.10	6.21
Mabea aff. *speciosa*	35	2.60	0.94	1.27	3.87
Vochysia vismiaefolia	5	0.37	2.41	3.26	3.63
Goupia glabra	7	0.52	2.24	3.02	3.54
Apeiba burchelii	28	2.08	1.06	1.43	3.51
Tapirira guianensis	20	1.49	1.45	1.95	3.44
Nectandra aff. *globosa*	23	1.71	1.03	1.39	3.10
Sclerolobium paraense	9	0.67	1.76	2.38	3.05
Virola michelii	20	1.49	3.46	1.53	3.02
Tachigalia alba	12	0.89	1.28	1.73	2.62
Lecythis pisonis	9	0.67	1.42	1.92	2.59
Jacaratia spinosa	10	0.74	1.33	1.80	2.54
Inga alba	11	0.82	1.20	1.63	2.45
Poraqueiba guianensis	24	1.78	0.49	0.66	2.44
Apuleia leiocarpa	10	0.74	1.13	1.52	2.26
Pogonophora schomburgkiana	11	0.82	1.06	1.43	2.25
Erisma uncinatum	7	0.52	1.28	1.73	2.25
Gustavia augusta	25	1.86	0.28	0.38	2.24
Cecropia distachya	20	1.49	0.48	0.64	2.13
Newtonia suaveolens	11	0.82	0.91	1.23	2.05
Protium sagotianum	16	1.19	0.54	0.73	1.92
Eschweilera cf. *collina*	10	0.74	0.87	1.18	1.92
Geissospermum sericeum	14	1.04	0.63	0.85	1.89
Micropholis guianensis	13	0.97	0.64	0.87	1.84
Symphonia globulifera	14	1.04	0.48	0.65	1.69
Neea sp.	14	1.04	0.41	0.55	1.59
Mouriri brachyanthera	15	1.11	0.32	0.44	1.55
Trichilia micrantha	14	1.04	0.30	0.41	1.45

Table 23. The 30 most abundant families of plants (trees and lianas) ≥ 10 cm dbh occurring in 3-ha (three 1-ha plots combined) in a primary forest in the Bragantina region, Pará, with number of individuals (N), number of species (Sp), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Families are ranked by CVI.

Family	N	Sp	RD (%)	BA (m^2)	RDo (%)	CVI
Lecythidaceae	298	11	22.12	14.25	19.23	41.35
Mimosaceae	86	16	6.38	8.23	11.13	17.51
Caesalpiniaceae	64	12	4.74	5.06	6.83	11.57
Sapotaceae	77	17	5.68	3.23	4.36	10.04
Euphorbiaceae	72	9	5.36	2.87	3.88	9.24
Vochysiaceae	21	4	1.56	4.58	6.19	7.75
Burseraceae	56	10	4.16	2.33	3.15	7.31
Moraceae	60	16	4.43	1.79	2.41	6.84
Myristicaceae	25	2	1.86	3.68	4.97	6.83
Chrysobalanaceae	43	8	3.18	2.45	3.31	6.49
Lauraceae	46	9	3.40	1.80	2.42	5.82
Anacardiaceae	38	5	2.82	2.13	2.88	5.70
Meliaceae	44	7	3.27	1.72	2.34	5.61
Apocynaceae	40	8	2.97	1.68	2.26	5.23
Celastraceae	18	2	1.34	2.48	3.35	4.69
Tiliaceae	34	3	2.52	1.58	2.13	4.65
Myrtaceae	36	13	2.66	1.16	1.57	4.23
Icacinaceae	33	2	2.45	0.86	1.16	3.61
Flacourtiaceae	17	4	1.26	1.13	1.54	2.80
Caricaceae	10	1	0.74	1.33	1.80	2.54
Melastomataceae	24	4	1.78	0.55	0.75	2.53
Fabaceae	5	5	0.35	1.45	1.97	2.32
Clusiaceae	20	4	1.48	0.57	0.77	2.25
Sapindaceae	21	5	1.55	0.43	0.59	2.14
Bignoniaceae	10	3	0.74	0.93	1.26	2.00
Sterculiaceae	15	5	1.10	0.63	0.86	1.96
Rubiaceae	13	3	0.96	0.28	0.39	1.35
Quiinaceae	13	3	0.96	0.24	0.33	1.29
Boraginaceae	6	3	0.44	0.54	0.74	1.18
Combretaceae	7	4	0.51	0.48	0.65	1.16

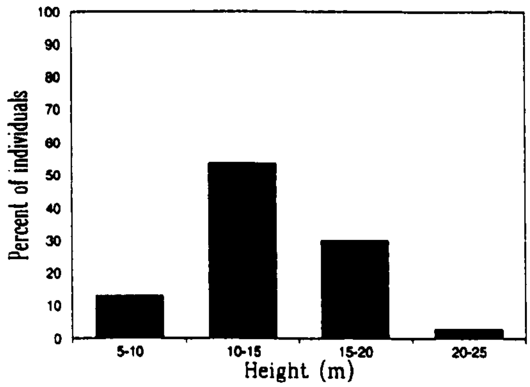

Figure 21. Distribution by height for individuals ≥ 10 cm dbh in 1-ha (two 0.5-ha plots combined) in a 40-years-old secondary forest of Bragantina region, Pará.

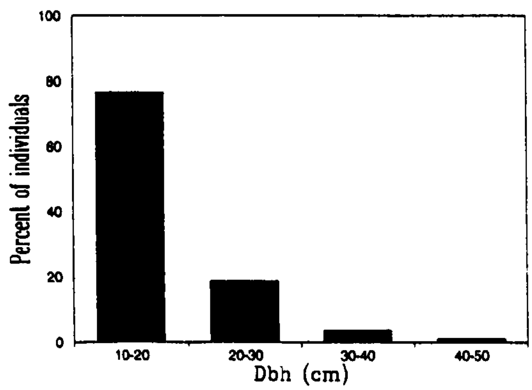

Figure 22. Distribution by dbh for individuals ≥ 10 cm dbh in 1-ha (two 0.5-ha plots combined) in a 40-years-old secondary forest of Bragantina region, Pará.

Table 24. The 30 most abundant tree species ≥ 10 cm dbh occurring in 1-ha (two 0.5-ha plots combined) in a 40-years-old secondary forest in the Bragantina region, Pará, with number of individuals (N), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Species are ranked by CVI.

Species	N	RD (%)	BA (m^2)	RDo (%)	CVI
Croton matourensis	97	19.67	3.5531	27.96	47.63
Tapirira guianensis	53	10.75	2.6683	21.00	31.75
Rollinia exsucca	31	6.28	0.6131	4.82	11.10
Margaritaria nobilis	30	6.08	0.5290	4.16	10.24
Guatteria poeppigiana	25	5.07	0.2968	2.33	7.40
Inga rubiginosa	18	3.65	0.3599	2.83	6.48
Byrsonima aerugo	14	2.84	0.3961	3.11	5.95
Vismia guianensis	17	3.44	0.2366	1.86	5.30
Cordia scabrida	15	3.04	0.2565	2.01	5.05
Dipteryx odorata	7	1.42	0.3561	2.80	4.22
Lacistema pubescens	15	3.04	0.1414	1.11	4.15
Zanthoxylum regnellianum	12	2.43	0.1783	1.40	3.83
Maximiliana maripa	4	0.81	0.3668	2.88	3.69
Inga edulis	9	1.82	0.1354	1.06	2.88
Matayba guianensis	9	1.82	0.1304	1.03	2.85
Inga thibaudiana	9	1.82	0.1101	0.86	2.68
Licania octandra	5	1.01	0.1984	1.56	2.57
Himatanthus sucuuba	7	1.42	0.1234	0.97	2.39
Thyrsodium paraense	8	1.62	0.0883	0.69	2.31
Stryphnodendron guianense	5	1.01	0.1508	1.19	2.20
Lecythis lurida	7	1.42	0.0914	0.72	2.14
Lecythis pisonis	7	1.42	0.0893	0.70	2.12
Hymenea parvifolia	5	1.01	0.1370	1.07	2.08
Ormosia paraensis	6	1.21	0.1080	0.85	2.06
Casearia decandra	7	1.42	0.0814	0.64	2.06
Inga alba	3	0.60	0.1685	1.32	1.92
Nectandra cuspidata	4	0.81	0.1008	0.79	1.60
Trattinickia rhoifolia	4	0.81	0.0862	0.67	1.48
Apeiba burchellii	4	0.81	0.0732	0.57	1.38
Coussarea ovalis	5	1.01	0.0441	0.34	1.35

were the Euphorbiaceae, Anacardiaceae and Mimosaceae (Table 25). The basal area occupied by all individuals was 12.71 m^2 ha^{-1}. *Croton matourensis* had the highest basal area (3.55 m^2) followed by *Tapirira guianensis* (2.67 m^2) (Table 24). The species-area curve (Fig 20) showed a flattening off after the first 15 subplots had been sampled (0.37 ha).

Discussion

Even after about 90 years of shifting cultivation, primary forest remnants persist in the Bragantina region. These fragments are the refuges of more than 200 tree species and support as many species as do the more widespread secondary forests in the same region (Table 21). They were similar to other eastern Amazonian primary forests (Table 26) in terms of numbers of individuals (≥10 cm dbh) (449 ha^{-1}), in basal area (25 m^2 ha^{-1}) and, with a mean value of 138 species ha^{-1}, were in the range (60-300 species ha^{-1}) of the *terra firme* Amazonian forests reviewed by Gentry (1988). Samples of *terra firme* forests of eastern Amazônia (for individuals ≥10 cm dbh) include representatives from 29 to 50 families ha^{-1} (Table 26). Those studies have shown that Burseraceae, Caesalpiniaceae, Euphorbiaceae, Fabaceae, Lecythidaceae, Moraceae and Sapotaceae were usually the most abundant families of plants in this region (Cain *et al.* 1956; Salomão *et al.* 1988; Mori *et al.* 1989). The *fazenda Monte Verde* forest included 52 families among the 1346 individuals sampled. In this study, the Lecythidaceae were the most abundant, with 23% of the individuals, having the highest contribution to the basal area (19%) and the highest CVI of all

Table 25. Families of trees ≥ 10 cm dbh occurring in 1-ha (two 0.5-ha plots combined) in a 40-years-old secondary forest in the Bragantina region, Pará, with number of individuals (N), number of species (Sp), relative density (RD), basal area (BA), relative dominance (RDo) and cover value index (CVI). Species are ranked by CVI.

Family	N	Sp	RD (%)	BA (m^2)	RDo (%)	CVI
Euphorbiaceae	135	6	27.38	4.24	33.34	60.72
Anacardiaceae	61	2	12.37	2.76	21.69	34.06
Annonaceae	58	4	11.76	0.97	7.65	19.41
Mimosaceae	46	7	9.33	0.95	7.49	16.82
Fabaceae	15	3	3.04	0.48	3.80	6.84
Malpighiaceae	14	1	2.84	0.40	3.12	5.96
Clusiaceae	18	2	3.65	0.24	1.93	5.58
Lecythidaceae	17	4	3.45	0.26	2.09	5.54
Boraginaceae	16	2	3.24	0.27	2.09	5.33
Lacistemaceae	15	1	3.04	0.14	1.11	4.15
Rutaceae	12	1	2.43	0.18	1.40	3.83
Palmae	4	1	0.81	0.37	2.89	3.70
Sapindaceae	12	4	2.43	0.16	1.27	3.70
Chrysobalanaceae	7	2	1.42	0.23	1.84	3.26
Apocynaceae	8	2	1.62	0.13	1.04	2.66
Caesalpiniaceae	6	2	1.22	0.16	1.28	2.50
Flacourtiaceae	8	2	1.62	0.09	0.71	2.33
Tiliaceae	7	1	1.42	0.11	0.85	2.27
Lauraceae	5	2	1.01	0.13	1.01	2.02
Moraceae	7	4	1.42	0.07	0.56	1.98
Burseraceae	4	2	0.81	0.09	0.68	1.49
Rubiaceae	5	2	1.01	0.04	0.35	1.36
Nyctaginaceae	3	2	0.61	0.04	0.29	0.90
Sapotaceae	2	2	0.41	0.03	0.26	0.87
Araliaceae	1	1	0.20	0.05	0.40	0.60
Celastraceae	2	1	0.41	0.02	0.16	0.57
Elaeocarpaceae	1	1	0.20	0.04	0.29	0.49
Quiinaceae	1	1	0.20	0.02	0.12	0.32
Myrtaceae	1	1	0.20	0.01	0.10	0.30
Connaraceae	1	1	0.20	0.01	0.09	0.29
Combretaceae	1	1	0.20	0.01	0.08	0.28

Table 26. Summary results for some phytosociological inventories in *terra firme* forests of eastern Amazônia for plants ≥ 10 cm dbh or ≥ 9.55 cm dbh[1]. n.d. no data.

Source	Location	Sample size (ha)	Number of				Basal area ($m^2 ha^{-1}$)
			Stems	Families	Genera	Species	
This study	Peixe Boi, Pará	3	1346	52	146	233	25
Black *et al.* 1950	Belém, Pará	1	423	31	65	87	n.d.
Pires *et al.* 1953	Castanhal, Pará	3.5	1482	47	130	179	n.d.
Cain *et al.* 1956	Mocambo, Pará	2	897	39	100	153	32.6
Pires 1966	Breves, Pará	1	516	36	n.d.	157	n.d.
Dantas & Muller 1979[1]	Altamira, Pará	0.5	300	29	n.d.	59	n.d.
Dantas *et al.* 1980[1]	Capitão Poço, Pará	1	504	39	86	121	n.d.
Silva *et al.* 1986	Carajás, Pará	1	516	38	96	128	27.7
Salomão 1991	Marabá, Pará	6	3147	46	157	237	19.8
Salomão *et al.* 1988	Carajás, Pará	1	484	39	83	122	21.6
Mori *et al.* 1989	Camaipi, Amapá	1	546	47	n.d.	205	35.1
Balée 1993	Canindé, Gurupi	1	475	41	n.d.	144	34.5
Almeida 1993	Caxiuanã, Pará	4	2441	50	n.d.	338	n.d.

families in the primary forest (46%). *Eschweilera coriacea* (15%) and *Lecythis idatimon* (12%) had the highest CVI in the primary forest. Other studies (Balée 1986; Cain *et al.* 1956; Dantas *et al.* 1980; Rodrigues 1963) included *Eschweilera coriacea* as the most important species in *terra firme* forests of eastern Amazônia. Many of the plant populations of the primary forest fragment are threatened because they are very small. Thirty-five percent of the species in this study were recorded from only one individual but is not clear if these species were truly rare throughout their range or if their rarity in the *fazenda Monte Verde* forest was a consequence of forest fragmentation. A high proportion of rare species was found by other researchers (Campbell *et al.* 1986 and Salomão 1991) in *terra firme* forest. R.P. Salomão (personal communication) found that one-third of the species in inventories of many plots (total area 35 ha) throughout Amazônia had only one individual. Primack & Hall (1992) found that the great majority (35% - 50%) of the tree species (≥ 10 cm dbh) recorded in Malaysian forests were rare on a local scale and that rare species had higher mortality rates than common ones.

Terra firme covered four times more land surface in Bragantina region prior to human settlement, but is represented by remnants that cover half the area of *igapó* remnants (Fig. 4). The persistence of *igapó* remnant in the landscape may be attributed to the difficulty of converting these forests to agricultural plots or pastures. A inventory made in 1 ha of a remnant *igapó* forest near to *Monte Verde* primary forest (I.C.G. Vieira unpublished) showed that the structure and floristic composition of these forests were completely different. Forty-four species ha^{-1} (trees ≥ 10 cm dbh) were presented in the *igapó* forest and only thirteen species (*Ampelocera edentula, Anacardium giganteum, Carapa guianensis, Cecropia sciadophylla, Combretum laxum, Eugenia* sp. *Licania heteromorpha, Protium decandrum, Sloanea grandiflora, Sterculia pruriens, Sterculia speciosa, Symphonia globulifera* and *Tapirira guianensis*) were represented in both types of forest. This pattern suggests that relatively few species are able to grow in the different soil conditions of both *terra firme* and *igapó*.

Shifting cultivation in the Bragantina region has long been recognized as having changed the original forest species composition (Lima 1954; Valverde & Dias 1967). After about 40-years-succession the secondary forest has fewer species and lower diversity than primary forest. There were 137 species ha^{-1} ($\geq$ 10 cm dbh) in the primary forest and 66 species in the 40-years-old secondary forest. The primary forest was dominated by *Eschweilera coriacea* and *Lecythis idatimon*. In contrast, the 40-years-old forest was dominated by large pioneers such as *Croton matourensis* and *Tapirira guianensis* which are characterised by fast growth rates and abundant occurrence in earlier successional stages (Chapter 6). Forty species $\geq$ 10 cm dbh (representing 61% of the total found in the 40-years-old forest and 17% of the ones found in the primary forest) were in both types of forest. These forty species can be divided into three groups: 77.5% had a higher density in the secondary forest (e.g. the large pioneers *Cordia scabrifolia, Croton matourensis, Didymopanax morototoni, Dipteryx odorata, Inga alba, Lecythis lurida, Trattinickia rhoifolia, and Zanthoxylum regnelianum*). The second group (only one species, *Rheedia acuminata*) had similar densities in both forests. The third group (20%) had a lower density in the secondary forest (*Apeiba burchelii, Apuleia leiocarpa, Escheweilera pedicellata, Lacmellea aculeata, Licania heteromorpha,* *Neea* sp., *Sapium poepigii and Talisia retusa*). Tropical woody plants that are restricted to primary forests have been shown to have a significantly higher mean seed weight than those in open or disturbed habitats (Foster & Janson 1975; I.C.G. Vieira *et al.*1996b). A comparison between 50 - 65-years-old secondary forests and primary forest in Panama (Knight 1975) revealed that although there were no differences in total species richness or abundance of shade-tolerant species, long-lived pioneers (large pioneers *sensu* Swaine & Whitmore 1988) were much more abundant in the secondary forest. In the upper Rio Negro, Saldarriaga *et al.* (1988) showed that even though species richness recovered rapidly in secondary succession, old secondary forests (> 30 years) differed from primary forests in their dominant species and had the large pioneer taxa *Jacaranda copaia, Goupia glabra* and *Vochysia* sp. as dominants and only secondary forests > 60 years old had species dominants that were equally common in primary forest. In the Mexican Chiapas highlands, a 40-years-old forest had 85% of the species richness of all vascular terrestrial plants found in primary forest (Gonzalez-Spinosa *et al.* 1991). Some of the primary tree species (e.g. *Eschweilera coriacea, Gustavia augusta, Trattinickia rhoifolia, Thyrsodium paraense*) were found in the 40-years-old forest while pioneer species such as *Casearia grandiflora, Casearia javitensis, Lacistema pubescens, Rollinia exsucca, Stryphnodendron guianensis, Vismia guianensis, Zanthoxylum rhoifolium* were absent in the primary forest. All the most species-rich families in the primary forest were less so in the 40-years-old forest (Tables 23 and 25). This is most evident for the Caesalpiniaceae, Lecythidaceae, Moraceae, Myrtaceae and Sapotaceae. The Annonaceae and Sapindaceae on the other hand, were more prominent in the 40-years-old forest.

After about 40 years under secondary succession, the basal area of the secondary forest was only 13 $m^2 ha^{-1}$ compared with 25 $m^2 ha^{-1}$ for the primary forest. These forests did not differ in the proportion of individuals in the smaller classes of 10-20 cm dbh and 20-30 cm dbh, however a larger number of individuals ($\geq$ 30 cm dbh) were found in the primary forest.

CHAPTER 8

MECHANISMS OF PLANT REGENERATION DURING SUCCESSION

Introduction

Cleared sites have four potential sources for regeneration: the seed bank, post-disturbance seed input, seedling and resprouting trunks and roots. The importance of the seed bank for the development of secondary succession has been emphasised by Uhl (1987), Young *et al.* 1987, Uhl & Jordan (1984), Victor & Jose (1992) and Rico-Gray & Garcia-Franco (1992). Several studies have investigated the seed rain in particular habitats or communities but little is known about its dynamics along a successional gradient. Vegetative sprouts are important in sites manually cleared for shifting cultivation (Rouw 1993) and have been regarded by some authors (Uhl *et al.* 1982b; Whitmore 1983) as being important in succession.

In this chapter I examine the abundance, life form composition and species richness in the soil seed bank and seed rain in 5, 10 and 20-years-old secondary forests and in primary forest and the regeneration from seedlings and sprouting in the secondary forests, and evaluate their relative importance in the establishment of woody species. The 40-years-old forest was left out of these studies because the site was remote and not available for long-term studies.

Methodology

Soil seed bank

Soil samples were collected at random in the three plots in each of 5, 10 and 20-years-old forests (Chapter 6). For the primary forest, the soil samples were collected at random along each of the three transects used for the vegetation survey (Chapter 7). Four soil samples of 20 cm x 20 cm were taken to a depth of 0-5 cm, and 5-10 cm in each of the sites (total of 12 samples/forest age-class/depth). All the samples were spread on separate trays, and put outside on a table covered with a white shade cloth and well ventilated. The samples were watered regularly. The samples were examined every 7 days in the first two months and every 14 days thereafter. After four months the soils in the trays were turned over and observed for two more months. All seedlings were identified as they emerged.

The diversity of the seed bank was evaluated by the Shannon-Wiener index and the similarity by the Sørensen index (Brower & Zar 1984). For each sample depth separately the seed bank data were first transformed to square root (Warr *et al.* 1993) and then analysed using a two-way nested analysis of variance with factor A (forest age-class) fixed, and factor B (replicate plots) as random (Zar 1996). A Tukey test was used to compare the mean of seed bank size among the four forest age-classes.

Seed rain

The seed rain was monitored in the same plots used for the seed bank. Four seed traps (cloth stretched on wood frames) of 1 m^2 were located randomly at 1 m from the ground level in each plot (total of 12 m^2 sampled/forest age-class). The traps were visited every 14 days from 1 April 1993 to 31 March 1994. All visible and healthy seeds were counted and extracted. The ones not identified were grown up in a glasshouse. Animal faeces and assorted fine debris in the traps were placed in a germination camera (FANEM model 347) with a constant temperature of 30°C and light and any seedlings which emerged were counted as present and identified. When intact fruits were recovered, the number of seeds contained within them was counted or was estimated using the average from a sample of fruits of the species. The square root transformed data were analysed by a one-way analysis of variance (Zar 1996) and a Tukey test was used to compare the mean of seed rain among the four forest age-classes. Diversity and similarity were analysed according as described for the seed bank.

Regeneration from seedlings and sproutings

In each of the secondary forest plots studied for seed bank and seed rain, two subplots of 1 m x 5 m (Total of 30 m^2/forest age-class) were laid out randomly and all plants < 5 cm dbh and higher than 1 m were identified and counted and a distinction was made between seedlings and sprouts (vegetative regrowth). Often the plants had to be pulled out or the soil around them had to be removed in order to check the form of regeneration. All plants ≥ 5 cm dbh recovered in the surveys in the same plots (Chapter 6) were also examined for evidence of cutting and resprouting.

Results

Seed bank

The number of germinable seeds m^{-2} of soil was significantly different between the forest age-classes at both depths ($F=19.39$ for 0-5 cm and 30.88 for 5-10 cm; $df=3$, $p< 0.001$). There were no significant differences between the seed bank of the plots inside each forest age-class ($F= 1.06$; $df= 8$; $p= 0.41$, for 0-5 cm; and $F= 0.5$, $df= 8$, $p= 0.85$, for 5-10 cm). The highest number of seeds was found in the 0-5 cm soil of the 5-years-old forest (1190 ± 284 seeds m^{-2}) and decreased with age to 137 ± 19 seeds m^{-2} in the primary forest (Table 27). The density of seeds at the lower depth (5-10 cm) was about half of that found in the top soil (Table 27). Between 30% and 40% of the seeds germinated after 4 weeks (Fig. 23). After turning over the soil at 16 weeks there was a new peak of germination and another decline.

Total seed bank species diversity and richness did not vary much with age between secondary forests nor were they different from primary forest (Table 27). Species numbers found in the top soil (0-5 cm) seed bank were 55, 57 and 63 for the 5, 10 and 20-years-old secondary forests and 44 for the primary forest. For the deeper samples the number of species ranged from 31 to 41 for the secondary forests and was 31 for the primary forest. All the seed species and numbers in the seed bank (0-10 cm) for each forest age-class are shown in Appendix 6.

The most common life form in most forest age-classes was herbs (Tables 28 and 29) but the number of herb seeds decreased as the succession developed: from 77 % in the 5-years-old forest to 40 % of the total seeds in the

Table 27. Mean numbers of seeds ($m^{-2} \pm SE$) at two different depths of soil and the numbers of species and diversity ($30\ m^{-2}$) of the seed bank in 5-years, 10-years, 20-years-old secondary forests and aprimary forest in the Bragantina region, Pará. The mean values followed by different letters in the rows are significantly different according to a Tukey test, $p<0.05$.

	Forest-age class			
Depth	5-years	10-years	20-years	Primary forest
0-5 cm	1190 ± 284a	546.9 ± 42b	450.5 ± 56.7b	137.5 ± 19c
5-10 cm	410.9 ± 78.2a	260.4 ± 6.2ab	162 ± 20.5b	64.1 ± 10.4c
No. of species	60	63	70	54
Species diversity (H')	1.20	1.30	1.42	1.31

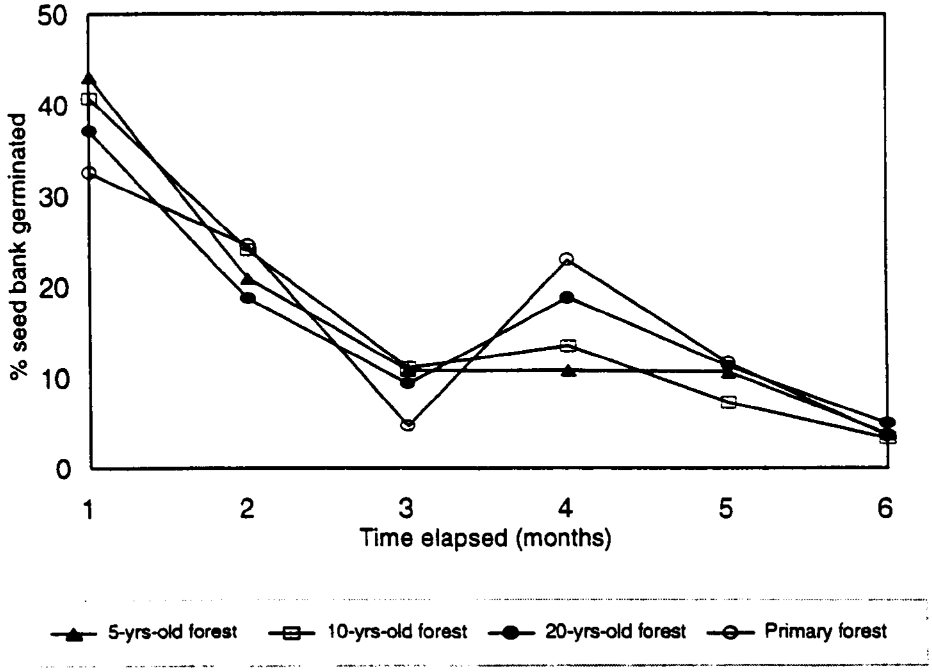

Figure 23. Distribution of germination of all seeds (N=6189) from all soil samples in each forest age-class over 6 months.

Table 28. The percentage of seeds and numbers of species of different life forms found in soil seed banks at 0-5 cm depth in 5-years, 10-years and 20-years-old secondary forests and a primary forest in the Bragantina region, Pará.

	Forest age-class							
	5-years		10-years		20-years		Primary forest	
Life forms	% of seeds	no. of spp.	% of seeds	no. of spp.	% of seeds	no. of spp.	% of seeds	no. of spp.
Epiphyte	0.04	1	0.09	1	4.74	2	0.00	0
Herb	76.95	31	59.50	24	47.86	32	39.77	19
Vine	0.48	4	3.42	7	14.45	6	1.51	2
Shrub	14.83	9	21.10	12	12.14	11	14.78	8
Tree	7.61	8	15.70	11	20.58	12	43.94	15
Unknown	0.09	2	0.19	2	0.23	1	0.00	0
Total	100.00	55	100.00	57	100.00	63	100.00	44

Table 29. The percentage of seeds and numbers of species of different life forms found in soil seed banks at 5-10 cm depth in 5-years, 10-years and 20-years-old secondary forests and a primary forest in the Bragantina region, Pará.

	Forest age-class							
	5-years		10-years		20-years		Primary forest	
Life forms	% of seeds	no. of spp.	% of seeds	no. of spp.	% of seeds	no. of spp.	% of seeds	no. of spp.
Epiphyte	2.92	1	0.00	0	1.29	3	0.00	0
Herb	82.76	18	85.00	22	82.64	25	54.47	17
Vine	0.13	1	0.20	1	0.64	2	0.82	1
Shrub	8.87	5	10.20	5	7.72	6	12.19	3
Tree	5.32	6	4.60	6	7.07	4	32.52	10
Unknown	0.00	0	0.00	0	0.64	1	0.00	0
Total	100.00	31	100.00	34	100.00	41	100.00	31

primary forest. The herb species richness were higher in the secondary forests (24-32 herb species) than in the primary forest (19). On the other hand, the proportion of tree seeds and species increased with forest age (Tables 28 and 29).

The most numerous seed bank species in the secondary forests were the herbaceous *Borreria verticillata* (Rubiaceae) > *Cyperus luzulae* (Cyperaceae) > *Lindernia crustacea* (Scrophulariaceae) > *Borreria latifolia* (Rubiaceae), > the tree *Cecropia palmata* (Moraceae) > the shrub *Clidemia hirta* (Melastomataceae). In the primary forest *Cecropia palmata* > *Clidemia hirta* > the herb *Paspalum conjugatum* (Gramineae) were the most abundant (Tables 30 and 31). *Cecropia palmata* accounted for 25% of the seed bank of the primary forest. Other successional woody species in the primary forest seed bank were: *Casearia decandra, Clidemia hirta, Solanum caavurana, Solanum crinitum, Solanum juripeba, Solanum stramonifolium, Trema micrantha, Vismia guianensis* and *Zanthoxylum rhoifolium*. The tree species *Apeiba burchelii, Conceveiba guianensis, Coussarea ovalis, Didymopanax morototoni, Goupia glabra, Jacaranda copaia, Maprounea guianensis, Ocotea cajumari, Rollinia exsucca, Sapium* sp., and *Sclerolobium paraense* were only found in the soil seed bank of the primary forest and in low densities (< 10 seeds m^{-2}). The species similarity amongst the soil seed banks of the forest age-classes varied from 0.48 to 0.69. As could be expected, similarity was higher for forests adjacent in the chronosequence.

Table 30. Mean numbers of seeds m^{-2} (N) of some common (with at least 45 seeds in all plots combined) species in the seed bank (0-5 cm) of the 5-years, 10-years, and 20-years-old secondary forests and a primary forest in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class. n.o. means not recorded in the sample plots.

	Forest age-class							
	5-years		10-years		20-years		Primary forest	
Species	N	range	N	range	N	range	N	range
Axonopus compressus	2	0-6	n.o.		69	19-144	23	6-37
Borreria latifolia	442	37-900	69	19-137	67	31-87	15	0-25
Borreria verticillata	1052	419-2443	198	56-381	29	12-44	8	0-25
Cecropia palmata	140	62-294	197	19-369	233	162-344	175	137-200
Clidemia hirta	227	175-281	317	281-381	135	81-162	50	25-94
Cyperus luzulae	490	419-620	162	81-219	196	44-356	4	0-6
Gouania pyrifolia	n.o.		4	0-6	179	19-481	n.o.	
Diodia ocimifolia	2	0-6	8	0-25	110	6-269	4	0-6
Irlbachia alata	321	12-706	42	0-100	29	0-87	n.o.	
Jacquemontia hirtiflora	n.o.		44	0-75	60	50-69	2	0-6
Lasiacis ligulata	117	31-269	8	0-12	8	0-19	8	6-12
Lindernia crustacea	492	19-1225	250	0-444	77	37-137	8	0-19
Mariscus flavus	48	6-94	185	56-337	60	44-75	27	12-37
Miconia ceramicarpa	104	6-250	60	0-150	10	6-25	6	0-19
Paspalum conjugatum	37	18-56	37	12-50	67	19-144	31	19-50
Peperomia pellucida	2	0-6	42	0-112	12	0-25	40	0-119
Philodendron sp.	n.o.		n.o.		85	0-256	n.o.	
Pterolepis trichotoma	246	44-450	8	0-25	17	0-31	n.o.	
Scleria secans	50	19-94	37	0-231	27	12-44	n.o.	
Stachytarphetta cayannensis	406	137-819	90	0-231	2	0-6	n.o.	
Vismia guianensis	46	25-75	44	6-88	25	6-62	19	12-25
Zanthoxylum rhoifolium	108	0-325	37	0-81	50	0-81	2	0-6
Other species (85 species)	622		446		454		167	

Table 31. Mean numbers of seeds m^{-2} (N) of some common species (with at least 20 seeds in all plots combined) in the seed bank (5-10 cm) of the 5-years, 10-years, 20-years old secondary forests and a primary forest in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class n.o. means not recorded in the sample plots.

	Forest age-class							
	5-years-old		10-years-old		20-years-old		Primary forest	
Species	N	range	N	range	N	range	N	range
Axonopus compressus	n.o.		27	0-56	37	12-88	19	0-44
Borreria latifolia	185	106-269	71	87-269	35	31-38	2	0-6
Borreria verticillata	273	131-544	119	37-212	6	0-12	4	0-12
Cecropia palmata	71	0-131	23	12-62	35	6-69	29	25-37
Clidemia hirta	127	94-150	98	19-162	37	12-56	27	6-44
Cyperus luzulae	227	131-331	162	81-212	106	44-137	n.o.	
Hymenophillum sp.	48	0-125	n.o.		2	0-6	n.o.	
Irlbachia alata	171	0-444	87	0-169	10	0-31	n.o.	
Lasiacis ligulata	35	12-75	13	6-25	15	6-25	2	0-6
Lindernia crustacea	119	75-200	117	44-219	33	31-37	8	0-12
Mariscus flavus	92	50-150	150	44-250	87	69-119	13	6-25
Miconia ceramicarpa	100	6-225	4	0-6	4	0-12	6	0-19
Paspalum conjugatum	25	19-38	17	12-19	104	81-137	48	12-100
Peperomia pellucida	n.o.	n.o.	27	12-37	35	12-50	8	0-25
Pterolepis trichotoma	52	31-87	29	0-87	n.o.		n.o.	
Scleria secans	10	0-19	27	0-62	4	0-12	n.o.	
Torenia crustacea	50	0-150	n.o.		n.o.		n.o.	
Other species (53 species)	137		116		149		112	

Seed rain

A total of 10,591 seeds of at least 70 species were caught in the seed rain traps in the 5-years-old secondary forests, 6,320 seeds of at least 93 species in the 10-years-old, 6,170 seeds of at least 104 species in the 20-years-old and 2,641 seeds of at least 134 species in the primary forest (Appendix 7). In the secondary forests, from 2% to 6.6% of the seeds remained unidentified and in the primary forest 21.4% of the seeds were unidentified. The mean number of seeds m^{-2} in the seed rain was significantly ($F=2.8$; $df=3$; $p<0.05$) different between the forest age-classes. The highest number of seeds was found in the 5-years-old forest (883 ± 230 seeds m^{-2}), and this value is significantly ($p<0.05$) different from the number of seeds in the primary forest (220 ± 80 seeds m^{-2}) (Table 32). On the other hand, the species richness and diversity were higher in the primary forest (133 species; $H'=1.35$) and lower in the 5-years-old forest (69 species; $H'= 0.91$) (Table 32). The species similarity amongst the seed rain of the secondary forests varied from 0.46 (between 5-years and 20-years-old forests) to 0.51 (between 5-years-old and 10-years-old forests and between 10-years-old and 20-years-old forests) and the species similarity between the seed rain of secondary forests and the primary forest ranged from 0.38 to 0.45, with increasing similarity with age.

The growth forms represented in the seed rain varied with the age of the forest (Table 33). In general, trees dominated the seed rain of all forest age-classes and the contribution of herbs, vines and shrubs was variable. Although most of the seeds were visible, there was a high contribution of small hidden seeds (Table 33), mainly of herbs, that could only be recorded after submitting

Table 32. Mean numbers of seeds ($m^{-2} \pm SE$), numbers of species and species diversity ($12\ m^{-2}$) of seed rain in 5-years, 10-years, 20-years-old secondary forests and a primary forest in the Bragantina region, Pará. The mean values followed by different letters in the rows are significantly different according to a Tukey test, $p < 0.05$.

	Forest-age class			
	5-years	10-years	20-years	Primary forest
Number of seeds	883 ± 230 a	527 ± 122 ab	514 ± 169ab	220 ± 80b
Number of species	70	93	104	134
Species diversity (H')	0.91	1.19	1.09	1.35

Table.33. Distribution of plant life forms among the visible, hidden and total seeds (N) and species (Sp) caught in the seed rain of 5-years, 10-years, 20-years and primary forest in the Bragantina region, Pará. Values are for the total area sampled of 12 m^2 in each age class of secondary forest.

Life-form	5-years-old						10-years-old						20-years-old						Primary forest					
	Visible		Hidden		Total		Visible		Hidden		Total		Visible		Hidden		Total		Visible		Hidden		Total	
	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp	N	Sp
Epiphyte	2	1	1	1	3	2	33	1	6	1	39	1	-	-	-	-	-	-	-	-	4	2	4	2
Herb	34	3	79	13	113	15	90	5	369	10	459	15	46	3	108	13	154	16	30	3	93	18	122	19
Vine	767	7	33	4	800	9	199	6	53	3	252	8	208	4	7	4	215	7	140	8	7	4	147	11
Shrub	2107	3	377	6	2484	8	-	-	691	7	691	7	32	3	154	7	186	9	142	4	69	5	211	8
Tree	5809	20	1175	8	6984	21	3761	23	828	14	4589	32	4200	32	1006	18	5206	44	1299	41	293	24	1593	57
Unidentified	41	13	166	2*	207	15	162	28	128	2*	290	30	286	26	123	2*	409	28	429	35	135	2*	564	37
Total	8760	47	1831	34	10591	70	4245	63	2075	37	6320	93	4772	68	1398	44	6170	104	2040	91	601	55	2641	134

* Almost certainly a substantial underestimate

them to light in a germination camera. However, having done this procedure, many of their seedlings could not be identified to genera or species and the group of unidentified species, although sorted to some extent into taxa, underestimated the species number.

Table 34 reveals that a few species dominated the seed rain in each forest age-class. In the 5-years-old, four species (*Cecropia palmata, Miconia* sp., *Myriaspora* sp. and *Vismia guianensis*) contributed to 71% of all seeds trapped. In the 10-years-old, five species (*Cecropia palmata, Clidemia hirta, Inga* sp., *Vismia guianensis* and *Zanthoxylum rhoifolium*) accounted for 66% of the seed rain. In the 20-years-old, the highest density was achieved by *Cecropia palmata, Didymopanax morototoni, Vismia guianensis* and *Zanthoxylum rhoifolium* which accounted for 70 % of the total seed rain. In the primary forest *Didymopanax morototoni* alone contributed to 35 % of all seeds trapped.

Fig. 24 and Tables 35 and 36 show the monthly variation in both the mean number of seeds m^{-2} and the mean number of species in the seed rain for each forest age-class. The month of the peak catch of seeds varied between the forest age-class. Species composition in the seed rain was very variable during the year, obscuring any phenological pattern in seed-rain diversity. During June, 267 seeds m^{-2} (23 species) were collected for the 5-years-old, 162 (19 species) for the 20-years-old and 55 (30 species) for the primary forest. Another peak of seed fall for the 5-years-old forest was in November (211 seeds m^{-2}; 20 species) and the peak of seeds for the 10- years-old forest was in October (124 seeds m^{-2}; 30 species). In many cases, peaks in seed rain were associated with a high fall of seeds from the species fruiting near the traps. Seeds of Compositae,

Table 34. Mean numbers of seeds m^{-2} (N) of some common species (with at least 50 seeds in all plots combined) in the seed rain of the 5-years, 10-years, 20-years-old secondary forests and a primary forest in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class. n.o. means not recorded in the plots.

	5-yrs-old		10-yrs-old		20-yrs-old		Primary forest	
Species	N	range	N	range	N	range	N	range
Ambelania acida	n.o.		n.o.		n.o.		4.7	0 - 14
Bignoniaceae	n.o.		0.3	0 - 0.5	n.o.		4.3	0 - 12.8
Cecropia palmata	92.75	14.5 - 249.5	68.3	32 - 95	88	28 - 120	8.3	7 - 10
Clidemia hirta	12.5	5.3 - 17.3	51.6	1.5 - 132.3	10	1.5 - 24.8	4.5	1.5 - 6.3
Commelina sp.	0.1	0 - 0.3	1.1	0 - 2.5	2.7	0 - 8	2.4	0 - 7.3
Convolvulaceae	28.3	0 - 84.5	1	0 - 2.5	n.o.		n.o.	
Cordia sp.	n.o.		2.9	0 - 8.8	1.9	0 - 5.8	0.1	0 - 0.3
Croton matourensis	n.o.		n.o.		12	0 - 35	n.o.	
Didymopanax morototoni	0.1	0 - 0.3	0.3	0 - 0.5	57.9	1.3 - 170.3	78	1.3 - 230.3
Ficus sp.	n.o.		22	0 - 66	n.o.		8.5	0 - 25.3
Gouania pyrifolia	28.1	0 - 84.3	9.8	0 - 29.3	14.9	0.5 - 42.3	0.3	0 - 0.8
Inga sp.	0.4	0 - 1.3	31.5	0.3 - 51.3	0.2	0 - 0.3	0.1	0 - 0.3
Lacistema pubescens	27.2	6.8 - 52	14.6	0.8 - 35.5	0.8	0 - 1.5	3.7	1 - 8.8
Lacmellea aculeata	n.o.		n.o.		8.3	0 - 24.8	0.1	0 - 0.3
Leguminosae	n.o.		2.4	0 - 6.3	0.4	0 - 1	4.6	0 - 13.8
Mabea angustifolia	1.7	0 - 5	0.4	0 - 1.3	2.4	0.3 - 4.3	n.o.	
Maprounea guianensis	n.o.		n.o.		6.1	0 - 18.3	n.o.	
Miconia ceramicarpa	1.3	0 - 3	25.8	0.8 - 75.3	2.2	0.5 - 4	3.4	1.3 - 6
Miconia minutiflora	93	0 - 265.5	12.8	0.5 - 36.8	21	3 - 54.5	3.7	2.3 - 5.8
Miconia sp.	86	0 - 188	n.o.		2.2	0 - 6.5	n.o.	
Mikania banisteriae	4.4	0 - 13.3	n.o.		n.o.		n.o.	
Morph 08*	3.1	0 - 9.3	1.6	0 - 2.5	0.3	0 - 1	0.5	0 - 1.5
Morph 34	n.o.		n.o.		11.4	0 - 34.2	n.o.	
Morph 65	n.o.		0.2	0 - 0.5	0.5	0 - 1.5	13.5	0.5 - 20.8
Myriaspora sp.	89.7	0 - 269	n.o.		0.5	0 - 1.5	n.o.	
Paullinia pinnata	n.o.		4.1	0 - 9.3	0.1	0 - 0.3	n.o.	
Piper aduncum	16.8	0.3 - 50	10.8	0.8 - 8.8	1.2	0 - 2	0.8	0 - 2
Psychotria sp.	n.o.		3.2	0 - 5.8	2.8	0 - 7.3	0.5	0 - 1.5
Rollinia exsucca	0.1	0 - 0.3	0.3	0 - 0.8	8.7	0 - 25.8	0.3	0 - 1
Sabicea sp.	4.7	0 - 13.5	n.o.		n.o.		n.o.	
Serjania sp.	n.o.		5.2	0.3 - 15	1.3	0 - 2.3	1.3	1 - 1.5
Siparuna guianensis	0.1	0 - 0.3	9.4	0 - 28.3	0.3	0 - 0.8	0.2	0 - 0.5
Solanaceae	n.o.		n.o.		n.o.		8.8	0 - 26.3
Tapirira guianensis	n.o.		14.6	0 - 43.3	3.5	1 - 7	0.8	0 - 2.5
Virola sebifera	1.2	0 - 3	0.2	0 - 0.5	0.6	0 - 1.8	2.3	0 - 6.8
Vismia guianensis	360.3	151.5 - 647.5	115	36.3 - 269	58.9	2.5 - 157.8	2.8	1.5 - 3.5
Zanthoxylum rhoifolium	n.o.		80	0 - 240	156	0.3 - 465	n.o.	
Other species (195 species)	35.53		37.27		37.06		61.58	

* Morph is used for each separate but unidentified taxon

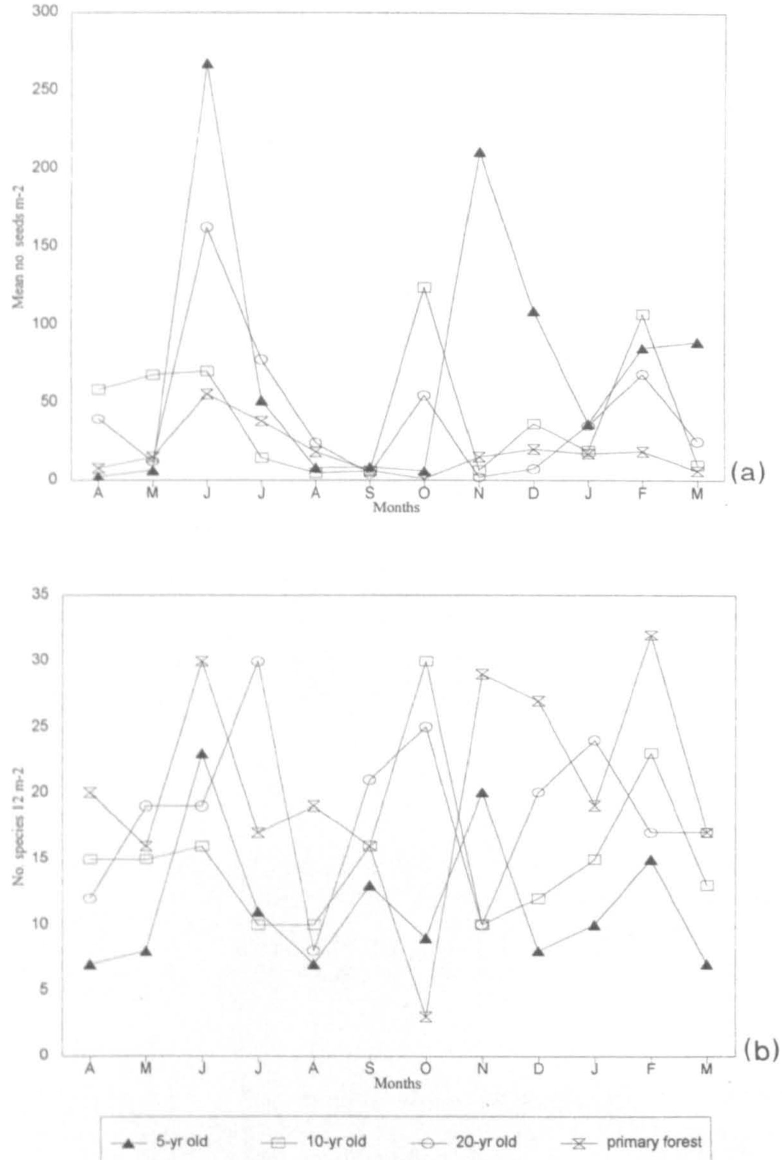

Figure 24. (a) Changes in the mean number of seeds m^{-2} $month^{-1}$ in the seed rain in the 5-years, 10-years, 20-years-old secondary forests and primary forest. (b) Changes in the number of species of seeds in the seed rain 12 m^{-2} $month^{-1}$ for each forest age-class.

Table 35. Mean numbers of seeds m^{-2} (N) per month in the seed rain of the 5-years, 10-years, 20-years-old secondary forests and a primary forest in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class.

	Forest age-class							
	5-years		10-years		20-years		Primary forest	
Month	N	range	N	range	N	range	N	range
April	2.5	0.7 - 4.5	58.4	3 - 168.5	39.4	5.8 - 88	7.7	1.8 - 15.8
May	6.4	1.7 - 14.5	67.9	1.7 - 130	12.5	7.8 - 19	15	0.8 - 41.5
June	267.2	22.5 - 29	70.3	1.2 - 111	162.3	28 - 416	55.2	4.2 - 144
July	51.3	20.8 - 95	14.6	0.3 - 36	77.7	7.5 - 6.5	38	1.5 - 111
August	8.4	2 - 19.5	4.9	1.3 - 10.3	24.3	0 - 51.5	18.5	3 - 45.3
September	9.0	1 -23.5	6.0	5.3 - 6.5	4.5	1.3 - 9	6.4	3 - 10
October	6.3	1.5 - 13.5	124.4	36.2 - 177	54.8	0.8 - 140	1.1	0 - 1.7
November	210.9	20.3 -467	6.7	0.5 - 16.7	2.1	0.5 - 5.3	15.4	12.7 - 19
December	109.3	5 - 199	36.6	0.3 - 107	7.8	5.7 - 12	20.3	13.2 - 33
January	36.4	13.3 - 71	19.1	0.3 - 28.5	35.3	3.8 - 60	17.3	8.5 - 26
February	85.6	61 - 122	107.2	82 - 132.5	68.4	6 - 130	18.7	10.7 - 27
March	89.3	2 - 263	10.4	3 - 21.7	25	6.7 - 51	6.5	1.3 - 13

Table 36. Mean numbers of species of seeds 12 m^{-2} (N) per month in the seed rain of the 5-years, 10-years, 20-years-old secondary forests and a primary forest in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class.

	Forest age-class							
	5-years		10-years		20-years		Primary forest	
Month	N	range	N	range	N	range	N	range
April	7	2 - 4	15	2 -11	12	5 - 6	20	3 - 14
May	8	3 - 4	15	4 -10	19	4 - 9	16	1 - 13
June	23	6 - 12	16	2 -12	19	6 - 11	30	6 - 16
July	11	2 - 7	10	1 - 6	30	3 - 18	17	4 - 13
August	7	2 - 3	10	1 - 6	8	0 - 6	19	3 - 10
September	13	3 - 6	16	3 - 10	21	2 - 14	16	3 - 10
October	9	2 - 4	30	7 - 24	25	2 - 19	3	0 - 3
November	20	8 - 12	10	2 - 8	10	1 - 8	29	11 - 16
December	8	3 - 3	12	1 - 6	20	5 - 9	27	9 - 16
January	10	3 - 6	15	1 - 10	24	4 - 15	19	6 - 12
February	15	6 - 9	23	10 -13	17	7 - 11	32	9 - 20
March	7	1 - 5	13	5 - 11	17	8 - 12	17	4 - 9

Melastomataceae and Piperaceae were common throughout the year and were mostly in the debris and faeces in the traps. Species of these last three families produce very small seeds and are dispersed mainly by birds and bats. Of the fruits of 108 species that was caught in the seed rain of the secondary forests 63 (58%) had fleshy or arillate fruits and 45 species (42%) had dry capsular fruits. Species with fleshy or arillate fruits are dispersed mainly by birds and bats (Swaine & Hall 1983) while capsular ones can have wind or self dispersal.

Regeneration from seedlings and sproutings

In the 5-years-old forest 300 individuals of 63 species and 33 families of small (> 1 m tall, < 5 cm dbh) woody plants were found on the six 5 m^2 areas sampled. In the 10-years-old forest the corresponding values were 548 individuals, 68 species and 37 families and in the 20-years-old forest 478 individuals, 66 species and 37 families (Appendices 8, 9 and 10). In the 5-years-old forest 46% of the small woody plants and 49% of the species were classified as seedlings and 54% of the individuals and 51% of the species were sprouts (Fig. 25). In the 10-years and 20-years-old forests, seedlings predominated in terms of individuals (80.6% to 81.8%) and species (65% to 78%) (Fig. 25). A check of larger plants (≥ 5 cm dbh) showed that individuals and species regenerated from sprouts were more abundant than those regenerated from seeds in all forest age-classes (Fig. 25). The most common life form in the forest age-classes of the smaller individuals were trees (60%-73%). Half of the trees

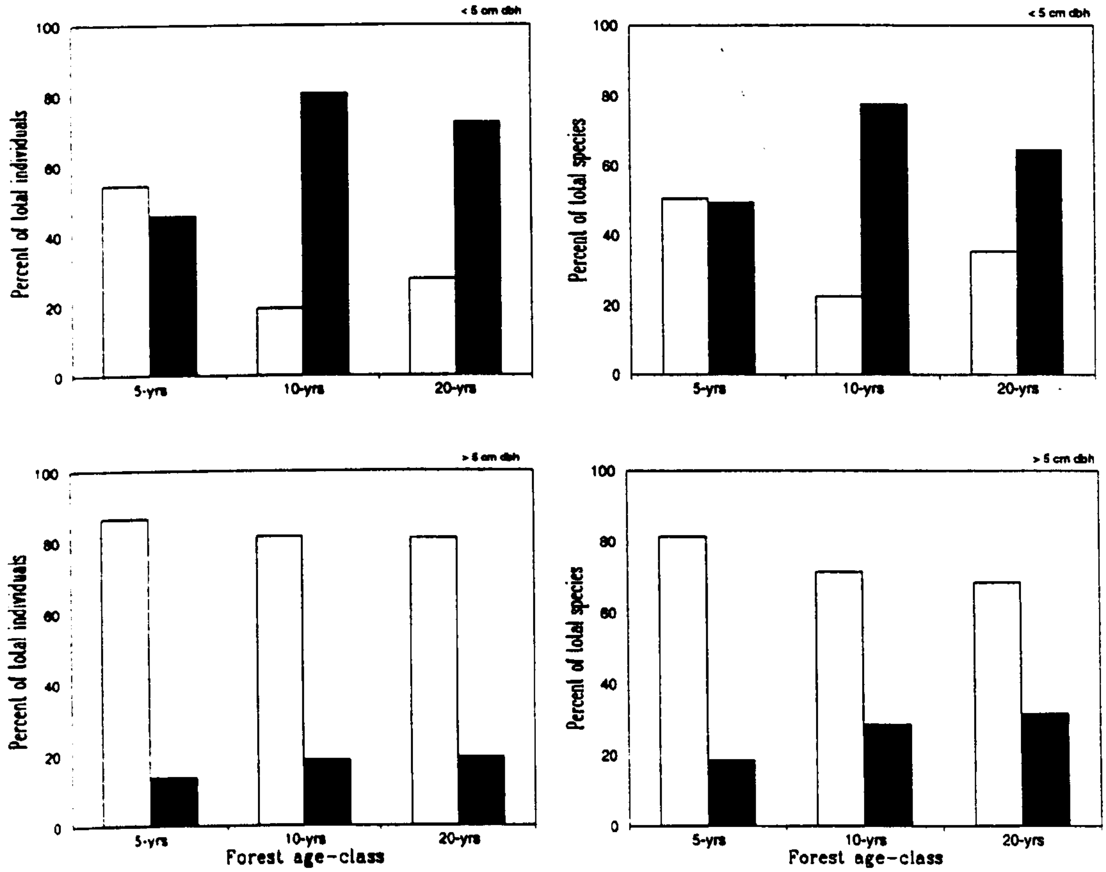

Figure 25. Percentage of total individuals and species regenerating from seedlings and sprouts in six replicate each of 5 m^2 (for individuals ≥ 1 m tall, < 5 cm dbh) and in each of three replicates of 250 m^2 (for individuals ≥ 5 cm dbh) in the 5-years, 10-years and 20-years-old secondary forests in the Bragantina region, Pará. The open histograms refer to sprouts and the solid histograms refer to seeds.

found in the 5-years-old forest were seedlings and half were sprouts and in the 10-years and 20-years-old about 60% of the trees were seedlings (Fig. 26).

Abundance and diversity of seedlings

The mean number of seedlings m^{-2} (≥ 1 m tall, < 5 cm dbh) were not significantly different ($F = 2.7$, df= 2, $p= 0.146$) between the forest age-classes (Table 37). The same is the case for the mean number of species ($F = 1.53$, df = 2, $p = 0.291$). For individuals ≥ 5 cm dbh there was a significant difference between forest age-class only for the mean number of species ($F= 5.06$; df=2; $p< 0.05$) (Table 38). The highest mean number of seedling species was found in the 10-years and 20-years-old forests (4.7 and 6.3 seedling species m^{-2}, respectively), and these values were significantly different ($p<0.05$) from the 5-years-old forest (1.7 seedlings species m^{-2}) (Table 38).

The seedlings in the 5-years-old forest belonged to 36 species (Appendix 8) and the most abundant were the trees *Rourea amazonica* (1.4 seedlings m^{-2}) and *Lacistema pubescens* (0.5 seedlings m^{-2}) and the herb *Psychotria colorata* (0.4 seedlings m^{-2}) (Table 39). In the 10-years-old forest there were 18 species of seedlings and in the 20-years-old forest there were 23 species (Appendices 9 and 10). The most abundant seedlings in the 10-years-old forest were the shrub *Myrcia bracteata* (7.1 m^{-2}) and the herbs *Pariana* sp. and *Scleria secans* (0.6 m^{-2}) and in the 20-years-old forest the most abundant seedlings were *Inga* sp. (3.2 m^{-2}) and *Myrcia bracteata* (1.6 m^{-2}) (Table 39). Species diversity were low in each forest age-class and did not vary much with age. The values of Shannon-

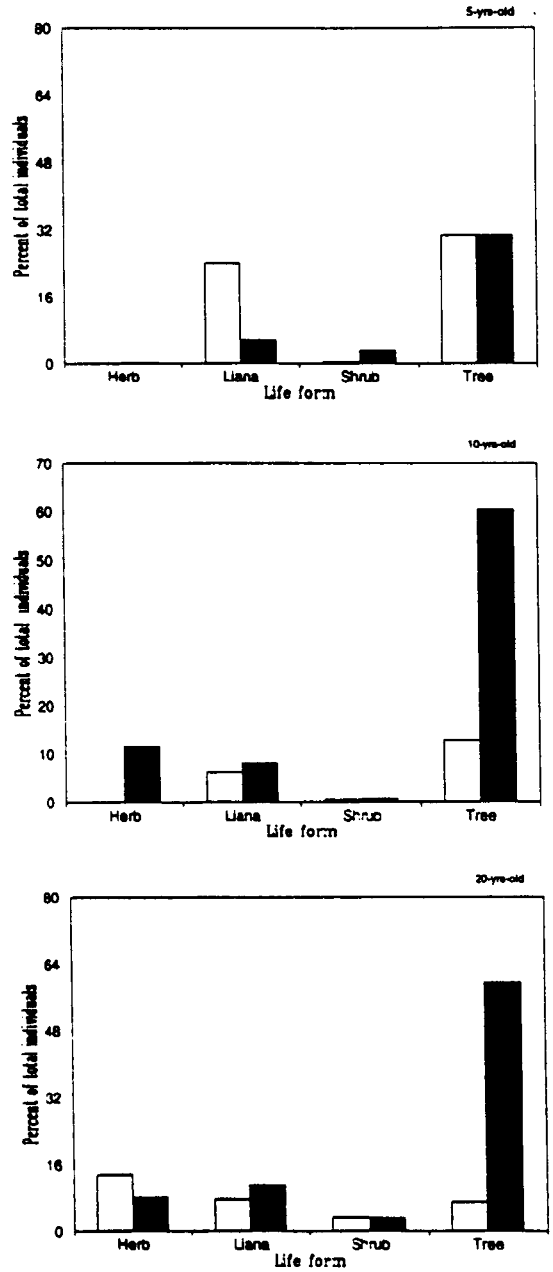

Figure 26. The percentage distribution of life forms among the individuals (≥ 1 m tall, < 5 cm dbh) regenerating from seedlings and sprouts in six replicates of 5 m^2 in the 5-years, 10-years and 20-years-old secondary forests in the Bragantina region, Pará. The open histograms refer to sprouts and the solid histograms refer to seeds.

Table 37. Mean numbers (with ranges in parentheses) of individuals and species of seedlings and sprouts m^{-2} of woody plants (≥ 1m tall, < 5 cm dbh) in six replicates of 5 m^2 in the 5-years, 10-years, 20-years-old secondary forests in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class.

	Individuals		Species	
Forest age-class	Seedlings	Sprouts	Seedlings	Sprouts
5-years-old	4.6 (1.4 - 7.5)	5.4 (4.3 - 6.1)	1.5 (0.5 - 2.1)	1.5 (1.2 - 2.0)
10-years-old	14.7 (7.7 - 25.5)	3.5 (0 - 7.5)	2.3 (2.0 - 2.5)	0.7 (0 -1.1)
20-years-old	11.5 (6.6 - 16.4)	4.4 (2.9 - 5.6)	2 (1.6 - 2.4)	1.1 (0.9 - 1.5)

Table 38. Mean numbers (with ranges in parentheses) of individuals and species of woody plants ≥ 5 cm dbh which had regenerated from seeds and sprouts in three replicates of 250 m^2 in the 5-years, 10-years, 20-years-old forests in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class. The mean values followed by different letters in the columns are significantly different according to Tukey test, $p < 0.05$.

	Individuals		Species	
Forest age-class	From seeds	From sprouts	From seeds	From sprouts
5-years- old	3.3 (1 - 7)a	21.3 (10 - 34)a	1.7 (1 - 3) a	7.3 (5 - 10) a
10-years-old	7.3 (3 - 10)a	32.3 (21 - 44)a	4.7 (2 - 6) b	11.7 (11 - 12) b
20-years-old	9.0 (5 - 13)a	38.0 (32 - 44)a	6.3 (4 - 8) b	13.7 (13 - 15) b

Table 39. Mean numbers of seedlings and sprouts m^{-2} of some common woody species ≥ 1 m tall, < 5 cm dbh (with at least 8 individuals in all plots combined) in the 5-years, 10-years and 20-years old forests in the Bragantina region, Pará. The ranges are for the values in the three plots in each forest age-class. n.o. means not recorded or less than 8 individuals recorded in all plots combined.

	5-years-old				10-years-old				20-years-old			
	seedlings		sprouts		seedlings		sprouts		seedlings		sprouts	
Species	N	range	N	range	N	range	N	range	N	range	N	range
Arrabidaea sp.	0.03	0-0.1	0.03	0-0.1	0.1	0-0.3	n.o.		0.43	0-1.3	n.o.	
Bernardinia fluminensis	0.03	0-0.1	n.o.		0.1	0-0.3	n.o.		0.23	0-0.7	n.o.	
Calyptranthes cf. *bipenis*	0.03	0-0.1	0.3	0-0.9	n.o		n.o.		n.o.		n.o.	
Cassipourea guianensis	n.o.		0.03	0-0.1	n.o		n.o.		0.03	0-0.1	n.o.	
Davilla kuntii	n.o.		1.03	0.4-2.2	0.53	0-1	0.43	0-0.9	0.13	0-0.4	0.36	0.3-0.4
Diodia sp.	0.03	0-0.1	n.o.		n.o.		n.o.		0.26	0-0.8	n.o.	
Gustavia augusta	n.o.		0.27	0-0.8	0.1	0-0.3	0.23	0-0.7	n.o.		n.o.	
Heisteria acuminata	n.o.		0.17	0-0.5	n.o		n.o.		0.13	0-0.3	n.o.	
Inga edulis	0.06	0-0.2	0.13	0-0.3	n.o.		n.o.		0.4	0-1.1	n.o.	
Inga sp.	n.o.		n.o.		n.o.		n.o.		3.2	0-9.6	n.o.	
Inga thibaudiana	n.o.		n.o.		0.4	0-0.9	0.36	0-1.1	0.23	0-0.3	n.o.	
Lacistema aggregatum	0.13	0-0.4	n.o.		n.o.		n.o.		n.o.		0.23	0-0.5
Lacistema pubescens	0.5	0-1.5	0.1	0-0.3	0.27	0.1-0.5	n.o.		0.2	0-0.4	0.1	0-0.3
Machaerium madeirense	n.o.		0.17	0-0.5	n.o.		0.06	0-0.2	n.o.		0.1	0-0.3
Memora flavida	0.06	0-0.2	0.13	0-0.3	n.o.		n.o.		0.27	0-0.8	0.03	0-0.1
Memora magnifica	n.o.		0.37	0-1.1	n.o.		n.o.		n.o.		0.13	0-0.2
Myrcia bracteata	n.o.		0.7	0-2.1	7.1	0.8-17.4	n.o.		1.6	0.6-3.6	n.o.	
Myrcia floribunda	0.13	0-0.4	0.13	0-0.4	n.o.		0.03	0-0.1	0.1	0-0.3	0.1	0-0.3
Myrciaria tenella	0.06	0-0.2	0.13	0-0.4	n.o.		n.o.		0.6	0-2	n.o.	
Panicum pilosum	0.13	0-0.4	n.o.		0.5	0-1.1	n.o.		n.o.		n.o.	
Pariana sp.	n.o.		n.o.		0.6	0-1.9	n.o.		0.27	0-0.8	n.o.	
Protium trifoliolatum	n.o.		n.o.		n.o.		n.o.		0.3	0-0.9	n.o.	
Psychotria colorata	0.4	0-0.7	n.o.		0.53	0-1.5	n.o.		0.27	0.2-0.8	n.o.	
Rourea amazonica	1.37	0-3.9	0.03	0-0.1	0.2	0-0.5	1.37	0-4.1	0.23	0-0.7	n.o.	
Rourea ligulata	n.o.		n.o.		0.5	0-1.5	n.o.		n.o.		n.o.	
Scleria secans	0.13	0-0.4	n.o.		0.6	0-1.8	n.o.		0.16	0-0.5	n.o.	
Smilax schomburgkiana	n.o.		0.23	0-0.7	0.1	0-0.3	0.36	0-1.1	n.o.		n.o.	
Tabebuia serratifolia	0.17	0-0.4	0.3	0-0.9	n.o.		no.		n.o.		n.o.	
Tabernaemontana angulata	0.03	0-0.1	n.o.		n.o.		n.o.		0.43	0-1.1	0.46	0-1.4
Trichilia micrantha	n.o.		n.o.		0.1	0-0.3	n.o.		0.37	0-0.6	n.o.	
Trichilia sp.	n.o.		n.o.		0.83	0-2.5	n.o.		0.06	0-0.2	n.o.	
Other species (99 species)	2.11		0.35		2.14		0.66		1.60		1.09	

Wiener indices were: 1.29 for the 5-years-old forest, 0.90 for the 10-years-old forest and 1.12 for the 20-years-old forest.

Abundance and diversity of sprouts

The mean numbers of sprouts m^{-2} ($\geq$ 1 m tall, < 5 cm dbh) were not significantly different ($F= 0.77$, $df= 2$, $p= 0.503$) between the forest age-classes. The same is the case for the mean number of species ($F= 1.83$, $df= 2$, $p= 0.240$). For individuals $\geq$ 5 cm dbh there was a significant difference between forest age-class only for the mean number of species ($F= 10$, $df= 2$, $p< 0.01$). The highest mean number of sprouting species was found in the 10-years and 20-years-old forests (11.7 and 13.7, respectively) (Table 38).

In the 5-years-old forest, there were 36 sprouting species (Appendix 8) and the most abundant species were the liana *Davilla kuntii* (1.0 sprout m^{-2}) and the shrub *Myrcia bracteata* (0.7 sprouts m^{-2}) (Table 39). Nine species (*Arrabidaea* sp., *Chrysophyllum sparsiflorum, Inga edulis, Lacistema pubescens, Memora flavida, Myrcia floribunda, Myrciaria tenella, Rourea amazonica* and *Tabebuia serratifolia*) were found as seedlings and sprouts. In the 10-years-old there were 58 sprouting species (Appendix 9) and in the 20-years-old forests there were 48 species (Appendix 10). Eight species in each of these two forests had both seedlings and sprouts. The most abundant sprouts in the 10-years-old were of *Rourea amazonica* (1.4 m^{-2}) and in the 20-years-old forests the most abundant sprouts was *Tabernaemontana angulata* (0.46 m^{-2}) (Table 39). The species diversity was low in each forest age-class and the Shannon-Wiener indices were: 1.19 for the 5-years forest, 1.04 for the 10-years and 1.27 for the 20-years-old forests.

Discussion

Seed bank

Some studies (Guevara & Gomez-Pompa 1972; Uhl *et al.* 1981; Putz 1983; Swaine & Hall 1983) showed that soil seed banks are important in the early stages of succession in the tropics but few data are available to assess temporal changes of the seed banks. In this study, the broad successional trend in the seed bank was a density peak at an early stage (5-years) followed by a decline to the lowest density in the primary forest. Guevara & Gomez-Pompa (1972) found the highest density of seeds in the soil seed bank of Veracruz, Mexico in a 5-years-old secondary forest. They took samples at 45 days intervals and found that seed density ranged from 1982 to 4051 m^{-2} compared with primary forest that ranged from 344 to 862. In Young *et al.*'s (1987) model the density of seeds in the soil began to increase after 12 weeks of deforestation, the soil seed densities had a peak after 4 to 7 years and then declined as some seeds lost their viability. Uhl (1987) found a marked decline in seed bank density during succession in San Carlos, Venezuela. In contrast, Rico-Gray & Garcia-Franco (1992) found no apparent successional trends in forest seed banks in Yucatan, Mexico while Abdulhadi & Lamb (1988) found higher density and species richness in the seed banks of old secondary forests (> 20 years) than mature forest or of 2-years-old secondary forests in Australia. Chandrashekara & Ramakrishnan (1993) found a significant increase in soil seed bank with gap age in Kerala, India.

The seed banks of the primary forest studied here were within the range (55-860 seeds m^{-2}) reported in forest seed banks from other tropical rain forests

(Guevara & Gomez-Pompa 1972; Hall & Swaine 1980; Uhl *et al.* 1981, 1982a; Putz 1983; Uhl & Clark 1983; Putz & Appanah 1987; Chandrashekara & Ramakrishnan 1993) and were mainly of woody pioneers. Seed banks are larger in the soils of secondary regrowth and disturbed agricultural sites, and mainly of forbs and grasses (Young *et al.* 1987; Garwood 1989; Skoglund 1992). The number of species found in the Bragantina primary forest (54 species) and secondary forests (60 - 70 species) were within the range reported by these authors (4 - 79 for primary forest and 8 - 67, for secondary forest or farms), but Garwood (1989) pointed out that in the primary forests the number of species significantly increases as total area sampled increases whereas in secondary forests it does not.

Forest disturbance can affect the size and composition of the successional woody species seed bank. Ewel *et al.* (1981) and Uhl *et al.* (1981) showed that forest burning reduces seed bank size and Saulei & Swaine (1988) found an initial depletion in soil seed bank after clearance of a primary forest in Papua New Guinea. When burned sites are farmed there is a predominance of herbs that have a short life and can produce seeds locally (Uhl & Clark 1983). This study and others (Young *et al.* 1987; Saulei & Swaine 1988) showed that as the secondary succession developed, however, the woody colonisers gradually increased in the seed bank and predominated in later stages.

In general, there is a decrease in seed density and number of species with depth (Putz 1983; Garwood 1989). In Bragantina, the lower depth (5-10 cm) had almost half of the number of seeds and 65% of the number of species compared with the 0-5 cm depth (Tables 27 and 28). Some species are more abundant near the surface, others in deeper layers, while some show an almost uniform distribution. Differences in the depth profile of the seed bank within and between sites have been attributed to differences in forest soil texture, cultivation history of field and successional changes in seed rain (Garwood 1989).

I observed that most of the species found in the seed bank had very small seeds (range 0.001 - 0.4 g; N= 19). According to Whitmore (1983) seeds with the ability to stay viable for a long time in the soil tend to be small and the group of species with persistent seed banks produce large numbers of well-dispersed seeds that have the capacity to remain dormant indefinitely. Mechanisms of dormancy for most pioneer species are unknown but for some, germination tests showed that there are precise light and temperature requirements (Vazquez-Yanes 1980). The abundant pioneer *Cecropia palmata*, (seed weight = 0.0021 g; c. 3000 seeds per infrutescence), had high germination in the light (89%) and no germination in the dark (I.C.G. Vieira *et al.* 1996b). By contrast, the pioneer *Vismia guianensis* (seed weight = 0.001 g; c. 130 seeds per fruit) showed low germination in the light (13%) and no germination in the dark. Uhl & Clark (1983) reported high germination (> 75%) for some pioneer species such as *Cecropia ficifolia, Vismia lauriformis,* and *Solanum stramonifolium* in light treatments.

From the 96 species found in the seed bank of the secondary forests up 20-years-old, 14 were trees and among them only four were pioneer species that also occurred in the primary forest (*Annona densicoma, Casearia decandra, Cecropia palmata, Croton matourensis)* and two were shade-bearing (*Neea* sp. and

Trichilia sp.). By comparison, only two pioneer tree species were found in the seed bank of degraded pastures near Paragominas, Pará (Nepstad *et al.* 1996b) and the same number in a 5-years-old secondary forest in Bragantina (Denich 1991). In common with other published results (Rico-Gray & Garcia-Franco 1992) there was relatively little similarity between the established vegetation and the seed bank. From the total of 140 tree species (≥ 5 cm dbh) recorded from the secondary forest plots (Chapter 6) only 14 occurred in the seed bank (*Banara guianensis, Casearia decandra, Casearia grandiflora, Cassia fastuosa, Cecropia palmata, Croton matourensis, Lacistema pubescens, Mabea angustifolia, Miconia minutiflora, Myriaspora egensis, Neea* sp., *Trema micrantha, Vismia guianensis,* and *Zanthoxylum rhoifolium*). This shows that the majority of tree species do not accumulate seeds in the soil and that the seed bank must make a limited direct contribution to the tree regeneration during the shifting cultivation succession in the Bragantina region.

Seed rain

The quantification of seed rain has scarcely been reported for tropical successional vegetation in spite of its importance (Young *et al.* 1987). In this study more seeds were collected from secondary forests than in primary forest (883, 527 and 514 seeds m^{-2} $year^{-1}$ for 5-years, 10-years and 20-years-old secondary forests respectively and 220 seeds m^{-2} $year^{-1}$ for primary forest). Young *et al.* (1987) found the same pattern but reported values much higher for secondary forests of 3 and 11-years-old (3366-3700 seeds m^{-2} $year^{-1}$ respectively) and for primary forest (1233 seeds m^{-2} $year^{-1}$). In Bragantina I found that the number of species increased with succession (from 70 species in the 5-years-old forest to 134 in the primary forest) but Young *et al.* (1987) reported that more species were trapped in the young vegetation than in the primary forest (75 vs 48), but they used only half as much trap surface area in the primary forest. The high proportion of vine and herb species in the seed rain of the Bragantina primary forest was probably due to the closeness of agricultural sites. Some studies dealing with seed rain were conducted in tree-fall gaps (Denslow & Gomez Diaz 1990; Martinez-Ramos & Soto-Castro 1993) or beneath the canopies of isolated trees (Guevara *et al.* 1986; Guevara & Laborde 1993; Vieira *et al.* 1994; Nepstad *et al.* 1996b). In building-phase forest patches, 48 species were found in the seed rain in a 8-years-old treefall gap, 51 species in a 20-years-old gap and 42-50 species in mature forest patches (Martinez-Ramos & Soto-Castro 1993). Augspurger & Franson (1988) found that the mean diversity of wind-dispersed species was not significantly different between gaps and forest sites (average of 10 species in both gaps and forest). The density of wind-dispersed seeds in the gaps was 328 seeds m^{-2}, and in the forest sites 207 seeds m^{-2}. Denslow & Gomez Diaz (1990) reported 588 seeds m^{-2} $year^{-1}$ in tree fall gaps in Costa Rica and she pointed out that these seeds may have originated from the early successional vegetation bordering the forest. Some studies showed that the deposition of seeds is concentrated under plants that serve as perch or feeding for animals. Nepstad *et al.* (1996b) found four hundred times more seeds fell into traps placed beneath woody plants in an abandoned pasture in eastern Amazônia than in the traps placed in the open. This large difference was associated with the presence of birds and bats attracted by the abundant fleshy fruiting of the isolated trees. Vieira *et al.* (1994) described a similar phenomenon of direct dispersal beneath the shrub *Cordia multispicata* which also produced fleshy fruits. In Mexican abandoned pastures there were 710 seeds m^{-2} beneath the canopies of four isolated standing trees (Guevara & Laborde 1993).

Immediately after clearing a site, all the seed rain is allochthonous, as the vegetation recovers, autochthonous seeds contribute to the seed rain (Young *et al.* 1987). The relative abundance in the seed rain of trees and other life forms varied between forest age-classes but trees contributed 66% to 84% of the total seeds and 30% to 43% of the species in secondary forests and 61% of total seeds and 44% of the species in primary forest (Table 33). Species with fleshy and arillate fruits dominated the seed rain of the secondary forests. Most wind and self dispersed seeds were vines and herbs, but some large pioneers and mature species had this mode of dispersal. The most common trees in the seed rain of the secondary forests were already present in the community: *Cecropia palmata, Lacistema pubescens, Miconia minutiflora, Tapirira guianensis* and *Vismia guianensis.* However, a few tree species found in the seed rain, in low densities, came from the primary forest, especially the wind-dispersed species *Chaunochiton klaperi* and *Erisma uncinatum* and the species *Cecropia obtusa, Inga alba, Laetia procera, Nectandra globosa, Pouroma palmata, Saccoglotis guianensis, Trichilia* sp., and *Virola sebifera* which were found in faeces in the traps and probably were carried by bats or birds. In the primary forest most of the tree seed species trapped were pioneers such as *Cecropia palmata, Clidemia hirta and Didymopanax morototoni* or species with abundant fruits in the canopy. In the forests of San Carlos, Venezuela where there were fewer pioneer seeds in the annual seed rain than in the upper 4-5 cm of the soil, seed rain probably accounts for only a small proportion of regeneration after disturbance (Uhl & Clark 1983). However seed rain was more important in young regrowth in a study in Costa Rica because the number of seeds in the annual seed rain was equal to or greater than that in the soil (Young *et al.* 1987).

Regeneration from seedlings and sproutings

Sprouting from stems and roots has been reported to be a common means of regeneration among tropical forest species following disturbance (Uhl *et al.* 1988; Putz & Brokaw 1989; Kauffman 1991) but the dynamics and structure of successional vegetation depend on the availability of various potential sources of colonisation (Noble & Slatyer 1980). In a shifting cultivation system, such as is practised in Bragantina the majority of cleared fields are cultivated immediately after burning, i.e. without removal of the stumps. As a result when the farms are left for fallows, the reproductive potential of the seed bank and of sprouting from stumps of woody species is high. Results of the field determination of the mode of propagation showed that the secondary forest flora consists of those species that sprout following cutting and burning, and those that are able to arrive by seed. From 81% to 86% of individuals and from 68% to 81% of the species ≥ 5 cm dbh arose predominantly from sprouts (Fig. 25). The smaller individuals in the secondary forests (≥ 1m tall, < 5 cm dbh) arose predominantly from seed, both in terms of number of individuals and number of species, with the exception of the 5-years-old forest (Fig. 25).

These data suggest that the secondary forests are initially composed of sprouting plants, with new plants arriving from seed as the secondary forests age. The percentage of sprouting plants < 5 cm dbh in the youngest forest was high because these sprouts had not yet advanced to the larger size category. Uhl *et al.* (1982a) working at San Carlos, Venezuela, found in a 3-years-old secondary forest that 54% of the individuals were sprouts and only 17% were sprouts in a 5-years-old forest in the same area (Uhl & Jordan 1984). Earlier work at San Carlos had shown that sprouting from cut stumps was the most common means of regeneration after forest cutting (Uhl *et al.* 1981). They found 6.37 sprouts m^{-2} vs only 0.95 seedlings m^{-2}. In Denich's (1991) studies in 5-years-old forests in the Bragantina region he found that the majority of individuals sprouted and the mean number of seedlings was 15 ± 8 m^2. Gorchov *et al.* (1993) found 1.79 seedlings m^{-2} and 0.46 sprouts m^{-2} in a rain forest after strip-cutting in the Peruvian Amazon.

Many species regenerated in the secondary forests only from seeds (44 species) or only from sprouts (48 species), while some (29) had both modes of propagation (Table 40). The sprouts can disappear from the fallow vegetation with the death of the vegetative plants, while seedlings have a chance to remain in the vegetation. Another important feature is that sprouts can rapidly cover the ground but seedlings have the highest growth rates (Stocker 1981). In an Australian rain forest Stocker (1981) found that by 23 months after burning, 82 tree species were present, 84 as shoots and 34 as seeds. Uhl *et al.* (1981) found that fire killed many sprouts in Venezuela and strongly reduced vegetative regrowth. Reduced species numbers were found in secondary forest on burned

Table 40. Tree species, with their mode of regeneration, occurring in the secondary forests (six 5-m^2 plots for plants < 5 cm dbh and three 250-m^2 plots for plants ≥ 5 cm dbh) of 5, 10 and 20-years-old combined for each dbh class in the Bragantina region, Pará.

Only from seeds	Only from sprouts	From seeds and sprouts
≥ 5 cm dbh	**≥ 5 cm dbh**	**≥ 5 cm dbh**
Brosimum guianensis	Andira retusa	Bauhinia jarensis
Byrsonima aerugo	Annona paludosa	Casearia pitumba
Cecropia distachya	Astrocaryum vulgare	Cordia scabrifolia
Cecropia palmata	Banara guianensis	*Croton matourensis
Jacaranda copaia	Bauhinia jarensis	Inga edulis
Maximiliana maripa	Casearia arborea	Lacistema pubescens
Ocotea glomerata	Casearia grandiflora	*Mabea angustifolia
Swartzia laurifolia	Cassia fastuosa	Myrcia splendens
Xylopia frutescens	Couratari guianensis	*Ormosia paraensis
	Cupania scrobiculata	Phyllanthus nobilis
< 5 cm dbh	Eschweilera pedicelatta	Rollinia exsucca
Abarema cochleatum	Eugenia muricata	Sapium lanceolatum
Annona densicoma	Guatteria poeppigiana	Tapirira guianensis
Aspidosperma desmanthum	Gustavia augusta	Zanthoxylum rhoifolium
Astrocaryum mumbaca	Himathanthus sucuuba	
Banara guianensis	Inga alba	**< 5 cm dbh**
Casearia arborea	Inga nitida	Casearia pitumba
Cordia scabrida	Inga thibaudiana	Cassipourea guianensis
Croton matourensis	Inga velutina	Chrysophyllum sparsiflorum
Cybianthus minutiflora	Jacaratia spinosa	*Gustavia augusta
Eugenia muricata	Lecythis lurida	Heisteria acuminata
Euterpe oleracea	Miconia minutiflora	Heliconia acuminata
Guapira sp.	Myrcia cuprea	Inga edulis
Guatteria poeppigiana	Myriapora egensis	*Inga thibaudiana
Inga heterophylla	Saccoglotis guianensis	Lacistema agregatum
Inga sp.	Stryphnodendron pulcherrimum	Lacistema pubescens
Inga velutina	Swartzia racemosa	*Lecythis lurida
Jacaranda copaia	Talisisa subalbens	*Miconia minutiflora
Mabea angustifolia	Terminalia amazonica	Myrcia bracteata
Maximiliana maripa	Trattinickia rhoifolia	Myrcia floribunda
Mendoncia hoffmannseggiana	Virola sebifera	Myrciaria tenella
Miconia alata	Vismia guianensis	Rollinia exsucca
Miconia minutiflora	Xylopia aromatica	Rourea amazonica
Miconia sp.		Tabebuia serratifolia
Myrcia eximia	**< 5 cm dbh**	Zanthoxylum rhoifolium
Myrcia fallax	Amphirrox longifolia	
Nectandra cuspidata	Calycolpus sp.	
Neea sp	Calyptranthes cf. bipenis	
Nelsonia sp.	Calyptrocarya bicolor	
Ormosia paraensis	Couratari guianensis	
Protium pilosum	Erythroxylum leptoneurum	
Protium trifoliolatum	Eschweilera pedicelatta	
Richardella macrophylla	Eugenia patriisi	
Rinorea passoura	Geissospermum sericeum	
Siparuna guianensis	Inga nitida	
Iriartea exorrhiza	Lacunaria crenata	
Symphonia globulifera	Metrodorea flavida	
Talisia longifolia	Myrcia laruotteana	
Thyrsodium paraense	Myrcia sylvatica	
Trichilia micrantha	Vismia guianensis	
Trichilia sp.		
Virola sebifera		

* These seven species were found with both modes of regeneration but in different classes of dbh, that is why they are cited in this table twice.

sites in Mindanao, Philippines (Kellman 1970) and in Kalimantan, Indonesia (Kartawinata *et al.* 1980). In general, the woody species are eliminated by intensive agriculture and regrowth comes to be dominated by weeds (Kellman 1980; Uhl *et al.* 1981). In Bragantina, whereas pioneer species predominated among secondary forest seedlings, the sprouts included some primary forest species such as *Andira retusa, Couratari guianensis, Eschweilera pedicelatta, Guatteria poeppigiana, Saccoglotis guianensis, Swartzia racemosa,* and *Talisia subalbens*. Many of these species had no or poor seed rain and seed bank and sprouting may represent the only way to regenerate in the secondary forests. In the Bragantina, a large number of woody species has regenerated from sprouts in secondary forests.

Seed bank, seed rain and the regeneration of species

The degree in which the seed bank and seed rain is involved in succession seems to vary (Skoglund 1992). Experimental studies in recently cleared forests (Uhl *et al.* 1981, 1982b; Young *et al.* 1987; Lawton & Putz 1988) have demonstrated that most of the woody colonising species originate from the seed bank. In my study its likely that some of the seed bank resulted from seed rain during the period of cultivation. This included the 15-17 species observed both in seed rain and seed bank. In the absence of longer term seed rain data and information on seed longevity it is impossible to quantify this contribution to the seed bank.

A comparison made with the number of species in the seed bank, seed rain and seedlings (Table 41) showed that there were more species (and tree

Table 41. Total number of species (with number of tree species in parentheses) in the seed bank, seed rain, and from seeds and sprouts of two size classes (≥ 5 cm dbh and ≥ 1 m tall, < 5 cm dbh) in the 5-years, 10-years and 20-years-old secondary forests in the Bragantina region, Pará.

Forest	Seed	Seed	≥ 5 cm dbh		≥ 1 m tall, < 5 cm dbh	
age-class	bank	rain	seeds	sprouts	seeds	sprouts
5-years	60 (9)	70 (21)	4 (4)	18 (18)	36 (19)	36 (25)
10-years	63 (12)	93 (32)	13 (13)	25 (25)	58 (36)	18 (9)
20-years	70 (12)	104 (44)	13 (13)	31 (30)	48 (30)	23 (10)

Table 42. The numbers of tree species in two or all three of seed bank, seed rain and seedlings in the 5-years, 10-years and 20-years-old secondary forests in the Bragantina region, Pará.

	5-years-old	10-years-old	20-years-old
Seed bank and seed rain	4	7	7
Seed bank and seedlings	4	3	2
Seed rain and seedlings	2	8	7
Seed bank, seed rain and seedlings	1	2	1

species) in the seed rain than in the seed bank or regenerating from seedlings. For smaller individuals (≥ 1m tall, < 5 cm dbh) more species were found regenerating from seedlings but the numbers were still low. For trees, the number of species of seedlings is similar to the number of species in the seed rain, but the numbers of common species are low (Table 42). The seed bank of secondary forests has seeds of 9-12 tree species of which 4-7 species were present in the seed rain and 2-4 as seedlings (Tables 41 and 42). On the other hand, 2-8 species occurred in both seed rain and as seedlings. The tree species in common with seed bank, seed rain and seedlings is very low, and only the species *Mabea angustifolia, Miconia minutiflora* and *Zanthoxylum rhoifolium* were present in all these stages. Because pioneer tree species have smaller seeds than primary forest trees (Foster & Janson 1985) it is not surprising that they dominate the seed bank and seed rain in secondary forests. Pioneer and late secondary forest species dominate less disturbed sites, while herb species dominate repeatedly burned and disturbed sites (Hall & Swaine 1980). In Papua New Guinea two-thirds of the tree seeds in the seed rain and seed bank of a small patch of old regrowth forest (~55-years-old) were from species abundant in the surrounding young vegetation (< 2-years-old) but absent from the patch (Saulei & Swaine 1988). In rain forests, the seed bank may be less important compared with the current seed rain in the recovery process (Putz & Appanah 1987). The abundance of seeds in the surface soil of young secondary forests has been reported by Young *et al.* (1987) to result from the high rate of input from the taller successional plants. In my study, the seed bank was higher than the seed rain (Tables 27 and 32) in all forest age-classes. Uhl &

Clark (1983) found that there was a low seed rain compared with seed bank size (180 seeds m^2 in the seed bank vs 50 seeds m^2 $year^{-1}$ in the seed rain) and they concluded that seed longevity may be considerably greater than 1 year for pioneer species. Cheke *et al.* (1979) also found that the seed bank numbers in the soil were much greater than those in the annual seed rain.

In the secondary forests studied, the species seems to posses different combinations of regenerative traits. The most abundant medium-pioneer species (such as *Cecropia palmata, Vismia guianensis* and *Zanthoxylum rhoifolium*) can be characterised by having large seed bank populations and high seed rain but no or few seedlings in the secondary forests (Fig. 27) while large pioneers (such as *Croton matourensis, Inga* sp. and *Tapirira guianensis*) have low seed rain and seed bank and some persistent seedling banks (Fig. 28) and the ability to sprout. Large mature-forest species such as *Gustavia augusta* and *Virola sebifera* were very poorly represented in the seed bank, seed rain and as seedlings (Fig. 29) and were more commonly found as sprouts in secondary forests. Other abundant pioneer species (such as *Croton matourensis, Lacistema pubescens, Inga thibaudiana, Miconia minutiflora, Mabea angustifolia, Myrcia bracteata, Rollinia exsucca, Siparuna guianensis, Zanthoxylum rhoifolium*) and four primary forest species (*Annona densicoma, Iriartea exorrhiza, Symphonia globulifera* and *Trichilia* sp.) were recorded as seeds in the seed bank or seed rain and were also presented as seedlings. Possible explanations for the apparent absence of the medium-pioneer species (with high seed bank and seed rain) as seedlings are: some individuals may have been excluded by the decision to ignore seedlings less than 1 m tall or high small seedling mortality from herbivory or shade or

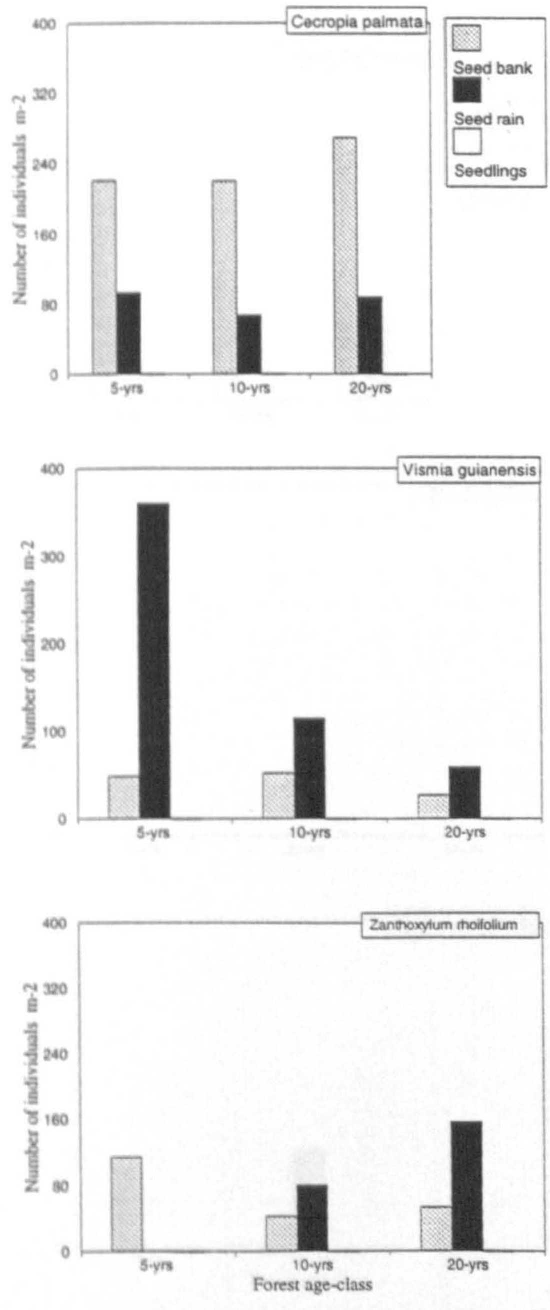

Figure 27. The mean number of individuals (≥ 1m tall, < 5 cm dbh) m^{-2} of three medium-pioneer species in the seed bank, seed rain and as seedlings in the 5-years, 10-years and 20-years-old secondary forests in the Bragantina region, Pará.

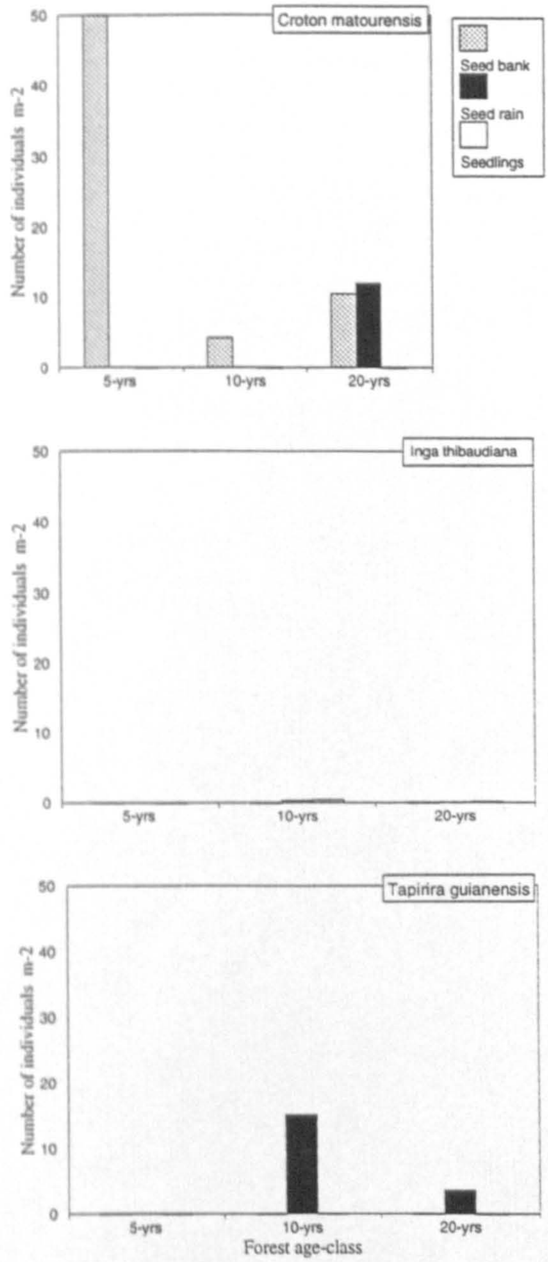

Figure 28. The mean number of individuals (≥ 1m tall, < 5 cm dbh) m^{-2} of three large-pioneer species in the seed bank, seed rain and as seedlings in the 5-years, 10-years and 20-years- old secondary forests in the Bragantina region, Pará.

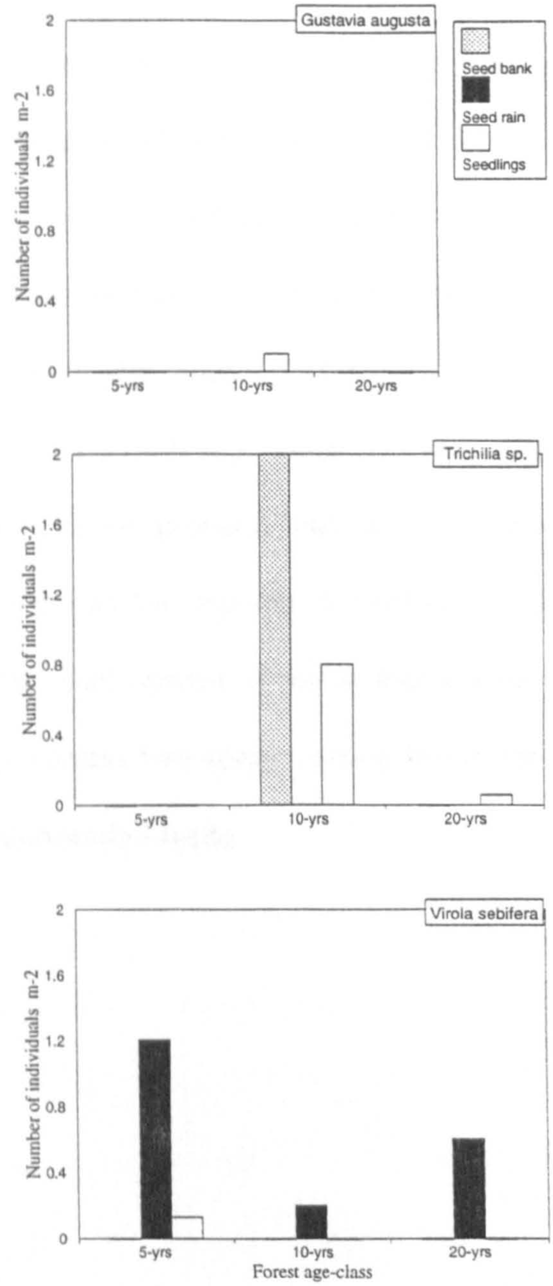

Figure 29. The mean number of individuals (≥ 1m tall, < 5 cm dbh) m^{-2} of three large mature-forest species in the seed bank, seed rain and as seedlings in the 5-years, 10-years and 20-years old secondary forests in the Bragantina region, Pará.

both. McClanahan & Wolfe (1993) found that some successional tree species present in the seed rain of open habitats in Florida had a high mortality and were not present as seedlings. The establishment of new individuals depends not only the dynamics of replacement in the upper strata, but also the ability of seedlings and sprouts to survive under competition.

In conclusion, the most abundant pioneer tree species in all successional stages sampled had a high seed bank and seed rain but failed to regenerate as seedlings while other pioneer and some primary species present in the secondary forests had the capacity to withstand repeated felling and burning, and regenerated from sprout. It seems that the basic structure of the forest or the presence of certain tree species along the chronosequence is maintained by a variety of regenerative traits.

CHAPTER 9

CONCLUDING REMARKS

Reports of scientific studies in the middle of this century (Egler 1961 Ackermann 1966; Penteado 1967) indicated that deforestation degraded the Bragantina region into a "ghost-landscape" or "desert", owing to shifting cultivation practices. Also, these studies reported a soil and floristic impoverishment of secondary forests (Penteado 1967; Lima 1954) that replaced the primary ones. However, more recent studies (Denich 1991; Nunez 1995) found that Bragantina's secondary forests which had been intensively used for traditional agriculture had a high species richness but a low biomass. In this thesis, a study of succession after shifting cultivation confirmed that the Bragantina landscape is dominated by secondary forests but secondary forests greater than 10 years old are more common than previously observed (Denich 1991), and probably belong to large landholders.

Fallow periods mark the end of the cropping and the beginning of plant succession and the regeneration of vegetation appeared to be dependent of the transfer of nutrients from the soil to the vegetation (Scott 1987). Burning secondary forests with at least eight previous cycles of cultivation, gave a high nutrient input to the soil. The most notable effects of burning were the increase in soil pH, calcium, magnesium and potassium and the loss of organic matter and exchangeable aluminium, all of which are typical for shifting cultivation systems (Roder *et al.* 1993). As secondary forests age, there was a significant increase in soil carbon and a slight increase in extractable phosphorus and exchangeable cations. Similar observations were made by researchers elsewhere (Nigeria, Aweto 1981b; India, Mishra & Ramakrishnan 1983b and Toky & Ramakrishnan 1983b). The stocks of total organic carbon and available phosphorus in the Bragantina forests are within the recorded values for tropical rain forests (Uhl & Jordan 1984; Martins *et al.* 1990; Thompson *et al.* 1992). However, the stocks of exchangeable potassium (10 kg ha^{-1}) were low and those of calcium (150 - 220 kg ha^{-1}) were high compared with the values found by other authors in Amazônia. Probably such high values of calcium in the soils of Bragantina's forests are due to the influence of the Pirabas Formation limestone that underlies the study area.

Changes in ecological patterns and strategies have featured in models of tropical succession (Gomez-Pompa & Vazquez-Yanes 1981; Ewel 1983). These authors have suggested that succession should be described in terms of three phases based on the dominance of ecological groups (herbs, shrubs and climbers; short-lived pioneers; and long-lived pioneers). Finegan (1996) using data mainly from northern Amazônia and Mexico made a model of forest succession over 100 years. He claimed that secondary forests may become as species rich as primary forests, although they have different species composition, suggesting that species richness and composition vary independently. He noted that long-term successional change may be determined by life-histories differences between tree species and that the presence of a tree in the third phase of succession depended on factors operating early in the succession. The factors are: initial site conditions, the ecology of dispersal, germination and interactions of the seedlings with the dominant species. My data largely support Finegan's (1996) model but this is scarcely surprising since his variables and conclusions are very broadly defined. Concerning woody species richness and diversity, the Bragantina secondary forests are similar to those described elsewhere with younger successional stages dominated by a few species and the species numbers and diversity increasing gradually during succession (Aweto 1981a; Mishra & Ramakrishnan 1983a; Uhl & Jordan 1984; Purata 1986; Saldarriaga *et al.* 1988). The structure of both successional and primary forests was characterised by a high density of small individuals, but the older forests showed an increased number of individuals in the larger size classes. The mean basal area of woody plants in young secondary forests was very low 4.23 m^2 ha^{-1} while the oldest forests (> 10 years) had 11 to 16.72 m^2 ha^{-1}. These values are 1.5 - 6 times less than mean basal area of the primary forest (25.4 t ha^{-1}).

In the Bragantina secondary forests, species composition varied greatly with age as was clearly shown by the ordination and classification techniques used. They defined four groups of woody plant species that occurred during the succession. The first two groups were formed by species with a high abundance in the secondary forests which consisted of medium and large pioneer species. The other two groups were large pioneer and mature forest species and were mostly restricted to the primary forests, with some large pioneers also found in the old secondary forests at low densities. Some primary species have been observed to establish together with or even before pioneer species in other tropical sites (Swaine & Hall 1983; Uhl & Jordan 1984). It is the tolerance model proposed by Connell & Slatyer (1977) which describes succession as a process whereby slower growing, more tolerant, late successional species invade and mature in the presence of the fast-growing less tolerant, pioneer species. Other studies (Purata, 1986; Kapelle *et al.* 1995) also recognised a gradient of successional processes in species composition. At the family level the differences between age classes were also great. In the primary forest all the most species-rich families (such as the Caesalpiniaceae, Lecythidaceae, Moraceae, Myrtaceae and Sapotaceae) were less so in the secondary forests. In the secondary forests the Mimosaceae had the highest number of species and together with the Lacistemaceae and Clusiaceae had the highest number of individuals.

Propagule availability is the key to understanding how species established in regrowth. The seed bank and seed rain analysed here, showed that there were an extraordinary number of seeds in the soil and seed rain and the values varied with forest age. In the youngest forests, the herbs dominated the seed bank and only 22% of them were from woody species. On the other hand, the oldest secondary forests had about 40% of woody species in the seed bank. Regarding seed rain, in general, woody species contributed to 87% to 89% of the total seeds and 50% to 60% of the species in secondary forests. The most common tree species in the seed rain of the secondary forests were already present in the community and had mainly fleshy and arillate fruits. Few tree species in the seed rain, in low densities, came from the primary forest through wind or animal vectors. An analysis of the total of 140 woody species ($\geq$ 5 cm dbh) recorded from all secondary forests combined, showed that only 10% occurred in the seed bank and 24% in the seed rain, indicating that the majority of tree species do not accumulate seeds in the soil or have restricted seed dispersal, and that both seed bank and seed rain make a limited direct contribution to the woody regeneration during succession in the Bragantina region. Sprouting, on the other hand, plays an important part in the recovery in the Bragantina region depending on the age of the secondary forest. The secondary forests are apparently initially composed of sprouting plants, with new plants arriving from seed as the secondary forests age. Many of the species with a high capacity to sprout had no or poor seed rain and seed bank and sprouting may represent their only means of regenerating in the secondary forests. The species in the secondary forests had a variety of species mechanisms. In general, the most abundant pioneers had large seed banks and high seed rain but no or few seedlings, with some of them regenerating as sprouts; while large pioneers and mature species were poorly represented in the seed bank, seed rain and as seedlings and were more commonly found as sprouts. Other less abundant pioneer species were recorded as seeds in the seed bank or seed rain and were also present as seedlings.

It must be said that traditional shifting cultivators do not use heavy equipment for clearing the forest and this means sprouting is possible. Where heavy equipment is used in eastern Amazônia, recovery of disturbed sites is much slower and plant establishment is highly dependent on seeds from the surrounding vegetation (Uhl *et al.* 1988; Nepstad *et al.* 1990; Nunez 1995). Another important point to observe is that the 5-years-old secondary forests more intensively used by the farmers, showed the poorest richness and diversity, the lowest floristic similarity with the primary forest, the lowest basal area and height, and a high predominance of herbs in their seed banks. It seems that if this young forest comes dominate the landscape, the recovery will be dominated by herbs as was observed in other agricultural sites by Kellman (1980) and Uhl *et al.* (1981).

Remnant primary forests of a few hectares each are spread over the region. One of these fragments was studied in this thesis and it is a refuge for more than 200 woody species, largely or entirely restricted to these fragments. The 272 tree species (≥ 5 cm dbh) found in the surveys in the transects and random walks in this fragment were classified (I.C.G. Vieira *et al.* 1996a) according to their capacity to maintain themselves in the slash and burn agricultural cycles. We defined "threatened" species as those trees restricted to the primary forest. "Favoured" species included those which were found in the primary forest and that also occurred in the secondary forests up to 40 years old. The trees that are "most threatened", i.e., which have both a low density of adult individuals and no regeneration in the primary forest, represented 22.4% of the total forest species. The "susceptible species", with a high adult density and good regeneration in the primary forest, represented 21.6% of the total forest tree species. The "species under risk", e.g. the trees with a low density or low regeneration in the forest reached 20.5%. Ninety-five (35%) species occurred in the secondary forests. Hence, almost one third of native tree flora is apparently "favoured" by agricultural activity and able to survive in the secondary forests around the remnant forest of *fazenda Monte Verde*. Besides the number of species, another indicator of the recuperation stage of the secondary forest tree flora is the relative abundance of each species. Of the 95 "favoured" species, 28 (29.4%) were among the 50 most abundant in the secondary forests of up to 40 years in age. Some general differences in ecological traits among those forest species "favoured" and "threatened" by agricultural activities were found. The ability to sprout following cutting and burning was the one which best differentiated (χ^2= 23.83; df= 1; p< 0.001) the groups (60 % of "favoured" species exhibited sprouting vs. only 35% of the "threatened" species). Seed weights of 90 of the forest tree species indicated that 17% of those species that did not appear in the secondary forests had very large seeds (>10 g); in fact, none of the large-seeded species were found in secondary forests. The apparent inability of trees with seeds >10 g in weight to colonize the secondary forests may be related to the shortage of dispersal vectors. The species of birds that visit secondary forests are small (<30 g) and mainly insectivorous (J. Roma, personal communication); the small seed-carrying birds that disperse seeds into the secondary forests may be unable to carry larger seeds, as has been documented in Paragominas, Pará (Nepstad *et al.* 1996b). The study of other fragments of primary forest in Bragantina will give a better idea of the tree species really threatened by agriculture practices.

The general conclusion is that past and present human activities in the Bragantina region have strongly influenced the ecosystem structure and processes by altering species composition and soil properties. But even after about 90 years of shifting cultivation, the region has the potential for forest regeneration partly because there is a diversity of regeneration strategies among the species. Also soil nutrient stocks in the secondary forests are able to recover to values similar to those in the primary forest. It may predicted that woody vegetation will persist in the Bragantina region while traditional practices of agriculture persist, and the role of remnant forests is very important to maintain a large number of species that do not have the capacity to regrow in secondary forests. If a land use plan for Bragantina could be implemented, it would be successful.

Abdulhadi, R. & Lamb, D. (1988). Soil seed stores in a rain forest succession. *Proceedings of the Ecological Society of Australia*, 15, 81-87.

Ackermann, F.L. (1964). Geologia e fisiografia da região Bragantina no Estado do Pará. *Cadernos da Amazônia*, INPA, Manaus, 2, 1-90.

Ackermann, F.L. (1966). *A depredação dos solos da Região Bragantina e na Amazônia*, Universidade Federal do Pará, Belém.

Adedeji, F.O. (1984). Nutrient cycles and successional changes following shifting cultivation practice in moist semi-deciduous forests in Nigeria. *Forest Ecology and Management*, 9, 87-89.

Almeida, S.S.; Lisboa, P.L.B. & Silva, A.S. L. (1993). Diversidade florística de uma comunidade arbórea na Estação Científica "Ferreira Pena", em Caxiuanã (Pará). *Boletim do Museu Paraense Emilio Goeldi, Botânica*, 9, 93-188.

Alves, D. S. & Skole, D.L. (1996). Characterizing land cover dynamics using multitemporal imagery. *International Journal of Remote Sensing*, 17, 835-839.

Augspurger, C.K. & Franson, S.E. (1988). Input of wind-dispersed seeds into lightgaps and forest sites in a Neotropical forest. *Journal of Tropical Ecology*, 4, 239-252.

Austin, M.P. (1977). Use of ordination and other multivariate descriptive methods to study succession. *Vegetatio*, 35, 165-175.

Aweto, A.O. (1981a). Secondary succession and soil fertility restoration in South-Western Nigeria. I- Succession. *Journal of Ecology*, 69, 601-607.

Aweto, A.O. (1981b). Secondary succession and soil fertility restoration in South-Western Nigeria. II- Soil fertility restoration. *Journal of Ecology*, 69, 609-614.

Aweto, A.O. (1981c). Secondary succession and soil fertility restoration in South-Western Nigeria. III- Soil and vegetation interrelationships. *Journal of Ecology*, 69, 957-963.

Balée, W. (1986). Análise preliminar de inventário florestal e a etnobotânica Ka'apor (Maranhão). *Boletim do Museu Paraense Emílio Goeldi, Botânica*, 2, 141-67.

Balée, W. (1993). *Footprints of the forest: Ka'apor ethnobotany - the historical ecology of plant utilization by an Amazonian people*. Columbia University Press, New York.

Bastos, T.X. (1972). O estado atual dos conhecimentos das condições climáticas da Amazônia brasileira. *Boletim Técnico IPEAN*, 54, 68-122.

Bigarella, J.J. & Ferreira, A.M.M. (1985). Amazon geology and the pleistocene and the cenozoic environments and paleoclimates. *Key Environments: Amazonia.* (eds. G.T. Prance & T. E. Lovejoy), pp. 49-71. Pergamon Press, Oxford.

Black, G.A.; Dobzhansky, T. & Pavan, C. (1950). Some attempts to estimate species diversity and population density of trees in Amazonian forests. *Botanical Gazette*, 111, 413-25.

Brinkmann, W.L.F. & Nascimento, J.C. (1973). The effect of slash and burn agriculture on plant nutrients in the tertiary region of central Amazonia. *Acta Amazonica*, 3, 55-61.

Brower, J.E. & Zar, J.H. (1984). *Field and Laboratory Methods for General Ecology.* 2nd edition. Wm. C. Brown Publishers, Iowa.

Brown, S. & Lugo, A. (1990). Tropical secondary forests. *Journal of Tropical Ecology*, 6, 1-32.

Budowski, G. (1965). Distribution of tropical American rain forest species in the light of successional processes. *Turrialba*, 15, 40-42.

Burguer, B. & Kitamura, E.P. (1987). Importância e viabiliadade de uma pequena agricultura sustentada na Amazônia oriental. *Tubinger Geographische Studien*, 95, 447-461.

Buschbacher, R.; Uhl, C. & Serrão, E.A.S. (1988). Abandoned pastures in eastern Amazônia. II. nutrient stocks in the soil and vegetation. *Journal of Ecology*, 76, 682-699.

Cain, S.A.; Castro, G.M.O.; Pires, J.M. & Silva, N.T. (1956). Application of some phytosociological techniques to Brazilian rain forests. *American Journal of Botany*, 43, 911-41.

Camargo, F.C. (1948). Terra e colonização no antigo e novo quaternário da zona da estrada de ferro de Bragança, Estado do Pará, Brasil. *Boletim do Museu Paraense Emilio Goeldi*, 10, 123-147.

Campbell, D.G.; Daly, D.C.; Prance, G.T. & Maciel, U.N. (1986). Quantitative ecological inventory of *terra firme* and *várzea* tropical forest on the Rio Xingu, Brazilian Amazon. *Brittonia*, 38, 369-393.

Chandrashekara, U.M. & Ramakrishnan, P.S. (1993). Germinable soil seed bank dynamics during the gap phase of a humid tropical forest in the western parts of Kerala, India. *Journal of Tropical Ecology*, 9, 455-467.

Cheke, A.A.; Nanakorn, W. & Yankoses, C. (1979). Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in northern Thailand. *Biotropica*, 11, 88-95.

Clarke, W.C. (1976). Maintenance of agriculture and human habitats within the tropical forest ecosystem. *Human Ecology*, 4, 247-259.

Clements, F.E. (1916). Plant succession. *Carnegie Institute Washington Publication* 242, Washington, DC.

Connell, J.M. & Slatyer, R.O. (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, 111, 1119-1144.

Correa, J.C. & Reichardt, K. (1989). The spatial variability of Amazonian soil under natural forest and pasture. *Geojournal*, 19, 423-427.

CSRA/SUDAM (Centro de Sensoriamento Remoto da Amazônia/ Superintendência de Desenvolvimento da Amazônia) (1988). *Levantamento da alteração da cobertura vegetal do Estado do Pará*. SUDAM, Belém.

Dantas, M. & Muller, N.R.M. (1979). Estudos fito-ecológicos do trópico úmido brasileiro. I- aspectos fitossociológicos de mata sobre terra roxa na região de Altamira. *Anais da Sociedade Botânica do Brasil*, 30, 205-218.

Dantas, M. Rodrigues, J.A. & Muller, N.R.M. (1980). Estudos fito-ecológicos do trópico úmido brasileiro:. II - aspectos fitossociológicos de mata sobre latossolo amarelo em Capitão Poço, PA. *Boletim de Pesquisa EMBRAPA/CPATU* 9, 1-19.

Denich, M. (1986a) Composição florística de capoeiras no município de Igarapé-Açu no Estado do Pará, *Documentos EMBRAPA/CPATU* 39, 1-16.

Denich, M. (1986b). A vegetação da Amazônia oriental com ênfase na vegetação antrópica. *Pesquisas sobre Utilização e Conservação do Solo na Amazônia Oriental*, (eds *EMBRAPA/CPATU-GTZ*), *Documentos EMBRAPA/CPATU*, 40, 43-69.

Denich, M. (1991). *A Importância de uma Vegetação Secundária Nova para o Incremento da Produtividade do Sistema de Produção na Amazônia Oriental Brasileira*. EMBRAPA /CPATU- GTZ, Belém- Pará.

Denslow, J. S. & Gomez Diaz, A.E.G. (1990). Seed rain to tree-fall gaps in a neotropical rain forest. *Canadian Journal of Forestry Research*, 20, 642-648.

Denslow, J.S. (1980). Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia*,3 46, 18-21.

Diniz, T.D. de A.S. (1986). Caracterização climática da Amazônia oriental. *Pesquisas sobre Utilização e Conservação do Solo na Amazônia Oriental.* (ed. EMBRAPA/CPATU-GTZ) *Documentos EMBRAPA/CPATU*, 40, 3-13.

Ducke A. & Black, G.A. (1953). Phytogeographical notes on the Brazilian Amazon. *Anais da Academia Brasileira de Ciências*, 25, 1-46.

Eastman, J.R. (1992). IDRISI. *Technical Reference and User's Guide.* Clark Univiversity Graduate School of Geography. Worcester, Massachusetts.

Eden, M.J. (1990). *Ecology and Land Management in Amazonia.* Belhaven Press, London.

Eden, M. J. (1974). Palaeoclimatic influences and the development savanna in southern Venezuela. *Journal of Biogeography*, 1, 95-109.

Eden, M.J. (1987). Traditional shifting cultivation and the tropical forest system. *Trends in Ecology and Evolution*, 2, 340-343.

Eden, M.J.; Furley, P.A.; Macgregor, D.F.M.; Milliken, W. & Ratter J.A. (1991). Effect of forest clearance and burning on soil properties in northern Roraima, Brasil. *Forest Ecology and Management*, 38, 283-290

Egler, E.G. (1961). A zona Bragantina no Estado do Pará. *Revista Brasileira de Geografia*, 23, 527-555.

Egler, F.E. (1954). Vegetation science concepts. I- initial floristic composition - a factor in old-field vegetation development. *Vegetatio*, 4, 412-417.

EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária). (1979). *Manual de Métodos de Análises de Solos.* Serviço Nacional de Levantamento e Conservação de Solos. Rio de Janeiro.

EMBRAPA (Empresa Brasileira de Pesquisa Agropecuária). (1981). *Mapas de Solos do Brasil.* Serviço Nacional de Levantamento e Conservação de Solos. Rio de Janeiro.

EMBRAPA/CPATU (Empresa Brasileira de Pesquisa Agropecuária/ Centro de Pesquisas Agroflorestais da Amazônia Oriental). (1969-1993). *Boletim Agroclimático. Sistema de Informações Agroclimatológicas.* Belém.

Ewel, J.J. (1976). Litterfall and leaf decomposition in a tropical forest succession in Eastern Guatemala. *Journal of Ecology*, 64, 293-308.

Ewel, J.J. (1979). Secondary forests: the tropical wood resource of the future. *Simpósio International sobre las Ciencias Forestales y su Contribucion al Desarrolo de la America Tropical.* (ed Manuel Chavarria), pp. 53-60. Editorial UNED, San Jose, Costa Rica.

Ewel, J.J.; Berish, C.; Brown, B.; Price, N. & Raich, J. (1981). Slash and burn impacts on a Costa Rican wet forest site. *Ecology*, 62, 816-829.

Ewel, J.J. (1983). Succession. *Tropical Rain Forest Ecosystems: Structure and Function* (ed. F. B. Golley), pp. 217-223. Elsevier.

Ewel, J.J.; Chai, P. & Lim, M.T. (1983). Biomass and floristics of three young second-growth forests in Sarawak. *Malasyan Forester*, 46, 347-364.

Falesi, I.; Baena, A.R.C.& Dutra, S. (1980). Consequências da exploração agropecuária sobre as condições físicas e químicas dos solos das microrregiões do nordeste paraense. *Boletim de Pesquisa da EMBRAPA/CPATU*, 14, 1-49.

Fearnside, P.M. (1993). Deforestation in Brazilian Amazon: the effect of population and land tenure. *Ambio*, 22, 537-545.

Fenner, M. (1985). *Seed Ecology*. Chapman and Hall, London.

FIBGE (Fundação Instituto Brasileiro de Geografia e Estatística). (1970). Censo Agropecuário - Pará. *VIII Recenseamento Geral - 1970, Série Regional*. volume 3, tomo 4. FIBGE, Rio de Janeiro.

FIBGE (Fundação Instituto Brasileiro de Geografia e Estatística). (1985). Censo Agropecuário - Pará. *Censos Econômicos de 1985*. volume 6. FIBGE, Rio de Janeiro.

FIBGE (Fundação Instituto Brasileiro de Geografia e Estatística). (1990). *Divisão do Brasil em Mesorregiões e Microrregiões Geográficas*. volume 2, tomo 1 - Região Norte. FIBGE, Rio de Janeiro.

FIBGE (Fundação Instituto Brasileiro de Geografia e Estatística). (1993). *Áreas dos Municípios por Unidade da Federação* FIBGE, Rio de Janeiro.

FIBGE. (Fundação Instituto Brasileiro de Geografia e Estatística). (1984). *Produção agrícola municipal - Culturas temporárias e permanentes*. vol.9 - 1982, tomo 1 - Região Norte. FIBGE, Rio de Janeiro.

Finegan, B. (1984). Forest succession. *Nature*, 312, 109-114.

Finegan, B. (1996). Pattern and process in neotropical secondary rain forests: the first 100 years of succession. *Trends in Ecology and Evolution*, 11, 119-124.

Foster, S.A. & Janson, C.H. (1985). The relationship between seed size and establishment conditions in tropical woody plants. *Ecology*, 66, 773-780.

Francisco, B.H.R.; Loewenstein, P.; Silva, O.F. da & Silva, G.G. da (1971). Contribuição a geologia da folha São Luis (SA 23) no Estado do Pará. *Boletim do Museu Paraense Emilio Goeldi, Ciências da Terra*, 17, 1-40.

Furch, K. & Klinge, H. (1989). Chemical relationships between vegetation, soil and water in contrasting inundation areas of Amazônia. *Mineral Nutrients in Tropical Forests and Savannas*. (ed J. Proctor), pp. 189-204. Blackwell Scientific Publications, Oxford.

Garwood, N.C. (1989). Tropical soil seed banks: a review. *Ecology of Soil Seed Banks* (eds M.A. Leck, V.T. Parker & R.L.Simpson), pp. 149-202. Academic Press, London.

Gentry, A.H. (1988). Tree species richness of upper Amazonian forests. *Proceedings of the National Academy of America*, 85, 156-159.

Gerold, G. (1994). Pedo-ecological changes of tropical forest-soils by different land-use impacts. *Interciencia*, 19, 297-301.

Gleason. H.A. (1927). Further views on the succession concept. *Ecology*, 8, 229-326.

Goes, A.M., Rossetti, D.F., Nogueira, A.C.R. & Toledo, P.M. (1990). Modelo deposicional preliminar da formação Pirabas no nordeste do Estado do Pará. *Boletim do Museu Paraense Emilio Goeldi, Ciências da Terra*, 2, 3-15.

Golley, F.B.; Ewel, J.J. & Child, G I. (1976). Vegetation biomass of five ecosystems in northeastern Colombia. *Tropical Ecology*, 17, 16-22.

Gomez-Pompa, A. (1971). Posible papel de la vegetación secundaria en la evolución de la flora tropical. *Biotropica*, 3, 125-135.

Gomez-Pompa, A. & Vazquez-Yanes, C. (1981). Successional studies of a rain forest in Mexico. *Forest Succession: Concepts and Applications*. (eds D.C. West, H.H. Shugart and D.B. Botkin), pp. 246-266. Springer-Verlag.

Gomez-Pompa, A. & Vazquez-Yanes, C. & Guevara, S. (1972). The tropical rain forest: a non-renewable resource. *Science*, 177, 762-765.

Gonzalez-Espinosa, M.; Quintana-Ascencio, P.F.; Ramirez-Marcial, N. & Gaytan-Guzman, P. (1991). Secondary succession in disturbed *Pinus-Quercus* forests in the highlands of Chiapas, Mexico. *Journal of Vegetation Science*, 2, 351-360.

Gorchov, D.L.; Cornejo, F.; Ascorra, C. & Jaramillo, M. (1993). The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio*, 107/108, 339-349.

Guevara, S. & Laborde, J. (1993). Monitoring seed dispersal at isolated trees in tropical pastures: consequences for local species availability. *Vegetatio*, 107/108, 319-338.

Guevara, S.; Purata, S.E. & van der Maarel, E. (1986). The role of remnant trees in tropical succession. *Vegetatio*, 66, 77-84.

Guevara, S. & Gomez-Pompa, A. (1972). Seeds from surface soils in a tropical region of Veracruz, Mexico. *Journal of the Arnold Arboretum*, 53, 312-335.

Grime, J.P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, Chicester.

Hall, J.B. & Okali, D.U.U. (1979). A structural and floristic analysis of woody fallow vegetation near Ibadan, Nigeria. *Journal of Ecology*, 67, 321-346.

Hall, J.B. & Swaine, M.D. (1980). Seed stocks in Ghanaian forest soils. *Biotropica*, 12, 256-263.

Hill, M.O. & Gauch, H.G. (1980). Detrended correspondence analysis: an improved ordination technique. *Vegetatio*, 42, 47-58.

Hill, M.O. (1979). TWINSPAN - *A Fortran Program for Arranging Multivariate Data in an Ordered Two-Way Table by Classification of the Individuals and Attributes*. Cornell University, Ithaca, New York.

Horn, H.S. (1976). Succession. *Theoretical Ecology* (ed R.M. May), pp. 187-204. Blackwell, Oxford.

Hurlbert, S.H. (1984). Pseudo replication and the design of ecological field experiments. *Ecological Monographs*, 54, 184-211.

INPE (Instituto Nacional de Pesquisas Espaciais). (1992). *Deforestation in Brazilian Amazon*. INPE, São José dos Campos, São Paulo.

IPEAN (Instituto de Pesquisas Agronômicas do Norte). (1975). *Zoneamento Agrícola da Microrregião 24*. IPEAN, Belém.

Jordan, C.F. & Russel, C.E. (1989). Jari: A pulp plantation in the Brazilian Amazon. *Geojournal*, 19, 429-435.

Jordan, C.F. (1985). Soils of the Amazon rain forest. *Key Environments: Amazonia* (eds Prance, G.T. & Lovejoy, T.C.), pp. 83-94. Pergamon Press, Oxford.

Jordan, C.F. (1989). Are process rates higher in tropical forest ecosystems? *Mineral Nutrients in Tropical Forests and Savannas*. (ed J. Proctor), pp. 202-205. Blackwell Scientific Publications, Oxford.

Kappelle, M.; Kennis, P.A.F. & Vries, R.A.J. (1995). Changes in diversity along a successional gradiente in a Costa Rican upper montane *Quercus* forest. *Biodiversity and Conservation*, 4, 10-34.

Kartawinata, K.; Riswan, S. & Soedjito, H. (1980). The floristic change after disturbance in lowland dipterocarp forest in East Kalimantan, Indonesia. *Tropical Ecology and Development* (ed J.I. Furtado), pp. 47-54. International Society of Tropical Ecology, Kuala-Lumpur.

Kauffman, J.B. (1991). Survival by sprouting following fire in tropical forests of the eastern Amazon. *Biotropica*, 23, 219-224.

Kellman, M.C. (1970). Secondary plant succession in tropical montane Mindanao. *Australian National University*, Publ. no. BG/2, Camberra.

Kellman, M.C. (1980). Geographic patterning in tropical weed communities and early secondary succession. *Biotropica* (Supplement), 12, 34-39.

Kent, M. & Coker, P. (1996). *Vegetation Description and Analysis. A Practical Approach.* John Wiley & Sons, New York.

Kidd, C.V. & Pimentel, D. (1992). *Integrated Resource Management: Agroforestry for Development*. (eds). Academic Press, San Diego, CA. 223pp.

Kleinman, P.J.A.; Pimentel, D. & Bryant, R.B. (1995). The ecological sustainability of slash-and-burn agriculture. *Agriculture, Ecosystems and Environment*, 52, 235-249.

Klinge, H. (1977). Fine litter production and nutrient return to the soil in three natural forests stands in eastern Amazon. *Geo-Eco-Trop*, 1, 159-167.

Knight, D.H. (1975). An analysis of late secondary succession in species-rich tropical forest. *Ecological Studies-Analysis and Synthesis* (eds F.B. Golley & E. Medina). vol 11, pp. 53-59. Springer-Verlag.

Lawton,, R.O. & Putz, F.E. (1988). Natural disturbance and gap-phase regeneration in a wind-exposed tropical cloud forest. *Ecology*, 69, 764-777.

Lima, R.R. (1954). *Os Efeitos das Queimadas sobre a Vegetação dos Solos Arenosos da Região da Estrada de Ferro de Bragança.* Instituto Agronômico do Norte (IAN), Belém.

Lucas, R.M.; Honzak, M.; Foody, G.M.; Curran, P.J. & Corves, C. (1993). Characterizing tropical secondary forest using multi-temporal Landsat sensor imagery. *International Journal of Remote Sensing*, 14, 3061-3067.

Margalef, R. (1963). On certain unifying principles in ecology. *American Naturalist*, 97, 357-374.

Martinez-Ramos, M. & Soto-Castro, A. (1993). Seed rain and advanced regeneration in a tropical rain forest. *Vegetatio*, 107/108, 299-318.

Martins, P.F.S. & Cerri, C.C. (1986). O solo de um ecossistema natural de floresta localizado na Amazônia oriental. I. Caracterização química e física. *Anais do I Simpósio do Trópico Umido*, vol. 1, pp. 271-286. EMBRAPA/CPATU, Belém.

Martins, P.F.S., Cerri, C.C., Volkoff, B. & Andreux, A. (1990). Efeito do desmatamento e do cultivo sobre características físicas e químicas do solo sob floresta natural na Amazônia oriental. *Revista IG São Paulo*, 11, 21-33.

Martins, P.F.S., Cerri, C.C., Volkoff, B., Andreux, F. & Chauvel, A. (1991). Consequences of clearing and tillage on the soil of a natural Amazonian ecosystem. *Forest Ecology and Management*, 38, 273-282.

Mattos, M.M. & Uhl, C. (1994). Economic and perspectives on ranching in the eastern Amazon. *World Development*, 22, 145-158.

Mausel, P.; Wu, Y.; Li, Y.; Moran E.F. & Brondizio, E.S. (1993). Spectral identification of successional stages following deforestation in the Amazon. *Geocarto International*, 8, 61-71.

McClanahan, T.R. & Wolfe, R.W. (1993). Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology*, 7, 279-287.

Medina, E. & Cuevas, E. (1989). Patterns of nutrient accumulation and release in Amazônian forests of the upper Rio Negro basin. *Mineral Nutrients in Tropical Forests and Savannas*. (ed J. Proctor), pp. 217-240. Blackwell Scientific Publications, Oxford.

Meggers, B.J. (1994). Archeological evidence for the impact of mega-Niño events on Amazonia during the past two millennia. *Climatic Change* 28, 321-338.

Mishra, B.K. & Ramakrishnan, P.S. (1983a). Secondary succession subsequent to slash and burn agriculture at higher elevations of north-east India.. I- Species diversity, biomass and litter production. *Acta Oecologica - Oecologia Applicata*, 4, 95-107.

Mishra, B.K. & Ramakrishnan, P.S. (1983b). Secondary succession subsequent to slash and burn agriculture at higher elevations of north-east India. II- Nutrient cycling. *Acta Oecologica - Oecologia Applicata*, 4, 237-245.

Mitja, D. & Hladik, A. (1989). Aspects de la reconstitution de la vegetation dans deux jacheres en zone forestiere africaine humide (Makoku, Gabon). *Acta Oecologica/Oecologia Generalis*, 10, 75-94.

Moran, E.F.; Brondizio, E. Mausel, P. (1994). Integrating Amazonian vegetation, land-use and satellite data. *Bioscience*, 44, 1-18.

Mori,, A.S. Rabelo, B.V., Tsou, C. & Daly, D. (1989). Composition and structure of an eastern Amazonian forest at Camaipi, Amapá, Brazil. *Boletim do Museu Paraense Emílio Goeldi, Botânica*, 5, 3-18.

Mueller-Dombois, D. & Ellenberg, H. (1974). *Aims and Methods of Vegetation Ecology*. John Wiley, New York.

Munsell Color Company (1954). *Munsell Soil Color Charts*. Baltimore.

Murphy, L.S. & Riley, J.P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, 27, 31-36.

Nepstad, D.C.; Moutinho, P.R.; Uhl, C.; Vieira, I.C.G. & Cardoso da Silva, J.M. (1996a). The ecological importance of forest remnants in an eastern Amazonian frontier landscape. *Forest Patches in Tropical Landscapes* (eds John Schelhas & Russell Greenberg), pp. 133-150. Island Press, Washington, DC.

Nepstad, D.C.; Uhl, C.; Pereira, C. & da Silva, J.M.C. (1996b). Barriers to tree establishment in an abandoned Amazonian pasture: seed availability, seed predation, herbivory and drought. *Oikos*, (in press).

Newton, K. (1960). Shifting cultivation and crops rotations in the tropics. *Papua and New Guinea Agronomic Journal*, 13, 81-118.

Noble, I.R. & Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, 43, 5-21.

Nobre, C.A. & Oliveira, A.S. (1986). Precipitation and circulation anomalies in South America and the 1982-83 El Niño/Southern oscillation episode. *Proceedings of the Second International Conference on Southern Hemisphere Meteorology. American Meteorological Society*, pp. 442-445. New Zeland.

Nobre, C.A.; Sellers, P.J. & Shukla, J. (1991). Amazonian deforestation and regional climate change. *Journal of Climate*, 4, 957-988.

Nortcliff, S., & Dias, A.C.D.C.P. (1988). The change in soil physical conditions resulting from forest clearance in the humid tropics. *Journal of Biogeography*, 15, 61-66.

Nunez, J.B.H. (1995). *Fitomassa e estoque de bioelementos das diversas fases de vegetação secundária, provenientes de diferentes sistemas de uso da terra no Nordeste Paraense, Brasil*. Msc. Thesis, Unversidade Federal do Pará, Belém.

Odum, E.P. (1969). The strategy of ecosystem development. *Science*, 164, 262-270.

Peet, R.K. (1974). The measurement of species diversity. *Annual Review of Ecology and Systematics*, 5, 285-307.

Penteado, A.R. (1967). *Problemas de Colonização e de Uso da Terra na Região Bragantina do Estado do Pará*, Universidade Federal do Pará, Coleção Amazônia, Série José Veríssimo. Pará.

Pickett, S.T.A. (1976). Succession: An evolutionary interpretation. *American Naturalist*, 110, 107-119.

Pires, J. M. (1966). The estuaries of the Amazon and Oyapoque rivers. *Proceedings of the Decca Symposium*, pp. 211-218. UNESCO, Roma.

Pires, J.M. & Prance, G.T. (1985). The vegetation types of the Brazilian Amazon. *Key environments: Amazonia* (eds G.T. Prance & T.E. Lovejoy), pp. 109-145. Pergamon Press, Oxford.

Pires, J.M. (1973). Tipos de vegetação da Amazônia. *Publicação Avulsa do Museu Paraense Emílio Goeldi*, 20, 179-202.

Pires, J.M.; Dobzhansky, T & Black, G.A. (1953). An estimate of the number of species of trees in an Amazonian forest community. *Botanical Gazette*, 114, 467-77.

Prance, G.T. (1977). The phytogeographic subdivisions of Amazonia and their influence on the selection of biological reserves. *Extinction is Forever* (eds G.T. Prance & T.S. Elias), pp. 195-213. New York Botanical Garden, Bronx.

Primack, R.B. & Hall, P. (1992). Biodiversity and forest change in Malaysian Borneo. *Bioscience*, 42, 829-837.

Purata, S.E. (1986). Floristic and structural changes during old-field succession in the Mexican tropics in relation to site history and species availability. *Journal of Tropical Ecology*, 2, 257-276.

Putz, F.E. & Appanah, S. (1987). Buried seeds, newly dispersed seed, and the dynamics of a lowland forest in Malaysia. *Biotropica*, 19, 326-33.

Putz, F.E. & Brokaw, N.V.L. (1989). Sprouting of broken trees on Barro Colorado Island, Panama. *Ecology*, 70, 508-512.

Putz, F.E. (1983). Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology*, 64, 1069-1074.

Ramakrishnan, P S. & Toky, O.P. (1981). Soil nutrient status of hill agro-ecosystems and recovery pattern after slash and burn agriculture (Jhum) in northeastern India. *Plant and Soil*, 60, 41-64.

Ramakrishnan, P.S. (1989). Nutrient cycling in forest fallows in north-eastern India. *Mineral Nutrients in Tropical Forests and Savannas* (ed J. Proctor), pp. 337-352. Blackwell Scientific Publications, Oxford.

Reiners, W.A., Bouwman, A.F.; Parsons, W.F.J. & Keller, M. (1994). Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecological Applications*, 4, 363-377.

Rico-Gray, V. & Garcia-Franco, J.G. (1992). Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. *Journal of Vegetation Science*, 3, 617-624.

Riswan, S.; Kenworthy, J.B. & Kartawinata, K. (1985). The estimation of temporal processes in tropical rain forest: a study of primary mixed dipterocarp forest in Indonesia. *Journal of Tropical Ecology*, 1, 171-182.

Roder, W., Calvert, O. & Dorji, Y. (1993). Effect of burning on selected soil parameters in a grass fallow shifting cultivation system in Bhutan. *Plant and Soil*, 149, 51-58.

Rodrigues, W. A. (1963). Estudo de 2,6 hectares de mata de *terra firme* da Serra do Navio, Território do Amapá. *Boletim do Museu Paraense Emílio Goeldi, Botânica*, 19, 1-44.

Rossetti, D.F., Goes, A.M. & Truckenbrodt, W. (1990). A influência marinha nos sedimentos barreiras. *Boletim do Museu Paraense Emilio Goeldi, Ciências da Terra*, 2, 17-29.

Rouw, A. de (1993). Regeneration by sprouting in slash and burn rice cultivation. Taï rain forest, Cote d'Ivoire. *Journal of Tropical Ecology*, 9, 387-408.

Saldarriaga, J.G. (1987). Recovery following shifting cultivation. Case study no.2: A century of succession in the Upper Rio Negro. *Amazonian Rain Forests. Ecosystem Disturbance and Recovery* (ed C. F. Jordan), pp. 24-33. Springer-Verlag, Berlin.

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. *Journal of Ecology*, 76, 938-958.

Salomão, R. P. (1991). Uso de parcelas permanentes para estudos de vegetação da floresta tropical úmida. I- Município de Marabá, Pará. *Boletim de Pesquisa do Museu Paraense Emilio Goeldi, Botânica*, 7, 543-604.

Salomão, R. P. (1994). *Estimativas de biomassa de uma floresta tropical úmida e florestas secundárias da Amazônia oriental*. MSc. thesis, Universidade Federal do Pará, Belém.

Salomão, R.P.; Silva, M.F.F.; Rosa, N.A. (1988). Inventário ecológico em floresta pluvial tropical de *terra firme*, Serra Norte, Carajás, Pará. *Boletim do Museu Paraense Emílio Goeldi, Botânica*, 4, 1-46.

Saulei, S.M. & Swaine, M.D. (1988). Dynamics of seed rain and soil seed banks during forest clearance and subsequent regrowth in the Gogol Valley, Papua New Guinea. *Journal of Ecology*, 76, 133-1152.

Scott, G. A. J. (1977). The importance of old-field succession biomass increments to shifting cultivation. *Great Plains Rocky Mountains Geographical Journal*, 61, 318-327.

Scott, G. A. J. (1987). Shifting cultivation where land is limited. Case study no.3: Campa Indian agriculture in the Gran Pajonal of Peru. *Amazonian Rain Forests. Ecosystem Disturbance and Recovery* (ed C. F. Jordan), pp. 34-45. Springer-Verlag, Berlin.

Seavoy, R.E. (1973). The shading cycle in shifting cultivation. *Annals of the Association of American Geographers*, 63, 522-528.

Silva, M.F.F.; Nanuza, L.M.; Cavalcante, P.B. & Joly, C.A. (1986). Estudos botânicos: histórico, atualidade e perspectivas. *Carajás: Desafio Político, Ecologia e Desenvolvimento*. pp. 184-207. Conselho de Desenvolvimento Científico e Tecnológico (CNPq), Brasília.

Sioli, H. (1973). Recent human activities in the Brazilian Amazon region and their ecological effects. *Tropical Forest Ecosystems in Africa and South America: A Comparative Review* (eds B.J. Meggers; E.S. Ayensu & W.D. Duckworth), pp. 321-324. Smithsonian Institution Press, Washington, DC.

Skoglund, J. (1992). The role of seed banks in vegetation dynamics and restoration of dry tropical ecosystems. *Journal of Vegetation Science*, 3, 357-360.

Skole, D. & Tucker, C. (1993). Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science*, 260, 1905-1910.

Stark, N. (1970). The nutrient content of plants and soils from Brazil and Surinam. *Biotropica*, 2, 51-60.

Steininger, M.K. (1996). Tropical secondary forest regrowth in the Amazon: age, area and change estimation with Thematic Mapper Data. *International Journal of Remote Sensing*, 17, 9-27.

Stocker, G.C. (1981). Regeneration of a north Queensland rain forest following felling and burning. *Biotropica*, 13, 86-92.

Stromgaard, P. (1986). Early secondary succession on abandoned shifting cultivator's plots in the miombo of south central Africa. *Biotropica*, 18, 97-106.

Swaine, M.D. & Hall J.B. (1983). Early succession on cleared forest land in Ghana. *Journal of Ecology*, 71, 601-627.

Swaine, M.D. & Whitmore, T.C. (1988). On the definition of ecological species groups in tropical rain forests. *Vegetatio*, 75, 81-86.

ter Braak, C.J.F. (1988). CANOCO - *A Fortram Program for Canonical Community Ordination by (Partial) (Detrended) (Canonical) Correspondence Analysis, Principal Correspondence Analysis and Redundancy Analysis (Version 2.0).* TNO Institute of Applied Computer Science, Wageninger.

Tergas, L.E. & Popenoe, H.L. (1971). Young secondary vegetation and soil interactions in Izabal, Guatemala. *Plant and Soil*, 34, 675-690.

Thompson, J.; Proctor, J.; Viana, V.; Milliken, W.; Ratter, J.A. & Scott, D.A. (1992). Ecological studies on a lowland evergreen rain forest on Maracá Island, Roraima, Brazil. I. Physical environment, forest structure and leaf chemistry. *Journal of Ecology*, 80, 689-703.

Toky, O.P. & Ramakrishnan, P.S. (1983a). Secondary succession following slash and burn agriculture in north-eastern India. I- biomass, litterfall and productivity. *Journal of Ecology*, 71, 735-745.

Toky, O.P. & Ramakrishnan, P.S. (1983b). Secondary succession following slash and burn agriculture in north-eastern India. II- nutrient cycling. *Journal of Ecology*, 71, 747-757.

Uhl, C. & Clark, K. (1983). Seed ecology of selected Amazon basin successional species. *Botanical Gazette*, 144, 419-425.

Uhl, C. & Jordan C.F. (1984). Succession and nutrient dynamics following forest cutting and burning in Amazonia. *Ecology*, 65, 1476-1490.

Uhl, C. (1987). Factors controlling succession following slash-and-burn agriculture in Amazonia. *Journal of Ecology*, 75, 377-407.

Uhl, C.; Buschbacher, R. & Serrão, E.A.S. (1988). Abandoned pastures in eastern Amazonia. I. patterns of plant succession. *Journal of Ecology*, 76, 663-681.

Uhl, C.; Clark, H. & Clark, K. (1982a). Successional patterns associated with slash-and-burn agriculture in the upper Rio Negro region the Amazon basin. *Biotropica*, 14, 249-254.

Uhl, C.; Jordan, C.; Clark, K.; Clark, H. & Herrera, R. (1982b). Ecosystem recovery in Amazon caatinga forest after cutting, cutting and burning, and bulldozer clearing treatments. *Oikos*, 38, 313-320.

Uhl. C.; Clark, K.; Clark, H. & Murphy, P. (1981). Early plant succession after cutting and burning in the upper Rio Negro region of the Amazon basin. *Journal of Ecology*, 69, 631-649.

USDA (United States Department of Agriculture) (1975). *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys.* Agriculture Handbook 436. USDA, Washington, D.C.

Valverde, O. & Dias, C.V. (1967). *A Rodovia Belém-Brasília. Estudo de Geografia Regional*. Instituto Brasileiro de Geografia. Rio de Janeiro.

Vazquez-Yanes, C. (1980). Notas sobre la autoecologia de los árboles pioneros de rápido crecimiento de la selva tropical lluviosa. *Tropical Ecology*, 21, 103-112.

Vetter Roland, E. & Botosso, P.C. (1989). El Niño may affect growth behavior of Amazonian trees. *Geojournal* 19, 419-421.

Victor, R.G. & Jose, G.G.F. (1992). Vegetation and soil seed bank of successional stages in tropical lowland deciduous forest. *Journal of Vegetation Science*, 3, 617-624.

Vieira, I.C.G.; Salomão, R.P.; Rosa, N.; Nepstad, D.C & Roma, J. & (1996a). O renascimento da floresta no rastro da agricultura. *Revista Ciência Hoje*, 119, 38-44.

Vieira, I.C.G.; Rabelo, N. & Rosa, N.A. (1996b). Características de frutos e sementes de espécies arbóreas da Amazônia. *Anais da I Reunião de Botânicos da Amazônia*. Belém. (in press).

Vieira, I.C.G.; Uhl, C. & Nepstad, D.C. (1994). The role of the shrub *Cordia multispicata* Cham. as a "succession facilitator" in an abandoned pasture, Paragominas, Amazônia. *Vegetatio*, 115, 91-99.

Vieira, L.S.; Santos, W.H.P.; Falesi, J.C. & Oliveira Filho, J.P.S. (1967). Levantamento de reconhecimento dos solos da Região Bragantina, Estado do Pará. *Pesquisa Agropecuária Brasileira*, 2, 1-63.

Vitousek, P.M. (1984). Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, 65, 285-298.

Walkley, A. & Black, I. (1934). An examination of Oegtjareff method for determining soil organic matter and a proposed modification of the chromic acid titration method. *Soil Science*, 37, 29-38.

Warr, S.J.; Thompson, K. & Kent, M. (1993). Seed banks as a neglected area of biogeographic research: a review of literature and sampling techniques. *Progress in Physical Geography*, 17, 329-347.

Whitmore, T.C. (1978). Gaps in the forest canopy. *Tropical Trees as Living Systems* (eds P.B. Tomlinson & M.H. Zimmermann), pp. 639-655. Cambridge University Press, Cambridge.

Whitmore, T.C. (1983). Secondary succession from seed in tropical forests. *Forestry Abstracts*, 44, 767-779.

Whitmore, T.C. (1984). *Tropical Rain Forest of the Far East*. 2nd edition. Clarendon Press, Oxford.

Williams-Linera, G. (1983). Biomass and nutrient content in two successional stages of tropical wet forest in Uxpanapa, Mexico. *Biotropica*, 15, 275-284.

Young, K.R.; Ewel, J.J.; Brown, B.J. (1987). Seed dynamics during forest succession in Costa Rica. *Vegetatio*, 71, 157-173.

Zar, J.H. (1996). *Biostatistical Analysis*. 3rd edition. Prentice-Hall, New Jersey.

APPENDICES

Appendix 1. List of species of woody plants (≥ 5 cm dbh) occurring in the 5-years, 10-years, 20-years and 40-years-old secondary forests in the Bragantina region, Pará, with their authorities, families and number of individuals in all plots sampled in each age.

Species	Family	Forest age-class 5-yrs	10-yrs	20-yrs	40-yrs
Abarema cochleatum (Willd) Barn. & Grim	Mimosaceae	-	3	3	-
Allophyllus sp.	Sapindaceae	-	2	-	-
Ambelania acida Aubl.	Apocynaceae	-	2	-	-
Andira retusa (Lam.) H.B.K.	Fabaceae	-	-	2	-
Annona paludosa Aubl.	Annonaceae	3	1	1	-
Apeiba burchellii Sprague.	Tiliaceae	-	-	2	-
Arthocarpus integrifolia L.F.	Moraceae	-	1	-	-
Astrocaryum mumbaca Mart.	Palmae	-	2	-	4
Banara guianensis Aubl.	Flacourtiaceae	29	2	1	3
Batesia floribunda Spruce ex Benth.	Caesalpiniaceae	-	-	1	-
Bauhinia guianensis Aubl.	Caesalpiniaceae	-	-	4	1
Bauhinia jarensis Wunderlin	Caesalpiniaceae	-	-	6	-
Bauhinia macrostachya Benth	Caesalpiniaceae	-	-	-	6
Bellucia grossularioides (L.) Triana	Melastomataceae	-	-	1	-
Brosimum guianense (Aubl.) Hub.	Moraceae	-	2	1	-
Byrsonima aerugo Sagot.	Malpighiaceae	-	-	1	3
Campomanesia sp.	Myrtaceae	-	-	2	-
Caryocar villosum (Aubl.) Pers.	Caryocaraceae	-	4	-	-
Casearia arborea (L.C. Rich) Urb.	Flacourtiaceae	-	2	-	-
Casearia decandra Jacq.	Flacourtiaceae	-	6	6	2
Casearia grandiflora Camb.	Flacourtiaceae	1	16	6	1
Casearia javitensis HBK	Flacourtiaceae	-	-	-	2
Casearia pitumba Sleumer.	Flacourtiaceae	-	3	1	-
Cassia fastuosa Willd.	Caesalpiniaceae	4	-	-	-
Cecropia distachya Huber	Moraceae	-	-	2	-
Cecropia palmata Willd.	Moraceae	27	2	5	-
Chrysophyllum sparsiflorum K.L.	Sapotaceae	-	-	-	1
Connarus perrottettii (DC.) Planchon.	Connaraceae	-	-	-	2
Cordia nodosa Lam	Boraginaceae	-	2	-	-
Cordia scabrida Mart.	Boraginaceae	-	-	-	5
Cordia scabrifolia A.DC.	Boraginaceae	4	3	17	-
Cordia sp.	Boraginaceae	-	6	-	-
Couratari guianensis Aubl.	Lecythidaceae	-	1	5	-
Coussarea ovalis Stande	Rubiaceae	2	2	-	3
Croton cajucara Benth.	Euphorbiaceae	-	-	5	-
Croton matourensis Aubl.	Euphorbiaceae	32	7	26	17
Cupania scrobiculata L.C. Rich.	Sapindaceae	-	1	6	6
Dalbergia subcymosa Ducke	Fabaceae	-	-	-	1
Didymopanax morototoni (Aubl.) Decne et Planch	Araliaceae	-	-	1	1
Dipteryx odorata (Aubl.) Willd.	Fabaceae	3	3	1	-
Eschweilera coriacea (DC.) Mart. et Berg.	Lecythidaceae	-	-	1	2
Eschweilera pedicellata (Richard) Mori	Lecythidaceae	1	2	1	1
Eschweilera sp.	Lecythidaceae	-	-	1	-
Eugenia muricata DC.	Myrtaceae	-	-	1	-
Eugenia patrisii Vahl.	Myrtaceae	-	-	1	-
Guarea sp.	Meliaceae	-	-	1	-
Gualteria poeppigiana Mart.	Annonaceae	1	2	1	27
Gustavia augusta L.	Lecythidaceae	-	-	10	5
Heisteria acuminata (H & B) Engl.	Olacaceae	-	-	2	-
Himatanthus sucuuba (Spruce) Woodson	Apocynaceae	-	1	6	4
Hippocratea sp.	Hippocrateaceae	-	-	2	-
Hymenaea parvifolia Hub.	Caesalpiniaceae	-	-	-	1
Inga alba (Sw.) Willd.	Mimosaceae	1	1	5	-

Species	Family	Forest age-class 5-yrs	10-yrs	20-yrs	40-yrs
Inga edulis Mart.	Mimosaceae	20	1	12	8
Inga heterophylla Willd.	Mimosaceae	-	-	-	7
Inga ingoides (Rich.) Willd.	Mimosaceae	11	-	8	-
Inga macrophylla HBK	Mimosaceae	-	-	-	2
Inga microcalyx Spruce.	Mimosaceae	-	-	2	-
Inga nitida Willd.	Mimosaceae	3	23	-	-
Inga rubiginosa (Rich.) DC.	Mimosaceae	-	9	3	3
Inga sp.	Mimosaceae	-	-	1	-
Inga thibaudiana DC.	Mimosaceae	1	26	32	5
Inga velutina Willd.	Mimosaceae	7	4	1	-
Jacaranda copaia (Aubl.) D. Don	Bignoniaceae	1	2	2	-
Jacaratia spinosa (Aubl.) A.DC.	Caricaceae	-	-	1	-
Lacistema aggregatum (Berg) Rusby	Lacistemaceae	1	-	-	1
Lacistema pubescens Mart.	Lacistemaceae	3	86	47	43
Lacmellea aculeata (Ducke) Monach.	Apocynaceae	-	-	2	1
Lacunaria jenmani (Oliv.) Ducke	Quiinaceae	-	-	-	1
Lecythis lurida (Miers.) Mori	Lecythidaceae	2	5	10	21
Lecythis pisonis Cambess.	Lecythidaceae	-	2	-	9
Licania kunthiana Hook. F.	Chrysobalanaceae	-	-	2	-
Licania octandra (Hoffmgg. ex R. & S.) Kuntze	Chrysobalanaceae	-	-	3	2
Lindackeria latifolia Bth.	Flacourtiaceae	-	4	1	-
Mabea angustifolia Spruce ex Benth.	Euphorbiaceae	1	4	1	1
Maquira coriacea (Karsten) C.C. Berg.	Moraceae	-	1	-	-
Maquira guianensis Aubl.	Moraceae	-	3	3	9
Margaritaria nobilis (L.F.) Muell. Arg.	Euphorbiaceae	-	-	-	6
Matayba discolor (Sprag.) Radlk.	Sapindaceae	-	2	-	-
Matayba guianensis Aubl.	Sapindaceae	3	-	-	8
Matayba sp.	Sapindaceae	-	-	7	-
Maximiliana maripa (C. Serra) Drude	Palmae	2	4	-	1
Maytenus guianensis K.L.	Celastraceae	-	-	-	1
Miconia minutiflora (Bompl.) DC.	Melastomataceae	-	-	2	-
Miconia sp.	Melastomataceae	-	-	1	-
Myrcia cf. *splendens* (Sw.) DC.	Myrtaceae	-	-	6	-
Myrcia cuprea (Berg.) Kiaerskou	Myrtaceae	1	-	2	-
Myrcia sp.	Myrtaceae	-	-	2	-
Myrcia sylvatica Meyer (DC.)	Myrtaceae	-	1	-	-
Myrciaria floribunda (Wert. ex Willd.) Berg.	Myrtaceae	-	-	2	-
Myriaspora egensis DC.	Melastomataceae	-	1	-	-
Myriaspora sp.	Melastomataceae	-	-	1	-
Nectandra cuspidata Nees	Lauraceae	1	-	2	2
Neea sp.	Nyctaginaceae	-	-	1	6
Ocotea glandulosa Lasser.	Lauraceae	-	-	4	-
Ocotea glomerata (Nees) Mez.	Lauraceae	-	1	-	-
Ormosia nobilis Tul.	Fabaceae	-	-	1	-
Ormosia paraensis Ducke	Fabaceae	-	1	2	-
Paullinia sp.	Sapindaceae	-	2	-	-
Phenakospermum guyannense (L.C. Rich.) Endl. ex Miq.	Musaceae	-	-	-	4
Phyllanthus nobilis Muell. Arg.	Euphorbiaceae	-	4	-	-
Platymiscium trinitatis Benth.	Fabaceae	-	-	-	1
Poecilanthe effusa (Huber.) Ducke	Fabaceae	-	-	-	1
Pogonophora schomburgkiana Miers. ex Benth.	Euphorbiaceae	-	1	-	7
Pseudolmedia murure Standl.	Moraceae	-	-	2	-
Pterocarpus rohrii Vahl.	Caesalpiniaceae	-	-	1	-
Quiina paraensis Pires et Froes.	Quiinaceae	-	-	1	-
Richardella macrophylla (Lam) Eyma	Sapotaceae	-	-	-	2
Rollinia exsucca (DC. ex Dunal) DC.	Annonaceae	4	41	18	21
Sacoglottis guianensis Benth.	Humiriaceae	12	-	-	-

Species	Family	Forest age-class 5-yrs	10-yrs	20-yrs	40-yrs
Sapium aff. *poeppigii* Hemsley	Euphorbiaceae	-	-	-	1
Sapium lanceolatum Hub.	Euphorbiaceae	-	7	6	1
Sclerolobium paraense Hub.	Caesalpiniaceae	-	1	-	-
Serjania paucidentata DC.	Sapindaceae	-	-	-	1
Sloanea grandiflora J.E. Smith	Elaeocarpaceae	-	-	-	2
Sloanea parviflora Planch. ex Benth.	Elaeocarpaceae	-	-	-	1
Spondias mombin L.	Anacardiaceae	6	-	-	-
Stryphnodendron cf. *pulcherrimum* (Willd) Hochr.	Mimosaceae	1	4	-	-
Stryphnodendron guianense (Aubl.) Benth.	Mimosaceae	1	-	11	1
Swartzia brachyrachis Harms	Caesalpiniaceae	-	-	1	-
Swartzia laurifolia Bentham	Caesalpiniaceae	1	1	-	2
Swartzia racemosa Benth.	Caesalpiniaceae	2	-	-	-
Tabebuia serratifolia (Vahl) Nichols.	Bignoniaceae	-	-	-	1
Talisia cf. *subalbens* Radlk.	Sapindaceae	-	2	-	-
Talisia retusa Cowan	Sapindaceae	-	-	2	-
Tapirira guianensis Aubl.	Anacardiaceae	13	9	8	12
Terminalia amazonica (J. Gmelin) Exell	Combretaceae	-	-	3	-
Thyrsodium paraense Huber	Anacardiaceae	-	2	3	8
Trattinickia rhoifolia Willd.	Burseraceae	4	1	-	2
Trema micrantha (L.) Blume	Ulmaceae	1	-	-	-
Unidentified		2	-	-	-
Virola sebifera Aubl.	Myristicaceae	2	-	-	-
Virola surinamensis (Rol.) Warb.	Myristicaceae	-	-	1	-
Vismia cayennensis (Jacq.) Pers.	Clusiaceae	-	-	-	1
Vismia guianensis (Aubl.) Choisy	Clusiaceae	56	75	20	8
Xylopia aromatica (Lam.) Mart.	Annonaceae	-	2	1	-
Xylopia frutescens Aubl.	Annonaceae	-	2	-	-
Xylopia sp.	Annonaceae	1	-	-	-
Zanthoxylum regnellianum Engl.	Rutaceae	-	-	-	7
Zanthoxylum rhoifolium Lam.	Rutaceae	3	33	8	-

Appendix 2. List of species of woody plants (≥ 5 cm dbh) occurring in the primary forest in the Bragantina region, Pará, with their authorities, families and number of individuals (N) in all plots combined.

Species	Family	N
Ambelania acida Aubl.	Apocynaceae	5
Ampelocera edentula Kuhlm.	Ulmaceae	2
Amphirrox surinamensis Eichl.	Violaceae	6
Andira retusa (Lam.) H.B.K.	Fabaceae	1
Aparisthmium cordatum (Juss.) Baill.	Euphorbiaceae	14
Apeiba burchellii Spreng.	Tiliaceae	4
Apeiba echinata Aubl.	Tiliaceae	1
Apuleia leiocarpa (Vog.) Macbr.	Caesalpiniaceae	2
Aspidosperma nitidum Benth. ex Muell	Apocynaceae	1
Astrocaryum mumbaca Mart.	Palmae	4
Astronium lecointei Ducke	Anacardiaceae	2
Banara guianensis Aubl.	Flacourtiaceae	1
Batocarpus cf. *amazonicus* (Ducke) Fosberg	Moraceae	1
Bauhinia jarensis Wunderlin	Caesalpiniaceae	4
Bauhinia macrostachya Benth.	Caesalpiniaceae	2
Bauhinia viridiflora Ducke	Caesalpiniaceae	1
Brosimum guianense (Aubl.) Huber	Moraceae	1
Brosimum lactescens (S. Moore) C.C.	Moraceae	1
Brosimum rubescens Taubert	Moraceae	1
Calyptranthes cf. *macrophylla* Berg	Myrtaceae	7
Calyptranthes sp.	Myrtaceae	5
Carapa guianensis Aubl.	Meliaceae	1
Caryocar glabrum (Aubl.) Pers.	Caryocaraceae	4
Caryocar villosum (Aubl.) Pers.	Caryocaraceae	1
Casearia javitensis H.B.K.	Flacourtiaceae	1
Casearia mariquitensis H.B.K.	Flacourtiaceae	1
Cassipourea guianensis Aubl.	Rhizophoraceae	1
Cecropia distachya Huber	Moraceae	2
Cecropia palmata Willd.	Moraceae	1
Cecropia sp.	Moraceae	1
Cedrela odorata L.	Meliaceae	1
Chamaecrista bahiae (Irwin) Irwin & Barneb.	Caesalpiniaceae	2
Clarisia ilicifolia (Spreng.) Lanj.	Moraceae	2
Clarisia racemosa R. Pav.	Moraceae	1
Conceveiba guianensis Aubl.	Euphorbiaceae	4
Cordia goeldiana Huber	Boraginaceae	1
Cordia scabrifolia A. DC.	Boraginaceae	1
Couepia guianensis ssp *divarica* (Hub.) Prance	Chrysobalanaceae	2
Couratari guianensis Aubl.	Lecythidaceae	4
Coussarea paniculata (Vahl.) Stand.	Rubiaceae	1
Cupania scrobiculata L.C.Rich.	Sapindaceae	4
Dendrobangia boliviana Rusby	Icacinaceae	3
Dialium guianense (Aubl.) Sandw.	Caesalpiniaceae	4
Didymopanax morototoni (Aubl.) Decne.et Planch.	Araliaceae	1
Diospyros melinonii (Hiern) A.C. Sm.	Ebenaceae	2
Diplotropis brasiliensis (Tul.) Benth.	Fabaceae	3
Dipteryx odorata (Aubl.) Willd.	Fabaceae	2
Drypetes variabilis With.	Euphorbiaceae	1
Enterolobium schomburgkii Benth.	Mimosaceae	1

Species	Family	N
Erisma uncinatum Warm.	Vochysiaceae	2
Eschweilera aff. *ovata* (Cambess.) Mier	Lecythidaceae	1
Eschweilera cf. *collina* (Benoist) Eyma	Lecythidaceae	3
Eschweilera coriacea (DC.) Mart. ex Berg.	Lecythidaceae	57
Eschweilera pedicellata (Richard) Mori	Lecythidaceae	5
Eugenia aff. *heterochroma* Diels.	Myrtaceae	1
Eugenia cf. *brachypoda* DC.	Myrtaceae	1
Eugenia cf. *feijoe* Berg.	Myrtaceae	2
Eugenia cf. *lambertiana* DC.	Myrtaceae	1
Eugenia cupulata Amsh.	Myrtaceae	1
Eugenia patrisii Vahl.	Myrtaceae	4
Eugenia schomburgkii Benth.	Myrtaceae	1
Eugenia sp.	Myrtaceae	1
Eugenia tapacumensis Berg.	Myrtaceae	1
Franchetella anibifolia (A.C. Sm.) Aubr.	Sapotaceae	2
Franchetella cf. *reticulata* (Engl.) Aubr.	Sapotaceae	1
Franchetella jariensis Pires	Sapotaceae	3
Franchetella sagotiana (Baill.) Eyma	Sapotaceae	5
Fusaea longifolia (Aubl.) Saff.	Annonaceae	5
Geissospermum sericeum (Sagot.) Benth.	Apocynaceae	10
Goupia glabra Aubl.	Celastraceae	5
Guarea kunthiana A. Juss	Meliaceae	2
Guatteria poeppigiana Mart.	Annonaceae	2
Gustavia augusta L.	Lecythidaceae	45
Hebepetalum humirifolium (Planch.) Benth	Linaceae	1
Heisteria acuminata (H. & B.) Engl.	Olacaceae	9
Helicostylis pedunculata Benoist.	Moraceae	2
Helicostylis scabra (Macbr.) C.C. Berg.	Moraceae	3
Helicostylis tomentosa (P. & E.) Rusby	Moraceae	3
Himatanthus sucuuba (Spruce) Woodson	Apocynaceae	4
Hippocratea cf. *ovata* Lam.	Hippocrateaceae	1
Hirtella racemosa Lam.	Chrysobalanaceae	2
Humiriastrum aff. *excelsum* Ducke	Humiriaceae	1
Hymenaea parvifolia Hub.	Caesalpiniaceae	2
Hymenolobium excelsum Ducke	Fabaceae	1
Ilex parviflora Benth.	Aquifoliaceae	1
Inga alba (Sw.) Willd.	Mimosaceae	2
Inga auristellae Harms.	Mimosaceae	1
Inga falcistipula Ducke	Mimosaceae	3
Inga gracilifolia Ducke	Mimosaceae	2
Inga nitida Willd.	Mimosaceae	1
Inga rubiginosa (Rich.) DC.	Mimosaceae	1
Inga thibaudiana DC.	Mimosaceae	2
Iriartea exorrhiza Drude	Palmae	1
Iryanthera sagotiana (Bth.) Warb.	Myristicaceae	2
Lacmellea aculeata (Ducke) Monach.	Apocynaceae	3
Lacmellea floribunda (Poeppig.) Bentg.	Apocynaceae	2
Lacunaria crenata (Tul.) A.C. Sm.	Quiinaceae	8
Lecythis idatimon Aubl.	Lecythidaceae	28
Lecythis lurida (Miers.) Mori	Lecythidaceae	8
Lecythis pisonis Cambess.	Lecythidaceae	1
Licania canescens R. Ben.	Chrysobalanaceae	7
Licania heteromorpha Benth.	Chrysobalanaceae	4

Species	Family	N
Licania kunthiana Hook. F.	Chrysobalanaceae	1
Licania menbranaceae R. Ben	Chrysobalanaceae	2
Licania octandra (Hoffmgg. ex R.S.) Kuntze	Chrysobalanaceae	2
Licania sp.	Chrysobalanaceae	3
Licaria armeniaca (Nees) Kost.	Lauraceae	2
Mabea speciosa Mull. Arg.	Euphorbiaceae	16
Mapouria cf. *fockeana* (Miq.) Brem	Rubiaceae	2
Maprounea guianensis Aubl.	Euphorbiaceae	2
Maquira guianensis Aubl.	Moraceae	3
Matayba cf. *guianensis* Aubl.	Sapindaceae	2
Matayba macrostylis Radlk.	Sapindaceae	1
Maytenus myrsinoides Reissek	Celastraceae	2
Miconia cf. *serialis* DC.	Melastomataceae	3
Miconia cf. *stenostachya* DC.	Melastomataceae	1
Miconia nervosa (SM.) Triana	Melastomataceae	1
Miconia poeppigii Triana	Melastomataceae	3
Miconia sp.	Melastomataceae	1
Micropholis guianensis Pierre	Sapotaceae	5
Micropholis venulosa (Mart. & Eich.)	Sapotaceae	1
Minquartia guianensis Aubl.	Olacaceae	2
*Mouriri brachyanthera*Ducke	Melastomataceae	5
Myrcia cf. *laruotteana* Camb.	Myrtaceae	1
Myrcia fallax (Rich.) DC.	Myrtaceae	1
Myrcia sylvatica (Meyer) DC.	Myrtaceae	3
Myrciaria tenella (DC.) Berg	Myrtaceae	2
Nectandra aff. *globosa* Mez.	Lauraceae	9
Neea sp.	Nyctaginaceae	6
Neoptychocarpus apodanthus (Kuhlm.) Bucheim	Flacourtiaceae	1
Newtonia psilostachya (DC.) Brenan	Mimosaceae	3
Newtonia suaveolens (Miq.) Brenan	Mimosaceae	3
Ocotea cajumari Mart.	Lauraceae	2
Ocotea caudata Mez.	Lauraceae	4
Parkia pendula Benth.	Fabaceae	1
Pithecellobium racemosum Ducke	Mimosaceae	1
Planchonella oblanceolata Pires	Sapotaceae	3
Planchonella prieurii (A. DC.) Pires	Sapotaceae	2
Pogonophora schomburgkiana Miers.ex Benth.	Euphorbiaceae	5
Poraqueiba guianensis Aubl.	Icacinaceae	10
Pourouma acuminata Mart.	Moraceae	5
Pourouma guianensis Aubl.	Moraceae	1
Pouteria echinocarpa W.A. Rich.	Sapotaceae	1
Pouteria engleri Eyma	Sapotaceae	1
Pouteria lasiocarpa (Mart.) Radlk.	Sapotaceae	1
Pradosia cf. *granulosa* Pires & Penning	Sapotaceae	1
Prieurela prieurii (A.DC.) Aubr.	Sapotaceae	1
Protium decandrum (Aubl.) March.	Burseraceae	8
Protium heptaphyllum (Aubl.) March.	Burseraceae	3
Protium pilosum (Cuatr.) Daly	Burseraceae	16
Protium sagotianum Marchand	Burseraceae	5
Protium sp.	Burseraceae	1
Protium spruceanum (Benth.) Engl.	Burseraceae	1
Protium tenuifolium (Engl.) Engl.	Burseraceae	6
Protium trifoliolatum Engl.	Burseraceae	11

Appendix 2 (cont.)

Species	Family	N
Prunus myrtifolia (L.) Urb.	Rosaceae	1
Pseudolmedia murure Standley	Moraceae	1
Pterocarpus rohrii Vahl.	Caesalpiniaceae	2
Qualea albiflora Warm.	Vochysiaceae	1
Qualea paraensis Ducke	Vochysiaceae	1
Rheedia acuminata (R. et P.) Pl. et Tr.	Clusiaceae	1
Rinorea neglecta Sandw.	Violaceae	7
Rinorea passoura (DC.) Kuntz.	Violaceae	1
Sagotia racemosa Baill.	Euphorbiaceae	3
Salacia cf. *martiana* Peyr.	Hippocrateaceae	2
Sandwithiodoxa egregia (Sandw.) Aubl.	Sapotaceae	5
Sapium cf. *poeppigii* Hemsley.	Euphorbiaceae	4
Siparuna decipiens (Tul.) A. DC.	Monimiaceae	1
Sloanea garckeana Schum.	Elaeocarpaceae	3
Sloanea parviflora Planch. ex Benth.	Elaeocarpaceae	2
Sloanea sp.	Elaeocarpaceae	2
Sterculia cf. *pilosa* Ducke	Sterculiaceae	1
Sterculia pruriens (Aubl.) Schum.	Sterculiaceae	14
Sterculia speciosa Schum.	Sterculiaceae	1
Swartzia brachyrachis Harms.	Caesalpiniaceae	2
Symphonia globulifera L. F.	Clusiaceae	3
Tabebuia serratifolia (Vahl.) Nichols.	Bignoniaceae	3
Tachigalia alba Ducke	Caesalpiniaceae	8
Tachigalia myrmecophila Ducke	Caesalpiniaceae	2
Tachigalia paniculata Aubl.	Caesalpiniaceae	5
Talisia cf. *macrophylla* (Mart.) Radlk	Sapindaceae	3
Talisia floribunda	Sapindaceae	1
Talisia retusa Cowan	Sapindaceae	5
Talisia subalbens Radlk.	Sapindaceae	1
Tapirira guianensis Aubl.	Anacardiaceae	7
Terminalia amazonica (J. Gmelin) Exell.	Combretaceae	1
Terminalia argentea C. Martius	Combretaceae	1
Terminalia guianensis Eichl.	Combretaceae	1
Theobroma speciosum Willd.	Sterculiaceae	9
Thyrsodium paraense Huber	Anacardiaceae	6
Trattinickia rhoifolia Willd.	Burseraceae	2
Trichilia cf. *quadrijuga* H.B.K.	Meliaceae	2
Trichilia micrantha Benth.	Meliaceae	11
Trichilia schomburgkii C. DC.	Meliaceae	7
Trichilia septentrionalis C. DC.	Meliaceae	1
Virola michelii Heckel	Myristicaceae	16
Vitex triflora Vall.	Verbenaceae	1
Vochysia vismiaefolia Spr.ex Warm.	Vochysiaceae	1
Xylopia aromatica (Lam.) Mart	Annonaceae	1
Zollernia paraensis Hub.	Caesalpiniaceae	1

Appendix 3. List of species used in DCA and TWINSPAN analysis with their numbers and codes.

No.	Code	Species
21	Trat rho	*Trattinickia rhoifolia*
40	Dipt odo	*Dipteryx odorata*
62	Inga alb	*Inga alba*
1	Spon mom	*Spondias mombin*
4	Anno pal	*Annona paludosa*
15	Cord sp.	*Cordia* sp.
33	Crot mat	*Croton matourensis*
39	Sapi lan	*Sapium lanceolatum*
41	Bana gui	*Banara guianensis*
45	Vism gui	*Vismia guianensis*
46	Sacc gui	*Saccoglotis guianensis*
66	Inga nit	*Inga nitida*
69	Inga vel	*Inga velutina*
72	Cecr pal	*Cecropia palmata*
79	Myrc cf.	*Myrcia* cf. *splendens*
84	Maxi mar	*Maximilana maripa*
88	Zant rho	*Zanthoxylum rhoifolium*
2	Tapi gui	*Tapirira guianensis*
12	Jaca cop	*Jacaranda copaia*
14	Cord sca	*Cordia scabrida*
22	Bauh gui	*Bauhinia guianensis*
50	Nect cus	*Nectandra cuspidata*
63	Inga edu	*Inga edulis*
65	Inga ing	*Inga ingoides*
7	Roll exs	*Rollinia exsucca*
13	Cord scb	*Cordia scabrifolia*
32	Crot caj	*Croton cajucara*
35	Mabe ang	*Mabea angustifolia*
36	Marg nob	*Margaritaria nobilis*
42	Case dec	*Casearia decandra*
43	Case gra	*Casearia grandifolia*
44	Lind lat	*Lindackeria latifolia*
48	Laci pub	*Lacistema pubescens*
61	Abar coc	*Abarema cochleatum*
64	Inga het	*Inga heterophylla*
68	Inga thi	*Inga thibaudiana*
70	Stry gui	*Stryphnodendron guianense*
71	Stry pul	*Stryphnodendron* cf. *pulcherrimum*
81	Neea sp3	*Neea* sp.
86	Cous ova	*Coussarea ovata*
87	Zant reg	*Zanthoxylum regnelianum*
91	Mata sp.	*Matayba* sp.
6	Guat poe	*Guatteria poeppigiana*
56	Lecy lur	*Lecythis lurida*
57	Lecy pis	*Lecythis pisonis*
67	Inga rub	*Inga rubiginosa*
73	Maqu gui	*Maquira guianensis*
3	Thyr par	*Thyrsodium paraense*
10	Hima suc	*Himatanthus sucuuba*
24	Bauh mac	*Bauhinia macrostachya*
27	Cary vil	*Caryocar villosum*
30	Lica oct	*Licania octandra*

Appendix 3 (cont.)

No.	Code	Species
89	Cupa scr	*Cupania scrobiculata*
90	Mata gui	*Matayba guianensis*
23	Bauh jar	*Bauhinia jarensis*
51	Cour gui	*Couratari guianensis*
53	Esch ped	*Eschweilera pedicellata*
11	Lacm acu	*Lacmelea aculeata*
37	Pogo sch	*Pogonophora schomburgkiana*
83	Astr mum	*Astrocaryum mumbaca*
54	Gust aug	*Gustavia augusta*
92	Tali ret	*Talisia retusa*
9	Geis ser	*Geissospermum sericeum*
25	Tach alb	*Tachigalia alba*
26	Tach pan	*Tachigalia paniculata*
49	Nect glo	*Nectandra* aff. *globosa*
77	Caly sp	*Calyptranthes* sp.
78	Euge pat	*Eugenia patrisii*
80	Neea sp1	*Neea* sp.
82	Heis acu	*Heisteria acuminata*
85	Lacu cre	*Lacunaria crenata*
93	Fran sag	*Franchetella sagotiana*
95	Sand egr	*Sandwithiodoxa egregia*
96	Ster pru	*Sterculia pruriens*
97	Theo spe	*Theobroma speciosum*
99	Amph sur	*Amphirrox surinamensis*
8	Ambe aci	*Ambelania acida*
19	Prot ten	*Protium tenuifolium*
74	Pour acu	*Pourouma acuminata*
75	Viro mic	*Virola michelii*
98	Apei bur	*Apeiba burchelii*
5	Fusa lon	*Fusaea longifolia*
16	Prot dec	*Protium decandrum*
17	Prot pil	*Protium pilosum*
18	Prot sag	*Protium sagotianum*
20	Prot tri	*Protium trifoliolatum*
28	Goup gla	*Goupia glabra*
29	Lica can	*Licania canescens*
31	Apar cor	*Aparisthimium cordatum*
34	Mabe spe	*Mabea* aff. *speciosa*
38	Sapi poe	*Sapium* cf. *poepigii*
47	Pora gui	*Poraqueiba guianensis*
52	Esch cor	*Eschweilera coriacea*
55	Lecy ida	*Lecythis idatimon*
58	Mour bra	*Mouriri brachyanthera*
59	Tric mic	*Trichilia micrantha*
60	Tric sch	*Trichilia schomburgkii*
76	Caly mac	*Calyptranthes* cf. *macrophylla*
94	Micr gui	*Micropholis guianensis*
100	Rino neg	*Rinorea neglecta*

Appendix 4. List of species of woody plants (≥ 10 cm dbh) occuring in the primary forest in the Bragantina region, Pará, with their authorities, families and number of individuals (N) in all transects sampled.

Species	Family	N
Acacia multipinnata Ducke	Mimosaceae	3
Aiouea sp.	Lauraceae	2
Allophyllus cf. *punctatus* (E.& P.) Radlk.	Sapindaceae	2
Amaioua guianensis Aubl.	Rubiaceae	1
Ambelania acida Aubl.	Apocynaceae	2
Ampelocera edentula Kuhlm.	Ulmaceae	8
Amphirrox surinamensis Eichl.	Violaceae	1
Anacardium giganteum Hanc. ex Engl.	Anacardiaceae	1
Andira retusa (Lam.) H.B.K.	Fabaceae	1
Aniba panurensis (Messner) Mez	Lauraceae	1
Aparisthmium cordatum (Juss.) Baill.	Euphorbiaceae	6
Apeiba burchellii Spreng.	Tiliaceae	28
Apeiba echinata Aubl.	Tiliaceae	3
Apuleia leiocarpa (Vog.) Macbr.	Caesalpiniaceae	10
Arrabidaea tuberculata DC.	Bignoniaceae	1
Aspidosperma cf. *eteanum* MGF.	Apocynaceae	1
Aspidosperma desmanthum Benth. ex Muell	Apocynaceae	9
Aspidosperma nitidum Benth. ex Muell	Apocynaceae	1
Astronium lecointei Ducke	Anacardiaceae	5
Bagassa guianensis Aubl.	Moraceae	1
Bauhinia guianensis Aubl.	Caesalpiniaceae	12
Bauhinia macrostachya Benth.	Caesalpiniaceae	4
Brosimum lactescens (S. Moore) C.C.	Moraceae	1
Brosimum rubescens Taubert	Moraceae	1
Calycolpus sp.	Myrtaceae	4
Calyptranthes sp.	Myrtaceae	5
Campomanesia cf. *aromatica* (Aubl.) Griseb Baech.	Myrtaceae	2
Carapa guianensis Aubl.	Meliaceae	4
Caryocar glabrum (Aubl.) Pers.	Caryocaraceae	6
Caryocar villosum (Aubl.) Pers.	Caryocaraceae	1
Casearia decandra Jacq.	Flacourtiaceae	1
Casearia mariquitensis HBK	Flacourtiaceae	6
Cecropia distachya Huber	Moraceae	20
Cecropia obtusa Trec.	Moraceae	1
Cecropia sciadophylla Mart.	Moraceae	1
Cedrela odorata L.	Meliaceae	1
Chamaecrista bahiae (Irwin) Irwin & Barneb.	Caesalpiniaceae	2
Clarisia racemosa R. Pav.	Moraceae	9
Combretum laxum Jacq.	Combretaceae	1
Combretum sp.	Combretaceae	1
Conceveiba guianensis Aubl.	Euphorbiaceae	3
Copaifera duckei Dwyer	Caesalpiniaceae	1
Cordia goeldiana Huber	Boraginaceae	4
Cordia scabrida Mart.	Boraginaceae	1
Cordia scabrifolia A. DC.	Boraginaceae	1
Couepia aff. *magnoliifolia* Benth.	Chrysobalanaceae	1
Couepia guianensis ssp *divarica* (Hub.)Prance	Chrysobalanaceae	8
Couratari aff. *multiflora* (Smith) Eyma	Lecythidaceae	5
Couratari guianensis Aubl.	Lecythidaceae	3
Coussarea paniculata (Vahl.) Stand.	Rubiaceae	11

Species	Family	N
Croton cajucara Benth	Euphorbiaceae	2
Croton matourensis (Aubl.) M. Arg.	Euphorbiaceae	4
Davilla kunthii St. Hil.	Dilleniaceae	3
Dendrobangia boliviana Rusby	Icacinaceae	9
Dialium guianense (Aubl.) Sandw.	Caesalpiniaceae	3
Didymopanax morototoni (Aubl.) Decne. et Planch.	Araliaceae	2
Diospyros artanthifolia Mart.	Ebenaceae	1
Diospyros melinonii (Hiern) A.C. Sm	Ebenaceae	5
Dipteryx odorata (Aubl.) Willd.	Fabaceae	1
Drypetes variabilis With.	Euphorbiaceae	2
Duguetia echinophora R.E. Fries	Annonaceae	1
Enterolobium schomburgkii Benth.	Mimosaceae	2
Erisma uncinatum Warm.	Vochysiaceae	7
Eschweilera aff. *ovata* (Cambess.) Mier	Lecythidaceae	7
Eschweilera amazonica R. Kunth.	Lecythidaceae	1
Eschweilera cf. *collina* (Benoist) Eyma	Lecythidaceae	10
Eschweilera coriacea (DC.) Mart. ex Berg	Lecythidaceae	124
Eschweilera pedicellata (Richard) Mori	Lecythidaceae	8
Eugenia cf. *feijoe* Berg.	Myrtaceae	3
Eugenia cf. *lambertiana* DC.	Myrtaceae	6
Eugenia mimius Mac. Vaugh	Myrtaceae	1
Eugenia patrisii Vahl.	Myrtaceae	3
Eugenia sp.	Myrtaceae	2
Ficus gomelleira Kunth.	Moraceae	1
Franchetella anibifolia (A.C. Sm.) Aubr	Sapotaceae	8
Franchetella gongrijpii Eyma	Sapotaceae	3
Franchetella jariensis Pires	Sapotaceae	12
Franchetella sagotiana (Baill.) Eyma	Sapotaceae	8
Geissospermum sericeum (Sagot.) Benth.	Apocynaceae	14
Goupia glabra Aubl.	Celastraceae	7
Guarea kunthiana A. Juss	Meliaceae	5
Guatteria poeppigiana Mart.	Annonaceae	3
Gustavia augusta L.	Lecythidaceae	25
Hebepetalum humirifolium (Planch.) Benth	Linaceae	1
Heisteria acuminata (H. & B.) Engl.	Olacaceae	4
Helicostylis cf. *elegans* (Macbr.) C.C. B	Moraceae	1
Helicostylis tomentosa (P. & E.) Rusby	Moraceae	9
Heteropteris sp.	Malphighiaceae	1
Himatanthus sucuuba (Spruce) Woodson	Apocynaceae	6
Hippocratea sp.	Hippocrateaceae	1
Humiriastrum aff. *excelsum* Ducke	Humiriaceae	4
Hymenaea parvifolia Hub.	Caesalpiniaceae	5
Inga alba (Sw.) Willd.	Mimosaceae	11
Inga falcistipula Ducke	Mimosaceae	4
Inga gracilifolia Ducke	Mimosaceae	9
Inga marginata Willd.	Mimosaceae	7
Inga nitida Willd.	Mimosaceae	1
Inga rubiginosa (Rich.) DC.	Mimosaceae	5
Inga thibaudiana DC.	Mimosaceae	4
Iriartea exorrhiza Drude	Palmae	1
Iryanthera sagotiana (Bth.) Warb.	Myristicaceae	5
Jacaranda copaia D. Don.	Bignoniaceae	5
Jacaratia spinosa (Aubl.) DC.	Caricaceae	10

Species	Family	N
Lacmellea aculeata (Ducke) Monach.	Apocynaceae	6
Lacunaria jenmanii (Oliv.) Ducke	Quiinaceae	2
Lacunaria crenata (Tul) A.C. Sm.	Quiinaceae	8
Laetia procera (P. et Endl.) Eichl.	Flacourtiaceae	8
Lecythis idatimon Aubl.	Lecythidaceae	96
Lecythis lurida (Miers.) Mori	Lecythidaceae	10
Lecythis pisonis Cambess.	Lecythidaceae	9
Licania canescens R. Ben.	Chrysobalanaceae	14
Licania heteromorpha Benth.	Chrysobalanaceae	11
Licania membranacea R. Ben	Chrysobalanaceae	2
Licania octandra (Hoffmgg. ex R.& S.) Kuntze	Chrysobalanaceae	3
Licania sp.	Chrysobalanaceae	3
Lindackeria paraensis Kuhlm	Flacourtiaceae	2
Luheopsis duckeana Burret	Tiliaceae	3
Mabea speciosa Mull. Arg.	Euphorbiaceae	35
Machaerium ferox (Mart. ex Benth) Ducke	Fabaceae	1
Machaerium sp.	Fabaceae	1
Mapouria sp.	Rubiaceae	1
Maprounea guianensis Aubl.	Euphorbiaceae	2
Maquira guianensis Aubl.	Moraceae	4
Maripa sp.	Convolvulaceae	1
Matayba cf. *guianensis* Aubl.	Sapindaceae	3
Matayba macrostylis Radlk.	Sapindaceae	10
Maytenus myrsinoides Reissek	Celastraceae	11
Metrodorea flavida Krause	Rutaceae	2
Miconia poeppigii Triana	Melastomataceae	4
Miconia cf. *serialis* DC.	Melastomataceae	4
Miconia sp.	Melastomataceae	1
Micropholis guianensis Pierre	Sapotaceae	13
Micropholis venulosa (Mart. & Eich.) Pires	Sapotaceae	1
Minquartia guianensis Aubl.	Olacaceae	6
Mouriri brachyanthera Ducke	Melastomataceae	15
Myrcia amazonica DC.	Myrtaceae	1
Myrcia cf. *laruotteana* Camb.	Myrtaceae	1
Myrcia sp.	Myrtaceae	1
Myrcia sylvatica (Meyer) DC.	Myrtaceae	6
Myrciaria tenella (DC.) Berg	Myrtaceae	1
Nectandra aff. *globosa* Mez.	Lauraceae	23
Nectandra aff. *pichurim* (H.B.K.) Mez	Lauraceae	1
Neea sp.	Nyctaginaceae	14
Newtonia psilostachya (DC.) Brenan	Mimosaceae	15
Newtonia suaveolens (Miq.) Brenan	Mimosaceae	11
Ocotea argyrophylla Ducke	Lauraceae	1
Ocotea cajumari Mart.	Lauraceae	10
Ocotea caudata Mez.	Lauraceae	5
Ocotea rubra Mez.	Lauraceae	2
Ocotea sp.	Lauraceae	1
Oenocarpus distichus Mart.	Palmae	2
Ormosia sp.	Fabaceae	1
Parahancornia amapa (Huber) Ducke	Anacardiaceae	1
Parinari rodolphii Huber	Chrysobalanaceae	1
Parkia gigantocarpa Ducke	Mimosaceae	1

Appendix 4 (cont.)

Species	Family	N
Parkia ulei (Harms.) Kuhlm.	Mimosaceae	2
Pithecellobium racemosum Ducke	Mimosaceae	8
Planchonella oblanceolata Pires	Sapotaceae	8
Planchonella prieurii (A.DC.)Pires	Sapotaceae	3
Pogonophora schomburgkiana Miers. ex Benth	Euphorbiaceae	11
Poraqueiba guianensis Aubl.	Icacinaceae	24
Pourouma acuminata Mart.	Moraceae	4
Pourouma guianensis Aubl.	Moraceae	1
Pourouma velutina Miq.	Moraceae	3
Pouteria echinocarpa W. A. Rich	Sapotaceae	1
Pouteria guianensis Aubl.	Sapotaceae	1
Pouteria heterosepala Pierre	Sapotaceae	1
Pouteria hispida Eyma	Sapotaceae	2
Pouteria lasiocarpa (Mart.) Radlk.	Sapotaceae	1
Pouteria sp.	Sapotaceae	1
Pradosia cf. *granulosa* Pires & Penning	Sapotaceae	2
Protium aff. *subserratum* (Engl.) Engl.	Burseraceae	2
Protium aracouchini (Aubl.) March.	Burseraceae	3
Protium decandrum (Aubl.) March.	Burseraceae	8
Protium pilosum (Cuatr.) Daly	Burseraceae	1
Protium sagotianum Marchand	Burseraceae	16
Protium sp.	Burseraceae	3
Protium tenuifolium (Engl.) Engl.	Burseraceae	11
Protium trifoliolatum Engl.	Burseraceae	6
Prunus myrtifolia (L.) Urb.	Rosaceae	3
Pseudolmedia murure Standley	Moraceae	2
Pterocarpus rohrii Vahl.	Caesalpiniaceae	3
Qualea albiflora Warm.	Vochysiaceae	2
Qualea paraensis Ducke	Vochysiaceae	7
Quiina cf. *duckei* Pires	Quiinaceae	3
Radlkoferella macrocarpa (Hub.) Aubr.	Sapotaceae	3
Rauwolfia paraensis Ducke	Apocynaceae	1
Rheedia acuminata (R. et P.) Pl. et Tr.	Clusiaceae	3
Saccoglottis guianensis Benth.	Humiriaceae	1
Sandwithiodoxa egregia (Sandw.) Aubl.	Sapotaceae	9
Sapium aff. *poeppigii* Hemsley	Euphorbiaceae	7
Sclerolobium paraense Hub.	Caesalpiniaceae	9
Simaruba amara Aubl.	Simarubaceae	3
Simaruba cf. *multiflora* A. Juss.	Simarubaceae	1
Sloanea garckeana Schum.	Elaeocarpaceae	7
Sloanea grandiflora J.E. Smith	Elaeocarpaceae	1
Solanum sp.	Solanaceae	1
Sterculia cf. *pilosa* Ducke	Sterculiaceae	1
Sterculia pruriens (Aubl.) Schum.	Sterculiaceae	7
Sterculia speciosa Schum.	Sterculiaceae	1
Strychnos cf. *jobertiana* Baill.	Loganiaceae	1
Strychnos sp.	Loganiaceae	1
Stryphnodendron barbadetiman (Vel.) Mart.	Mimosaceae	1
Stryphnodendron pulcherrimum Hochr.	Mimosaceae	2
Symphonia globulifera L. F.	Clusiaceae	14
Tabebuia serratifolia (Vahl.) Nichols.	Bignoniaceae	4
Tachigalia alba Ducke	Caesalpiniaceae	12
Tachigalia myrmecophila Ducke	Caesalpiniaceae	1

Appendix 4 (Cont.)

Species	Family	N
Tachigalia paniculata Aubl.	Caesalpiniaceae	2
Talisia retusa Cowan	Sapindaceae	5
Talisia subalbens Radlk.	Sapindaceae	1
Tapirira guianensis Aubl.	Anacardiaceae	20
Teuerminalia amazonica (J. Gmelin) Exell.	Combretaceae	3
Terminalia argentea C.Mart.	Combretaceae	2
Tetracera willdenowiana Stend.	Dilleniaceae	1
Tetragastris altissima (Aubl.) Swart.	Burseraceae	2
Tetrapterys cf. *discolor* (Mey) DC.	Malphighiaceae	1
Theobroma grandiflorum (Willd. ex Spreng.) K.	Sterculiaceae	1
Theobroma speciosum Willd.	Sterculiaceae	5
Thyrsodium paraense Huber	Anacardiaceae	11
Tovomita aff. *schomburgkii* Pl. et Tr.	Clusiaceae	1
Trattinickia rhoifolia Willd.	Burseraceae	4
Trichilia cf. *rubra* C. DC.	Meliaceae	2
Trichilia micrantha Benth.	Meliaceae	14
Trichilia schomburgkii C. DC.	Meliaceae	13
Trichilia septentrionalis C. DC.	Meliaceae	5
Trymatococcus cf. *oligandrus* (R. Ben.) Lanj.	Moraceae	1
Virola michelii Heckel	Myristicaceae	20
Vismia cayennensis (Jacq.) Pers.	Clusiaceae	2
Vitex triflora Vall.	Verbenaceae	1
Vochysia vismiaefolia Spr.ex Warm.	Vochysiaceae	5
Xylopia nitida Dun.	Annonaceae	1
Zanthoxylum regnellianum Engl.	Rutaceae	3

Appendix 5. List of species of woody plants (≥ 10 cm dbh) occurring in a 40-years-old secondary forestin the Bragantina region, Pará, with their authorities, families and number of individuals (N) sampled.

Species	Family	N
Abarema cochleatum (Willd) Barn. & Grim.	Mimosaceae	1
Apeiba albiflora Ducke	Tiliaceae	3
Apeiba burchellii Sprague.	Tiliaceae	4
Apuleia leiocarpa (Vog.) Macbr.	Clusiaceae	1
Batocarpus amazonicus (Ducke) Fosberg	Moraceae	1
Buchenavia aff. *tetraphylla* (Aublet.)Howard.	Combretaceaea	1
Byrsonima aerugo Sagot.	Malpighiaceae	14
Casearia decandra Jacq.	Flacourtiaceae	7
Cecropia palmata Willd.	Moraceae	1
Connarus perrottettii (DC.) Planchon.	Connaraceae	1
Cordia scabrida Mart.	Boraginaceae	15
Cordia scabrifolia A. DC.	Boraginaceae	1
Couratari guianensis Aubl.	Lecythidaceae	2
Coussarea ovalis Stande	Rubiaceae	5
Croton matourensis Aubl.	Euphorbiaceae	97
Cupania scrobiculata L.C. Rich.	Sapindaceae	1
Didymopanax morototoni (Aubl.) Decne et Planch	Araliaceae	1
Dipteryx odorata (Aubl.) Willd.	Fabaceae	7
Enterolobium schomburgkii Benth.	Mimosaceae	1
Eschweilera pedicellata (Richard) Mori	Lecythidaceae	1
Eugenia sp.	Myrtaceae	1
Guatteria poeppigiana Mart.	Annonaceae	25
Himatanthus sucuuba (Spruce) Woodson	Apocynaceae	7
Hymenaea parvifolia Hub.	Caesalpiniaceae	5
Inga alba (Sw.) Willd.	Mimosaceae	3
Inga edulis Mart.	Mimosaceae	9
Inga rubiginosa (Rich.) DC.	Mimosaceae	18
Inga thibaudiana DC.	Mimosaceae	9
Lacistema pubescens Mart.	Lacistemaceae	15
Lacmellea aculeata (Ducke) Monach.	Apocynaceae	1
Lacunaria jenmani (Oliv.) Ducke	Quiinaceae	1
Lecythis lurida (Miers.) Mori	Lecythidaceae	7
Lecythis pisonis Cambess.	Lecythidaceae	7
Licania heteromorpha Benth.	Chrysobalanaceae	2
Licania octandra (Hoffmgg. ex R. & S.) Kuntze	Chrysobalanaceae	5
Lindackeria paraensis Kuhlm.	Flacourtiaceae	1
Maprounea guianensis Aubl.	Euphorbiaceae	1
Maquira guianensis Aubl.	Moraceae	4
Margaritaria nobilis (L.F.) Muell. Arg.	Euphorbiaceae	30
Matayba guianensis Aubl.	Sapindaceae	9
Maximiliana maripa (C. Serra) Drude	Palmae	4
Maytenus guianensis K.L.	Celastraceae	2
Nectandra cuspidata Nees	Lauraceae	4
Neea sp.	Nyctaginaceae	3
Ocotea glomerata (Nees) Mez.	Lauraceae	1
Ormosia paraensis Ducke	Fabaceae	6
Platymiscium trinitatis Benth.	Fabaceae	2
Pogonophora schomburgkiana Miers. ex Benth.	Euphorbiaceae	3
Pouteria hispida Eyma	Sapotaceae	1

Appendix 5 (cont.)

Species	Family	N
Pseudolmedia murure Standl.	Moraceae	1
Rheedia acuminata (R. et P.) Pl. et Tr.	Clusiaceae	1
Richardella macrophylla (Lam) Eyma	Sapotaceae	1
Rollinia exsucca (DC. ex Dunal) DC.	Annonaceae	31
Sapium lanceolatum Hub.	Euphorbiaceae	3
Sapium cf. *poeppigii* Hemsley	Euphorbiaceae	1
Sloanea parviflora Planch. ex Benth.	Elaeocarpaceae	1
Stryphnodendron guianense (Aubl.) Benth.	Mimosaceae	5
Talisia cf. *subalbens* Radlk.	Sapindaceae	1
Talisia retusa Cowan	Sapindaceae	1
Tapirira guianensis Aubl.	Anacardiaceae	53
Thyrsodium paraense Huber	Anacardiaceae	8
Trattinickia rhoifolia Willd.	Burseraceae	4
Vismia guianenis (Aubl.) Choisy	Clusiaceae	17
Xylopia longifolia (Sagot) R. & Tries	Annonaceae	1
Xylopia sp.	Annonaceae	1
Zanthoxylum regnellianum Engl.	Rutaceae	12

Appendix 6. List of species occurring in the seed bank (0 - 10 cm) of 5-years, 10-years and 20-years-old secondary forests and a primary forest (PF) in the Bragantina region, Pará, with their authorities, families and number of seeds sampled in each forest age-class.

Species	Family	5-yrs	10-yrs	20-yrs	PF
Ageratum conyzoides L	Compositae	1	-	-	-
Andropogon bicornis L.	Gramineae	-	-	-	1
Annona densicoma Mart.	Annonaceae	-	-	2	-
Apeiba burchellii Sprague	Tiliaceae	-	-	-	1
Axonopus compressus (Sw.) Beauv.	Gramineae	2	13	51	20
Banara guianensis Aubl.	Flacourtiaceae	3	5	6	-
Blepharodon nitidum (Vell.) Macbr.	Asclepiadaceae	3	-	-	-
Borreria latifolia (Aubl.) Schum.	Rubiaceae	301	67	49	8
Borreria verticillata (L.) Mey	Rubiaceae	636	154	17	6
Calytrocarya bicolor T. Koyama	Cyperaceae	-	-	-	2
Calytrocarya sp.	Cyperaceae	-	-	-	2
Casearia decandra Jacq.	Flacourtiaceae	-	5	2	12
Casearia grandiflora Camb.	Flacourtiaceae	-	7	1	-
Cassia fastuosa Willd.	Mimosaceae	1	-	-	-
Cassia obtusifolia L.	Mimosaceae	-	-	2	-
Cecropia palmata Willd.	Moraceae	101	106	129	98
Cestrum laevigatum Schlecht.	Solanaceae	-	6	7	4
Cissampelos fasciculata Benth.	Menispermaceae	-	-	2	-
Clidemia hirta (L.) D. Don	Melastomataceae	170	199	83	37
Commelina sp.	Commelinaceae	1	-	2	-
Conceveiba guianensis Aubl.	Euphorbiaceae	-	-	-	1
Conyza bonariensis (L.) Cronquist	Compositae	7	-	1	1
Cordia multispicata Cham.	Boraginaceae	1	-	-	-
Costus arabicus L.	Zingiberaceae	5	1	1	1
Coussarea ovalis Stande.	Rubiaceae	-	-	-	2
Coutoubea spicata Aubl.	Gentianaceae	-	1	-	-
Croton matourensis Aubl.	Euphorbiaceae	24	2	5	1
Croton miquelensis Feguson.	Euphorbiaceae	-	1	1	-
Croton trinitatis Millsp.	Euphorbiaceae	-	1	1	-
Cyperus chalaranthus Presl.	Cyperaceae	-	5	21	-
Cyperus diffusus Vahl.	Cyperaceae	-	3	22	-
Cyperus filifolius Willd.	Cyperaceae	5	13	1	2
Cyperus ligularis L.	Cyperaceae	6	-	-	-
Cyperus luzulae Rottb.	Cyperaceae	344	156	145	2
Cyperus sphacelatus Rottb.	Cyperaceae	7	6	3	-
Davilla kunthii St. Hil.	Dilleniaceae	-	2	-	-
Desmodium canum (G.Mel.) Schinz. et. Tkellesh.	Fabaceae	1	-	-	-
Didymopanax morototoni (Aubl.) Decne et Pl.	Araliaceae	-	-	-	1
Digitaria horizontalis Willd.	Gramineae	-	-	-	3
Dioclea virgata (Rich.) Amsh.	Fabaceae	1	3	1	-
Diodia ocimifolia (Willd. ex R.) Bren.	Rubiaceae	54	4	6	4
Emilia sonchifolia (L.) DC. Ex Wright.	Compositae	1	-	2	-
Eupatorium odoratum L.	Compositae	3	6	3	1
Geophila aff. *cordata* Miq.	Rubiaceae	-	1	-	-
Geophila sp.	Rubiaceae	-	-	1	-
Gouania pyrifolia Reiss.	Rhamnaceae	-	2	87	-
Goupia glabra Aubl.	Celastraceae	-	-	-	5
Heliconia psittacorum L. F.	Musaceae	-	-	1	-
Hymenophyllum sp.	Hymenoplyllaceae	24	1	1	-

Appendix 6 (cont.)

Species	Family	5-yrs	10-yrs	20-yrs	PF
Hyptis atrorubens Poit.	Labiatae	5	-	19	10
Ichnanthus pallens (Sw.) Munro ex Benth.	Gramineae	-	-	2	-
Irlbachia alata (Aubl.) Maas.	Gentianaceae	236	62	19	-
Jacaranda copaia (Aubl.) D. Don.	Bignoniaceae	-	-	-	4
Jacquemontia hirtiflora (Mart. et Gal.) O'Donnell.	Convolvulaceae	-	22	30	1
Lacistema pubescens Mart.	Lacistemaceae	4	-	-	1
Lasiacis ligulata Hitch. & Chase	Gramineae	73	10	11	5
Lindernia crustacea F. Muell.	Scrophulariaceae	293	176	53	8
Mabea angustifolia Spruce ex Benth	Euphorbiaceae	1	2	-	-
Macfadyena ungnis-catii (L.) A. Gentry	Bignoniaceae	-	-	-	3
Mandevilla hirsuta (L. C. Rich.) K. Schum.	Apocynaceae	6	1	-	-
Maprounea guianensis Aubl.	Euphorbiaceae	-	-	-	1
Mariscus flavus Vohl.	Cyperaceae	67	161	71	19
Mariscus ligularis (L.) Urb.	Cyperaceae	7	8	-	-
Miconia ceramicarpa (DC.) Cogn.	Melastomataceae	98	31	7	6
Miconia minutiflora (Bonpl.) DC.	Melastomataceae	-	1	-	-
Microtea debilis Swartz.	Phytocalaceae	-	-	1	-
Mikania banisteriae DC.	Compositae	-	3	2	-
Myriaspora egensis DC.	Melastomataceae	1	1	-	2
Neea sp.	Nyctaginaceae	-	-	1	-
Ocotea cajumari Mart.	Lauraceae	-	-	-	1
Ouratea castaneaefolia (DC.) Engl.	Ochnaceae	1	-	-	-
Panicum pilosum Swartz.	Gramineae	16	1	2	1
Paspalum amazonicum Trin.	Gramineae	1	-	2	3
Paspalum conjugatum Berg.	Gramineae	30	26	82	38
Paspalum decumbens Swartz.	Gramineae	-	-	1	-
Passiflora misera H.B.K.	Passifloraceae	1	-	-	1
Pavonia malacophylla (Link. et Otto) Garcke	Malvaceae	-	1	2	-
Peperomia pellucida (L.) H.B.K.	Piperaceae	1	33	23	23
Philodendron sp.	Araceae	-	-	42	-
Phyllanthus niruri L.	Euphorbiaceae	4	-	-	-
Polygala monticola H.B.K.	Polygalaceae	2	-	1	-
Polypodium decumanum Willd.	Polypodiaceae	-	-	2	-
Pothomorphe umbellata (L.) Miq.	Piperaceae	1	-	1	-
Pseudabutilon spicatum R. E. Fries.	Malvaceae	-	1	2	-
Psychotria colorata (Willd. ex R. & S.) M. Arg.	Rubiaceae	-	-	-	6
Pterolepis trichotoma (Rottb.) Cogn.	Melastomataceae	143	18	8	-
Rolandra argentea Rotth.	Compositae	3	-	-	-
Rollinia exsucca (DC. ex Dunal) DC.	Annonaceae	-	-	-	1
Sabicea aspera Aubl.	Rubiaceae	1	4	5	-
Sapium sp.	Euphorbiaceae	-	-	1	
Scleria pterota Presl.	Cyperaceae	4	-	4	-
Scleria secans (L.) Urb.	Cyperaceae	29	79	15	-
Sclerolobium paraense Hub.	Caesalpiniaceae	-	-	-	2
Selaginella calcarata A. Br.	Selaginellaceae	1	15	22	-
Sida glomerata Commers.	Malvaceae	-	4	-	-
Solanum asperum Vahl.	Solanaceae	-	-	1	-
Solanum caavurana Vell.	Solanaceae	-	1	15	2
Solanum crinitum Lam.	Solanaceae	-	1	-	1
Solanum juripeba L.C. Rich.	Solanaceae	1	7	6	5
Solanum sp.	Solanaceae	-	1	-	-
Solanum stramonifolium Jacq.	Solanaceae	3	1	-	2
Stachytarpheta cayannensis (Rich.) Vahl.	Verbenaceae	201	43	1	-

Appendix 6 (cont.)

Species	Family	5-yrs	10-yrs	20-yrs	PF
Torenia crustacea F. Muell.	Scrophulariaceae	27	-	-	-
Trema micrantha (Sw.) Blume	Ulmaceae	4	11	4	3
Trichilia sp.	Meliaceae	-	1	-	-
Triumfetta althaeoides Lam.	Tiliaceae	-	1	-	-
unidentified1		-	1	-	-
unidentified2		-	1	-	-
unidentified3		-	-	2	-
unidentified4		-	-	2	-
unidentified5		1	-	-	-
unidentified6		1	-	-	-
Urena lobata L.	Malvaceae	-	2	-	-
Vismia guianensis (Aubl.) Choisy	Clusiaceae	23	25	13	16
Wulffia baccata (L. F.) Kuntze	Compositae	27	6	7	-
Xiphidium coeruleum Aubl.	Haemodoraceae	-	-	3	1
Xylopia nitida Dun.	Annonaceae	-	-	10	3
Zanthoxylum rhoifolium Lam.	Rutaceae	55	20	26	2

Appendix 7. List of species occurring in the seed rain of 5-years, 10-years, 20-years-old secondary forest and a primary forest (PF) in the Bragantina region, Pará, with their authorities, families and number of seeds sampled in each forest age-class.

Species	Family	5-yrs	10-yrs	20-yrs	PF
Acacia paniculata Willd.	Mimosaceae	-	-	-	3
Acrocomia sclerocarpa Drude	Palmae	-	-	4	-
Aechmea sp.	Bromeliaceae	-	-	-	1
Alibertia edulis (L. C. Rich.) A. Rich.	Rubiaceae	-	1	-	-
Ambelania acida Aubl.	Apocynaceae	-	-	-	56
Ananas ananasoides (Bachen.) L. B. Smith.	Bromeliaceae	-	-	1	-
Annonaceae	Annonaceae	2	-	6	-
Arrabidaea sp.	Bignoniaceae	-	-	12	-
Asplenium serratum L.	Polypodiaceae	-	-	-	1
Asplundia sp.	Cyclanthaceae	1	-	-	-
Astronium lecointei Ducke	Anacardiaceae	-	-	-	3
Banara guianensis Aubl.	Flacourtiaceae	-	21	2	2
Banisteriopsis sp.	Malpighiaceae	-	-	3	-
Basanacantha spinosa (Jacq.) Karst.	Rubiaceae	-	-	6	-
Bauhinia jarensis Wunderlin	Caesalpiniaceae	-	-	1	2
Bauhinia macrostachya Benth.	Caesalpiniaceae	-	-	2	-
Bignoniaceae	Bignoniaceae	-	3	3	51
Borreria latifolia (Aubl.) Schum.	Rubiaceae	-	-	-	2
Borreria verticillata (L.) Mey.	Rubiaceae	-	-	-	1
Campsoneura sp.	Myristicaceae	-	-	-	34
Casearia decandra Jacq.	Flacourtiaceae	1	3	3	1
Casearia sp.	Flacourtiaceae	-	2	-	-
Cecropia obtusa Trec.	Moraceae	-	1	13	11
Cecropia palmata Willd.	Moraceae	1113	820	1056	100
Cedrela odorata L.	Meliaceae	-	-	-	1
Cestrum sp.	Solanaceae	-	7	-	-
Chaunochiton kapleri (Sagt. ex Engl.) Ducke	Olacaceae	1	-	-	1
Clidemia hirta (L.) D. Don.	Melastomataceae	150	619	120	54
Clusia grandifolia Engl.	Clusiaceae	-	-	-	3
Combretum sp.	Combretaceae	-	-	-	24
Commelina sp.	Commelinaceae	1	13	32	29
Coniza sp.	Compositae	10	-	-	2
Convolvulaceae	Convolvulaceae	339	12	-	-
Cordia multispicata Cham.	Boraginaceae	23	6	-	-
Cordia sp.	Boraginaceae	-	35	23	1
Costus arabicus L.	Zingiberaceae	-	1	1	6
Croton matourensis Aubl.	Euphorbiaceae	-	-	144	-
Cybianthus sp.	Myrsinaceae	-	-	1	-
Dichapetalum rugosum (Vahl.) Prance	Dichapetalaceae	-	6	-	34
Didymopanax morototoni (Aubl.) Decne. et Planch.	Araliaceae	1	3	695	937
Diodia sp.	Rubiaceae	-	-	-	1
Doliocarpus sp.	Dilleniaceae	8	1	-	-
Duguetia sp.	Annonaceae	9	-	2	-
Erisma uncinatum Warm.	Vochysiaceae	-	-	2	1
Eschweilera collina Eyma	Lecythidaceae	-	-	-	6
Eschweilera coriacea (A. DC.) Mart. ex Berg.	Lecythidaceae	-	-	-	3
Eschweilera sp.	Lecythidaceae	-	-	-	2
Eugenia sp.	Myrtaceae	-	-	-	7
Eupatorium odoratum L.	Compositae	2	-	-	-
Euphorbiaceae	Euphorbiaceae	-	6	4	-
Euterpe oleracea Mart.	Palmae	-	-	-	1
Fevillea sp.	Cucurbitaceae	1	-	-	-
Ficus gomelleira Kunth. et Bouche.	Moraceae	-	-	-	2
Ficus maxima P. Miller	Moraceae	-	-	-	2
Ficus sp.	Moraceae	-	264	-	102

Species	Family	5-yrs	10-yrs	20-yrs	PF
Geissospermum sericeum (Sagot.) Benth.	Apocynaceae	-	-	-	1
Geophilla sp.	Rubiaceae	5	-	3	-
Gnetum sp.	Gnetaceae	-	-	-	2
Gouania pyrifolia Reiss.	Rhamnaceae	337	118	179	3
Gramineae	Gramineae	-	38	-	-
Guarea sp.	Meliaceae	-	-	-	1
Guatteria schomburgkiana Mart.	Annonaceae	-	-	2	-
Heisteria sp.	Olacaceae	-	-	-	1
Hippocratea cf. *ovata* Lam.	Hippocrateaceae	-	-	-	3
Inga alba (SW.) Willd.	Mimosaceae	-	9	2	-
Inga gracilifolia Ducke	Mimosaceae	-	-	-	3
Inga macrophylla H.B.K.	Mimosaceae	-	2	2	3
Inga sp.	Mimosaceae	5	378	2	1
Inga stipularis DC.	Mimosaceae	-	-	1	-
Inga thibaudiana DC.	Mimosaceae	-	3	-	-
Iriartea exorrhiza Drude	Palmae	-	5	1	1
Irlbachia alata (Aubl.) Mass.	Gentianaceae	22	1	2	2
Iryanthera sp.	Myristicaceae	-	-	-	1
Jacaranda copaia (Aubl.) D. Don	Bignoniaceae	-	-	-	4
Jacaratia spinosa (Poepp.) A.DC.	Caricaceae	-	-	-	4
Jacquemontia hirtiflora (Mart. ex Gal.) O'Donell	Convolvulaceae	2	-	-	-
Lacistema pubescens Mart.	Lacistemaceae	326	175	9	44
Lacmellea aculeata (Ducke) Monach.	Apocynaceae	-	-	99	1
Laetia procera (Poepp. et Endl.) Eichl.	Flacourtiaceae	1	-	-	-
Lauraceae	Lauraceae	6	1	13	2
Lecythis idatimon Aubl.	Lecythidaceae	-	-	-	17
Leguminoseae	Leguminosae	-	29	5	55
Licania heteromorpha Benth.	Chrysobalanaceae	2	-	3	4
Lindernia crustacea F. Muell.	Scrophulariaceae	2	10	18	2
Mabea angustifolia Spruce ex Benth.	Euphorbiaceae	20	5	29	-
Mabea sp.	Euphorbiaceae	8	28	13	-
Mabea speciosa Mull. Arg.	Euphorbiaceae	-	-	-	12
Macffadyena ungnis-catii (L.) A. Gentry	Bignoniaceae	-	-	-	1
Mandevilla hirsuta (L. C. Rich.) K. Schum.	Apocynaceae	2	-	-	-
Manihot sp.	Euphorbiaceae	-	1	-	-
Mansoa difficilis (Cham.) DC.	Bignoniaceae	-	-	-	1
Maprounea guianensis Aubl.	Euphorbiaceae	-	-	73	-
Margaritaria nobilis (L. F.) Muell. Arg.	Euphorbiaceae	-	-	1	-
Maximiliana maripa (C. Serra) Drude	Palmae	2	-	-	-
Maytenus sp.	Celastraceae	-	-	-	6
Miconia ceramicarpa (DC.) Cogn.	Melastomataceae	16	309	26	41
Miconia ciliata (Rich.)	Melastomataceae	11	-	3	5
Miconia minutiflora (Bonpl.) DC.	Melastomataceae	1118	154	252	44
Miconia sp.	Melastomataceae	1028	-	26	-
Mikania banisteriae var. *gabrieli* (Backer) G.M. Barroso	Compositae	53	-	-	-
Mikania sp.	Compositae	-	1	-	-
Morph 01*		-	5	-	-
Morph 02		-	-	1	1
Morph 03		-	-	18	10
Morph 04		-	-	-	1
Morph 05		3	4	9	1
Morph 06		-	3	-	-
Morph 07		-	-	-	1
Morph 08		37	19	4	6
Morph 09		-	-	-	2
Morph 10		-	-	1	-
Morph 12		-	-	-	3
Morph 13		-	-	5	-
Morph 14		-	1	2	-

Species	Family	5-yrs	10-yrs	20-yrs	PF
Morph 16		3	1	-	-
Morph 20		-	-	-	7
Morph 22		-	-	-	4
Morph 24		-	-	2	-
Morph 26		-	-	-	8
Morph 27		-	-	2	-
Morph 28		-	2	-	-
Morph 29		-	1	1	-
Morph 30		-	17	-	-
Morph 34		-	-	137	-
Morph 35		4	18	-	5
Morph 37		-	2	1	-
Morph 38		1	5	-	2
Morph 39		1	-	1	-
Morph 40		1	10	-	8
Morph 41		-	-	13	-
Morph 42		-	-	-	8
Morph 43		1	10	26	2
Morph 44		-	-	5	-
Morph 45		1	2	-	1
Morph 46		-	3	-	1
Morph 47		-	-	-	1
Morph 48		-	1	-	2
Morph 49		-	1	-	-
Morph 50		-	1	-	-
Morph 51		-	1	-	-
Morph 52		-	-	-	3
Morph 53		-	1	-	-
Morph 54		-	-	1	-
Morph 55		-	-	2	-
Morph 56		-	-	-	1
Morph 57		-	1	-	-
Morph 58		-	-	1	-
Morph 59		-	-	-	1
Morph 60		-	1	-	1
Morph 61		-	-	1	1
Morph 62		1	-	-	47
Morph 63		-	-	1	-
Morph 64		-	-	1	-
Morph 65		-	2	6	162
Morph 66		-	-	-	21
Morph 67		16	-	-	-
Morph 69		-	5	-	-
Morph 70		-	8	-	-
Morph 71		-	-	17	-
Morph 72		-	-	20	-
Morph 73		-	-	-	10
Morph 74		-	-	-	3
Morph 75		-	-	-	7
Morph 76		-	25	-	-
Morph 77		6	2	-	-
Morph 78		-	-	-	3
Morph 79		-	-	-	23
Morph 80		-	-	-	22
Morph 81		-	-	2	-
Myrcia bracteata (Rich.) DC.	Myrtaceae	-	3	-	-
Myriaspora sp.	Melastomataceae	1076	-	6	-
Myrtaceae	Myrtaceae	-	-	2	18
Nectandra aff. *globosa* Mez.	Lauraceae	-	-	1	-

Species	Family	5-yrs	10-yrs	20-yrs	PF
Neea sp.	Nyctaginaceae	-	-	-	1
Newtonia suaveolens (Miq.) Brenan.	Mimosaceae	-	-	1	32
Norantea sp.	Marcgraviaceae	-	7	6	-
Ocotea caudata Mez.	Lauraceae	-	1	-	1
Ocotea glomerata (Nees) Mez.	Lauraceae	-	14	-	-
Paspalum conjugatum Berg.	Gramineae	1	-	-	-
Paullinia pinnata L.	Sapindaceae	-	49	1	-
Paullinia sp.	Sapindaceae	-	-	-	9
Phyllanthus niruri L.	Euphorbiaceae	-	1	5	-
Phyllanthus urinari L.	Euphorbiaceae	5	1	2	3
Pilea microphylla Griseb.	Urticaceae	7	1	6	14
Piper aduncum L.	Piperaceae	202	43	14	10
Piper marginatum Jacq.	Piperaceae	2	-	5	-
Posoqueria sp.	Moraceae	-	-	1	1
Pothomorphe umbelata (L.) Miq.	Piperaceae	8	28	5	7
Pourouma palmata P. et E.	Moraceae	-	1	-	-
Protium sp.	Burseraceae	-	-	-	8
Psychotria sp.	Rubiaceae	-	38	34	6
Pterolepis trichotoma (Rotth.) Cogn.	Melastomataceae	3	4	6	-
Rheedia sp.	Clusiaceae	-	-	-	4
Rinorea neglecta Sandw.	Violaceae	-	-	-	16
Ripsalles sp.	Cactaceae	2	39	-	-
Rolandra argentea Rottw.	Compositae	1	-	1	1
Rollinia exsucca (DC. ex Dunal) DC.	Annonaceae	1	3	104	4
Sabicea sp.	Rubiaceae	56	-	-	-
Saccoglottis guianensis Benth.	Humiriaceae	-	-	1	-
Sapindaceae	Sapindaceae	1	-	-	1
Sapotaceae	Sapotaceae	-	-	-	1
Schizolobium amazonicum (Hub.) Ducke	Caesalpiniaceae	12	-	-	-
Scleria sp.	Cyperaceae	23	6	6	1
Sclerolobium paraense Hub.	Caesalpiniaceae	-	-	-	5
Selaginella sp.	Selaginellaceae	1	-	-	1
Serjania sp.	Sapindaceae	-	62	15	16
Siparuna guianensis Aubl.	Monimiaceae	1	113	3	2
Solanaceae	Solanaceae	-	-	-	105
Solanum stramonifolium Jacq.	Solanaceae	-	3	-	1
Stachytarphetta cayannensis (Rich.) Vahl.	Verbenaceae	-	-	2	5
Stryphnodendron guianense (Aubl.) Benth.	Mimosaceae	-	1	-	-
Swartzia laurifolia Bentham	Caesalpiniaceae	-	-	1	-
Symphonia globulifera L. F.	Clusiaceae	-	-	3	14
Tabebuia serratifolia (Vahl.) Nichols.	Bignoniaceae	-	-	2	-
Tapirira guianensis Aubl.	Anacardiaceae	-	175	42	10
Thyrsodium paraense Hub.	Anacardiaceae	-	-	4	-
Torenia crustacea F. Muell.	Scrophulariaceae	8	-	-	-
Trichilia sp.	Meliaceae	-	-	-	18
Undetermined, morphs not separated		129	109	119	129
Vigna unguiculata L.	Fabaceae	2	-	-	-
Virola michelii Heckel	Myristicaceae	-	-	2	2
Virola sp.	Myristicaceae	-	-	-	1
Virola sebifera Aubl.	Myristicaceae	14	2	7	27
Vismia cayennensis (Jacq.) Pers.	Clusiaceae	-	1	-	1
Vismia guianensis (Aubl.) Choisy.	Clusiaceae	4324	1381	707	33
Wulffia baccata (L. F.) Kuntz.	Compositae	1	12	6	1
Xylopia sp.	Annonaceae	8	18	-	-
Xyphidium sp.	Haemodoraceae	-	-	-	1
Zanthoxylum rhoifolium Lam.	Rutaceae	-	961	1871	-

* Morph is used for each separate but unidentified taxon.

Appendix 8. List of species occurring as sprouts and seedlings in the 5-years-old secondary forest in the Bragantina region, Pará, with their authorities, families and number of sprouts and seedlings.

Species	Family	sprouts	seedlings
Annona densicoma Mart	Annonaceae	-	1
Arrabidaea sp.	Bignoniaceae	1	1
Banara guianensis Aubl.	Flacourtiaceae	-	1
Bernardinia fluminensis (Gard.) Planch.	Connaraceae	-	1
Calycolpus sp.	Myrtaceae	4	-
Caliptranthes cf. *bipenis* Berg.	Myrtaceae	10	-
Calytrocarya bicolor T. Koyama	Cyperaceae	1	-
Casearia pitumba Sleumer	Flacourtiaceae	1	-
Cassipourea guianensis Aublet	Rhizophoraceae	1	1
Chrysophyllum sparsiflorum K. L.	Sapotaceae	1	2
Clidemia hirta L.D. Don.	Melastomataceae	-	3
Croton matourensis Aubl.	Euphorbiaceae	-	1
Dalbergia aff. *subcymosa* Ducke	Fabaceae	-	1
Davilla kunthii St. Hill.	Dilleniaceae	31	-
Diodia sp.	Rubiaceae	-	1
Erythroxylum leptoneurum O. E. Schultz.	Erythroxylaceae	1	-
Eugenia patrisii Vahl.	Myrtaceae	1	-
Gouania pyrifolia Reiss.	Rhamnaceae	1	-
Guatteria poeppigiana Mart.	Annonaceae	-	2
Gustavia augusta L.	Lecythidaceae	8	-
Heisteria cf.*acuminata* (H. & B.) Engler	Olacaceae	5	-
Heliconia acuminata L. C. Rich.	Musaceae	2	-
Inga edulis Mart.	Mimosaceae	4	2
Lacistema agregatum Berg. Rusby	Lacistemaceae	-	4
Lacistema pubescens Mart.	Lacistemaceae	3	15
Lecythis lurida (Miers.) Mori	Lecythidaceae	1	-
Lygodium sp.	Schizaeaceae	2	-
Mabea angustifolia Spruce ex Benth.	Euphorbiaceae	-	1
Machaerium madeirense Pittier	Fabaceae	5	-
Machaerium quinata (Aubl.) Sandw.	Fabaceae	-	3
Mandevilla hirsuta (A. Rich.) Schum.	Apocynaceae	1	-
Memora flavida (DC.) Bur et Schum.	Bignoniaceae	4	2
Memora magnifica (Mart. ex DC.) Burret	Bignoniaceae	11	-
Metrodorea flavida Krause	Rutaceae	1	-
Miconia minutiflora (Bompl.) DC.	Melastomataceae	1	-
Miconia sp.	Melastomataceae	-	1
Mikania cf.psilostachya DC.	Compositae	-	1
Myrcia bracteata (Rich.) DC.	Myrtaceae	21	-
Myrcia falax (Rich.) DC.	Myrtaceae	-	1
Myrcia floribunda (West. ex Willd.) Berg.	Myrtaceae	4	4
Myrcia laruotteana Camb.	Myrtaceae	1	-
Myrciaria tenella (DC.) Berg.	Myrtaceae	4	2
Neea sp.	Nyctaginaceae	-	2
Panicum pilosum Swartz.	Gramineae	-	4
Prionostemma aspera (Lam.) Miers.	Hippocrateaceae	6	-
Psychotria colorata (Willd. ex R.&S.)M. Arg.	Rubiaceae	-	12
Richardella macrophylla (Lam.) Eyma	Sapotaceae	-	1
Rollinia exsucca (DC. ex Dunal) DC.	Annonaceae	2	-
Rourea amazonica (Backer) Radlk.	Connaraceae	1	41
Sabicea glabrescens Benth. ex Char.	Rubiaceae	1	2

Appendix 8 (cont.)

Species	Family	sprouts	seedlings
Scleria secans (L.) Urb.	Cyperaceae	-	4
Serjania tenuifolia Radlk.	Sapindaceae	-	3
Smilax schomburgkiana Kunth.	Smilacaceae	7	-
Solanum caavurana Vell.	Solanaceae	-	1
Strychnos cf. *tomentosa* Benth.	Loganiaceae	2	-
Tabebuia serratifolia (Vals.)Nichols.	Bignoniaceae	9	5
Tabernaemontana angulata Mart. ex M. Arg.	Apocynaceae	-	1
Tetracera volubilis Mart ex M. Arg.	Dilleniaceae	-	4
Virola sebifera Aubl.	Myristicaceae	-	4
Vismia guianensis (Aubl.) Choisy	Clusiaceae	2	-
Wulffia sp.	Compositae	-	2
Zanthoxylum rhoifolium Lam.	Rutaceae	2	-

Appendix 9. List of species occurring as sprouts and seedlings in the 10-years-old secondary forest in the Bragantina region, Pará, with their authorities, families nd number of sprouts and seedlings.

Species	Family	sprouts	seedlings
Abarema cochleatum (Willd.) Bar. & Grim.	Mimosaceae	-	1
Annona densicoma Mart.	Annonaceae	-	5
Arrabidaea sp.	Bignoniaceae	-	3
Bauhinia jarensis Wunderlin	Caesalpiniaceae	1	-
Casearia arborea (L. C. Rich.) Urban	Flacourtiaceae	-	1
Casearia pitumba Sleumer.	Flacourtiaceae	1	1
Cassipourea guianensis Aublet.	Rhizophoraceae	-	3
Clidemia hirta (L.) D. Don	Melastomataceae	-	1
Cybianthus cf. *minutiflorus* Mez.	Myrsinaceae	-	1
Davilla kunthii St. Hill.	Dilleniaceae	13	16
Doliocarpus dentatus (Aubl.) Standl.	Dilleniaceae	2	-
Erythroxylum macrophyllum Cav.	Erythroxylaceae	-	1
Euterpe oleracea Mart.	Palmae	-	2
Forsteronia sp.	Apocynaceae	-	1
Gouania pyrifolia Reiss.	Rhamnaceae	1	-
Guatteria poeppigiana Mart.	Annonaceae	2	2
Gustavia augusta L.	Lecythidaceae	7	3
Heliconia acuminata L. C. Rich.	Musaceae	-	1
Inga nitida Willd.	Mimosaceae	1	-
Inga thibaudiana DC.	Mimosaceae	11	12
Inga velutina Willd.	Mimosaceae	-	3
Iriartea exorrhiza (Mart.) H. Wende.	Palmae	-	1
Jacaranda copaia (Aubl.) D. Don	Bignoniaceae	-	2
Lacistema pubescens Mart.	Lacistemaceae	-	8
Lacunaria crenata (Tul.) A. C. Sm.	Quiinaceae	1	-
Lecythis lurida (Miers.) Mori	Lecythidaceae	-	1
Machaerium cf. *inundatum* (Mart. ex Benth.) Ducke	Fabaceae	-	1
Machaerium madeirense Pittier	Fabaceae	2	-
Machaerium quinata (Aubl.) Sandw.	Fabaceae	1	1
Maximiliana maripa (C. Serra) Drude	Palmae	-	3
Memora allamandiflora Bur. et K. Scum.	Bignoniaceae	-	1
Mendoncia cf. *hoffmannsegiana* Nees	Acanthaceae	-	1
Miconia alata (Aubl.) DC.	Melastomataceae	-	1
Miconia ceramicarpa (DC.) Cogn.	Melastomataceae	-	1
Miconia minutiflora (Bonpl.) DC.	Melastomataceae	-	2
Myrcia bracteata (Rich.) DC.	Myrtaceae	-	212
Myrcia eximia DC.	Myrtaceae	-	1
Myrcia floribunda (West. ex Willd.) Berg.	Myrtaceae	1	-
Myrcia sylvatica (Meyer) DC.	Myrtaceae	5	-
Nectandra cuspidata Nees	Lauraceae	-	1
Neea sp.	Nyctaginaceae	-	5
Nelsonia sp.	Acanthaceae	-	4
Newtonia suaveolens (Miq.) Brenam	Mimosaceae	-	2
Ormosia paraensis Ducke	Fabaceae	-	1
Ouratea paraensis Aubl.	Ochnaceae	-	1
Panicum pilosum Swarz.	Gramineae	-	15
Pariana sp.	Gramineae	-	19
Piper ottonoides Yunckel	Piperaceae	-	1
Protium pilosum (Cuatr.) Daly	Burseraceae	-	1
Psychotria barbiflora DC.	Rubiaceae	-	1

Appendix 9 (Cont.)

Species	Family	sprouts	seedlings
Psychotria colorata (Willd. ex R.& S.) M. Arg.	Rubiaceae	-	16
Pueraria phaseoloides Benth.	Fabaceae	-	2
Rinorea passoura (DC.) Kuntz.	Violaceae	-	1
Rollandra argentea Rotth.	Compositae	-	1
Rollinia exsucca (DC. ex Dunal) DC.	Annonaceae	-	1
Rourea amazonica (Backer) Radlk.	Connaraceae	41	6
Rourea ligulata Backer	Connaraceae	-	15
Sabicea glabrescens Benth. ex Char.	Rubiaceae	2	1
Scleria secans (L.) Urb.	Cyperaceae	-	18
Siparuna guianensis Aubl.	Monimiaceae	-	3
Smilax schomburgkiana Kunth.	Smilacaceae	11	3
Talisia longifolia (Bth.) Radlk.	Sapindaceae	-	1
Tetracera volubilis L.	Dilleniaceae	3	-
Trichilia micrantha Benth.	Meliaceae	-	3
Trichilia sp.	Meliaceae	-	25
Vismia guianensis (Aubl.) Choisy	Clusiaceae	2	-
Wulffia baccata (LF.) Kuntze	Compositae	-	1
Zanthoxylum rhoifolium Lam.	Rutaceae	-	1

Appendix 10. List of species occurring as sprouts and seedlings in the 20-years-old secondary forest in the Bragantina region, Pará, with their authorities, families and number of sprouts and seedlings.

Species	Family	sprouts	seedlings
Aegiphila scandens Mold.	Verbenaceae	1	-
Amphirrox longifolia Spreng.	Violaceae	3	-
Annona densicoma Mart.	Annonaceae	-	1
Arrabidaea sp.	Bignoniaceae	-	13
Aspidosperma desmanthum Benth. ex Muell. Arg.	Apocynaceae	-	1
Astrocaryum mumbaca Mart.	Palmae	-	2
Bauhinia jarensis Wunderlin	Caesalpiniaceae	-	6
Bernardinia fluminensis (Gard.) Planch.	Connaraceae	-	7
Calathea sp.	Maranthaceae	1	-
Calycolpus sp.	Myrtaceae	1	-
Casearia arborea (L.C. Rich.) Urban.	Flacourtiaceae	-	1
Cassipourea guianensis Aublet.	Rhizophoraceae	7	1
Cordia scabrida Mart.	Boraginaceae	-	1
Costus arabicus L.	Zingiberaceae	1	-
Couratari guianensis Aubl.	Lecythidaceae	2	-
Dalbergia aff.*subcymosa* Ducke	Fabaceae	1	1
Davilla kunthii St. Hill.	Dilleniaceae	11	4
Diodia sp.	Rubiaceae	-	8
Eschweilera pedicellata (Richard.) Mori	Lecythidaceae	1	-
Eugenia muricata Berg.	Myrtaceae	-	1
Geissospermum sericeum (Sagot.) Benth.	Apocynaceae	1	-
Guapira sp.	Nyctaginaceae	-	1
Heisteria cf. *acuminata* (H.& B.) Engler	Olacaceae	-	4
Heliconia acuminata L.C. Rich.	Musaceae	1	1
Humirianthera duckei Huber	Icacinaceae	1	-
Ichnanthus pallens (Swartz.) Doell. & Mart.	Gramineae	-	1
Inga edulis Mart.	Mimosaceae	-	12
Inga heterophylla Willd.	Mimosaceae	-	3
Inga sp.	Mimosaceae	-	96
Inga thibaudiana DC.	Mimosaceae	-	4
Lacistema agregatum (Berg.) Rusby	Lacistemaceae	7	-
Lacistema pubescens Mart.	Lacistemaceae	3	6
Machaerium madeirense Pittier.	Fabaceae	3	-
Machaerium quinata (Aubl.) Sandw.	Fabaceae	1	-
Machaerium sp.	Fabaceae	-	1
Mansoa difficilis (Cham.) DC.	Bignoniaceae	4	-
Memora allamandiflora Bur.et K. Schum.	Bignoniaceae	4	-
Memora flavida (DC.) Bur et Schum.	Bignoniaceae	1	8
Memora magnifica (Mart. ex DC.) Burret	Bignoniaceae	4	-
Mendoncia cf. *hoffmannsegiana* Nees.	Acanthaceae	-	1
Miconia minutiflora (Bompl.) DC.	Melastomataceae	-	3
Moutabea guianensis Aubl.	Polygalaceae	-	1
Myrcia bracteata (Rich.) DC.	Myrtaceae	-	48
Myrcia floribunda (West ex Willd.) Berg.	Myrtaceae	3	3
Myrciaria tenella Berg.	Myrtaceae	-	20
Olyra latifolia L.	Gramineae	4	-
Ormosia paraensis Ducke	Fabaceae	-	2
Palicourea sp.	Rubiaceae	2	-
Pariana sp.	Gramineae	39	8

Appendix 10 (cont.)

Species	Family	sprouts	seedlings
Paullinia sp.	Sapindaceae	-	1
Piper ottonoides Yunckel	Piperaceae	-	2
Protium pilosum (Cuatr.) Daly	Burseraceae	-	3
Protium trifoliolatum Engl.	Burseraceae	-	9
Psychotria barbiflora DC.	Rubiaceae	-	2
Psychotria colorata (Willd. ex R.& S.) M. Arg.	Rubiaceae	-	8
Rourea amazonica (Backer) Radlk.	Connaraceae	-	7
Rourea sp.	Connaraceae	-	5
Scleria secans (L.) Urb.	Cyperaceae	10	5
Serjania sp.	Sapindaceae	1	-
Siparuna guianensis Aubl.	Monimiaceae	-	1
Symphonia globulifera L. F.	Clusiaceae	-	1
Tabernaemontana angulata Mart.	Apocynaceae	14	13
Thyrsodium paraense Huber	Anacardiaceae	-	3
Trichilia micrantha Benth.	Meliaceae	-	11
Trichilia sp.	Meliaceae	-	2
Zanthoxylum rhoifolium Lam.	Rutaceae	-	3