# SPATIAL AND TEMPORAL ANALYSIS OF FLORISTIC COMPOSITION AND DYNAMICS IN SOME LOWLAND AMAZONIAN FORESTS

**Barbara Vinceti**

A THESIS SUBMITTED FOR THE DEGREE OF DOCTOR OF PHILOSOPHY
THE UNIVERSITY OF EDINBURGH
2003

# *Declaration*

---

This thesis has been composed by myself from the results of my own work, except where stated otherwise, and has not been submitted in any other application for a degree.

Barbara Vinceti
October, 2003

## *Dedication*

*I dedicate this thesis to my brother Luca, my parents and some very precious friends, scattered around on this planet.*

## Oda a una mañana del Brasil
da *NAVEGACIONES Y REGRESOS (1959)*

*Esta es una mañana*
*del Brasil. vivo adentro*
*de un violento diamante,*
*toda la transparencia*
*de la tierra*
*se materializó*
*sobre*
*mi frente,*
*apenas si se mueve*
*la bordada verdura,*
*el rumoroso cinto*
*de la selva:*
*ancha es la claridad, como una nave*
*del cielo, victoriosa.*

*todo crece,*
*los árboles,*
*el agua,*
*los insectos,*
*el dia.*
*todo termina en hoja.*
*se unieron*
*todas*
*las cigarras*
*que nacieron, vivieron*
*y murieron*
*desde que existe el mundo,*
*y aquí cantan*
*en un solo congreso*
*con voz de miel,*
*de sal,*
*de aserradero,*
*de violin delirante.*
......................

*deshabitadas*
*tierras,*
*cristal*
*verde*
*del mundo,*
*en alguna*
*región*
*un ancho rio*
*se despeña*
*en plena soledad,*
*los saurios cruzan*
*las aguas pestilentes,*
*miles de seres lentos*
*aplastados*
*por la*
*ciega espesura*
*cambian de planta, de agua,*
*de pantano, de cueva,*
*y atraviesan el aire*
*aves abrasadoras.*
.......................

Pablo Neruda (1904-1973)

# Abstract

Recent research has suggested that apparently undisturbed tropical forests, remote from areas of deforestation or other significant human influences, are undergoing unexpected changes. These observed changes may already be having significant impacts on terrestrial carbon stocks, fluxes, and biodiversity. However, the findings have proved controversial, partly because a rather limited number of permanent sample plots (PSPs) have been monitored for short periods.
This work is centred on tree-by-tree data collated from long-term forest PSPs from several lowland Neotropical sites, spanning a wide gradient of environmental conditions across the Amazon basin, covering variable census intervals.

The aim of the analysis is to: (1) investigate the role played by the main environmental variables in determining the observed geographical patterns of rainforest floristic composition, diversity and structure, (2) characterize temporal and regional patterns of forest dynamics, and changes in forest dynamics and basal area (BA), (3) explore potential shifts in species composition over time, due to mechanisms other than natural successional processes.

With regard to floristic aspects, the present work reveals that: (1) large-scale patterns in the abundance of the most important tree families are identifiable, with fast-growing families dominating in highly dynamic forest stands studied in western Amazonia (WA); (2) the number of dry months seems to be the best predictor for alpha-diversity across the sites investigated, (3) soil seems to be playing a major role in determining floristic diversity, at local scale; (4) significant structural differences exist between forests stands located in drier and wetter sites.

With regard to forest dynamics and BA, the study shows that: (1) turnover is much higher in western than in central Amazonian (CA) plots, (2) stand BA and turnover appear to have been significantly increasing in the last two decades in almost all PSPs examined, regardless of environmental conditions, (3) mortality and recruitment have both increased in every region, but the increase is not significant for mortality rates, (4) the spatial patterns and temporal trends observed do not seem to be significantly affected by potential biases and errors in PSP measurements, (5) the recorded increase in BA productivity does not seem to be directly associated with the increased occurrence of fast-growing species.

With regard to changes in species composition, this thesis shows that: (1) rapid fluctuations in population density of some common abundant species are occurring, although they are less marked than those found in other tropical forest PSPs, (2) the population density of the most abundant species is increasing in WA plots, driven by a recruitment wave, whereas it is decreasing in CA plots, due to mortality exceeding recruitment rates, (3) pioneer species are showing an increasing occurrence over time in almost all sites.

The overall findings suggest that the $CO_2$ "fertilization" effect may be the main factor responsible for the changes observed in the tropical forest plots examined, but a wider and longer sampling effort of PSPs would be needed to better test this phenomenon, and understand the potentially profound changes in the ecology of tropical rainforests that would derive from it.

# Acknowledgements

Going back in time to the beginning of a long story, I would like to thank my professor of Silviculture, at the University of Florence, Pietro Piussi, who first suggested me to run the risk of venturing up north to Edinburgh, and to Maurizio Mencuccini who did not hesitate in organizing my reception. Maurizio has always provided extremely insightful technical advice, psychological support and has been almost constantly available during the course of my experience in Scotland.

I would like to thank my supervisor Yadvinder Malhi, who managed to instill in me enthusiasm and curiosity for tropical forests, he himself undergoing a process of stupefied discovery of these complex fascinating natural systems, at the time I started my thesis. He managed to convince me that I should come on board and has been always extremely encouraging. I learned a bit of his way of looking at things with calm and optimism.

A crucial supporter has been my very good friend and flatmate Sandra Patiño. We shared a lot of time and she showed me how someone can be so deeply in love with nature.

Following facts along their evolvement, this point of the story gets crowded with friends, who shared accommodation with me: Ana Efstathiou, Caroline Wood, Sandeep Vadher, Robert Bois, Dimistris Dimoliatis; who shared coffee with me: Alasdair Hardy, Franz Conen, Caroline Nichol, Johanna Pulli, Dimitris Zianis; shared beer: Mark Rayment, Natalia Gomez, Craig Barton, Sara Strati, Daniela Famulari, Sandeep Vadher; and played games, Mark's kids, who gave me the most joyful and serene moments during my stay in Edinburgh.

Many thanks for the extreme availability and support to some staff members of IERM: Connie Fox, Sheila Wilson, Allister Kydd, Dave Haswell, John Anthony, Derek Scott.

A very special thanks to the colleagues from the RAINFOR network: Oliver Phillips, always very enlightening and prompt in replying, Tim Baker, extremely helpful and supportive, Simon Lewis, acute and constructively critical. Their advice, critical comments and patience have been fundamental in helping me to keep focused on the thesis, while being involved in another full-time job during the last year of my PhD. They got soon used to sending me printout copies of my chapters, full of scribbles, to my Mediterranean address. Thanks also to the various colleagues from the tropical regions, who have been collating data from forest permanent sample plots and made available an invaluable capital of information, which has been in part examined in this thesis.

Many thanks to the Rotary Foundation that provided financial support to part of my learning experience in Edinburgh and in particular to my tutor, Glen Stewart who helped me discovering aspects of the Scottish culture unknown to me.

Final thanks to my present colleagues, who have given me enough freedom to complete the work, and to my friends in Rome who have morally supported me throughout the last stages of the writing up.

# *Table of contents*

---

# *List of figures*

# List of tables

---

## *List of symbols and abbreviations*

| | |
|---|---|
| BA | basal area |
| PSP | permanent sample plot |
| C | carbon |
| CA | central Amazonia |
| WA | western Amazonia |
| WA-NP | western Amazonia – North Peru |
| WA-SP | western Amazonia – South Peru |
| SA | south Amazonia |
| EA | eastern Amazonia |
| BIONTE | Biomassa e Nutrientes Florestais |
| BDFFP | Biological Dynamics, of Forest Fragments Project |
| CA | Correspondence analysis |
| DCA | Detrended Correspondence Analysis |
| RA | Reciprocal averaging |
| $N_0$ | stem number at the initial census |
| $N_f$ | stem number at the final census |
| $N_s$ | number of stems that survived between census intervals |
| ln | logarithm to the base e (exp) |
| Stem $r_m$ | stem annual mortality rate |
| Stem $r_r$ | stem annual recruitment rate |
| BA $r_m$ | basal area annual mortality rate |
| BA $r_r$ | basal area annual recruitment rate |
| $BA_0$ | basal area at the initial census |
| $BA_f$ | basal area at the final census |
| $BA_s$ | basal area of stems that survived between census intervals |
| $\text{Stem.}_t$ | stem turnover rate |
| $\text{BA.}_t$ | basal area turnover rate |
| $\Delta$BA rel | basal area relative change |
| $d_0$ | initial diameter |
| $d_f$ | final diameter |
| p.o.m. | point of measurement |
| P | precipitation |
| $P_g$ | rate of population change |

# *Chapter 1. Introduction*

---

## 1.1. Introduction

Human alteration of the Earth is substantial and growing. The carbon dioxide released into the atmosphere is causing significant perturbation of the natural cycle of carbon between land, atmosphere and oceans. A deeper understanding of the impact that changes in atmospheric composition and climate may be having on terrestrial vegetation is needed. Present and foreseeable responses from different ecosystems need to be analysed to interpret the perturbations that human-induced alterations are provoking.

## 1.2. The global carbon cycle, trends in atmospheric $CO_2$, land sinks

Humanity contributes in adding $CO_2$ to the atmosphere by mining and burning fossil fuels, and by converting forests and grasslands to agricultural or to other low-biomass ecosystems. The records of atmospheric $CO_2$ measured from 1958 until the present at Mauna Loa Observatory, Hawaii (Keeling et al. 2001) irrefutably establishes the presence of a significant upward trend in atmospheric $CO_2$ concentrations. The atmospheric $CO_2$ has been around 280±10 ppm for several thousands years before the Industrial Era (circa 1750), then it has risen to 367 ppm in 1999, reaching a concentration that has not been exceeded during the past 420,000 years, and likely not during the past 20 million years (Prentice et al. 2001). Increases in similar proportion of other greenhouse gases, especially methane, nitrous oxide, and chlorofluorocarbons, have also been observed.

A persistent feature of global carbon cycle calculations is an imbalance in the calculated $CO_2$ emissions, atmospheric accumulation of $CO_2$, and modelled ocean uptake (Broecker et al. 1979; Schimel 1995).

Global $CO_2$ budget calculations are based on the most recent estimates of land-atmosphere fluxes. Estimates show in the 1990s an atmospheric increase of $3.2 \pm 1.0$ Pg of C $a^{-1}$, an emission of ca. $6.4 \pm 0.4$ Pg of C $a^{-1}$, an ocean uptake of $-1.7 \pm 0.5$ Pg of C $a^{-1}$, a $CO_2$ release due to land-use change during the 1980s of about 1.7 of Pg of C $a^{-1}$, and an amount that ranges from -3.8 to 0.3 Pg of C $a^{-1}$ that is unaccounted for (Prentice et al. 2001). This "missing" carbon cannot yet be unambiguously attributed to a clearly identified sink but increased growth, under elevated $CO_2$ conditions, has been often assumed to be the primary mechanism underlying the "residual terrestrial sink" (Fan et al. 1998; Gifford 1994; Lloyd 1999).

It has been argued that a fraction of carbon that is missing in global carbon cycle calculations may be taken up and stored by terrestrial vegetation through a stimulation of productivity due to the $CO_2$ "fertilisation" effect (Lloyd 1999). This effect would lead to an increase in terrestrial carbon storage, in vegetation and or/soils, in the range from 0.5 to 4.0 Gt C $a^{-1}$ (Gifford 1994).

However, the magnitude of this stimulation is likely to depend on the availability of soil water and nutrients (Oren et al. 2001) and hence current magnitude and the long-term nature of this uptake is uncertain. Globally, there appears to be a net release of carbon into the atmosphere during El Niño years, and a net uptake during cooler years (Braswell et al. 1997; Vukicevic et al. 2001). Most of this interannual variability appears to be driven by the tropical terrestrial biosphere (Bousquet et al. 2000).

## 1.3. Evidence for a tropical carbon sink

Accumulated evidence over the past two decades has suggested that extratropical Northern Hemisphere land areas are making a significant contribution to the global uptake of anthropogenic $CO_2$. In the tropics, results are constrained by sparse measurements, but specific studies suggest the existence of a carbon sink in tropical forests (AA.VV. 2001).

The methods used to identify carbon sinks provide independent evidence for the existence of a terrestrial residual sink but are currently generating slightly dissimilar estimates of the magnitude and location of the sink. Individual inventory studies in mature forests show that carbon stocks in such forests are increasing (Lugo and Brown 1993). Recent micrometeorological research suggests that there may be a large net carbon sink in mature Amazonian forests (Grace et al. 1995b; Grace et al. 1995a; Malhi et al. 1998), though a degree of uncertainty still persists in assessing the magnitude of gaseous exchanges between canopies and atmosphere. Biomass inventories in old-growth tropical forests suggest that such an effect does indeed exist (Phillips et al. 1998a). Methodological limitations and difficulties are implicated in all the approaches adopted. Nevertheless, forest biomass studies represent a valid integration to other methods used to assess the effects of global change on forests. The large dataset collated and studied by Phillips et al. (1998) contains further information from forest permanent sample plots (PSPs) that has not yet been explored. Part of the same dataset will be analysed in this work, in order to understand the origin of the observed apparent increase in the biomass of old-growth forests (e.g., methodological biases, natural forest dynamics, or global atmospheric change).

## 1.4. Biomass and turnover studies

Although changes in tropical forest biomass and turnover have been highlighted in some studies, the mechanisms of change have not been explored in detail. Constraints in elucidating the functioning of tropical forest ecosystems and in interpreting signals of change derive from the limited amount of ground-based information, the large amount of spatial and temporal variation (Hall et al. 1998; Sheil 1996), the extremely patchy nature of tropical forest ecosystems (White and Pickett 2001), and the lack of consistent protocols (Clark 2002; Phillips et al. 2002a).

## 1.5. Studies on forest compositional change

Whatever the role of tropical forests with respect to carbon sequestration, their species composition is likely to be shifting in response to global atmospheric changes. Research on tropical forest ecosystems suggests that local and regional forest dynamics are linked to changing climatic factors (Clark and Clark 1994; Condit 1998). Unusual droughts and variation in rainfall are increasingly recognized as important in tropical forests (Condit et al. 1996a; Nakagawa et al. 2000; Williamson et al. 2000). There is evidence for an individually differentiated response of species to elevated $CO_2$ (Körner and Bazzaz 1996; Wurth et al. 1998), and competition is likely to be modified. Insights into potential changes in species composition can come from (i) understanding the current species distribution in tropical forests and its relation to climate, (ii) searching for evidence of any shift in recent decades. The species-specific information necessary to make predictions of the impact of future climate scenarios is not available for most tropical forests and the picture is complicated by biogeographical and evolutionary factors that contribute to shaping the landscape (Carrion et al. 2001; Colinvaux et al. 1996; van der Hammen and Hooghiemstra 2000; Whitlock and Millspaugh 2001).

## 1.6. The present study

This work is based on part of a large set of tree-by-tree data collated from long-term forest PSPs in several lowland Neotropical sites, compiled by Phillips et al. (1998).

The database spans a wide gradient of environmental conditions across the Amazon basin, covering variable census intervals, and offers a unique opportunity to tackle some major questions on the potential changes affecting the dynamics and the floristic composition of some Amazonian tropical rainforest PSPs.

In this study, a new analysis of above-ground biomass changes in space and time is presented. The potential impacts of current anthropogenic changes in atmospheric composition and climate on tropical forest ecosystems are explored, analysing spatial and temporal patterns of change in rainforest biomass and floristic composition. Forest dynamics is disaggregated into single ecosystem processes (recruitment, mortality, and growth) to identify the mechanisms leading to the observed changes in BA over time. The role played by the main environmental variables in determining the observed geographical patterns of rainforest floristic composition, diversity and structure within the Amazon Basin is investigated. Changes in species population expected to be associated with the observed changes in forest biomass are identified and described. The methodologies adopted to carry out forest inventories and to analyse forest data are reviewed and discussed with the objective to identify the main biases most likely to affect the assessments of forest biomass changes.

## 1.7. Specific questions addressed

The main questions addressed in the present study are:

1. How are current patterns of forest diversity related to environmental factors?

Rainforest species composition and structure vary spatially across the Amazon Basin, under the influence of environmental factors. It is fundamental to understand the relative importance of soil types and climate in shaping forest stand characteristics, in order to be able to predict the direction of changes in tropical forest ecosystems. A spatial analysis of the floristic composition and structure of several lowland Amazonian plots is shown in Chapter 4.

2. Are there significant changes in forest biomass and dynamics in the studied plots, over time?

A detailed analysis of stand dynamic variables (mortality, recruitment, turnover) is fundamental to interpret the mechanisms behind any observed changes in BA and dynamics over time. Spatial and temporal trends in BA and dynamics changes are analysed in Chapter 5.

3. Is there any evidence that the observed changes are due to recovery from disturbance, or to an increase in production driven by global atmospheric change?

The assessment of BA growth within different size classes, and the joint analysis of rates of change in total stand BA and stem density provides clues on potential causes of BA and dynamics change over time (see Chapter 5).

4. Are any observed changes in forest biomass and dynamics associated with some particular functional groups?

Some groups of species are likely to be differently affected by changes in atmospheric composition and climate. Some groups in particular, are expected to be advantaged in the competition for resources (i.e., fast-growing species), and therefore to be contributing more than others to any observed change in stand BA and dynamics over time. Their contribution to stand BA and dynamics changes is analysed in Chapter 5.

5. To what extent could methodological biases influence the measurements of changes in BA and dynamics over time?

Forest inventories have been considered susceptible to flaws, and models used to define the variables that describe forest dynamics have been found to be time-dependent. The artifactual direction of change, most likely to derive from incorrect adoption of proper protocols, has been carefully analysed. The various biases that can affect BA measurements and data analysis have been examined in detail to determine their occurrence and potential magnitude (see Chapter 6).

6. Is there evidence that tropical forest diversity and species composition is being affected by global atmospheric changes? Are particular taxonomic groups showing marked changes in population density over time?

Forest tree species are expected to respond differently to the pressure of a rapidly changing atmospheric composition and of an increased frequency of drought, with some elements of the flora playing an increasingly dominant role in rainforest ecosystems. Signals of a potential floristic shift are analysed across stands from different regions of the Amazon basin, characterized by different climatic regimes, in order to assess and interpret the impact of the global change (see Chapter 7).

# Chapter 2. Literature review

---

## 2.1 Introduction

The first part of the present chapter offers a description of the main environmental characteristics of the Amazon basin and of some agents of change that may be having an influence on the dynamics and species composition of old-growth forests (i.e., enhanced atmospheric concentration of carbon dioxide, climate change, and other agents of disturbance). A fully detailed description of the permanent sample plots used in the present work is given later in Chapter 3.

The second part of this chapter presents a description of the floristic composition and structure of some lowland Amazonian forests, together with a review of the main hypotheses explaining current patterns of floristic composition and species richness found across the Amazon basin. In the same section, the methodology used in the present work to analyse floristic patterns is described. This part introduces the findings presented and discussed later in Chapter 4.

The next section of the present chapter offers a review of the main results from long-term studies on tropical forest basal area and dynamics. This part relates to the analysis of changes in basal area and turnover through time, presented in Chapter 5.

Then, methodological difficulties related to investigations in tropical forest permanent sample plots are also presented and anticipate those discussed in Chapter 6, that is an application of some tests to the dataset used in this thesis, with the objective to detect the potential effect of biases and artefacts on the results presented.

The final section provides a review of studies on the potential influence of global change on rainforest species composition and introduces the analysis carried out in Chapter 7.

## 2.2 The Amazon rainforest and its environment

Forests cover about 35% of the earth's surface. Globally, forests store over 80% of the earth's terrestrial organic carbon (Olson et al. 1983) and more than 60% of the global phytomass (Esser 1992). The largest area of forests (42%) is laid at low latitudes, and more than half of this area is in tropical America. Brazil has the second largest extension of forests, accounting for ~10% of the total (Fearnside 1992). The South American rainforests are located in three main areas, of which the largest lies in the Amazon and Orinoco basins, stretching from the lower slopes of the Andes east to the Guianas and south to about 15°S in western Brazil and northeastern Bolivia. The Amazon Basin encompasses nearly 6 000 000 km$^2$ of South America and most of its surface is covered by the largest block of tropical rainforests (4 000 000 km$^2$), which constitutes 58% of their global extension (Whitmore 1990). A second block lies across the Andes on the Pacific coasts of Ecuador and Colombia, extending northwards through Central America, as far as Veracruz in southernmost Mexico (19°N). The Atlantic coast of Brazil has a third block, a strip less than 50 km wide on the coastal mountains, extending to the vicinity of Rio de Janeiro.

The extent of Amazonian *terra firme* forests (i.e. forest not permanently or seasonally flooded) is considerable (Prance 1987). It was estimated in 1973 as 3 303 000 km$^2$ by Pires, (quoted in Goodland and Irwin 1975). This forest type is located on well-drained plateaus and slopes descending towards stream beds; it is characterised by a high diversity of tree species and a mosaic of distinctive structural and floristic communities that result from variation in edaphic, climatic, topographic, geologic and geographic conditions.

### *Climate*

In the humid tropical forest biome, mean annual rainfall ranges from a minimum of 1500 mm in the lowlands to about 10 000 mm in middle elevations due to orographic rain on front ranges (Richards 1952). Seasonal patterns of rainfall are thought to be far more important than temperature in serving as proximal cues for biological activities (Hartshorn 1992). When rainfall is less than 100 mm/month, evapotranspiration exceeds water uptake by plants, and this initiates an effective dry season. Even with this low level of rainfall it may take up to one month for the soil to dry out sufficiently to cause moisture stress in plants (Hartshorn 1992). The duration of the dry season is sometimes defined as the period for which precipitation is < 100 mm, but in fact, the length of the dry period is usually longer as it takes time for the soil to recharge its moisture reserves (Malhi et al., review b). A striking feature of rainfall records from tropical regions is the great year-to-year variation (Hartshorn 1992; Walsh and Newbery 1999). Strong interannual variation is typical in tropical South America and it is linked to the variation of atmospheric circulation (Rao and Hada 1990). Studies of extreme climatic events in the Amazon Basin have been carried out (Marengo and Hastenrath 1993) to explore the mechanisms that regulate climate anomalies. Pluviometric sites, maintained by the National Agency for Electric Energy (Agência Nacional de Energia Elétrica, ANEEL), and located in the main Brazilian part of the Amazon region, provide some information on the strength of the El-Niño phenomenon. They reveal that the central-northern zone apparently experiences stronger El-Niño effects than the southern zone (Sombroek, in press). Their frequency is illustrated in table 2.1.

| Year | Intensity | Regions |
|---|---|---|
| 1908 | weak ? | Sena Madureira (Acre) |
| 1911 | weak ? | Manaus (Amazon) |
| 1916 | weak ? | Sena Madureira (Acre), Taperinha (Para) |
| 1925-27 | very strong | Fonte Boa (Amazon), Erunepé, Sao Gabriel de Cachoeira (Amazon) |
| 1930 | weak ? | Parentins (Amazon) |
| 1936 | weak ? | Manicoré (Amazon) |
| 1939-40 | weak ? | Barcelos (Amazon) |
| 1942 | weak ? | Taperinha (Para) |
| 1951-52 | weak ? | Porto Velho (Rondonia), Taperinha (Para) |
| 1957-58 | weak ? | Itacoatiara (Amazon), Parentins (Amazon) |
| 1963 | weak ? | Porto Velho (Rondonia), Taperinha (Para) |
| 1967-68 | Moderate | Coari (Amazon), Humaitá (Amazon), Manaus (Amazon) |
| 1971-72 | Moderate | Boa Vista (Roraima), Porto Velho (Rondonia), Taraucá (Acre) |
| 1976 | Moderate | Rio Branco (Acre) |
| 1980-81 | weak | Tapauá (Amazon), Sao Felix de Araguaya (Mato Grosso) |
| 1983 | Strong | Everywhere |
| 1987-88 | weak | Açailandia (Maranhão) |
| 1991-92 | Moderate | Prainha (Para); Humaitá (Amazon), Coari (Amazon), Caracarai (Roraima), Barcelos (Amazon) |
| 1995-96 | weak | Apui (Amazon) |
| 1997-98 | Strong | Everywhere |

Table 2.1. El-Niño related droughts in the Amazon Basin from (Sombroek, in press).

### *Soil*

The proportional extent of soils with moderate to very low fertility in the moist lowland tropics is far greater (1146 x $10^6$ ha, ca. 77%) than that occupied by relatively fertile soils (223 x $10^6$ ha, ca. 15%) (Vitousek and Sanford 1986). Figure 2.1 shows the relative extent of soil types of various fertilities. The majority of rainforests in the Brazilian Amazon occur on heavily weathered, nutrient-poor soils (Brown 2001), and if compared to rainforests on richer substrates, they tend to have lower nutrient budgets and a higher proportion of nutrients contained in the living material of the ecosystem (Klinge 1976). Soils can vary considerably over distances of as little as 10 m (Longman and Jenik 1987), and pedogenetic processes are affected mostly by local features of topography, parent material or water conditions. Many of the soils of the humid tropics impose very few physical limitations on plant growth but are of low nutrient availability. Weathering is rapid because of high temperatures and copious percolation of rainwater. Soils tend to be often more fertile in the seasonally dry tropics (Terborgh 1992). Leaching is severe during the rainy season, and when the rains cease, the soil begins to dry out, aided by the transpiration of plants. Roots withdraw more and more of the water stored in the soil column and the partially compensatory upward flow carries with it freshly dissolved minerals from the weathering rock below.

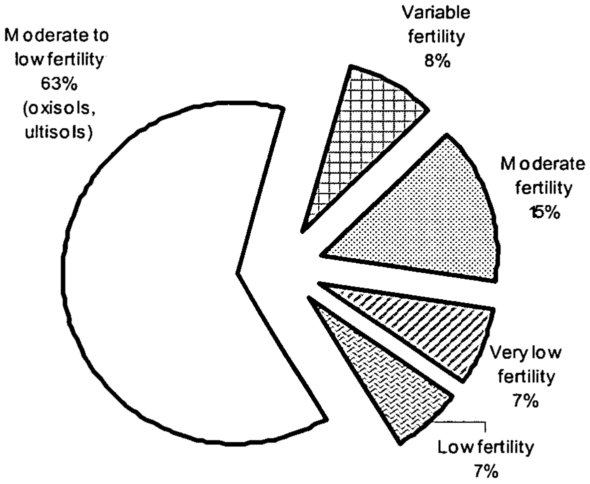


Figure 2.1. Major soils grouped by fertility, with corresponding percentage of total area (1489 millions of ha), modified from (Sanchez 1981).

There is no general agreed system of soil classification and nomenclature but two major international systems are in wide use at present: the legend of the Soil Map of the World (FAO-UNESCO 1974, 1988) and the Soil Taxonomy (Soil Survey Staff 1975, Soil Management Support Service 1990). On a global scale of soil diversity, nearly two-thirds of all tropical soils are classified as oxisols and ultisols (Figure 2.2), two types that contain clays with little content of soluble minerals.

The moderate to strong acidity interferes with the ability of roots to take up nutrients. Oxisols will become irreversibly hardened if cleared of natural vegetation and allowed to dry. They are characterized by being deep, red or yellowish, without distinct horizons, very strongly weathered and therefore with a very low cation-exchange capacity (by definition they have less than 10% of the original weatherable minerals remaining) They consist mainly of quartz, kaolinite, Fe and Al oxides, and organic matter. They usually have little content of silt, thus, they hold little water that is available to plants. Ultisols are low nutrient kaolinite rich, clay-enriched subsoils that occur mainly in humid areas, with a horizon of accumulation of black or reddish amorphous materials. They generally have marks of intense leaching, and a low supply of bases. The release of bases by weathering usually is equal to or less than the removal by leaching, and most of the bases commonly are held in the vegetation and the upper few centimeters of the soils. Base saturation in most ultisols decreases with increasing depth because the vegetation has concentrated the bases at a shallow depth. Very few have many primary minerals that contain bases other than some micas. Psamments are sandy soils that lack pedogenic horizons, usually dominated by quartz sands.

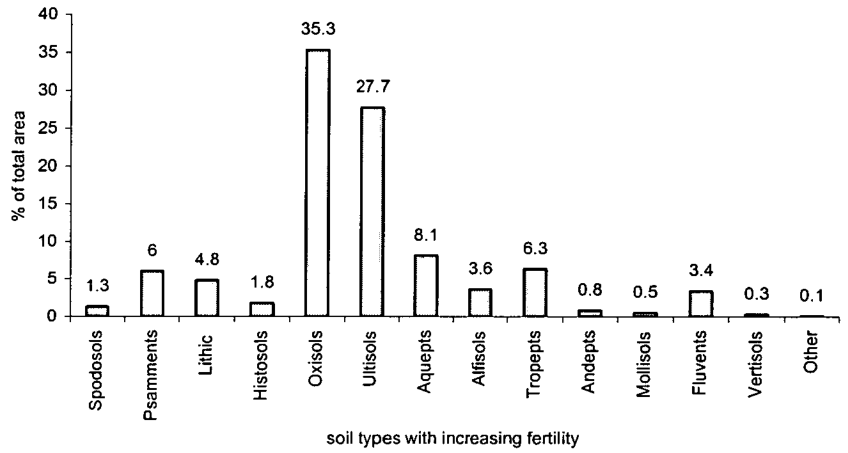


Figure 2.2. Major soils of the tropics and corresponding percentage of total area (1 489 millions of ha), modified from (Sanchez 1981). Soil types are displayed along a gradient of increasing fertility from very low to moderate.

## 2.3 Agents of change in old-growth forests

### 2.3.1. The enhanced carbon dioxide in the atmosphere

The dramatic anthropogenic release of carbon trapped by both prehistoric ecosystems (i.e. fossil fuels) and modern-day vegetation has led to a 31% increase in concentrations of atmospheric carbon dioxide ($CO_2$) from a preindustrial concentration of ca. 280 ppm to 368 ppm in 2000. This concentration has certainly not been exceeded during the past 420 000 years, and probably not during the past 20 million years. Moreover, the rate of increase in $CO_2$ concentration during the past century is at least an order of magnitude greater than the world has seen for the last 20 kyr (Prentice et al. 2001). $CO_2$ is the most important of the greenhouse gases that are increasingly trapping solar heat and warming the global climate. In addition to climatic warming, this extra carbon dioxide may have a number of direct effects on terrestrial ecosystems.

The $CO_2$ at present and predicted concentrations is hypothesised to have a direct “fertilization” effect on plant growth (Dixon et al. 1994). However, the overriding issue is whether effects on plant growth will trigger effects on magnitudes of global carbon sources and sinks. The role played by different types of forests in the overall carbon budget and for how long their present role will be maintained are still unanswered questions, although the different approaches adopted to tackle these issues are progressing towards a converging result.

Four major approaches have been used to estimate the biospheric-atmospheric exchange of $CO_2$ in natural ecosystems: 1) eddy covariance measurements (Fan et al. 1990; Grace et al. 1995a; Grace et al. 1995b; Malhi et al. 1998; Malhi et al. 1999; Miranda et al. 1997), 2) inverse modelling (Bousquet et al. 2000; Fan et al. 1998; Keeling et al. 1996; Rayner et al. 1999; Tans et al. 1990), 3) spatially explicit ecosystem modelling (Cao and Woodward 1998; Melillo et al. 1993; Tian et al. 1999), 4) forest biomass inventories (Brown and Lugo 1992; Fearnside 1997a; Fearnside 1997b; Melillo et al. 1993; Phillips et al. 1998a). This study is based on this last approach.

### ***Effects of enhanced $CO_2$ on terrestrial vegetation***

The increase in atmospheric $CO_2$ has direct effects on carbon assimilation (Curtis 1996; Farquhar et al. 1980; Mooney et al. 1999), and indirect effects on water-use efficiency (Farquhar 1997; Körner 2000), and on the interaction between the carbon and nitrogen cycles (Hungate et al. 1999; Körner 2000; Norby et al. 1999; Vitousek and Field 1999). The direct effects on photosynthesis can be expressed by plants in a faster development or in an increased final mass. Both types of response have been observed (Masle 2000). Water-use efficiency is enhanced by the partial closure of stomata induced by high $CO_2$ concentration. The consequent reduction of water loss during transpiration leads to an increased ratio of carbon gain to water loss and to a lengthening of the duration of the growing season in water-limited ecosystems. Nitrogen-use efficiency is also improved and it seems that increased $CO_2$ concentration stimulates nitrogen fixation (Hungate et al. 1999; Vitousek and Field 1999).

A distinction between relative and absolute effects has to be taken into account (Körner 1993). There is increasing evidence that water- or temperature- stressed plants are more responsive to $CO_2$ increase than unstressed plants (Polley et al. 1993). Water shortage may enhance the relative effect of rising $CO_2$ on growth, when compared to a nonstressed control. However, the absolute growth increment under moist conditions is likely to be many times larger (Körner 1993).

There is also a problem in scaling to be considered. Studies in natural plant communities confirm that leaf and individual responses do not necessarily translate into community and ecosystem responses (Körner 1993). In fact, despite the relatively strong effects of elevated $CO_2$ on growth (Idso and Idso 1994; Schimel and Sulzman 1995), ecosystem carbon storage may be less responsive to increased levels of atmospheric $CO_2$. The notorious difficulties in observing below-ground processes in the field contribute to obscuring the overall picture. Therefore, it is difficult to test whether ecosystems commonly possess the ability to enhance nitrogen- and water-use efficiency under stress while a major portion of annual net productivity is shunted to grow more and larger roots. Initial experiments examining root growth of tree seedlings in chambers containing high $CO_2$ (Norby et al. 1986) indicate not only greater growth of roots than shoots, but also a greater mobilization of nutrients necessary for growth in the soil solution. Additional carbon is expected to enter the soil by the acceleration of ontogeny, by a more rapid shoot death, and by enhanced root turnover and production of exudates (Allen et al. 2000; Koch and Mooney 1996).

Upper thresholds of carbon storage in ecosystems are likely to be imposed by limitations of a mechanical and physiological nature. There are physical limits to the amount of organic carbon that can be held in soils (Scholes et al. 1999) and the enhancement of photosynthetic rates is likely to be negligible at $CO_2$ atmospheric concentration above a certain threshold (800-1,000 ppm or lower) (Körner 2000). Furthermore, limited availability of nutrients and water can considerably limit C sequestration in young forest stands (Oren et al. 2001), that are supposed to provide a substantial contribution to the buffering of carbon emissions. Furthermore, a reason for uncertainty about the long-term strength of actual carbon sinks stems from the general expectation that the increased above-ground net primary productivity will be partially counterbalanced by an increased rate of turnover of the biomass, as the upper limits in productivity are approached.

In Chapter 5 of this thesis, trends in BA change over time are analysed to assess the response of some tropical forest stands to enhanced atmospheric carbon dioxide, and their capability to sequester carbon.

### ***Response of tropical forest ecosystems to $CO_2$***

The $CO_2$ response of tropical biomes deserves high priority as almost half of the carbon in global biomass is found in the tropics and subtropics (Brown and Lugo 1982) and predictions assume that responses are more pronounced the warmer the climate (Gifford 1992; Koch and Mooney 1996; Rawson 1992). Uncertainties persist regarding the influence of $CO_2$ on the productivity of plant species from tropical ecosystems, because the response to rising $CO_2$ varies largely between plants grown individually and in competing arrays or in glasshouse-maintained micro-ecosystems (Arnone and Körner 1995; Bazzaz 1990; Lovelock et al. 1998; Wurth, Winter, and Körner 1998).

A few studies have been carried out in a tropical natural environment. Reekie and Bazzaz (1989) studied competition and patterns of resource use among seedlings of tropical trees under ambient and elevated $CO_2$, using five relatively fast growing early successional species. The results of their study suggest that $CO_2$ influenced the competitive outcome largely through its effects on canopy architecture, producing an increase in mean height of the canopy of some of the studied species. Wurth et al. (1998) tested the prediction that plants growing in deep shade and high temperature, such as in the understory of humid tropical forests, are particularly sensitive to rising atmospheric $CO_2$. Leaf carbon balance should be improved in very low light, under elevated $CO_2$, because in deep shade the higher concentration of $CO_2$ reduces photorespiration, increases quantum yield and thus, decreases the light compensation point of photosynthesis (Long and Drake 1991; Wong and Dunin 1987). Although small in absolute terms, the large relative effects detected could induce far-ranging changes in community dynamics in a forest. In the long term this suggests that atmospheric $CO_2$ enrichment is likely to influence species composition of tropical forests, regardless of the overall biomass responses (Hattenschwiler and Körner 1996; Körner 1995; Körner 1998).

Experiments have been mainly conducted on seedlings and the growth stimulation induced by $CO_2$, observed in natural tropical environments, has been found to characterize the early phase of recruitment (Wurth, Winter, and Körner 1998).

Atmospheric $CO_2$ enrichment is thought to also have indirect connections with enhanced forest dynamics, through the potential greater survival or aggressiveness of some functional groups, such as lianas. Lianas are known to be strongly carbon limited until they reach the top layer of the canopy (Bigelow 1993; Pimm and

Sudgen 1994), and may be showing a considerable response to increased atmospheric carbon dioxide (Phillips et al. 2002b).

### *Differentiated responses of species to elevated $CO_2$*

Individual species respond differently to elevated $CO_2$ (Körner and Bazzaz 1996; Wurth, Winter, and Körner 1998) and the strength of the response of photosynthesis to the enhanced atmospheric concentration of $CO_2$ depends on the photosynthetic pathway used by plants. For the individual competitor there are many features that ultimately determine success. Structural features such as leaf angle and size, bud position, internode length, branching patterns, bud dominance hierarchy and adult plant size can be more significant than the photosynthetic behaviour of a sunlit leaf. Qualities completely different from those investigated by gas-exchange analysis may determine whether a species will become dominant in a natural plant community (Farquhar 1997; Pritchard et al. 1999). The $CO_2$ "fertilisation" effect is likely to manifest itself by inducing changes in competitive advantages among species. Bazzaz (1979) studied the ecophysiological properties of plants occurring at different successional stages and found that the dominant taxa of late successional stages in forests tended to have a very reduced photosynthetic capacity compared with pioneers (Bazzaz 1979). Looking at species interactions, Bazzaz (1990) investigated the effects of simultaneous changes in $CO_2$ and temperature, at the population level, on annual crops, and observed that $CO_2$ magnified the intensity of plant-plant interactions and enhanced the growth of the remaining dominant individuals.

Körner (1993) presents compelling arguments for producing a hierarchy of species responses based on ecological functional properties of classes of species. According to him, growth advantages conferred on one species must result in growth losses in less-competitive species in a complex but predictable way. The fundamental problem is that there is presently no ecological theory that can successfully predict the outcomes of competition at any specified time or place, when it occurs under conditions of $CO_2$ fertilisation.

There is evidence that plants with low intrinsic growth rates are less responsive to $CO_2$ increases than are rapidly growing plants. Non-native species such as invasive plants and crop species would seem to be advantaged (Dukes and Mooney 1999; Poorter 1993). Phillips and Gentry (1994) suggest that there will be an increasing predominance of light-demanding plants and climbers and the eventual extinction of some slow-growing shade-tolerant trees. The light-demanding trees have less dense wood than the shade lovers (Woodcock et al. 2000; Woodcock 2000). Thus, mature tropical forests would be likely to sequester less carbon per unit area than expected because of the preponderance of low density species. These forests may ultimately act as sources for atmospheric carbon.

The picture is very complex though, because responses to $CO_2$, which would lead to a particular species composition, would act in conjunction with responses to changes in water availability and competition for other resources, which would promote a different array of species.

In the present study, potential evidence for a differentiated response of species to changes in atmospheric composition is analysed in Chapter 7, where signals of a shift in forest species composition through time are investigated.

### 2.3.2. The effect of climate change

Climate change scenarios derived from global circulation models predict that global warming is unlikely to alter the climate of aseasonal tropical rainforests significantly. However, models indicate temperature rises of ca. 2°C by 2100, a decline in annual rainfall, and prolonged seasonal drought in part of the equatorial tropics covered by seasonal forests, especially in Amazonia (Hulme and Viner 1998). Current trends are likely to induce an overall increase in rainfall. However, some areas will experience a sharp decline in rainfall but climate models do not agree on specific regional locations.

Fairly predictable patterns of rainfall seasonality in humid tropical forest regions may be interrupted or overridden by unpredictable events such as the penetration of polar air masses into the outer tropics or the El Niño Southern Oscillation (ENSO) that results from the interaction between atmosphere and ocean in the tropical Pacific. ENSO is the primary mode of global climate variability in the 2 to 7 year time band. Its activity and periodicity have varied considerably through time. The apparent "shift" in temperature of the tropical Pacific around 1976 to warmer conditions (which appeared to continue to 1998), coincided with more frequent, intense and persistent ENSO events (IPCC 2001). Analysis of a 15,000 year record of deposits in an alpine lake in south-western Ecuador, derived from ENSO event-related debris slides, indicates that the return period of warm-phase ENSO events shortened from around 15 years in 15 000-7 000 yr BP to 2-8.5 years from 5 000 yr BP to the present (Kestin et al. 1998; Rodbell et al. 1999; Torrence and Webster 1999). There is also evidence of recent unusual ENSO behaviour in comparison to that of previous decades. The El-Niño episodes since the mid-1970s have been relatively more frequent than the opposite La Niña episodes (IPCC 2001). Local climate data for some tropical forest plots are analysed in Chapter 3, to detect the occurrence of anomalies in rainfall regime at different sites, and to highlight trends in mean annual precipitation over time.

### 2.3.3. Other agents of change

Some factors other than climate change could play a key role in locally shaping the structure and the floristic composition of highly diverse communities such as tropical forests. Seven distinct categories of non-deforestation threats to tropical forest biodiversity have been identified (Phillips 1997): i) selective extraction of plants; ii) selective extraction of animals; iii) biological invasions; iv) fragmentation; v) climate change; vi) changing atmospheric composition, and vii) changing tree turnover rates. Large tracts of apparently unperturbed primary forests could be undergoing long-term changes due to successional evolution (Connell 1978; Sheil 1999). Recovery from past disturbance such as fire or the presence of human settlements and natural processes of stable colonization by vegetation of areas previously perturbed by river dynamics, could also be taking place.

Pristine sites, chosen to investigate the natural evolution of primary forests could be affected by perturbation taking place in neighbouring areas (Laurance et al. 1998a). Declines or increases in species occupying surrounding areas would affect the type of seed dispersed over long distances. The fragmentation or the clearing of the forest in surrounding areas would deprive the monitored stands of external input of seeds (Hubbell 1979; Warner and Chesson 1985).

Substitution of species could occur under the pressure of short-term local dynamics (closure of a large natural treefall gap and consequent reduction of light-demanding species, seed dispersal and availability) (Denslow 1980; Hubbell et al. 1990; Hubbell et al. 1999; Sousa 1984). If the size of forest permanent sample plots is small (less than 0.35 – 0.5 ha), large intrinsic fluctuations in dynamic processes and floristic composition are more likely to occur.

Regulatory mechanisms that control spatial patterns of species richness (e.g. density-dependent mechanisms) would also have a role in determining local declines or rises in tree populations (Condit et al. 1992). Some of these phenomena could be separately discerned, but sometimes their effects on species composition would not be distinguishable from generally recognized shifts in vegetation structure and composition due to the readjustment of plant communities to climatic changes.

Thus, the mechanisms driving changes can sometimes be difficult to identify and quantify. Degradatory processes can greatly alter tropical forest ecology in unexpected ways by direct and indirect effects. The interaction between two or more processes can generate impacts different from those triggered by single processes alone, having an amplified impact on biodiversity. Some of the factors that determine major changes in tropical forest ecosystems have been defined by Phillips (1997) as "invisible threats", as they are not visible on remotely-sensed images, and therefore detected only by a careful monitoring on the ground.

Changes in stand dynamics and turnover have been addressed in the present work, through the analysis of ground measurements carried out in forest permanent sample plots. Basal area and turnover changes over time are discussed in Chapter 5. The occurrence of recovery from past disturbance is tested in Chapter 6, and changes in species composition over time are investigated in Chapter 7.

## 2.4 Floristic composition and structure of tropical rainforest

### 2.4.1 Hypotheses on the origin and maintenance of species diversity

Lowland tropical evergreen forests are extremely diverse communities in which single species form a very small portion of the whole stand. Several hypotheses have been elaborated to explain the origin of the high species diversity found in tropical rainforests. Some of the causal factors have been summarized by Givnish (1999), with climate reputed to be the main driver for the observed diversity patterns:

- high species richness is favoured where the climate is stable, and therefore extinction rates are low;
- a stable climate contributes to enhancing speciation rates via resource-partitioning;
- the stability of favourable climatic conditions, with the associated reduced extinction rates and enhanced speciation rates, causes a "storage effect" that results in an accumulation of species (species packing), enlarging the overall species-pool.

The mechanisms responsible for the maintenance of diversity over time have been grouped into two main clusters of theories:

- equilibrium theories (niche models): species coexistence is promoted via resource and space partitioning over gradients, and different timing in their biological cycle. Coexistence is also enabled through mechanisms of density or distance-dependent mortality that prevents self-replacement by offspring trees at the same location (Connell 1971; Janzen 1970). Species coexistence in wetter tropical forests may be facilitated by the absence of competition for moisture combined with year-round pest pressure and low understory light levels, which reduce growth rates and the potential for competition for resources (Givnish 1999).
- Non-equilibrium (lottery models): species are similar in their requirements, life-histories and responses to environmental conditions and species co-occurrence is explained by chance factors and frequency in environmental disturbance (Chesson and Warner 1994; Hubbell and Foster 1986a; Pacala and Tilman 1994).

A complement to these two groups of theories derives from the concept of species storage effect, otherwise known as the species-pool concept. The species-pool is linked to the potential immigration of species into an area, and is the result of extinctions and speciation processes. Zagt and Werger (1996) propose a mix of the two elements (stochastic and deterministic) in a temporal succession as a mechanism maintaining high species diversity. Pre-gap conditions are mainly stochastic, therefore local availability of seeds and seedlings, together with seedlings mortality are driven by chance factors, as resource availability is rather uniform. In the post-gap stage, interspecific differences in resources requirements are made evident due to the more diversified environment and resource availability. Different growth rates are more manifest and competitive ability is stimulated. Zagt and Werger (1996) observed that studies in support for theories that assume randomness to be the force organizing communities are usually derived from trees that are either large or well established. In contrast, support for theories that assume species-specific differences in growth and survival frequently comes from studies on seedlings. Zagt and Werger (1996) focus their attention on seedlings, considered much more responsive to resource availability and subject to critical demographical constraints, and show how chance and species-specific factors vary during the stages of seedling regeneration in the understory and in gaps. A recent work on tropical pioneer species suggests seed size-dependent trade-off between dispersal (selecting for large seed number), and emergence-establishment success (selecting for large seed size) to be selectively operating in a first stage of recruitment. In a second stage, a trade-off between growth rate and susceptibility to herbivores acts as a post-establishment mechanism that allows the coexistence of a wide range of pioneer species with a large variation in seed size (Dalling and Hubbell 2002).

Most of the questions on the origin and maintenance of diversity are still unanswered due to a lack of data at varying spatial scales.

### 2.4.2. Potential factors regulating species richness

Trends in tropical forest variability have been extrapolated from floristic inventories, and attempts have been made to explore what factors contribute most in regulating diversity. Positive correlation links some of the factors identified (e.g., forest stature with fertility, rainfall with latitude and longitude), while other variables are negatively correlated (e.g., number of stems ha$^{-1}$ and average diameter at breast height). It has been shown that the number of woody species per unit area in a relatively uniform sample tends to:

- increase with forest stature, as shown by Duivenvoorden (1995) for lowland sites in Colombia with similar climate but strongly divergent soil characteristics;
- decrease with increasing average diameter at breast high over the sample area (Condit et al. 1996b; Duivenvoorden 1995);
- increase with soil fertility in the Neotropics when the effects of rainfall have been controlled (Clinebell et al. 1995; Duivenvoorden 1995; Gentry 1988);
- increase with the rate of tree turnover, including mortality and recruitment (Phillips et al. 1994a);
- increase with altitude in regions receiving moderate to high precipitation (Gentry 1988; Vazquez and Givnish 1998), and decreases with increasing latitude (Gentry 1988; Gentry 1992);
- increase with rainfall and decrease with seasonality in mature lowland forests (Clinebell et al. 1995; Gentry 1988);

- increase with the number of individuals present in a sample (Condit et al. 1996b; Lieberman et al. 1985a);
- increase with time following catastrophic disturbances (Terborgh et al. 1996).

The rate at which species composition shifts with distance (beta diversity) in a relatively uniform habitat is greater in richer communities at lower elevations (Vazquez and Givnish 1998).

The strongest patterns seem to be at global, continental, and regional rather than local scales. For edaphic factors for example, while specialization of plant species to extremely different adjacent soil conditions is well known (Newbery et al. 1986), there is much less information on the effect of edaphic factors on plant species distribution where the gradients are not too extreme.

Some already known patterns of diversity, that operate at different temporal and spatial scales, have been conceptualised. Temporal scales can be distinguished between ecological (that seems to control and mirror more closely the present situation), and an evolutionary scale that does not have evident traces in the present time (Givnish 1999). Furthermore, drivers for diversity operate at different spatial scales: while macro-climate factors control the floristic richness of a region, soil and topography determine micro-scale local variation in forest species composition. Historical biogeographical factors also play a role at continental and regional level. In Asian tropical forests, Ashton found a decline at a regional scale in species-richness with the length of the dry season (Ashton 1996). At a smaller scale, he found a great variation in species richness clearly associated with habitat variation. In other studies, the same rainfall-diversity correlation is found, but the picture is complicated by inverse relationships between rainfall and fertility (Hall and Swaine 1976; Huston 1980). Nevertheless, in the Neotropics, while species diversity tends to positively correlate with rainfall, the positive relationship between tree species and soil fertility is weak (Wright 1992). Thus, the amount of rainfall remains potentially a better predictor of diversity.

Phillips et al. (1994a) do not find a strong relationship between rainfall and diversity, but rather a positive correlation between diversity and productivity. Similarly, after having examined 106 lowland forest inventories, some authors (ter Steege et al. 2000) find rainfall to be a poor predictor of large-scale patterns in diversity, when sites with less than 2000 mm of annual rainfall are excluded.

### 2.4.3. Floristic patterns within the Amazon basin

In the Neotropics, tree species are distributed within a total of 140 families (Mass and Westra 1993). Amazonian forests are the largest and most diverse in the tropics, with up to 473 tree and liana species in a single hectare (Condit et al. 1996b; Gentry 1988; Phillips et al. 1994a). Gentry (1994) observed that although the variability in structure and composition is very high, Neotropical forests are floristically very similar to one another, and a few families dominate most forest sites. The evidence that a few higher taxa can dominate immense areas of forest, as is typical for the temperate counterparts, challenges the common belief that the Amazonian vegetation is a small-scale mosaic of unpredictable composition and structure.

An extreme is represented by some *terra firme* sites with particular substrates such as podzols, white sands and soil overlying limestone or ultrabasic rocks, characterized by tendencies to single-species dominance (Richards 1996a).

The striking floristic homogeneity of the Amazonian flora is evident from studies of the upper Amazonian *terra firme* forests. Pitman et al. (1999) have analysed the distribution of common and rare species on a N-S axis at the foothill of the Andes, comparing sample plots from South Peru (Manu) and Ecuador (Yasuni) and have found evidence for predictable oligarchies of species that dominate several thousands of square kilometres at each site. They came to the conclusion that most tree species in that region are habitat generalists, occurring over large areas of the Amazonian lowlands at low densities but large absolute population sizes. Although most species are locally scarce, showing landscape–scale densities of $< 1$ individual $ha^{-1}$, most trees belong to a small set of ubiquitous common species.

Looking at Western Amazon sites, Pitman et al. (2001) found a disproportionate number of species concentrated in a few families: Palms, Moraceae, Myristicaceae and Violaceae. One interesting aspect in their study is that, despite the predictability of tree community composition over large areas in Amazonian Ecuador and Peru, the environmental conditions in their tree plots were not at all uniform. They had to reconcile the findings from a growing number of studies that show species-specific habitat preferences with their observation on the widespread dominance of a small spectrum of species. They suggest that while the majority of species at their sites are highly sensitive to environmental heterogeneity, the small number of common species that form the large-scale oligarchies, are largely indifferent to it, and perhaps common for that reason (Brown 1984; Hubbell and Foster 1986b). Their findings also indicate that the regulation of relative abundance is controlled by ecological factors more than non-equilibrium chance-based dynamics.

Terborgh and Andresen (1998) examined compositional variation in tree communities of tropical South America, with a primary focus on the Amazon Basin. They have found clear geographic and edaphic patterns emerging from their analysis, allowing some preliminary generalisations about the organization of the Amazonian tree flora. They looked at the dissimilarity of forest composition, both at local and regional scales, and observed that dissimilarity between sites increases with distance for both flooded and unflooded forests. They also noticed that tree communities of inundated forests tend to be more similar to *terra firme* forests within the same geographical region than to the inundated forests of adjacent regions. This is quite an unexpected result, in contrast with the strong adaptive gradient found between the leached, acidic, and drought-prone soils of the uplands, and the young, fertile, moist and neutral soils of floodplains (Lieberman et al. 1985a; Terborgh, Foster, and Nunez 1996; Tuomisto et al. 1995).

### 2.4.4 Some interpretations of floristic patterns in the Amazon basin

When looking at patterns of plant biodiversity, an important distinction should be made, as evidenced by recent work by Whittaker et al. (2001), between diversity expressed as a simple inventory of species and diversity expressed as taxonomic distinctiveness. Species richness could be related to contemporary ecological processes and controls (O'Brien 1998), while the explanation for biogeographical patterns of distinctiveness requires theories focusing on evolution of historical contingencies (Bush 1994; Whittaker, Willis, and Field 2001; Willis and Whittaker 2002a).

Most scenarios postulate at least some degree of fragmentation of Amazonian forests caused by climatic changes due to Pleistocene glaciations. The disruption of continuity in the Amazonian forest cover would have been provoked by drying (Haffer 1969; Prance 1973a), catastrophic flooding (Frailey et al. 1988) or marine intrusion (Vuilleumier 1971). According to other scenarios, the Amazonian forest did not fragment, but the cooling of the glacial-period climates triggered repeated invasions of subtropical elements (Bush 1994; Colinvaux et al. 1996), that ultimately would have caused a fragmentation of lowland populations if not lowland forests themselves. The isolation of forests or populations would have generated refuge areas where populations diverged to the point of speciation and where today a high degree of endemism is displayed. This re-expansion of the forest from refugia would have determined the formation of "secondary contact zones" (Haffer 1997), accommodating species originated in distinct regions. Manaus has been considered as a refuge by Prance (Prance 1973b) and as a "contact zone" by Haffer (1997).

The case is far from being solved and more inventories from under-sampled areas of the Amazon are necessary to disentangle the complexity of the floristic patterns. Numerous criticisms have also been expressed on the methodologies applied to define and delimit phytogeographic regions and refuge areas. The location of refugia is controversial and it seems not to coincide with zones of past high stability but rather with areas of high disturbance (Bush 1994), located in peripheral regions of the Amazon, and colonized by species adapted to colder climates during the Pleistocene glaciations. In addition, the role refugia have actually played in shaping the present patterns of diversity is also uncertain. Recent paleoecological and molecular evidence has increasingly led to the questioning of this well-established paradigm. It seems that the isolation produced by full-glacial refugia may have had a greater influence on current patterns of diversity in temperate regions than in tropical zones (Willis and Whittaker 2002b). The analysis of pollen sediments deposited by the Amazon river on the ocean floor of the Atlantic has revealed that the lowland tropical forests were not extensively replaced by savanna vegetation during glacial periods (Colinvaux et al. 1996), but rather that forests dominated throughout. An alternative explanation for the patterns of endemicity within the lowland Amazonia has been found in the rise of sea level during warm phases of the Quaternary and late Tertiary periods (10 to 12 million years ago). The transgression of the ocean into the forested regions would have produced a fragmentation of the vegetation that encouraged speciation through geographic isolation (Nores 1999).

Whatever the role of refugia in determining the current patterns of endemic species in the Amazon Basin, some authors have pointed attention to other biases that could have led to a wrong identification of hot spots of species diversity. The biases could be attributed to the concentration of the sampling efforts in particular regions well represented by botanical collections and, according to Nelson (1990), mistakenly considered as refugia.

Furthermore, Tuomisto and Ruokolainen (1997) argued that current ecological conditions are more important to explain the actual geographic distribution of species, while others point attention to events more ancient than the Pleistocene climate changes, such as the Tertiary orogenies that gave rise to the major river channels of the Amazon basin and isolated the humid coastal regions of Colombia, Ecuador, Venezuela, and Atlantic Brazil (Dalling and Hubbell 2002).

The theories presented are all compatible with the concept of the Manaus region as an area of convergence and other factors evidenced by de Oliveira and Daly (1999), reinforce this argument: the location at the confluence of three great rivers, the marked difference in soils on either sides of the Rio Solimões near Manaus, and the climatic barrier of the so called "transverse dry belt", that is, a NE-SW band of lower and more seasonal rainfall running east of Manaus and crossing the Rio Amazonas. Also Ashton (1996), while analysing patterns of species diversity all across the tropical belt and looking for explanation in climate and biogeography, noticed the exceptional number of species at Manaus that would have been unexpected simply looking at the climate of the region and could find explanation in the high site heterogeneity and in the source-sink effect. The source-sink effect was described by Pulliam (1988) and would explain the rarity of species that are on the edge of their ecological distribution or expanded into sub-optimal habitats. Propagules of species arriving from elsewhere establish by chance beyond ecotones at the edge of their preferred habitat and can sustain local populations showing negative growth. In source/sink systems, a source has a positive local recruitment rate in the absence of immigration, and thus provides a net surplus of emigrants. A sink has negative local recruitment and so would not persist in the absence of a dispersal subsidy from elsewhere. In Pulliam's model and most examples, the sources and sinks are defined by habitat quality (productivity). A large proportion of a metapopulation can exist in sink habitats, if the source patches are sufficiently productive to subsidize the sinks. These source/sink systems can also be defined in the time domain: source patches act as persistent refugia, from which populations expand outward during good times (though often to sink habitats), and contracting back during less favorable times.

Asthon (1996) remarks that history must be taken into account comparing species richness across different regions, as an equilibrium between extinction and immigration rates may take thousands of years to achieve. Speciation rates are unlikely to increase species-richness substantially, because stand density does not change with the number of species. Therefore, addition of new species must decrease the density of those already there. Immigration rates are known to be particularly slow in tropical forest species that are typical of the most mature stages of forest succession.

At a local scale, where soil is expected to play a major role in shaping forest species composition, spatial factors can also play a role in explaining species patterns. Many soil-independent processes (Condit 1996), like herbivory, seed dispersal by animals, plagues and attacks by fungi, species migration, colonization and competition for space and light in dynamic forest ecosystems affect species composition at scales wide enough to influence species composition in neighboring plots.

In Chapter 4 of the present work, patterns of floristic diversity have been explored from a large set of data from PSPs scattered through the Amazon basin, and compared with previous studies, to test the hypotheses of quite distinct regional dominance by certain specific taxonomic elements. Some of the PSPs have never been used to explore floristic and structural patterns. The complexity of the floristic composition of 91 sample plots is disentangled using Detrended Correspondence Analysis (DCA). The observed floristic gradients are correlated to environmental variables to detect their role in regulating floristic composition. At a local scale, a dataset from the BDFFP experiment, near Manaus, has been used to explore the relationships between soil characteristics and species composition.

### 2.4.5 Methodology for the floristic analysis

In Chapter 4, multivariate analysis is used to assess the floristic relationships between plots from different regions of the Amazon Basin. Multivariate analysis is an important tool for community ecology, permitting the simultaneous treatment of all variables and a summary of data structure, with minimal loss of information (Pielou 1984).

Ordination is a procedure for adapting a multidimensional swarm of data points in such a way that when it is projected onto a two-dimensional space, any intrinsic pattern the swarm may possess becomes apparent. The swarm as a whole can be modified to make its internal pattern more clearly perceptible, and the effect is to give different weights to the several species that constitute a community. There are many possible ways for mapping a multi-dimensional scatter diagram in two dimensions. What differentiates one ordination technique from another is the system used for assigning weights to the species.

Reciprocal averaging (RA) and correspondence analysis (CA) are alternative names for the same ordination technique, extremely popular for ordinating ecological data and studying species distribution along gradients. The fundamental model assumes unimodal responses of species to environmental gradients that are not studied directly but inferred from species composition data. RA is a form of eigenanalysis (Palmer 1993). Its computational approach is rather simple (Fig 2.3).

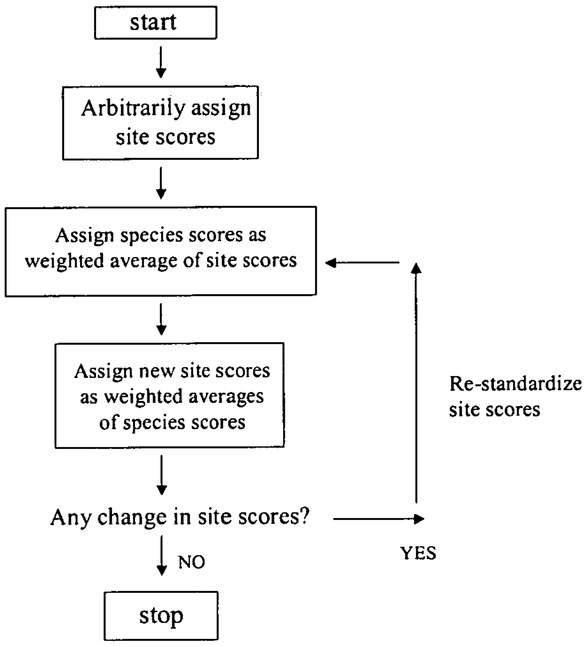


Figure 2.3. Steps in the process of reciprocal averaging.

In a one-dimensional ordination, a score is arbitrary assigned to each quadrat (plot) so that the quadrats can be ordered ("ordinated") along a single axis according to these scores. A weight is attributed to each species according to its abundance in a site (plot), and to each species is attributed a score, which is the weighted average of the quadrat scores. New site scores are assigned as the weighted average of all the species that occur in the site. Again, the weights are species abundances. The algorithm continues reciprocally averaging (and re-standardizing) site and species scores, until there is no noticeable change in species and sites scores from one iteration to the next. Quadrats and the species are ordinated simultaneously. Scores are assigned to each quadrat and to each species in such a way as to maximize the correlation between quadrat scores and species scores.

The result is the first CA axis solution. Given a data set, an identical solution will result from any set of initial arbitrary numbers. Computation of the second axis is essentially the same, except that the linear effects of the first axis are factored out. The first axis produces the maximum possible correlation between sites and species scores (Pielou 1984). Second and higher axes also have a maximal site-species correlation subject to the constraint that axes are orthogonal. Eigenvalues associated with each axis equal the correlation coefficient between species scores and site scores (Pielou 1984). An eigenvalue close to 1 will represent a high degree of correlation between species and sites, and an eigenvalue close to 0 will indicate very little correspondence.

Detrended correspondence analysis (DCA) overcomes the two defects of ordinary RA (ter Braak 1986). When data from a long gradient are ordinated by principal component analysis (PCA) or RA, they show a typical *arch effect* (sometimes called *horseshoe effect*) (Fig. 2.4).

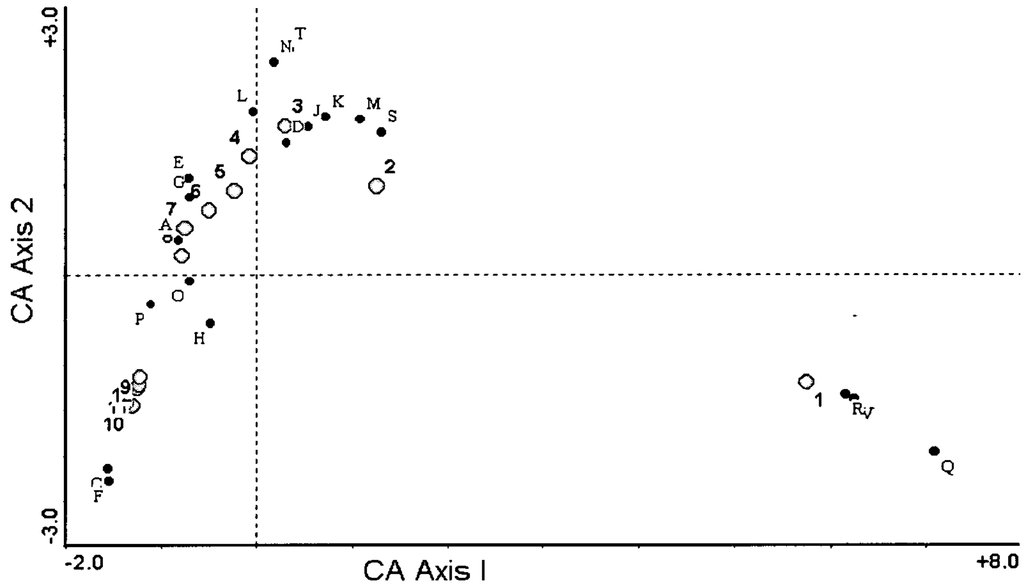


Figure 2.4. Examples of a long gradient and the arch effect in Correspondence Analysis (CA) representation (modified from Palmer, M., http://www.okstate.edu/artsci/botany/ordinate/).

The arch effect is a distortion or artifact in an ordination diagram, in which the second axis is an arched function of the first axis. It is caused by the unimodal distribution of species along gradients, which means the species has one optimal environmental condition. The single long gradient accounts for a high proportion of the variance. The arch created by the second axis is probably spurious and has no real ecological meaning. Another defect of RA consist of the contraction of scale at each of the extremes in the two-dimensional representation of the data swarm: the points at the ends tend to be more closely spaced than those at the middle and this variation in space does not correspond to any variation in the steepness of the environmental gradient. When the gradient represented is short, species response tend to be linear, while the representation of a long gradient determines unimodal responses. Nevertheless, steeper small gradients that occur and overlap with the extremes of the main long gradient produce the contraction of points at the ends of the biplot (Fig. 2.4).

The Detrended Correspondence Analysis (DCA) is a technique developed to flatten out the misleading arch and corrects the contraction in scale, applying the requisite adjustments. The procedure consists of systematic data manipulation (Hill 1979), carried out in order to force an ordination into a form that accords as well as possible with intuitive expectations. Various artifices are adopted such as cutting the first axis into segments and re-setting the average of each segment to zero (Hill and Gauch 1980).

### 2.4.6 The stand structure of tropical forests

Together with floristic composition, variation in tropical forest stand structure has been observed and documented by various authors. Tropical rainforest structure is known to vary with soil type (Tuomisto et al. 1995), soil nutrients (Laurance et al. 1999), climate (Gentry 1982), disturbance regime (Lugo and Scatena 1996), successional status (Saldarriaga et al. 1988), topographic position (Austin et al. 1996), and human impact (Brown et al. 1995; Laurance et al. 1997). It is mainly edaphic factors and tree falls that create patches of characteristic structure on all old-growth tropical rainforest landscapes. It is therefore difficult to extrapolate representative values for landscapes, from a few small plots, often < 1 ha in size. Nevertheless, the proper sample size for structure and biomass studies has been tested by some authors, and tropical rainforest studies have been explicitly designed for extrapolation to landscape scales (Brown et al. 1995; Grace et al. 1995b; Laurance et al. 1997).

Clark and Clark (2000) demonstrated mesoscale variation in forest structure and biomass within 600 ha of tropical rainforest in La Selva. The influence of edaphic factors in shaping the structure of the forest was particularly evident when old alluvial and recent alluvial soils were compared, showing a range from a maximum of 477.6 stems $ha^{-1}$, to a minimum of 312.5 stems $ha^{-1}$ respectively. The variation in basal area was also considerable, although not always correlated with the stem number, showing a range from 26 to 16.4 $m^2$ $ha^{-1}$ for the old alluvial and the recent alluvial soil type respectively.

It has been widely observed that greater availability of moisture on rainier, less seasonal sites, and of nutrients on more fertile sites, should reduce the whole-plant compensation points. Thus, it increases shade-tolerance (Burslem et al. 1996; Wright 1992), and permits more individuals to persist in the understory (Condit et al. 1996a). Givnish (1999) suggests that heavy annual rainfall would promote slightly more open upper canopies and denser understoreys, by favouring higher rates of tree falls. Heavy rainfall would reduce the mechanical strength of wetted soils and reduce the depth of root penetration in the soil, especially on poorly drained sites. In addition, high precipitation could determine an increase in rates of growth in tree height, as indicated mainly by qualitative observations and measurements of understory light (Coomes and Grubb 1998). Givnish (1999) found a highly significant increase in total stem density with precipitation but the trend shown becomes non-significant if the smallest trees are excluded (<20 cm of dbh), and almost non-significant when trees with dbh ≤ 10 cm are excluded from the analysis. In Asian tropical forests, Ashton (1996) compared stand structure and dynamics of plots from different regions and found consistently fewer trees in smaller size classes in forests with seasonal climates. He also found a higher fluctuation in mortality in small size trees.

In the present study, forest stand structure is examined for 91 rainforest PSPs, most of which derive from a considerable compiling effort of forest inventories from different regions of the Amazon Basin. Additional plots from tropical regions other than the Neotropics have been added to allow a Pantropical comparison.

## 2.5. Basal area change and turnover

Two main assumptions slowed progress toward resolving the question of whether tropical forests are sources or sinks of atmospheric carbon: the steady-state atmosphere assumption and the steady-state forest assumption (Gillepsie et al. 1992). The first assumption has been recently discredited by developments in the field of atmospheric sciences that showed how carbon concentration in the atmosphere has been changing on all time-scales during the Earth's history (Gillepsie, Brown, and Lugo 1992). However, during the past ~ 11 000 years, natural variation in $CO_2$ has been small (from 260 ppm at the Holocene minimum to 280 ppm in the pre-industrial period).

The steady-state forest assumption excluded a large portion of tropical forests from consideration in the global carbon cycle because biomass and biomass accumulation rates were supposed not to have changed over time in all these tropical forest lands not undergoing active land-use change. Undisturbed forests were unrealistically assumed to be in a steady state with respect to carbon exchange with the atmosphere. Lugo et al. (1992) pointed out that leaching of carbon to deep soil profiles and rivers would prevent any forest from permanently being in a carbon neutral state with the atmosphere and it is reasonable to expect that over vast land areas forests tend to operate as sources and sinks alternatively over time, under the influence of climatic factors.

Inventory studies indicate that carbon accumulation in Northern Hemisphere forests may be as high as –0.8 Pg of C $a^{-1}$ (IPCC 2001) while an earlier review of individual regional and national studies gave a range of –0.6 to –0.9 Pg of C $a^{-1}$ (Dixon et al. 1994). The picture from the tropical regions is also unclear. Recent micrometeorological research suggests that there may be a large net carbon sink in mature Amazonian forests (Grace et al. 1995b; Grace et al. 1995a; Malhi et al. 1998), even though a degree of uncertainty still persists in assessing the magnitude of gaseous exchanges between canopies and atmosphere.

### 2.5.1 Basal area change in tropical rainforests

Basal area seems to be a valuable surrogate measure of total biomass (Brown et al. 1989; Gillepsie, Brown, and Lugo 1992) and has been used as an effective measure for changes in biomass in tropical forests (Phillips et al. 1998a).

Observations over variable census intervals of basal area gains (due to growth and recruitment of new individuals) and losses (due to mortality) have shown clues of a stand basal area increase through time (Phillips et al. 1998a). Data from 153 permanent forestry plots, 97 from Amazonia, have been collated, and a total of more than 100 000 individual trees, all of them in mature undisturbed forests, has been analysed. The definition “undisturbed” derives from observations of the stem diameter distribution, which is found to be typically J-shaped in tropical forests not undergoing successional processes, not recovering from disturbance, and not undergoing any type of anthropogenic perturbation (Meyer 1952). However, a certain degree of disturbance from traditional shifting cultivation in the distant past cannot be excluded, and the slow accumulation of basal area, found in the sites studied by Phillips et al. (1998), could therefore have origins different from processes such as $CO_2$ fertilization.

### 2.5.2 Carbon sequestered in the Pantropical region

The entire Pantropical dataset analysed by Phillips et al. (1998) shows an increase in biomass (0.77 ±0.44 t $ha^{-1}$ $a^{-1}$), but there are regional differences. The trend is more significant in the Neotropics. For Amazonian inventories, Phillips et al. (1998) suggested a biomass gain from the 1970s, with an average accumulation rate of 0.97 ± 0.58 t $ha^{-1}$ $a^{-1}$. On the contrary, Paleotropical sites (tropical Africa, Asia, Australia) did not show significant changes (-0.18 ± 0.59 t $ha^{-1}$ $a^{-1}$). However, recent reanalysis of a more extensive Pantropical dataset shows basal area changes in African plots that are consistent in direction and magnitude with those observed for the Neotropical plots (Lewis et al., in prep.). The study by Phillips et al. (1998a) shows that in the Neotropics the mean value of biomass change has been positive for 21 out of 26 years (from 1971 to 1996) for the lowland Neotropics (paired t test, $P < 0.01$), and in 20 out of 22 years (1975-1996) for Amazonia (paired t test, $P < 0.001$).

Furthermore, the dynamics leading to the observed accumulation of basal area remain unclear because the spatial and temporal extents of the measurements are quite limited.

Despite the observed trends of basal area accumulation, any tropical forest sink appears vulnerable to factors such as the increased deforestation, logging, fragmentation, regional drying and warming, intensification of El Niño phenomena, and upper limits to forest productivity imposed by fertility and soil water availability. The present study offers more insight into some regions of the Amazon basin, with a separate analysis of the various components of forest dynamics, and providing spatial patterns of BA net change. A large network of permanent biomass plots is rapidly building up to enable more adequate investigations and tackle the main unanswered questions (Malhi et al. 2002).

### 2.5.3 Tropical forests turnover

Since the mid 20th century, a significant amount of information has been gathered on the dynamics of humid tropical forests. Rates of tree mortality and recruitment have been compiled and turnover rates calculated. Turnover rates are averages of mortality and recruitment rates and measure how fast individuals are moving through the population, not just how fast they die (Phillips et al. 1994a; Phillips 1996). The total number of individuals may remain more or less constant, even though the turnover increases.

Tree recruitment and tree mortality are not smooth, continuous processes. In a mature forest, tree growth, and especially tree death, are clumped in time and space. Therefore, there is inevitably background noise that may obscure underlying changes. To detect those changes in tree turnover, a large Pantropical sample of permanent tree plots, each regularly surveyed and re-censused over decades, is necessary to draw conclusions. A significant upward trend since 1960 in average measured rates of turnover of tropical forests trees $\geq$ 10 cm in diameter has been found (Phillips 1996; Phillips 1998; Phillips and Gentry 1994). This has proved to be a controversial finding (Phillips 1995; Sheil 1995a), but one which could have important implications for biodiversity and atmospheric change (Pimm and Sudgen 1994).

Phillips and Gentry (1998) looked at 22 mature forest sites with more than two inventories and found that forest turnover has generally increased since the 1950s. They also concluded that relatively shade-intolerant trees, with low-density wood and low carbon density, could benefit. If sustained over a large area and over a substantial period, this change could have a significant impact.

The increase in turnover coincides with an accelerating build up of carbon dioxide in the atmosphere (Keeling, Chin, and Whorf 1996). The effect of rising atmospheric $CO_2$ concentrations on tree turnover could be caused as much by stimulated liana growth as by tree growth (Phillips et al. 2002b). Whatever factor is mostly responsible for the patterns observed, the relevant aspect is that "intact" tropical forests are responding to global changes.

Changes in BA and turnover across several PSPs from tropical forest have been already analysed (Phillips et al. 1998a; Phillips and Gentry 1994), but a detailed exploration of the mechanisms leading to the observed changes is missing. Some questions in particular are addressed in the present study (Chapter 5). The spatial and temporal patterns in stem density and BA changes have been analysed jointly with forest stem dynamics (turnover). This analysis enables us to distinguish between changes in forest biomass due to recovery from disturbance, following a successional process, and changes in BA that may be caused by enhanced growth, perhaps in response to the enhanced carbon dioxide concentrations in the atmosphere. Changes in turnover and basal area are decomposed into the component processes of recruitment, mortality and growth. Analogously, the single components of forest stand structure are investigated separately to distinguish between the role played by large-stemmed trees that account for most of the forest biomass, and the role played by small-stemmed individuals in leading to the observed BA changes over time (Chapter 5). An updated interpretation on current forest dynamics change is presented and methodological issues are discussed (Chapter 6). The role of some groups of species with distinctive growth strategies (palms and pioneers species) is also examined to predict some floristic changes that could precede structural changes (Chapter 5 and 7).

## 2.6. Methodological issues in permanent sample plot studies

Long-term forest sample plots are a very useful tool in detecting and monitoring changes in dynamics and biomass. However, the complexity of the rainforest vegetation combined with the nature of the methods used to measure tropical forest stands mean that artefacts and mis-interpretation are a constant danger. A recent critique has argued that some of these old forest plot data sets have significant problems in interpretation because of the use of non-standardised methodologies (Clark 2002). The controversies surrounding long-term plot data centre around whether artefactual errors of experimental design, measurement or interpretation can explain some or all of the observed patterns of basal area accumulation in old-growth tropical forests (Condit 1997; Hall et al. 1998; Phillips 1995; Phillips 1996; Phillips and Sheil 1997; Sheil 1995a). The most controversial issues refer to possible improper measurement of trees with bole defects or buttresses. With respect to forest stand dynamics, some controversies exist on the use of equations that are census interval-dependent to estimate mean rates of tree recruitment and mortality. They could lead to artefactual changes in turnover through time, and make it difficult to compare these rates across sites with very different census intervals. In this review some of the most common artefacts that affect long-term plot studies are presented. Sheil (1995b) identifies three main types of artefacts. Two are methodological in origin: (1) error, bias or inconsistency in measurements, related to poor techniques and inconsistencies in methodology, the latter quite likely to occur in long term studies because methods tend to change; (2) physical alteration of the vegetation produced during field research activity. A third artefact is related to the interpretation and manipulation of the data in the process of data analysis.

A summary list of the sources for the most common errors and biases of the three types thoroughly analysed by Sheil (1995) is presented in Table 2.2.

**First type:**

1. poor species identification (mis-identification or species concept too broad)
2. poor quality of measurement due to very irregular shape of stems, broken stems, multiple stems, presence of stranglers, spines, buttresses
3. poor quality of measurements due to a fluctuating point of measurement, not permanently marked
4. poor quality of measurements due to tape stretch
5. lack of precision in measurements reading (high or low unit precision, rounding of values)
6. obscuring effect of hydrostatic stem flex (shrinkage/swelling) on real growth
7. "ghosts" recruits and mortalities due to a bad marking of boundaries and loss of tree tags

**Second type:**

1. disturbance on stem from nails for tags and paint to define the point of measurement
2. disturbance to understory vegetation by removal of herbs, cutting of lianas
3. disturbance to the ground (increased seed germination, trampling of seedlings, breakage of young stems)
4. loss of representativeness due to clear marking of plot

**Third type:**

1. statistical problems due to lack of replication and small plot size
2. statistical problems due to variable census intervals that affect calculation of mortality and recruitment rates
3. arbitrary removal of outliers in growth analysis caused by the very skewed nature of increment distribution
4. adoption of arbitrary criteria for the removal of "too negative" increments
5. problems caused by seasonal variations in stem growth and related to comparisons of growth when measurement periods do not cover an integral number of years

Table 2.2. List of the most common errors and biases in the adoption of measurement protocol for forest permanent sample plots (modified from Sheil 1995).

To the above-listed common errors and biases, an additional source of potential bias should be added, that is the way the location for plot establishment is chosen. A general tendency to select mature-phase, gap free tracts of forests ("majestic forest bias") has been observed, and attempts have been made to test how this methodological issue would affect local and regional characterization of forest stand dynamics (see Chapter 6, paragraph 6.2.1).

Some of the methodological issues identified are more crucial than others in estimates of BA change. All these potential errors and biases have been identified and analysed for their most likely effect on basal area measurements, and consequently on biomass change (Phillips et al. 2002a). The assessment proposed by Phillips et al. (2002a) is based on the possibility to predict and model the likely patterns that the artefacts would cause in the plot data, and to explicitly test for such patterns in the data. The evaluation of potential biases proposed was done by fragmenting the composite phenomenon of BA change into its main parts (i.e., growth, recruitment and mortality). Then, each component was separately screened in order to detect the "footprint" of typical artefacts in the data structure (Phillips et al. 2002a).

In this thesis, some of the tests suggested by Phillips et al. (2002a) have been used and applied to an expanded dataset (Chapter 6).

## 2.7. Changes in tropical forests species composition

The current distribution of the world's flora reflects a complicated history of interacting factors. They encompass both past and present climate, physical and chemical influences from soil and water, evolutionary history and interactions with other organisms, including humans. It is widely recognized that the inherent variability of climate in the tropics strongly influences the distribution and dynamics of forests in these regions (Clark and Clark 1994; Phillips and Gentry 1994;Bruijnzeel and Veneklaas 1998; Condit, Hubbell, and Foster 1996a; Vitousek and Matson 1992).

Recent results suggest that local and regional forest dynamics are linked to changing climatic factors (Clark and Clark 1994; Condit et al. 1995a; Condit, Hubbell, and Foster 1996a; Condit, Hubbell, and Foster 1996a; Condit 1998; Vitousek and Matson 1992; Walsh and Newbery 1999). Seasonal patterns of rainfall and drought will probably be more important than the total quantity of precipitation. Moist tropical forests in Amazonia and elsewhere are subjected to increasingly severe drought episodes through the El Niño Southern Oscillation and, possibly, through deforestation-driven reductions in rainfall. The effects of this trend on tropical forest canopy dynamics, emissions of greenhouse gases and on other ecological functions are potentially large, but poorly understood. Shifts in functional composition and biodiversity are expected as a result of climate changes and increased $CO_2$ (Condit, Hubbell, and Foster 1996a; Körner 2000), but so far there is no evidence of widespread compositional change in old-growth forests. It is not clear if this is due to the absence of evidence or the inadequacy of monitoring.

Compared with the flora of the temperate zones, relatively little is known about how different tropical forests types will respond to future climate change. A few studies on species compositional shift have been carried out, and most of these are focused on capturing the successional development of forest recovering from major disturbances (Sheil 1999; Sheil et al. 2000; Swaine et al. 1987a; Swaine et al. 1987b), or recurring perturbations, such as cyclones (Burslem and Whitmore 1999).

Hypotheses have been expressed on the potential shift on the competitive balance between different functional groups. Fast-growing species are expected to be advantaged (Phillips and Gentry 1994), and many invasive plant species share traits that could increase their dominance in a changing climate (Dukes and Mooney 1999). Rapid anthropogenic climate change might disadvantage species that cannot quickly extend their ranges into newly suitable regions, such as plants with long generation times.

The observed accelerated turnover of tropical forests coincides with an accelerated buildup of $CO_2$, and could be either the result of increased tree growth at the ecosystem level, or the enhanced growth of some functional groups such vines, that are known to affect tree-fall rates (Phillips and Gentry 1994). Some life forms (e.g., epiphytes) have been observed to be particularly susceptible to climate change (Benzing 1998). In a recent study across Amazonian tropical forest PSPs, evidence for an increasing occurrence of large lianas has been shown (Phillips et al. 2002b), as previously hypothesised by the same authors (Phillips and Gentry 1994). An increase in liana and early successional species is likely to have an impact on carbon balance, as fast-growing trees have less dense wood, and on forest structure. A decrease of small-stemmed treelets and shrubs with affinities for moist microhabitats was noted within the 50-ha PSPs of Barro Colorado Island (Condit, Hubbell, and Foster 1996a), and in tropical forest of Sarawak (Nakagawa et al. 2000), indicating a change in the size-structure of the forest, associated with drought events. However, some studies show that mature large trees may have a rather superficial horizontal root distribution and acquire water from shallower layers of the soil than roots of smaller individuals, as observed in a Panamanian seasonal forest (Meinzer et al. 1999). Some findings seem to indicate higher mortality rates in large- than in small-sized trees, experienced during droughts in Asian (Leighton and Wirawan 1986), African (Swaine 1992), and Neotropical (Condit, Hubbell, and Foster 1995a) forests. One of the possible explanations could be a greater exposure of the crown to intense sunlight and evaporation, in large- versus small-sized trees.

The impact of strong droughts has been recorded in Amazonian forests, but changes in mortality have not been studied at the species or genus level (Laurance et al. 2001). On the contrary, the change in abundance of common species with dbh >10 cm, and specifically, the decline in moisture-dependent guilds has been recorded in Panama (Condit, Hubbell, and Foster 1996a), and patterns of local species extinction have been modelled (Condit 1998).

There is a need for more adequate long-term tropical forest studies that cover suitable temporal and spatial scales for detecting signals of major compositional shifts. At present, given the size and temporal scale of existing monitoring experiments, it seems difficult to distinguish between the expected impacts of global changes and other processes of recovery from past disturbance or of species substitution that would occur on a local scale as part of the natural evolution of dynamic forest systems. The present study is intended to show hints of within-site variation in species composition, and to test if the direction of compositional change is consistent in sites across the Amazon basin (Chapter 7).

# *Chapter 3. Description of the study sites*

## 3.1. Introduction

In this chapter, the study sites are described, with a more detailed insight into those sets of 1-ha forest plots where most of the analysis is centred. The main environmental features (climate and soil) of each study site are presented and compared. Rainfall data derived from an historical series are analysed to detect trends of change in local precipitation across different localities of the Amazon Basin.

## 3.2. Study sites

The database used in the present work is a mosaic of data derived from different projects. The work focuses particularly on a set of permanent sample plots (PSPs) from the Amazon Basin, but other sites have been included in part of the analyses to allow Pantropical comparison of some rainforest characteristics and to extrapolate some generalization on tropical forest functioning. The PSPs are located in regions quite distinct climatically, as the isohyets map shows (Fig. 3.1). Values of mean monthly precipitation (mm/ month) are shown in the map of figure 3.1, by different colors.

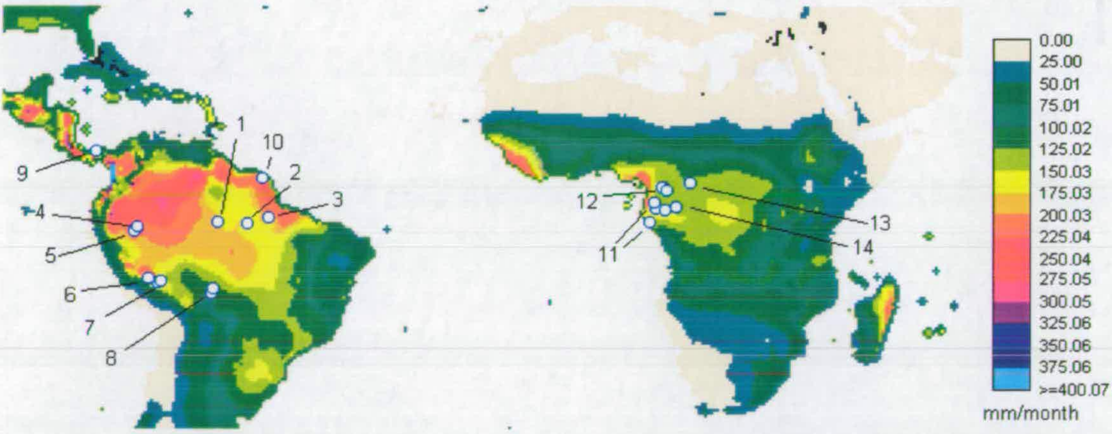


Figure 3.1. Map with isohyets. South American study sites are indicated together with some African plots used for a comparison of forest stand structure across continents. Refer to table 3.1 in text for the name of PSPs sites.

Within the Amazon Basin, total annual rainfall is typically 2000 mm, but ranges between 4000 mm in the northwest and is less than 1200 mm at the savanna fringes. Annual mean rainfall data for each region are reported later in Table 3.4.

Four clusters of PSPs are identified: (1) an Eastern Amazonian group with tall forests on old, nutrient-poor, well-drained soils in a moderately seasonal climate occasionally subject to drought; (2) a Central Amazonian cluster of similar sites, on old, nutrient-poor soil and a rainfall regime with a short dry period (3) a North Western Amazonian group around N Peru, located in a region with high rainfall and little or no dry season, (4) a South Western Amazonian group of sites located around S Peru and NE Bolivia, with forest often standing on richer soil near the base of the Andes and on the Brazilian crystalline shield, in a region subject to a more seasonal rainfall regime.

The sources of data, names of collaborators, their institutions, and the specific objectives of each initiative are specified in Table 3.1.

Most of the PSPs are from *terra firme* forest communities, standing on soil of different maturity, from plateau of ancient formation to recent floodplains, including one example of *terra firme*-swamp edge (see table 3.2, where location, size and forest type are listed).

The amount of information available for each PSP varied from tree-by-tree data for several consecutive censuses to simple floristic lists or diameter size distributions, with stems lumped by dimensional classes. Therefore, out of the total of 92 forest PSPs, only fractions of the whole database were used to test the different hypotheses explored in the present work. The sub-sets of data used for the three main analyses of the present study are listed below (see appendix 1 with a detailed list):

- analysis of floristic relationships in forest communities across the Amazon Basin: 68 PSPs, covering 12 localities.
- Analysis of stand structure: 91 PSPs, covering 23 localities. The analysis spans a wider range of sites whose structural data were extracted directly from the literature to allow a Pantropical comparison.
- Analysis of forest stand dynamics: 37 PSPs, covering 8 localities.

Most of the PSPs used for the structural analysis are from Neotropical sites (Almeida et al. 1993; Chave et al. 2001; Condit et al. 1999; Higuchi et al. 1997; Killeen 1996; Laurance et al. 1999; Phillips 1993). The additional PSPs used to compare forest stand structure across the tropical belt are from African and Asian locations (Condit et al. 1999; Lejoly 1994; Lejoly 1996; Reitsma 1988; Sonke 1998).

A few plots with more than one census were excluded from the analysis of stand dynamics, because the longest census interval was too short, or because they were isolated forest fragments, likely to be perturbed by edge effects and characterized by mortality rates much higher than those observed in more continuous tracts of primary forest.

The PSPs used for the analysis of forest dynamics are shown in table 3.3. In the same table, PSPs are divided between "older plots" and "more recent" ones, to distinguish between different periods of establishment. The "older PSPs" contribute most of the data (32 PSPs). They were monitored for almost two decades and are mainly from the Central Amazon (Manaus) and south Peru (Tambopata). "More recent" plots are fewer. They were established in the early 1990s and contribute only partially to the analysis of dynamics, covering mostly Northern and Southern Peruvian sites.

To allow the analysis of temporal patterns in forest dynamics, the longest census intervals was divided in two shorter consecutive periods, for which mortality, recruitment, growth and turnover rates were calculated. In table 3.3 the two main clusters of PSPs are described in different columns, where the midyear of both periods is indicated, together with the midyear of the longest census interval.

| Site or project | Code (map) | Country | State | Principal investigators | Institution/ sources | Priority of projects |
|---|---|---|---|---|---|---|
| BDFFP | 1 | Brazil | Amazonas | William Laurance | BDFFP, INPA | Impacts of fragmentation on species composition and dynamics |
| BIONTE | 1 | Brazil | Amazonas | Niro Higuchi | INPA | Impacts of silvicultural treatments on biomass and growth |
| Tapajos | 2 | Brazil | Para | Natalino Silva | CIFOR | Impacts of silvicultural treatments on biomass and growth |
| Caxiuana | 3 | Brazil | Para | Samuel Almeida | Museu Goeldi, Belem (Para) | Floristic characterization, analysis of dynamics |
| Allpahuayo | 4 | Peru | Loreto | Oliver Phillips, RodolfoVasquez | UL/PFP/IIAP | Floristic characterization, analysis of dynamics |
| Mishana | 4 | Peru | Loreto | Oliver Phillips, RodolfoVasquez | UL/PFP | Floristic characterization, analysis of dynamics |
| Sucusari | 5 | Peru | Loreto | Oliver Phillips, RodolfoVasquez | UL/PFP | Floristic characterization, analysis of dynamics |
| Yanamono | 5 | Peru | Loreto | Oliver Phillips, RodolfoVasquez | UL/PFP | Floristic characterization, analysis of dynamics |
| Cuzco Amazonico | 6 | Peru | Madre de Dios | Oliver Phillips, RodolfoVasquez, Percy Nunez | UL/PFP/UNSAAC | Floristic characterization, analysis of dynamics |
| Tambopata | 7 | Peru | Madre de Dios | Oliver Phillips, Rodolfo Vasquez | UL/PFP | Floristic characterization, analysis of dynamics |
| BOLFOR | 8 | Bolivia | Santa Cruz | Leano, Fredericksen | BOLFOR | Impacts of silvicultural treatments on biomass and growth |
| BCI | 9 | Panama | | | Condit *et al.* (1999) | |
| Pasoh | | Malaysia | | | Condit *et al.* (1999) | |
| Nourages | 10 | French Guiana | | | Chave *et al.* (2001) | |
| Oveng | 11 | Gabon | | | Reitsma (1988) | |
| Doussala | 11 | Gabon | | | Reitsma (1988) | |
| Lope' | 11 | Gabon | | | Reitsma (1988) | |
| Ekobakoba | 12 | Cameroun | | | Reitsma (1988) | |
| Djolimpoum | 12 | Cameroun | Dja | | Sonke (1998) | |
| Mekas | 12 | Cameroun | Dja | | Sonke (1998) | |
| Alat-Makay | 12 | Cameroun | Dja | | Sonke (1998) | |
| Djomedjoh | 12 | Cameroun | Dja | | Sonke (1998) | |
| Ngotto | 13 | RCA | | | Lejoly (1994) | |
| Odzala | 14 | Congo | | | Lejoly (1996) | |

Table 3.1. List of the sources of the compiled database used for the present work. The institutions, the principal investigators, and the main objectives of each project that provided the data for the present study, are indicated.

| FOREST | REGION | COUNTRY | ENVIRONMENT-VEGETATION | LAT | LONG | ALT | AREA | # PSPs |
|---|---|---|---|---|---|---|---|---|
| Los Fierros Bosque I and II | Santa Cruz | Bolivia | tall evergreen forest, sandstone colluvium | -14.6 | -60.9 | 200 | 1 | 2 |
| BIONTE | Amazonas | Brazil | terra firme clay | -2.60 | -60.2 | 100 | 1 | 3 |
| BDFFP | Amazonas | Brazil | terra firme clay | -2.50 | -60.0 | 125 | 1 | 27 |
| Tapajos | Para | Brazil | terra firme clay | -2.80 | -55.0 | 80 | 0.25 | 12 |
| Caxiuana 6 | Para | Brazil | terra firme, sandy-clay | -1.70 | -51.5 | 50 | 1 | 1 |
| Caxiuana 7 | Para | Brazil | terra firme,sandy-clay | -1.70 | -51.5 | 50 | 1 | 1 |
| Tambopata1 | Madre de Dios | Peru | terra firme, clay | -12.8 | -69.7 | 260 | 1 | 1 |
| Tambopata6 | Madre de Dios | Peru | terra firme, upland sandy-clay | -12.8 | -69.7 | 270 | 1 | 1 |
| Tambopata4 | Madre de Dios | Peru | recent alluvium, Holocene floodplain | -12.8 | -69.7 | 250 | 1 | 1 |
| Tambopata0 | Madre de Dios | Peru | recent (Holocene) floodplain | -12.8 | -69.7 | 255 | 1 | 1 |
| Tambopata 2 | Madre de Dios | Peru | terra firme- permanent swamp edge | -12.8 | -69.7 | 255 | 0.4 | 1 |
| Tambopata3 | Madre de Dios | Peru | sandy-clay terra firme | -12.8 | -69.7 | 270 | 1 | 1 |
| YanamonoA | Loreto | Peru | old floodplain, silty-clay | -3.40 | -72.9 | 140 | 1 | 1 |
| YanamonoB | Loreto | Peru | silty-clay, nutrient-rich, adequate drainage | -3.40 | -72.9 | 140 | 1 | 1 |
| Mishana | Loreto | Peru | terra firme, white sand | -3.80 | -73.5 | 150 | 1 | 1 |
| Indiana | Loreto | Peru | silty-clay, nutrient-rich, adequate drainage | -3.50 | -73.8 | 140 | 1 | 1 |
| Allpahuayo B | Loreto | Peru | sandy-clay, well drained | -4.00 | -73.4 | 170 | 1 | 1 |
| Allpahuayo A | Loreto | Peru | sandy-clay, poorly drained | -4.00 | -73.4 | 160 | 1 | 1 |
| Allpahuayo C | Loreto | Peru | white sand, nutrient-poor, excessively drained (varillal) | -4.00 | -73.4 | 170 | 1 | 1 |
| Sucusari A | Loreto | Peru | terra firme, sandy-clay | -3.20 | -72.9 | 150 | 1 | 1 |
| Sucusari B | Loreto | Peru | terra firme, sandy-clay | -3.20 | -72.9 | 150 | 1 | 1 |
| Sucusari C | Loreto | Peru | alluvial, silty, nutrient poor, varzea, seasonally flooded by black water river | -3.20 | -72.9 | 140 | 1 | 1 |
| Sucusari D | Loreto | Peru | sandy-clay, intermediate nutrient status, well-drained plateau and ridge-top forest | -3.20 | -72.9 | 150 | 1 | 1 |
| Sucusari E | Loreto | Peru | sandy-clay, poorly-drained oligotrophic plateau forest, irregular topography, intermediate nutrient status | -3.20 | -72.9 | 150 | 1 | 1 |
| Cuzco Amazonico 2e | Madre de Dios | Peru | recent falluvium, Holocene floodplain | -12.6 | -69.1 | 200 | 1 | 1 |
| Cuzco Amazonico 2u | Madre de Dios | Peru | recent falluvium, Holocene floodplain | -12.6 | -69.1 | 200 | 1 | 1 |
| Cuzco Amazonico 1e and 1u | Madre de Dios | Peru | recent falluvium, Holocene floodplain | -12.6 | -69.2 | 200 | 1 | 2 |
| Huanchaca Dos I and II | Santa Cruz | Bolivia | gallery forest | -13.9 | -60.8 | 800 | 1 | 2 |
| Huanchaca Dos Isla al Frente I and II | Santa Cruz | Bolivia | gallery forest | -14.5 | -83.4 | 800 | 1 | 2 |
| Caxiuana 5, 8-13 | Para | Brazil | terra firme,sandy-clay | -1.70 | -51.5 | 50 | 1 | 7 |
| Caxiuana A-B | Para | Brazil | terra firme | -1.70 | -51.5 | 50 | 1 | 2 |

Table 3.2. *(Continued)*

| FOREST | REGION | COUNTRY | ENVIRONMENT-VEGETATION | LAT | LONG | ALT | AREA | # PSPs |
|---|---|---|---|---|---|---|---|---|
| Pakitza, Manu River, plot 1 | Madre de Dios | Peru | terra firme, old terrace | -11.90 | -71.30 | 300 | 1 | 1 |
| Nouragues | Nourages | French Guiana | terra firme | 4.80 | -52.70 | 100 | 22 | 2 |
| BCI | Barro Colorado Island | Panama | Clay | 9.20 | -79.90 | 150 | 50 | 1 |
| Pasoh | Pasoh | Malaysia | Clay | 2.90 | 102.3 | 90 | 50 | 1 |
| Oveng | | Gabon | Clay | 0.70 | 11.40 | 580 | 1 | 1 |
| Doussala | | Gabon | sandy-clay | -3.10 | 10.60 | 480 | 1 | 1 |
| Lope' | | Gabon | Sandy | -0.40 | 11.50 | 250 | 1 | 1 |
| Ekobakoba | | Cameroon | sandy-clay | 0.40 | 13.10 | 520 | 2.5 | 1 |
| Djolimpoum (L1-4) | Djolimpoum | Cameroon | n.a. | 3.30 | 12.90 | 590 | 2.5 | 1 |
| Mekas (L5-6) | Mekas | Cameroon | n.a. | 3.20 | 12.50 | 640 | 2.5 | 1 |
| Alat-Makay (L7-8) | Alat-Makay | Cameroon | n.a. | 2.90 | 13.30 | 560 | 2.5 | 1 |
| Djomedjoh (L9) | Djomedjoh | Cameroon | n.a. | 3.00 | 13.60 | 660 | 2.5 | 1 |
| Ngotto | | CAR | n.a | 4.00 | 17.00 | | ? | ? |
| Odzala | | Congo | n.a | 0.50 | 14.53 | 500 | ? | ? |

Table 3.2. List of all the sites included in the present work. For each analysis presented in different chapters, a separate sub-set of plots has been considered.

| Site | code | Tot ha | first census | Last census | longest interval | Older PSPs |  | More recent PSPs |  | midyear |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  |  | 1st int. | 2nd int. | 1st int. | 2nd int. | longest int. | 1st int. | 2nd int. | 1st int. | 2nd int. |
| BDFFP1201 | BD12 | 3 | Apr-81 | Apr-99 | **18** | 4.8 | 7.9 | / | / | 1990.0 | 1988.4 | 1995.1 | / | / |
| BDFFP1301 | BD13 | 6 | Jun-83 | Feb-97 | **13.7** | 3.8 | 9.9 | / | / | 1989.9 | 1984.9 | 1992.1 | / | / |
| BDFFP3402 | BD34 | 9 | Nov-85 | Nov-98 | **13.1** | 5.3 | 7.8 | / | / | 1991.6 | 1987.7 | 1994.1 | / | / |
| BDFFP2303 | BD23 | 2 | Apr-85 | Sep-97 | **12.5** | 5.4 | 7.1 | / | / | 1991.3 | 1987.7 | 1993.5 | / | / |
| Bionte1 | BI1 | 1 | May-86 | May-99 | **13** | 5 | 8 | / | / | 1992.5 | 1988.5 | 1995.0 | / | / |
| Bionte2 | BI2 | 1 | May-86 | May-99 | **13** | 5 | 8 | / | / | 1992.5 | 1988.5 | 1995.0 | / | / |
| Bionte4 | BI4 | 1 | May-86 | May-99 | **13** | 5 | 8 | / | / | 1992.5 | 1988.5 | 1995.0 | / | / |
| Tambopata0 | T0 | 1 | Oct-83 | Jul-00 | **16.8** | 7.8 | 9 | / | / | 1991.4 | 1986.9 | 1995.5 | / | / |
| Tambopata1 | T1 | 1 | Nov-79 | Sep-94 | **21.6** | 7.9 | 9 | / | / | 1989.8 | 1987.0 | 1995.5 | / | / |
| Tambopata3 | T3 | 1 | Sep-83 | Jul-00 | **17** | 7.9 | 9.1 | / | / | 1991.5 | 1987.0 | 1995.5 | / | / |
| Tambopata4 | T4 | 1 | Sep-83 | Jul-00 | **16.9** | 7.9 | 9 | / | / | 1991.5 | 1987.0 | 1995.5 | / | / |
| YanamonoA | YA1 | 1 | Jun-83 | Jan-01 | **17.7** | 7.8 | 9.9 | / | / | 1991.9 | 1986.9 | 1996.1 | / | / |
| Tambopata6 | T6 | 1 | Oct-83 | Sep-98 | **15.9** | / | / | 7.7 | 7.2 | 1990.5 | 1986.9 | 1994.4 | / | / |
| AllpahuayoA | AL1 | 1 | Nov-90 | Jan-01 | **10.2** | / | / | 5.3 | 4.9 | 1995.1 | / | / | 1992.7 | 1998.6 |
| AllpahuayoB | AL2 | 1 | Nov-90 | Jan-01 | **10.2** | / | / | 5.3 | 4.9 | 1995.1 | / | / | 1992.7 | 1998.6 |
| SucusariA | SU1 | 1 | Feb-92 | Jan-01 | **8.9** | / | / | 3.9 | 5 | 1996.5 | / | / | 1994.0 | 1998.5 |
| SucusariB | SU2 | 1 | Feb-92 | Jan-01 | **8.9** | / | / | 3.9 | 5 | 1996.5 | / | / | 1994.0 | 1998.5 |
| Cuzco Amazonico 1e | CA11 | 1 | May-89 | Oct-98 | **9.4** | / | / | 5.3 | 4.1 | 1996.3 | / | / | 1991.6 | 1996 |
| Cuzco Amazonico 1u | CA12 | 1 | May-89 | Oct-98 | **9.4** | / | / | 5.3 | 4.1 | 1996.3 | / | / | 1991.6 | 1996 |
| Cuzco Amazonico 2e | CA21 | 1 | May-89 | Oct-98 | **9.4** | / | / | 5.3 | 4.1 | 1996.3 | / | / | 1991.6 | 1996 |
| Cuzco Amazonico 2u | CA22 | 1 | Jun-89 | Oct-98 | **9.3** | / | / | 5.3 | 4.0 | 1996.3 | / | / | 1991.6 | 1996 |
| Caxiuana6 | CX6 | 1 | May-94 | May-99 | **5** | Only structural and floristic analysis |  |  |  | 1996.5 | / | / | / | / |
| Caxiuana7 | CX7 | 1 | May-95 | May-99 | **4** | Only structural and floristic analysis |  |  |  | 1997.0 | / | / | / | / |
| BDFFP1101 | BD101 | 1 | Feb-81 | Apr-99 | **18.1** | Only structural and floristic analysis |  |  |  | 1990.1 | / | / | / | / |
| BDFFP1102 | BD102 | 1 | Feb-81 | Apr-99 | **18.1** | Only structural and floristic analysis |  |  |  | 1990.1 | / | / | / | / |
| BDFFP1103 | BD103 | 1 | Mar-81 | Apr-99 | **18.1** | Only structural and floristic analysis |  |  |  | 1990.1 | / | / | / | / |
| BDFFP1109 | BD119 | 1 | Aug-81 | Jun-99 | **17.8** | Only structural and floristic analysis |  |  |  | 1989.9 | / | / | / | / |
| BDFFP3304 | BD33 | 2 | Mar-84 | May-98 | **14.2** | Only structural and floristic analysis |  |  |  | 1991.1 | / | / | / | / |
| BDFFP1113 | BD113 | 1 | Jun-87 | Apr-97 | **10.3** | Only structural and floristic analysis |  |  |  | 1992.2 | / | / | / | / |
| Tambopata2 | T2 | 1 | Oct-83 | Sep/Oct-98 | **15** | Only floristic analysis |  |  |  | 1990.5 | / | / | / | / |

Table 3.3. List of plots with more than 1 census, used for the analysis of plot dynamics and for the comparison of dynamics in two consecutive periods. Length and midyear are indicated for each time interval.

## 3.3. Climate data

Climate data for the study sites were extracted from an observational dataset that covers global land areas, excluding Antarctica, compiled by the Climatic Research Unit of the University of East Anglia (UK). The dataset was "constructed" from station observations that cover the period 1901-1998 (Hulme and Viner 1998). Data were interpolated onto a 0.5° grid. For the present study, only the period 1960-1998 was considered. The series is available from the IPCC Data Distribution Centre (http://ipcc-ddc.cru.uea.ac.uk/cru_data/datadownload/download_index.html).

In Figure 3.2 (a,b) is shown the rainfall regime for a series of study sites, representative of different regions of the Amazon Basin.

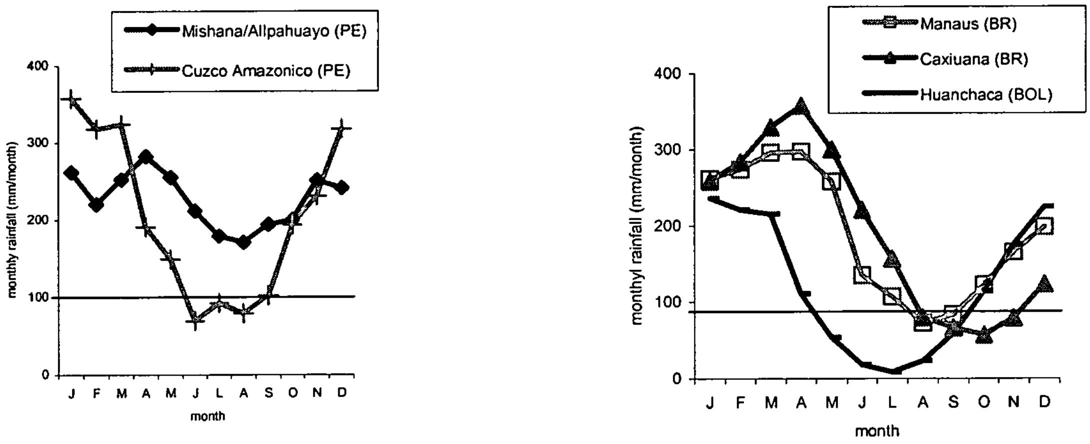


Figure 3.2 (a, b). Rainfall patterns for 5 localities across the Amazon Basin. BR = Brazil, PE = Peru, BOL = Bolivia. Data are from the historical series compiled by Hulme and Viner (1998). The black line helps the identification of those months considered as dry, that is, with less than 100 mm of rainfall.

It can be expected that wet tropical forests experience water limitation effects when monthly precipitation goes below 100 mm, as studies on transpiration seem to indicate (e.g., Hodnett et al. 1996; Malhi et al., review b). Months with less than 100 mm of rainfall are therefore considered as dry. Rainfall patterns are seasonal in the south and east parts of the studied region; for several months of the year, rainfall rates drop below 100 mm /month. On the contrary, rainfall regime is aseasonal in the western part of the Amazon region, where precipitation never goes below this critical threshold. The main features of the local climate (annual precipitation and number of dry months) are summarized in table 3.4, for most of the regions represented in the dataset.

| COUNTRY | SITE | REGION | # DRY MONTHS | MEAN ANNUAL PRECIPITATION |
|---|---|---|---|---|
| Bolivia (Santa Cruz) | Los Fierros | SA | 6.5 | 1313 |
| Bolivia (Santa Cruz) | Huanchaca | SA | 5.8 | 1454 |
| Brazil (Para) | Tapajos | EA | 4.7 | 2067 |
| Brazil (Para) | Caxiuana | EA | 2.8 | 2508 |
| Peru (Madre de Dios) | Cuzco Amazonico | WA-SP | 3.5* | 2451* |
| Brazil (Manaus) | Manaus (BDFFP / BIONTE) | CA | 2.4 | 2387 |
| Peru (Madre de Dios) | Tambopata | WA-SP | 4.1* | 2248 * |
| Peru (Madre de Dios) | Pakitsa | WA-SP | 3.5* | 2300* |
| Peru (Loreto) | Allpahuayo / Indiana / Mishana | WA-NP | 0.9 | 2885 |
| Peru (Loreto) | Sucusari / Yanamono | WA-NP | 0.6 | 2840 |
| Panama | BCI | CAA | 3.5 | 2912 |
| Malaysia | Pasoh | AS | 2.9 | 1885 |
| Congo | Odzala | AF | 4.2 | 1597 |
| Gabon | Oveng/Doussala/Lope/Ekobakoba | AF | 4.7 | 1775 |
| Cameron | Dja | AF | 4.7 | 1632 |
| Central African Republic | Ngotto | RCA | 4.3 | 1673 |
| French Guiana | Nourages | FG | 2.5 | 3430 |

Table 3.4. Mean number of dry months and the mean annual precipitation (mm) for the study sites. The value of annual rainfall for Tambopata, Cuzco Amazonico and Pakitsa are accompanied by an asterisk to indicate that the value from the historical dataset differs considerably from the values recorded by local stations (see text). Regions: AF= Africa, AS= Asia, CA= Central Amazon, CCA= Central America, EA Eastern Amazon, FG= French Guiana, SA= Southern Amazon, WA-NP= Western Amazon North Peru, WA-SP= western Amazon South Peru.

The series extracted from the historical dataset overestimates mean annual rainfall for those sites located at the foot of the Andes. Therefore, for a few sites (those with an asterisk in table 3.3) values from local station were used.

## 3.4. Most important study sites

In the next paragraphs, the three main clusters of PSPs that contribute most of the data for this study are described: (1a) Manaus (Amazonas, Brazil) and (1b) Caxiuana (Parà, Brazil), (2) Madre de Dios Department (Tambopata, Cuzco Amazonico, South Peru), and (3) Loreto Department, Iquitos area (Allpahuayo, Sucusari, Yanamono, Mishana, Indiana, North Peru). Their geographical span is shown in Fig. 3.3. The majority of the PSPs are located near Manaus and were established within the frame of two main projects: Biological Dynamics of Forest Fragments Project (BDFFP - 27 ha) and Biomassa e Nutrientes Florestais (BIONTE - 3 ha).

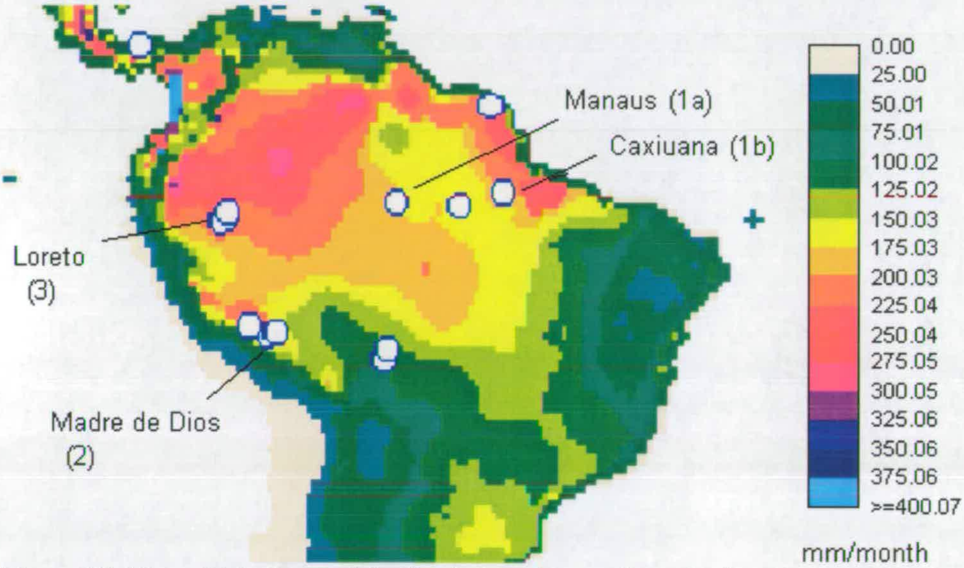


Figure 3.3. Map with isohyets of the South American main study sites.

### *(1a) Manaus, Amazonas (BDFFP & BIONTE projects)*

The BDFFP (Biological Dynamics of Forest Fragments Project) was established in 1979 to study the long-term effects of forest fragmentation on the Amazon ecosystem. The study area (Fig. 3.4) is surrounded by large expanses (> 200 km) of continuous forest to the west, north, and east.

The project is operated within a 20 x 50 kilometres area including 66 permanent, one-hectare study plots, located in continuous forest fragments ranging from 1 to 100 hectares. The fragments were isolated in the early 1980s, by distances of 70-1000 m from the surrounding forest by clearing the intervening vegetation to establish cattle pastures. Reserves ranging from 1 to 1000 ha in area were delineated in nearby continuous forest to serve as experimental controls. Of the 66 plots, 39 were located in forest fragments and 27 in continuous forest (controls) (Laurance et al. 1998b) (see appendix 2 for a detailed list of the BDFFP plots analysed). More than 56 000 trees were measured, marked, identified, and monitored.

Only those plots located at more than 300-400 m from any edge were chosen for the present study, in order to exclude any perturbation due to forest edge effects.

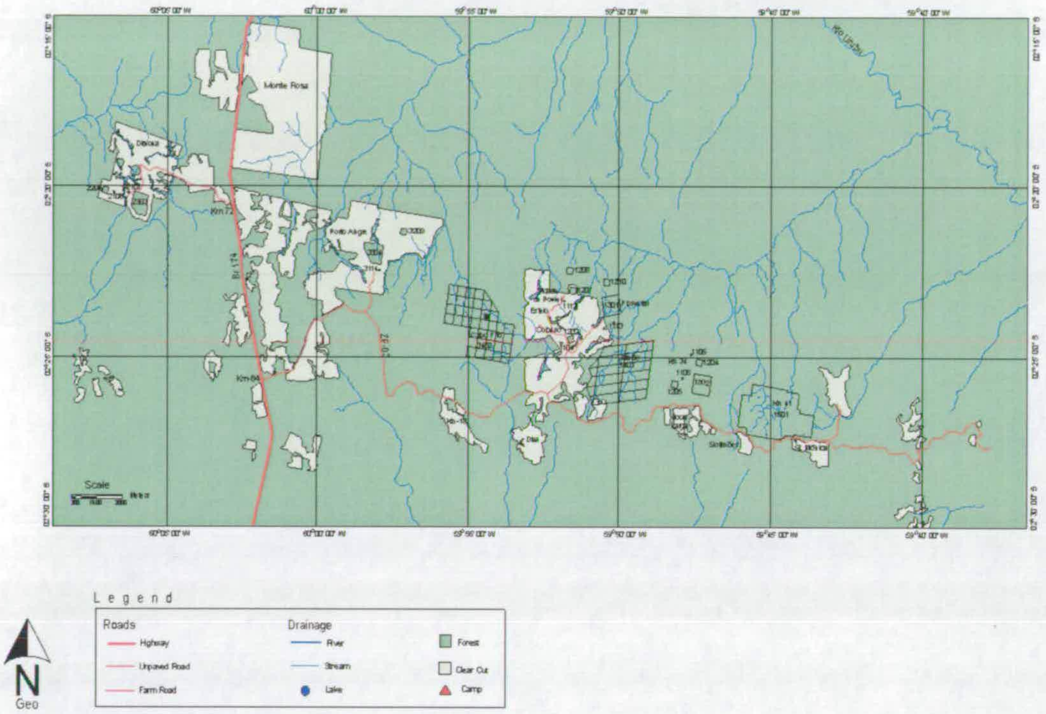


Figure 3.4. Map of Biological Dynamics of Forest Fragments project (Manaus, Brazil) reserves and plots. Source: INPE Landsat TM 5,4,3 RGB 1995.

The BIONTE (Biomass and Forest Nutrients) project was developed within a bilateral agreement between Brazil and the United Kingdom, and was administered by Niro Higuchi at INPA (Instituto Nacional de Pesquisa da Amazonia). The objective was to assess the effects of selective logging on the cycles of nutrients and water, and the physical, chemical and biological properties of soil. The characteristics of the vegetation, soil and topography are similar to those found within the BDFFP sample plots.

### *(1b) Caxiuana (Parà)*

Caxiuana gained the status of reserve in the mid 1980s. The area is characterized by a very high diversity due to its remoteness and low population density. The 33 000 ha of reserve are mainly covered by a dense lowland *terra firme* forest (ca. 90% of the surface) whose floristic richness is one of the highest within the eastern side of the Amazon basin. The site is administered by the Estação Ferreira Penna of the Museu Paraense Emìlio Goeldi (MPEG, Belem, Brazil).

### *(2) Madre de Dios Department (Tambopata, Cuzco Amazonico)*

The two south Peruvian sites are located in the department Madre de Dios. The 6 PSPs from Tambopata studied in the present work are part of a larger sampling effort, started more than 20 years ago and aimed at covering all forest types. They are located inside the Zona Reservada Tambopata, part of the Zona Reservada-Candamo-Tambopata, an area of about 1.5 million ha characterised by lowland and montane forest (Phillips et al. 1994b). Very dissimilar forest types coexist in a relatively small area and enhance its floristic richness. The overall variability in forest structure and composition is attributable to a variable degree of perturbation from the river flooding and to different stages of maturity of soil profiles. Generally, moving from the lower floodplain to the upper floodplain, increasing stature, structural complexity and species richness are observed. The main forest types encompassed by the plots included in the present study are (from Phillips 1994):

- upland sandy-clay *terra firme*: sandy-clay soil; little or no indication of past flooding (T3 and T6).
- Old floodplain forest: clay soil, subjected to flooding within the last 200 years (T1).
- Upper floodplain forest: alluvial, clay soil, tall forest, very rarely flooded (T4).
- Middle floodplain forest: tall forest, recent floodplain, flooded occasionally (T0).
- Seasonally water-logged swamp forest: oxbow lakes filling in (T2).

The four PSPs of Cuzco Amazonico are characterized by climatic conditions similar to those found in Tambopata. Soils are of more recent origin, being mostly formed on young floodplains and seasonal swamps.

### *(3) Loreto Department*

The Iquitos region of western Amazonia is mainly located within the Loreto Department. The area is mostly characterized by flat or gently undulating *terra firme*, with seasonally or permanently flooded habitats along rivers, lakes, and swamps, and with elevation varying from 110 to 180 m above sea level. An exceptionally diverse mosaic of biotopes characterizes the region. The flora of the “Zona Reservada Allpahuayo-Mishana", a 57 000 ha national reserve, located 25 km southwest of Iquitos in northeastern Peru, is very diverse and has been described in detail (Vasquez and Phillips 2000; Vazquez 1997). The extreme floristic diversity covaries with high spatial variation in soil properties (Gentry and Ortiz 1993; Salo 1993). Characteristic substrates include upland white sand, upland lateritic soil, non-inundated alluvial soil, and "tahuampa" - floodplains seasonally inundated by either suspension-rich white water or suspension-poor black water. The uplands of Allpahuayo-Mishana can be classified into two major types: those on sandy soils and those on clay soils (Vazquez 1997). The PSPs studied here, located within the Allpahuayo Forest Reserve, show a topographic range that includes both the clay rich, valley soils and the well drained sandy soils, with distinctive variation in structure and species composition (Mishana, Allpahuayo). The PSPs in Yanamono and Sucusari have more uniform, clay rich soils but extremely high diversity of species per hectare.

### *Cross-description of sites*

The selected sites span wide landform and rainfall gradients. The three main regions identified are characterized by a different rainfall regime. Values of mean annual precipitation and seasonality vary considerably, with a maximum precipitation and the shortest dry season in the western northern Peruvian cluster of PSPs, and a minimum annual rainfall and the longest dry season in the southern part of Amazon basin, where the Bolivian PSPs are located. Tambopata and Cuzco Amazonico also show a long dry season (between 3 and 4 dry months), while Caxiuana and Manaus have an intermediate length of the dry season, but lower values of mean annual rainfall.

Next to climate, soils are the second powerful factor controlling both the distribution and the composition of tropical forests. A large soil gradient is captured by the geographical distribution of the study sites. Within the Guyana and Brazilian shields, active weathering of the crystalline basement rocks results in areas with relatively high nutrient concentrations, whereas the sedimentary lowland areas that border the crystalline shield are derived from weathered shield material, and are comparatively infertile (Sombroek 2000). Lowland infertile areas are typically characterized by plateau formations of ancient origin with prevalent oxisols. The PSPs from central and eastern part of the Amazon are located within these land forms. By contrast, the soils of western Amazonia derive from the Andean Cordillera and have higher fertility and higher ion exchange capacities. In particular, Tambopata and Cuzco Amazonico, in the southern Peruvian part of the western Amazon, show very young soils of alluvial origin.

Large differences also occur within the above-described main land forms. For instance, in the Iquitos area of the Peruvian Amazon the small hills characteristically have white, sandy soils, whereas clay rich soils with higher nutrient concentrations are found in the lowest sites (Vormisto et al. 2000). The most limiting macro-nutrient in many Amazonian soils is thought to be phosphorus rather than nitrogen (Vitousek 1984; Lloyd and Farquhar 2000), but micronutrients are also likely to play an important role.

The south Peruvian PSPs in Tambopata seem to be affected by river dynamics, being in part exposed to seasonal flooding, while the main factor of perturbation for the Central Amazon PSPs (Manaus) studied here is human presence that triggers the conversion of forest land into pasture. The area is accessible by road and it is therefore exposed to anthropogenic threats. However, the BIONTE plots are located within a continuous forest and the selected BDFFP fragments are far from forest margins (300-400 m).

## 3.5. Trends in rainfall regime

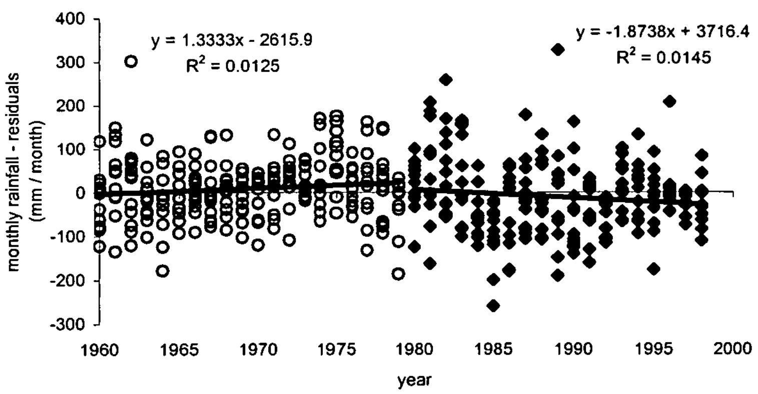
Regional climatic regimes, their interannual, interdecadal and perhaps intercentennial variability in rainfall, and the regularity and intensity of drought can have a major impact on forest structure and adaptation of the vegetation to changeable conditions. Time series analysis was carried out on the historical series of rainfall data extracted from the database compiled by Hulme and Viner (1998). The analysis was applied to sites that are representative of different climate regimes within the Amazon Basin, to test the degree of sensitivity to perturbation due to anomalies in precipitation, such as ENSO events, in different regions.

Meterological observations in the tropics have only been abundant over the last 40 years, therefore the analysis of rainfall temporal patterns was focused on the period

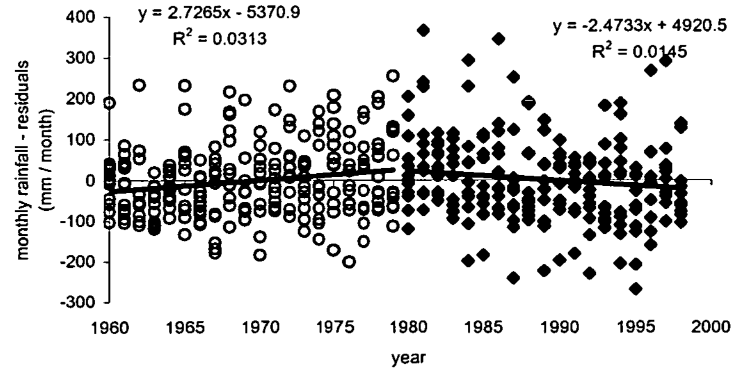
1960-1998. An average annual cycle was derived from mean monthly precipitation values calculated over the entire selected period. For each year, monthly residuals were calculated and plotted in Figure 3.5, a-e. Trends were examined separately for the two periods 1960-1979 and 1980 – 1998, as a recent analysis of mean climate and climatic trends in the tropics (Malhi et al., in review c) reveals contrasting temperature trends for the last versus the first two decades of the time interval analysed. In this study, temperature values showed a net cooling up until the mid-1970s, especially in the Western Amazon, followed by a period of strong warming, experienced by all tropical regions.

The dataset studied in the present work does not reveal any statistically appreciable precipitation patterns. Nevertheless, the first two decades show a slight tendency to an increase in precipitation while the last two decades show either stable or decreasing precipitation, in most of the regions explored.

Mishana - Allpahuayo (Peru) (a)



Cuzco Amazonico (Peru) (b)



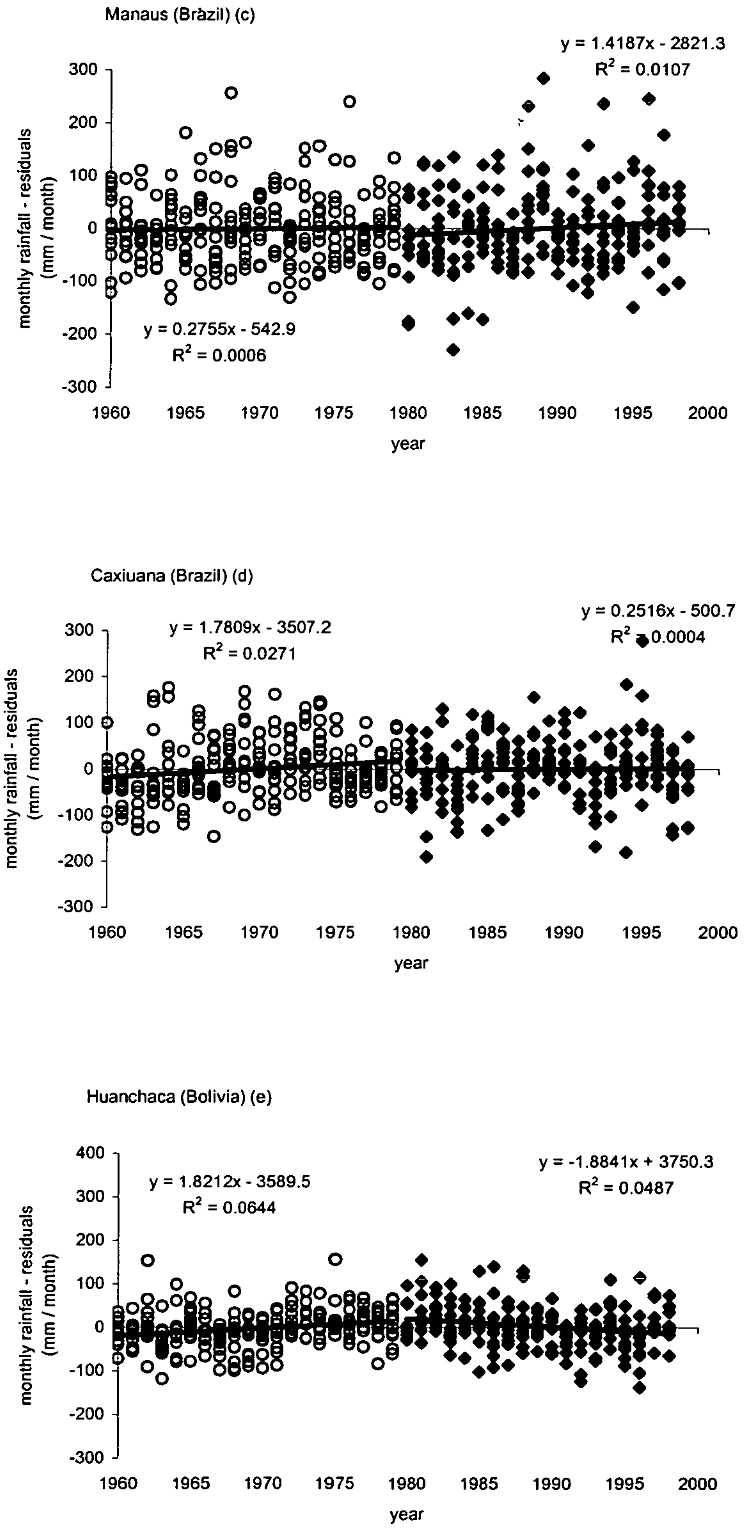


Figure 3.5 (a-e). Monthly residuals for rainfall values, plotted versus time for two consecutive periods 1960-1979, 1980-1998.

The second period examined is characterized by more negative residuals, showing higher frequency of monthly rainfall values that are lower than average. This could be due to a higher frequency of dry events, such as El Niño, in the second period examined. Indeed, during the 1960s and 70s, only weak and moderate El Niño effects have been recorded in some regions of the Amazon Basin, while during the course of the 1980s and 90s, two strong events were detected all across the Amazonian region, precisely in 1983, and in 1997-98 (see Chapter 2, Table 2.1).

However, monthly precipitation data have strong limitations for the assessment of rainfall regimes; periods of drought may be more critical for understanding the interactions between climate and tropical ecology and function. In most tropical terrestrial ecosystems, a more relevant environmental control than total precipitation *per se* is the duration (period with < 100 mm / month) and intensity (how much the precipitation drops below the 100 mm / month threshold) of the dry season. In addition, the dry season length does not represent the importance of soil "memory", i.e. whether a soil is fully hydrated or only partially hydrated in the months preceding a dry month.

Looking at the past, other climatic variables seem to have played a major role in shaping the composition of forests across the Amazon Basin and controlling their extension. Palynological data have been used to reconstruct how the plant population of the Amazon responded to the global warming at the onset of the Holocene (Colinvaux et al. 2000). The results of these studies seem to indicate that the Amazon Basin was never arid and remained forested throughout glacial times. The reduced precipitation was never enough to fragment the forest in the Amazon lowlands. Precipitation was not constant but reduced temperature alone should have moderated the cycle "evaporation followed by renewed precipitation" thought to be responsible for heavy showers in parts of lowland Amazon (Nimer 1989). The population changes within Amazonian and Central Brazilian plant communities over the global change are most easily attributable to temperature. Pollen data reveal changes in species population that mainly consisted of heat intolerant species extending their distribution to higher elevations.

It must always be possible that the rise in CO2 was also involved in causing the observed changes, but there is no evidence for this.

To conclude, it must be said that more refined analyses would be required to capture the relationships between climate and vegetation. These should consider other climatic variables, together with rainfall patterns. The present analysis is only an attempt to contextualize the analyses of tropical forest floristic composition and dynamics, which follow in the next chapter, and to detect signals of major rainfall trends affecting the Amazon region.

### 3.6 Conclusions

The PSPs used for the present study broadly cover very distinct environmental conditions. The dataset collated constitutes the valuable outcome of the on-going work of several research groups, and, although not spanning the whole range of soil and climate that characterizes the Amazon basin, it offers a valuable amount of information for the investigation of the main spatial and temporal patterns of forest structure, biomass and dynamics in relation to controlling environmental factors.

The analyses presented in the next chapters are among the few existing examples of investigations based on long-term observations of a large set of tropical rainforest stands, distributed across a wide area.

The floristic and structural aspects are analysed in Chapter 4, the patterns in basal area and turnover change through time are described in Chapter 5, methodological issues are deeply treated in Chapter 6, and finally the potential impacts of global changes on species composition are described in Chapter 7.

# Chapter 4. Floristic composition, diversity, and structure of some Amazonian forest plots

---

## 4.1. Introduction

It is fundamental to understand the relative importance of soil types and climate in shaping forest stand characteristics, in order to be able to predict the direction of changes in tropical forest ecosystems. The floristic makeup of a tropical forest has implications for the amount of carbon stored, depending on the relative proportion of high and low-wood density families. This information combined with estimates of forest turnover allows quantification of residence time of carbon in the forest and storage capacity.

In this chapter, the role played by the main environmental variables in determining the observed geographical patterns of rainforest floristic composition, diversity and structure within the Amazon Basin is investigated. The relationship between species richness and rainfall regimes is analysed to enable predictions on possible changes in forest diversity as a consequence of changing environmental conditions. Historical factors that could be responsible for present distribution of dominant elements of the Amazonian flora in different regions are also explored. Later in this work, potential signals of change in sample plot species composition are analysed.

Results are compared with published studies to identify a general picture of floristic diversity at different taxonomic levels. Potential explanations and regulating mechanisms that led to the current distribution of rainforest species richness are reviewed in Chapter 2, and the analysis presented here is aimed at testing to what extent these general rules are valid for the Amazon Basin. The role of some environmental versus biogeographical factors in determining the observed peaks in species diversity in certain regions is examined.

Species richness is also analysed at a smaller scale, using a cluster of plots from the same locality, to explore the role played by local factors (e.g., soil variability) in regulating floristic diversity.

A third element explored is the structure of rainforest stands. Structural characteristics of forest stands across various regions of the Amazon basin are analysed and compared with those of forest stands from other tropical regions, exploring especially the relationship between variability in forest structure and environmental factors. As illustrated in the review of Chapter 2, at present only a few studies on the structural variation of tropical forest stands are available. Thus, this work represents an important contribution to the understanding of the structural features of tropical forest plots, given the large geographical coverage of the PSPs investigated.

## 4.2. Methodology

### 4.2.1. Detrended correspondence analysis

A Detrended Correspondence Analysis (DCA) was used to disentangle the complexity of the floristic composition of 68 Amazonian PSPs. This statistical analysis is reviewed in Chapter 2. Classification and ordination techniques have been often used to detect associations at the same locality and to unveil floristic patterns throughout the range of similar vegetation types at regional levels (e.g., Oliveira-Filho 1993; Ratter et al. 1996).

Several studies have been carried out in Brazil, relating floristic and structural variation to environmental factors within riverine forests and the associated vegetation (Felfili 1995), or the floristic composition of several forest types (Silva and Shepherd 1986). In addition, a very large set of data, composed of 106 floristic lists, not only from Brazil but also from some neighbouring countries, was used to understand the origin of the flora of Central Brazil (Oliveira-Filho and Ratter 1995). Terborgh and Andresen (1998) also used DCA to look at similarities in species composition of flooded and unflooded forests, within and across regions. They applied DCA to the 16 most important families in 39 plots spread across Brazil, French Guyana and Central America. The same approach and the same set of families was used by ter Steege et al. (2000) to analyze 94 forest tree plots, from Amazonia and the Guiana shield, distributed among four substrates and characterized by more than 2000 mm of annual rainfall (ter Steege et al. 2000).

The preparation of the dataset used for floristic assessment in the present study followed the protocol set up by Terborgh and Andresen (1998). Plot data were entered at the species level, listing named taxa, and a truncated sample was taken from each plot.

In order to weight plots equally, a number of individuals equal to the ones contained in the hectare of forest with the lowest density (479 trees/ha) were extracted. The selection was done attributing a random number to each tree in the plot, then ranking the random numbers, and finally selecting the first 479 to represent the plot in the analyses.

The truncated data sets were collapsed into genera or families to be treated at different taxonomic levels. Data were ordered via detrended correspondence analysis (DCA) using the program CANOCO for Microsoft 4.0 (ter Braak and Smilauer 1998). Analyses were conducted at different taxonomic levels and using various truncated and transformed data sets. First, all the plots and the families were used for the DCA. Then, a selection of 16 well-represented families, defined as the most representative within the entire Amazon Basin in previous studies (Terborgh and Andresen 1998; ter Steege et al. 2000), was used to run a second DCA and to compare the results from the present study with other findings.

As revealed by previous studies (Terborgh and Andresen 1998), ordination based on the generic and species level data are of little interpretability and utility for broad continent-wide comparisons. If species-level data are used, plots tend to cluster tightly within localities, because stands in different regions share only a few species. Species-level data were here used only to ordinate plots within one site to test for edaphic effects, where the density of sampling is high and the continuity between plots allows a more detailed analysis of floristic composition (BDFFP, Manaus).

Differences in the abundance of the 16 major tree families were analysed by dividing the total sample of 68 plots into 5 main regions (South Amazon, Central Amazon, Eastern Amazon, Western Amazon-North Peru, Western Amazon-South Peru), and using ANOVA with the Tukey's test for multiple comparisons. The use of ANOVA would require that the sample be selected independently and at random. Although this is not the case for the present analysis, the test was carried out to compare results with the findings from previous studies (see Ter Steege et al. 2000), where a set of the most representative families was selected, and their abundance compared across Amazonian regions. An additional test for spatial auto-correlation would be required to check for the effect of spatial proximity on the degree of similarity found within sites compared. The same test for spatial auto-correlation carried out by Ter Steege et al. (2000) suggested that none of the plots used in their study were really spatially independent (no matter the distance) but were ordered on a gradient. This is likely to apply also to the dataset used in this study.

With a total of 68 PSPs, five major regions were characterized, although samples were not balanced and the degree of floristic representativeness varied across regions. The regions identified are: Central Amazon, (30 PSPs); Eastern Amazon (14

PSPs), with Tapajos (3) and Caxiuana (11); the southern fringes of the Amazon Basin (6 PSPs), with two Bolivian sites, Huanchaca (4) and Los Fierros (2); Western Amazon (18 PSPs), with two clusters of plots, one in south Peru (10), with Tambopata (6) and Cuzco Amazonico (4), and a second cluster in north Peru (8), with Allpahuayo (2), Sucusari (2), Yanamono (2), Indiana (1), and Mishana (1).

To summarize, DCA was applied to two different datasets for three different analyses as follows:

a. The entire set of plots (68) and the entire number of woody families (85).
b. A set of plots from Central Amazon (26) and the total number of species contained in this sub-sample of plots (254).
c. The scores from the DCA of the plots from Central Amazon (26) were correlated with soil characteristics (% of sand and clay).

For most of the variables calculated and used to characterise different plots, sites and regions, the multiple comparisons were carried out using a non-parametric test, as the strongly unbalanced samples were expected to be non-normally distributed. The Kruskal-Wallis test is a generalization of the procedure used by the Mann-Whitney test and, like Mood's median test, offers a nonparametric alternative to the one-way analysis of variance and performs a hypothesis test of the equality of population medians for a one-way design (two or more populations), looking for differences among the populations' medians (Sokal and Rohlf 1974). The Kruskal-Wallis test is more powerful (the confidence interval is narrower, on average) than Mood's median test for analyzing data from many distributions, including data from the normal distribution, but is less robust against outliers.

### 4.2.2. Floristic characterization of PSPs

Only plots with more than 70% of the individuals identified to family and genus level were used for the floristic analysis. The resulting list of individuals from each plot was used for a further selection of a truncated sub-sample of individuals for the DCA. The spelling of species scientific names was standardized. For some of the unidentified species it was possible to allocate collections to morphospecies (i.e., a morphological concept, despite the lack of a specific name). All the individuals that could not be attributed to a species or morphospecies were discarded. A family importance value (FIV) was calculated for individual plots and for sites. FIV was calculated from the formulae below (Dallmeier 1992; Mori et al. 1983a; Mori et al. 1983b):

FIV = relative diversity + relative density + relative dominance (1)

Where:

Relative diversity = (# of species of a family / total # of species of the sample) x 100
Relative density = (# of individuals of a family / total # of individuals of the sample) x 100
Relative dominance = (basal area of a family / total basal area of the sample) x 100

The total numbers of families and genera were estimated after subtracting the non-identified stems. The total number of species in each PSP was also calculated. When not all the individuals were identified, an estimated number of species $ha^{-1}$ was determined. The "most likely value" of total species (later referred to as the number of "expected species") was estimated using the equation below (Vasquez and Phillips 2000):

total # of species = (total # of trees) x (# identified species) / (# identified trees) (2)

The equation is based on the assumption that the rate of accumulation of species, with an increasing sampling effort (i.e. increasing number of trees included in the sample), is constant. The ratio number of species : number of trees is assumed to remain equal within one hectare, leading to an underestimate of the total number of species on small-sized PSPs. The use of the equation above implies errors on the conservative side because the most difficult plants to identify tend to be the rarest, and therefore it is likely that the ratio of species to individuals will be greater for non-identified plants than it is for identified plants. In addition, given the small plot dimension, the species-accumulation curve, if drawn, would be far from reaching the asymptotic point, at such a limited spatial extension of forest samples. With progressively increasing sample sizes, well above 1 ha, the equation would lead to an overestimate of total species richness, as the species-area curve reaches a plateau. A further element of uncertainity derives from species spatial aggregation that affects they way new species accumulate with increasing plot area.

In terms of the main objectives of the present study, the simplification introduced was judged acceptable and preferable to the alternative of simply ignoring unidentified trees.

### 4.2.3. Pioneer species and palms

To understand and to be able to predict the dynamics and productivity of tropical forests is a major current challenge for ecologists. To develop realistic forest-dynamics models, and to assess the response of plant functional types to climatic change in tropical forests, require collapsing the great number of tree species in any tropical wet or moist forest into a much smaller set of tree types, or functional groups (cf. Condit, Hubbell, and Foster 1996a; Vanclay 1991a).

Two main broad groups of species have been identified along a continuum of species' behaviour (shade -tolerant and –intolerant or "pioneer" species), basing the distinction on the most broadly applicable diagnostic trait, which is the light requirement for seed germination (Swaine and Whitmore 1988). Tropical pioneer trees have been defined as species requiring high irradiance for establishment and growth to maturity (Swaine and Whitmore 1988). A suite of physiological and demographic characteristic traits accompanies this: long seed dormancy, and large seed banks, high photosynthetic and growth rates, rapid and continuous leaf production, early and long flowering time, and rapid acclimation to environmental variation. Two types of specific variation are particularly important within this group, and relate to the minimum size of disturbance required for successful establishment, leading to the distinction between so-called small-gap and large-gap pioneers (Brokaw 1987), and the longevity and the maximum stature of adults.

In this study, pioneer species were distinguished by local botanists and experts, analysing a complete list of species inventoried across all the locations studied (Oliver Phillips, Rodolfo Vasquez and Abel Monteagudo, William Laurance). A list of 61 strictly gap-dependent pioneer species derived from a floristic inventory of Guianan forests (Paracou) (Molino and Sabatier 2001) was added. Appendix 3 shows the final lists of pioneer species used, which derives from the merging of the individual lists above-mentioned. A standard definition for "pioneer" species was provided as a reference for the screening of species lists and a code was attributed to each pioneer species as follows: 1 = species that colonize big natural gaps in primary forests, 2 = species that colonize secondary forests, edges of roads, recently stabilized river banks, and other perturbed areas, 3 = species found in both the circumstances described above. The resulting pioneer category was quite broad, with species that need gaps to establish but have very different ecologies, including long lived, hard wooded species, found in mature looking forests, such as *Bertholletia* sp., *Dinizia* sp. and *Jacaranda* sp., that establish and grow rapidly to canopy height in treefall gaps and then persist as canopy dominants, possibly for several centuries, to short lived, canopy height species, such as *Cecropia* sp., which reach heights of 30 m or more and may persist for 30-50 years.

Palms are one of the most diverse and prominent families in Neotropical lowland rainforests (Gentry 1988; Kahn and De Granville 1992; Henderson 1995), whose abundance of large arborescent palms distinguishes them from most Paleotropical forests (Gentry 1988; Kahn and De Granville 1992). Palms are especially diverse in the western Amazon, perhaps due to higher rainfall (Henderson 1995). Several studies have shown that habitat specialization is important for maintaining high palm diversity in the Neotropics. In Costa Rica, the distribution of five of seven subcanopy and canopy palms was related to topographic or edaphic factors (Clark et al. 1995) and several studies have also shown or suggested that treefall gaps are an important ecological factor for palms (Kahn 1986; Kahn and De Granville 1992), although the dependency on large treefalls for their recruitment has been shown not to be true for all tall arborescent palms (Svenning 1999a). Palms and palmoid species of highly diverse palm communities in Ecuador were shown to have distributions strongly influenced by microhabitat heterogeneity, especially by variation in topography (Svenning 1999b). On a landscape-scale, Clark et al. (1995) found the highest local richness of palms in the least fertile soils (although La Selva soils are more fertile than in most of the Amazon Basin).

Palms are found to be more frequent on slope crests and steeper slopes where recent gaps have also been found to be more frequent. In a Central Amazon forest, Kahn and Castro (1985) found substantially higher palm densities on slope crests than at midslope, with the lowest densities on the plateaus; they speculated that higher densities at slope crests reflected the greater gap formation on these more wind-prone sites. Similarly, in a Puerto Rican montane forest, Basnet (1992) found that stem density of palms $\geq 10$ cm in dbh and saplings decreased significantly from ridges to slopes to valley positions.

### 4.2.4. Forest structure

Some structural characteristics of forest stands were analysed on the largest sample of plots available for this study, including not only Neotropical sites but also some African and Asian PSP data. The number of large trees was determined in each plot, defining a cutoff used by other researchers (Brown and Lugo 1992; Clark and Clark 1996). Any division point to distinguish large trees would be partially arbitrary but it has been observed that most of the trees above 70 cm in dbh are relatively frequent in PSPs of one hectare and usually have emergent crowns (Clark and Clark 1992) that are therefore exposed to a different environment from the rest of the canopy.

### 4.2.5. Hypotheses to be tested

Hyp.1 –Given the high differentiation in soil and climate between the various regions of the Amazon basin, different families and genera are expected to dominate different parts of Amazonian forests, and some floristic groups, such as pioneer species and palms, are expected to be more represented in highly dynamic forest stands.

Hyp.2 – Family and species richness is expected to be higher in aseasonal and fertile areas. However, the current floristic diversity may not be entirely explicable by analysing present day environmental conditions. Some biogeographical factors that have affected the evolution of the Amazonian flora are expected to better explain present day floristic composition in some sites.

Hyp.3 – At a local scale, floristic composition is expected to reflect closely the variation of edaphic conditions.

Hyp.4 – Forest structure is expected to show a relationship with environmental conditions and stand dynamics. Specifically, mean stem size is expected to be lower in aseasonal dynamic forests of western Amazon. Total basal area is expected to decline with increasing stem density, due to the lower frequency of large stemmed trees.

## 4.3. Results

### 4.3.1. Floristic characterization of some Amazonian PSPs

The questions asked in this section are:

- Are there regional patterns in floristic composition across the Amazon Basin?
- What are the regional patterns in families and in genera?
- What is the fraction of species that are shared/unique between regions?
- Are some functional groups more abundant in certain regions?

Five major regions were identified, as described earlier in this chapter, characterized by distinct climatic regimes (see map with isohyets, in Fig. 3.1, in Chapter 3).

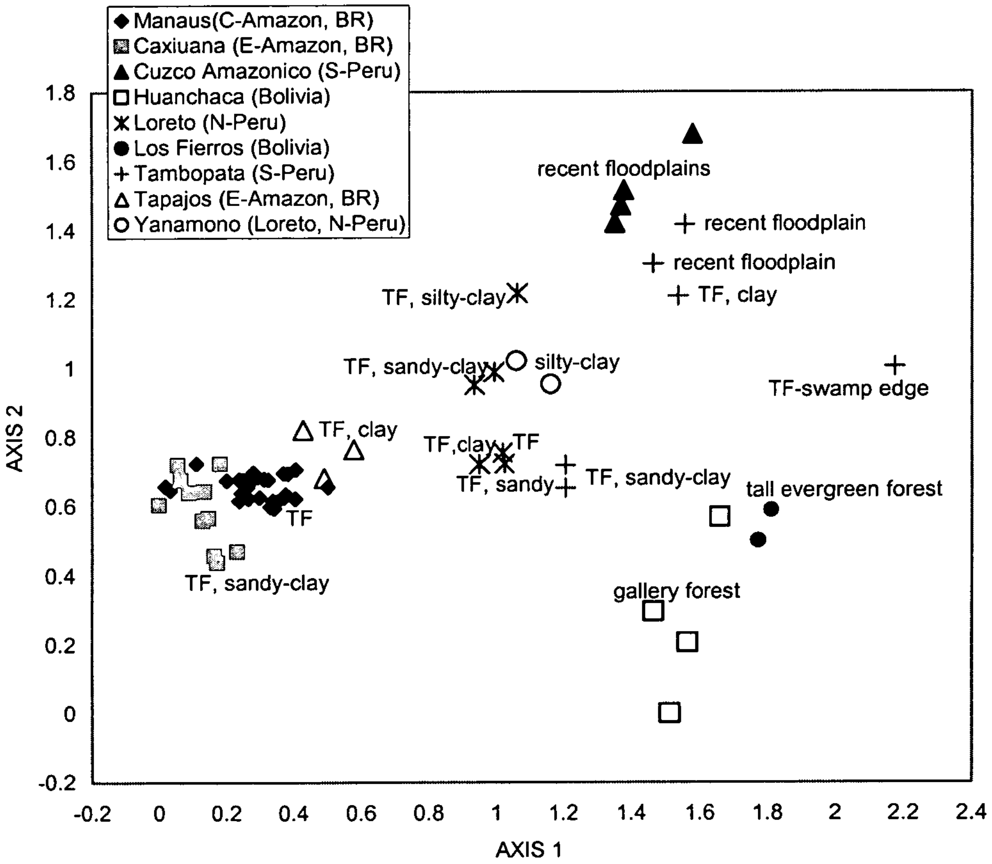


Figure 4.1. Results of a Detrended Correspondence Analysis carried out using family composition data (a total of 85 families) from 68 1-ha plots (equal number of 479 stems). Plots are located along the two axes according to relative abundance of different families in their floristic inventories. Loreto = Allpahuayo, Sucusari, TF = terra firme.

Data from all the plots available (68) and all the families (85), for a total of 38693 stems, were used to calculate the local importance of families. An equal sample of stems (479) from each plot, for a total of 32572 stems, was then used to produce a matrix table to be fed into CANOCO 4.0. Fig. 4.1 offers a visual representation of the outputs of the detrended correspondence analysis (DCA). The output of the ordination exercise roughly resembles a flipped geographic map of the Amazon.

Tight clustering of plots reveals a high local abundance of the same families. PSPs located in the Central and Eastern Amazon cluster tightly on the left side of the graph, revealing a great similarity in floristic composition. This is shown also in Table 4.2, where the results of the ANOVA are presented. Conversely, PSPs from the Western Amazon are more scattered on the right hand side of the graph (Fig. 4.1). The Bolivian PSPs are floristically quite dissimilar from other regions, and dissimilar to each other.

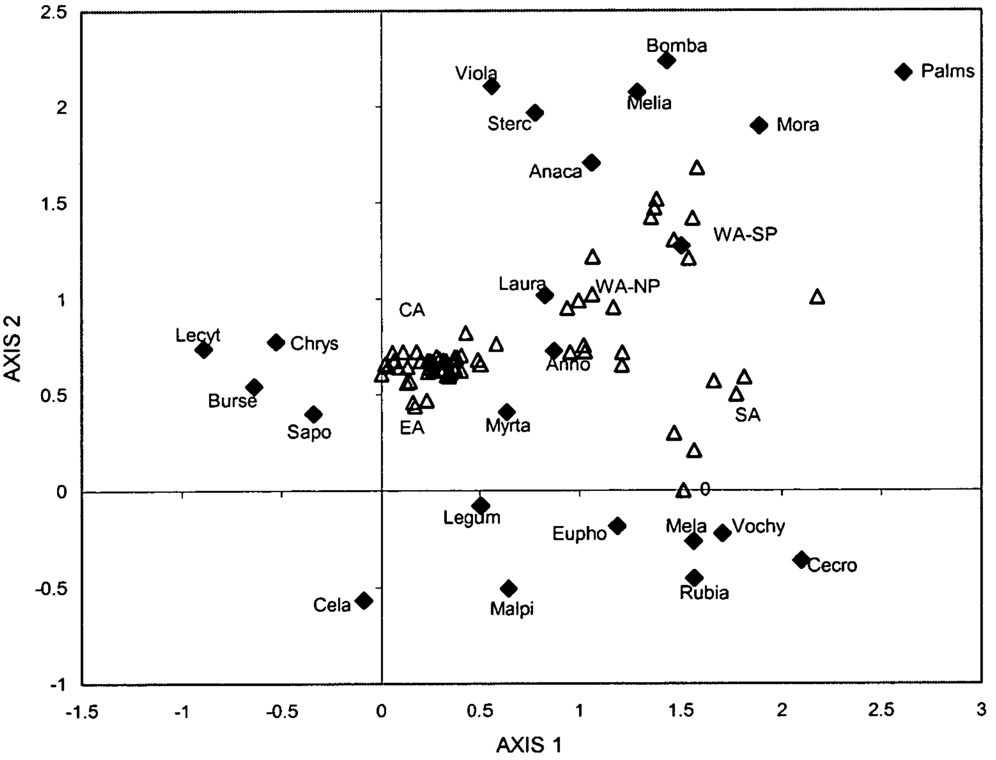


Figure 4.2. Results of a Detrended Correspondence Analysis carried out using family composition data (a total of 85 families, diamonds) from 68 1-ha plots (equal number of 479 stems, triangles). Labels show the 23 highly represented families. Plots gravitate in the two-dimensional space around those families that are most abundant in their floristic inventories.

In Figure 4.2, PSPs are shown in the diagram together with families. The first axis shows a gradient along which families are distributed according to their peak in frequency. The space in the diagram surrounding a family identifies a region where its highest relative dominance is found. Those PSPs falling within this space are dominated by that family.

Families tightly clustered tend to occur together in a forest stand, while species quite distant on the graph tend to replace each other. Lecythidaceae, Sapotaceae, Chrysobalanaceae and Burseraceae usually co-occur and are shown to dominate PSPs from CA and EA, distributed on the left hand side of the graph. Moraceae, Palms, and Myristicaceae form another group of co-occurring families, and are particularly abundant in WA, as shown by the geographic range of PSPs located in the right hand side of the diagram. Leguminosae occupy a central position in the graph. This means that the family is well represented in the vast majority of PSPs. The degree of stretching in families' dispersion on the graph is influenced by the weight of some rare families, but the exclusion of these had no discernible effect on the ordination. The more central the position of a family in the graph, the more complete is the representation of their distribution along the gradient explained by the first axis, with low frequencies at the ends of the axis and a peak in the middle. For some families, the peak in distribution is not encompassed by the analysis, and falls somewhere outside the virtual gradient represented along the first axis of the DCA. These families tend to occupy the extreme margins in the swarm of PSPs shown in the diagram.

The patterns generated by various permutations of the dataset and analytical methods were fundamentally similar (e.g. including only a selection of most represented families, or using a selection of 16 families indicated in the literature as representative, from other trans-Amazonian studies).

Details on the DCA are reported in Table 4.1. The first two axes of the DCA explain 28.5% of total variance in the data. The first axis has an eigenvalue above 0.3, and this denotes a good separation of families on the first axis.

| DCA | AXIS 1 | AXIS 2 | AXIS 3 | AXIS 4 |
|---|---|---|---|---|
| Eigenvalues | 0.312 | 0.115 | 0.065 | 0.032 |
| lenght of gradient | 2.177 | 1.678 | 1.396 | 1.235 |
| Cumulative percentage of variance | 20.8 | 28.5 | 32.9 | 35 |

Table 4.1. Summary table of DCA of 68 plots and 85 families.

The total value of the cumulative percentage of variance is relatively low and this is probably due to some noise in the data. The length of the gradient is expressed in standard deviation units. A gradient is a spatially varying aspect of the environment, which is expected to be related to species composition. Environmental gradients correspond to the *x-axes* in a simultaneous portrayal of all species response curves along an environmental gradient. A whole gradient (i.e. a complete species turnover) is normally captured when its length corresponds to 4 standard deviation units (ter Braak and Smilauer 1998). Therefore, what is displayed along the first axis of the DCA is a partial environmental gradient (length = 2.177). One plot stands as an outlier on the far right hand side of the graph (Fig. 4.1), and this is due to its peculiar floristic composition, dominated by a single family, as is typical of extreme environments such as a swamp forest. A distinction into two sub-groups is apparent within WA PSPs (Fig. 4.1.). It can probably be explained by the geographic distance between plots, and by the type of disturbance affecting forest stands. The WA cluster spans a wide range of environmental conditions, from the Bolivian *terra firme* plots in the lower part of the cluster, not perturbed by periodic flooding but occasionally affected by fire, to the seasonally flooded sites and recent (Holocene) floodplains in the upper part of the cluster. The Peruvian cluster of PSPs is mostly located in the upper part of the graph and divided into a northern cluster, more central, and a southern cluster, in more marginal position. The swarm of Bolivian PSPs lay in an isolated position, in the lower part of the graph.

### 4.3.2. Dominant families and genera

Eight families emerge as most important on the basis of the FIV calculated for each single plot. In Figures 4.3 (a-d), families that have the highest FIV (a), relative diversity (b), relative density (c), and relative dominance (d) in each region are displayed.

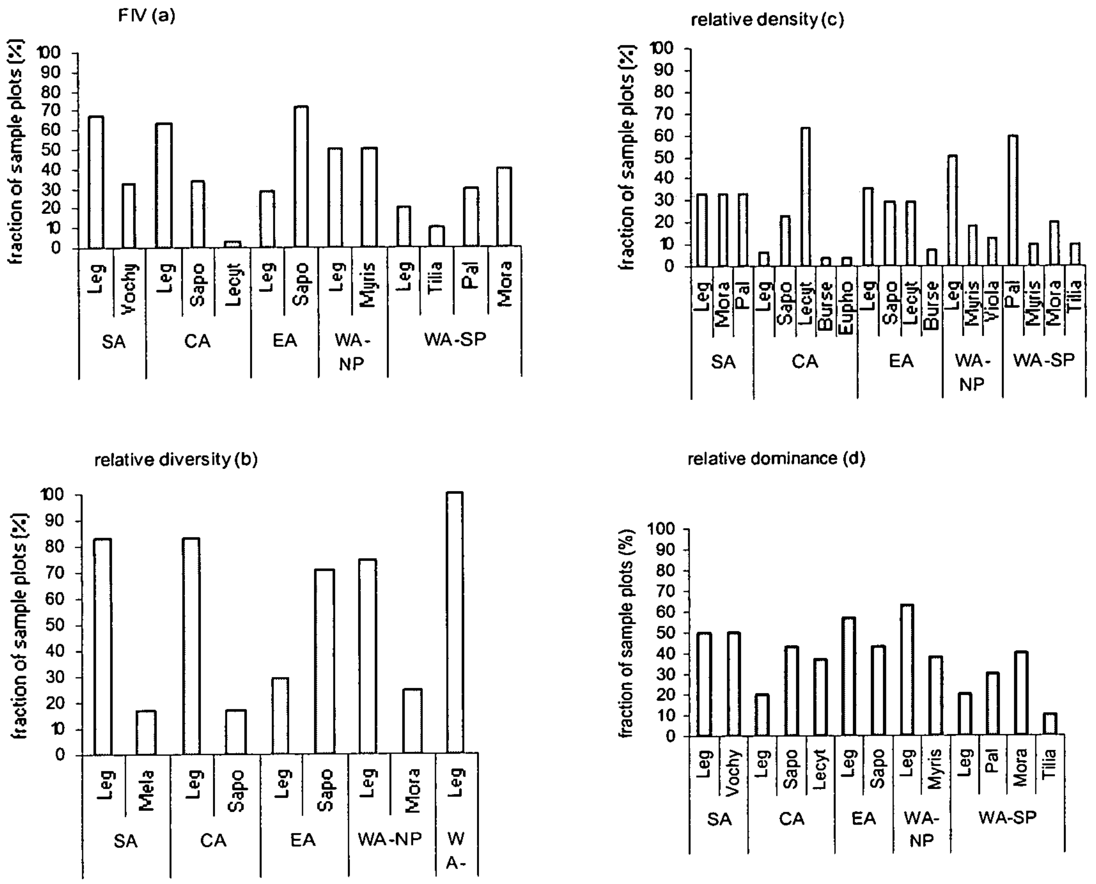


Figure 4.3. (a-d). Fraction of PSPs from each region where certain families have the highest family importance value (FIV) (a), the highest family relative diversity (b), the highest family relative density (c), the highest family relative dominance (d).

Bars in the diagrams show the percentage of PSPs from each region where a certain family has the highest value with respect to each parameter.

Patterns are quite consistent within regions. The most important families are easily identifiable: Leguminosae, Sapotaceae, Myristicaceae and Moraceae. Leguminosae have high FIV in every region (Fig. 4.3, a), tend to be the most diverse family in almost every region with the exception of the Eastern Amazonian PSPs (Fig. 4.3, b), and dominate a considerable fraction of plots in every region (Fig. 4.3, d). In the SA, EA, and WA-NP plots, Leguminosae show the highest FIV in 67%, 63% and 50% of the PSPs respectively, while their importance is less pronounced in CA and WA-SP where respectively Sapotaceae and Moraceae show the highest FIV in 71% and 40% of the PSPs (Fig. 4.3,a). In EA region, Sapotaceae is the most diverse family in the majority of plots (Fig. 4.3,b). Only 1 or 2 families dominate with respect to highest diversity in every region (Fig. 4.3, b). The highest relative density is shared among a wider range of families in each region: Lecythidaceae has the highest density in most of the PSPs in the CA region (63% of the plots), Leguminosae in the WA-NP region (50% of the plots), and Palms in the WA-SP region (50%); abundant families in the SA and EA region show more homogeneous values of relative density across plots (fig. 4.3,c). Leguminosae have the largest share in BA in the majority of plots in two regions (WA-NP and EA), Sapotaceae in CA, Moraceae in WA-SP (Fig. 4.3,d). Table 4.2 shows what part of the flora is unique to a region and what part is shared across regions, with respect to main families. It shows the results of a one-way ANOVA on the average number of individuals of 16 major families in random samples of 479 trees from 68 small 1-ha plots, in 5 Amazonian regions.

| **Region** | **SA** | **WA-NP** | **WA-SP** | **CA** | **EA** | **P** |
|---|---|---|---|---|---|---|
| **N. of plots** | 6 | 8 | 10 | 10 | 14 | |
| Annonaceae | 16.7 | 18.0 | 19.4 | 16.1 | 17.9 | 0.875 |
| Bombacaceae | 2.5 (a) | 8.4 (a) | 17.4 (b) | 7.4 (a) | 0.6 (a) | < 0.001 |
| Burseraceae | 2.3 (a) | 18.6 (a) | 6.1 (a) | 44.2 (b) | 38.9 (b) | < 0.001 |
| Chrysobalanaceae | 2.8 (a) | 10.1 (a) | 6.7 (a) | 24.1 (b) | 24.4 (b) | < 0.001 |
| Euphorbiaceae | 22.0 (a) | 28.1 (a) | 13.0 (b) | 16.9 (ab) | 4.9 (b) | < 0.001 |
| Lauraceae | 10.3 | 18.6 | 18.5 | 20.9 | 16.1 | 0.024 |
| Lecythidaceae | 0.3 (a) | 21.8 (a) | 4.7 (a) | 78.1 (b) | 68.0 (b) | < 0.001 |
| Leguminosae | 47.3 (ab) | 56.0 (b) | 33.2 (a) | 56.5 (b) | 70.4 (b) | < 0.001 |
| Meliaceae | 1.5 (a) | 14.5 (b) | 10.4 (ab) | 5.4 (a) | 4.1 (a) | 0.001 |
| Moraceae | 41.7 (a) | 26.0 (ab) | 53.2 (a) | 17.9 (b) | 13.1 (b) | < 0.001 |
| Myristicaceae | 1.3 (a) | 61.6 (c) | 23.4 (b) | 9.8 (a) | 9.5 (a) | < 0.001 |
| Palmae | 63.3 (ac) | 37.0 (a) | 81.4 (c) | 5.9 (b) | 0.5 (b) | < 0.001 |
| Rubiaceae | 24.2 (a) | 11.3 (b) | 5.4 (b) | 4.2 (b) | 9.1 (b) | < 0.001 |
| Sapotaceae | 17.7 (a) | 21.8 (a) | 22.4 (a) | 59.6 (b) | 73.0 (c) | < 0.001 |
| Sterculiaceae | 0.0 (a) | 10.5 (b) | 7.4 (c) | 6.3 (b) | 6.2 (b) | 0.001 |
| Violaceae | 5.5 | 15.6 | 20.8 | 13.8 | 33.1 | 0.027 |

Table 4.2. Average number of individuals of 16 major tree families in random samples of 479 trees from 68 1-ha plots in five Amazonian regions: SA= South Amazon, CA= Central Amazon, EA= Eastern Amazon, WA-NP= Western Amazon, North Peru, WA-SP= Western Amazon, South Peru. Regions that show the same symbol associated to the value are not significantly different from each other; differences are significant for regions accompanied by different symbols. P indicates the level of significance tested with one-way ANOVA.

Annonaceae, Lauraceae and Violaceae do not seem to differ significantly in relative density from region to region, whereas for all the other families differences are significant. Burseraceae, Chrysobalanaceae and Lecythidaceae are far more abundant in plots from Central and Eastern Amazon basin. Conversely, Myristicaceae are scarce in the South, Central and Eastern Amazon, while quite abundant in the western Amazon, especially in the most aseasonal sites of North Peru. Palmae and Moraceae are both abundant in the Western Amazon, particularly in North Peru, but reach a peak in the most southern plots of Bolivia, whereas they are not frequent in Central and Eastern Amazon. Sapotaceae tend to vary considerably in abundance across regions, from the southern fringes of the Amazon, where they are less represented, to the Central and Eastern Amazon where they are extremely abundant. In the sample of plots examined, out of 85 families analysed, 43 were found in plots in every one of the regions. Another group of 42 less frequent families is displayed in Tab. 4.3. They were not encountered within the PSPs of every region. Given the limited number of PSPs, this result only implies that they are less frequent, and not necessarily that they are absent from a certain region.

The Bolivian plots (SA) show a higher degree of uniqueness of their flora, presenting the greatest number of families not shared by other regions (Table 4.3), such as: Aquifoliaceae, Convolvulaceae, Marcgraviaceae, Strelitziaceae, Trigoniaceae. The Bolivian plots included in the analysis occupy an extreme position within the gradient explored, being located at the dry southern fringe of Amazonia.

| FAM | REGIONS | | | | |
|---|---|---|---|---|---|
| Rosaceae | WA-NP | WA-SP | CA | | SA |
| Araliaceae | WA-NP | WA-SP | | EA | SA |
| Caricaraceae | WA-NP | WA-SP | | EA | SA |
| Staphyleaceae | WA-NP | WA-SP | | | SA |
| Caryocaraceae | WA-NP | WA-SP | CA | EA | |
| Ebenaceae | WA-NP | WA-SP | CA | EA | |
| Icacinaceae | WA-NP | WA-SP | CA | EA | |
| Lacistemaceae | WA-NP | WA-SP | CA | EA | |
| Linaceae | WA-NP | WA-SP | CA | EA | |
| Monimiaceae | WA-NP | WA-SP | CA | EA | |
| Simarubaceae | WA-NP | WA-SP | CA | EA | |
| Sterculiaceae | WA-NP | WA-SP | CA | EA | |
| Bixaceae | WA-NP | WA-SP | | EA | |
| Capperaceae | WA-NP | WA-SP | | | |
| Piperaceae | WA-NP | WA-SP | | | |
| Sabiaceae | WA-NP | WA-SP | | | |
| Solanaceae | WA-NP | WA-SP | | | |
| Erythroxylaceae | WA-NP | | CA | | SA |
| Rhizophoraceae | WA-NP | | CA | EA | |
| Hugoniaceae | WA-NP | | CA | | |
| Opiliaceae | WA-NP | | CA | | |
| Rhabdodendraceae | WA-NP | | CA | | |
| Menispermaceae | WA-NP | | | EA | |
| Aquilariaceae | WA-NP | | | | |
| Cyatheaceae (palmoid) | WA-NP | | | | |
| Lythraceae | | WA-SP | | | SA |
| Proteaceae | | WA-SP | CA | EA | |
| Asteraceae | | WA-SP | | | |
| Dialypetalanthaceae | | WA-SP | | | |
| Phytolaccaceae | | WA-SP | | | |
| Urticaceae | | WA-SP | | | |
| Connaraceae | | | CA | EA | SA |
| Styracaceae | | | CA | | SA |
| Dilleniaceae | | | | EA | SA |
| Loganiaceae | | | | EA | SA |
| Polygalaceae | | | | EA | SA |
| Aquifoliaceae | | | | | SA |
| Convolvulaceae | | | | | SA |
| Marcgraviaceae | | | | | SA |
| Strelitziaceae | | | | | SA |
| Trigoniaceae | | | | | SA |
| Duckeodendraceae | | | CA | | |

Table 4.3. List of families that occur only in some of the regions, therefore not common to all. CA= Central Amazon, EA= Eastern Amazon, WA-NP= Western Amazon North Peru, WA-SP= Western Amazon South Peru, SA= Southern Amazon.

At the genus level, patterns of floristic dominance are also clearly identifiable (Table 4.4.). *Eschweilera* is particularly frequent within the CA region, in the great majority of plots sampled. *Iriartea* is extremely frequent in half the South Peruvian PSPs analysed. Within the other three regions, the most common genera dominate about 1/3 of the plots sampled.

| Region | N. PSPs | Family | Genus | % of PSPs in the region |
|---|---|---|---|---|
| CA | 30 | Lecythidaceae | Eschweilera | 80.0 |
| EA | 14 | Sapotaceae | Pouteria | 35.7 |
| WA-NP | 8 | Myristicaceae | Iryanthera | 37.5 |
| WA-SP | 10 | Palmae | Iriartea | 50.0 |
| BOL | 6 | Moraceae | Pseudolmedia | 33.3 |

Table 4.4. Summary table of most abundant genera in each region. The percentage reported refers to the fraction of 1-ha sample plots where the indicated genus shows the highest density of individuals per ha. The number shown corresponds to the number of plots. CA= Central Amazon, EA= Eastern Amazon, WA-NP= Western Amazon North Peru, WA-SP= Western Amazon South Peru, SA= Southern Amazon.

### 4.3.3. Some distinct functional groups (pioneer species and palms)

The contribution of pioneer species (for a complete list, see appendix 3) to the total number of individuals and total BA $ha^{-1}$ differs considerably between the five regions of the Amazon Basin identified (Table 4.5.). Pioneer species are most abundant in SA, where they represent more than 22% of the stems. In WA, both in south and in north Peru, the percentage is halved. In PSPs from CA and EA, only 3.4% of total stems belong to pioneer species.

| N. Plots | Region | mean N (%) pioneers on tot N trees | mean BA (%) pioneers on tot BA |
|---|---|---|---|
| 30 | Central Amazon | 3.4 | 3.7 |
| 14 | Eastern Amazon | 3.5 | 7.2 |
| 8 | Western Amazon (NP) | 7.5 | 9.5 |
| 10 | Western Amazon (SP) | 11.6 | 16.4 |
| 6 | Southern Amazon (Bolivia) | 22.1 | 15.8 |

Table 4.5. Summary table with average % of pioneer species on the total number of individuals $ha^{-1}$, and on total basal area $ha^{-1}$, for 5 regions of the Amazon Basin.

A very similar ranking is shown in the contribution of pioneer species to stem and stand BA. The highest BA of pioneer species is found in south Peruvian PSPs. EA and WA-SP PSPs show large-stemmed individuals from the pioneer guild (on average 5-6 stems of pioneers $ha^{-1}$ with dbh > 90 cm), while large-stemmed pioneers do not occur in PSPs from the other regions. The Bolivian plots show the highest stem density of pioneer species but most of the contribution to total stand BA derives from small-stemmed individuals. The largest pioneer individuals belong to the following genera: *Ficus* and *Bertholletia* in WA-SP, with stems above 100 cm of dbh; *Dinizia*, *Bertholletia*, *Goupia*, and *Trattinickia* contain the largest individuals among pioneer species in EA, with trees above 100 cm dbh. In CA and WA-NP the species with largest diameter are from the same genera above-mentioned, but rarely reach 70 cm dbh. In SA the largest pioneers reach about 60 cm dbh and belong mainly to the genera *Jacaranda*, *Apeiba*, *Hyeronima* and *Didymopanax*.

A multiple comparison of pioneer species occurrence across regions was carried out (Kruskal-Wallis test, Tukey's test) and statistically significant differences were found between regions ($P < 0.001$). With regard to both % of stems and BA $ha^{-1}$, median values are the highest for SA plots (N% = 24.67, BA% =14.06), followed by progressively decreasing values in WA-SP plots (N% = 10.57, BA% =15.12), WA-NP (N% = 8.84, BA% =11.49), EA (N% = 2.58, BA% =5.19), and CA (N% = 2.30, BA% =2.99). Values for regions are quite distinct, except for EA and CA that show a similar contribution of pioneers to stem density, and for SA and WA-SP, that present similar median values in pioneer species' contribution to total stand BA.

The abundance of Palms was also compared across regions (Table 4.6). The ranking is similar for the two variables described, with the highest value in the Southern fringes of the Peruvian and Bolivian Amazon.

| N. Plots | Region (Palms) | mean N (%) Palms on tot N trees | mean BA (%) Palms on tot BA |
|---|---|---|---|
| 10 | Western Amazon (SP) | 17.0 | 12.5 |
| 6 | Southern Amazon (Bolivia) | 13.0 | 5.5 |
| 8 | Western Amazon (NP) | 7.6 | 5.2 |
| 14 | Central Amazon | 1.3 | 0.5 |
| 30 | Eastern Amazon | 0.1 | 0.04 |

Table 4.6. Summary table with average relative density and relative dominance of palms on the total number of individuals $ha^{-1}$, and on total basal area $ha^{-1}$, for 5 regions of the Amazon Basin. Relative density = (# of individuals of a family / total # of individuals of the sample) x 100; relative dominance = (basal area of a family / total basal area of the sample) x 100.

Palms are not absent in the eastern Amazonia PSPs but, within the sample of inventories explored, they tend to be small-stemmed (e.g., *Astrocaryum* sp.) and are therefore not recorded, as the minimum diameter considered is 10 cm dbh. Spatial patterns in palms occurrence were investigated (Kruskall-Wallis test, Tukey's test), and statistically significant differences between regions were found ($P < 0.001$). As for pioneer species, spatial patterns in BA mirror those found for stem density and the ranking of sites is the same. Median values are the highest for WA-SP plots (%N = 15.9, %BA =13.1), followed by progressively lower values: SA plots (%N = 12.3, %BA =5.0), WA-NP (%N = 8.2, %BA =4.3), CA (%N = 1.0, %BA =0.3), and EA (%N = 0.0, %BA =0.0).

Pioneer species and Palms tend to co-occur, being most abundant in the same regions. They usually occur with higher frequencies in sites with high stem turnover rates (see Chapter 5).

### 4.3.4 Patterns in total species richness across the Amazon basin

The following questions are addressed in the next paragraphs:

- Are there regional patterns in species richness? At which taxonomic level?
- Can patterns be related to environmental factors? Are there other factors that might play a role (e.g., biogeography)?

The variation in total species richness across different Amazonian regions was investigated and the relationships with climatic factors explored. The total number of families was correlated with the amount of annual rainfall and the number of dry months $a^{-1}$. To avoid the so called "species paradox", where the number of species (or families) increases simply as a function of the number of individuals sampled, a sub-sample with an equal number of stems was randomly selected from each plot and tested. The threshold in the number of stems selected (479) corresponds to the number of trees with dbh $\geq$ 10 cm in the least dense plot. A total of 68 floristic inventories corresponding to an equivalent number of PSPs was selected. PSPs were lumped by localities and the mean number of families $ha^{-1}$ calculated. Table 4.7 shows the average number of families $ha^{-1}$, the number of dry months and the mean annual precipitation for each locality. Values extracted from a standard sub-sample of stems were compared to those referred to the entire 1-ha PSP.

The values of mean annual precipitation for Tambopata and Cuzco Amazonico derive from local meteorological stations. The value provided by the historical dataset used for the present study (described in Chapter 2, paragraph 2.3.2) seems to be partially biased for these two sites. Values of mean annual rainfall are generated by the interpolation of precipitation from meteorological stations located at the foot of the Andes and extrapolated to the region. This leads to an overestimate of actual values and data from local stations were used instead.

| Locality | Region | Plots N | equal (479) | | unequal (tot N) | | Dry months N | Ann.prec. mean |
|---|---|---|---|---|---|---|---|---|
| | | | mean N fam | SE Mean | mean N fam | SE Mean | | |
| Allpahuayo, Mishana,Indiana | WA-NP | 4 | 46.0 | 1.8 | 52.5 | 1.3 | 0.9 | 2885 |
| Sucusari | WA-NP | 2 | 45.0 | 4.0 | 51.0 | 5.0 | 0.6 | 2840 |
| Yanamono | WA-NP | 2 | 44.5 | 2.5 | 52.5 | 1.5 | 0.6 | 2840 |
| Tambopata | WA-SP | 6 | 40.5 | 1.1 | 44.5 | 1.1 | 4.1* | 2248* |
| Manaus | CA | 30 | 40.4 | 0.5 | 46.7 | 0.4 | 2.4 | 2387 |
| Cuzco Amazonico | WA-SP | 4 | 39.3 | 0.5 | 43.0 | 0.4 | 3.5* | 2451* |
| Tapajos | EA | 3 | 38.0 | 0.6 | 41.3 | 0.9 | 4.7 | 2067 |
| Caxiuana | EA | 11 | 37.5 | 0.7 | 41.6 | 0.8 | 2.8 | 2508 |
| Huanchaca | SA | 4 | 35.3 | 1.7 | 40.0 | 1.8 | 5.8 | 1454 |
| Los Fierros | SA | 2 | 32.0 | 1.0 | 37.5 | 2.5 | 6.5 | 1313 |

Table 4.7. Summary table with mean number of families (from equal and unequal samples of stems per plot), number of dry months and mean annual precipitation (mm) for each locality. The value of annual rainfall for Tambopata and Cuzco Amazonico is accompanied by an asterisk to indicate that the value from the historical dataset differs considerably from the values recorded by local stations (see text). Regions: CA= Central Amazon, EA Eastern Amazon, SA= Southern Amazon, WA-NP= Western Amazon North Peru, WA-SP= western Amazon South Peru.

The relationship between the number of families and mean annual rainfall is strong, whether samples both equal (Fig. 4.4.) or unequal in size (results not shown) are used. Sites with less than 2000 mm $a^{-1}$ show the lowest number of families (Bolivia: Los Fierros and Huanchaca). Family richness is positively correlated with annual precipitation and negatively correlated with seasonality, but it was not possible to distinguish the effect of total precipitation and seasonality because they strongly covary. The highest diversity is found in sites with rainfall between 2500 and 3000 mm $a^{-1}$ and with less then 1 dry month. The regression of mean number of families on mean annual rainfall in each site is quite strong: $y = 0.0074x + 23.058$; $R^2 = 0.77$, with $R^2$ based on locality means and not considering within-site variance.

Data were further lumped by regions to have larger and more balanced samples from each area. Differences in the total number of families between regions are significant ($P < 0.001$) as shown by the Kruskal-Wallis test (Tukey's test), using both an equal sample of stems (479), and an unequal sample of individuals from each forest sample plot (total number of trees $ha^{-1}$).

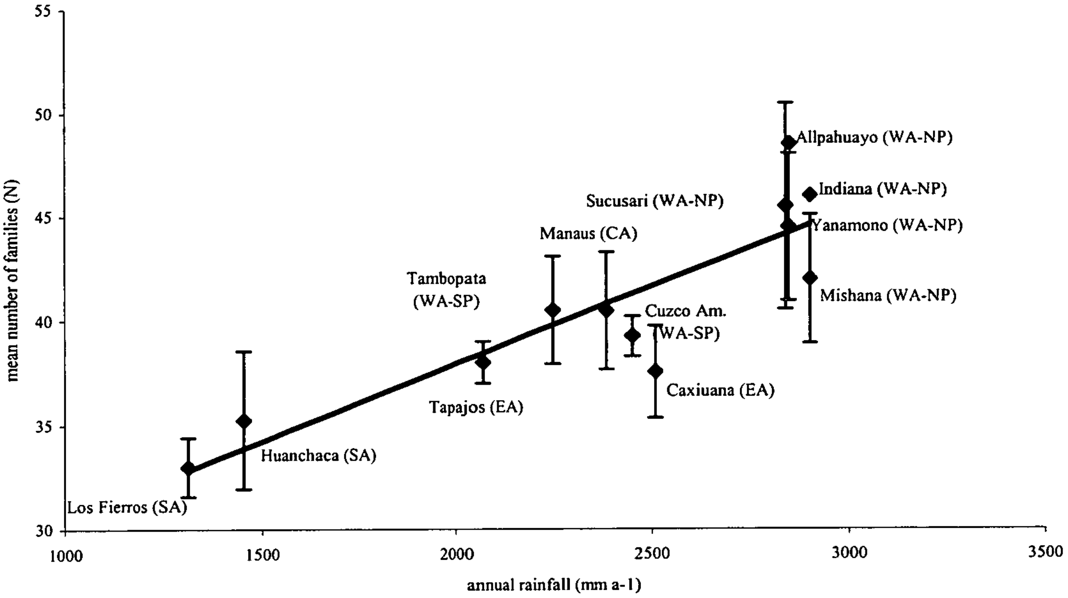


Figure 4.4. Relationship between the average number of tree families (lianas are excluded) in each site (with mean values obtained from an equal sample of 479 stems from each of the 68 selected PSPs) and the mean annual rainfall for each site. Bars indicate standard deviation.

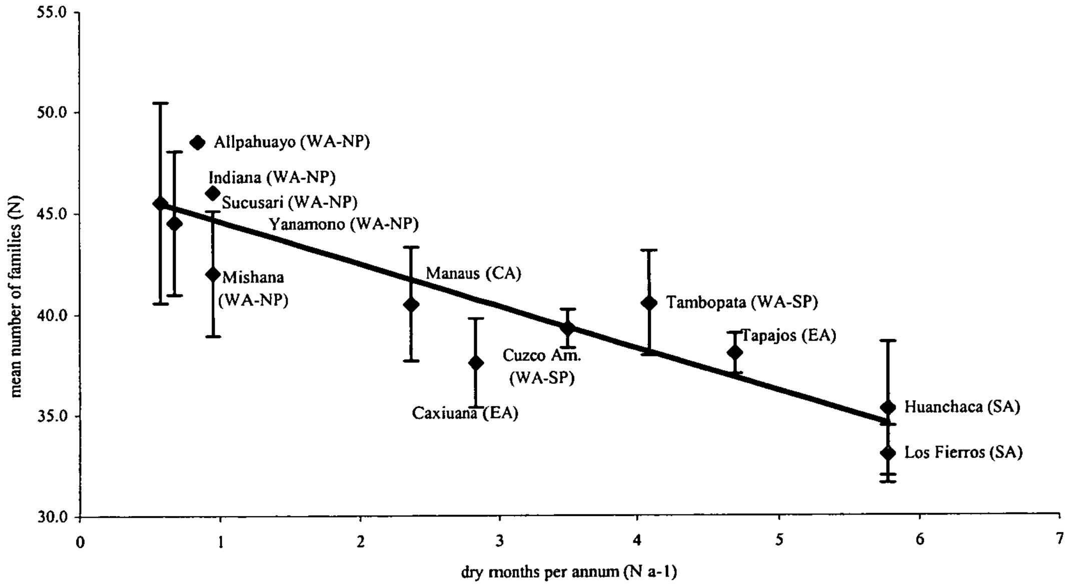


Figure 4.5. Relationship between the average number of families in each site (with mean values obtained from an equal sample of 479 stems from each plot) and the number of dry months. Bars indicate standard deviation.

Median values are the highest for WA-SP plots (equal sample = 46.5, unequal sample = 52.0), followed by CA plots (equal sample = 40.5, unequal sample = 47.0), WA-SP (equal sample = 40.0, unequal sample = 43.5), EA (equal sample = 38.0, unequal sample = 41.0), and SA (equal sample = 33.0, unequal sample = 39.0).

The mean total number of families $ha^{-1}$ in each region, derived from an equal number of stems in each plot, was correlated with the mean number of dry months. Figure 4.5 shows the strong inverse relationship ($y = -2.101x + 46.655$; $R^2 = 0.81$, with $R^2$ based on between-site variance).

The relationship between floristic richness and climate was tested also at species level. Table 4.8 shows the number of "expected" species in an equal number of stems in each locality (see paragraph 4.2. for a definition of "expected" species).

| Locality | Region | Plots N | "Expected" Species mean N | SE mean |
|---|---|---|---|---|
| Allpahuayo, Mishana, Indiana | WA-NP | 4 | 238.00 | 23.30 |
| Caxiuana | EA | 11 | 155.88 | 7.08 |
| Cuzco Amazonico | WA-SP | 4 | 146.76 | 4.88 |
| Huanchaca | SA | 4 | 124.90 | 25.00 |
| Los Fierros | SA | 2 | 147.80 | 25.70 |
| Manaus | CA | 30 | 257.10 | 7.25 |
| Sucusari | WA-NP | 2 | 289.20 | 17.40 |
| Tambopata | WA-SP | 6 | 175.82 | 5.20 |
| Tapajos | EA | 3 | 128.60 | 8.96 |
| Yanamono | WA-NP | 2 | 281.80 | 21.60 |

Table 4.8. Mean number of "expected" species in each region.

Species diversity increases with a decreasing length of the dry season, mirroring the patterns already illustrated for families (Fig. 4.6.), but the decline is much steeper. Differences between regions are statistically significant (Kruskal-Wallis test, H= 41.80, P= 0.000).

Where the dry period exceeds 3 months $a^{-1}$, the total number of species is never more than 150. On the other hand, where the dry season lasts for less than 1 month $a^{-1}$, the number of "expected" species $ha^{-1}$ almost doubles.

Manaus represents an exception with more than 250 species $ha^{-1}$ and 3 dry months $a^{-1}$. The $R^2$, based on between-site variance, is 0.84 if all the localities are considered ($y = -35.123x + 286.08$), and 0.93 when Manaus is excluded ($y = -33.961x + 275.21$). diversity. A methodological artifact could be partially responsible for the observed correlation.

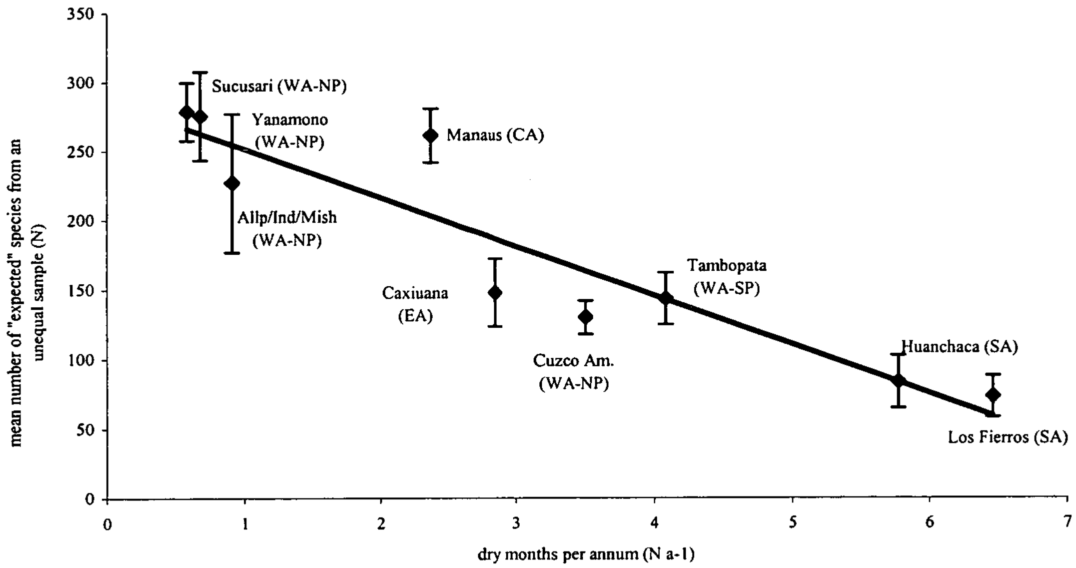


Figure 4.6. Relationship between the average number of "expected" species in each site (with mean values obtained from an unequal sample from each plot) and the number of dry months. Bars indicate standard deviation.

The length of the dry season seems to be a better predictor of family diversity than annual rainfall, and also performs well as a predictor of species-level

The quality of the floristic survey could vary considerably among sites, leading to different accuracy in the identification of species. However, subspecies and varieties were discarded in the counting of species, as only some inventories showed further taxonomic differentiations below the species level. Logically, stem density is likely to have an influence on the number of species $ha^{-1}$ and PSPs with highest species diversity are also characterized by high stem density. To avoid this artifact, the relationship between the number of dry months and the number of "expected" species in each PSPs was tested for equal samples of individuals (Fig. 4.7). The negative correlation is maintained ($y= -28.483x + 252.99$; $R^2= 0.89$, with $R^2$ based on between-site variance), and has a higher $R^2$ than using an unequal sample of stems per plot.

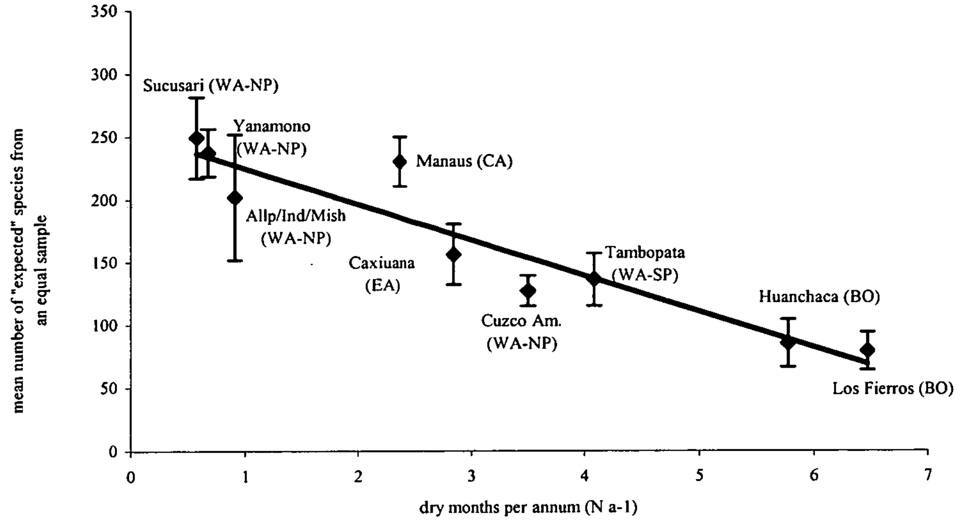


Figure 4.7. Relationship between the average number of "expected" species in each site (with mean values obtained from an equal sample of 479 stems from each plot) and the number of dry months. Bars indicate standard deviation.

Even after accounting for any stem density effect, the species richness found in PSPs near Manaus is higher than expected and presumably factors other than present-day environmental conditions contribute to generating the floristic richness observed in the region (e.g., recent historical changes in climate, or longer term biogeographical factors), as suggested by various authors (see discussion in paragraph 4.4).

### 4.3.5. Local patterns of floristic diversity

The questions addressed in the next paragraphs are the following:

- Are there local patterns in floristic composition within a site?
- Can these patterns be related to local edaphic factors?

A DCA was run with species-level data for a cluster of PSPs from the Central Amazon (BDFFP project, Manaus), to detect local relationships between floristic composition and local environmental factors. The chosen PSPs are fairly homogeneous in stand characteristics and floristic composition.

A total of 254 species, represented by more than 10 individuals, was fed into the DCA and, from this sample, the most abundant species were selected to explore within site beta-diversity. The floristic gradient is shown along the first axis of the

DCA in Fig. 4.9. Two families occur with highest stem density in all PSPs blocks (Lecythidaceae and Burseraceae) with the exception of block 3304, dominated by Euphorbiaceae and Bombacaeae. This presumably determines its isolation along the second axis of the DCA in Fig. 4.9. The first two most abundant species in all PSP blocks are *Protium hebetatum* (Burseraceae), and *Eschweilera coriacea* (Lecythidaceae).

A substitution of species is evident in Fig. 4.8, where the progressively decreasing density of some species is accompanied by an opposite trend for others, moving from one block to another along the first axis. The two most important species are not shown, as they are homogeneously highly frequent in all PSPs clusters, and therefore not suitable to detect the main floristic differences between the examined PSPs blocks.

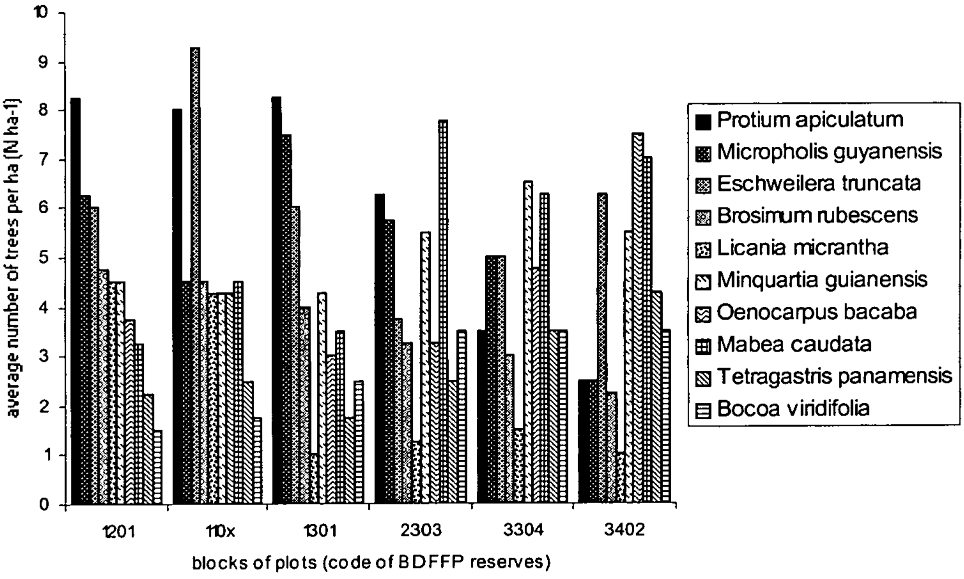


Figure 4.8. Average occurrence of individuals of 10 very abundant species, (out of 254 species with > 10 stems fed into the DCA), found in 26 1-ha plots, clustered in 6 reserves from the BDFFP experiment (Manaus, Brazil). The display of PSPs blocks along the $x$-axis mirrors the sequence along the first axis of the DCA (see Fig. 4.9).

Only species with more than 10 individuals across all the PSPs (254) were fed into the DCA. This was done to avoid weighting by rare species. Unimodal methods are statistical methods that are designed to analyse data arising from unimodal response curves or surfaces. Unimodal means "with one mode" and is used to indicate a response curve or surface with one peak. In unimodal methods, rare species may have an unduly large influence on the analysis. Their influence can be reduced by checking the "Downweighting of rare species" box in Canoco for Windows 4.0 (ter Braak and Smilauer 1998).

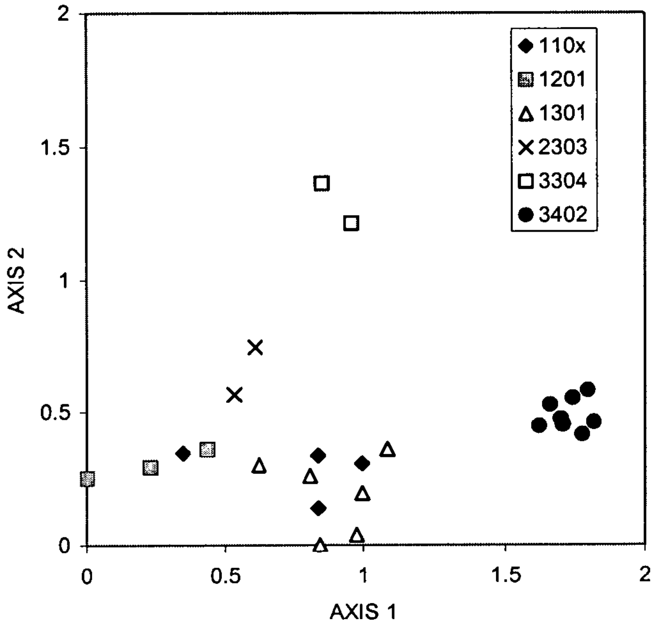


Figure 4.9. Results of a DCA run using species composition data (254 species with > 10 stems) from 26 1-ha plots, for BDFFP (Manaus, Brazil) PSPs. Plots are distributed in the two-dimensional space according to their floristic composition. Different block of PSPs are identified by different symbols.

The resulting scatterplot (Fig. 4.9) resembles a geographic map of the BDFFP reserves. The clusters define distinct blocks of plots geographically separated, as shown in the map of BDFFP reserves (see map in Fig. 3.4 in Chapter 3). Two main gradients are shown in Fig. 4.9. The first axis explains the most variation in the data (length of gradient = 1.73) (Table 4.9), but still a low percentage of the total variance (17.3).

| DCA | AXIS 1 | AXIS 2 | AXIS 3 | AXIS 4 |
|---|---|---|---|---|
| Eigenvalues | 0.232 | 0.87 | 0.059 | 0.041 |
| Length of gradient | 1.733 | 1.16 | 1,071 | 1.098 |
| Cumulative percentage of variance | 17.3 | 23.7 | 28.1 | 31.2 |

Table 4.9. Summary table of DCA of 27 plots in Manaus and 254 species.

The effect of soil characteristics was explored. Only soil texture data were uniformly available for all PSPs, therefore the relationship between plots' scores on the first DCA axis and the percentage of sand was tested. The percentage of sand in the soil is negatively correlated with the amount of clay, which can be considered a proxy for soil fertility. The amount of sand also affects water drainage in the soil and can be looked at as a proxy for water supply to the plant. Therefore, a high content of sand would sugget a considerable leaching, low fertility and limited water availability. Figure 4.10 shows the floristic index (i.e., DCA value on first axis) negatively correlated with a progressively more sandy soil texture.

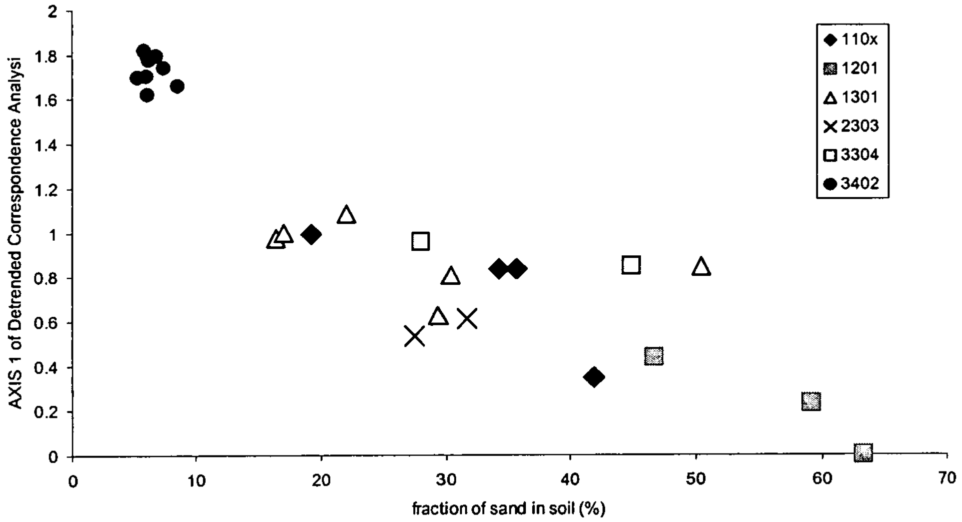


Figure 4.10. Relationship between the percentage of sand in the soil and the scores from a Detrended Correspondence Analysis (DCA) run with species-level data from 26 1-ha plots (BDFFP project, Manaus, Brazil). Symbols correspond to different blocks of PSPs.

The relationship showed a very strong regression between the two variables ($y = -0.0284x + 1.7751$, $R^2 = 0.83$). Within the BDFFP plots, floristic variability therefore seems to be well explained by soil characteristics, when these are approximately described by the percentage of sand (cf. Laurance et al. 1999 show similar results for the relationship between biomass and soil texture). The gradient along the second axis of the DCA shown in Fig 4.9 seems to be due to other factors that may contribute in determining the assemblage of species analysed. Distance between plots and topography are the most likely explanatory variables for the observed floristic variation. Those blocks dispersed in the middle and upper parts of the graph in Fig.

4.9 are geographically isolated from the others, and although not too dissimilar in soil characteristics, they probably are affected by different surrounding conditions (species-pool), and different dispersal of species common in other blocks.

### 4.3.6. Structural variation in tropical rainforest PSPs

After exploring the floristic variability of different PSPs scattered across the Amazon basin, the variability in forest stand structure was investigated on a total of 91 PSPs. They are mainly derived from studies carried out in the Brazilian and Peruvian Amazon, but also in French Guiana and other tropical zones (West Africa, Malaysia, Panama). All the plots show a characteristic stem-diameter distribution (inverse-J shape), typical of non-perturbed tracts of forest (Richards 1996b). The small classes are abundantly represented, indicating a good regeneration, and only a few individuals reach dimensions of ≥ 100 cm of diameter (emergents). Two examples of diameter distribution from 1-ha plots of different regions are presented in Figure 4.11.

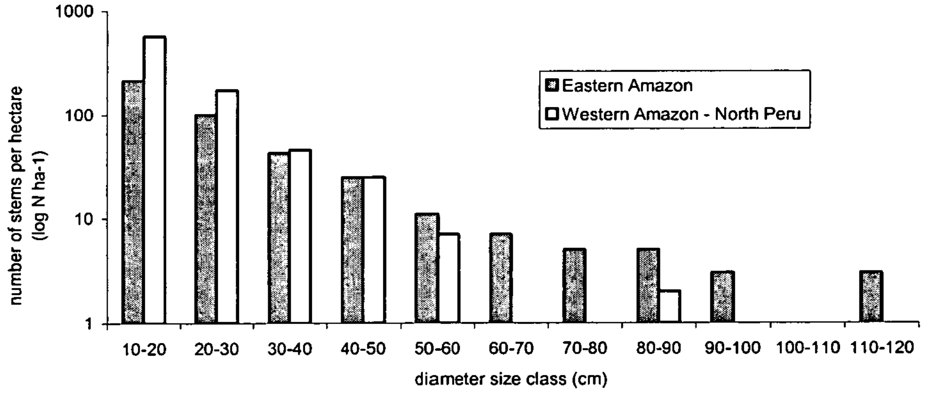


Figure 4.11. Stem diameter distribution in 2 1-ha sample plots from different localities, with extreme values in diameter frequencies, as an example of the typical reversed J-shaped structure of mixed uneven aged stands.

Some parameters were adopted to define the structural characteristics of different stands. Their values for each PSP are listed in Table 4.10. In Table 4.11, the same parameters are shown for 7 main regional clusters of PSPs. The variation in total number of stems is greater than the variation in total BA. Mishana shows an exceptionally high stem density, while the African PSPs have almost half the number of stems $ha^{-1}$. BA varies from a maximum of 37 $m^2$ $ha^{-1}$ in Lope (Cameroon), to a minimum of 25 $m^2$ $ha^{-1}$ in Cuzco Amazonico (Peru). A high contribution to total stem density and total BA derives from small-stemmed trees in various Western Amazonian PSPs and in central Amazonian plots (Manaus). Conversely, African PSPs and those PSPs located in drier sites of the Neotropics show an opposite pattern (Table 4.10).

| Locality | Country | N Plots | N tot trees/ha ≥10 cm dbh | Stdev N tot | N trees ≥70 cm dbh | BA trees ≥ 70 cm dbh (m2) | N trees ≥ 100 cm dbh | BA trees ≥100 cm dbh (m2) | tot BA (m2) (all stems) | Stdev tot BA | mean BA (m2) (all stems) | ratio N trees <20/>70 cm dbh | ratio BA trees <20/ >70 cm dbh |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Odzala | Congo | 1 | 304.9 | | 3.8 | | 1.7 | | | | | 43.6 | |
| Oveng, Doussala, Lope, Ekobakoba | Gabon | 4 | 429.8 | 39.8 | 19.0 | 15.3 | 6.4 | 8.1 | 37.7 | 3.5 | 0.088 | 12.2 | 0.3 |
| Dja | Cameroun | 9 | 516.4 | 62.1 | 15.0 | 9.9 | 3.4 | 3.9 | 32.6 | 3.3 | 0.063 | 21.6 | 0.5 |
| Ngotto | CAR (**) | 1 | 556.0 | | 12.0 | | 6.0 | | | | | 29.0 | |
| BCI (*) | Panama | 1 | 428.7 | | | | 3.3 | | 31.8 | | 0.074 | | |
| Nourages | French Guiana | 2 | 528.4 | 8.4 | 12.8 | | 3.5 | | | | | 24.8 | |
| Pasoh | Malaysia | 1 | 577.5 | | | | 1.1 | | 30.3 | | 0.052 | | |
| Caxiuana | Brazil | 11 | 492.0 | 31.7 | 11.4 | 8.2 | 3.1 | 3.9 | 31.9 | 2.3 | 0.065 | 27.4 | 0.6 |
| Tapajos | Brazil | 3 | 499.0 | 25.0 | 9.0 | 6.3 | 2.3 | 2.6 | 27.6 | 3.8 | 0.056 | 41.1 | 1.0 |
| Huanchaca | Bolivia | 4 | 625.0 | 81.8 | 11.8 | 8.4 | 3.8 | 4.1 | 30.1 | 1.7 | 0.049 | 43.8 | 1.0 |
| Los Fierros | Bolivia | 2 | 607.5 | 26.2 | 12.0 | 8.8 | 4.0 | 4.1 | 28.2 | 3.3 | 0.047 | 42.8 | 0.8 |
| Manaus | Brazil | 30 | 609.9 | 45.5 | 5.0 | 3.0 | 0.6 | 0.7 | 27.9 | 2.1 | 0.046 | 99.3 | 2.9 |
| Cuzco Amazonico | Peru | 4 | 512.8 | 40.48 | 6.7 | 4.2 | 1.8 | 1.8 | 25.0 | 2.2 | 0.049 | 52.6 | 1.5 |
| Tambopata | Peru | 5 | 545.6 | 27.9 | 6.2 | 5.0 | 1.6 | 2.4 | 27.5 | 1.9 | 0.051 | 55.4 | 1.2 |
| Allpahuayo | Peru | 3 | 570.3 | 59.7 | 2.7 | 1.8 | 0.7 | 0.6 | 25.8 | 2.4 | 0.045 | 173.5 | 5.0 |
| Indiana | Peru | 1 | 571.0 | | 11.0 | 6.6 | | | 32.0 | | 0.056 | 31.6 | 0.9 |
| Pakitsa | Peru | 1 | 577.0 | | 7.0 | 4.6 | 2.0 | 1.7 | 27.2 | | 0.047 | 45.9 | 1.2 |
| Yanamono | Peru | 2 | 585.5 | 20.5 | 7.5 | 4.1 | 0.5 | 0.5 | 30.3 | 1.0 | 0.052 | 48.1 | 1.4 |
| Sucusari | Peru | 5 | 596.2 | 27.5 | 4.8 | 2.7 | 0.2 | 0.2 | 27.9 | 1.7 | 0.047 | 129.2 | 3.8 |
| Mishana | Peru | 1 | 829.0 | | 4.0 | 2.4 | 1.0 | 0.9 | 28.7 | | 0.035 | 143.3 | 3.7 |

Table 4.10. Table of structural parameter values for each locality. For some plots, where metadata are from the literature, some values are missing. These plots are underlined in the list. (*) Barro Colorado Island, (**) Central African Republic. The N tot trees, N trees ≥ 70, N trees ≥ 100 of individuals $ha^{-1}$ is not always an integer number, as sometimes it is a mean value.

| Region | N Plots | N tot Trees/ha ≥10 cm dbh | Stdev N tot | N trees ≥70 cm dbh | BA trees ≥ 70 cm dbh (m2) | N trees ≥ 100 cm dbh | BA trees ≥100 cm dbh (m2) | tot BA (m2) (all stems) | Stdev tot BA | mean BA (m2) (all stems) | ratio N trees <20/>70 cm dbh | Ratio BA trees <20/ >70 cm dbh |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CAA | 1 | 428.7 | | | | 3.3 | | 31.80 | | 0.074 | | |
| AF | 15 | 481.8 | 81.96 | 15.1 | 11.54 | 4.3 | 5.20 | 34.19 | 4.05 | 0.071 | 21.05 | 0.45 |
| EA | 14 | 493.5 | 29.61 | 10.9 | 7.80 | 2.9 | 3.60 | 30.96 | 3.12 | 0.063 | 30.33 | 0.71 |
| FG | 2 | 528.4 | 8.44 | 12.8 | | 3.5 | | | | | 24.78 | |
| WA-SP | 10 | 535.6 | 37.03 | 6.5 | 4.62 | 1.7 | 2.10 | 26.46 | 2.15 | 0.049 | 53.32 | 1.32 |
| AS | 1 | 577.5 | | | | 1.1 | | 30.30 | | 0.052 | | |
| WA-NP | 12 | 605.3 | 77.84 | 5.2 | 3.01 | 0.4 | 0.37 | 28.18 | 2.46 | 0.047 | 119.78 | 3.45 |
| CA | 30 | 609.9 | 45.53 | 5.0 | 2.96 | 0.6 | 0.72 | 27.94 | 2.14 | 0.046 | 99.30 | 2.92 |
| SA | 6 | 619.2 | 65.08 | 11.8 | 8.58 | 3.8 | 4.12 | 29.46 | 2.22 | 0.048 | 43.48 | 0.89 |

Table 4.11. Summary table of structural parameter values, for each region. For some plots, where metadata are from the literature, some values are missing. AF= Africa, AS= Asia, CA= Central Amazon, CCA= Central America, EA Eastern Amazon, FG= French Guiana, SA= Southern Amazon, WA-NP= Western Amazon North Peru, WA-SP= western Amazon South Peru. The N tot trees, N trees ≥ 70, N trees ≥ 100 of individuals $ha^{-1}$ is not always an integer number, as sometimes it is a mean value.

The relationship between stem density and BA was tested for a sample of 87 plots from different regions (Fig. 4.12). The two variables do not seem to show any significant correlation.

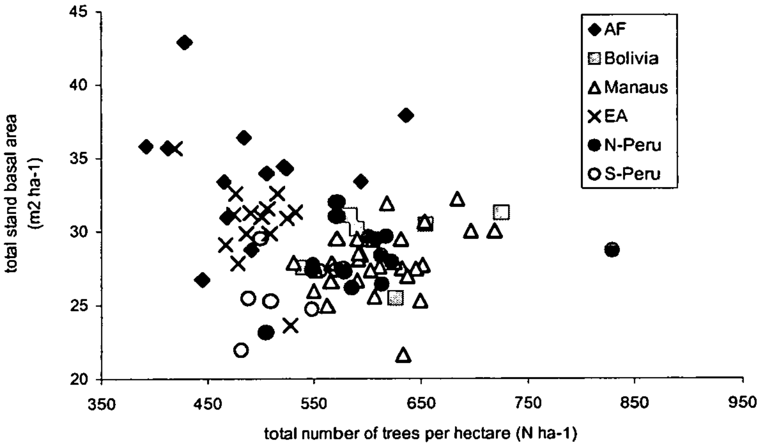


Figure 4.12. Relationship between BA and mean values of stem density in 87 1-ha PSPs from the Neotropical region.

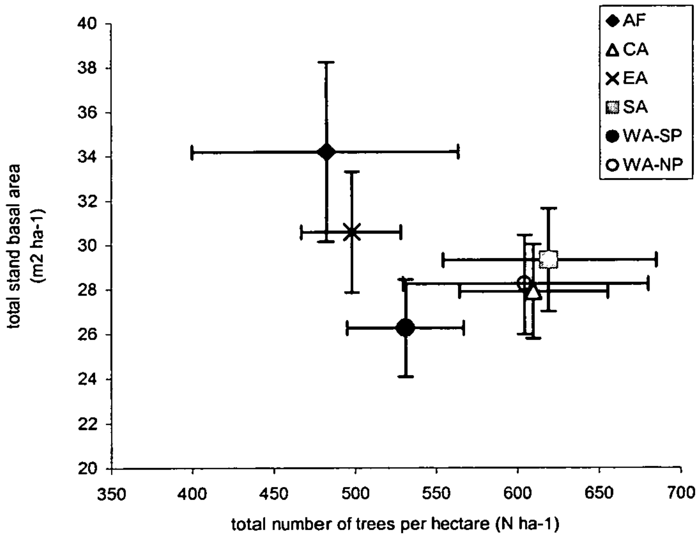


Figure 4.13. Relationship between BA and total number of stems in 87 1-ha PSPs from the Pantropical region. Bars indicate standard deviation.

Average values of stem density and BA for each site were calculated (Fig. 4.13). Mean stand BA values tend to decline with an increasing number of stems up to an average of 550 stems ha$^{-1}$ (Pearson's r = 0.66), then mean BA increases again to reach intermediate values with increasing density of stems (Pearson's r = 0.54) (Fig. 4.13). The correlation between the total stand BA and the total number of large trees ha$^{-1}$ is shown for 85 1-ha PSPs in Figure 4.14 (Pearson's r = 0.709).

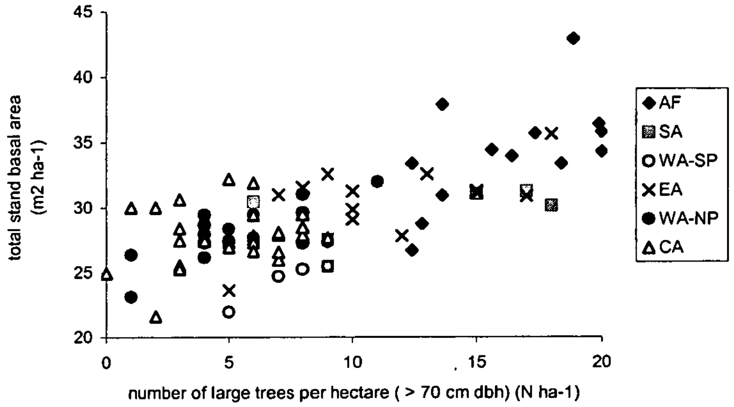


Figure 4.14. Relationship between the number of large-stemmed trees (>70 cm of dbh) ha$^{-1}$ and the stand total BA in 85 1-ha PSPs from the Neotropics.

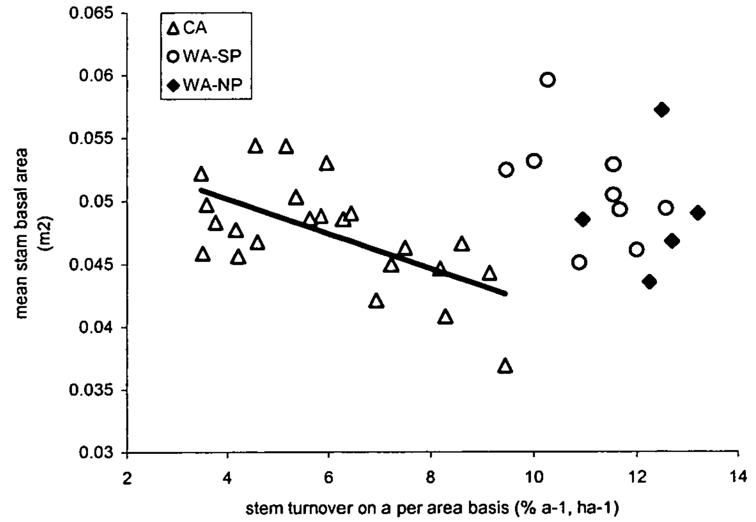


Figure 4.15. Relationship between mean stand basal area and mean turnover rate in 37 1-ha PSPs from the Neotropical region. The regression line shows the trend within the Central Amazonian sites only.

Big trees seem to be more frequent in forest with higher values of BA, although they contribute << 50 % of BA in most of the Amazonian PSPs studied (Table 4.10 and 4.11).

An inverse correlation was expected to relate stand turnover with mean tree size, with highly dynamic forests characterized by shorter life-cycles and smaller trees. Turnover was calculated on a per area basis (annual mean of stem dead and recruited in a hectare). This relationship was tested for all 37 PSPs for which turnover values were available. The expected relationship was not evident (Fig. 4.15), maybe due to the limited sample of PSPs used in this work, especially those from WA, not representing the whole range of stand turnover and mean size values. However, a significant decline of mean BA was found within the CA cluster of PSPs (23): $y = -0.0014x + 0.0557$, $R^2 = 0.391$, $F = 23.45$, $P < 0.001$).

Environmental factors are expected to be responsible for determining forest structure and biomass, in particular precipitation and soil. However, no direct correlation was found between total stand BA and precipitation (expressed as the number of dry months or the mean annual rainfall), but a higher number of large-stemmed trees was found in sites with a dry season of more than 3 months (Fig. 4.16)..

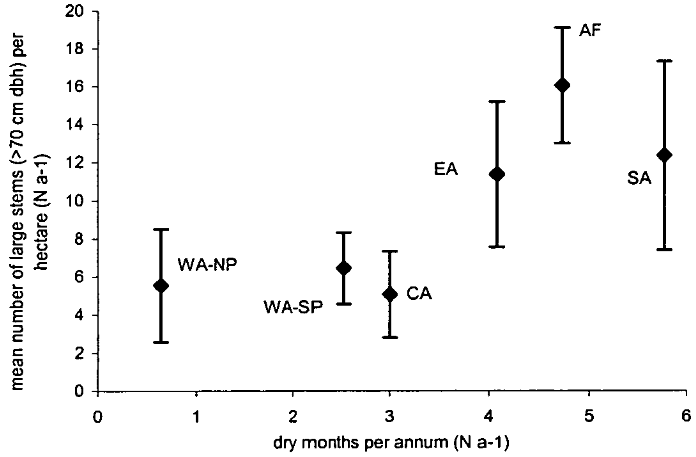


Figure 4.16. Relationship between number of dry months and the number of large-stemmed trees (>70 cm of dbh), in 85 1-ha PSPs from the Neo- and Paleotropics. Bars indicate standard deviation.

The same relationship was tested between the length of the dry season and the mean basal area of large-stemmed trees (>70 cm dbh) (Fig. 4.17), and a similar trend was found.

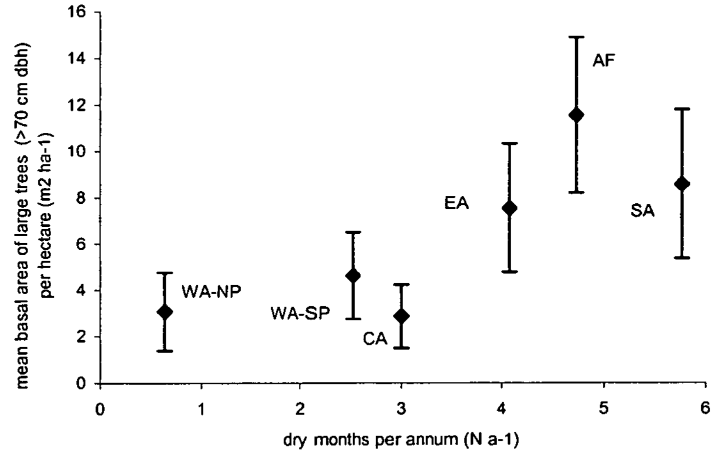


Figure 4.17. Relationship between number of dry months and the BA of large-stemmed trees (>70 cm of dbh), in 85 1-ha PSPs from the Neo- and Paleotropics. Bars indicate standard deviation.

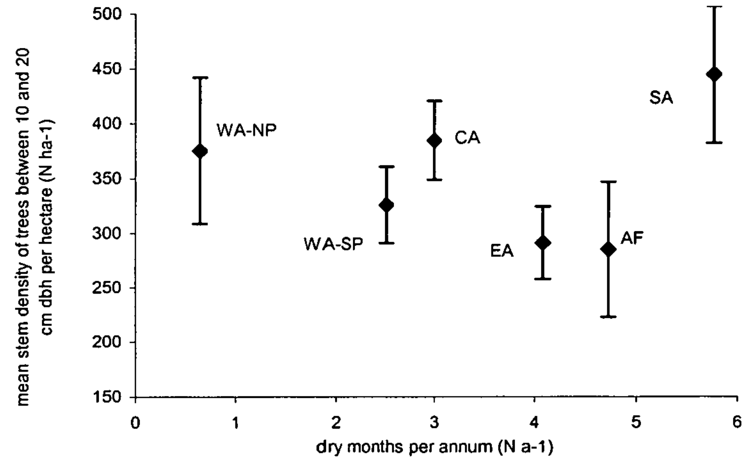


Figure 4.18. Relationship between number of dry months and the stem density small trees (10-20 cm of dbh), in 85 1-ha PSPs from the Neo- and Paleotropics. Bars indicate standard deviation.

On the other hand, the number of trees between 10-20 cm of dbh was not correlated with rainfall or length of the dry season, as shown in Fig. 4.18, indicating that the lower mean size in wetter forest PSPs is simply due to a smaller fraction of big trees. Thus, it seems that big trees tend to be more frequent in sites with less precipitation. However, mean size is poorly correlated with the length of the dry season.

In Fig. 4.17, PSPs in CA and SA, show values lower than expected for both density and BA of large trees. The sample is limited in size and poorly performing in representing a potential variation of mean stand BA. It seems that extending the analysis to a larger sample of PSPs, mean BA values show a general negative relationship, although quite noisy, with the length of the dry season up to a threshold of about 6 dry months; then mean total BA values drop (Malhi's *pers. comm.* from observation on a larger sample of Trans-Amazonian PSPs). This is particularly evident in SA plots.

## 4.4. Discussion

### 4.4.1. Floristic patterns across the Amazon basin

The questions addressed with regard to the major floristic patterns are:

a) What are the main floristic patterns?
b) What are the main causal factors (environment, biogeography)?
c) Why are certain families more abundant in certain regions?
d) What factors cause higher abundance of pioneer species in certain regions?

Together with a striking floristic similarity, large-scale patterns in the abundance of the most important tree families in lowland Amazonian forests are clearly recognizable, as shown in other studies (ter Steege et al. 2000). While Lecythidaceae, Sapotaceae, Chrysobalanaceae and Burseraceae dominate in Eastern and Central Amazon (in the present study, the localities of Manaus, Caxiuana and Tapajos), Palms, Moraceae and Myristicaceae dominate the lowland forests of Western Amazonia (the localities from Loreto and Madre de Dios departments in Peru) and, to a certain extent, the South Amazonian plots studied (Los Fierros and Huanchaca in Bolivia). Leguminosae are slightly more abundant in the Central and Eastern Amazonian PSPs, but have a major role, with respect to stem density and to share of total BA, all across the Amazonian lowland rainforests studied.

The present study confirms what emerged from previous floristic analyses on trans-Amazonian floristic patterns (ter Steege et al. 2000; Terborgh and Andresen 1998). A main W-E floristic gradient underlies the distribution of PSPs along the first axis of the DCA plane, in agreement with observations in other studies (ter Steege et al. 2000; Terborgh and Andresen 1998). The gradient in family dominance described in Fig. 4.2 could have several explanations: geographic position, forest physiognomy, degree of disturbance, and evolutionary history of the South American flora.

Geographic distance partially explains the dispersion of the plots, as the western sites are clearly separated from the eastern ones (Fig. 4.1). The tight clustering of the three groups of PSPs from CA and EA could be due to high similarity in forest physiognomy (exclusively *terra firme* forest), and the absence of regular perturbations due to river dynamics. Conversely, WA plots may be more dispersed on the DCA biplot plane due to a higher landscape diversity between plots (Fig. 4.1). The WA cluster includes a wider range of physiognomic types: a seasonally flooded forest, a stand located on recent floodplains, and a swamp forest represented by an isolated point in the graph, because it is dominated by a single family, as is typical of recently inundated forests (Richards 1996c) (in this case, the family Tiliaceae dominates the stand). Within the WA group, a geographic separation divides the cluster between north and south Peruvian PSPs, with two exceptions: *terra firme* forests from the south of Peru are more similar to *terra firme* stands from the north of Peru than to more recently disturbed forests from the same area. This does not support the findings of Terborgh and Andresen (1998) who compared *terra firme* and inundated forests and surprisingly found that tree communities of inundated forests tend to resemble more closely *terra firme* forests within the same geographical region than inundated forests from adjacent regions. In the present work, the sampling density for the two types of forests (flooded and unflooded) is too low and unbalanced to allow further exploration of the results from Terborgh and Andresens's work (1998).

The high degree of floristic uniformity within the CA and EA plots is evident also at genus-level. A few genera tend to be dominant (*Eschweilera* in CA and *Pouteria* in EA PSPs). WA plots are more diverse at genus level (Table 4.4). The Bolivian plots (SA) form a very dispersed cluster on their own, sharing part of the most common families. The lack of tight clustering could be due to the different physiognomy of the forests investigated (tall evergreen forest and gallery forest), and to the different history of the evolution of vegetation in this southern fringe of the Amazon basin. The moderate level of tree species diversity recorded for lowland humid forest communities in Bolivia and the abundance of species that are widely distributed across the Amazon Basin (some Moraceae and Palms, such as *Pseudolmedia laevigata* and *Iriartea deltoidea*) can lead to various interpretations. Such characteristics would support the assumption that these forests have only recently, in a biogeographical time frame, become established and would also conform to the hypothesis that Amazonian forest vegetation has expanded southward quite recently, during the Holocene (Prado and Gibbs 1993). The Bolivian PSPs examined are within a region whose forests are less than 1000 years old (Mayle et al. 2000). Likewise, there is widespread evidence that much of lowland Bolivia has been subject to recurrent catastrophic disturbance caused by the fluvial dynamics of both major and secondary river systems (Hanagarth 1993), although this is not the case of Los Fierros PSPs. The most likely perturbing factor at the dry southern margins of the Amazon Basin, represented here by Los Fierros and Huanchaca PSPs from the Bolivian Amazon, seems to be occasional fires.

Other authors have identified different gradients in stand floristic composition across the Amazon basin, sometimes providing contrasting evidence on the direction of the steepest gradient. Regional differences in family composition of forests within the Amazon basin were recognized by Gentry (1990), but more detailed insights come from more recent studies. Pitman et al. (2001) noted a more rapid change in tree species composition along an E-W than along a N-S axis in western Amazonia. This pattern has been explained by a supposed higher gross similarity of edaphic and climatic conditions found moving from north to south along the Andean piedmont, than moving eastwards (Pitman et al. 1999; Terborgh and Andresen 1998). Pitman found also a species overlap between adjacent different habitats with as few as 15% of species completely restricted to one habitat or another.

The gradients in family composition described in this work could be of both ecological and historical origin. Families that dominate a region are not absent in other regions but are simply less diverse and less abundant. This seems to suggest that historical factors are not so crucial in explaining current floristic patterns, as they should tend to determine the presence or absence of taxa and not variation in their relative abundance.

Disturbance regime could be responsible for the gradient. Families with pioneer-like characteristics (small seeds, light wood, short regeneration times), such as Moraceae, dominate in more disturbed regions, especially in Western Amazonia, over slower growing and large-seeded families such as Chrysobalanaceae and Lecythidaceae. Analysing a dataset partially overlapping with the one used for the present study, a marked wood density gradient was found, moving from Eastern to Western Amazonia, with a dominance of low-wood density families in the Western part and a greater representation of high-density families in the Eastern part of the Amazon basin (Baker et al, in review). A similar pattern was found by ter Steege and Hammond (2001a) at a regional level, in the lowland tropical rainforests of Guyana.

With respect to the occurrence of some functional groups, pioneer species are found to occur more frequently in the WA and SA regions (Peru and Bolivia). In WA, their presence is likely associated to a certain degree of disturbance, due to high rainfall. The perturbation associated with high rainfall is generated by different mechanisms that seem to have an influence on forest composition and structure. High precipitation may stimulate higher production, may cause unstable rooting and frequent windstorms, and all these three circumstances would lead to a faster stand dynamics, with more rapid growth and death of trees, and therefore maintaining conditions favourable to the regeneration of fast-growing species.

In SA, the abundance of pioneer species could be due to a different factor, such as the transitional location of rain forest / dry forest / savanna of the PSPs analysed in the present study.

Palms tend to be highly represented in sites where pioneer species are also particularly frequent. The presence of pioneer species and palms was examined in relation to forest stand dynamics (see Chapter 5). Within the 5 sites investigated in this work, their co-occurrence seems to be highest within the very dynamic Peruvian plots (Table 4.7), also characterized by high diversity, as found by Phillips et al. (1994a) and shown in Chapter 5.

### 4.4.2. Patterns in species richness (alpha-diversity)

The main questions addressed are:

a) What does explain variation in diversity?
b) Can we separate climate from paleohistorical factors in explaining actual patterns of floristic diversity? How would they have operated to give the present patterns?
c) Could sampling density explain the observed patterns?

Most of the studies on floristic richness within the Amazon basin have focused on Western Amazonia. Only one attempt precedes the one shown in this work, in comparing the floristic richness of PSPs from Western and Eastern Amazonia (ter Steege et al. 2000).

The observed patterns of diversity found across the Amazon Basin indicate that the total number of tree families $ha^{-1}$ varies considerably across regions. The varying degree of accuracy in species identification, found within the database used for the present study, could be partially responsible for the observed patterns of diversity. However, most of the unidentified individuals were at least attributed to a family. Thus, when a full identification of all the individuals is not available, the total number of forest tree families ha$^{-1}$ tends to be a less biased value than the total number of species ha$^{-1}$. To avoid biases due to different sample size, trends were explored for both an equal and unequal pool of stems per plot, since in accordance with previous findings (Condit et al. 1996b; Denslow 1995), in this study the number of families and species ha$^{-1}$ was found to be positively correlated with the number of stems ha$^{-1}$. The patterns were found to be robust in both cases.

The present study supports and confirms the existing findings on the main floristic patterns observable across the Amazon Basin. The Western Amazon has been identified as a region of extreme diversity, but the present work shows how other parts of the Amazon basin can present extreme values of alpha diversity, as is the case of Central Amazonia.

Different mechanisms could be operating with different intensity across the various regions of the Amazon Basin. The main distinction is between present-day environmental causes (climate and soil) and historical factors.

A general good predictor for tree species diversity is found to be the amount of annual rainfall or the number of dry months a$^{-1}$, as indicated by several authors (Clinebell et al. 1995; Duivenvoorden 1996; Gentry 1988). The number of families increases with an increasing amount of annual rainfall and decreases with an increasing number of dry months (Fig. 4.5), in agreement with the already observed increase of woody species with increasing rainfall and decreasing seasonality (Clinebell et al. 1995; Duivenvoorden 1996; Gentry 1988). Moreover, the same trend emerges looking at the total number of species (or "expected" species when the identification of all individuals is not complete). Only the greatly diverse PSPs from Central Amazonia constitute a slight deviation from the general positive correlation between richness of the flora and rainfall. The positive relationship between rainfall and diversity has been explained by some authors through the assumption that rainfall is a proxy for productivity (Clinebell et al. 1995; Gentry 1988), although this is not always necessarily true since the relationship between rainfall and fertility is complex, with aseasonal sites affected by extreme soil nutrient leaching for example. Some authors did not find a relationship between richness and rainfall and dismissed annual mean rainfall values as good predictor of species diversity (Phillips et al. 1994a; ter Steege et al. 2000; ter Steege and Hammond 2001a). Ter Steege et al.

(2000) argue that the sample they used to explore climate-diversity relationships did not cover areas with extreme precipitation, and it seems that 90% of the Amazon is not characterized by extreme environmental conditions. However, the present study encompasses primarily sites located close to extreme environmental conditions, such as the very seasonal Bolivian forests, the aseasonal WA-NP PSPs, and offers an adequate representation of intermediate sites with short dry season but low annual precipitation and, vice versa, sites with limited length of the dry season but lower mean annual rainfall.

Ecological and historical factors are difficult to distinguish, as some of the areas that should host high diversity due to current climatic conditions, were likely to host high diversity even under past conditions. Geologically active zones at the foot of the Andes were very rich in the past but are also rich today due to present-day precipitation and high fertility. It has been shown that the surface alluvium in western Amazonia has been deposited over a long time span, from Neogene time to the present, as quoted by Rasanen et al. (1992) from Hoorn (1988) and Dumont (1989). Four retroarc intraforeland basins were identified in Western Amazonia, all formed during the Cenozoic evolution of the Andes mountains, with the present day basin relief developed in Miocene-Pliocene time as reported by Rasanen et al. (1992). A wide continuum of depositional regimes has characterized the Amazonian foreland, with periods of deposition particularly intense in certain parts of the intraforeland (the modern Pastaza-Marañon floodbasin, the Pastaza fan, Pleistocene deposition in the proximal part of Madre de Dios-Beni basin). The Pastaza-Marañon intraforeland basin located west of Iquitos, seems to have in its central parts, one of the world's largest areas of Holocene aggradation in an inland basin.

The relative importance of each hypothesis is difficult to test. Better characterization of soil and local climate is needed and comparative studies should be carried out to establish whether the regional diversity is actually higher than would be expected on the basis of high habitat differentiation, before invoking historical factors. We need to know which taxa or regions deviate from the patterns expected on the basis of present-day ecological conditions, otherwise we risk asking the wrong questions. The part of diversity unexplained by present ecological conditions can be attributed to the effect of history (changes in climate, geology, dispersal, soil formations, etc.) and other unmeasured factors.

Contemporary factors, such as habitat differentiation, could be a cause for high regional diversity. This seems to be the case of Tambopata (South Peru), as the site shows great variation in hydrology and topography due to river dynamics.

Some elements that have historically contributed to the evolution of forest composition could be currently still operating and influence species richness. For instance, the presence of disturbance is considered a factor that promotes by itself a higher species richness (Molino and Sabatier 2001), increasing the number of species that require perturbation for their regeneration. Some findings from tropical forest stands in French Guiana support this hypothesis as lower diversity was found to be associated with lower abundance of pioneers (ter Steege et al. 2000). This could be the case of the Western Amazonian PSPs explored in this work. A higher level of disturbance could have promoted a great representation of fast growing species, characterized by short regeneration times, and induced high species richness of such pioneer-like taxa.

In contrast to Western Amazonia, in Central Amazonia, some biogeographical factors may have played a major role. For example, the unexpectedly high richness of Central Amazonian PSPs could be linked to the so called "mid-domain effect" that is thought to operate at the centre of a biogeographical region. This clearly suggests that even in the absence of major environmental gradients, a peak in diversity should be observable at the centre of a biogeographical region versus extreme regions (Colwell and Lees 2000). This effect has been defined as " the increasing overlap of species ranges towards the center of a shared geographic domain due to geometric boundary constraints in relation to the distribution of species' range sizes and midpoints". Colwell & Lees (2000) affirm that only once the effects of geometry are removed, can environmental and historical influences on species richness gradients be looked at afresh. In testing this effect in specific cases, a crucial requisite is that species must collectively share the same boundaries.

Other effects have been detected and analyzed. Historical factors could be exerting their influence also through an "area effect". The size of the area covered by continuous forests, not separated by other formations or fragmented by a dendritic grid of rivers and small streams or large river mouths, affects speciation and extinction rates. The hypothesis also predicts that, within the tropics, regions with greater area covered by continuous forest should have greater species richness. According to this biogeographical principle, more habitat differentiation and more genetic variation are found in large areas, contributing to increasing speciation rates.

Rosenzweig proposed that increasing land area decreases extinction rates in two ways: (i) large areas of similar habitat lead to large species distributions and large total population sizes, reducing the impact of random population fluctuations, (ii) large areas increase the number of refugia in which populations can survive local environmental disturbances (Rosenzweig 1995). He also proposed that larger species ranges increase allopatric speciation, because large ranges are more likely than small ranges to be interrupted by geographic/climatic barriers.

Central Amazon could be manifesting this effect. However, it is not clear if Manaus is located at the intersection of two biogeographical regions, as some authors have speculated. With regard to this point, the results from this study seem to be in agreement with the hypothesis of a superposition of different geographic distribution patterns in the Manaus region, an area of confluence of distinct phytogeographic provinces (de Oliveira and Daly 1999). Previous studies have found many Neotropical plant species to reach their range limits in the Manaus region, e.g. from Guyana (Mori 1991) and from western and eastern Amazon forest (Prance 1994). Regional studies on the distribution of tree species in the Manaus region reveal that the flora from this area contains elements from both western and eastern Amazonia (de Oliveira and Daly 1999).

The peculiar floristic richness of the area around Manaus is feeding the debate on the mechanisms that have led to the present patterns of Amazonian diversity. Indeed, the observed patterns do not permit inference of whether current distributions are the results of previously broader distribution that have retracted or expansions of distributions that were formerly more limited. Wider sampling efforts are also necessary to dismiss any bias due to the concentration of floristic surveys in certain regions on the outcomes of diversity studies (Nelson et al. 1990). The density of the studies in the Amazon should be increased. It has been noted by some authors (Ashton 1969; Tuomisto and Ruokolainen 1997) that ecological homogeneity is easily accepted for the tropics even at such scales that would be considered heterogeneous if the study was made in the temperate zone.

### 4.4.3. Local patterns in floristic diversity

The issues explored are:

a) Do soils explain much of the local variation in forest floristic composition?

b) Are there other factors that may be responsible for the observed floristic variation?

Within single localities, where climate conditions are similar, soil variation is expected to play a significant role in determining the observed floristic diversity. In this analysis, in agreement with most floristic studies at local- and meso-scale, soil plays a major role in controlling relative abundance of species.

In the BDFFP plots, near Manaus, the percentage content of sand in soil (or the percentage of clays, due to the inverse correlation between the two variables) is capable of explaining much of the variability in species composition between forest reserves located not more than 30 km apart, and which appear extremely similar floristically if analysed at family level (Fig. 4.1).

Previous studies on the BDFFP plots revealed a main gradient in the study area, discriminating sites with varying proportions of clay (with clayey soils having higher concentrations of total N, organic C, most cations, and lower aluminium). Clays have more binding sites for cations, largely because clay content is positively correlated with organic matter, which is an important determinant of cation exchange capacity in soils with clays of low activity, like in the Amazonian ferralsols (Sombroek 2000).

Another two gradients in soil parameters were found within BDFFP plots, but resulted to be less significant. They mainly described the continuum in soil pH (with more acidic sites having less total P and higher $Al^{3+}$ and $Ca^{2+}$), and the variation from soil with high available water capacity to those with more phosphate.

Soil variation was found to be the only significant predictor for the variation in above-ground biomass, across the *terra firme* forests of the BDFFP plots, located on nutrient-poor ferralsols. It accounted for a third of the two-fold variation in the biomass observed, with total nitrogen as the most important single variable responsible for the variability (Laurance et al. 1999).

Together with a direct effect of fertility on productivity, a second influence on species composition has been hypothesized as a mechanism by which biomass varies across plots. A positive association between fertile soils and the frequency of large emergent species that contain a high fraction of forest biomass has been suggested (Clark and Clark 1996). Nevertheless, in the present study, a correlation between the frequency of very big trees and the texture of the soil was not found in the data from the BDFFP plots (result not shown). For these plots, a strong secondary gradient, not explained by soil texture, emerged from the DCA biplot in Fig. 4.9, and could be due to the variation in pH as found by Laurance et al. (1999).

Although fine-scale environmental heterogeneity is an important component of local diversity, there is also a purely spatial component to floristic diversity. It is a basic biogeographic observation that distance between communities and species turnover are positively correlated (Cox and Moore 2000). Thus, even in the absence of other factors, the species composition of eastern and western Amazonian forests is expected to differ considerably through long-term limits on species dispersal ability. Similar dispersal limitation processes could drive spatial floristic differentiation at much smaller, within-site scales.

Thus, the natural distribution of a species is limited by more than physiology and is restricted by the actual opportunities for dispersal and establishment, by herbivore and pathogen pressure, climatic irregularities and by competition with other species.

Water and nutrient availability are the most ubiquitously variable factors in lowland tropical rainforests and thus likely to limit the distribution of many species. Since rainfall and soil fertility tend to covary (due to leaching under high rainfall) it is difficult to segregate their effects on individual species. A significant challenge confronting ecologists is the integration of mechanisms acting at multiple scales.

Examples of experimental evidence of control of rainfall and soil on species distribution are given by various authors, at regional (Veenendaal and Swaine 1996) and landscape level (ter Steege et al. 1993).

In upper Amazonia, Gentry (1988) (see also Tuomisto 1995) suggested that forests are a fine-grained mosaic of many different forest types, each characterized by local assemblages of edaphic specialists. However, spatial studies on canopy trees in Colombian forests (Duivenvoorden 1994) and Peruvian Amazonia (Pitman et al. 1999) show that beta-diversity for tree species is low, especially in the well-drained upland forests, which are the most widespread forest type in this region. Condit et al. (2000, 2002) found higher beta-diversity in Panama than in Western Amazonia, due to high habitat variation that increases species turnover relative to Amazonia, where population densities seem to be bounded by as yet unidentified processes. Dispersal limitation and stochastic events, although coupled with strong regional gradients in precipitation, often overridden by the effect of surficial geology and local soil attributes, are shown to be highly correlated with forest species composition in Panama (Pyke et al. 2001). A strong influence of dispersal limitation is suggested at intermediate scales for both regions. A confounding factor is given by the often found covariance between environmental variables and distance. Distance seems to play a more important role over short distance (< 5 km) while only precipitation and geology were found to be useful for predicting species-level floristic variation at broader scales.

More data would be necessary to separate edaphic, from climate and from spatial factors utilizing various forms of analytic approach, constructing distance matrices, using Non-Metric Multidimensional Distance Scaling Ordination (NMDS, Kruskal 1964), and treatment of data that would reveal the confounding effect of spatial autocorrelation (Harms et al. 2001), as attempted by Phillips (in review a), at a landscape scale.

### 4.4.4. Patterns in forest structure

The issues addressed are:

a) What are the causes of the variation in stand structure found within a large sample of PSPs from lowland tropical rainforest sites?
b) What environmental factors are responsible for the observed variation in structure?

General trends can be observed when the structure of the several PSPs from different localities is compared. The variation in stem number and basal area was found to be greater within the SA PSPs, presumably because the sample from the two southern Amazonian locations explored spans a wide gradient of environmental conditions.

Plots from AF, EA, and SA have high frequencies of large-stemmed trees, while CA and WA-NP plots fall on the other extreme. Plots from WA-SP on average have an intermediate frequency of trees ≥ 70 cm in dbh.

It seems that drier sites have bigger and fewer trees but CA forests are an exception to the rule, having intermediate-high density of stems $ha^{-1}$. Similarly, SA plots do not fit in the trend, as they show both high stem density $ha^{-1}$, and high abundance of relatively big trees. Some authors show differences in diameter and density between flooded and unflooded sites. The inundated sites are generally characterized by fewer and small trees (Balslev et al. 2001), and normally the number is also lower in nutrient-rich soils but mean diameter is greater.

In the present study, both the differences at a continental and regional level are significant, although the role played by the environmental variables is not immediately interpretable because the resolution of soil and climate data used is not fine enough to relate them to variation in forest structure within regions.

Excluding one site from the analysis, the negative correlation found between the lower density of small-stemmed trees and the length of the dry season could find an explanation in the impact exerted by periods of drought on small trees. This effect would be greater on understory tropical plants than in canopy individuals because of competition. The variable and potentially severe dry season in Neotropical moist forest has been found to be sufficiently intense to severely limit soil moisture availability for understory plants (Tobin et al. 1999). Findings on differentiated mortality on the basis of tree size during drought are not consistent and the evidence that small trees suffer high mortality in a drought is not fully supported by the results shown here.

Different rooting depth and variable topographic local conditions control plant responses to soil moisture depletion. Stable-isotope studies have revealed that trees of different size classes belonging to the same species can preferentially tap different sources of soil water (Dawson 1996a) and that source water utilization can change seasonally in species with dimorphic root morphology (Dawson 1996b), that is, with a root system developed both vertically and horizontally.

Studies on the partitioning of soil water among canopy trees in a seasonally dry tropical forest have shown that contrary to expectations, smaller trees were preferentially tapping deeper sources of soil water than larger trees (Meinzer et al. 1999). Larger trees seem to rely primarily on water taken from the upper portions of the soil profile and potential risks of developing severe water deficits seems to be mitigated by various factors. First, the extensive horizontal area explored by large root systems of big trees and second, the stem diurnal water storage which is greater in large-stemmed trees. The preferential exploration of the upper part of the soil in larger trees may be explained by the higher nutrient demand associated with maintenance of a large crown leaf area which imposes a selective pressure to maximise root density in the superficial more nutrient rich portion of the soil. Other work suggests that differences in rooting depth may be related to niche differentiation, such that shallow rooting trees can make use of light precipitation events (Stratton et al. 1996).

Another recent study indicates that smaller trees can exploit soil resources far from their main stem, with the bulk of water uptake occurring in the top half metre of the soil profile (Sternberg et al. 2002).

Looking at mortality patterns in drier versus wetter areas, the loss was found to be much higher in small-stemmed trees than in other size classes in both environmental conditions, with a greater loss in very wet areas, compensated by higher recruitment rates (see Chapter 5, section 5.4.3). However, some studies showed that the ratio of mortality in the drought of 97/98 compared to the pre-drought period was highest in trees > 40 cm in dbh (Nakagawa et al. 2000).

Reports in the literature are quite contradictory. However, the different responses across different size classes and life-forms (e.g., trees versus shrubs), different sites, with different tree species communities and different soil conditions can be explained assuming that various mechanisms are operating. Recurrent droughts could have triggered adaptation processes that have conditioned the suite of species occurring at present, making them more robust in response to dry events. The converse may be true where periodic strong drought has not been experienced.

Soil properties also confound any generality in results. Where soils are deep, deep rooting may be expected as a successful drought tolerance mechanism, but when deep exploration is impeded by hardened layers, larger water-demanding trees could become more vulnerable to drought than shrubs.

Fertility could be also responsible for the observed differentiation in structure. Soils tend to be often more fertile in the seasonally dry tropics (Terborgh 1992), where, during the dry season the soil begins to dry out, aided by the transpiration of plants. Roots withdraw more and more of the water stored in the soil column and the partially compensatory upward flow carries with it freshly dissolved minerals from the weathering rock below. Leaching is also less in drier locations. This could favour greater dimensions for highly competitive individuals.

Fire may also be an important factor in shaping forest structure, killing small trees in dry areas, although this hypothesis is not supported by results displayed here. SA plots are located in a region recurrently disturbed by fire and show the highest density of small-stemmed trees.

Despite the amplitude and richness of the sample explored in the present study, spanning very different climatic regions of the Amazon Basin, further tests ought to be carried out, based on a wider set of PSPs distributed across the major environmental gradients. The measurement protocol should include the sampling of other variables that are fundamental for describing forest functioning (e.g., soil, precipitation). An improved identification and a further enlargement of the sample would help in better understanding how diversity is distributed and what factors are driving the existing regional differences. Continent-wide datasets derived from long-term studies on forest growth and dynamics only now are becoming available. Networking initiatives are already in place and are aimed at gathering and collating the existing information available from the wide set of PSPs established in South America and in other parts of the tropics (Malhi et al. 2002).

## 4.5 Conclusions

1. Large-scale patterns in the abundance of the most important tree families in lowland Amazonian forests are identifiable and consistent with previous studies. Lecythidaceae, Sapotaceae, Chrysobalanaceae and Burseraceae tend to dominate in the Eastern and Central Amazonian PSPs studied, while Palms, Moraceae and Myristicaceae dominate the lowland forests of Western Amazonia and, to a certain extent, the South Amazonian plots studied.
2. Palms and pioneers co-occur in Western Amazonian PSPs. Their high frequency in this region is probably associated with a higher turnover.
3. At a local scale, soil plays a major role in regulating floristic diversity, as shown for a subset of PSPs from Central Amazonia (BDFFP sample plots), where the content of sand in the soil explains great part of the floristic differentiation of plots located within a few kilometres from each other.
4. A strong relationship was found between climate and family richness. A correlation was also found between the length of the dry season and species richness, with the number of dry months identified as the best predictor for alpha-diversity. Aseasonal sites tend to show a higher number of families and species ha$^{-1}$.
5. The structural analysis does not reveal clear relationships between stem density and total basal area ha$^{-1}$.
6. The frequency of large-stemmed trees (> 70 cm of dbh) was found to be higher in forest stands located in drier sites, within the sample of plots examined.
7. Mean tree size does not show a correlation with stand turnover. More dynamic forests (Western Amazonian PSPs) were expected to have a higher density of small-stemmed trees, but some plots from the Central Amazon (Manaus, Brazil) show a high fraction of small stems despite their low turnover rates.

# Chapter 5. Basal area positive change: where and why

---

## 5.1 Introduction

Understanding dynamics and basal area (BA) changes is fundamental to interpret the response of tropical forests to the pressure of global changes in atmospheric composition and climate. Tropical forest ecosystems undergoing major changes are likely to show some degree of variation in BA and dynamics (mortality, recruitment, turnover). BA of trees is a well-substantiated surrogate measure of total biomass in tropical forests (Brown, Gillepsie, and Lugo 1989; Gillepsie, Brown, and Lugo 1992) and has been used as an effective measure for changes in biomass in tropical forests. The analysis of forest dynamics provides insight into the mechanisms leading to the observed variation of BA over time.

Evidence already published suggests that there are ongoing changes in these parameters (Phillips et al. 1998a; Phillips et al. 2002b; Phillips and Gentry 1994). However, previous findings gave a general Neotropical picture of BA accumulation (Phillips et al. 1998a), without exploring the geographical extent of the concerted changes recorded, whether they were general throughout the Amazon or restricted to one region or environmental zone. In addition, it was not explored whether BA accumulation was due to increased gains (recruitment, growth), or decreased losses (mortality), or due to an increase in both, with positive changes outweighing negative changes. With regard to forest dynamics, Phillips and Gentry (1994) showed how estimated turnover rates increased in the last few decades, but did not explore whether these were attributable to an increase of recruitment, mortality or both.

The present analysis goes beyond what has already been shown, separately analysing the different processes that lead to the observable BA changes (tree mortality, recruitment and growth), and highlighting regional differences. Changes are explored across a large number of permanent sample plots (PSPs), clearly demarcated forest stands whose evolution could be monitored through time. A joint analysis of BA and stem density changes was carried out to give insight into explanations for such changes ($CO_2$ fertilization effect versus recovery from disturbance hypothesis), and to test the effect of potential artefacts as responsible factors for the observed turnover increase (e.g., “majestic forest” effect) (Phillips et al. 2002a).

Some groups of species, such as pioneer species and palms with markedly distinct ecological traits and particularly dependent on gap formation for their regeneration and establishment (Swaine and Whitmore 1988; Svenning 1999a), and therefore more likely to occur in disturbed tracts of forests, were separately investigated to test whether their behaviour departed significantly from that of the much larger group of shade-tolerant, slow-growing species. Fast–growing species in particular are expected to become progressively more dominant within forests characterized by accelerated turnover. This hypothesis is supported by evidence of an increase in density and relative dominance of large lianas over time in some PSPs from the Neotropics (Phillips et al. 2002b).

Here, the relationship between the density of fast-growing species and stand mean turnover rates across a large set of PSPs was investigated.

Data may not be sufficient to provide a complete picture of edaphic and climatic gradients and observations are limited to a few plots, which may not reflect a region as a whole. Yet the dataset provides a first assessment of BA and turnover changes across space and time, highlighting some major differences between two distinct Amazonian regions, the Western and the Central/Eastern part of the basin.

### 5.1.1 Permanent sample plots

Permanent sample plots have a central role in many investigations whose objective is to disentangle the ecological complexity of tropical forests (Condit et al. 1996b; Condit et al. 1999; Hubbell, Condit, and Foster 1990). The expense of establishing and maintaining PSPs leads to a limited number of replications and often to small plot sizes, but both the number and size of plots is likely to increase (Condit 1995). A catalytic factor has been the renewed interest in the role of tropical forests in the global carbon cycle. The practical aspects of the establishment of PSPs have been widely treated (Alder and Synnott 1992; Dallmeier 1992; Manokaran et al 1990; Manokaran et al. 2001; Vanclay 1991b), but the adequate representation of the dynamic behaviour of these ecosystems remains a challenging issue. The intrinsic limitations of PSP studies have been increasingly considered and evaluated (Clark 2002; Hall et al. 1998; Sheil 1995b; Phillips et al. 2002a), and the use of more robust and appropriate statistical techniques has been suggested (Sheil 1995b).

However, networks of long-term research sites representing a variety of major forest types have been recommended by scientists from a range of disciplines, from taxonomists who seek to rapidly identify the vast number of unknown species in tropical forests, to climatologists who need basic figures on gas exchange and carbon storage in tropical ecosystems. Examples of these networks are already in place

(Condit 1995; Malhi et al. 2002) and can undoubtedly contribute to partially answering several questions on tropical forests growth, regeneration, diversity and sensitivity to global changes, although some issues require much larger-scale research efforts to be addressed properly (e.g., demography of rare species, community variation at large scales).

In this work, a large set of PSPs data is used to highlight temporal and spatial patterns of change in forest dynamics, after having carefully considered the methodological issues related to measurement protocols adopted in tropical forest sample plots (see next paragraph and the detailed analysis of Chapter 6).

### 5.1.2. Comparison of dynamics across time and space

The development of the modern concept of rain forests as dynamic systems of ever-changing mature, gap and building phases owes much to Aubreville's hypothesis of a "mosaic" theory of regeneration (Aubreville 1938). Dynamics are extremely variable across different types of tropical rainforests, and, at a smaller scale, within the same forest type as a function of local perturbation and local habitat characteristics. Temporal changes are also recorded and a key question is whether they constitute fluctuations around average conditions or long-term trends. The assessment of changes in forest dynamics requires careful treatment of raw data from PSPs. Various sources of methodological biases and errors have been identified and shown to affect the analysis of PSPs (Clark 2002; Sheil 1995b; Sheil and May 1996). Most of the potential biases and errors have been discussed in Chapter 6.

Mortality estimates have been found to be highly variable over short temporal intervals (Brokaw 1983). Careful analyses of change in mortality rates should be ideally based on data from plots re-censused on an annual basis, but this is rarely the case.

Furthermore, the most common model adopted to estimate mortality rates is not independent of the time interval between two consecutive censuses (Sheil et al. 1995; Sheil and May 1996). The model assumes a simple population in which each member has an equal and constant probability of dying over a unit of time. The probability of loss of individual members is not constant in heterogeneous populations, such as mixed species stands. However, even monospecific stands with mixed size or age, and with phenotypically differentiated populations, or with populations in heterogeneous environments, are likely not to show equal probability of death of individuals. Tropical forests are extremely heterogeneous and the consequence on mortality estimates is a decline in measured rates with increasing census interval. The artefact is more severe when a fraction of the population has a much higher mortality rate than the average. The tendency to a decline in measured mortality with increasing census interval has been tested and quantified for a large set of PSPs from tropical forests (Lewis et al., in prep.), including also the present database. A correction factor has been introduced to account for a variable length of the census interval and the effect has been shown not to alter the overall pattern of increasing turnover. The length of the time interval has been shown to affect also the quantification of biomass production over time (Malhi et al., in review a), with production declining with an increasing length of the period between two censuses (see Chapter 6 for a more detailed identification and discussion of all biases and errors affecting PSPs measurements and plot data analysis).

Ideally, the same period of time should be covered by inventories carried out in different sites, that is the dates of first and last inventory should roughly coincide across plots to enable comparisons over a period affected by the same climatic regimes and perturbations. Only a few long-term plot studies in the tropics are characterized by quite regular re-censuses. In particular, when the size of the plot is very large, it could take several years before completing the task, therefore census intervals tend to vary extremely between populations of trees within the same plot (Kubo et al. 2000).

Another element of heterogeneity is introduced when measurement intervals do not cover an integral number of years, so that the seasonal variation of rates could obscure long-term trends. It would be recommendable to carry out forest censuses during the early dry season, before trees shrink, but this is not always possible. With respect to susceptibility to stem flexing, a temporary stem character that is controlled by turgidity and moisture stress in the individual (Hubbell and Foster 1994; Wright 1991), shallow rooted understory trees seem to be more affected.

The methodological difficulties encountered in estimating BA change are discussed separately in Chapter 6. In the same chapter, the repercussions of methodological biases on final results are assessed and some tests for detecting and removing them are discussed. The suggested tests are presented, discussed and applied to a dataset larger than the one used in a recently publish paper, annexed to this work (Phillips et al. 2002a).

### 5.1.3. Hypotheses to be tested

In the present chapter the following hypotheses are tested:

Hyp.1: BA and stand dynamics in tropical forests ecosystems are revealing signals of a potential response to changes of an anthropogenic nature (Phillips et al. 1998a; Phillips and Gentry 1994). The observed BA accumulation and turnover increase over time may be due to various mechanisms, such as changes in BA and stem gain and losses, or both phenomena. Here, the main drivers leading to the recorded changes are identified; it is tested whether BA accumulation is due to increased BA gains (i.e., recruitment, growth) or BA losses (i.e., mortality), or both, and whether turnover increase is due to increased stem recruitment or increased stem mortality or both.

Hyp.2: observed changes in forest basal area, dynamics and structure may be consistent with a $CO_2$ fertilization effect (Phillips et al. 1998a), or with a natural disturbance-recovery dynamics of tropical forests, as most tropical forest locations have probably experienced severe anthropogenic or natural disturbance at least once within the Holocene (Clark 1996; Meggers 1994; Sanford et al. 1985). Here it is tested which of the two explanations is better supported by the observed patterns.

Hyp.3: patterns of change in BA and turnover have not been spatially explored within the Amazon Basin. Here, it is tested whether patterns of change are consistent with respect to the different climatic, edaphic, and geographic regions within Amazonia. Changes are expected to be greater in areas where rainfall and soil fertility are less limiting factors.

Hyp.4: some groups of species, such as pioneer species and palms, are expected to undergo more marked changes, being advantaged by an increased forest turnover (Phillips 1997; Phillips et al. 2002b). Here it is tested whether there have been significant shifts in the relative proportion of pioneers or palms.

The above listed hypotheses were tested answering the following specific questions:

- Is there a change in BA over time?
- Are forest dynamics (recruitment, mortality, turnover) changing?
- Are BA changes caused by changes in growth, recruitment or mortality?

- How are BA changes distributed across size classes?
- Are trees getting bigger or more numerous?
- Are there spatial patterns across regions in BA and dynamics change?
- Are BA and dynamics changes attributable to particular functional groups?

## 5.2 Study sites

The list of sites selected for the analysis presented in this chapter is shown in Chapter 3. Specifically, Table 3.1 lists the sources of different datasets used for the analysis; Table 3.3 lists the sites selected for the analysis of dynamics and the census intervals used for comparison of dynamic processes; in paragraph 3.4, a more detailed description of the most important sites is provided. As previously mentioned, most of the data for the present work derive from the activities of several research teams. Only a few plots were re-censused and mapped by the author of this thesis, specifically: 3 plots of the BIONTE project (Manaus, Brazil), and 4 plots in Tambopata (Madre de Dios District, Peru). The dataset compiled and chosen for the analysis of dynamics has the following characteristics:

a. PSPs have a size of 1 hectare;
b. PSPs have at least three censuses;
c. the minimum recorded stem size is the same ( $\geq$ 10 cm of dbh) from the first census onward (for the BIONTE plots, the first census had to be discarded because the minimum diameter recorded was 25 cm);
d. each census includes all the individuals that reached the minimum size, with no selection for particular species (e.g. timber species);
e. all plots are surrounded by tracts of forests that undergo equivalent protection to remove edge effects (e.g. from the BDFFP project database, only plots located at least 300-400 m from forest edges were selected for the analysis, fragments that were too small or isolated were discarded;
f. different researchers were responsible for the maintenance of each site through time, but the methodology should not have changed significantly. Improvements can be found in the database, when checking for the quality of diameter measurements. For some plots it is know that, from the time the present analysis was carried out, further improvements in data quality were independently introduced by the owners of the datasets, through cross-checking of internal consistencies and improvement in species identification;

g. all plots are located in areas of lowland rainforest, mostly *terra firme* but not exclusively (see Table 3.2 for plots description).

The selected pool of PSPs that matched the required characteristics was spatially clustered in three main regional blocks, with distinct climate and edaphic conditions. The regions identified are: Central Amazon, (23), and Western Amazon (14), with two sub-clusters of plots, one in south Peru (9), with Tambopata (5) and Cuzco Amazonico (4), and a second cluster in north Peru (5), with Allpahuayo (2), Sucusari (2), Yanamono (1).

## 5.3 Methodology

Dynamic properties of different plots were compared and analysed over time. First, stem dynamics was analysed, then BA change, finally stem and BA changes were explored jointly. BA accumulation and turnover were disaggregated into single factors (recruitment, growth and mortality), and these were analysed separately. The list below reports the variables calculated and compared:

| **STEMS** | **Equation** |
|---|---|
| Stem density (N $ha^{-1}$) | |
| Stem density annual change (N $ha^{-1}$, $a^{-1}$) | (1a) |
| Stem density annual relative change (N% $ha^{-1}$, $a^{-1}$) | (2a) |
| Stem mortality (% $a^{-1}$) | (3a) |
| Stem recruitment (% $a^{-1}$) | (4a) |
| Stem turnover (% $a^{-1}$) | (5a) |
| Diameter increments (cm $a^{-1}$) | (6) |
| | |
| **BASAL AREA** | |
| BA ($m^2$ $ha^{-1}$) | |
| BA annual net change ($m^2$ $ha^{-1}$, $a^{-1}$) | (1b) |
| BA annual relative change (%$m^2$ $ha^{-1}$, $a^{-1}$) | (2b) |
| BA mortality (% $a^{-1}$) | (3b) |
| BA recruitment (% $a^{-1}$) | (4b) |
| BA turnover (% $a^{-1}$) | (5b) |

Census intervals vary between plots. Two main periods were identified to allow a better analysis of temporal trends in changes. The two intervals cover years before and after 1990-91, with first and last census dates slightly variable from plot to plot. However, midyears of the two resulting census intervals are rather synchronous. Net annual BA change was calculated for the longest census interval, as well as for the two consecutive periods identified. Some of the PSPs were only established in the early 90s, therefore the second period includes a larger sample (37 PSPs) which encompasses both long-established (29 PSPs) and more recently established PSPs (8 PSPs). The more recently established PSPs contribute to increase the representativeness of the Western Amazonia sites, which have smaller sample sizes than the Central Amazonian block.

The equations used to calculate mortality and recruitment have been found to be time dependent (Sheil et al. 1995), with higher rates estimated over short versus long census intervals. With regard to the analyses shown here, the influence of time is mitigated by a longer time interval in the second versus the first period analysed. This enhances the probability that any increasing trends in mortality and turnover will be genuine trends.

The diameter increments of each individual tree were screened to detect "anomalous" diameter measurements. All trees with a negative diameter change and that shrank by more than 5% of the initial diameter or grew by over 7.5 cm $a^{-1}$ were discarded from BA net change calculation (Condit et al. 1993a; Condit et al. 1993b). Basal area is usually computed by using diameter at breast height (dbh), that is the tree stem diameter commonly measured at 1.3 m above ground, and inclusive of bark. A variation in BA indicates a corresponding change in total stand biomass, as long as there are no large changes in forest structure and composition (Brown et al. 1992; Brown, Gillepsie, and Lugo 1989; Gillepsie, Brown, and Lugo 1992). Turnover is another measure of forest dynamism and is defined as the mean rate of mortality and recruitment of tree stems (generally with $\geq$ 10 cm in dbh) and/ or BA. Net annual stem density change was calculated as:

$$\Delta N / \Delta t = (N_f - N_0) / \Delta t \qquad (1a)$$

and relative stem density change was calculated as:

$$\Delta N_{rel} = ((N_f - N_0) * 100 / N_0) / \Delta t \qquad (2a)$$

where $N_0$ is the stem number at the beginning of the period $\Delta t$, $N_f$ is the stem number at the end of the period. Stem annual mortality rates were calculated as follows (Condit, Hubbell, and Foster 1995a; Lieberman et al. 1985b; Phillips et al. 1994a):

$$\text{stem } r_m = (\ln (N_0) - \ln (N_s)) / \Delta t \qquad (3a)$$

where $N_s$ is the number of stems that survived during $\Delta t$. Annual recruitment rates have been calculated as (Condit et al. 1999):

$$\text{stem } r_r = (\ln(N_f) - \ln(N_s)) / \Delta t. \qquad (4a)$$

This model has been widely adopted and recently criticized (Sheil and May 1996), as discussed earlier in this chapter. Basal area mortality and recruitment were calculated using the same formula, and substituting $N_0$ with $BA_0$, $N_f$ with $BA_f$, and $N_s$ with $BA_s$. Therefore, BA mortality rates were calculated as:

$$BA\ r_m = (\ln(BA_0) - \ln(BA_s)) / \Delta t \qquad (3b)$$

and BA recruitment rates were calculated as:

$$BA\ r_r = (\ln(BA_f) - \ln(BA_s)) / \Delta t \qquad (4b)$$

Turnover was calculated as the mean of mortality and recruitment rates (Phillips 1996), for stems and BA respectively:

$$\text{stem}_t = (\text{Stem } r_m + \text{Stem } r_r) / 2 \qquad (5a)$$

$$BA_t = (BA\ r_m + BA\ r_r) / 2 \qquad (5b)$$

Net annual BA change was calculated as:

$$\Delta BA / \Delta t = (BA_f - BA_0) / \Delta t \qquad (1b)$$

and BA relative change was calculated as:

$$\Delta BA \text{ rel} = ((BA_f - BA_0) * 100 / BA_0) / \Delta t. \qquad (2b)$$

For individual stems, diameter increment rates were calculated as:

$$\Delta d / \Delta t = (d_f - d_0) / \Delta t \qquad (6)$$

where $d_0$ and $d_f$ are the initial and final diameter for the interval $\Delta t$ considered.
Increment rates for individual stems were calculated to assess the quality of diameter measurements and to be able to discard from the analyses those individuals that did not fall within the upper and lower thresholds defined to eliminate the most likely erroneous diameter measurements (Condit, Hubbell, and Foster 1993a).
Spatial patterns were analysed for stem density and BA change, for all plots together and lumping PSPs by regions. The significance of regional differences was tested applying the Kruskal-Wallis test to changes recorded over time.
The multiple comparisons of sites were carried out using a non-parametric test, as the strongly unbalanced samples were expected to be non-normally distributed. The Kruskal-Wallis test is a nonparametric version of the one-way ANOVA and compares median instead of mean values (Sokal and Rohlf 1974) (see also the methods section in Chapter 4). Temporal and spatial patterns in forest stand dynamics were also analysed. Mean rates of recruitment, mortality and turnover change were compared between the two intervals and the statistical significance of any difference was tested. Regional differences were also investigated using the Kruskal-Wallis test. The contribution of different tree size classes to the overall stand BA change over time was determined. A detailed analysis of the various components, positive (BA growth and recruitment) and negative (BA mortality), driving overall BA change was carried out. Growth rates of trees surviving from the first to last census were determined. Examples of different mechanisms of BA accumulation were shown, using as a model two sample plots from different regions, characterized by different stand dynamics.

### 5.3.1. Pioneer species

The group of pioneer species was identified as described earlier in Chapter 4 (paragraph 4.2), where the main distinctive characteristics of this guild are described. For this study, a list of pioneer species was compiled with the help of local botanists and experts, analysing a complete list of species inventoried across all the locations studied (Oliver Phillips, Rodolfo Vasquez and Abel Monteagudo, William Laurance). To this, another list of 61 strictly gap-dependent pioneer species derived from a floristic inventory of Guianan forests (Paracou) (Molino and Sabatier 2001) was added.

## 5.4 Results

The following results are presented:

1. Changes in stem density and basal area.
2. Temporal and spatial patterns in recruitment, mortality and turnover.
3. Basal area changes by size class.
4. Changes in some functional groups.

### 5.4.1. BA and stem density change

The positive net changes in stem density and BA recorded are higher in the second time interval, with values extracted from 29 PSPs for the first interval, and 37 PSPs for the second time interval (stem density change: 1st interval = 0.71 stems $ha^{-1}$ $a^{-1}$, 2nd interval = 1.08 stems $ha^{-1}$ $a^{-1}$; BA net change: 1st interval = 0.09 $m^2$ $ha^{-1}$ $a^{-1}$, 2nd interval = 0.13 $m^2$ $ha^{-1}$ $a^{-1}$) but differences are not significant. Over the longest census interval, mean BA change is significantly different from zero (0.11 ± 0.021 $m^2$ $ha^{-1}$ $a^{-1}$, $P <0.001$), while the stem density increase is not statistically significant (0.84 ± 0.432 stems $ha^{-1}$ $a^{-1}$).

Significant differences between regions were recorded for both net annual stem density and BA change, over the second period (Kruskal-Wallis test for stem density change, $H = 9.50$, $P < 0.05$; for BA, $H = 16.13$, $P< 0.001$, 37 PSPs) and the longest time interval (Kruskal-Wallis test for stem density, $H = 7.89$, $P < 0.05$; for BA, $H = 14.55$, $P< 0.001$, 37 PSPs), while differences were not significant over the first period (29 PSPs).

For each variable and period examined, changes recorded showed the highest median value in the WA-SP plots over the longest census interval (stem change = 2.98 stems, $ha^{-1}$ $a^{-1}$, BA change = 0.21 $m^2$ $ha^{-1}$ $a^{-1}$), intermediate values for the CA plots (stem change = 0.53 stems, $ha^{-1}$ $a^{-1}$, BA change = 0.01 $m^2$ $ha^{-1}$ $a^{-1}$), and the lowest value for the WA-NP (stem change = -3.71 stems, $ha^{-1}$ $a^{-1}$ BA change = -0.05 $m^2$ $ha^{-1}$ $a^{-1}$), over the same period.

Mean BA accumulation rates were compared for the two main blocks of PSPs (WA and CA) with a Mann-Whitney test, which revealed slightly higher values in WA but no significant differences.

Stem density change and BA relative change were analysed jointly. A general positive linear relationship between BA change and stem change was found (y =

0.7348x + 0.2992, $R^2$=0.51), with a slope of the regression line significantly different from zero.

The relative changes for the two variables did not show the same sign in all PSPs (Fig. 5.1). The five cases found are listed below, indicating the percentage of PSPs falling in each category:

a) relative positive change of both BA and stem density (59.5 %)
b) relative negative stem density change and positive BA change (18.9%)
c) relative negative change for both BA and stem density (13.5%)
d) relative positive change in BA and no change in stem density (5.4%)
e) relative positive change of stem density and no change in BA (2.7%)

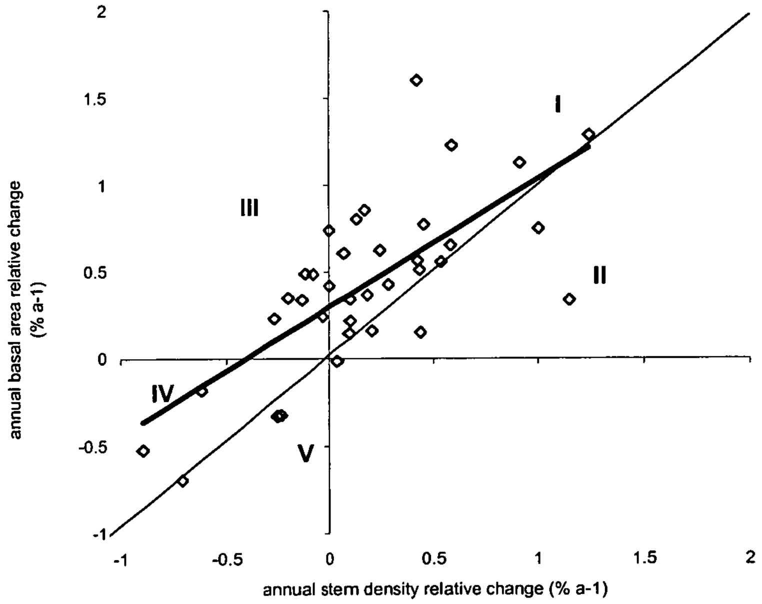


Figure 5.1. BA change (%) versus stem density change (%) over the longest census interval for 37 1-ha PSPs from the Amazon basin. Line 1:1 and regression line (thicker) are shown.

The three quadrants occupied by the swarm of points can be further split and described as follows:

**I** - stem density increases proportionally less than BA, over time. The bulk of the forest stand is growing and mortality is not reducing density (48.6% of all PSPs).

**II** – Stem density increases proportionally more than BA. A few big trees are lost through mortality and BA loss is partially compensated by recruitment of several small trees (10.8% of all PSPs).

**III** – Stem density decreases, while BA increases. Some trees die and the reduced stem density stimulates the growth of individuals surrounding the gaps produced, largely compensating the BA lost through mortality. It seems to be the typical case of thinning through successional evolution of the stand (18.9% of all PSPs).

**IV** – Stem density decreases proportionally more than BA. Some middle-sized trees die and their falling involves many small-stemmed individuals. Several individuals are affected by mortality but the overall BA loss is less than proportional (8.1% of all PSPs).

**V** – Stem density decreases proportionally less than BA. Only a few trees die and mostly from medium- or large-sized classes (5.4% of all PSPs).

Two plots showed no change in stem density and positive relative change in BA, indicating that no recruitment took place while standing trees increased their size.

The majority of PSPs falls in the area **I**, showing a prevalent tendency for an increase of both stem density and BA with a more marked positive change in BA than in stem density.

### 5.4.2. Temporal and spatial patterns in recruitment, mortality, and turnover

Stem dynamic rates were found to be all significantly higher in the second period, with values extracted from a sample of 29 PSPs for the first period, and 37 PSPs for the second period (stem recruitment: 1st interval = 1.46 ± 0.12 (SE) % $a^{-1}$, 2nd interval = 1.74 ± 0.16 (SE) % $a^{-1}$; stem mortality: 1st interval = 1.33± 0.12 (SE) % $a^{-1}$, 2nd interval = 1.55 ± 0.13 (SE) % $a^{-1}$; stem turnover: 1st interval = 1.40 ± 0.11 (SE) % $a^{-1}$, 2nd interval = 1.65 ± 0.13 (SE) % $a^{-1}$).

BA dynamic rates were also found to be higher in the second interval tested (BA recruitment: 1st interval = 0.32 ± 0.03 (SE) % $a^{-1}$, 2nd interval = 0.39 ± 0.04 (SE) % $a^{-1}$; BA mortality: 1st interval = 0.93 ± 0.13 (SE) % $a^{-1}$, 2nd interval = 1.35 ± 0.14 (SE) % $a^{-1}$; BA turnover: 1st interval = 0.83 ± 0.07 (SE) % $a^{-1}$, 2nd interval = 0.94 ± 0.08 (SE) % $a^{-1}$), but only for BA recruitment rates were differences significant.

Spatial patterns were tested comparing the two main blocks of PSPs (WA and CA) with Mann-Whitney U-test applied to stem and BA recruitment and mortality rates. The test showed for every variable significant difference between the two regions. Median values for each region and the results of the test are listed: stem recruitment, CA = 1.06, WA = 2.6, W = 385, P<0.001; stem mortality, CA = 0.93, WA = 2.19, W = 284, P<0.001; BA recruitment, CA = 0.24, WA = 0.72, W = 420.5, P<0.001; BA mortality, CA = 0.9, WA = 2.2, W = 409.5, P<0.001.

A multiple comparison of the three main regional clusters of PSPs (CA, WA-NP and WA-SP) was carried out using the Kruskal-Wallis test to identify differences for the same variables examined above, over the longest census interval (37 PSPs). The test revealed significant differences for stem recruitment (H = 23.75, P< 0.001), mortality (H = 23.61, P< 0.001) and turnover rates (H = 23.30, P< 0.001). With regard to BA, the test showed significant differences between regions over the longest census interval for BA recruitment (H = 24.66, P< 0.001), BA mortality (H = 22.39, P< 0.001), BA turnover (H = 23.64, P< 0.001), BA annual net change of trees surviving from the beginning to the end of the census interval (H = 24.37, P< 0.001) and BA annual net change of surviving trees + BA annual change due to recruitment (H = 23.61, P< 0.001). For both BA and stem density dynamics, values are significantly higher in WA plots than CA plots.

One plot from WA (AllpahuayoA) was affected by exceptional mortality during the second interval examined (between 1996 and 2001), but the exclusion of this plot from the analysis does not introduce significant changes.

### TURNOVER

Turnover rates for stems and BA were compared. Stem turnover showed higher rates than BA turnover in every plot (Fig. 5.4). This was expected as smaller trees exhibit the fastest turnover rates, and proportionately contribute more to overall plot stem density than to overall plot basal area.

A gradient from less to more dynamic plots is observable in Fig. 5.2, with CA plots in the lower part of the graph, and WA plots in the upper part. Stem turnover is significantly higher in western than in central Amazonia (2.31 ± 0.08 % $a^{-1}$, n = 23, and 1.06 ± 0.07 % $a^{-1}$, n = 14, mean ± standard error, t = -11.05, P<0.001). BA turnover is also significantly higher in western than central Amazonia (1.43 ± 0.05 % $a^{-1}$, n = 23, and 0.63 ± 0.05 % $a^{-1}$, n = 14, mean ± standard error, t = -10.60, P<0.001).

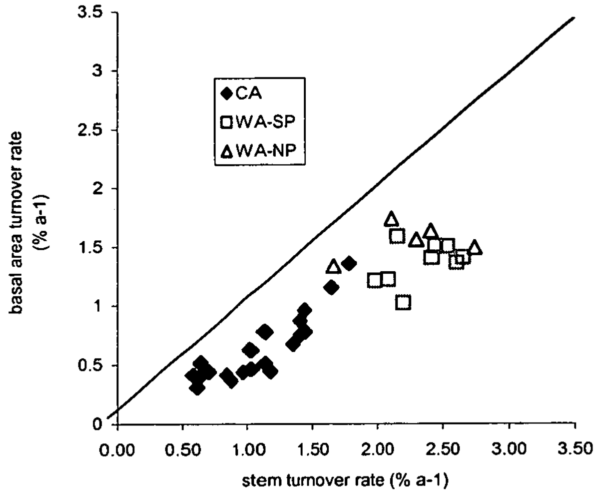


Figure 5.2. Basal area turnover rate versus stem turnover rate over the longest census interval for 37 1-ha PSPs from the Amazon basin, divided in three main regions: CA= Brazilian PSPs, WA-SP=Western Amazonian South Peruvian PSPs, WA-NP=Western Amazonian North Peruvian PSPs. Line is 1:1.

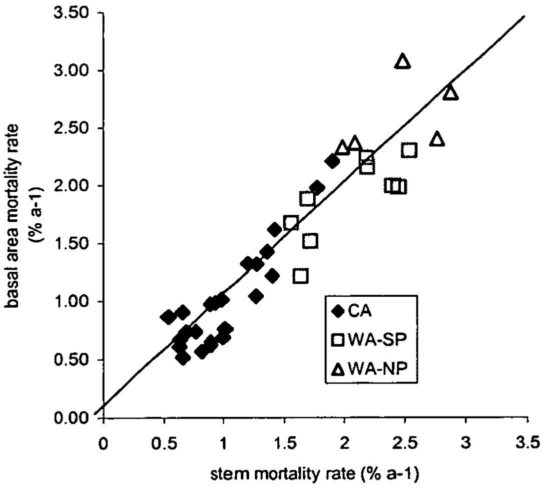


Figure 5.3. BA mortality rate versus stem mortality rate over the longest census interval for 37 1-ha PSPs from the Amazon basin, divided in three main regions: CA= Brazilian PSPs, WA-SP=Western Amazonian South Peruvian PSPs, WA-NP=Western Amazonian North Peruvian PSPs. Line is 1:1.

For both regions, stem turnover rates have increased significantly in the second versus the first census interval (in CA, 0.96 ± 0.08 % $a^{-1}$, and 1.12 ± 0.08 % $a^{-1}$, mean ± standard error, paired t test t = -2.25, P<0.05, in first and second census respectively; in WA, 2.11 ± 0.08 % $a^{-1}$, and 2.51 ± 0.15 % $a^{-1}$, mean ± standard error, t = -2.26, P<0.05, in first and second census respectively), where the first interval contains only "older" PSPs and the second interval contains also "more recent" PSPs.

MORTALITY

Stem and basal area mortality rates tend to fall on a 1:1 line, showing a gradient from less (CA) to more dynamic plots (WA) (Fig. 5.3). Within WA plots, mortality rates are higher for WA-NP.

RECRUITMENT

Recruitment rates tend to be much higher for stems than for BA, as shown in Fig 5.4. The marked deviation visible in the graph is originated by the fact that stem recruitment is (by definition) referred to the smallest trees that reach the threshold required to be included in the forest census. Values tend to cluster by region, as for mortality and turnover. A gradient is found with Central Amazonian plots showing the lowest recruitment rates, and WA-SP plots the highest rates.

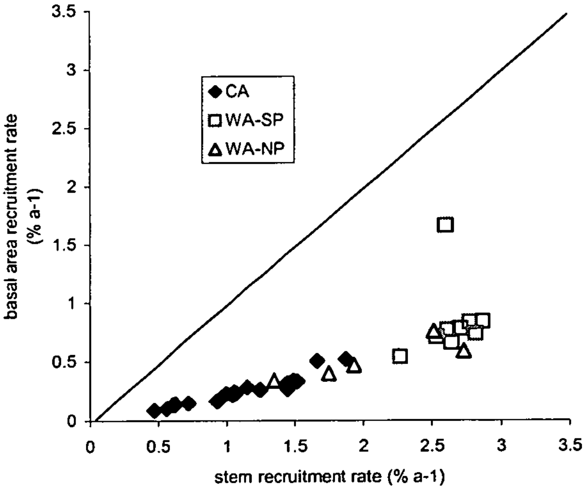


Figure 5.4. Basal area recruitment rate versus stem recruitment rate over the longest census interval for 37 1-ha PSPs from the Amazon basin, divided in three main regions: CA= Brazilian PSPs, WA-SP=Western Amazonian South Peruvian PSPs, WA-NP=Western Amazonian North Peruvian PSPs. Line is 1:1.

Mortality and recruitment were compared, calculating both variables on a per area basis. Annual stem losses and gains are generally balanced within the CA cluster of

PSPs, while within the WA group, two opposite patterns characterizes the two sub-groups: WA-SP plots present a greater BA annual gain through recruitment than an annual BA loss by mortality; on the contrary, most of WA-NP plots show BA loss greater than BA recruitment (Fig. 5.5). Overall, changes in stem density over time are more marked in WA than CA plots, due to a larger imbalance between mortality and recruitment. However, the measured changes in stem density through time over the whole sample of plots are not significant, as shown earlier in this chapter.

With regard to BA, annual losses are greater than gains on an area basis, in all plots (Fig. 5.6), and mostly so in WA-NP plots.

Annual BA losses are by far greater than BA gains by recruitment, therefore the generally observed BA accumulation at stand level is mainly determined by the increasingly positive contribution of trees that survive from the initial to the final census. Changes over time in BA growth of surviving trees and BA growth plus recruitment were calculated. Values were found to be significantly higher in the second census interval than in the first period examined (BA annual net change of trees surviving from the beginning to the end of the census interval: 1st interval = 0.36 ± 0.02 (SE) % $a^{-1}$, 2nd interval = 0.41 ± 0.02 (SE) % $a^{-1}$; and BA annual net change of surviving trees + BA annual change due to recruitment: 1st interval = 0.44 ± 0.03 (SE) % $a^{-1}$, 2nd interval = 0.52 ± 0.03 (SE) % $a^{-1}$), where the first interval contains only "older" PSPs and the second interval contains also "more recent" PSPs.

The relative change in BA showed a correlation with the relative stem density change over the longest census interval, as shown earlier in Figure 5.1, but BA accumulation rates over the longest census interval do not show a correlation with stem turnover rates for the same period. However, ideally a larger sample should be explored to detect a potential correlation between the two variables.

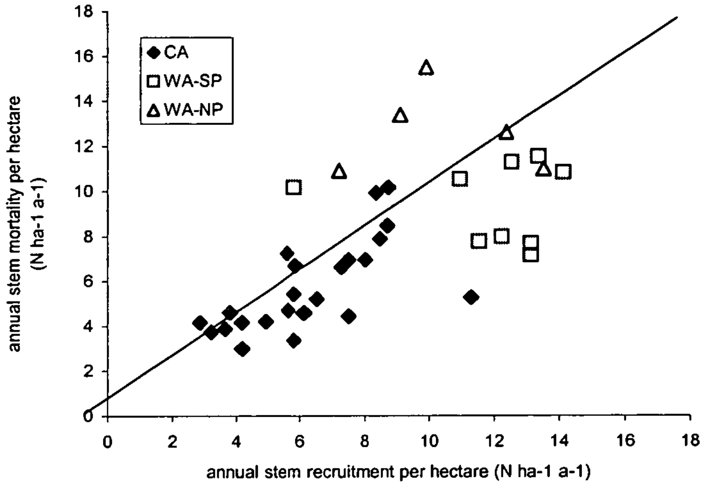


Figure 5.5. Stem annual mortality versus stem annual recruitment on a per area basis, calculated over the longest census interval for 37 1-ha PSPs from the Amazon basin. They are divided in three main regions: CA= Brazilian PSPs (23), WA-SP=Western Amazonian South Peruvian PSPs (9), WA-NP=Western Amazonian North Peruvian PSPs (5). Line is 1:1.

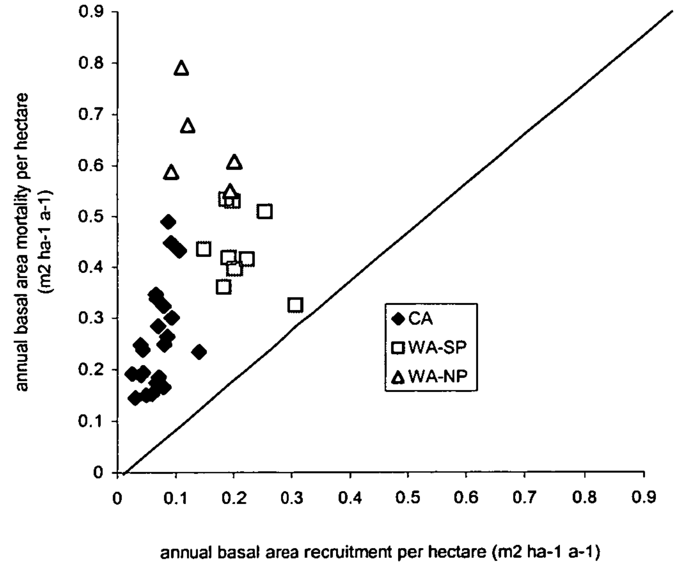


Figure 5.6. BA annual mortality versus BA annual recruitment on a per area basis, calculated over the longest census interval for 37 1-ha PSPs from the Amazon basin. They are divided in three main regions: CA= Brazilian PSPs (23), WA-SP=Western Amazonian South Peruvian PSPs (9), WA-NP=Western Amazonian North Peruvian PSPs (5). Line is 1:1.

### 5.4.3. Basal area changes by size class

The results shown above seem to indicate that mostly the enhanced growth of surviving trees is contributing to stand BA accumulation, but which size class is mostly responsible for the positive BA net increase?

To address this point, BA annual growth in each size class was analysed for a cohort of individuals that survived from first to final inventory (Fig 5.7). Surviving individuals were allowed to grow into the next size class, in order to identify which size class contributed most to production.

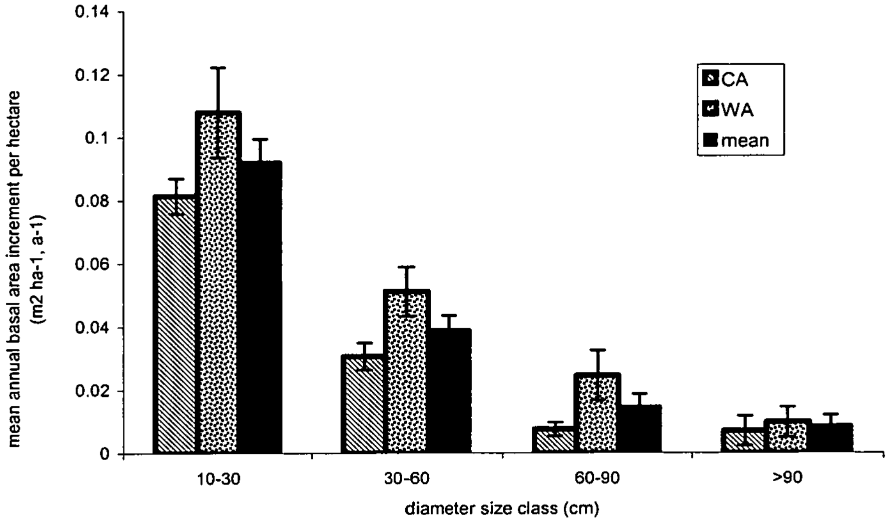


Figure 5.7. Mean annual BA increment ha$^{-1}$ and per size class of trees surviving from first to last inventory, in 37 1-ha PSPs, 24 from the Brazil, and 14 from Peru. Mean BA annual growth ha$^{-1}$ for all PSPs together is shown. Size classes: 1=10-30; 2= 30-60; 3= 60-90; 4=>90 cm of dbh. Bars indicate limits of 95% confidence interval.

In both regions, BA growth rates of surviving trees were negatively correlated with stem size, with small-sized stems contributing more than larger stems to stand BA gain over the longest census interval. Stand BA change was then examined in each size class, including all stems, not just the cohort of surviving trees (Fig. 5.8).

In all size classes, BA growth rate seemed higher in WA. This difference appeared to be related to soil fertility (Malhi et al., in review a). The relative difference in stem productivity seemed to be greatest in the large size class (60-90 cm), with CA plots showing a mean annual BA net change 69.3% lower than WA plots, followed by the intermediate size class (30-60 cm ) with a 40.0% lower BA net change in CA versus WA plots.

Within-class net changes were first considered without taking into account the contribution to BA change due to individuals moving in and out of a specific size class, and of trees dying and being recruited (Fig 5.8). For every plot, initial and final BA values in each size-class were calculated, then the annual balance over time was determined, and an annual value of BA net change per $ha^{-1}$ was calculated.

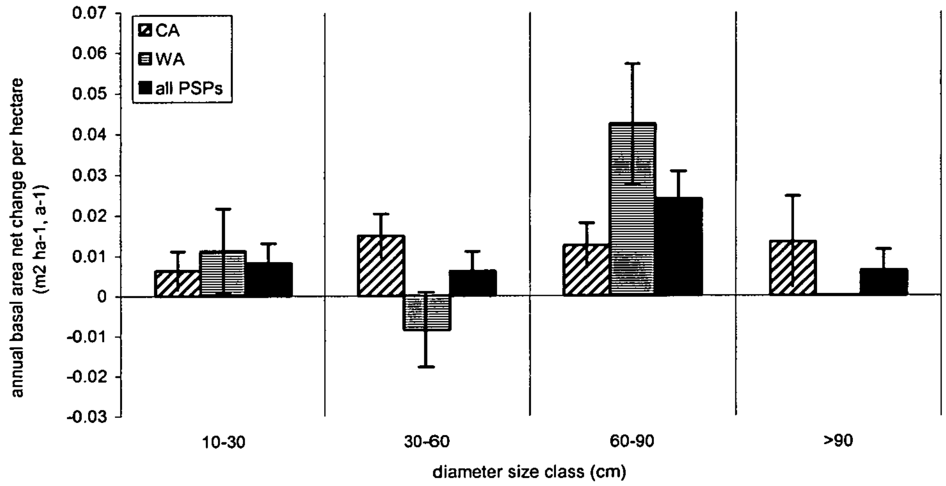


Figure 5.8. Mean annual BA net change $ha^{-1}$ per size class over the longest census interval, in 37 1-ha PSPs, 24 from Brazil, and 14 from Peru. Mean BA net change $ha^{-1}$ for all PSPs together is shown. Size classes: 1=10-30; 2= 30-60; 3= 60-90; 4=>90 cm of dbh.

Over the whole sample of PSPs (37 PSPs), all size classes showed an average positive increase in BA (Fig. 5.8), with a maximum annual stand BA positive change for stems between 60 and 90 cm of dbh. However, a regional divergence was found between CA and WA plots, specifically in the size-class where maximum BA net change culminates (second size class in CA, and third one in WA), and in the BA balance of medium-stemmed trees (30-60 cm of dbh), which is negative in WA plots. The mechanisms leading to the observed BA balance in each size class were further analysed. Two plots were chosen from the two main regions, as indicative of growth, recruitment and mortality patterns (Fig. 5.9 and 5.10).

In each class, BA change was sub-divided into various components separately quantified: a) BA total gain and loss, b) BA gain and loss due to trees moving in and out of a size class, c) BA gain due to growth of trees within a size class, d) BA loss due to death of some individuals, and (e) the final balance between total BA losses and gains in each size-class.

The balance is negative in both plots for class 1; the CA plot presents a positive net BA in class 2 and 4; the WA plot presents a negative net BA change in class 2, while change becomes positive in the two largest size classes (3 and 4), showing a maximum in class 4.

In both sample plots, moving from small- to large-sized classes, the contribution to positive BA change is progressively more associated with trees moving in a class from the one immediately preceding, while within-class growth plays a decreasing role moving towards larger size classes. The same is true for mortality; it decreases with increasing size in both plots, and moving towards larger size classes, losses are determined more by trees shifting out from a class to join the next, than by within-class mortality. Mortality is higher in WA plots, and the amount of BA moving from one class to the next is also higher, reflecting higher growth and dynamic rates.

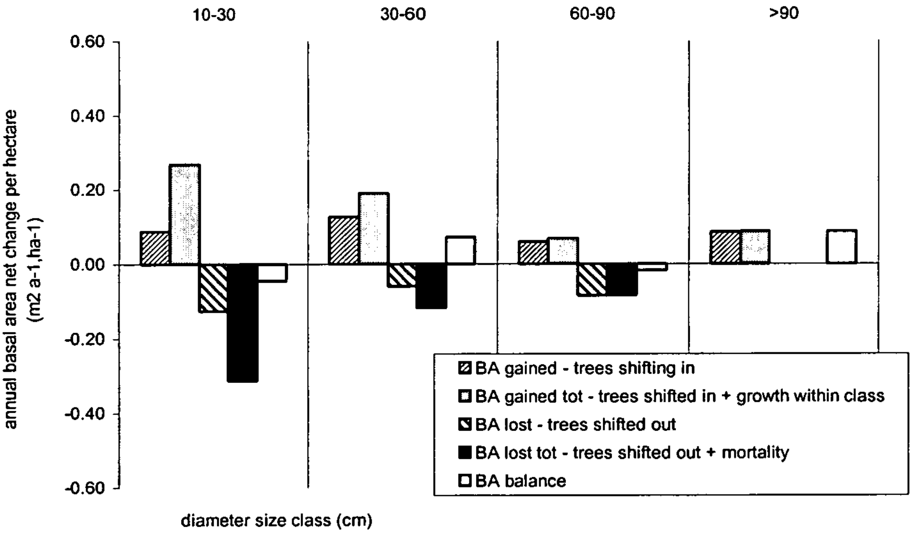


Figure 5.9. Mean annual BA net change ha$^{-1}$ for various components of total BA net change in 4 size classes, over a period of 5.3 years: total BA gain due to BA shifted in through growth of trees from one class to the next, and to growth of trees within the same class (BA gained by shift of growing trees is also shown by a separate bar); total loss of BA due to trees that died and trees that moved out from a class into the next. The final balance (BA total gains - BA total losses) is also shown. Values are taken from a representative sample plot from the Central Amazon (BDFFP 1201.1, Manaus). Size classes: 1=10-30; 2= 30-60; 3= 60-90; 4=>90 cm of dbh.

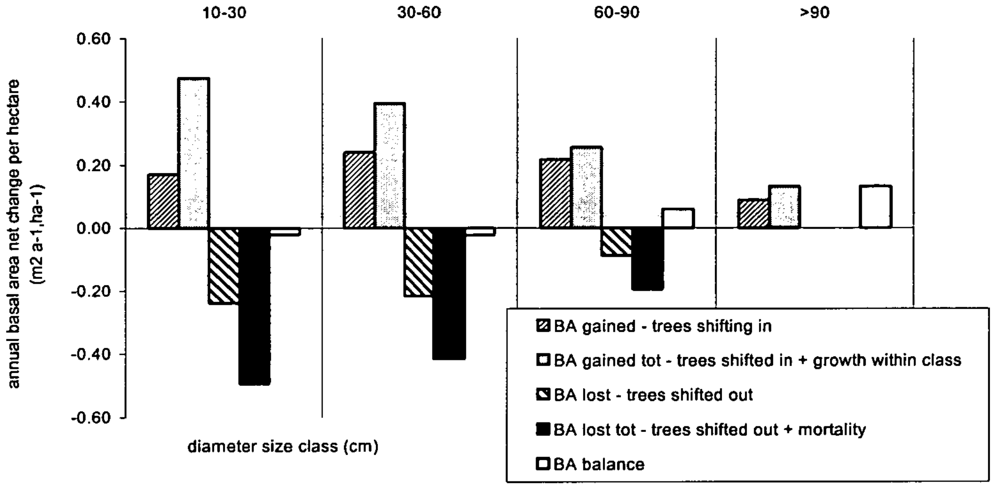


Figure 5.10. Mean annual BA net change $ha^{-1}$ for various components of total BA net change in 4 size classes, over a period of 7.7 years: total BA gain due to BA shifted in through growth of trees from one class to the next, and to growth of trees within the same class (BA gained by shift of growing trees is also shown by a separate bar); total loss of BA due to trees that died and trees that moved out from a class into the next. The final balance (BA total gains - BA total losses) is also shown. Values are taken from a representative sample plot from the Western Amazon, (Tambopata 6, South Peru). Size classes: 1=10-30; 2= 30-60; 3= 60-90; 4=>90 cm of dbh.

### 5.4.4. Changes in some functional groups

The role played by some groups of fast-growing species was investigated in different regions. The contribution of pioneer species and palms to stand BA net change was analysed in 37 1-ha PSPs, distributed from Western to Central Amazonia. Results are shown in figures 5.11 and 5.12. In both graphs, plots are displayed on the *x*-axis along a gradient of decreasing total stand BA net change per year, with a black line indicating the switch from positive to negative BA annual net change.

Out of 31 PSPs with annual positive BA net change, 22 show also positive change in BA of pioneer species. However, positive BA change in pioneers is not confined to plots showing BA accumulation. Over the whole sample of plots, no correlation was found between the relative stand BA change and relative change for the selected group of species. It is interesting to note that the two plots with most negative stand BA annual net change, falling on the extreme right hand side of the graph (Fig. 5.11), are characterised by the greatest absolute loss of pioneer species' BA.

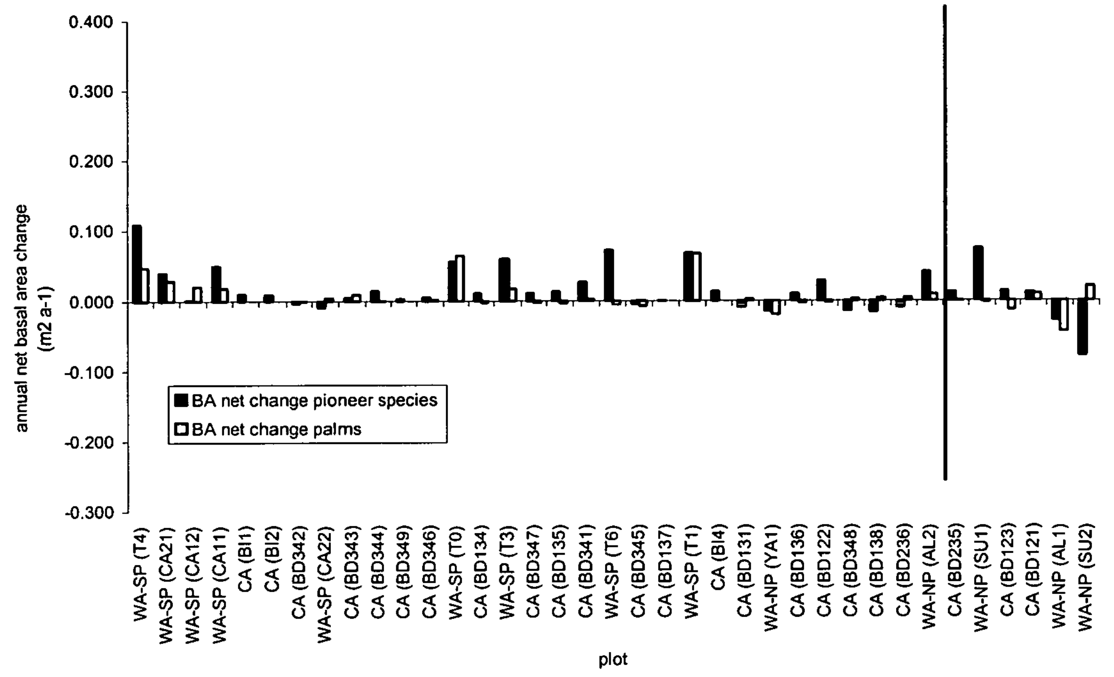


Figure 5.11. Annual net basal area change of pioneer species and palms in 37 1-ha PSPs from the Western and Central Amazon. Plots displayed along the $x$-axis following a gradient of progressively lower stand BA change, with a switch from positive to negative annual BA net change in correspondence of the vertical line; plots on the left hand side of the line have positive BA change, those plots on the right of the line show increasingly more negative annual BA net change. The dotted line indicates the main pattern of total stand BA change.

With regard to palms, annual net and relative BA change showed no correlation with stand annual net and relative BA change. Sixteen plots in total show positive change in palms' BA, and 14 of these show also positive BA change at stand level.

Spatial patterns were investigated. The most marked increase in BA of pioneers over time, both in absolute and relative terms, was found in the WA south Peruvian PSPs, with Tambopata showing the highest mean annual increase (0.073 ± 0.01 $m^2$ $a^{-1}$), followed by Cuzco Amazonico (0.020 ± 0.014 $m^2$ $a^{-1}$).

Net changes in BA of pioneers and palms showed a correlation (Pearson's r = 0.47); both groups of species presented the most marked net BA positive change in some south Peruvian plots (Tambopata).

The same pattern was found for the annual BA net change of palms, with the highest increase in Tambopata (0.038 ± 0.014 $m^2$ $a^{-1}$) and Cuzco Amazonico (0.018 ± 0.005 $m^2$ $a^{-1}$), indicating a trend of increase for both groups in highly dynamic plots, where pioneer species and palms are already well represented. Relative BA changes of pioneer species were more pronounced in some central Amazonian plots (BD343, BD134, BD121), but the same regional cluster presented also the most negative values of stand BA relative change (BD138) (Fig. 5.12). The relative change in BA of pioneer species was expected to show a relationship with the increase in stem turnover but no significant correlation was detected. No correlation was found between relative changes in basal area of pioneers and palms.

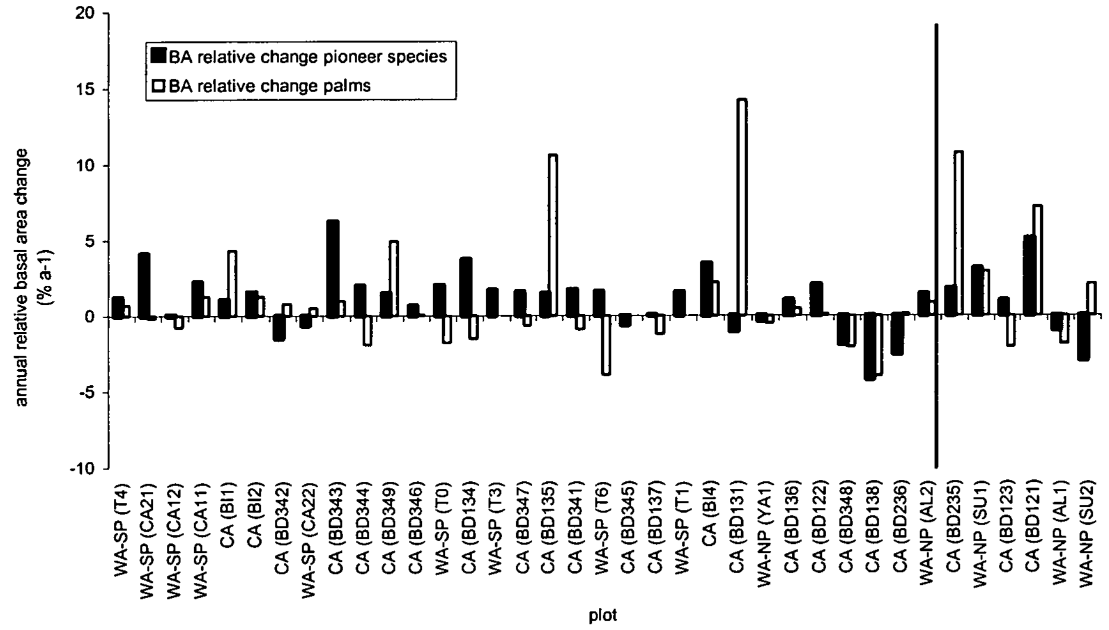


Figure 5.12. Annual relative basal area change of pioneer species and palms, in 37 1-ha PSPs from the Western and Central Amazon. Plots displayed along the $x$-axis following a gradient of progressively lower stand BA change, with a switch from positive to negative annual BA net change in correspondence of the vertical line; plots on the right hand side of the line have positive BA change, with higher values on the left hand side; those plots on the left of the line show increasingly more negative annual BA net change.

## 5.5 Discussion

Over the sample plots studied, BA accumulation through time is a widespread phenomenon. The net increase in BA is found to be statistically significant over the longest census interval, and more pronounced during the last decade explored. This evidence is supported by previous findings of Phillips et al. (1998a). They showed, across a Pantropical dataset, an increase in biomass of 0.77 ± 0.44 t $ha^{-1}$ $a^{-1}$, with a more significant trend in the Neotropics. More recent analyses of Pantropical data have indicated, for a set of the Paleotropical PSPs, that changes are consistent in direction and magnitude with those observed for the Neotropical plots (Lewis et al., in prep.). The present analysis expands those previous findings, exploring in detail the mechanisms leading to the observed BA changes.

Over the whole set of PSPs studied, the observed BA positive net change appears to be distributed across stem size classes. The greatest BA net positive change was found in large-stemmed trees (dbh between 60 and 89 cm dbh) (Fig. 5.8), however, when the various components contributing to the observed BA change in each size class are disaggregated (see Fig. 5.9 and 5.10), the growth of surviving trees is found to be much higher in small and medium-sized trees (10-30, and 30-60 cm dbh). This finding supports the results from some studies on the *in situ* response to elevated $CO_2$ in tropical forest understory plants, showing a responsive behaviour of plants growing near the photosynthetic light compensation point (Wurth, Winter, and Körner 1998), therefore indicating that an improved carbon balance should be more visible in stems with shaded crowns, such as small-stemmed trees, or trees in juvenile stages.

The net BA increase in all size classes argues against any single methodological bias or error due to inappropriate diameter measurement and data treatment. More specifically, the artefact introduced by buttresses "creeping" can be excluded as a sole responsible factor in the BA changes recorded, as the increase in BA is not confined to very large trees where the artefact is more likely to occur. Methodological issues have been treated with great detail in Chapter 6, where different sources of biases in measurements are discussed with great detail and tested, and it is shown, through a simulation, the limited effect of buttress creeping on final figures of BA accumulation, especially in the Peruvian plots. However, within-size class dynamics differed from site to site; BA net change was found to be positive for all the four size classes in the CA plots, while the WA dataset showed an average negative BA change in medium-stemmed trees.

The data show that the increase in BA over time is the net result of an increase in both BA gains (recruitment and growth), and BA losses (mortality). BA recruitment in particular, increased significantly over the longest census interval, while mortality also increased, but not significantly.

Positive changes in BA over time appear not to be linked to the abundance of fast growing species, as no positive correlation was found between the occurrence of palms and pioneers and BA accumulation rates. However, for 71% of the plots showing stand BA positive change, an increase in BA of pioneer species was also recorded, although this increase is not confined to plots that show BA accumulation. The most significant positive changes in BA of pioneer species and palms were recorded in WA-SP plots. This increasing contribution of fast-growing species to total stem density and total BA could be a consequence of the more pronounced increase in turnover found in highly dynamic sites, where pioneer species and palms are already well represented, and may be further favoured by an accelerated dynamism of the forest. However, the greatest relative increase in palms and pioneer species was found in CA plots, where these two groups of species are less abundant in absolute terms.

Forest dynamics are also changing over time. Old-growth forests of Amazonia seem to be experiencing accelerated tree turnover and this finding is consistent with what emerged from previous studies that explored different time-scales and larger spatial extents, showing a Pantropical doubling of mean forest stand dynamic rates in the 1990's compared with the 1950's (Phillips 1996; Phillips and Gentry 1994). Artifacts related to the time-dependency of dynamic rates, described and commented on by various authors (Phillips 1995; Sheil 1995a; Sheil and May 1996; Lewis et al., in prep.), have been discarded applying recommended tests (Phillips et al. 2002a), which prove that methodological procedures leave the observed trends unaffected.

Both stems and BA show an increase in turnover through time, although, as mentioned earlier, the positive change in BA mortality is not significant over time. Stem density is found to be increasing but not significantly, and growth of surviving trees was found to be significantly higher during the second time interval. Therefore, there is a tendency for trees in a plot to become more markedly larger than more numerous over time, with a significant increase in mean BA between initial and final census across all plots.

The synchronous positive net BA change and turnover increase argues against a bias related to the tendency to choose "majestic" forests for ecological studies, and also against the hypothesis of a general recovery from a catastrophic disturbance, as suggested (Clark 2002a) to be a potential explanation for the BA accumulation observed. In the first of the circumstance mentioned above, one would see mortality of large-stemmed trees but the resulting increase in mortality rate would be unlikely to be accompanied by an increase in biomass. On the other side, the second hypothesis would explain the BA accumulation, but could not explain the sustained increase in recruitment rates.

Despite the limited geographic distribution, the sites analysed are well suited to highlight the main characteristics of forest stands located on different substrates and regulated by different climatic regimes.

The analysis of spatial differences in BA change and turnover increase shows that the rates of BA accumulation for CA plots, characterized by lower dynamic rates, are comparable to those recorded for the more fertile aseasonal sites of WA-NP, characterized by higher turnover rates. Environmental factors such as low soil fertility and a pronounced dry season in CA do not seem to significantly limit net BA change, as would be expected considering environmental conditions. The increases in BA were greater in WA than in CA plots, but differences were not significant. Also, the increase in turnover estimates was more pronounced in the already-dynamic forests of the western Amazon.

Spatial differences were also tested sub-dividing the total sample of PSPs in to three clusters (WA-SP, WA-NP, and CA); differences between sites were found to be significant only for the second period examined, potentially indicating an increasingly marked differentiation in the regional response to global environmental changes in Amazonian tropical lowland forests.

The spatial patterns found in forest dynamics may be either an ecological response to the different prevailing climate and soil conditions found in WA and CA regions, or the result of biogeographical factors playing a role in shaping floristic patterns of the Amazon basin.

Western Amazonian PSPs show a much higher stem and BA turnover than those located in the Central Amazonian region. Differences in soil fertility and climate regime can partially explain the observed distinct dynamisms found in plots from the two main regions explored. Richer soils may determine a greater turnover in locations that benefit from ample moisture supply and good soil nutrition, with a greater above-ground forest productivity supporting faster turnover rates (Phillips et al. 1994a). The highest dynamic rates were found in plots from South Peru where the climate is seasonal and would probably pose some limits to forest productivity. Nevertheless, the effect of a seasonal climate in the South of Peru can be overridden by a strong effect of richer soils, found close to the Andes.

Other factors have also been mentioned by Phillips et al. (in review b) as responsible for the higher turnover in Western Amazonian plots, such as windstorms (Nelson et al. 1994), saturated soil conditions, topography (Gale and Barford 1999), and biogeography. With respect to this factor, it has been shown earlier in this work

(Chapter 4) and by other authors (Baker et al., in review; ter Steege and Hammond 2001b) how the Amazon basin is characterized by a clear gradient in family composition, with low wood density families dominating on richer soils in the south-west part of the Amazon basin (e.g., Cecropiaceae, Leguminosae Mimosaceae), and high wood density families dominating the Eastern part (e.g., Leguminosae Caesalpinaceae, Lecythidaceae, Chrysobalanaceae).

However, as shown earlier in Chapter 4, the relative density of some elements of the flora changes across sites, but very few taxonomic groups are confined to some particular sites, indicating that migration has not been seriously limited by long-term physical impediments to dispersal across the Amazon Basin. This seems therefore to suggest that large scale variation in edaphic conditions may have played a major role in determining the current floristic gradients, where some soil characteristics concur with other factors (i.e., climate) in determining specific forest dynamic conditions that support phylogenetically distinct groups, well- adapted to the prevailing environmental conditions, as commented also by Phillips et al. (in review a).

With regard to changes in turnover and BA accumulation, these are apparently increasingly more manifest through time over large areas in different regions.

Climate changes, manifest through El Niño events, have only marginally affected the western and southern regions of the Amazon basin. In addition, significant changes in rainfall patterns have not been detected in the study sites (see Chapter 3), therefore climate change is unlikely the main factor responsible for the recorded positive changes in BA. The role of a perturbation in the climatic regime on stand BA trends is extremely difficult to test, as the response of tree growth to fluctuations in precipitation patterns is affected by various factors and hidden by methodological issues. Furthermore, annual tree diameter measurements would be necessary and this is rarely the case in rainforest PSPs. The increase in BA over time might have various explanations. Some factors have been discarded (N-deposition, increased or decreased PAR, increased Saharan dust deposition) due to their uncertain effects on the vegetation and the limited spatial occurrence (Phillips et al., in review a). The large scale of the phenomenon, the growth response of trees surviving through the period studied, and the increase in recruitment rates recorded in both western and eastern Amazonian plots seem to lead to the conclusion that the increased $CO_2$ concentration in the atmosphere induced a “fertilization” effect. This could be an ephemeral phenomenon (soil and climatic potential constraints are to be considered), but it seems to be increasingly manifested in the study sites. As commented earlier (and also in Chapter 6, paragraph 6.4.1), the increase in BA recorded in most of the PSPs is unlikely to be explained by a successional process, where biomass builds up and stem density progressively decreases as a consequence of "self-thinning". Lewis et al. (in review) suggested that these results fit with the model of resource limited forests, proposed by Enquist & Niklas (2001). They show how despite a wide variation in species diversity, abundance and biomass, tree-dominated communities present nearly identical size-frequency distribution and standing biomass. They only vary in the degree of partitioning of a limited amount of resources, rather than increases (or decreases) in community biomass, potentially linked to local environmental conditions. According to these authors, the combination of different life strategies within the communities reflects the way partitioning of resources varies across communities.

The observed patterns of change in forest dynamics and stand structure were found to match predictions of growth as a driver in a system stimulated by an increased availability of resources (Lewis et al., in review). The response could be driven by different factors, maybe operating synergistically in a very complex way, and related to physiological mechanisms, such as changes in the photosynthetic response as shown especially for seedlings and saplings (Wurth, Winter, and Körner 1998), or to changes in carbon allocation from roots to shoots (Lloyd and Farquhar 1996).

However, as reported by Phillips et al. (in review a), the recorded increase in turnover appears to be faster than expected according to predictions of an increase in atmospheric $CO_2$, as shown by recent experiments (Curtis and Wang 1998). There is clearly a need to support the present findings with further investigations extended to a network of sites that will allow us to carry out more balanced experiments, including more forest PSPs in the aseasonal and dynamic western Amazonia. The protocol for measuring and monitoring PSPs needs to be improved and integrated by the collection of local soil and climate data. Diameter measurements should be better synchronized, and carried out in the proper season, to avoid methodological difficulties due to stem "shrinkage", when water availability is reduced (Baker et al. 2003). Refined modelling exercises should be carried out in order to better test the likely upper and lower boundaries of ecophysiological responses of tropical forest ecosystems to changes in atmospheric composition and climate. This would enable comparison of the magnitude of observed responses with predictions (Lewis et al., in prep.; Malhi et al., in review a).

## 5.6 Conclusions

1. Stand BA and turnover appear to be significantly increasing over time in almost all PSPs examined in the present study.
2. Regional patterns in turnover are found with the Western Amazonian plots studied, characterized by a much more pronounced dynamism than the Central Amazonian plots.
3. The more dynamic forests seem to be linked to richer soils. Recruitment and mortality showed a tendency to increase on substrates of varying fertility, but the largest absolute increases were recorded on richer soils. The main differences in recruitment, mortality and turnover between eastern and western plots crudely respect the distinction between poor soils, typically found in the eastern and central Amazon, and richer soils more common in the western part of the Amazon basin.
4. The influence of climate in controlling BA accumulation is unclear, although its effect is likely to be minimal in the study sites. The rainfall data do not reveal any significant change in the period studied.
5. Stand dynamics are not significantly correlated with the observed accumulation of BA over time. Rates of change in BA and turnover rates over time are higher in WA plots, but not significantly greater than values found in less dynamic Central Amazonian plots, analogously experiencing BA accumulation.
6. BA changes are distributed across all size classes, demonstrating that measurement biases are unlikely to be responsible for the observed patterns. Although BA net changes in each size class are slightly different between Western and Central Amazonian plots, the mechanisms responsible for stand growth and BA partitioning across stem size classes are analogous.
7. BA accumulation appears to be due more to a greater growth of individuals than to an increased stem density. It seems possible to reject the hypothesis of a general recovery from a major disturbance, while the hypothesis of a potential "fertilization" from the enhanced $CO_2$ concentration in the atmosphere is supported by the findings in this work.
8. Regardless of climate regime, forests in both seasonal and aseasonal climate regimes have shown a significantly increasing dynamism.
9. The role played by environmental factors is uncertain. Less fertile and seasonal Central Amazonian plots show high BA accumulation rates, comparable to those recorded in aseasonal plots from the western North Peruvian Amazonian region,

and those found in south Peruvian plots located on fertile soils. The sample size of the WA cluster of PSPs is probably too small to show such differences.

10. The recorded BA accumulation is not directly associated with the increased occurrence of fast growing groups of species, such as pioneers and palms. The increase in pioneer species and palms, found in most of the plots across various sites, but mainly recorded in south Peruvian plots, could be a consequence of the general increase in turnover rates, more marked in highly dynamic sites of the southern Amazon.

# Chapter 6. Some methodological issues

## 6.1. Introduction

In the present chapter the potential methodological difficulties in permanent sample plot (PSP) measurement and data processing are discussed. In the first part, the protocol used in the establishment of PSPs is analysed to highlight the repercussions that the choice of size, location and shape of the PSPs have on the inventory data. The methodology commonly adopted in measuring trees is reviewed and the protocol adopted for data processing is also illustrated, with the objective to detect noise and biases occurring in different phases of PSPs inventories, from the establishment of plots to tree measurement.

In the second part of the chapter, some recommended tests (Phillips et al. 2002a) are applied to the data, to assess the occurrence of artefacts in basal area (BA) change analyses shown in Chapter 5.

### 6.1.1 The main artefacts in permanent sample plot measurements

The main three types of biases occurring in PSPs measurements, as identified and summarized by Sheil (1995), have been presented in the literature review of Chapter 2 (paragraph 2.5). In this section, the main sources of biases are presented and described, together with their likely effect on plot's BA change estimates (Table 6.1). Phillips et al. (2002a) have proposed some tests to be applied to detect common biases in PSPs censusing and to assess their magnitude. The author of this thesis has contributed to the design of some of the tests suggested in that paper, re-presented in this chapter. Here the analysis is extended to a larger dataset than the one used by Phillips et al. (2002a).

In Table 6.1, the main sources of errors and biases with both positive and negative direction are listed. The present chapter will focus only on detecting and estimating the effects of positive biases in BA calculations.

| Origin/source | Description of bias/error | Direction of bias |
|---|---|---|
| ***Site selection*** | "majestic forest bias" (selection of mature-phase, gap-free sites) | Negative |
| | "progressive fragmentation and edge effects | Negative |
| | "immature forest bias" (biased selection of successional forest) | Positive |
| ***Plot establishment and tree measurements*** | Impact on vegetation inside the plot, field data collection (especially swelling around nails used to place tags on stems) | Positive |
| | Impact on vegetation (soil compacting, climbing and collecting trees, etc.) | Negative |
| | Incomplete recensusing | Negative |
| | Improved measurements of buttressed trees | Negative |
| | "buttress creep" (bole irregularities move up with time) | Positive |
| | Basal area inflation due to a disproportionately rapid radial increment of buttresses | Positive |
| ***Post-measurements checking data and publication*** | Reducing extreme increments | Negative |
| | Rounding-up of negative increments ("false negatives" are equalled to zero) | Positive |
| | Selective reporting of plots subjected to catastrophic disturbance | Negative |

Table 6.1. List of the main sources of bias in BA change estimates.

## 6.2. Sources of noises and biases in permanent sample plot inventories

### 6.2.1. Plot size and shape

The size of sample plots is very relevant when some PSPs structural and dynamic properties are analysed. Mortality and recruitment of trees can be very irregular at small spatial and temporal scales (Brokaw 1983), and the mean size of a gap is a particularly relevant element in this respect. Different patches of forests hold a diverse and dynamic population of stems of tree species with different ecological characteristics and exposed to a different degree of competition for resources not uniformly available. The definition of an adequate plot size is fundamental to capture an acceptable part of this environmental and vegetational variation. The influence of plot shape has not been explored extensively, especially in the tropics (Condit et al. 1996b), whereas the effects of plot size on estimates of plant diversity have been assessed in detail (Kilburn 1966). Species-accumulation curves show that rectangular quadrats have more species than square quadrats of the same area (Condit et al. 1996b), and the narrower the rectangle, the more the species contained in it per unit area (Condit et al. 1998). Long, rectangular plots tend to contain a greater range of forest structure and composition than square plots of the same area (Laurance et al. 1998c), because they are more likely to capture variations in topography, soil and drainage conditions, variation in degree of perturbation (gaps, treefalls, etc). On the other hand, square plots are in fact easier to map and establish, and are less likely to be biased by edge effect which occur when uncertainties on whether to exclude or include trees along a margin arise (Laurance et al. 1998c). The way a forest permanent sample plot is established has therefore significant consequences on the outcomes of the investigations and has to be carefully pondered in the interpretation of the data. The PSPs used in the present study were exclusively square in shape.

### 6.2.2. Plot location

To analyse BA changes over time, it is fundamental to consider the stage of development of the forest included in the PSPs used for the calculations. If mature-phase forests were not included, plots would naturally show an increase in BA simply as a result of successional processes. The total exclusion from the investigation of sites that underwent past perturbation is not achievable with certainty, and the evaluation of disturbance depends on the temporal scale considered (how far in the past?). At least, it seems possible to test whether the recovery from disturbance could itself explain positive changes in BA, or the observed pattern is driven by a biased selection of successional sites. Two tests have been proposed by Phillips et al. (2002a) to explore the possibility to attribute the observed BA changes to genuine region-wide phenomena of forest recovery from large-scale disturbance. Their application to the data used in the present study is shown in sections 6.4.1, 6.4.2. and 6.4.3. of this chapter.

### 6.2.3. Diameter measurements

Measuring diameters is problematic, as stem irregularities are very frequent. Good measurements of stem dbh are critical, since diameter increment is the difference between measured dbh in two censuses. Buttressed trees in particular often pose serious measurement problems as they progressively affect the point of measurement (by convention located at 1.30 m from the ground) and produce an increasingly more marked inflation of dbh measurement (Clark and Clark 1996; Sheil 1995b). Their diameter could be measured with a relaskop, or better, a ladder should be used to reach a point of measurement (p.o.m.) located at least 50 cm above the point of insertion of the buttresses. The use of a digital camera has also been tested satisfactorily (Malhi *pers. communication*).

To what extent was this good practice followed in establishing and re-censusing the plots described in the present study? The most common bias is caused by the tendency for some foresters and ecologists to measure trees at a standard 1.3 m above ground, regardless of any stem deformity. Different people usually carry out the PSPs measurements each time, and the protocol is not necessarily consistent.

There is evidence for a general improvement in the standard protocol adopted for forest measurements. If some biases affect the database, this is more likely to have happened in the past inventories. With respect to the dataset from the Western Amazon used for this study, a proper protocol was used from the time the plots were established. For stems with buttresses at 1.30 m, standard diameter measurements have been replaced by relaskopic measurements. The moving of the p.o.m. is recorded and in case of irregularities at the p.o.m., the exact point where diameter measurements are conducted is specified. Whenever diameter measurements are a result of an estimate due to the inaccessibility of the stem (e.g., dbh measurements of *Socratea exorrhiza* are usually quite difficult because of the thorny stilt roots typical of this species), this is specified in the data. In the Bionte dataset, trees have been properly measured above buttresses in all inventories. In the BDFFP plots, some biases, such as the rounding up of negative diameter measurements, have been detected in the first inventories (W. Laurance, *personal communication*) but the protocol has been increasingly refined with time, so the quality of dbh measurements has improved (see paragraph 6.4.6). The whole database from the BDFFP project has been screened and improved in the quality of dbh measurements and in the taxonomic identification of species.

The way diameters are measured is a crucial element in BA change and growth calculations. In a recent critique (Clark 2002), the erroneous application of the protocol for PSP measurements has been claimed to have lead to significant overestimates of forest-wide BA changes. The outputs of a simulation of the impact of buttresses on BA calculation are presented in section 6.4.3 of this chapter.

### 6.2.4. Impact of general disturbance

The various stages of PSP establishment and measurement are all likely to have an impact on BA change calculations as they alter the vegetation. Lines and paths cut through and around the plot increase local accessibility to people and animals. The physical damage produced by specimens' removal, tree-climbing, branch cutting, slashing of bark to help species, identification, and walking repetitively inside the PSP, especially along preferential corridors in correspondence of the boundaries or along some trajectories that intersect the plot, generates a perturbation. Cutting of lianas and climbers is likely to have an influence on stem competition, stem growth and tree-fall (Putz and Mooney 1991). Demarcation of the plot may be essential to avoid destructive practices but permanent marks to identify PSP boundaries should produce a minimum visual impact, to avoid attracting attention to the plot.

The operations of mapping tree position and topography further increase the problems of trampling of seedlings, soil compaction, alteration of local ground-litter conditions for germination, and alteration of light gradient to the ground. Botanical collection may also have an impact on the vegetation, unsterilized telescopic plant collecting poles are usually used to cut representative small branches, and sometimes iron-spiked tree-climbing gear is utilized to gain access to the canopy. A study on the mortality rate of collected and noncollected trees in the Peruvian Amazon (Phillips et al. 1998b), has shown that, at least in the short-term, the collection of voucher specimens from tropical moist forest trees does not seem to affect their survivorship, despite the physical damage produced. Nevertheless, the initial or cumulative impact of research activities on tree survivorship in permanent plots needs to be monitored, as few data exist.

After repeated censuses have been carried out, ongoing researcher perturbation may cause the system studied to become progressively less representative of wider tracts of forests. The consequences of intense research activities are likely to have particular significance in long-term studies. These methodological limitations have been recognized (Hall et al. 1998; Sheil 1995b), but are still difficult to quantify. As suggested by Phillips et al. (2002a) it should be possible to detect the impact of methodology, when more than one census is available: increments of climbed or collected trees should decline with the time and mortality should increase, as growth would be depressed by the impact of collection and the spreading of infections. The other types of disturbance (e.g. trampling of seedlings, soil compaction) would be detectable through a general decline in growth and an increased mortality, especially localized where the perturbation has been more severe. However, with respect to BA calculations, these impacts are likely to produce a negative bias and lead to underestimation of any genuine positive trend in BA.

One positive bias in BA calculations due to research artefacts has been identified. The localized swelling of stems around the nails used to attach tags to them, especially if nails are located very close the point of measurement, would produce an overestimate of diameter measurements. As shown by Phillips et al. (2002a), this does not seem to be the case for most of the Neotropical sites previously analysed to detect changes in BA. When changes in p.o.m. have been recorded, this artifact is less likely to have occurred. The BA inflation due to swelling around the nails should increase with time and not be manifest in recruitment. This whole issue is presented later in the discussion of results (paragraph 6.4.5).

## 6.3. Sources of biases in data processing

### 6.3.1. Plot data "harmonization"

The checking and correction of PSP data is the first stage of data processing. Careless measures create a bias and a random error component. The procedure of correction, in datasets containing more than one census, is also referred to as "harmonization" (Sheil 1995b), and consists of a careful evaluation of consistency between data from the last inventory and the previous ones. Thus, diameter measurements are examined to see if they follow a coherent sequence with records before and after. In addition, names of species and codes for individuals are checked to verify the consistency. Increments for each tree are calculated and thresholds for maximum and minimum acceptable values defined. In seasonal tropical climates, where soil water availability is periodically low, seasonal fluctuations in tree stem diameter has been shown to be significant; a 10-fold difference in soil water availability (determined measuring soil matric potential) between measurement occasions can lead to a 4% bias in estimates of annual growth (Baker et al. 2003). Negative changes in diameter are not impossible (hydrostatic stem flex, shedding of bark) (Sheil 1997), and need not necessarily be corrected, but criteria have to be defined to determine whether some individuals should be included in calculations. Sheil (1995) considered as acceptable those values of diameter changes contained between –0.2 and + 4 cm $a^{-1}$, while Condit et al. (Condit, Hubbell, and Foster 1993a; Condit, Hubbell, and Foster 1993b) eliminated from calculations those stems that shrank by more than 5% of the initial diameter $a^{-1}$ or grew by over 7.5 cm $a^{-1}$. The second approach was adopted in the present study for the calculation of growth and BA change. Discarded data, not used for growth analysis, were still included in the calculation of mortality rates and static population statistics. There are also examples in the literature of a systematic exclusion from growth analysis of very large trees, being characterized by massive buttresses and likely sources of inaccuracies (Taylor et al. 1996).

The accuracy of measurements and the quality of the database can be assessed verifying the frequency of the rounding to the nearest integral unit in diameter measurements, and the incidence of "rounding up" of negative measurements (Phillips et al. 2002a). This bias is generated by the wrong assumption that negative increment calculations are unacceptable and should therefore be entered as zero, either during fieldwork or afterwards, during the stage of data processing. Rounding errors can be detected by plotting the size frequency distribution of diameter measurements. This analysis was applied to one plot in Phillips et al. (2002a); here the assessment is extended to three plots (see section 6.4.6), to demonstrate the general improvement in the accuracy of tree diameter measurements over time.

## 6.4. Tests for positive biases in BA calculation

It has been argued by Phillips et al. (2002a) that each methodological issue is likely to leave a specific trace in the data and ultimately affect BA calculation, positively or negatively in a systematic way. It should be therefore possible to detect artefacts and assess their potential impact on final calculations.

Their results are shown in this section. The tests carried out are the following:

1. Analysis of "self-thinning" and of BA area accumulation rates to assess the effect of the "immature forest" bias on BA calculations.
2. Simulation of various scenarios of buttresses occurrence and magnitude to evaluate the impact of buttress creep on BA calculations.
3. Analysis of contribution from different tree size classes to total BA accumulation to evaluate the role played by big trees (by definition, those stems with > 70 cm of dbh) in the positive trend in BA.

Stem swelling around nails is also discussed in this chapter (see section 6.4.5.), among the potential positive biases affecting BA net change calculations.

The data used for each test are the following:

- self-thinning test on "immature forest" sites: 37 PSPs

- simulation of buttress creep: Brazilian data (BDFFP, 4 PSPs; Bionte, 3 PSPs), Peruvian data (Tambopata, 1 PSP), equilibrium (for 1 plot, real data have been manipulated to get to equilibrium conditions)
- BA accumulation by size classes: 23 PSPs chosen among those 1-ha plots with a longer census interval.

### 6.4.1. TEST 1a – "Self-thinning"

A biased selection of immature forest sites could generate erroneous estimates of forest-wide BA accumulation. The tendency would be for the plots to accumulate biomass simply as a normal result of successional processes and not as a real phenomenon of BA accumulation triggered by other causes. One way to test whether the selected sites are merely undergoing a recovery from a local major disturbance would be to compare their demography and BA change with successional sites. The self-thinning rule, where stem density declines as succession advances, has been widely described for mono-specific and multispecies stands in temperate and tropical forests, as reported by Phillips et al. (2002a) from various studies (Drake and Mueller Dombois 1993; Kiyoshi and Kihachiro 1999). This phenomenon is the result of competition of growing stems. Typically occurring in even-aged stands recovering from major disturbance, as during primary and secondary successions, the thinning affects smaller trees that are out-competed by larger individuals. The overall increase in BA observed over time should be accompanied by a decreasing number of stems. The process seems to be more complicated in species-rich forests where the decrease in stem number could be manifest later. In fact, the rich spectrum of shade-tolerant species that can survive in a suppressed state is likely to delay the decrease in tree density. Despite the lack of census intervals long enough to detect this phenomenon, a more immediate "self-thinning" should anyway take place (Phillips et al. 2002a). Mainly dominant and co-dominant canopy trees that are competing for growing space from the early stages of succession would undergo a reduction in density. The present test shows how the rate of change in stem density of some Amazon forest sites varies as a function of the rate of change in stand basal area. The test has been extended from 10 PSPs in Phillips et al. (2002a) to 37 1-ha Amazonian PSPs. Results are presented in Figure 6.1.

Most of the sites gaining BA are also increasing in stem density (59.5 %), indicating that the plots do not host successional forests. Plots were distributed across the other three quadrants as follows: 2.7% in quadrant II, 13.5% in quadrant III, 18.9% in quadrant IV, and 5.4% do not show variation in annual stem density rate of change but an increase in the annual rate of change in BA. The sites that gained most BA have also experienced a large increase in stem density (Pearson's $r = 0.665$, $P < 0.001$).

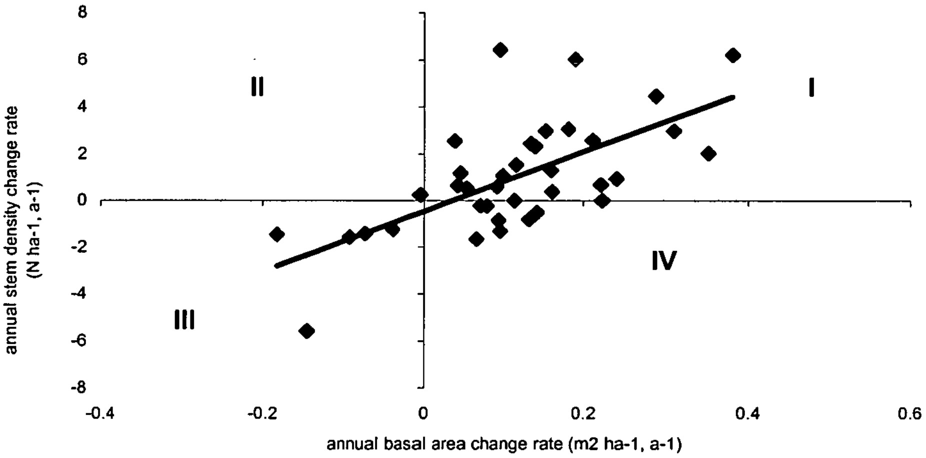


Figure 6.1. Rate of stem density change versus rate of BA change, in 37 1-ha Neotropical PSPs.

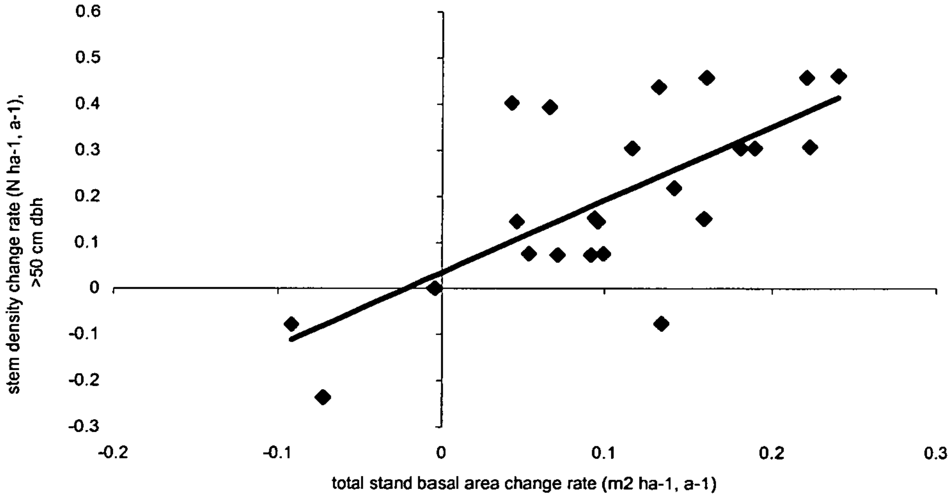


Figure 6.2. Rates of stem density change versus BA rate of change, in 23 1-ha Neotropical PSPs, for stems of >50 cm of dbh.

The pattern is equally apparent for those dominant and codominant canopy trees, defined as trees with >50 cm of dbh. Their stem density also increases with an increasing total stand BA rate of change, as shown for a sub-sample of 23 PSPs with the longest census interval, in Figure 6.2 (Pearson's correlation coefficient = 0.70, $P < 0.001$). Plots are distributed across quadrants in these proportions: 82.6% in quadrant I, 0% in quadrant II, 8.7% in quadrant III, 4.3% in quadrant IV, and 4.3% do not show variation in annual stem density rate of change but an increase in the annual rate of change in BA.

These results are contrary to what should be expected if self-thinning was taking place in an even-aged late-successional forest. Such a forest would accumulate biomass as a consequence of a cohort of large canopy trees increasingly suppressing smaller trees and competing with one another.

### 6.4.2. TEST 1b – Stand BA accumulation rates

A way to disprove that the selected sites are merely undergoing a recovery from a local major disturbance would be to compare their rates of BA accumulation with those derived from direct studies of late secondary successional sites of known age.

If the recorded BA accumulation rates are observed to be lower for lowland tropical sites known to be younger than those analysed in the present work, then the biomass increase observed in the former is unlikely to be driven by secondary succession.

There are few reliable measures of biomass accumulation in late successional forests to compare with. However, average estimates can be gained from the literature. Phillips et al. (2002a), quoting works by Brown and Lugo (1990), Hughes et al. (1999), Johnson et al. (2000), and Salimon and Brown (2000), reports that most secondary forests acquire at least 50% of aboveground biomass within 30 yr and the rate of increase declines rapidly with age.

Phillips et al. (2002a) estimated that maturing successional forests after 300 yr can accumulate, as a result of successional process, just ~3 kg $ha^{-1}$ $a^{-1}$, equivalent to 0.0014% of the biomass. This value was obtained by simulating biomass accumulation rates for late secondary succession, using an exponential model from Salimon and Brown (2000), fitted to secondary forests in Acre (southwest Brazil). The model was constructed by analyzing chronosequences and estimating the biomass of secondary forest stands of known time since abandonment. Standing live aboveground biomass was calculated using allometric equations developed by Uhl et al. (1988) (one equation specific for the genus Cecropia and another one for all the other secondary species), and accounting for floristic and structural changes. The total aboveground stand biomass at maturity was estimated to be between 250 and 320 Mg $ha^{-1}$. These estimates correspond to typical values for mature forest stand in

Acre (Brown et al. 1992), but are also representative of most lowland Amazonian rainforest stands. The prevalent soil type found in the forest stands used to build the model of biomass accumulation were Ultisols with patches of Oxisols, therefore resembling the most common edaphic conditions found across the sites presented in this study.

The estimates of biomass accumulation are more than two orders of magnitude less than the mean rate of increase recorded in the Neotropical sites analyzed in the present work (from the data used in the present work the average BA net accumulation rate is of 0.12 $m^2$ $ha^{-1}$ $a^{-1}$, for primary plots, equivalent to 0.4 % of biomass).

Aboveground biomass recovery of secondary forests is a well studied process (Brown and Lugo 1990). It has been observed that a typical sequence of events occurs in all successions, and suggests that many forest functions and characteristics (species richness and biomass) may resemble old-growth conditions long before species composition does (Guariguata and Ostertag 2001; Kennard 2002). In general, secondary forests rapidly accumulate up to 100 Mg $ha^{-1}$ of biomass within 15-20 years after abandonment (Brown and Lugo 1990; Silver et al 2000). Along a chronosequence in Central Panamà, Denslow and Guzman (2000) reported a peak in tree BA at intermediate stand ages (70 years), followed by a decline in 100-year old stands, to eventually reach somewhat lower, old-growth values. In the study by Denslow and Guzman (2000), stand structural changes followed the biomass accumulation model described by Peet (1992) as a shifting mosaic in which tree establishment and mortality are moderately synchronous and maximum biomass accumulation occurs in intermediately aged stands. Studies of the first 20 years of tropical successions (Richards 1955, 1996; Brown and Lugo 1990; Ewel 1980) suggest that canopy closure is rapid and maximum leaf biomass is attained within eight years; that dominance of a few species of pioneer trees is established early (two years), but begins to break up within less than 25 years; and that long-lived secondary and primary species may be present early, but begin to dominate with the demise of the first cohort of pioneers.

However, factors such as climate and past land use (Brown and Lugo 1990; Silver et al 2000) tend to affect the rate of biomass accumulation, which varies from site to site. The timing and the duration of the events described above depend on seed source, land-use history, and site productivity, but in general secondary forests that originated after shifting cultivation grow faster than secondary forests developed in abandoned pastures (Fearnside and Guimares 1996). If past disturbance has occurred in the sites presented in this study, it is more likely to be attributable to shifting cultivation than to substitution of forest with pastures, therefore the expected consequence would be fast biomass accumulation rates, followed by present day biomass accumulation rates lower than those currently observed by looking at changes in BA over time in the PSPs presented in this study.

### 6.4.3. TEST 2 – "Buttress creep"

The progressive vertical growth of buttresses has been indicated as possible cause of the BA accumulation observed. The effect should be increasingly manifest as the irregularity begins to affect the point of measurement during the time interval between inventories. This is particularly true when careless measurements are carried out without appropriately shifting the point of measurement.

Trees tend to progressively deform from below. At the time of plot establishment, the p.o.m. for buttressed trees should properly be placed 50 cm above the point of insertion of buttresses, but during the monitoring period, the irregularity begins to progressively affect the stem at the p.o.m. If re-measurement teams are careless and fail to shift the p.o.m., the positive bias in net change stand BA estimates should become more evident with time and produce a considerable inflation in net BA change, as an increasing number of p.o.m. would become affected by stem irregularities. No such trend is apparent in the cluster of Neotropical plots used for the present analysis (Figure 6.3). In Fig. 6.3, the annual net BA change $ha^{-1}$ over time intervals of different length, is shown for each of the 37 plots. Thus, each plot is represented by more than one point, each corresponding to a progressively longer time interval. Annual BA net change is positive for most measurements, although negative values were recorded, especially over shorter time intervals.

The overall impact of poor diameter measurements on estimates of BA changes has been quantified in some PSPs, used as examples, extracting the mean number of trees affected by buttresses within 1-ha forest plots, and comparing BA values derived from a "biased" and an improved measurement protocol. BA values obtained from relaskopic dbh measurements, on a p.o.m. which has been changed over time to avoid buttress creeping or/and nail swelling, were compared to BA values obtained from tape dbh measurements at 1.3 m above ground, regardless of the occurrence of buttresses in the proximity of the p.o.m.).

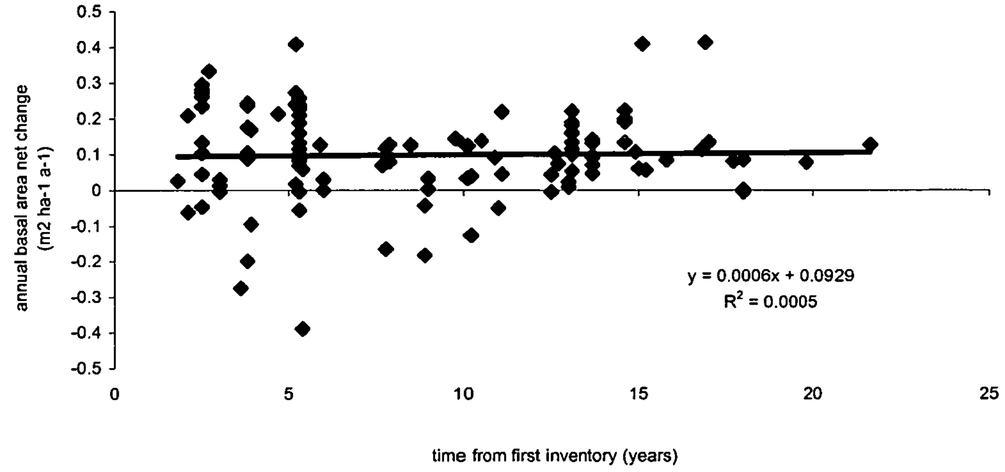


Figure 6.3. Annual BA net change $ha^{-1}$ versus time from first census in 37 1-ha PSPs from the Amazon basin. Each plot is therefore represented by more than one point.

| Plot | N. buttressed trees | Mean N. buttressed trees /site | % ot total N. stems/ha | Annual net BA change (non corrected values) | Annual net BA change (corrected values) |
|---|---|---|---|---|---|
| Cuzco Amazonico 1e | 9 | | 1.8 | 0.289 | 0.296 |
| Cuzco Amazonico 1u | 18 | | 3.5 | 0.328 | 0.309 |
| Cuzco Amazonico 2e | 10 | | 2.1 | 0.514 | 0.520 |
| Cuzco Amazonico 2u | 16 | 10.8 | 2.8 | 0.298 | 0.209 |
| Tambopata 0 | 6 | | 1.1 | 0.110 | 0.110 |
| Tambopata 1 | 6 | | 1.1 | 0.091 | 0.089 |
| Tambopata 3 | 3 | | 0.5 | 0.084 | 0.090 |
| Tambopata 4 | 3 | | 0.6 | * | NA |
| Tambopata 6 | 0 | 3.6 | 0.0 | | |
| Allpahuayo A | 8 | | 1.3 | | NA |
| Allpahuayo B | 9 | 8.5 | 1.5 | | NA |
| Sucusari A | 10 | | 1.7 | | NA |
| Sucusari B | 5 | 7.5 | 0.8 | -1.50 | -1.84 |
| **Min** | 0 | 3.6 | 0.0 | | NA |
| **Max** | 18 | 10.8 | 3.5 | | NA |

Table 6.2. Frequency of buttressed trees in 13 South Peruvian PSPs. The mean number of trees affected by buttresses in each site is indicated and the BA changes over the longest census interval are shown from census data with both biased and improved dbh measurements. The asterisk identifies one PSP were no dbh relaskopic measurements were found. For some PSPs the comparison was not possible as no changes in p.o.m. were recorded, therefore values are not available (NA).

For some older plots, improved relaskopic measurements have been adopted in the last few inventories and changes in p.o.m. over time, to avoid buttress creeping, have been recorded. For these plots it is possible to extract "biased" and correct dbh measurement series and compare them, to gain insight into the magnitude of the effect of buttress creeping on stand BA calculations.

"Biased" dbh series are obtained attributing to trees affected by buttresses a growth rate that equals the mean growth rate in the early census intervals, letting trees grow as in the past and without changing the p.o.m..

Correct dbh series derive from relaskopic dbh measurement applied to a new p.o.m. unaffected by buttresses during more recent inventories. In order to enable the estimate of BA change over time, despite the change in p.o.m., a new BA value has been calculated for the intermediate censuses, "correcting" previous dbh values in intermediate censuses using a mean relative growth rate. The growth rate was extrapolated using the initial dbh tape measurement (with no buttress effect) and the final corrected dbh measurement (relaskopic measurement above buttresses), and calculating a mean annual dbh increment. The effect of the improved protocol on the calculation of relative BA change over time is assessed comparing "corrected" and "biased" annual net changes in BA over time. Results are shown in table 6.3. The values of annual net BA change are not systematically smaller or larger in the improved versus the "biased" set of data, but the direction of change is the same for the two protocols, and the magnitude of the change is similar between the two sets.

In one plot, indicated by an asterisk in Table 6.3, no trees with dbh relaskopic measurements were found. In some recently established PSPs, the dbh of large trees was measured with the relaskop from the first census and the p.o.m. was not changed all through the monitoring period, therefore the comparison between "biased" and correct protocol did not show changes.

Thus, even if erroneous measurements around buttresses are common (and we have given evidence above that they are not), they only have a modest effect on the net magnitude of the predicted carbon sink. This error should be avoided and corrected for where possible, but it is unlikely that measurement errors can explain the increases in basal area measured in the plots rejected by Clark (2002) as being apparently erroneously measured, and data from these plots should definitely not be rejected.

We reach the conclusion that any poorly measured plot can still give a reasonably reliable estimate of change in basal area, as long as the nature of the type of measurement error does not change systematically with time.

### 6.4.4. BA accumulation by size class

BA inflation could be attributed to a wide range of potential field-measurement errors on BA change estimates. The combined effect of several errors (BA inflation and buttress creep) was empirically tested, by evaluating net change by size class, assuming that buttresses are disproportionately large and frequent on larger diameter trees (Clark 2002), and therefore the effects of buttress creep should be especially marked in trees with large diameters. For all the plots used in the analysis of forest stand dynamics in the present work (37 1-ha PSPs), net biomass accumulation attributable to different size classes was quantified (see Chapter 5, section 5.4.3.). Similarly to what is shown by Phillips et al. (2002a) on a different selection of sites, the analysis in the present work reveals a large variation between plots, in the contribution to overall BA change from different diameter size classes, but it emerges clearly that BA gains are not limited to large trees. Furthermore, the BA net accumulation rate is not increasing with time as would be expected if the effect were merely attributable to biases in large trees measurements, with no or irrelevant positive contribution from small and medium size trees, and progressively larger errors in larger trees measurements (see graph in Fig. 6.3, showing annual BA net change over time from first census).

### 6.4.5. Swelling around nails

The swelling of stems around nails could generate an error in BA change estimates if the point of measurement is close to where nails used to hold tags are placed. If teams are careless in remeasuring trees, failing to move the points of measurement if bole irregularities arise over time, the artefact could partially explain the apparent BA increase. If this were the case, the effect should be manifest in a considerably higher BA increase observed over the first measurement, due to the increasing production of reaction tissue by the plant. Few trees are recruited and tagged at each new census, therefore the potential bias due to swelling around nails is likely to be less pronounced in all the following census intervals. . Mean rates of BA change were calculated over progressively longer census intervals for 37 1-ha Neotropical PSPs. While BA annual net changes would be expected to be significantly smaller over longer time intervals versus the first census period, the values obtained are not significantly different. This finding seems to disprove the existence of a "cumulated" bias due to swelling around nails. .

### 6.4.6. Test for accuracy in diameter measurements

It is important to evaluate how accurately diameter measurements are carried out when monitoring individual stem growth and stand BA changes over time. It is possible to evaluate *a posteriori* how precisely the protocol has been applied. A selection of PSPs was used to evaluate the occurrence of:

- ➢ approximation of diameter measurements (4 plots, BDFFP, Bionte, Tambopata, Cuzco Amazonico);
- ➢ rounding up of diameter increments (3 plots from BDFFP).

A common bias occurring in dbh measurements is the approximation to the closest integer values. This can be seen from raw data, plotting frequency distributions of diameter measurements. Sudden peaks in measurement frequency would be evident in correspondence with integer values, in the case of flawed datasets, whereas lower frequencies often coincide with some fractional values that immediately precede the integer values. Some examples of dbh measurement distributions are shown in Figure 6.5 (a,b) and 6.6 (a.b), for two Brazilian and two Peruvian plots respectively. Some peaks in frequency are evident for integer dbh values, but within none of the datasets presented do they recur systematically. In one plot only (Tambopata), peaks in the dbh measurement distribution tend to occur more frequently every 5 cm along the *x*-axis. For this plot, a simulation was run to quantify how much the approximation in diameter measurements affects the estimates of BA change. Randomly determined values (between –0.99 and 0.99) were added to diameter measurements of stems that were part of the observed peaks in the initial and final census (see Fig. 6.6 a), and a new value of BA was calculated from both censuses. These new values were compared to those calculated from the original data. The difference in the BA had a negligible range of –0.42 % and 0.95 % of the value calculated from the original diameter measurements, leaving the positive balance in BA substantially unaffected.

#### ***Rounding up of dbh negative increments***

Biases in diameter measurements could be generated by incorrectly assuming that negative values in diameter "growth" must be rejected. This error could be introduced while working in the field, when the crosschecking with previous diameter measurements is carried out there, or during the post-measurement analysis and harmonization of field data. Negative values are entered as zero values. This rounding-up of negatives should be evident when plotting the size-frequency distribution of diameter increments between successive censuses. In the case of bias, data should show an overrepresentation of individuals characterized by no growth, and an underrepresentation of trees with small negative growth values. The bias can be approximately quantified and comparison between different measurement periods could be carried out to assess the quality of the database over time.

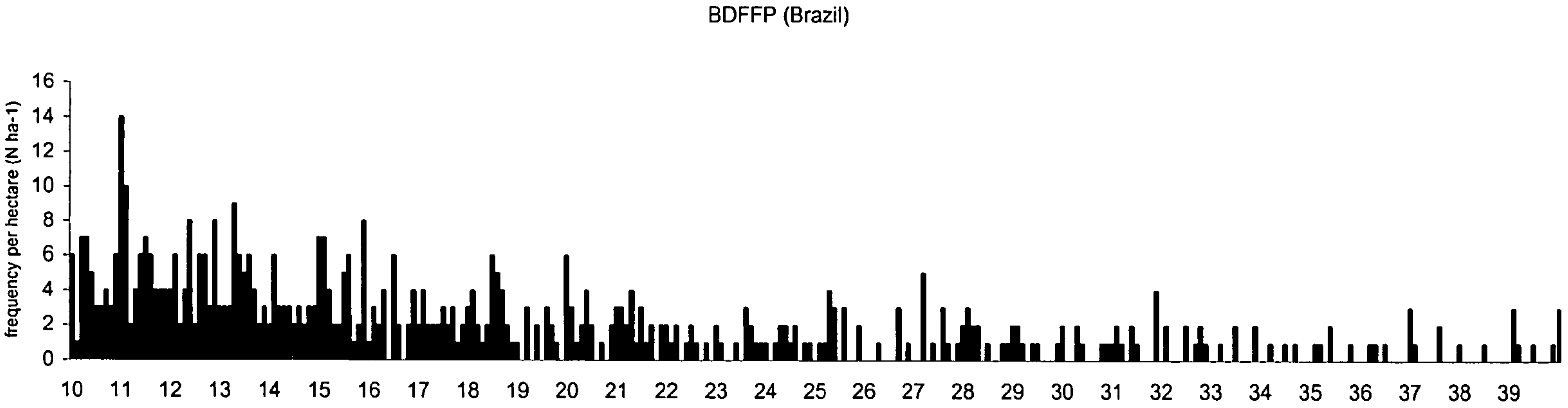
The number of trees rejected as unacceptable (both excessive positive and negative increments) is shown in Table 6.3 for 21 plots from the BDFFP experiment, as an example of the range and maximum possible size of the error that could have occurred in the estimate of BA positive change over time. Increments were discarded by checking both excessive positive and negative increments, independently for two consecutive periods that were compared in other analyses. The number of trees per interval refers to the number of stems surviving from the initial to the final inventory, and for which the calculation of increment was therefore possible. The threshold used to discard potentially erroneous dbh measurements are those adopted by other authors (Condit et al. 1999).

Trees rejected for positive biases are less frequent than the negative ones, and this leads to a potential systematic over-estimate of BA net change (whose magnitude is presented in the last column of Table 6.3), as trees positively biased are discarded less frequently. The difference between initial and final BA values, for each cluster of PSPs from the BDFFP experiment, was calculated both discarding and keeping the supposedly erroneous measurements. The two values of BA annual net change over time were compared. The table shows the difference between the two values, expressed as a percentage. In one reserve (1301) the value of net BA change estimated for the first interval appears to be considerably affected by the exclusion of the supposedly erroneous values, although this seems to be an extreme case due to serious negligence in dbh measurements. Analyzing individually each plot of reserve 1301, it seems the biased measurements are homogeneously spread across plots, and probably attributable to the negligent work of one specific team.

It has to be noted that in none of the plots of the BDFFP reserves presented in Table 6.3 does the value of the net BA change turn from negative to positive as a consequence of having removed supposedly erroneous dbh measurements.

| BDFFP reserve | N (ha) | interval | N (trees) | N total trees rejected | Negative | Positive | %diff. BA |
|---|---|---|---|---|---|---|---|
| 1201 | 3 | 1st | 1727 | 3 | 3 | | 1.8 |
| 1201 | 3 | 2nd | 1585 | 4 | 4 | | 2.0 |
| 1301 | 6 | 1st | 3654 | 26 | 25 | 1 | 17.3 |
| 1301 | 6 | 2nd | 3416 | 5 | 5 | | 3.6 |
| 2303 | 2 | 1st | 1280 | 1 | 1 | | 0.02 |
| 2303 | 2 | 2nd | 1235 | 4 | 3 | 1 | 1.26 |
| 3402 | 9 | 1st | 4881 | 14 | 14 | | 2.71 |
| 3402 | 9 | 2nd | 4808 | 9 | 9 | | 5.49 |

Table 6.3. Fraction of excessively positive and negative diameter increments excluded from the analysis of BA change for 12 plots from 4 reserves of the BDFFP experiment (Manaus, Brazil), over two census periods for each reserve. Trees were discarded separately for two consecutive time intervals. The number of trees with positive and negative bias in dbh measurement is indicated in separate columns. %diff. BA is the percentage correction to the net BA change caused by discarding trees and indicates the maximum potential over-estimation due to the removal of the supposedly erroneous dbh measurements.



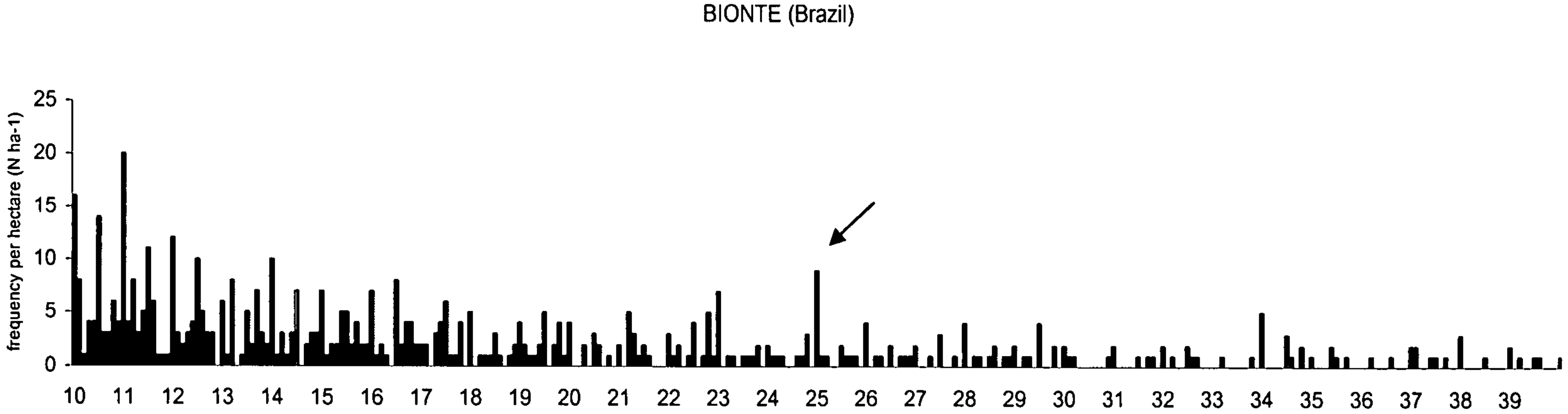


Figure 6.4 (a,b). Frequency distribution of dbh measurements in some Brazilian plots (BDFFP (1101), Bionte (BNT-01)).

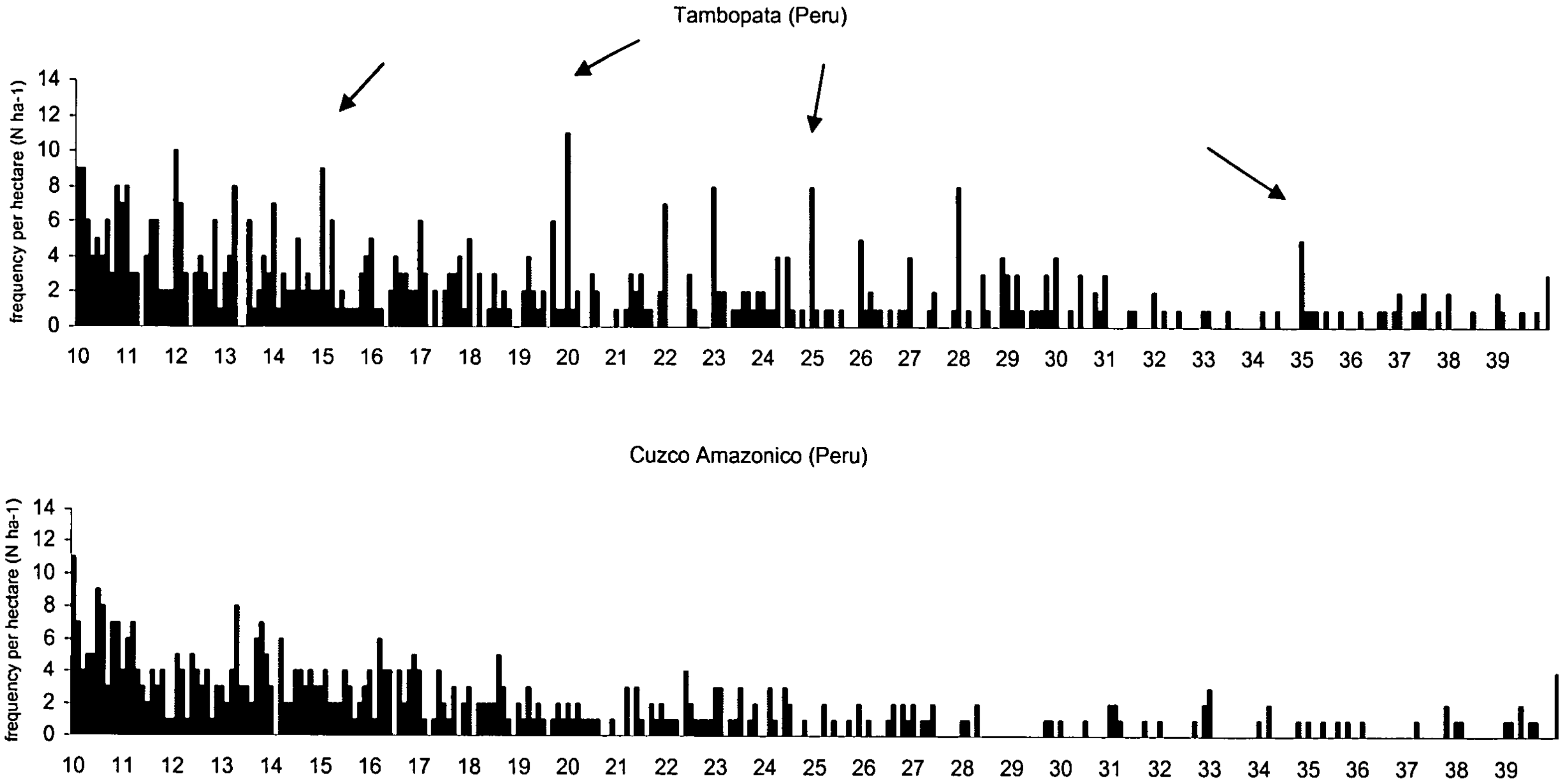
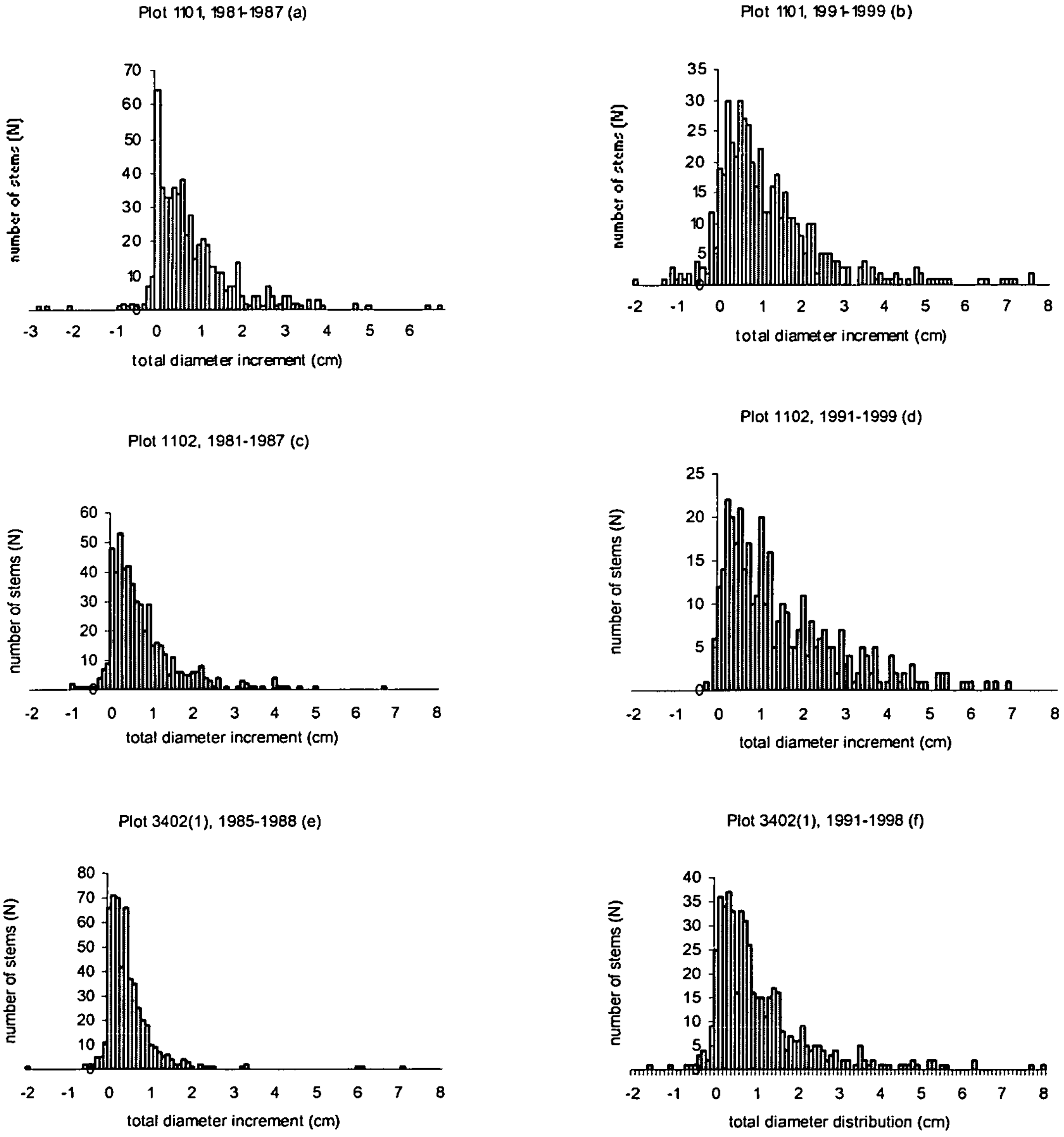


Figure 6.5 (a,b). Frequency distribution of dbh measurements in some Peruvian plots, (Tambopata (4), Cuzco Amazonico (2e)).

Some evidence for improvements in diameter measurements are provided in Phillips et al. (2002a). A more accurate protocol seems to have been applied in more recent censuses, as shown in preliminary checks on the BDFFP data (Manaus, Brazil), used also in the present work. Three examples are presented from the BDFFP database, showing the expected decrease in the frequency of zero values (Figure 6.7).



Plot 1101, 1981-1987 (a)

Plot 1101, 1991-1999 (b)

Plot 1102, 1981-1987 (c)

Plot 1102, 1991-1999 (d)

Plot 3402(1), 1985-1988 (e)

Plot 3402(1), 1991-1998 (f)

Figure 6.6 (a-f). Size-frequency distribution of diameter increments for some selected Brazilian plots (BDFFP 1101, 1102, 3402).

As reported in Phillips et al. (2002a), the high frequency of zero values tends to be the effect of rounded measurements, both slightly negative and slightly positive, thus reducing the impact of flawed measurements on stand BA calculations. Considering as flawed the negative measurements and potentially biased those increments that equal zero, the fraction of erroneously measured stems changes, for the three plots shown, from an average of 16.2% to an average of 9.4% of the total number of stems, from the first to the second period tested, indicating a mean reduction of wrong measurements of 6.8% through time. The decrease of diameter measurements equal to zero is particularly pronounced, diminishing on average from 10.8% to 3.9% of the total stems censused, during the first and second interval respectively. However, it is necessary to consider the different length of the time intervals presented in Fig. 6.7. ($1^{st}$ interval = 4-6 years, $2^{nd}$ interval = 7-8 years). The frequency distribution of increments would be expected to shift to the right with an increasing census interval. Nevertheless, the large fraction of zero increments during the first time interval does not seem plausible, considering the six-year span, and there was a halving of zero increment values despite a simple increase of two years in census interval in the $2^{nd}$ period in each of the three examples given. This leads me to think that a genuine improvement in diameter measurements has occurred.

Removing from the census those stems with negative increments and increments that equal zero, the calculated value of annual BA gain at stand level would be higher in each of the three PSPs in Fig. 6.7, for each of the two intervals explored. Disregarding potentially erroneous measurements, the annual BA gain would be on average 7.0 % and 3.4% higher, during the first and second census interval respectively. However, the magnitude of this additional gain cannot be compared between census intervals of different length, as the estimated productivity of surviving stems was found to be dependent on the length of time interval between consecutive inventories, as explained in the next sections.

## 6.5. Other methodological issues in PSPs measurements

### 6.5.1. Census interval dependency of stand dynamic rates

As already pointed out in other sections of this work, the comparisons of commonly used estimates of recruitment, mortality and turnover rates are problematic when census intervals are unequal, because estimates depend on the time interval between censuses. The inverse relationship between mortality rates and time interval between censuses was identified by various authors (Sheil, Burslem, and Alder 1995; Sheil and May 1996), and was explored further by Lewis et al. (in prep.). A correction factor for mortality was identified and the influence of the time dependency of mortality was quantified on a large Pantropical dataset. The effect was found to be negligible and did not change the overall picture of an increasing turnover through time, for most of the PSPs studied, which in part were used for this work.

The effect of the length of the time interval was also observed on forest stand productivity, found to be negatively correlated with the length of the census interval. The estimated total stem production between two censuses derives from the wood growth of trees that survived from the first census to the second census, plus the biomass of trees that appeared only in the second census. However, at least two factors are not considered in the calculation of stem production: (i) the growth of stems that were never recorded between the two censuses as they were recruited and died before the second census and (ii) the stem production in trees that died prior to the second census. Therefore, the direct calculation implies an underestimate whose magnitude is positively correlated with an increasing time interval between censuses, and is expected to be greater in more dynamic forests, where growth rates and the number of stems dying are higher. The influence of the census interval on estimates of forest productivity was observed and quantified for three Central Amazonian PSPs that had annual diameter measurement (BIONTE dataset, Manaus, Brazil) by Malhi et al. (in review a).

## 6.6 Conclusions

There are several biases that could originate from inappropriate selection of sites and erroneous application of the measurement protocols.

The correct protocol to be used for the establishment of PSPs was described and the way it has been applied to the PSPs analysed in this work was discussed. Some tests were proposed to show the impact of major flaws and tackle the hypothesis of methodological issues interfering with the observed accumulation of basal area in some PSPs across the Amazon Basin.

The suggested tests were applied to a collated dataset derived from different studies. The results from these tests do not suggest that the observed accumulation of basal area over time, shown in Chapter 5, is a measurement artefact.

# Chapter 7. Analysis of potential shifts in rainforest species composition

---

## 7.1. Introduction

Global change may already be showing measurable changes in tropical rainforest dynamics and floristic composition. Consideration of experimental and theoretical evidence suggests that climate and atmospheric changes may be having a number of effects. In the present chapter, fluctuations in population density and BA through time for the most common species in some selected sample plots from two distinct Amazonian regions are analysed and compared.

The dynamics and stability of species composition of tropical rainforests have been addressed by ecologists for a long time (Richards 1952) and still receive considerable attention. Tropical forests are no longer thought as stable and unchanging communities. Dramatic changes in forest composition at long-time scales are associated with climatic shifts (Bush et al. 1992), and the study of compositional dynamics is fundamental to reach an understanding of ecological processes that regulate the maintenance of species richness (Connell 1978; Phillips and Sheil 1997). The dynamic evolution of the assemblage of species is crucial in the evaluation of the possible consequences of recent anthropogenic changes in the tropics, such as deforestation, forest fragmentation and climatic change.

Communities and ecosystems are dynamic in space and time and individual species affect community and ecosystem dynamics at different spatial and temporal scales with the ultimate result of changes in species diversity being associated with changes in ecosystem structure and function. However, very limited empirical data are available to test the relationship between species diversity and ecosystem function and stability (Naeem et al. 1994).

Temporal dynamics have been well documented in both ecological and evolutionary time (Delcourt and Delcourt 1991; Pickett et al. 1987). There is ample evidence that many types of communities are subject to complex disturbance regimes, and that post-disturbance succession is occurring at a variety of spatial and temporal scales (Pickett and White 1985). However, regional wide dynamics of change due to global change are extremely difficult to detect as they are confounded with more localized patterns of species change. Finally, long time periods may be needed to completely differentiate global signals from background stochastic variation.

Elevated $CO_2$ has the potential to modify the relationship between diversity and productivity. Rising $CO_2$ concentrations may lead more responsive species to become dominant in the landscape (Bazzaz and Miao 1993). Less diverse communities may take up less additional $CO_2$ in an elevated $CO_2$ environment (Stocker and Körner 1999).

What has been described for grassland communities can be applied to tree communities, re-framing the observed dynamics into proper spatial and temporal scales. The complexity of forest change makes difficult any extrapolation of long-term patterns from short-term observations. Among the reasons are the prominent role of stochastic events such as tree falls, and their influence on vegetation structure and composition.

Four main approaches have been used to predict changes in the distribution and dominance of species under climate change:

- small-scale experiments that study species dynamics under altered precipitation regimes or simulated warming;
- identification of functional traits that are related to tolerance of different climates;
- modelling of species' future ranges based on aspects of their current ranges and predictions of climate change;
- long-term observations of changes in species composition and the correlation of these changes with interannual or interdecadal climate variation.

Here I will concentrate on long-term observations of species composition derived from forest permanent sample plots. Not much is known on tree species fluctuations in rainforest stands and, as stated by Sheil (2000), the ecology of long-term change in tropical rainforests appears to be based more on plausible arguments than upon empirical facts.

Establishing clear changes in floristic composition in tropical rain forest is a difficult task because the majority of species in any area are represented only by a few individuals. Rare species are thought to be more prone to local extinctions induced by environmental fluctuations (Swaine, Lieberman, and Putz 1987b), having a narrower ecological range than more common generalists. Simply by their scarcity, rare species are more likely to disappear from plot records, and equally they are likely to reappear due to immigration.

Changes over time in population size of species on 1-ha PSPs have been described for some tropical forests, with only a few species presenting small imbalance between recruitment and mortality, indicating a certain degree of stability in terms of density and species composition (Caballe and Martin 2001; Swaine, Hall, and Alexander 1987a).

Successional mechanisms driving the evolution of forest species composition have been described for sites with long enough periods of observation (Taylor et al. 1996). In these rainforest plots, an increasing proportion of shade-tolerant species relative to seral species, and a reduced stem turnover have been observed, as expected in forest successional development.

Some studies have highlighted the ecological implications of climatic change in tropical forests, especially changes in drought patterns, showing ways to assess the expected impact, analysing the response of functional types (Condit, Hubbell, and Foster 1996a), structural forest components (Condit, Hubbell, and Foster 1995a; Condit, Hubbell, and Foster 1996a), and tree distribution relative to precipitation patterns (Condit 1998).

Knowledge of the ecological range and the ecophysiological profiles of some species would enable speculation on the foreseeable fluctuations in species composition within the ecosystem. Studies on the response of single species to disturbance and high atmospheric $CO_2$ concentration have been carried out. It has been shown, through investigations of long-term tree ring chronologies from sympatric tropical dry-forest trees with contrasting phenologies, that annual growth is strictly dependent on annual and/or monthly variation in local precipitation, and patterns of growth reflect unique degrees of sensitivity to monthly rainfall and rainfall during previous years (Enquist and Leffler 2001). Although plant responses are species-specific, highly sensitive to rainfall fluctuations, and highly variable from year to year, they have been shown to be generally concordant across species and life-stages in six tropical species studied at La Selva (Clark and Clark 1994). Analysed over a period of 8 years, mean annual increments for the six species showed significant congruence in temporal variation, although no correlation was found between annual rainfall and the growth patterns observed.

With respect to exposure to elevated $CO_2$, there is evidence of individual species responses with potential repercussions on forest composition, although changes may occur rather slowly (Arnone and Körner 1995). Studies on representative species in tropical ecosystems seem to indicate that elevated $CO_2$ favours fast-growing species at the expense of slower-growing species, more through an increase in photosynthetic rates and leaf starch concentration and reduction in leaf area ratio than by accumulation of plant biomass (Lovelock et al. 1998). The results of Lovelock et al. (1998) indicate that $CO_2$ modifies biomass allocation patterns, with the extent of the modification being partially dependent on the successional status of the species, but also varying within the successional group. In contrast, some investigators assert that species are likely to respond similarly to elevated $CO_2$, based on two types of interactions between carbon and nitrogen availability that act in different directions (Lloyd and Farquhar 1996), emphasising the role of nutrient supply in determining the overall plant's response. The same authors note that, if other things were equal, the growth of plants with high respiratory costs, such as slow-growing plants, should respond more strongly to elevated $CO_2$ concentrations than that of plants with lower respiratory costs.

Single species-specific responses cannot be clearly identified, as other factors could play a more relevant role. Species respond differently to elevated $CO_2$ not only because of differences in growth rates, but also because of differences in a whole range of characteristics, including nutrient acquisition strategies and carbohydrate storage capacities (Diaz 1995). Although pioneer species are indicated as ill-equipped to tolerate water stress (Swaine, Lieberman, and Putz 1987b), and are shown to decline in abundance more often than shade-tolerant species after a sequence of dry years and long dry seasons (Condit, Hubbell, and Foster 1996a), they may yet be benefiting if their water-use efficiency is being stimulated by a $CO_2$-enriched environment.

However, the way in which competitive abilities are altered through different types of perturbing events could be more relevant in shaping species composition and structure of the ecosystem than mere physiological processes. Other mechanisms could further favour a greater dominance of early-successional species over late-successional species, such as their intrinsic rapid and long-distance dispersal that may facilitate rapid range shifting (Dukes and Mooney 1999), in response to changing conditions, or to the apparent trend to increasing turnover rates in tropical forests (Phillips and Gentry 1994).

A change in size-class structure of the forest associated with the impact of a severe drought has been observed in a tropical forest in Sarawak, with death of trees correlated with size class, affecting more small trees than large trees, although mortality caused by drought was less size dependent than mortality in non-drought periods, indicating that factors other than drought can play a critical role (Nakagawa et al. 2000).

Data on mortality, recruitment and turnover of single species populations are available (Burslem and Whitmore 1999; Newbery et al. 1999; Taylor et al. 1996) but, with the exception of rare cases (Sheil, Jennings, and Savill 2000), observations generally cover periods of time too short to investigate slow-acting long-term processes and changes. The limited sample sizes also makes it difficult to evaluate within site variability in species mortality and growth rates, and the influence of tree size and microenvironmental conditions.

Are species-specific differences in mortality rate general attributes of the species *per se*, or are they imposed on a given population by the local environment? For individual trees, growth tends to be fairly conservative through time (Swaine, Hall, and Alexander 1987a; Swaine, Lieberman, and Putz 1987b), but large inter-tree differences within species populations attributable to genetic variability and site factors makes it difficult to distinguish clearly between intrinsic properties of species and characteristics purely induced by local circumstances. Demographic comparisons are needed for individual species at various sites. If rates of change in local populations were shown to be intrinsic, that is, constant features of the species sampled, they would have a much higher predictive value.

Permanent sample plot (PSPs) data offer a unique opportunity to detect some signals of apparent change. The compilation of information on species population dynamics and compositional evolution of tropical forests is still a worthy operation. Most of the results from local studies may not be useful for generalisations, but some phenomena may reflect more widespread processes. This can be judged only by comparing patterns from several long-term studies.

### 7.1.1 Questions addressed

In this chapter, the following questions have been tackled:

1. Are there significant variations in overall species richness over time?
2. Are there significant shifts in common, abundant species, and are these shifts in a common direction in the two study areas?
3. Are the observed changes in population density driven by mortality or recruitment?

4. Is there a relationship between the rate of stem turnover and the rate of population change?
5. Which species are showing the most rapid changes, and do these species cluster into distinct taxonomic or functional groups?
6. Are there significant shifts in the relative abundance of pioneer species, and are these shifts consistent across study regions?

## 7.2. Methodology

### 7.2.1. Selection of sites

Sites were selected according to the following discriminant variables:

- length of longest census interval;
- contiguity in space and homogeneity in species composition.

The length of time analysed had to be long enough to enable a comparison between consecutive periods. Hence, only plots with the longest series of diameter measurements, among the available PSPs, were chosen for the analysis of floristic change over time (for a complete list of PSPs, see Chapter 3, Table 3.1 and 3.2). The selection of plots within regional clusters helped to ensure that they were sufficiently similar in species composition to enable the selection of species with a significant stem density.

The PSPs analysed are from two regions: Central Amazonia (Manaus, Brazil, BDFFP projects dataset), and South Western Amazonia (Tambopata, Madre de Dios department, Peru). The following plots had the required characteristics for the analysis:

- Brazilian PSPs: two blocks of five contiguous 1-ha plots from the BDFFP project near Manaus (reserves 3402 and 1301, for a total of 10 PSPs).
- Peruvian PSPs: one group of five 1-ha PSPs, from Tambopata: Tambo0, Tambo1, Tambo3, Tambo4, Tambo6 (5 PSPs in total).

The longest census interval was divided into two periods for comparison (see Chapter 3, Table 3.3). The two regional clusters of PSPs were different in size, therefore not easily comparable. However, separate analyses and comparisons between the two regions were carried out, and some attempts to seek generalizations were made.

### 7.2.2. Selection of species

Within each site, data from the selected PSPs were pooled together to extract representative species populations that matched a minimum size. Stems not fully identified were discarded, but those attributed to morphospecies were included. Within species, a distinction between subspecies and varieties was maintained.

The comparison between the two regions presented some difficulties. Species diversity, and the way it is spread across taxonomic levels (families, genera and species), varied across plots. Plots with very high species richness had lower population density for most of the species, and therefore a smaller number of species was adequately represented. Moreover, the sample size from the two sites was unbalanced (ten 1-ha PSPs from Manaus, and five 1-ha plots from the Western Amazon). Even pooling together all stems from the Peruvian plots, the resulting number of species occurring with a significant number of individuals was far lower than for the Brazilian sites. Therefore, to allow a better comparison between sites, three PSPs clusters, each with five 1-ha plots, were identified (one from Tambopata – Western Amazon, South Peru, and two from the BDFFP experiment - Central Amazon, Brazil). All species with ten or more individuals (within a cluster of 5 PSPs) in at least one observation time, were extracted from these clusters, and population changes for the selected species were investigated. The number of species, and the corresponding total number of individuals, extracted using the above-described criteria, were similar across PSP clusters, and therefore samples were comparable (see Table 7.1).

| Country | N. Plots | Plot code | N. Species | N. Stems | % of tot N. Stems |
|---|---|---|---|---|---|
| Brazil1 | 5 | reserve 3402 (1-to 5) | 53 | 1027 | 42.7 |
| Brazil2 | 5 | reserve 130:1 (1,4 to 7) | 48 | 1066 | 40.7 |
| Peru | 5 | 0,1,3,4,6 | 59 | 1594 | 64.3 |

Table 7.1 – Fractions of species with ≥10 trees in at least one census in a cluster of 5 1-ha PSPs, and corresponding number of individuals selected from each 5-ha cluster of PSPs.

### 7.2.3. Pioneer species

As mentioned earlier in Chapter 4 (paragraph 4.2 on methodology), the identification of "pioneer" species was possible thanks to personal communications of local botanists and experts (Oliver Phillips, Rodolfo Vasquez and Abel Monteagudo, William Laurance). A list of 61 strictly gap-dependent pioneer species derived from a floristic inventory of Guianan forests (Paracou) (Molino and Sabatier 2001) was also included and merged into the final list derived from the collation of all individual contributions of various experts (see Appendix 3).

### 7.2.4. Statistical analysis

Changes in species richness over time were analysed extracting a sub-sample of an equal number of stems from the two consecutive censuses compared (initial and final one). The selected individuals were randomly extracted from the total sample of individuals in each plot, equal to the minimum number of stems found across the censuses compared.

This was done to remove the effect of total stem density $ha^{-1}$ on species richness, although the total stem density has been shown not to vary significantly from first to last inventory in Chapter 5, paragraph 5.4. Then, a best estimate of total species richness was determined for the sub-sample, in order to remove the artifacts due to a more or less complete species identification in different inventories of the same plot.

Fluctuations over time for smaller samples of abundant species (species with >10 trees at first census, and the first 50 most abundant species) were investigated, determining rates of population change, over the longest census interval, using the following equation (Condit et al. 1999):

$$Pg = (\ln(N_f) - \ln(N_0)) / \Delta t \qquad (7.1)$$

where $N_f$ and $N_0$ are the final and initial stem density, respectively. Mean growth rates were calculated for single species populations. Growth was calculated as the mean annual dbh increment, excluding individuals that decreased in size by more than 5 % $a^{-1}$ or increased by more than 7.5 mm $a^{-1}$.

The above-mentioned criteria, used to discard potentially "erroneous" dbh increment measurements, have been documented in detail (Condit et al. 1999).

For the estimate of species population mortality, recruitment and turnover, the equations presented in Chapter 5 (paragraph 5.3) were adopted.

Changes in population size of individuals from families, genera and species occurring in both sites were analysed and compared, with a particular emphasis on those species that showed a rapid change in population density, and on fast-growing species.

Finally, mean increments for common species were compared to look for the effect of exogenous (environmental) versus endogenous (phylogenetic) controls on growth of the same elements of the flora from the two main regions analysed in this chapter.

## 7.3. Results

### 7.3.1. Variation in species richness over time

The comparison of species richness within the same plot over time revealed some methodological difficulties due to a variable quality of species identification across consecutive inventories. Within an equal randomly selected sample of stems extracted from the initial and final census, the number of identified stems and the corresponding number of taxa was calculated (morphospecies, varieties and subspecies were considered as distinct elements of the flora). The number of identified individuals decreased over time in 11 out of 15 PSPs. The fraction of identified stems, calculated on the total number of stems of the randomly extracted sample, varied from the first to last census between 69.8 % (1.19% SE) and 66.0 % (1.13% SE) in the Brazilian plots, and from 95.99% (1.44% SE) to 95.88 % (1.19% SE) in the Peruvian plots. This means that for the Brazilian PSPs the final inventory of species has been less accurate than the first, while for the Peruvian plots, the fraction of identified stems was similar across inventories, and generally higher in absolute terms.

Within the same equal sample of stems, randomly extracted from the initial and final census, also the number of species showed a decrease over time, on average by 1.84% (0.91% SE) in the Brazilian plots, and by 4.37% (1.42% SE) in the Peruvian plots. Only within the Peruvian cluster of plots was a real decline in species richness recorded. This result was not biased by differences in the fraction of identified species found in different censuses. Indeed, the proportion of identified stems was a similar fraction of the total number of stems per ha, over time. However, the observed decrease in total number of species $ha^{-1}$ was not significant.

### 7.3.2. Variation in population density of common, abundant species

The focus was then shifted to common, abundant species, supposedly more easily identifiable than rare, endemic species, therefore less affected by artefacts due to a declining quality of the floristic identification within the same plot. The rate of change in population density was examined for species with ten or more individuals for two sites (two 5-ha PSPs clusters from Manaus (Brazil), and one 5-ha cluster of PSPs from Tambopata (Peru). Table 7.1 shows the number of species selected for each site and the corresponding number of stems at the initial census.

Rates of population change over the longest census interval for the three samples of abundant species were calculated with equation (7.1) and multiplied by 100. Values were compared between the two sites. Fluctuations in stem density of abundant species are illustrated in Figures 7.1 (a) and fluctuations in BA are illustrated in Figures 7.1 (b).

Curves were compared with a $\chi^2$ test, calculated using intervals of one percentage point wide from $-2$ to $+2$, and combining all rates $< -2$ and $> +2$, obtaining 6 intervals in total. The two Brazilian clusters were compared with each other, and then separately compared to the Peruvian cluster. The two sites showed contrasting trends, for both stem density and BA changes. The two series of histograms from the Brazilian PSPs are not significantly different from each other, but both differ singificantly from the histograms representing the Peruvian cluster of PSPs (d.f. = 5, $P < 0.001$, $\chi^2$ test on stem density for Brazil1 and Peru = 26.28; $\chi^2$ test on stem density Brazil2 and Peru = 36.15; $\chi^2$ test on BA for Brazil1 and Peru = 16.40; $\chi^2$ test on BA for Brazil2 and Peru = 21.20). Most of the abundant species showed a declining population density over time in the two Brazilian clusters of PSPs, and an increase in the Peruvian cluster. BA changes presented different patterns; values of annual BA change were balanced over time in both regional samples, with a more considerable fraction of species with no BA change in the Brazilian cluster of PSPs. The different length of the observation period may play a role here. The census interval is shorter in the two Brazilian clusters of PSPs (13.1 and 13.7 years, in Brazil1 and Brazil2 respectively), than in the Peruvian cluster (17.4 years). However, census intervals are within the same order of magnitude, while the proportion of species with no changes in stem density and BA over time seems to differ between sites more than expected merely on the basis of a variable length of the time interval covered.

Thus, the considerable decrease in stem density was not accompanied by a proportional decline in BA. This revealed a reduction of stems occurring mostly in small-sized classes, indicating a progressive decline in the regeneration of abundant species.

It seems that the species composition of the studied plots may be changing. Regardless of total species richness, which could be a stable parameter over time, considerable fluctuations within the population of some species were observed.

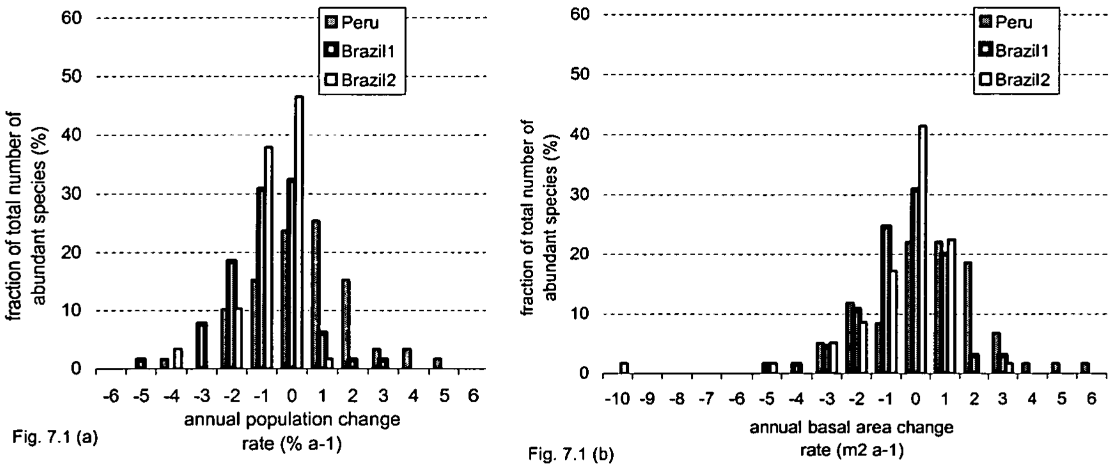


Fig. 7.1 (a)

Fig. 7.1 (b)

Figure 7.1 (a and b) – (a) Fractions of the populations of species with 10 or more individuals in at least one observation time, with different annual % of change in stem number, over the longest census interval; (b) fractions of the population of species with 10 or more individuals in at least one observation time, with different annual % of change in BA, over the longest census interval. Abundant species are selected from three clusters of 5 1-ha PSPs, representing two regions (the samples Brazil 1 and Brazil 2 from BDFFP project, Central Amazon; sample Peru from Tambopata, South Peru).

### 7.3.3. Dynamics of abundant species

The dynamics of abundant species was further analysed and imbalances between gains and losses were investigated for all abundant species with ≥ 10 stems. The separate or aggregate analysis of the two Brazilian clusters of PSPs did not show substantial differences, therefore samples were lumped to estimate dynamic rates. Mean mortality and recruitment rate estimates were significantly different between sites: mean mortality rate was 0.9 % ± 0.1 $a^{-1}$ for the Brazilian PSPs, and 1.8 % ± 0.2 $a^{-1}$ for the Peruvian PSPs ($t = -3.84$, $P < 0.001$); mean recruitment rate was 0.5 % ± 0.1 $a^{-1}$ in Brazilian PSPs and 2.7 % ± 0.3 $a^{-1}$ in Peruvian PSPs ($t = -8.12$, $P < 0.001$). Mortality and recruitment rates of abundant species were more correlated with each other in the Peruvian cluster of plots (Pearson's r= 0.59), than in the Brazilian cluster (Pearson's r= 0.40).

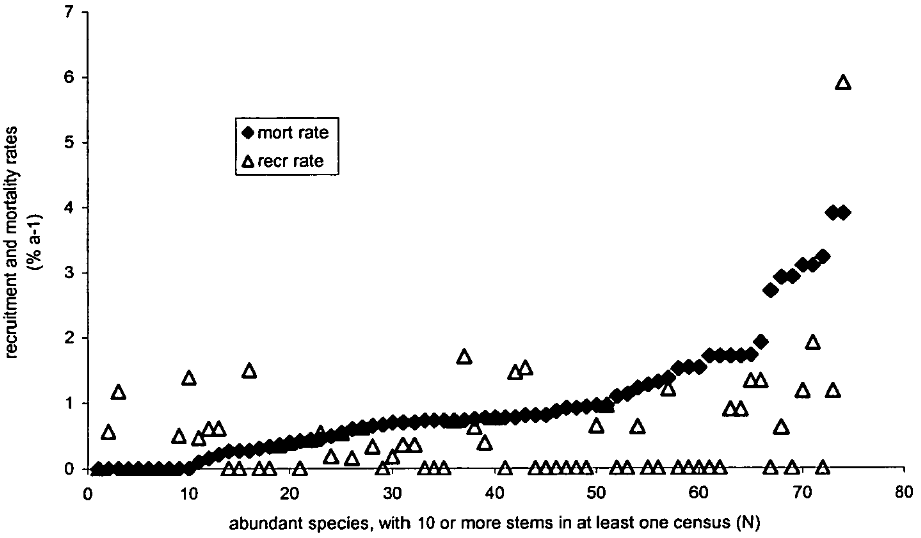


Figure 7.2 – Recruitment and mortality rates for species with 10 or more stems in at least one census (74 species), in two Brazilian clusters of 5 1-ha PSPs (Brazil1 and Brazil2, from BDFFP project). Species are displayed along a gradient of increasing mortality rates on the *x*-axis, and for each one are provided estimates of mortality (◆) and recruitment (Δ) rates.

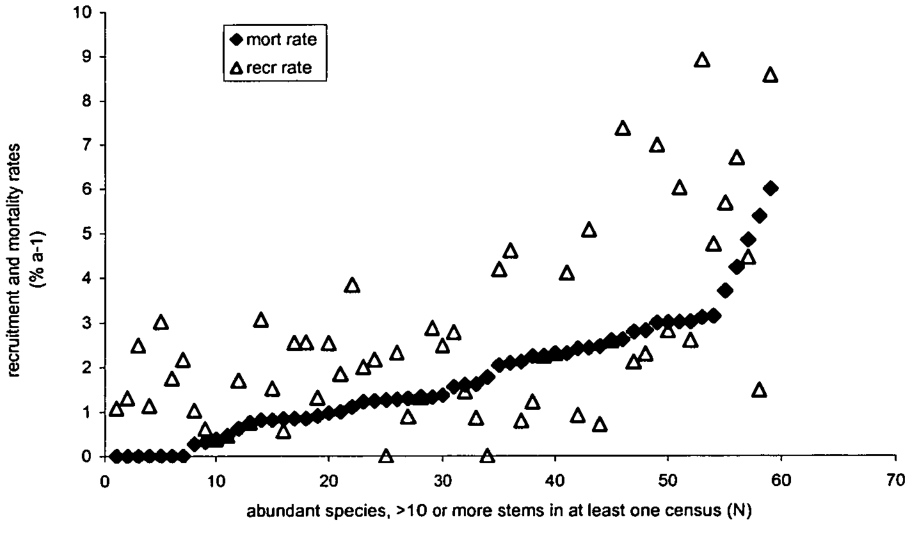


Figure 7.3 - Recruitment and mortality rates for species with 10 or more stems in at least one census (59 species), in the Peruvian PSPs. Species are ranked along a gradient of increasing mortality rates on the *x*-axis, and for each one are provided estimates of mortality (◆) and recruitment (Δ) rates.

Recruitment rates were higher than mortality rates, throughout the longest measurement period for 61% of the species in the Peruvian plots, and for only 17.6% of the species in the Brazilian PSPs. Mortality and recruitment rates are shown for all abundant species in Fig 7.2 and 7.3, ranked along the *x*-axis by mortality rate.

Thus, for the selected set of abundant species, mortality seemed to prevail over recruitment in the Brazilian PSPs, while the opposite was true for the Peruvian PSPs. But what was the relationship between stem density and BA trends over time? Were the species declining in stem density also losing BA in a similar fashion?

The relationship between the two values was found to be linear and presented a statistically significant association, as shown in Fig. 7.4 and 7.5. For species with >10 stems, annual population change and BA change showed a correlation in both sites (Pearson's r = 0.79, P <0.001, for the Brazilian PSPs, and Pearson's r = 0.64, P < 0.001, for the Peruvian PSPs), as found at stand level for all individuals (see Chapter 5). A great part of the species from the Brazilian plots fell in the upper left hand quadrant (22.9% of species), showing a declining stem density and an increasing BA, as would be expected from a "self-thinning" process (Fig. 7.4). However, the a larger proportion showed a decline for both variables (29.2%).

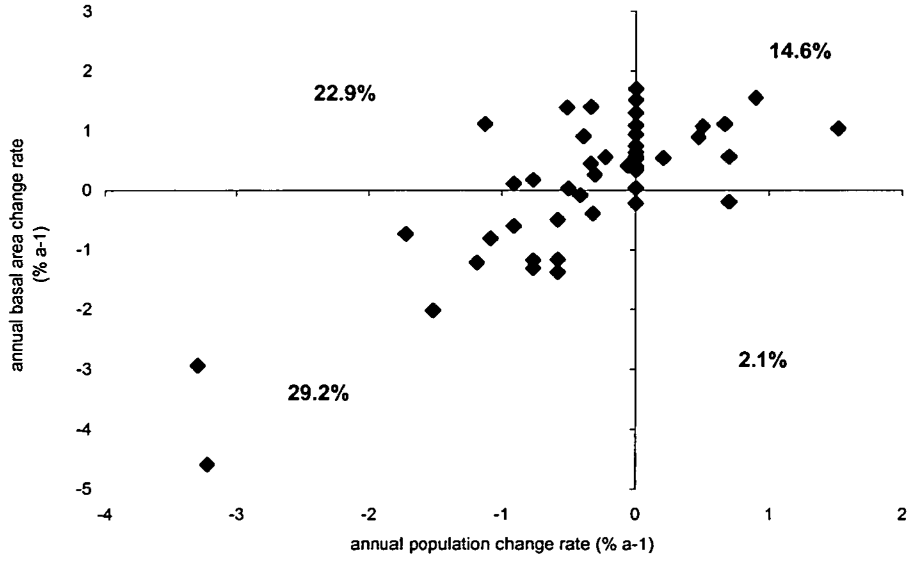


Figure 7.4 – Annual BA change versus annual population change for 74 core species (10 or more stems in at least one census) in two Brazilian clusters of 5 1-ha PSPs, over the longest census interval. Percentages in various quadrants indicate the fraction of plots falling in each of them.

A considerable number of species (29.2 %) showed no variation in rates of change of population density over time accompanied by an increasing annual basal area change over time; a small proportion of species showed an increase in both stem density and BA (14.6%), and a limited fraction of species (2.08 %) showed a decreasing annual basal area change and no variation over time in the annual population change rate. Only a small fraction of core species in the Peruvian plots fell in quadrant II (11.9%), while more than half fell in quadrant I (52.5 %), showing both an increasing stem density and BA (Fig. 7.5); some species showed no variation in annual population change rate, accompanied by an increasing annual basal area change (10.2%) or a decreasing annual basal area change (1.69%).

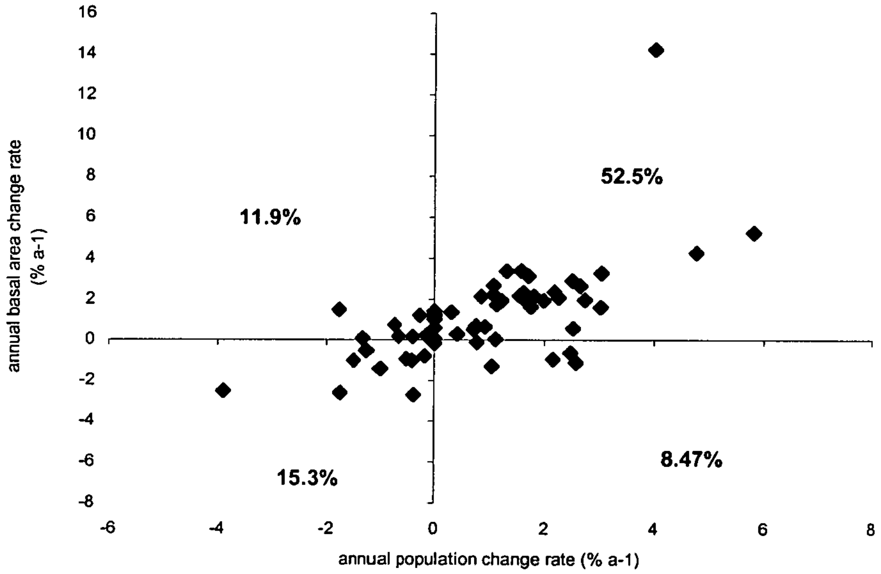


Figure 7.5 - Annual BA change versus annual population change for 59 core species (10 or more stems in at least one census) in the 6 Peruvian plots, over the longest census interval. Percentages in various quadrants indicate the fraction of plots falling in each of them.

Therefore, the current species composition seems to be shaped by different mechanisms in the two sites compared, with mortality mostly responsible for the observed changes in population density of abundant species in the Brazilian plots, and a pulse of recruitment driving species population size fluctuation, in the Peruvian plots. Some species were found to be changing over time more rapidly than others, and their characteristics and dynamics were explored.

### 7.3.4. Dynamics of rapidly changing species

The fluctuation in stem density and BA of the 15 most rapidly changing species was analysed. Tables 7.2, 7.3 and 7.4 show lists of rapidly changing species from the two locations, their stem density at each census, their mean and maximum size, their mean annual increment, and their dynamics. Species were ordered according to an increasing rate of annual population change.

The direction of change seemed consistent across inventories. Decline and increase were progressively more manifest over the three consecutive censuses. Within the set of species selected from both sites, annual population change was not correlated with mean annual increment, and only slightly correlated with turnover. However, most of the species selected are represented by a small number of stems and dynamic rates calculated for small populations have a high statistical error. The effect of chance could easily produce extreme values in species population change. Stochastic catastrophic events could drastically reduce the stem density or small species populations, especially if these have an aggregated distribution.

| Fam | Gen | Spe | inv. 1 (N) | inv. 2 (N) | inv. 3 (N) | Mean dbh (cm) | max dbh (cm) | dbh incr (cm a$^{-1}$) | mort. rate (%) | recr. rate (%) | turn. rate (%) | pop change (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Violaceae | Rinorea | racemosa | 10 | 10 | 13 | 11.2 | 13.6 | 0.01 | 3.9 | 5.9 | 4.9 | 2.00 |
| Vochysiaceae | Vochysia | obidensis | 9 | 9 | 11 | 24.9 | 35.1 | 0.39 | 0.0 | 1.5 | 0.8 | 1.53 |
| Violaceae | Amphirrhox | surinamensis | 10 | 12 | 12 | 12.3 | 15.4 | 0.05 | 0.0 | 1.4 | 0.7 | 1.39 |
| Moraceae | Helianthostylis | sprucei | 12 | 12 | 10 | 13.8 | 19.2 | 0.03 | 1.4 | 0.0 | 0.7 | -1.39 |
| Myrtaceae | Calyptranthes | macrophylla | 11 | 11 | 9 | 16.2 | 25.6 | 0.14 | 1.5 | 0.0 | 0.8 | -1.53 |
| Euphorbiaceae | Drypetes | variabilis | 11 | 9 | 9 | 15.0 | 21.5 | 0.09 | 1.5 | 0.0 | 0.8 | -1.53 |
| Legum. Caes. | Tachigali | plumbea | 15 | 13 | 12 | 28.4 | 59.1 | 0.50 | 1.7 | 0.0 | 0.9 | -1.70 |
| Sapotaceae | Pouteria | cladantha | 15 | 14 | 12 | 19.5 | 31.7 | 0.13 | 1.7 | 0.0 | 0.9 | -1.70 |
| Myrtaceae | Myrcia | grandis | 18 | 19 | 14 | 18.7 | 33.5 | 0.12 | 3.1 | 1.2 | 2.1 | -1.92 |
| Moraceae | Naucleopsis | caloneura | 31 | 30 | 24 | 13.4 | 20.o | 0.05 | 2.0 | 0.0 | 1.0 | -1.95 |
| Annonaceae | Fusaea | longifolia | 12 | 11 | 9 | 13.6 | 17.7 | 0.08 | 2.2 | 0.0 | 1.1 | -2.20 |
| Moraceae | Pseudolmedia | laevis | 11 | 9 | 8 | 17.6 | 35.4 | 0.13 | 2.4 | 0.0 | 1.2 | -2.43 |
| Legum. Mim. | Inga | paraensis | 10 | 9 | 7 | 18.5 | 34.0 | 0.41 | 3.9 | 1.2 | 2.5 | -2.72 |
| Euphorbiaceae | Pausandra | macropetala | 22 | 18 | 15 | 11.7 | 15.7 | 0.07 | 2.9 | 0.0 | 1.5 | -2.92 |
| **Palmae** | **Oenocarpus** | **bacaba** | **28** | **24** | **16** | **14.3** | **19.1** | **0.07** | **4.3** | **0.0** | **2.1** | **-4.27** |

Table 7.2 – Most rapidly changing populations in the Brazilian PSPs (5 1-ha plots from BDFFP 3402 block of PSPs). Pioneer species are in bold characters. Stem density is shown for the first, intermediate and final inventory (inv. 1, 2, 3 respectively), mean first census interval length = 4.9 years, mean second census interval length = 8.1 years; mean and maximum dbh refer to the first census; dbh incr. = mean annual increment between initial and final inventory; mort. rate = mortality rate; recr. rate = recruitment rate; turn. rate= turnover rate; pop. change= annual rate of population change.

| Fam | Gen | Spe | inv. 1 (N) | Inv. 2 (N) | inv. 3 (N) | mean dbh (cm) | max dbh (cm) | dbh incr (cm a-1) | mort. rate (%) | recr. rate (%) | turn. rate (%) | pop change (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Legum. Mim. | Zygia | racemosa | 13 | 13 | 16 | 26.2 | 51.9 | 0.14 | 0.6 | 2.1 | 1.3 | 1.52 |
| Burseraceae | Protium | apiculatum | 23 | 24 | 26 | 16.4 | 29 | 0.11 | 0.0 | 0.9 | 0.4 | 0.89 |
| Legum. Caes. | Swartzia | reticulata | 10 | 10 | 11 | 14.9 | 23.2 | 0.05 | 0.8 | 1.5 | 1.1 | 0.70 |
| **Palmae** | **Euterpe** | **precatoria** | 10 | 12 | 11 | 12.1 | 14.1 | 0.00 | 0.8 | 1.5 | 1.1 | **0.70** |
| Sapotaceae | Ecclinusa | guianensis | 21 | 21 | 23 | 20.3 | 47.8 | 0.11 | 0.4 | 1.0 | 0.7 | 0.66 |
| Lauraceae | Sextonia | rubra | 9 | 10 | 8 | 36.0 | 98.6 | 0.03 | 1.8 | 1.0 | 1.4 | -0.86 |
| Euphorbiaceae | Conceveiba | hostmannii | 17 | 17 | 15 | 17.5 | 39.6 | 0.06 | 0.9 | 0.0 | 0.5 | -0.91 |
| Chrys. | Couepia | caryophylloides | 17 | 17 | 15 | 28.9 | 47.8 | 0.11 | 0.9 | 0.0 | 0.5 | -0.91 |
| Moraceae | Naucleopsis | caloneura | 29 | 29 | 25 | 12.9 | 18.o | 0.03 | 1.1 | 0.0 | 0.5 | -1.08 |
| Lauraceae | Ocotea | amazonica | 14 | 14 | 12 | 17.1 | 27.9 | 0.17 | 1.1 | 0.0 | 0.6 | -1.13 |
| **Palmae** | **Oenocarpus** | **bacaba** | 40 | 42 | 34 | 13.9 | 20.9 | 0.01 | 2.1 | 0.9 | 1.5 | **-1.19** |
| Legum. Caes. | Eperua | glabriflora | 16 | 15 | 13 | 29.5 | 59.5 | 0.07 | 1.5 | 0.0 | 0.8 | -1.52 |
| Legum. Papil. | Paramachaerium | ormosioides | 19 | 18 | 15 | 21.1 | 38.4 | 0.07 | 1.7 | 0.0 | 0.9 | -1.73 |
| Myristicaceae | Virola | calophylla | 14 | 14 | 9 | 14.8 | 23.5 | 0.05 | 3.2 | 0.0 | 1.6 | -3.23 |
| Annonaceae | Fusaea | longifolia | 11 | 10 | 7 | 14.7 | 25.8 | 0.04 | 3.3 | 0.0 | 1.6 | -3.30 |

Table 7.3 – Most rapidly changing populations in the Brazilian PSPs (5 1-ha plots from BDFFP 1301 block of PSPs). Pioneer species are in bold characters. Stem density is shown for the first, intermediate and final inventory (inv. 1, 2, 3 respectively), mean first census interval length = 4.9 years, mean second census interval length = 8.1 years; mean and maximum dbh refer to the first census; dbh incr. = mean annual increment between initial and final inventory; mort. rate = mortality rate; recr. rate = recruitment rate; turn. rate= turnover rate; pop. change= annual rate of population change, Chrys.= Chrysobalanaceae.

| Fam | Gen | Spe | inv. 1 (N) | inv. 2 (N) | inv. 3 (N) | mean dbh (cm) | max dbh (cm) | dbh incr (cm a-1) | mort. rate (%) | recr. rate (%) | turn. rate (%) | pop change (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Palmae** | **Oenocarpus** | **mapora** | 10 | 15 | 26 | 10.9 | 12.7 | -0.01 | 3.1 | 8.9 | 6.0 | **5.80** |
| **Palmae** | **Euterpe** | **precatoria** | 34 | 44 | 75 | 14.5 | 18.5 | 0.03 | 2.6 | 7.4 | 5.0 | **4.76** |
| Legum. Caes. | Sclerolobium | bracteosum | 8 | 18 | 15 | 13.7 | 18.8 | 1.53 | 3.0 | 7.0 | 5.0 | 4.00 |
| **Moraceae** | **Castilla** | **ulei** | 6 | 9 | 10 | 19.7 | 37.0 | 0.21 | 0.0 | 3.0 | 1.5 | **3.03** |
| **Cecropiaceae** | **Pourouma** | **guianensis** | 21 | 27 | 34 | 22.1 | 42.7 | 0.54 | 3.0 | 6.0 | 4.5 | **3.02** |
| **Palmae** | **Socratea** | **exorrhiza** | 53 | 66 | 84 | 16.2 | 23.8 | 0.02 | 1.1 | 3.8 | 2.5 | **2.74** |
| Myristicaceae | Virola | calophylla | 9 | 9 | 14 | 17.1 | 29.6 | 0.21 | 2.4 | 5.1 | 3.8 | 2.65 |
| **Cecropiaceae** | **Pourouma** | **cecropifolia** | 11 | 14 | 17 | 23.1 | 35.9 | 0.23 | 6.0 | 8.6 | 7.3 | **2.58** |
| **Cecropiaceae** | **Pourouma** | **minor** | 85 | 99 | 127 | 23.6 | 65.8 | 0.42 | 2.1 | 4.6 | 3.3 | **2.52** |
| Clusiaceae | Calophyllum | brasiliense | 10 | 13 | 15 | 26.3 | 52.5 | 0.38 | 0.0 | 2.5 | 1.3 | 2.50 |
| Clusiaceae | Symphonia | globulifera | 10 | 12 | 15 | 23.0 | 37.2 | 0.41 | 4.2 | 6.7 | 5.5 | 2.47 |
| Monimiaceae | Siparuna | decipiens | 40 | 51 | 58 | 13.1 | 20.6 | 0.05 | 0.8 | 3.1 | 1.9 | 2.26 |
| Annonaceae | Oxandra | xylopioides | 12 | 10 | 9 | 21.1 | 37.2 | 0.09 | 2.5 | 0.7 | 1.6 | -1.75 |
| **Bignoniaceae** | **Jacaranda** | **copaia** | 12 | 10 | 9 | 40.7 | 72.0 | 0.79 | 1.8 | 0.0 | 0.9 | **-1.77** |
| Burseraceae | Protium | aracouchini | 9 | 10 | 5 | 11.3 | 13.1 | 0.06 | 5.4 | 1.5 | 3.4 | -3.90 |

Table 7.4 – Most rapidly changing populations in the Peruvian PSPs (5 1-ha plots). Pioneer species are in bold characters. Pioneer species are in bold characters. Stem density is shown for the first, intermediate and final inventory (inv. 1, 2, 3 respectively); mean first census interval length= 5.3 years, mean second census interval length= 4.8 years; mean and maximum dbh refer to the first census; dbh incr. = mean annual increment between initial and final inventory; mort. rate = mortality rate; recr. rate = recruitment rate; turn. rate= turnover rate; pop. change= annual rate of population change.

Nevertheless, among the 15 most rapidly changing species, the fraction of species with a declining stem density is higher in the two Brazilian clusters of PSPs (80%

and 67% of declining species) than in the Peruvian cluster (20% of declining species). Within the Peruvian sample plots, positive and negative changes are more significant both in relative terms (most of the species increasing in number almost double their stem density), and absolute terms (3 pioneer species, *Socratea exorrhiza, Euterpe precatoria* and *Pourouma minor*, show an increase of 29, 41 and 42 individuals, respectively). On the other hand, within the two Brazilian clusters, fluctuations are more marginal. This could be a signal of different processes affecting the two sites, but a much larger sample of stems would be needed to draw any significant conclusions.

### 7.3.5. Variation in the relative abundance of pioneer species

The list of rapidly changing species included some pioneers. They showed a marked increase in population size in the Peruvian plots, where Cecropiaceae and Palmae in particular presented a steadily increasing stem density. Trends for pioneers were less clear in the Brazilian plots. Pioneers were not adequately represented within the pool of abundant species and were therefore separately analysed in a larger sample of plots (Central Amazonian sites = 23 1-ha PSPs, Western Amazonian sites = 14 1-ha PSPs). Figure 7.6 presents a profile of the fractional contribution of pioneer species to the total number of individuals and total stand BA, for all the main sites studied in this work. The fraction of pioneers was higher in the more dynamic plots from Western Amazonia than Central Amazonian plots. This pattern mirrors what was shown in Chapters 4 and 5, using a different approach. In most WA locations, stems of pioneers seemed to reach larger diameters, revealing a floristic dominance of large-sized on small-sized pioneers.

Changes in the contribution of pioneer species to total stem density (Fig. 7.7) and stand BA (Fig. 7.8) were investigated over time. The two regional samples were not perfectly balanced in size; yet they were sufficiently large to show a common increasing occurrence of pioneers, potentially reflecting some larger scale trends.

Mean annual BA changes were positive in most locations, with the exception of some NW Amazonian plots. Stem density declined in two Western Amazonian sites, but BA decreased only in one. Tambopata, where the total contribution of pioneers is the highest, also showed the greatest mean annual changes.

Thus, pioneer species seemed to show increasing abundance over time, although a bigger sample would be necessary to prove the extent of this signal of floristic change.

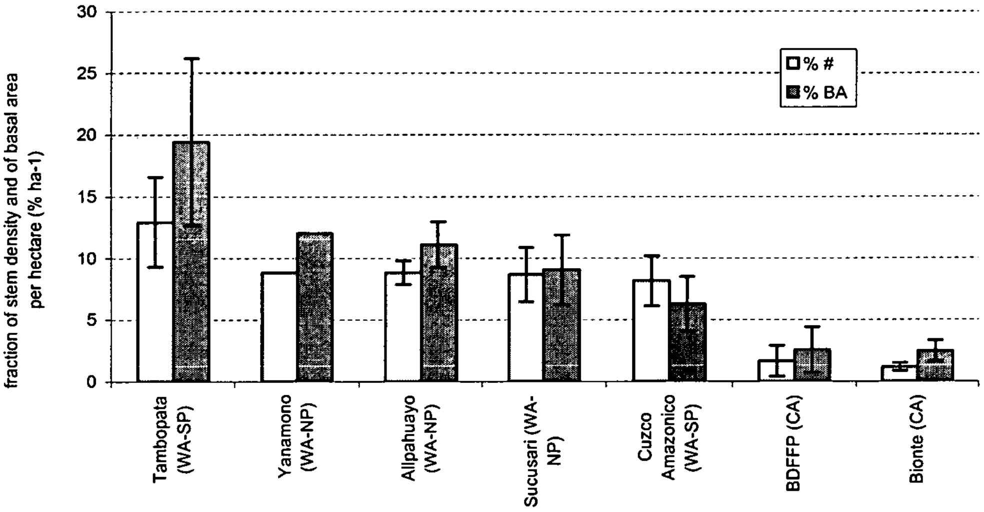


Figure 7.6 – Fractional contribution of pioneer species to total stand stem density and BA (37 PSPs). The floristic profile refers to the initial census in each plot.

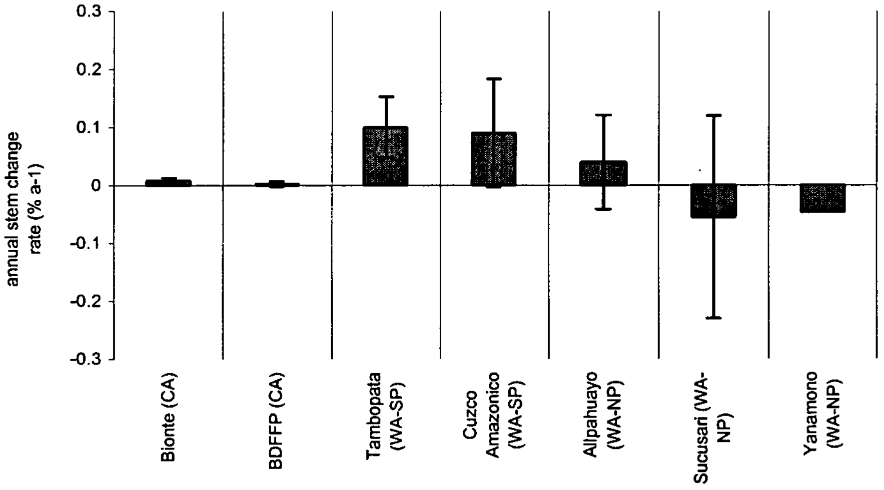


Figure 7.7 – Mean annual change in fractional contribution of pioneer species to total stand stem density (37 PSPs).

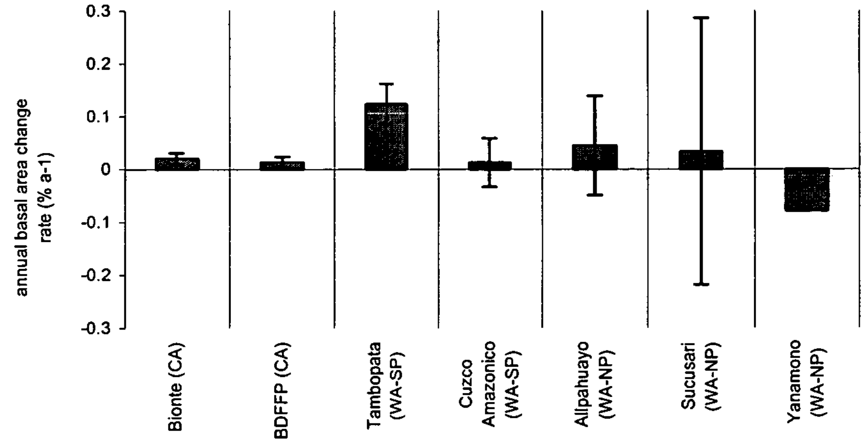


Figure 7.8 – Mean annual change in fractional contribution of pioneer species to total stand BA (37 PSPs).

The increase in density of pioneers was expected to be manifest at a different pace across the Amazon basin, under the regulation of various factors (e.g., phylogeny, dispersal, environment, etc.). Changes in the dominance of fast growing species were expected to be more evident where this group of species is already well represented and where forest dynamics is faster. The role of exogenous versus endogenous (phylogenetic) controls on the behaviour of taxa was examined. The performance of common elements of the flora was compared across sites to highlight the influence of environmental conditions. The population dynamic rates of species occurring in both the main regions analysed in this chapter were compared. Mean turnover rates for families with 10 or more stems at first census, in both sites, were estimated and compared between the two datasets. Mean turnover rates were also calculated for common genera with 10 or more stems in both sites (see Appendix 4 for a complete list of families and genera).

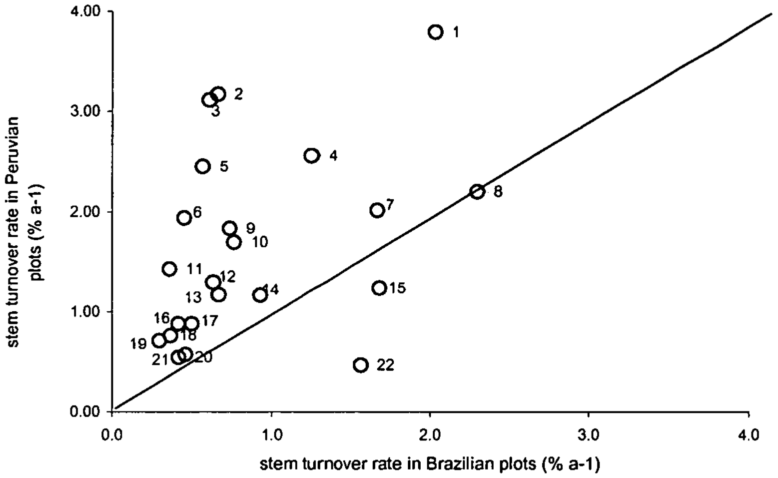


Figure 7.9 – Mean turnover estimates of plant families for the longest census interval in Peruvian versus Brazilian PSPs, for 22 families with 10 or more stems, occurring in both sites. 1 = Cecropiaceae, 2 = Myristicaceae, 3 = Leg. Caesalpinaceae, 4 = Flacourticeae, 5 = Bombacaceae, 6 = Monimiaceae, 7 = Violaceae, 8 = Palmae, 9 = Annonaceae, 10 = Meliaceae, 11 = Tiliaceae, 12 = Moraceae, 13 = Lauraceae, 14 = Euphorbiaceae, 15 = Rubiaceae, 16 = Olacaceae, 17 = Sapotaceae, 18 = Lecythidaceae, 19 = Chrysobalanaceae, 20 = Elaeocarpaceae, 21 = Apocynaceae, 22 = Burseraceae.

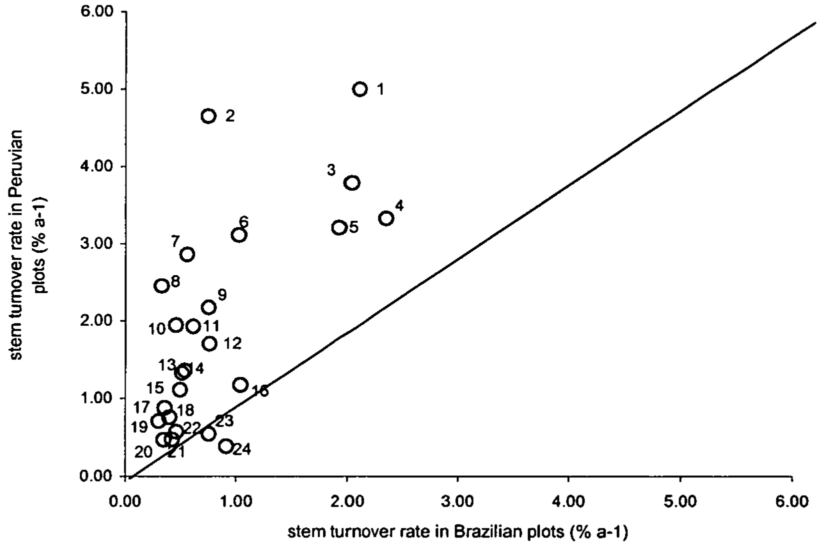


Figure 7.10 - Mean turnover estimates of plant genera for the longest census interval in Peruvian versus Brazilian PSPs, for 24 genera with 10 or more stems, occurring in both sites. 1 = Euterpe, 2 = Virola, 3 = Pourouma, 4 = Oenocarpus, 5 = Rinorea, 6 = Tachigali, 7 = Iryanthera, 8 = Matisia, 9 = Mabea, 10 = Siparuna, 11 = Helicostylis, 12 = Aspidosperma, 13 = Pseudolmedia, 14 = Pouteria, 15 = Hevea, 16 = Ocotea, 17 = Heisteria, 18 = Eschweilera, 19 = Licania, 20 = Tetragastris, 21 = Brosimum, 22 = Sloanea, 23 = Guarea, 24 = Micropholis.

A total of 22 families were found to occur in both sites analysed in this chapter. Mean turnover estimates were significantly higher in the Peruvian PSPs (paired t test, t =-3.93, P< 0.001), but values were correlated between sites, denoting a similar ranking of families on the basis of dynamics. Only three families showed higher turnover rates in Central Amazonia plots (*Burseraceae, Rubiaceae, Palmae*, the latter with extremely high value of mortality rate in CA PSPs) (Fig. 7.9).

A total of 24 genera were found to be in common to both sites. Mean turnover rates were higher within the Peruvian PSPs (paired t test, t =-6.64, P< 0.001), but values were strongly correlated between sites (Fig 7.10).

Dynamic rates, calculated for small populations, have a high statistical error, as mentioned earlier. However, differently for the analysis exposed in paragraph 7.3.4, where population changes were examined at species level, a much larger sample of individuals was investigated to look at families and genera. At family level, turnover rates were estimated on a total of 5814 and 1392 stems, from the Brazilian and Peruvian PSPs respectively (with an average number of stems per family of 263 and 67 respectively); at genus level, turnover rates were estimated on a total of 2821 and 807 stems from the Brazilian and Peruvian PSPs respectively (with an average number of stems per genus of 118 and 34 respectively). The two samples were unbalanced and probably not large enough to draw significant conclusions. However, earlier in this thesis (Chapter 5), turnover rates were shown to be higher in the Peruvian PSPs than in the Brazilian PSPs from a regional- to a stand-scale. The patterns shown in Fig. 7.9 and 7.10 support the same findings, at a finer scale.

Overall, these results indicate that rapid turnover species are consistently increasing in almost all locations and trends are likely to be progressively more evident in highly dynamic forests, where a potential substitution of species, triggered by global changes, is likely to occur faster, due to higher mortality and recruitment rates.

## 7.4. Discussion

The analysis of potential fluctuations in species richness for the same plot over time turned out not to be feasible due to the varying quality of the floristic identification, from the initial to the final census. With regard to shifts in species composition in natural forests, the evidence suggests that changes occur slowly, without catastrophic disturbance. Most species show little change in density over the periods studied, and few depart significantly, at least over the relatively short time scale treated, from apparent equilibrium in recruitment and mortality.

The length of the observation period seems to be a crucial factor. The available data are inadequate for an evaluation of long-term stability or equilibrium in population levels and species composition of tropical forests. However, the fluctuation in population size of abundant species can provide clues on future trends in forest species compositional change.

Very few of the abundant species analysed from a Central Amazonian and a south Western Amazonian cluster of plots, have undergone drastic changes in population density. The investigations on shifts in species composition are normally limited to abundant species, therefore the number of species analysed, the size of their populations and their representativeness of dynamic processes influencing forest stands depend on the extension of the tract of forest analysed and the contiguity of the areas studied. The small size of the sample plots investigated constrains the analysis of abundant species to a limited number of individuals that reach a minimum population size. In addition, the spatial turnover of species is a factor that varies considerably across different Amazonian regions (Condit et al. 2000), and would influence the selection of a set of species well represented and suitable for the analysis. Anyway, despite the slow apparent changes at the level of individual species, it has to be taken into account how even small barely detectable changes at plot scale might have a far greater impact on a global scale.

Local processes of immigration and extinction of species, succession, the change in the frequency of dry events, and changes in atmospheric composition are among the main factors responsible for local and regional evolution of the floristic composition, occurring in the plots investigated. The identification of the relative weight of these variables in shaping the flora is a complex operation, especially when the period of observation is limited and information is missing.

With respect to climate, as shown in Chapter 3, the two sites analysed in this chapter have not experienced any major change in rainfall regime in the last two decades, although the impact of strong drought has been shown in some central Amazonian forests partially included in the dataset used for this study (Laurance et al. 2001). Laurance et al. (2001) recorded increased mortality rates, near forest edges especially.

A considerable fraction of species was observed to be decreasing in abundance in the Brazilian PSPs analysed here, while most of the species showed an increasing population density in the Peruvian PSPs. Rates of change in single species populations were found to be strongly correlated with recruitment rates in the

Peruvian plots, and with mortality in the Brazilian plots. This suggests two different mechanisms operating and leading to a species substitution, one decimating species no longer matched with their environment, the other promoting species progressively showing advantageous strategies in coping with changing environmental conditions. Many species in the Brazilian PSPs were showing a considerable increase in basal area over time, despite a lack of recruitment, maybe indicating favourable growth condition at later stages of development. Small-sized individuals for some species could be more strongly affected by dry events. It has been shown that drought is likely to affect more the understory (Condit, Hubbell, and Foster 1996a), at least in more seasonal forests, as could be the case in Manaus, although a similar number of dry months $a^{-1}$ characterizes the South Peruvian plots investigated here. However, the present findings on the response of understory versus canopy trees are quite controversial. Some authors have shown that canopy species are more vulnerable to drought (Condit, Hubbell, and Foster 1995a; Leighton and Wirawan 1986; Swaine 1992), supposedly because their crowns are more exposed to direct sunlight and evaporation. Annual measurements of growth and survival of species would be necessary to interpret species-specific, size-dependent responses.

The response of species to changes in the environment (especially $CO_2$ enhancement) is species-specific but local soil physical and biological conditions, together with local climate, are likely to override the influence of elevated $CO_2$. Different mechanisms responsible for shaping floristic composition could have a prominent role in different locations. The many interactive influences of $CO_2$ enrichment and other factors complicate predictions. The increasing population density of the most abundant species in the Peruvian plot, due to recruitment rates higher than mortality rates, is consistent with finding from recent experiments on *in situ* $CO_2$ enrichment in the understory of a humid tropical forest in Panama (Wurth, Winter, and Körner 1998). Results seemed to suggest a stimulation of tree recruitment in deep shade. The higher fertility of the Peruvian plots versus the Brazilian plots investigated could have been stimulating further the recruitment process observed. If true for other species, including vines (Phillips et al. 2002b), the positive response could enhance forest turnover as was suggested by various studies (Phillips 1996; Phillips and Gentry 1994).

Predicted changes in species abundance are expected to take more time to become apparent in relatively low-productivity systems (Arnone and Körner 1995), and this would probably be the case of low-turnover systems as compared to high-turnover ones. Differences in mean turnover rates of abundant species were observed, with higher values in the Peruvian versus the Brazilian plots, mirroring the different dynamic rates recorded for Western and Central Amazonian plots at stand level, observed and discussed earlier in Chapter 5. These characteristics seem to indicate a potentially increasing evidence for compositional changes in the Peruvian PSPs than in the Brazilian PSPs.

Experiments by Arnone and Körner (Arnone and Körner 1995) seem to suggest that groups of species more than single species tend to be either gaining or losing their share of community biomass. A few examples of tropical species functional grouping can be found in the literature, although for modelling purposes this seems the only possible way to represent the behaviour of a complex ecosystem. A study based on plant functional types in BCI (Panama) revealed only a sharp change over time of the moisture-dependent guild, but did not reveal any change in forest structure (Condit, Hubbell, and Foster 1996a). Over 13 years, neither total stem density, wood volume, proportion of deciduous species, nor proportion of understory species changed in an appreciable way (Condit et al. 1995b). This may indicate that a slow change in species composition precedes any detectable change in the overall structure. From the same study, a decline in total density of pioneers was observed, although this was not consistent through time.

Contrary to what was found in BCI, in both sites studied in this work, among the most rapidly changing species, pioneers appeared to be gaining higher stem density over time, more evidently so within the Peruvian plots, where mainly pioneers and palms were among the species with more markedly increasing population density. In the Brazilian plots, the most significant absolute population change is associated with a palm, *Oenocarpus bataua*, which is losing a considerable number of individuals through time. Extracting and pooling all fast growing species by site, a pattern of increasing stem density and basal area over time was detected in almost every location, with a few exceptions (WA-NP plots).

The perspective of coherent responses of species and functional groups to elevated $CO_2$ are not very promising. Data available today from crop cultivars and tree seedlings, suggest that among the most unlikely things to happen is that two plant species or two cultivars respond identically to $CO_2$ enrichment. No reliable functional groups with respect to $CO_2$ responsiveness have been identified. Even among quite obvious groups, such as $C_3$ and $C_4$ species, legumes and non-legumes, or evergreen and deciduous species, trends are inconsistent, as reported in a recent review by Körner (2000). Things are further complicated by the fact that the differential responsiveness of members of such functional groups may vary with the availability of other resources (Körner 1996), especially soil conditions. In the more static, nutrient-limited Brazilian plots studied, environmental constraints could be overriding $CO_2$ effects, leading to a decreasing density of abundant species. The effect of dry events could alter species population dynamics in different ways in relation to general environmental conditions.

Functional groups could be established on the basis of comparative bioassays for the effect of drought (or other stresses) on species performance (growth and survival). Mechanisms for drought resistance associated with traits that delay desiccation and traits that provide tolerance to desiccation could be identified and would form the basis for a clustering of species. However, Engelbrecht (2001) studying 28 species in BCI did not find any correlation between rooting depth (chosen as a trait for plasticity in response to drought) and drought resistance. Hacke et al. (2001) did not find a significant correlation between vulnerability to xylem embolism and wood density (used as a proxy for the former); furthermore, the relation between vulnerability to xylem embolism and drought resistance has not yet been empirically established. However, the possibility of grouping species on the basis of their response to enhanced $CO_2$ and drought should be further tested in nature. Modelling based on median responses, and most of the time concentrated on dominant species, does not seem to lead to clear answers. Seedling data seem to be unsuitable substitutes for advanced adult-tree responses. The consequences for experimentalists are to study *in situ* and accept the challenge of greater variability and lower precision, but gaining greater relevance accounting for the complexity of responses, which depend on tree age, neighbours, microbial partners, soil resources, and atmospheric conditions.

The increase of pioneers could have implications for the carbon balance of rainforests, as fast-growing species have less dense wood and therefore a lower C storage potential, and in addition, also the structure of a forest would be likely to change.

It seems not possible as yet to distinguish neatly between natural forest dynamics and signals of a more global trend by looking at the PSPs examined. The increasing abundance of pioneer species should be tested by analysing a larger dataset and increasing the number of replications in each site. Furthermore, species responses should be better examined by analysing the ecological range of fast changing species, and by better monitoring of signals of increase in pioneers, distinguishing between slightly different life-strategies within the pioneer group, and enlarging the geographic basis of the investigation. Larger and longer experiments are needed, although more PSP data are being made available through the work of networks that, by merging the efforts of various research groups, help with collating information carried out at various Pantropical locations. This enables the interpretation of large scale phenomena taking place in tropical rainforests under the pressure of global changes.

## 7.5. Conclusions

1. Fluctuations in population density of some common abundant species, within a Peruvian (WA) and Brazilian (CA) clusters of PSPs, showed opposite patterns. In the Peruvian cluster, most of the abundant species experienced an increase in recruitment rates over time, while increased mortality rates seemed to be driving population change of the most frequent species, within the Brazilian cluster.
2. Fluctuations in stem density were less pronounced than BA changes over time for the same species. Despite an increasing or declining abundance over time, most of the species maintained an almost unchanged contribution to total stand BA.
3. Pioneer species showed an increasing occurrence in the final versus the initial census, both in terms of stem density and BA, across most of the study sites.
4. Turnover rates of families and genera occurring in both WA and CA clusters of PSPs, were found to be much higher in the Peruvian plots, mirroring patterns found at stand level and partially explained by a higher soil fertility found moving towards the foot of the Andes. This seems to indicate that signals of pronounced changes in floristic composition are likely to be detected earlier and more easily in more dynamic forest stands.

# Chapter 8. General conclusions

---

## Conclusions

Much current research is trying to understand the role of forests in the global carbon cycle, and to predict the direction of changes and the potential of tropical forests to sequester carbon under the pressure of global changes. The work reported in this thesis represents an attempt to document current patterns of tropical forest floristic composition, basal area and dynamics, to understand the role played by environmental factors in determining potential changes in productivity in tropical forest ecosystems, to interpret how species could be responding to global changes, to anticipate how the structure of a forest stand could change as a consequence of floristic changes, and to identify which areas of lowland Amazonian forests are likely to be more sensitive to global changes.

Floristic diversity across the Amazon basin was analysed and some patterns were found, revealing a clear dominance of different families in different parts of the Amazonian lowland forests. Pioneer species and palms were found to be particularly abundant in the western Amazonian sites, probably due to the higher dynamism found in forest plots in this region, which in turn appears to be associated with richer edaphic conditions.

A strong relationship was identified between climate and species richness, with the length of the dry season identified as the best predictor of alpha-diversity, found to be higher in aseasonal western Amazonian sites. However, some central Amazonian plots also displayed high species richness, exceptional if only environmental factors were considered. At the local level, within floristically homogeneous sites, species composition appeared to be controlled by soil characteristics.

Forest structure varied across tropical forest regions, perhaps under the influence of climate regime. The occurrence of large-stemmed trees was found to be higher in forests stands located in the drier sites. The structural analysis did not reveal clear relationships between stem density and total basal area ha$^{-1}$, and trees mean size did not appear to be correlated with stand turnover.

Stand basal area and turnover showed signals of significant increase over time in several locations analysed in the present study, and indicated the potential influence of some causal agents operating at a very large scale. The effect of climate in controlling basal area accumulation is unclear, although this is likely to be minimal in the study sites, as the rainfall data did not reveal any significant change in the period studied. The main differences in recruitment, mortality and turnover between eastern and western plots seemed to follow the distinction between poor soils, typically found in the eastern and central Amazon, and richer soils more common in the western part of the Amazon basin. Recruitment and mortality showed a tendency to increase on substrates of varying fertility, but the largest absolute increases were recorded on richer soils. Stand dynamics were not significantly correlated with the observed accumulation of basal area over time, and basal area increase appeared to be due more to a greater growth of individuals than to an increased stem density.

The observed basal area accumulation was not directly associated with the increased occurrence of fast growing groups of species, such as pioneers and palms. However, these two groups, pioneer species especially, were found to increase in most of the plots across various sites, although more remarkably in south Peruvian plots. This showed potential links with the general increase in turnover rates, more marked in highly dynamic sites of the southern Amazon.

Some tests were applied to investigate the potential role of methodological artefacts in biasing the observed accumulation of basal area in the plots studied. The tests suggested that measurement artefacts were unlikely to be responsible for the observed positive change in basal area. The geographical co-occurrence of the increase in stem density with the increase in basal area indicated that for most study sites it is possible to exclude biases due to the "majestic forest" effect.

In addition, the present study seemed to indicate against the hypothesis of a general recovery from a major disturbance, as all tree size classes are showing a positive change in basal area, in favour of the hypothesis of a potential "fertilization" from an enhanced $CO_2$ concentration in the atmosphere. The hypothesized "fertilization" effect might operate through various physiological mechanisms and affect all forest ecosystems, but the influence may be particularly important in tropical regions where productivity is intrinsically high.

It has been suggested that plants may respond by investing a greater proportion of their extra carbon into the production of roots and root exudates to increase their nutrient supply. Increased atmospheric $CO_2$ may also result in enhanced water-use efficiency, which would lengthen the growing season of plants in seasonally dry regions. A key uncertainty is the extent to which the fertilization effect is limited by availability of nutrients.

Independent of whether global change is inducing a tropical forest carbon sink, the atmospheric changes are likely to be causing modifications in the ecological balance of ecosystems, with consequences for ecosystem function and species diversity. Laboratory studies show that responsiveness to high $CO_2$ varies between species. Moreover, current changes in the C balance of tropical forests might be expected to coincide with generalized shifts in functional composition, but there is no evidence to date for widespread changes in composition except in forest fragments and edges. This absence of evidence might imply evidence of absence – or it might simply reflect our failure to adequately monitor forest behaviour.

Fluctuations in population density of some common abundant species were observed and showed different regional patterns. In the Peruvian cluster, most of the abundant species experienced an increase in recruitment rates over time, while increased mortality rates seemed to be driving population change of the most abundant species, within the Brazilian cluster. Longer observation periods would be necessary to determine whether any species shift is part of a natural fluctuation within the system or the result of a geographically-wide response to global change.

Despite an increasing or declining abundance over time, most of the species maintained an almost unchanged contribution to total stand basal area. Turnover rates of common species were found to be much higher in the Peruvian plots, mirroring patterns found at the stand level and partially explained by higher soil fertility. Mean values of stem density and basal area of pioneer species showed an increase over time in all the study sites, with an exception for some north Peruvian locations. This could signal increasing predominance of light-demanding plants and climbers in most locations, and the eventual extinction of some slow-growing, shade-tolerant trees, with repercussions on forest carbon stocks. Light-demanding trees have less dense wood than the shade lovers, and therefore mature tropical forests are likely to sequester less carbon per unit area than would be expected because of the increase of low-density species. A change in species composition would ultimately also affect forest structure, further contributing to changes in carbon stocks, in tropical forest ecosystems.

The comparison of elements of the flora common to both study sites analysed here, revealed generally higher mean turnover rates and higher mean annual increments in individuals from the western south Peruvian plots versus central Amazonian plots. This seems to suggest that floristic changes are likely to become more manifest earlier in highly dynamic forests, where a more rapid substitution of species might occur.

The picture is complicated, however, because responses to $CO_2$, which would lead to a particular species composition, would act in conjunction with responses to changes in water availability and competition for other resources, which would promote a different array of species. In addition, studies in natural plant communities confirm that leaf and individual responses do not necessarily translate into community and ecosystem responses. Moreover, changes may be transient and of an uncertain long-term direction. It has been predicted that the Amazon forest will increase in biomass, but will suffer large-scale dieback later in this century, as drought-temperature effects become important, leading to a rapid acceleration of global warming.

Monitoring and understanding what is happening on the ground in Amazonian forests today is crucial, both for the future of these forests and possibly for the global climate. Many of the existing permanent sample plots were initially censused in the 1980s and 1990s, and although they are already yielding valuable scientific information, their full potential will be realised if they can be monitored for several more decades. The permanent sample plots used for the present study cover very distinct environmental conditions and the dataset collated constitutes the outcome of the on-going work of several research groups. Although not spanning the whole range of soil and climate that characterizes the Amazon basin, the dataset offers a valuable amount of information for the investigation of the main spatial and temporal patterns of changes in forest structure, biomass and dynamics in relation to global change. The analysis does not yet provide adequate understanding and explanation for the potential ecological changes occurring in tropical forests. Long term monitoring would be required, together with an expansion of the network of plots to cover wider gradients of environmental conditions, and provide a better representation of different types of forest stands. More information would be needed from each site (local climate, soil, etc.). The protocol used to gather data for the present study has already been refined and applied to the most recent inventories of the study sites analysed. Ways to cluster tropical forest species into useful functional groups should be found to enable modelling and interpretation of species responses to changes in climate and atmospheric composition.

Some issues could be better addressed, provided that more data were available: (a) the effect on large unperturbed areas and forest fragments of deforestation occurring in neighbouring areas, (b) the basal area growth and total net primary production on a larger set of plots covering a larger range of different environmental conditions, (c) the species compositional change, using an approach based on functional groups, (d) the effect of climate on growth and mortality, analysing annual diameter measurements for some selected plots, (e) the behaviour of some common species occurring in different sites, in order to identify factors that limit forest productivity and would therefore limit the potential carbon sink.

# *Literature cited*

---

AA.VV. (2001). Atmospheric Inversion Calculation Performed for IPCC Third Assessment Report Chapter 3 (The Carbon Cycle and Atmospheric CO2), Technical Reports. **2**. Max-Plank-Institute fur Biogeochemie, Jena, Germany.

Alder, D. and Synnott, T. J. (1992). Permanent sample plots techniques for mixed tropical forests. 124 p. Oxford Forestry Institute, G.B. Tropical Forestry Paper no. 25.

Allen, A. S., Andrews, J. A., Finzi, A. C., Matamala, R., Richter, D. D., and Schlesinger, W. H. (2000). Effects of free-air CO2 enrichment (FACE) on belowground processes in a Pinus taeda forest. *Ecological Applications* **10**: 437-448.

Almeida, S. S., Lisboa, P. L. B., and Silva, A. S. L. (1993). Diversidade floristica de uma comunidade arborea na estacao cientifica "Ferreira Penna", em Caxiuana (Para'). *Boletim do Museu Paraense Emilio Goeldi* **9**: 93-128.

Arnone, J. A. and Körner, Ch. (1995). Soil and biomass carbon pools in model communities of tropical plants under elevated CO2. *Oecologia* **104**: 61-71.

Ashton, P. S. (1969). Speciation among tropical forest trees: some deductions in the light of recent evidence. Lowe-McConnel, R. H. Speciation in tropical environments. Biological Journal of the Linnean Society. pp. 155-196. London, Academic Press. *Biological Journal of the Linnean Society.* Vol 1, numbers 1& 2.

Ashton, P. S. (1996). Niche specificity among tropical trees: a question of scales. Newbery, D. M., Prins, H. H. T., and Brown, N. D. Dynamics of Tropical Communities. The 37th symposium of the British Ecological Society, Cambridge University. pp. 491-515. Blakwell Science, Oxford, UK.

Aubreville, A. (1938). La forêt coloniale: les forêts de l'Afrique occidentale française. *Annales, Academie des Sciences Coloniales* **9**:1-124.

Austin, M. P., Pausas, J. G., and Nicholls, A. O. (1996). Patterns of tree species richness in relation to environment in southeastern New South Wales, Australia. *Australian Journal of Ecology* **21**: 154-164.

Baker, T. R., Affum-Baffoe, K., Burslem, D. F. R. P., and Swaine, M. D. (2003). Phenological differences in tree water use and the timing of tropical forest inventories: conclusions from patterns of dry season diameter changechangechangedensity. *Forest Ecology & Management* **171**: 261-274.

Baker, T. R. and et al. (in review). Spatial pattern in neotropical biomass: interpolations across the Amazon from inventory data accounting for variation in forest structure and wood density. *Global Change Biology.*

Balslev, H., Luteyn, J., Ollgaard, B., and Holm-Nielsen, L. B. (2001). Composition and structure of adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Botanica* **92**: 37-57.

Basnet, K. (1992). Effect of topography on the pattern of trees in Tabonuco (Dacryodes excelsa) dominated rain forest in Puerto Rico. *Biotropica* **24**: 31-42.

Bazzaz, F. A. (1979). The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**: 351-371.

Bazzaz, F. A. (1990). The response of natural ecosystems to the rising global CO2 levels. *Annual Review of Ecological Systems* **21**: 167-196.

Bazzaz, F. A. and Miao, S. L. (1993). Successional status, seed size, and responses of tree seedlings to CO2, light, and nutrients. *Ecology* **74**: 104-112.

Benzing, D. H. (1998). Vulnerabilities of tropical forests to climate change: The significance of resident epiphytes. *Climate Change* **39**: 519-540.

Bigelow, S. W. (1993). Leaf nutrients in relation to stature and life form in tropical rain-forest. *Journal of Vegetation Science* **4**: 401-408.

Bousquet, P., Peylin, P., Ciais, P., Le Quere, C., Friedlingstein, P., and Tans, P. P. (2000). Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science* **290**: 1342-1346.

Braswell, B. H., Schimel, D. S., Linder, E., and Moore, B. (1997). The response of global terrestrial ecosystems to interannual temperature variability. *Science* **278**: 870-872.

Broecker, W. S, Takahashi, T., Simpson, H. J., and Peng, T-H. (1979). Fate of fossil fuel carbon dioxide and the global carbon budget. *Science* **206**: 409-418.

Brokaw, N. V. L. (1983). Treefalls: frequency, timing, and consequences. Leigh, E. G., Rand, S. A., and Windsor, D. M. The ecology of a tropical rainforest: seasonal rhythms and long-term changes. pp. 101-108. Oxford University Press, Oxford, UK.

Brokaw, N. V. L. (1987). Gap-phase regeneration of three pioneer species in a tropical forests. *Journal of Ecology* **75**: 9-19.

Brown, I. F., Martinelli, L. A., Thomas, W. W., Moreira, M. Z., Ferreira, C. A. C., and Victoria, R. A. (1995). Uncertainty in biomass of Amazonian forests: an example from Rondonia, Brazil. *Forest Ecology & Management* **75**: 175-189.

Brown, I. F., Nepstad, D. C., Pires, I. D., Luz, L. M., and Alechandre, A. S. (1992). Carbon storage and land-use in extractive reserves, Acre, Brazil. *Environmental Conservation* **19**: 307-315.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *American Naturalist* **124**: 255-279.

Brown, K. S. (2001). Soils and vegetation. Whitmore, T. C. and Prance, G. T. Biogeography and Quaternary History in Tropical America. pp. 19-45. Oxford Monographs in Biogeography 3, Oxford Science Publication, Oxford, UK

Brown, S., Gillepsie, A. J. R., and Lugo, A. E. (1989). Biomass estimation methods for tropical forests with applications to forest inventory data. *Forest Science* **35**: 881-902.

Brown, S. and Lugo, A. E. (1982). The storage and production of organic-matter in tropical forests and their role in the global carbon cycle. *Biotropica* **14**: 161-187.

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

Brown, S. and Lugo, A. E. (1992). Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. *Interciencia* **17**: 8-18.

Bruijnzeel, L. A. and Veneklaas, E. J. (1998). Climatic conditions and tropical, montane forest productivity: The fog has not lifted yet. *Ecology* **79**: 3-9.

Burslem, D. F. R. P., Grubb, P. J., and Turner, I. M. (1996). Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica* **28**: 636-648.

Burslem, D. F. R. P. and Whitmore, T. C. (1999). Species diversity, susceptibility to disturbance and tree population dynamics in tropical rain forest. *Journal of Vegetation Science* **10**: 767-776.

Bush, M. B. (1994). Amazonian speciation: a necessary complex model. *Journal of Biogeography* **21**: 5-17.

Bush, M. B., Piperno, D. R., Colinvaux, P. A., de Oliveira, P. E., Krissek, L. A., Miller, M. C., and Rowe, W. E. (1992). A 14 300-yr paleological profile of a lowland tropical lake in Panama. *Ecological Monographs* **62**: 251-275.

Caballe, G. and Martin, A. (2001). Thirteen years of change in trees and lianas in a Gabonese rainforest. *Plant Ecology* **152**: 167-173.

Cao, M. K. and Woodward, F. I. (1998). Net primary and ecosystem production and carbon stocks of terrestrial ecosystems and their responses to climate change. *Global Change Biology* **4**: 185-198.

Carrion, J. S., Munuera, M., Dupre, M., and Andrade, A. (2001). Abrupt vegetation changes in the Segura Mountains of southern Spain throughout the Holocene. *Journal of Ecology* **89**: 783-797.

Chave, J., Riera, B., and Dubois, M. A. (2001). Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *Journal of Tropical Ecology* **17**: 79-96.

Chesson, P. L. and Warner, R. R. (1994). Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist* **117**: 923-943.

Clark, D. A. (2002). Are tropical forests an important carbon sink? Reanalysis of the long-term plot data. *Ecological Applications* **12**: 3-7.

Clark, D. A. and Clark, D. B. (1992). Life-history diversity of canopy and emergent trees in a Neotropical rain-forest. *Ecological Monographs* **62**: 315-344.

Clark, D. A. and Clark, D. B. (1994). Climate-induced annual variation in canopy tree growth in a Costa-Rican tropical rain-forest. *Journal of Ecology* **82**: 865-872.

Clark, D. A., Clark, D. B., Sandoval, R., and Castro, M. V. (1995). Edaphic and human effects on landscape-scale distributions of tropical rain-forest palms. *Ecology* **76**: 2581-2594.

Clark, D. B. (1996). Abolishing virginity. *Journal of Tropical Ecology* **12**: 735-739.

Clark, D. B. and Clark, D. A. (1996). Abundance, growth and mortality of very large trees in neotropical lowland rain forest. *Forest Ecology & Management* **80**: 235-244.

Clark, D. B. and Clark, D. A. (2000). Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology & Management* **137**: 185-198.

Clinebell, R. R., Phillips, O. L., Gentry, A. H., Stark, N., and Zuuring, H. (1995). Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation* **4**: 56-90.

Colinvaux, P. A., de Oliveira, P. E., Moreno, J. E., Miller, M. C., and Bush, M. B. (1996). A long pollen record from lowland Amazonia: forest and cooling in glacial times. *Science* **274**: 85-88.

Colwell, R. K. and Lees, D. C. (2000). The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology & Evolution* **15**: 70-76.

Condit, R. (1995). Research in large, long-term tropical forest plots. *Trends in Ecology & Evolution* **10**: 18-21.

Condit, R. (1996). Defining and mapping vegetation types in mega-diverse tropical forests. *Trends in Ecology & Evolution* **11**: 4-5.

Condit, R. (1997). Forest turnover, diversity, and CO2. *Trends in Ecology & Evolution* **12**: 249-250.

Condit, R. (1998). Ecological implications of changes in drought patterns: Shifts in forest composition in Panama. *Climate Change* **39**: 413-427.

Condit, R., Ashton, P. S., Manokaran, N., Lafrankie, J. V., Hubbell, S. P., and Foster, R. B. (1999). Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. *Philosophical Transactions Series B-Biological Sciences* **354**: 1739-1748.

Condit, R., Hubbell, S. P., and Foster, R. B. (1992). The recruitment near conspecific adults and the maintenance of tree and shrub diversity in a Neotropical forest. *The American Naturalist* **140**: 261-286.

Condit, R., Hubbell, S. P., and Foster, R. B. (1993a). Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *Forest Ecology & Management* **62**: 123-143.

Condit, R., Hubbell, S. P., and Foster, R. B. (1993b). Mortality and growth of a commercial hardwood El-Cativo, Prioria-copaifera, in Panama. *Forest Ecology & Management* **62**: 107-122.

Condit, R., Hubbell, S. P., and Foster, R. B. (1995a). Mortality-rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* **65**: 419-439.

Condit, R., Hubbell, S. P., and Foster, R. B. (1995b). Wood volume and production of tropical timber species: data from a large, permanent plot in Panama. *Journal of Tropical Forest Science* **7**: 599-622.

Condit, R., Hubbell, S. P., and Foster, R. B. (1996a). Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science* **7**: 405-416.

Condit, R., Hubbell, S. P., and Foster, R. B. (1996a). Changes in tree species abundance in a Neotropical forest: Impact of climate change. *Journal of Tropical Ecology* **12**: 231-256.

Condit, R., Hubbell, S. P., Lafrankie, J. V., Sukumar, R., Manokaran, N., Foster, R. B., and Ashton, P. S. (1996b). Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots. *Journal of Ecology* **84**: 549-562.

Condit, R., Loo, de Lao, Leigh, E. G., Foster, R. B., Sukumar, R., Manokaran, N., and Hubbell, S. P. (1998). Assessing forest diversity from small plots: Calibration using species-individual curves from 50 ha plots. In: Dallmeier, F., Comiskey, J.A. (Eds), Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies. **20**: 247-268. Man and the Biosphere Series, UNESCO, Paris, and The Parthenon Publishing Group, New York.

Condit, R., Pitman, N., Leigh, E. G., Chave, J., Terborgh, J. W., Foster, R. B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H., Losos, E., and Hubbell, S. P. (2000). Beta-diversity in tropical forest trees. *Science* **295**: 666-669.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and rain forest trees. denBoer, P. J. and Gradwell, G. R. Dynamics of populations. pp. 298-312. Pudoc, Wageningen, The Netherlands.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302-1310.

Coomes, D. A. and Grubb, P. J. (1998). Responses of juvenile trees to above-ground and below-ground competition in nutrient-starved Amazonian rain forest. *Ecology* **79**: 768-782.

Cox, C. B. and Moore, P. D. (2000). Biogeography: an ecological and evolutionary approach. Sixth edition: 316 p., Blackwell Science, Oxfird, UK.

Curtis, P. S. (1996). A meta-analysis of leaf gas exchange and nitrogen in trees grown under elevated carbon dioxide. *Plant Cell and Environment* **19**: 127-137.

Curtis, P. S. and Wang, X. (1998). A meta-analysis of elevated $CO_2$ effects on woody plant mass, form, and physiology. *Oecologia* **113**: 299-313.

Dalling, J. W. and Hubbell, S. P. (2002). Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology* **90**: 557-568.

Dallmeier, F. Editor. (1992). Long-term monitoring of biological diversity in tropical forest areas: Methods for establishment and inventory of permanent plots. 72 p. UNESCO, Paris. MAB Digest, 11.

Dawson, T. E. (1996a). Determining water use by trees and forests role from isotopic, energy balance and transpiration analyses: the roles of tree size and hydraulic lift. *Tree Physiology* **16**: 263-272.

Dawson, T. E. (1996b). Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia* **107**: 13-20.

de Oliveira, A. A. and Daly, D. C. (1999). Geographic distribution of tree species occurring in the region of Manaus, Brazil: implications for regional diversity and conservation. *Biodiversity and Conservation* **8**: 1247-1259.

Delcourt, H. R. and Delcourt, P. A. (1991). Quaternary Ecology, a paleoecological Perspective. 242 p., Chapman & Hall, London, UK.

Denslow, J. S. (1980). Gap partitioning among tropical rainforest trees. *Biotropica* **12**: 47-55.

Denslow, J. S. (1995). Disturbance and diversity in tropical rain-forests - The density effect. *Ecological Applications* **5**: 962-968.

Denslow J.S., Guzman S. (2000) Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence. Panama. *Journal of vegetation science* **11**:201-212.

Diaz, S. (1995). Elevated $CO_2$ responsiveness, interactions at the community level and functional type. *Journal of Biogeography* **22**: 289-295.

Dixon, R. K., Brown, S., Houghton, R. A., Solomon, A. M., Trexler, M. C., and Wisniewski, J. (1994). Carbon pools and flux of global forest ecosystems. *Science* **263**: 185-190.

Drake, D. R. and Mueller Dombois, D. (1993). Population development of rain forest trees on a chronosequence of Hawaiian lava flows. *Ecology* **74**: 1012-1019.

Duivenvoorden, J. F. (1994). Vascular plant species counts in the rain forests of the Middle Caqueta area, Colombia Amazonia. *Biodiversity and Conservation* **3**: 685-715.

Duivenvoorden, J. F. (1995). Tree species composition and rain forest-environment relationships in the middle Caqueta area, Colombia, NW Amazonia. *Vegetatio* **120**: 91-113.

Duivenvoorden, J. F. (1996). Patterns of tree species richness in rain forests of the middle Caqueta area, Colombia, NW Amazonia. *Biotropica* **28**: 142-158.

Dukes, J. S. and Mooney, H. A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology & Evolution* **14**: 135-139.

Dumont, J. F. (1989). Neotectanica y dinamica fluvial de la baja Amazonia Peruana. *Boletin de la Sociedad Geologica del Peru* **80**: 51-64.

Engelbrecht, B. M. J. (2001). Drought resistance in seedlings of 28 tropical woody plant speciesresponses to climatic variation. Euroworkshop: Functional Grouping of Tropical Trees. Edinburgh, UK.

Enquist, B. J. and Leffler, A. J. (2001). Long-term tree ring chronologies from sympatric tropical dry- forest trees: individualistic responses to climatic variation. *Journal of Tropical Ecology* **17**: 41-60.

Enquist, B. J. and Niklas, K. J. (2001). Invariant scaling relations across tree-dominated communities. *Nature* **410**: 655-660.

Esser, G. (1992). The role of the tropics in the global carbon budget: impacts and possible developments. In: Goldammer, J. G (ed) Tropical forests in transition. Ecology of Natural and Anthropogenic disturbance processes. Pp. 225-252. Birkhaeuser Verlag, Berlin, Germany.

Ewel, J.J. (1980) Tropical succession: manifold routes to maturity. *Biotropica* **12**:2-7.

Fan, S. M., Gloor, M., Mahlman, J., Sarmiento, J. L., Takahashi, T., and Tans, P. P. (1998). A large terrestrial carbon sink in North America implied by atmospheric and ocean carbon dioxide data and models. *Science* **282**: 442-446.

Fan, S. M., Wofsy, S. C., Bakwin, P. S., Jacob, D. J., and Fitzjarrald, D. R. (1990). Atmosphere-biosphere exchange of CO2 and O3 in the central- Amazon-forest. *Journal of Geophysical Research-Atmospheres* **95**: 16851-16864.

Farquhar, G. D. (1997). Carbon dioxide and vegetation. *Science* **278**: 1411-1411.

Farquhar, G. D., von Caemmerer, S. V., and Berry, J. A. (1980). A biochemical-model of photosynthetic CO2 assimilation in leaves of C3 plants. *Planta* **149**: 78-90.

Fearnside, P. M. (1992). Carbon Emissions and Sequestration in Forests: Case Studies from Seven Developing Countries. Vol. 2, Greenhouse Gas Emissions from Deforestation in the Brazilian Amazon. LBL-32758 UC-402, Energy and Environment Division, Lawrence Berkeley Laboratory. 73 p. , Berkeley, University of California, CA, USA.

Fearnside P.M., Guimares, W.M. (1996) Carbon uptake by secondary forests in Brazilian Amazonia. *Forest Ecology and Management* **80**:35-46.

Fearnside, P. M. (1997a). Greenhouse gases from deforestation in Brazilian Amazonia: Net committed emissions. *Climate Change* **35**: 321-360.

Fearnside, P. M. (1997b). Wood density for estimating forest biomass in Brazilian Amazonia. *Forest Ecology & Management* **90**: 59-87.

Felfili, J. M. (1995). Diversity, structure and dynamics of a gallery forest in Central Brazil. *Vegetatio* **117**: 1-15.

Frailey, C. D., Lavina, E. L., Rancy, A., and Filho, J. P. S. (1988). A proposed Pleistocene/Holocene lake in the Amazon basin and its significance to Amazonian geology and biogeography. *Acta Amazonica* **18**: 119-143.

Gale, N. and Barford, A. S. (1999). Canopy tree mode of death in a western Ecuadorian rain forest. *Journal of Tropical Ecology* **15**: 415-436.

Gentry, A. H. (1982). Patterns of neotropical plant species diversity. *Evolutionary Biology* **15**: 1-84.

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

Gentry, A. H. (1992). Tropical forest biodiversity - Distributional patterns and their conservational significance. *Oikos* **63**: 19-28.

Gentry, A. H. (1994). Floristic similarities and differencies between southern and central America and upper and central Amazonia. Gentry, A. H. Four Neotropical Forests. pp. 141-157. Yale University Press, Yal, USA.

Gentry, A. H. and Ortiz, R. (1993). Patrones de composición florística en la Amazonia Peruana. Kalliola, R., Puhakka, M., and Danjoy, W. Tropical Amazonía Peruana: Vegetación húmeda tropical en el llano subandino. pp. 155-166., PAUT and ONERN, Jyväskylä, Finland.

Gifford, R. M. (1992). Interaction of carbon dioxide with growth-limiting environmental factors in vegetation productivity: implications for the global cargbon cycle. *Advances in Bioclimatology* **1**: 24-58.

Gifford, R. M. (1994). The global carbon-cycle - A viewpoint on the missing sink. *Australian Journal of Plant Physiology* **21**: 1-15.

Gillepsie, A. J. R., Brown, S., and Lugo, A. E. (1992). Tropical forest biomass estimation from truncated stand tables. *Forest Ecology & Management* **48**: 69-87.

Givnish, T. J. (1999). On the causes of gradients in tropical tree diversity. *Journal of Ecology* **87**: 193-210.

Glenn-Lewin, D. C., Peet, R. K., and Veblen, T. T. (eds.) (1992). Plant succession. Theory and prediction. 352 p. Chapman & Hall, London, UK.

Goodland, R. J. A. and Irwin, H. S. (1975). Amazon jungle: Green hell to red desert: An ecological discussion of the environmental impact of the highway construction program in the Amazon Basin. 155 p., Elsevier Scientific Publishing, New York, USA.

Grace, J., Lloyd, J., Mcintyre, J. A., Miranda, A., Meir, P., Miranda, H., Moncrieff, J. B., Massheder, J., Wright, I., and Gash, J. H. C. (1995a). Fluxes of carbon-dioxide and water-vapor over an undisturbed tropical forest in south-west Amazonia. *Global Change Biology* **1**: 1-12.

Grace, J., Lloyd, J., Mcintyre, J. A., Miranda, A. C., Meir, P., Miranda, H. S., Nobre, A. D., Moncrieff, J. B., Massheder, J., Malhi, Y., Wright, I., and Gash, J. H. C. (1995b). Carbon-dioxide uptake by an undisturbed tropical rain-forest in southwest Amazonia, 1992 to 1993. *Science* **270**: 778-780.

Guariguata M.R., Ostertag R. (2001) Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* **148**:185-206.

Hacke, U. G., Sperry, J. S., Pockman, W. T., Davis, S. D., and McCulloch, K. A. (2001). The effects of plant composition and diversity on ecosystem processes. *Oecologia* **126**: 457-461.

Haffer, J. (1969). Speciation in Amazonian forest birds. *Science* **165**: 131-137.

Haffer, J. (1997). Contact zones between birds of southern Amazonia. Remsen, J. V. Jr. Studies in Neotropical Ornithology Honouring Ted Parker. pp. 281-306. . Ornithological Monographs No.48, Washington, DC, USA.

Hall, P., Ashton, P. S., Condit, R., Manokaran, N., and Hubbell, S. P. (1998). Signal and noise in sampling tropical forest structure and dynamics. Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies. Vol **20**, pp. 63-78. Man and the Biosphere Series, UNESCO, Paris, and The Parthenon Publishing Group, New York.

Hall, P. and Swaine, M. D. (1976). Classification and ecology of closed-canopy forest in Ghana. *Journal of Ecology* **64**: 913-951.

Hanagarth, W. (1993). Acerca de la Geoecología de las Sabanas del Beni e el Noreste de Bolivia. 186 p. Instituto de Ecología, La Paz, Bolivia.

Harms, K. E., Condit, R., Hubbell, S. P., and Foster, R. B. (2001). Habitat association of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* **89**: 947-959.

Hartshorn, G. S. (1992). Possible effects of global diversity in tropical forests. Peters, R. L. Global warming and biological diversity. pp. 137-146. Yale University Press, Yale, USA.

Hattenschwiler, S. and Körner, Ch. (1996). System-level adjustments to elevated CO2 in model spruce ecosystems. *Global Change Biology* **2**: 377-387.

Henderson, A. (1995). The Palms of the Amazon. 226 p., Oxford University Press, Oxford, UK.

Higuchi, N., Santos, J. C., Ribeiro, R. J., Freitas, J.V., Vieira, G.; Coic, A.; Minette, L.J. (1997). Crescimento e incremento de uma floresta Amazonica de terra-firme manejada experimentalmente. In: Higuchi, N.; Ferraz, J.B.S., Antony, L., Luizao, F., Luizao, R., Biot, Y., Hunter, I., Proctor, J., Ross, S. (Eds). Biomassa e nutrientes florestais: relatório final. INPA / DFID, p.88-132, Manaus, Brazil.

Hill, M. O. (1979). DECORANA - A FORTRAN Program for Detrended Correspondence Analysis and Reciprocal Averaging. Cornell University, Ithaca, New York, USA.

Hill, M. O. and Gauch, H. G. Jr. (1980). Detrended Correspondence Analysis: an improved ordination technique. *Vegetatio* **42**: 47-58.

Hodnett, M. G., Oyama, M. D., Tomasella, J., and de O.Marques Filho, A. (1996). Comparisons of long-term soil water storage behaviour under pasture and forest in three regions of Amazonia. Gash, J. H. C., Nobre, C. A., Roberts, J. M., and Victoria, R. L. Amazonian deforestation and climate. pp. 57-77, Wiley, New York, USA.

Hoorn, C. (1988). Nota preliminar sobre la edad de los sedimentos Terciarios de la zona de Araracuara (Amazonas). *Boletin Geologico* **29**: 87-95.

Hubbell, S. P. (1979). Tree dispersion, adundance, and diversity in a tropical dry forest. *Science* **203**: 1299-1309.

Hubbell, S. P., Condit, R., and Foster, R. B. (1990). Presence and absence of density dependence in a Neotropical tree community. *Philosophical Transactions Series B-Biological Sciences* **330**: 269-281.

Hubbell, S. P. and Foster, R. B. (1986a). Biology, chance and history and the structure of tropical rainforest tree communities. Diamond, J. M. and Case, T. J. Community Ecology. pp. 314-329, Harper and Row, New York, USA.

Hubbell, S. P. and Foster, R. B. (1986b). Commonness and rarirty in a Neotropical forest: implications for tropical tree conservation. Soule, M. E. Conservation Biology: the science of scarcity and diversity. pp. 205-232. , Sinauer Associates, Sunderland, Massachussetts, USA.

Hubbell, S. P. and Foster, R. B. (1994). Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. Gentry, A. H. Four Neotropical Forests. Chapter 26, p. 522-541. Yale University Press, Yale, USA.

Hubbell, S. P., Foster, R. B., OBrien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J., and de Lao, S. L. (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* **283**: 554-557.

Hughes, R. F., Kauffman, J. B., and Jaramillo, V. J. (1999). Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* **80**: 1892-1907.

Hulme, M. and Viner, D. (1998). A climate change scenario for the tropics. *Climatic Change* **39**: 145-176.

Hungate, B. A., Dijkstra, P., Johnson, D. W., Hinkle, C. R., and Drake, B. G. (1999). Elevated CO2 increases nitrogen fixation and decreases soil nitrogen mineralization in Florida scrub oak. *Global Change Biology* **5**: 781-789.

Huston, M. A. (1980). Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography* **7**: 147-157.

Idso, K. E. and Idso, S. B. (1994). Plant-responses to atmospheric CO2 enrichment in the face of environmental constraints - A review of the past 10 years research. *Agricultural and Forest Meteorology* **69**: 153-203.

IPCC - Intergovernmental Panel for Climate Change. (2001). Climate Change. The Scientific Basis. The third assessmnet report of IPCC working group I. 881 pp., Cambridge University Press, Cambridge, UK.

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist* **104**: 501-528.

Johnson, C. M., Zarin, D. J., and Johnson, A. H. (2000). Post-disturbance aboveground biomass accumulation in global secondary forests. *Ecology* **81**: 1395-1401.

Kahn, F. (1986). The life forms of Amazonian palms in relation to forest structure and dynamics. *Biotropica* **18**: 214-218.

Kahn, F. and De Castro, A. (1985). The palm community in a forest of central Amazonia. *Biotropica* **17**: 210-216.

Kahn, F. and De Granville, J.-J. (1992). Palms in forest ecosystems of Amazonia. 226 p., Springer-Verlag. Ecological studies, Berlin, Germany.

Keeling, C. D., Bacastow, R. B., and Whorf, T. P. (2001). Measurements of the concentration of carbon dioxide at Mauna Loa Observatory,Hawaii. Clark, W. C. Cardon Dioxide Review: 1982. pp. 377-385., Oxford University Press, New York, USA.

Keeling, C. D., Chin, J. F. S., and Whorf, T. P. (1996). Increased activity of northern vegetation inferred from atmospheric CO2 measurements. *Nature* **382**: 146-149.

Kennard D.K. (2002) Secondary forest succession in a tropical dry forest: patterns of development across a 50-year chronosequence in lowland Bolivia. *Journal of tropical ecology* **18**:53-66.

Kestin, T. S., Karoly, D. J., Yang, J. I., and Rayner, N. A. (1998). Time-frequency variability of ENSO and stochastic simulations. *Journal of Climate* **11**: 2258-2272.

Kilburn, P. D. (1966). Analysis of species-area relations. *Ecology* **47**: 831-843.

Killeen, T. J. (1996). Historia natural and biodiversidad de Parque Nacional "Noel Kempff Mercado", Santa Cruz, Bolivia and climatic factors. Missouri Botanical Garden/FAN/TNC. Plan de Manejo-Componente Cientifico. Santa Cruz, Bolivia.

Kiyoshi, U. and Kihachiro, K. (1999). Long-term growth dynamics of natural forests in Hokkaio, northern japan. *Journal of Vegetation Science* **10**: 815-824.

Klinge, H. (1976). Root mass estimation in lowland tropical rainforests of Central Amazonia, Brazil. III. Nutrients in fine roots from giant humus podzol. *Tropical Ecology* **16**: 28-38.

Koch, G. W. and Mooney, H. A. (1996). Responses of terrestrial ecosystems to elevated CO2: a synthesis and summary. Koch, G. W. and Mooney, H. A. Carbon dioxide and terrestrial ecosystems. pp. 415-428., Academic Press, . New York.

Körner, Ch. (1993). CO2 Fertilization: the great uncertainty in future vegetation development. Solomon, A. M. and Shugart, H. H. Vegetation dynamics and global change. pp. 53-70., Chapman & Hall, London, UK.

Körner, Ch. (1995). Biodiversity and CO2: global change is under way. *Gaia* **4**: 234-243.

Körner, Ch. (1996). The response of complex multispecies systems to elevated CO2. Walker, B. H. and Steffen, W. L. Global change in terrestrial ecosystems. pp. 20-42. IGBP series number 2, Cambridge University Press, Cambridge, UK.

Körner, Ch. (1998). Tropical forests in a CO-2-rich world. *Climate Change* **39**: 297-315.

Körner, Ch. (2000). Biosphere responses to CO2 enrichment. *Ecological Applications* **10**: 1590-1619.

Körner, Ch and Bazzaz, F. A. (1996). Carbon dioxide, populations, and communities. 488 pp. Academic Press, San Diego, USA.

Kruskal, J. B. (1964). Nonmetric multidimensional scaling: a numerical method. *Psychometrika* **89**: 947-959.

Kubo, T., Kohyama, T., Potts, M. D., and Ashton, P. S. (2000). Mortality rate estimation when inter-census intervals vary. *Journal of Tropical Ecology* **16**: 753-756.

Laurance, W. F., Fearnside, P. M., Laurance, S. G., Delamonica, P., Lovejoy, T. E., Rankin-de Merona, J. M., Chambers, J. Q., and Gascon, C. (1999). Relationship between soils and Amazon forest biomass: A landscape-scale study. *Forest Ecology & Management* **118**: 127-138.

Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. M., and Hutchings, R. W. (1998c). Influence of plot shape on estimates of tree diversity and community composition in central Amazonia. *Biotropica* **30**: 662-665.

Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. M., and Laurance, S. G. (1998b). Rain forest fragmentation and the dynamics of Amazonian tree communities. *Ecology* **79**: 2032-2040.

Laurance, W. F., Ferreira, L. V., Rankin-de Merona, J. M., Laurance, S. G., Hutchings, R. W., and Lovejoy, T. E. (1998a). Effects of forest fragmentation on recruitment patterns in Amazonian tree communities. *Conservation Biology* **12**: 460-464.

Laurance, W. F., Laurance, S. G., Ferreira, L. V., Rankin-de Merona, J. M., Gascon, C., and Lovejoy, T. E. (1997). Biomass collapse in Amazonian forest fragments. *Science* **278**: 1117-1118.

Laurance, W. F., Williamson, G. B., Delamonica, P., Oliveira, P., Lovejoy, T. E., Gascon, C., and Pohl, L. (2001). Effects of a strong drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology* **17** : 771-785.

Leighton, M. and Wirawan, N. (1986). Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982-1983 El Nino Southern Oscillation event. Prance, G. T. Tropical rain forests and the world atmosphere. pp. 75-102., Westview Press, Boulder,Colorado.

Lejoly, J. (1994). Mise en place des transects en vue des inventaires de biodiversité dans la forêt de Ngotto (République centrafricaine). Projet Ecofac (Conservation et utilisation rationnelle des écosystèmes forestiers en Afrique Centrale). 109 p., Agreco-CTFT, Bruxelles, Belgium.

Lejoly, J. (1996). Biodiversité végétale dans le Parc National d'Odzala (Congo) Projet Ecofac (Conservation et utilisation rationnelle des écosystèmes forestiers en Afrique Centrale). 127 p., Agreco-CTFT, Bruxelles, Belgium.

Lewis, S., Phillips, O. L., Sheil, D., Vinceti, B., Baker, T., Brown, S., Graham, A. W., Higuchi, N., Hilbert, D. W., Laurance, W. F., Lejoly, J., Malhi, Y., Monteagudo, M. A., Nunez, P., Sonke, B., Nur Supardi, M. N., Terborgh, J. W., and Vasquez, R. M. (in prep.). Tropical forest tree mortality, recruitment and turnover rates: calculation, interpretation, and comparison when census intervals vary. *Journal of Ecology.*

Lewis, S., Phillips, O. L., Malhi, Y., and et al. (in review b). Global change and tropical forest dynamics: a framework for evaluating causal mechanisms and detecting their effects. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences.*

Lieberman, D., Lieberman, M., Hartshorn, G. S., and Peralta, R. (1985b). Growth rates and age-size relationships of tropical wet forest trees in Costa Rica. *Journal of Tropical Ecology* **73**: 915-924.

Lieberman, M., Lieberman, D., Hartshorn, G. S., and Peralta, R. (1985a). Small-scale altitudinal variation in lowland wet tropical forest vegetation. *Journal of Ecology* **73**: 505-516.

Lloyd, J. (1999). Current perspectives on the terrestrial carbon cycle. *Tellus Series B-Chemical and Physical Meteorology* **51**: 336-342.

Lloyd, J. and Farquhar, G. D. (1996). The CO2 dependence of photosynthesis, plant growth responses to elevated atmospheric CO2 concentrations and their interaction with soil nutrient status .1. General principles and forest ecosystems. *Functional Ecology* **10**: 4-32.

Lloyd, J. and Farquhar, G. D. (2000). Do slow-growing species and nutrient-stressed plants consistently respond less to elevated CO2? A clarification of some issues raised by Poorter (1998). *Global Change Biology* **6**: 871-876.

Long, S. P. and Drake, B. G. (1991). Effect of the long-term elevation of CO2 concentration in the field on the quantum yield of photosynthesis of the C3 sedge, Scirpus-olneyi. *Plant Physiology* **96**: 221-226.

Longman, K. A. and Jenik, J. (1987). Tropical forest and its environment. 2nd ed. 347 pp., Longman Scientific & Technical, Essex, UK.

Lovelock, C. E., Winter, K., Mersits, R., and Popp, M. (1998). Responses of communities of tropical tree species to elevated CO2 in a forest clearing. *Oecologia* **116**: 207-218.

Lugo, A. E. and Brown, S. (1993). Management of tropical soils as sinks or sources of atmospheric carbon. *Plant and Soil* **149**: 27-41.

Lugo, A. E. and Scatena, F. N. (1996). Background and catastrophic tree mortality in tropical moist, wet, and rain forests. *Biotropica* **28**: 585-599.

Malhi, Y., Baker, T., Phillips, O. L., Almeida, S. S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C., Di Fiore, A., Higuchi, N., Killeen, T. J., Laurance, S., Laurance, W. F., Lewis, S., Merccado-Montoya, L. M., Monteagudo, M. A., Neill, D. A., Nunez, P., Patino, S., Pitman, N., Quesada, C. A., Silva, J. N. M., TorresLezama, A., Vasquez, R. M., Terborgh, J. W., Vinceti, B., and Lloyd, J. (in review a). The Above-Ground Wood Productivity and Net Primary Productivity of 100 Neotropical Forests. *Global Change Biology* (in review).

Malhi, Y., Baldocchi, D. D., and Jarvis, P. G. (1999). The carbon balance of tropical, temperate and boreal forests. *Plant Cell and Environment* **22**: 715-740.

Malhi, Y., Nobre, A. D., Grace, J., Kruijt, B., Pereira, M. G. P., Culf, A. D., and Scott, S. (1998). Carbon dioxide transfer over a Central Amazonian rain forest. *Journal of Geophysical Research-Atmospheres* **103**: 31593-31612.

Malhi, Y., Pegoraro, E., Nobre, A. D., Pereira, M. G. P., Grace, J., Culf, A. D., and Clement, R. (in review b). The water and energy dynamics of a central Amazonian rainf forest. *Journal of Geophysical Research-Atmospheres.*

Malhi, Y., Phillips, O. L., Lloyd, J., Baker, T., Wright, J., Almeida, S., Arroyo, L., Frederiksen, T., Grace, J., Higuchi, N., Killeen, T., Laurance, W. F., Leaño, C., Lewis, S., Meir, P., Monteagudo, M. A., Neill, D. A., Nunez, P. V., Panfil, S. N., Patiño, S., Pitman, N., Quesada, C. A., Rudas-Ll, A., Salomão, R., Saleska, S., Silva, N., Silveira, M., Sombroek, W. G., Valencia, R., Vasquez, R. M., Vieira, I. C. G., and Vinceti, B. (2002). An international network to understand the biomass and dynamics of Amazonian forests (RAINFOR). *Journal of Vegetation Science* **13**: 439-450.

Manokaran, N., Lafrankie, J. V., Kochummen, K. M., Quah, E. S., Klahn, J. E., Ashton, P. S., and Hubbell, S. P. (2001). Methodology for the fifty hectare research plot at Pasoh Forest Reserve. Forest Research Institute Malaysia, Research Pamphlet No. 104, 66 p., ISSN-0126-8196. Kuala Lumpur, Malaysia.

Marengo, J. A. and Hastenrath, S. (1993). Case-studies of extreme climatic events in the Amazon Basin. *Journal of Climate* **6**: 617-627.

Masle, J. (2000). The effects of elevated CO2 concentrations on cell division rates, growth patterns, and blade anatomy in young wheat plants are modulated by factors related to leaf position, vernalization, and genotype. *Plant Physiology* **122**: 1399-1415.

Mass, P. J. M. and Westra, L. Y. Th. (1993). Neotropical plant families., 290 pp., Koeltz Scientific Books, Koenigstein, Germany.

Mayle, F. E., Burbridge, R., and Killeen, T. (2000). Millennial-scale dynamics of southern Amazonian rain forests. *Science* **290**: 2291-2294.

Meggers, B. J. (1994). Archaeological evidence for the impact of mega-Nino events on Amazonia during the past 2 millennia. *Climatic Change* **28**: 321-338.

Meinzer, F. C., Andrade, J. L., Goldstein, G., Holbrook, N. M., Cavelier, J., and Wright, S. J. (1999). Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Oecologia* **121**: 293-301.

Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., and Schloss, A. L. (1993). Global climate-change and terrestrial net primary production. *Nature* **363**: 234-240.

Meyer, H. A. (1952). Structure, growth, and drain in balanced uneven-aged forests. *Journal of Forestry* **50**: 85-92.

Miranda, A. C., Miranda, H. S., Lloyd, J., Grace, J., Francey, R. J., Mcintyre, J. A., Meir, P., Riggan, P., Lockwood, R., and Brass, J. (1997). Fluxes of carbon, water and energy over Brazilian cerrado: An analysis using eddy covariance and stable isotopes. *Plant Cell and Environment* **20**: 315-328.

Molino, J. F. and Sabatier, D. (2001). Tree Diversity in Tropical Rain Forests: A Validation of the Intermediate Disturbance Hypothesis. *Science* **294**: 1702-1704.

Mooney, H. A., Canadell, J., Chapin, F. S., Ehleringer, J. R., Körner, Ch, McMurtie, R. E., Parton, W. J., Pitelka, L. F., and Schulze, E. D. (1999). Ecosystem Physiology Responses to Global Change. Steffen, W. L., Canadell, J., Ingram, J. S. I., and Walker, B. H. Implications of Global Change for Natural and Managed Ecosystems: A Synthesis of GCTE and Related Research. pp. 141-189. IGBP Book Series No. 4, Cambridge University Press, London.

Mori, S. A. (1991). The Guyana lowland floristic province. *C.R.Soc.Biogeogr* **67**: 67-75.

Mori, S. A., Boom, B. M., de Carvalho, A. M., and dos Santos, T. S. (1983b). Southern Bahian moist forests. *Botanical Review* **49**: 155-232.

Mori, S. A., Boom, B. M., de Carvalino, A. M., and dos Santos, T. S. (1983a). Ecological importance of Myrtaceae in an Eastern Brazilian wet forest. *Biotropica* **15**: 68-70.

Naeem, S., Thompson, L. J., Lawler, S. P., and Woodfin, R. M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature* **368**: 734-737.

Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubo, T., Kato, T., Maeda, T., Sato, K., Miguchi, H., Nagamasu, H., Ogino, K., Teo, S., Hamid, A. A., and Seng, L. H. (2000). Impact of severe drought associated with the 1997-1998 El Nino in a tropical forest in Sarawak. *Journal of Tropical Ecology* **16**: 355-367.

Nelson, B. W., Ferreira, L. V., da Silva, M. F., and Kawasaki, M. L. (1990). Endemis centres, refugia and botanical collection density in Brazilian Amazonia. *Nature* **345**: 714-716.

Nelson, B. W., Kapos, V., Adams, J. B., Oliveira, W. J., Braun, O. P., and Doamaral, L. (1994). Forest disturbance by large blowdowns in the Brazilian Amazonia. *Ecology* **75**: 853-858.

Newbery, D. M., Kennedy, D. N., Petol, G. H., Madani, L., and Ridsdale, C. E. (1999). Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. *Philosophical Transactions Series B-Biological Sciences* **354**: 1763-1782.

Newbery, D. M., Renshaw, E., and Brunig, E. F. (1986). Spatial pattern of trees in kerangas forest, Sarawak. *Vegetatio* **65**: 77-89.

Norby, R. J., ONeill, E. G., and Luxmoore, R. J. (1986). Effects of CO2 enrichment on the growth and mineral-nutrition of Quercus-alba seedlings in nutrient-poor soil. *Plant Physiology* **82**: 83-89.

Norby, R. J., Wullschleger, S. D., Gunderson, C. A., Johnson, D. W., and Ceulemans, R. (1999). Tree responses to rising CO2 in field experiments: implications for the future forest. *Plant Cell and Environment* **22**: 683-714.

Nores, M. (1999). An alternative hypothesis for the origin of Amazonian bird diversity. *Journal of Biogeography* **24**: 475-485.

OBrien, E. M. (1998). Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography* **25**: 379-398.

Oliveira-Filho, A. T. (1993). Gradient analysis of an area of coastal vegetation in the state of Paraiba, northeastern Brazil. *Edinburgh Journal of Botany* **50**: 217-236.

Oliveira-Filho, A. T. and Ratter, J. A. (1995). A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. *Edinburgh Journal of Botany* **52**: 141-194.

Olson, J. W., Watts, J. A., and Allison, L. J. (1983). Carbon in live vegetation of Major World Ecosystems. Report ORNL-5862. Oak Ridge National Laboratory, Oak Ridge, Tennessee, USA.

Oren, R., Ellsworth, D. S., Johnsen, K. H., Phillips, N., Ewers, B. E., Maier, C., Schafer, K. V. R., McCarthy, H., Hendrey, G., McNulty, S. G., and Katul, G. G. (2001). Soil fertility limits carbon sequestration by forest ecosystems in a CO2-enriched atmosphere. *Nature* **411**: 469-472.

Pacala, S. and Tilman, D. (1994). Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. *The American Naturalist* **143**: 222-257.

Palmer, M. W. (1993). Putting things in even better order - The advantages of canonical correspondence-analysis. *Ecology* **74**: 2215-2230.

Peet R.K. (2000) Community structure and ecosystem function. In: Glenn-Lewin, D.C., Peet, R.K. & Veblen, T.T. (eds.) *Plant succession: theory and prediction*, pp. 103-151. Chapman and Hall, London.

Phillips, O. L. (1993). Comparative valuation of tropical forests in Amazonian Peru. PhD Thesis, Washington University, Missouri Botanical Garden, St. Louis, Missouri, USA.

Phillips, O. L. (1995). Evaluating turnover in tropical forests - Response. *Science* **268**: 894-895.

Phillips, O. L. (1996). Long-term environmental change in tropical forests: increasing tree turnover. *Environmental Conservation* **23**: 235-248.

Phillips, O. L. (1997). The changing ecology of tropical forests. *Biodiversity and Conservation* **6**: 291-311.

Phillips, O. L. (1998). Increasing tree turnover in tropical forests as measured in permanent plots. In: Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies. Vol. **20**, pp. 221-245. Man and the Biosphere Series, UNESCO, Paris, and The Parthenon Publishing Group, New York.

Phillips, O. L. (in review a). Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology*.

Phillips, O. L., Arroyo, L., Higuchi, N., Killeen, T., Laurance, W. F., Lewis, S., Lloyd, J., Malhi, Y., Monteagudo, M. A., Neill, D., Nunez, P. V., Silva, J. N. M., Terborgh, J. W., Vasquez, R. M., Alexiades, M., Almeida, S., Brown, S., Chave, J., Comiskey, J. A., Czimczik, C., Di Fiore, A., Erwin, T., Kuebler, C., Laurance, S. G., Nascimento, H. E. M., Palacios, W. A., Patino, S., Pitman, N., Olivier, J., Quesada, C. A., Saldias, M., TorresLezama, A., and Vinceti, B. (in review b). Carbon sink for a century. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*.

Phillips, O. L. and Gentry, A. H. (1994). Increasing turnover through time in tropical forests. *Science* **263**: 954-957.

Phillips, O. L., Gentry, A. H., Reynel, C., Wilkin, P., and Galvezdurand, C. (1994b). Quantitative ethnobotany and Amazonian conservation. *Conservation Biology* **8**: 225-248.

Phillips, O. L., Hall, P., Gentry, A. H., Sawyer, S. A., and Vasquez, R. M. (1994a). Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences of the United States of America* **91**: 2805-2809.

Phillips, O. L., Malhi, Y., Higuchi, N., Laurance, W. F., Nunez, P. V., Vasquez, R. M., Laurance, S. G., Ferreira, L. V., Stern, M. J., Brown, S., and Grace, J. (1998a). Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science* **282**: 439-442.

Phillips, O. L., Nunez, P., and Timana, M. E. (1998b). Tree mortality and collecting botanical vouchers in tropical forests. *Biotropica* **30**: 298-305.

Phillips, O. L. and Sheil, D. (1997). Forest turnover, diversity and CO2. *Trends in Ecology & Evolution* **12**: 404.

Phillips, O. L., Malhi, Y., Vinceti, B., Baker, T., Lewis, S., Higuchi, N., Laurance, W. F., Nunez, P. V., Vasquez, R. M., Laurance, S., Ferreira, L. V., Stern, M. J., Brown, S., and Grace, J. (2002a). Changes in growth of tropical forests: evaluating potential biases. *Ecological Applications* **12**: 576-587.

Phillips, O. L., Vasquez, R. M., Arroyo, L., Baker, T., Killen, T., Lewis, S., Malhi, Y., Monteagudo, M. A., Neill, D. A., Nunez, P. V., Alexiades, M., Ceron, C., Di Fiore, A., Erwin, T., Jardim, A., Palacios, W. A., Saldias, M., and Vinceti, B. (2002b). Increasing dominance of large lianas in Amazonian forests. *Nature* **418**: 770-774.

Pickett, S. T. A., Collins, S. L., and Armesto, J. J. (1987). Models, mechanisms and pathways of succession. *Botanical Review* **53**: 335-371.

Pickett, S. T. A. and White, P. S. (1985). The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York.

Pielou, E. C. (1984). The Interpretation of Ecological Data: A Primer on Classification and Ordination. 288 pp., Wiley-Interscience Publisher, New York.

Pimm, S. L. and Sudgen, A. M. (1994). Tropical diversity and global change. *Science* **263**: 933-934.

Pitman, N. C. A., Terborgh, J. W., Silman, M. R., and Nunez, P. V. (1999). Tree species distributions in an upper Amazonian forest. *Ecology* **80**: 2651-2661.

Pitman, N. C. A., Terborgh, J. W., Silman, M. R., Nunez, P. V., Neill, D. A., Ceron, C. E., Palacios, W. A., and Aulestia, M. (2001). Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* **82**: 2101-2117.

Polley, H. W., Johnson, H. B., Marino, B. D., and Mayeux, H. S. (1993). Increase in C3 plant water-use efficiency and biomass over glacial to presentCO2 concentrations. *Nature* **361**: 61-64.

Poorter, H. (1993). Interspecific variation in the growth-response of plants to an elevated ambient CO2 concentration. *Vegetatio* **104**: 77-97.

Prado, D. E. and Gibbs, P. E. (1993). Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden* **80**: 902-927.

Prance, G. T. (1973b). A review of the phytogeographic evidence for Pleistocene climate changes in the neotopics. *Annals of the Missouri Botanical Garden* **69**: 594-624.

Prance, G. T. (1973a). Phytogeographic support for the theory of Pleistocene forest refuges in teh Amazon basin, based on the evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae and Lecythidaceae. *Acta Amazonica* **3**: 5-28.

Prance, G. T. (1987). Vegetation. Whitmore, T. C. and Prance, G. T. Biogeography and Quaternary History of tropical America. pp. 28-44., Claredon Press, Oxford, UK.

Prance, G. T. (1994). A comparison of the efficacy of higher taxa and species numbers in the assessment of biodiversity in the Neotropics. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **345**: 89-99.

Prentice, I. C. and et al. (2001). The carbon cycle and atmospheric carbon dioxide. Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., and Johnson, C. A. Climate Change 2001 - The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Pp. 185-237, Cambridge University Press, Cambridge, UK.

Pritchard, S. G., Rogers, H. H., Prior, S. A., and Peterson, C. M. (1999). Elevated CO2 and plant structure: a review. *Global Change Biology* **5**: 807-837.

Pulliam, H. R. (1988). Sources, sinks and population regulation. *American Naturalist* **132**: 652-661.

Putz, F. E. and Mooney, H. A. Editors. (1991). The biology of vines. Leigh, E. G., Rand, S. A., and Windsor, D. M. The ecology of a tr ecology of a tropical rainforest: seasonal rhythms and long-term changes. 526 p., Cambridge University Press, Cambridge.

Pyke, C. R., Condit, R., Aguilar, S., and Lao, S. (2001). Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science* **12**: 553-566.

Rao, V. B. and Hada, K. (1990). Characteristics of rainfall over Brazil - Annual variations and connections with the southern oscillation. *Theoretical and Applied Climatology* **42**: 81-91.

Rasanen, M., Neller, R., Salo, J., and Jungner, H. (1992). Recent and ancient fluvial deposition systems in the Amazonian foreland basin, Peru. *Geological Magazine* **129**: 293-306.

Ratter, J. A., Bridgewater, S., Atkinson, R., and Ribeiro, J. F. (1996). Analysis of the floristic composition of the Brazilian cerrado vegetation II: comparison of the woody vegetation of 98 areas. *Edinburgh Journal of Botany* **53**: 153-180.

Rawson, H. M. (1992). Plant-responses to temperature under conditions of elevated CO2. *Australian Journal of Botany* **40** : 473-490.

Rayner, P. J., Enting, I. G., Francey, R. J., and Langenfelds, R. (1999). Reconstructing the recent carbon cycle from atmospheric CO2, delta C-13 and O-2/N-2 observations. *Tellus Series B-Chemical and Physical Meteorology* **51**: 213-232.

Reitsma, J. M. (1988). Forest vegetation of Gabon. Tropenbos Technical Series 1, The Tropenbos Foundation, Ede, The Netherlands.

Richards, P. W. (1952). The tropical rain forest: an ecological study. 575 pp., Cambridge University Press, Cambridge, UK.

Richards, P.W. (1955) The secondary succession in the tropical rain forest. *Science Progress* **43**:45-57.

Richards, P. W. (1996c). Composition of primary rain forests: II. The tropical rain forest. An ecological study. pp. 308-338. Second edition, Cambridge University Press, Cambridge, UK.

Richards, P. W. (1996a). Regeneration. The tropical rain forest. An ecological study. pp. 49-69. Second edition, Cambridge University Press, Cambridge, UK.

Richards, P. W. (1996b). Structure of primary rain forest. The tropical rain forest. An ecological study. pp. 23-48. Second edition, Cambridge University Press, Cambridge, UK.

Rodbell, D. T., Seltzer, G. O., Anderson, D. M., Abbott, M. B., Enfield, D. B., and Newman, J. H. (1999). An similar to 15,000-year record of El Nino-driven alluviation in southwestern Ecuador. *Science* **283**: 516-520.

Rosenzweig, M. L. (1995). Species diversity in space and time. 436 pp., Cambridge University Press, Cambridge, UK.

Saldarriaga, J. G., West, D. C., Tharp, M. L., and Uhl, C. (1988). Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology* **76**: 938-958.

Salimon, C. I. and Brown, I. F. (2000). Secondary forests in western Amazonia: significant sinks for carbon released from deforestation? *Interciencia* **25**: 198-202.

Salo, J. (1993). Notas en la historia de la exploración científica y teorías en la selva baja peruana. Kalliola, R., Puhakka, M., and Danjoy, W. Tropical Amazonía Peruana: Vegetación húmeda tropical en el llano subandino. pp. 23-31, PAUT and ONERN, Jyväskylä, Finland.

Sanchez, P. A. (1981). Soils of the humid tropics. Department of Anthropology. Blowing in the wind: Deforestation and long-range implications. pp. 347-410. William and Mary, Williamsburg, Vancouver, British Columbia.

Sanford, R. L., Saldarriaga, J. G., Clark, K. E., Uhl, C., and Herrera, R. (1985). Amazon rain-forest fires. *Science* **227**: 53-55.

Schimel, D. S. (1995). Terrestrial ecosystems and the carbon-cycle. *Global Change Biology* **1**: 77-91.

Schimel, D. S. and Sulzman, E. (1995). Variability in the earth climate system - decadal and longer timescales. *Reviews of Geophysics* **33**: 873-882.

Scholes, R. J., Schulze, E. D., Pitelka, L. F., and Hall, D. O. (1999). Biogeochemistry of terrestrial ecosystems. Wall, D. H., Steffen, W. L., Canadell, J., and Ingram, J. S. I. The terrestrial biosphere and global change. pp. 271-303. Cambridge University Press, Cambridge, UK.

Sheil, D. (1995b). A critique of permanent plot methods and analysis with examples from Budongo-forest, Uganda. *Forest Ecology & Management* **77**: 11-34.

Sheil, D. (1995a). Evaluating turnover in tropical forests. *Science* **268**: 894-894.

Sheil, D. (1996). Species richness, tropical forest dynamics and sampling: questioning cause and effect. *Oikos* **76**: 587-590.

Sheil, D. (1997). Long-term growth and rainfall in a Ugandan moist forest: seasonal rhythms and flexing stems. *Commonwealth Forestry Review* **76**: 121-127.

Sheil, D. (1999). Developing tests of successional hypotheses with size- structured populations, and an assessment using long-term data from a Ugandan rain forest. *Plant Ecology* **140**: 117-127.

Sheil, D., Burslem, D. F. R. P., and Alder, D. (1995). The interpretation and misinterpretation of mortality-rate measures. *Journal of Ecology* **83**: 331-333.

Sheil, D., Jennings, S., and Savill, P. (2000). Long-term permanent plot observations of vegetation dynamics in Budongo, a Ugandan rain forest. *Journal of Tropical Ecology* **16**: 765-800.

Sheil, D. and May, R. M. (1996). Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* **84**: 91-100.

Silva, A. F. and Shepherd, G. J. (1986). Comparações florísticas entre algumas matas brasileiras utilizando análises de agrupamento. *Revista Brasileira de Botanica* **9**: 81-86.

Silver W.L., Ostertag R., Lugo A.E. (2000) The potential for carbon sequestration through reforestation of abandoned tropical agricultural and pasture lands. *Restoration ecology* **8**(4):394-407.

Soil Survey Staff (1999). Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys, 2nd edition. Agriculture Handbook No. 436. Washington: United States Department of Agriculture.

Sokal, R. R. and Rohlf, F. (1974). Nonparametric methods in lieu of single classification anova. Biometry. The principles and practice of statistics in biological research. Second edition. pp. 429-445. W.H. Freeman and Company, San Francisco, USA.

Sombroek, W. G. (in press). Annual rainfall and dry-season strenght in the Amazon region and their environmental consequences. *Ambio.*

Sombroek, W. G. (2000). Amazon landforms and soils in relation to biological diversity. *Acta Amazonica* **30**: 81-100.

Sonke, B. (1998). Etudes floristiques et structurales des forêts de la Réserve de Faune du Dja (Cameoun). PhD Thesis, Universite libre de Bruxelles, Belgium.

Sousa, W. P. (1984). The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**: 353-391.

Sternberg, L. S. L., Moreira, M. Z., and Nepstad, D. C. (2002). Uptake of water by lateral roots of small trees in an Amazonian tropical forest. *Plant and Soil* **238**: 151-158.

Stocker, R. and Körner, Ch. (1999). A field study of the effects of elevated CO2 and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology* **5**: 95-105.

Stratton, L. C., Goldstein, G., and Meinzer, F. C. (1996). Temporal and spatial partitioning of water resources among eight woody species in a Hawaiian dry forest. *Oecologia* **124**: 309-317.

Svenning, J. C. (1999b). Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* **87**: 55-65.

Svenning, J. C. (1999a). Recruitment of tall arborescent palms in the Yasuni National Park, Amazonian Ecuador: are large treefall gaps important? *Journal of Tropical Ecology* **15**: 355-366.

Swaine, M. D. (1992). Characteristics of dry forest in West Africa and the influence of fire. *Journal of Vegetation Science* **3**: 365-374.

Swaine, M. D., Hall, J. B., and Alexander, I. J. (1987a). Tree population dynamics at Kade, Ghana. *Journal of Tropical Ecology* **3**: 331-345.

Swaine, M. D., Lieberman, D., and Putz, F. E. (1987b). The dynamics of tree populations in tropical forest - A review. *Journal of Tropical Ecology* **3**: 359-366.

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

Tans, P. P., Fung, I. Y., and Takahashi, T. (1990). Observational constraints on the global atmospheric CO2 budget. *Science* **247**: 1431-1438.

Taylor, D. M., Hamilton, A. C., Whyatt, J. D., Mucunguzi, P., and BukenyaZiraba, R. (1996). Stand dynamics in Mpanga Research Forest Reserve, Uganda, 1968- 1993. *Journal of Tropical Ecology* **12**: 583-597.

ter Braak, C. J. F. (1986). Canonical correspondence-analysis - A new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67**: 1167-1179.

ter Braak, C. J. F. and Smilauer, P. (1998). Canoco Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (version 4). Centre for Biometry, Wageningen, The Netherlands.

ter Steege, H. and Hammond, A. S. (2001a). Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology* **82**: 3197-3212.

ter Steege, H. and Hammond, A. S. (2001b). Character convergence, diversity, and disturbance in tropical rainforest in Guyana. *Ecology* **82**: 3197-3292.

ter Steege, H., Jetten, V. G., Polak, A. M., and Werger, M. J. A. (1993). Tropical rain-forest types and soil factors in a watershed area in Guyana. *Journal of Vegetation Science* **4**: 705-716.

ter Steege, H., Sabatier, D., Castellanos, H., van Andel, T., Duivenvoorden, J. F., de Oliveira, A. A., Ek, A. R., Lilwah, R., Maas, P., and Mori, S. (2000). An analysis of the floristic composition and diversity of Amazonian forests including those of the Guiana Shield. *Journal of Tropical Ecology* **16**: 801-828.

Terborgh, J. W. (1992). Diversity and the tropical rain forest. 242 p., Scientific American Library, New York, USA.

Terborgh, J. W. and Andresen, E. (1998). The composition of Amazonian forests: patterns at local and regional scales. *Journal of Tropical Ecology* **14**: 645-664.

Terborgh, J. W., Foster, R. B., and Nunez, P. V. (1996). Tropical tree communities: A test of the nonequilibrium hypothesis. *Ecology* **77**: 561-567.

Tian, H. Q., Melillo, J. M., Kicklighter, D. W., McGuire, A. D., and Helfrich, J. V. K. (1999). The sensitivity of terrestrial carbon storage to historical climate variability and atmospheric CO2 in the United States. *Tellus Series B-Chemical and Physical Meteorology* **51**: 414-452.

Tobin, M. F., Lopez, O. R., and Kursar, T. A. (1999). Responses of tropical understory plants to a severe drought: Tolerance and avoidance of water stress. *Biotropica* **31**: 570-578.

Torrence, C. and Webster, P. J. (1999). Interdecadal changes in the ENSO-monsoon system. *Journal of Climate* **12**: 2679-2690.

Tuomisto, H. and Ruokolainen, K. (1997). The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. *Biodiversity and Conservation* **6**: 347-357.

Tuomisto, H., Ruokolainen, K., Kalliola, R., Linna, A., Danjoy, W., and Rodriguez, Z. (1995). Dissecting Amazonian biodiversity. *Science* 269: 63-66.

Uhl C, Buschbacher R, Serrão EAS (1988) Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *Journal of Ecology* **76**: 663-681.

van der Hammen, T. and Hooghiemstra, H. (2000). Neogene and Quaternary history of vegetation, climate, and plant diversity in Amazonia. *Quaternary Science Reviews* **19**: 725-742.

Vanclay, J. K. (1991a). Aggregating tree species to develop diameter increment equations for tropical rain-forests. *Forest Ecology & Management* **42**: 143-168.

Vanclay, J. K. (1991b). Data requirements for developing growth models for tropical moist forests. *Commonwealth Forestry Review* **70**: 248-271.

Vasquez, R. M. and Phillips, O. L. (2000). Allpahuayo: Floristics, structure, and dynamics of a high- diversity forest in Amazonian Peru. *Annals of the Missouri Botanical Garden* **87**: 499-527.

Vazquez, J. A. and Givnish, T. J. (1998). Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *Journal of Ecology* **86**: 999-1020.

Vazquez, R. (1997). Flórula de las Reservas Biológicas de Iquitos, Perú. Monographs in Systematic Botany 1046 p., Missouri Botanical Garden Press, St. Louis, Missouri, USA

Veenendaal, E. M. and Swaine, M. D. (1996). Limits to tree species distribution in lowland tropical rainforest. Newbery, D. M., Prins, H. H. T., and Brown, N. D. Dynamics of Tropical Communities. The 37th symposium of the British Ecological Society, Cambridge University. pp. 163-191. Blakwell Science, Cambridge, UK.

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

Vitousek, P. M. and Field, C. B. (1999). Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry* **46**: 179-202.

Vitousek, P. M. and Matson, P. A. (1992). Tropical forests and trace gases: potenatial interactions between tropical biology and the atmospheric sciences. *Biotropica* **24**: 233-239.

Vitousek, P. M. and Sanford, R. L. (1986). Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics* **17**: 137-167.

Vormisto, J., Phillips, O. L., Ruokolainen, K., Tuomisto, H., and Vasquez, R. M. (2000). A comparison of fine-scale distribution patterns of four plant groups in an Amazonian rainforest. *Ecography* **23**: 349-359.

Vuilleumier, B. S. (1971). Pleistocene changes in the fauna and flora of South America. *Science* **1973**: 771-779.

Vukicevic, T., Braswell, B. H., and Schimel, D. S. (2001). A diagnostic study of temperature controls on global terrestrial carbon exchange. *Tellus Series B-Chemical and Physical Meteorology* **53**: 150-170.

Walsh, R. P. D. and Newbery, D. M. (1999). The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions Series B-Biological Sciences* **354**: 1869-1883.

Warner, R. R. and Chesson, P. L. (1985). Coexistence mediated by recruitment fluctuations - A field guide to the storage effect. *American Naturalist* **125**: 769-787.

White, P. S. and Pickett, S. T. A. (2001). The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida, USA.

Whitlock, C. and Millspaugh, S. H. (2001). A paleoecologic perspective on past plant invasions in Yellowstone. *Western North American Naturalist* **61**: 316-327.

Whitmore, T. C. (1990). An Introduction to Tropical Rain Forests. Oxford University, Oxford, UK.

Whittaker, R. J., Willis, K. J., and Field, R. (2001). Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* **28**: 453-470.

Williamson, G. B., Laurance, W. F., Oliveira, A. A., Delamonica, P., Gascon, C., Lovejoy, T. E., and Pohl, L. (2000). Amazonian tree mortality during the 1997 El Nino drought. *Conservation Biology* **14**: 1538-1542.

Willis, K. J. and Whittaker, R. J. (2002a). Species diversity - Scale matters. *Science* **295**: 1245-1248.

Willis, K. J. and Whittaker, R. J. (2002b). The refugial debate. *Science* **287**: 5457-5459.

Wong, S. C. and Dunin, F. X. (1987). Photosynthesis and transpiration of tres in a eucalypt forest stand: CO2, light, and humifity responses. *Australian Journal of Plant Physiology* **14**: 619-632.

Woodcock, D. W. (2000). Wood specific gravity of trees and forest types in the southern Peruvian amazon. *Acta Amazonica* **3**: 589-599.

Woodcock, D. W., dos Santos, G., and Reynel, C. (2000). Wood characteristics of Amazon forest types. *Iawa Journal* **21**: 277-292.

Wright, S. J. (1991). Seasonal drought and the pheonology of understory shrubs in a tropical moist forest. *Ecology* **72**: 1643-1657.

Wright, S. J. (1992). Seasonal drought, soil fertility and the species density of tropical forest plant-communities. *Trends in Ecology & Evolution* **7**: 260-263.

Wurth, M. K. R., Winter, K., and Körner, Ch. (1998). In situ responses to elevated CO2 in tropical forest understorey plants. *Functional Ecology* **12**: 886-895.

Zagt, R. J. and Werger, M. J. A. (1996). Community structure and the demography of primary species in tropical rainforest. Newbery, D. M., Prins, H. H. T., and Brown, N. D. Dynamics of Tropical Communities. The 37th symposium of the British Ecological Society, Cambridge University. **8**: 193-219. Blakwell Science, Cambridge, UK.

## Appendix 1

List of sites with specification of the different analysis they have been included in: (1) Struc.: analysis of structure, (2) Flor.: analysis of floristic composition, (3) Dyn.: analysis of dynamics, with distinction between primary and More recent PSPs sites.

| # | plot | code | country | Region | (1) Struc. | (2) Flor. | (3) Dyn. |
|---|---|---|---|---|---|---|---|
| 1 | BDFFP 1201(1) | BD121 | Brazil | Amazonas | * | * | Older PSPs |
| 2 | BDFFP 1201(2) | BD122 | Brazil | Amazonas | * | * | Older PSPs |
| 3 | BDFFP 1201(3) | BD123 | Brazil | Amazonas | * | * | Older PSPs |
| 4 | BDFFP 1301(1) | BD131 | Brazil | Amazonas | * | * | Older PSPs |
| 5 | BDFFP 1301(4) | BD134 | Brazil | Amazonas | * | * | Older PSPs |
| 6 | BDFFP 1301(5) | BD135 | Brazil | Amazonas | * | * | Older PSPs |
| 7 | BDFFP 1301(6) | BD136 | Brazil | Amazonas | * | * | Older PSPs |
| 8 | BDFFP 1301(7) | BD137 | Brazil | Amazonas | * | * | Older PSPs |
| 9 | BDFFP 1301(8) | BD137 | Brazil | Amazonas | * | * | Older PSPs |
| 10 | BDFFP 2303(5) | BD235 | Brazil | Amazonas | * | * | Older PSPs |
| 11 | BDFFP 2303(6) | BD236 | Brazil | Amazonas | * | * | Older PSPs |
| 12 | BDFFP 3402(1) | BD341 | Brazil | Amazonas | * | * | Older PSPs |
| 13 | BDFFP 3402(2) | BD342 | Brazil | Amazonas | * | * | Older PSPs |
| 14 | BDFFP 3402(3) | BD343 | Brazil | Amazonas | * | * | Older PSPs |
| 15 | BDFFP 3402(4) | BD344 | Brazil | Amazonas | * | * | Older PSPs |
| 16 | BDFFP 3402(5) | BD345 | Brazil | Amazonas | * | * | Older PSPs |
| 17 | BDFFP 3402(6) | BD346 | Brazil | Amazonas | * | * | Older PSPs |
| 18 | BDFFP 3402(7) | BD347 | Brazil | Amazonas | * | * | Older PSPs |
| 19 | BDFFP 3402(8) | BD348 | Brazil | Amazonas | * | * | Older PSPs |
| 20 | BDFFP 3402(9) | BD349 | Brazil | Amazonas | * | * | Older PSPs |
| 21 | Bionte1 | BI1 | Brazil | Amazonas | * | * | Older PSPs |
| 22 | Bionte2 | BI2 | Brazil | Amazonas | * | * | Older PSPs |
| 23 | Bionte4 | BI4 | Brazil | Amazonas | * | * | Older PSPs |
| 24 | Tambopata0 | T0 | Peru | Madre de Dios | * | * | Older PSPs |
| 25 | Tambopata1 | T1 | Peru | Madre de Dios | * | * | Older PSPs |
| 26 | Tambopata3 | T3 | Peru | Madre de Dios | * | * | Older PSPs |
| 27 | Tambopata4 | T4 | Peru | Madre de Dios | * | * | Older PSPs |
| 28 | Tambopata6 | T6 | Peru | Madre de Dios | * | * | Older PSPs |
| 29 | Tapajos1 | TP1 | Brazil | Tapajos | * | * | Older PSPs |
| 30 | Tapajos2 | TP2 | Brazil | Tapajos | * | * | Older PSPs |
| 31 | Tapajos3 | TP3 | Brazil | Tapajos | * | * | Older PSPs |
| 32 | YanamonoA | YA1 | Peru | Loreto | * | * | Older PSPs |
| 33 | AllpahuayoA | AL1 | Peru | Loreto | * | * | More recent PSPs |
| 34 | AllpahuayoB | AL2 | Peru | Loreto | * | * | More recent PSPs |
| 35 | Cuzco Amazonico 1e | CA11 | Peru | Madre de Dios | * | * | More recent PSPs |
| 36 | Cuzco Amazonico 1u | CA12 | Peru | Madre de Dios | * | * | More recent PSPs |
| 37 | Cuzco Amazonico 2e | CA21 | Peru | Madre de Dios | * | * | More recent PSPs |
| 38 | Cuzco Amazonico 2u | CA22 | Peru | Madre de Dios | * | * | More recent PSPs |
| 39 | Sucusari A | SU1 | Peru | Loreto | * | * | More recent PSPs |
| 40 | Sucusari B | SU2 | Peru | Loreto | * | * | More recent PSPs |
| 41 | Tambopata2 | T2 | Peru | Madre de Dios |  | * |  |
| 42 | Bol (H1-1) | BH11 | Bolivia | Santa Cruz | * | * |  |
| 43 | Bol (H1-2) | BH12 | Bolivia | Santa Cruz | * | * |  |
| 44 | Bol (H2-1) | BH21 | Bolivia | Santa Cruz | * | * |  |
| 45 | Bol (H2-2) | BH22 | Bolivia | Santa Cruz | * | * |  |

Appendix 1 *(Continued)*

| | Plot | code | country | Region | Struc.(1) | Flor.(2) | Dyn.(3) |
|---|---|---|---|---|---|---|---|
| 46 | Bol (LF-1) | BF1 | Bolivia | Santa Cruz | * | * | |
| 47 | Bol (LF-2) | BF2 | Bolivia | Santa Cruz | * | * | |
| 48 | Caxiuana10 | CX10 | Brazil | Para | * | * | |
| 49 | Caxiuana11 | CX11 | Brazil | Para | * | * | |
| 50 | Caxiuana12 | CX12 | Brazil | Para | * | * | |
| 51 | Caxiuana13 | CX13 | Brazil | Para | * | * | |
| 52 | Caxiuana5 | CX5 | Brazil | Para | * | * | |
| 53 | Caxiuana7 | CX7 | Brazil | Para | * | * | |
| 54 | Caxiuana6 | CX6 | Brazil | Para | * | * | |
| 55 | Caxiuana8 | CX8 | Brazil | Para | * | * | |
| 56 | Caxiuana9 | CX9 | Brazil | Para | * | * | |
| 57 | CaxiuanaA | CX1 | Brazil | Para | * | * | |
| 58 | CaxiuanaB | CX2 | Brazil | Para | * | * | |
| 59 | YanamonoB | YA2 | Peru | Loreto | * | * | |
| 60 | AllpahuayoC | AL3 | Peru | Loreto | * | | |
| 61 | Indiana | IN | Peru | Loreto | * | * | |
| 62 | Mishana | MI | Peru | Loreto | * | * | |
| 63 | Barro Colorado Island | BCI | Panama | | * | | |
| 64 | Dja L1 | DJL1 | Cameroon | | * | | |
| 65 | Dja L2 | DJ2 | Cameroon | | * | | |
| 66 | Dja L3 | DJ3 | Cameroon | | * | | |
| 67 | Dja L4 | DJ4 | Cameroon | | * | | |
| 68 | Dja L5 | MK5 | Cameroon | | * | | |
| 69 | Dja L6 | MK6 | Cameroon | | * | | |
| 70 | Dja L7 | AM7 | Cameroon | | * | | |
| 71 | Dja L8 | AM8 | Cameroon | | * | | |
| 72 | Dja L9 | DJM9 | Cameroon | | * | | |
| 73 | Doussala | DS | Gabon | | * | | |
| 74 | Ekobakoba | EK | Gabon | | * | | |
| 75 | FG10 | FG10 | French Guiana | Nourages | * | | |
| 76 | FG12 | FG12 | French Guiana | Nourages | * | | |
| 77 | Lope' | LP | Gabon | | * | | |
| 78 | Ngotto | NG | Rep.Centrafricana | | * | | |
| 79 | Odzala | OD | Congo | | * | | |
| 80 | Oveng | OV | Gabon | | * | | |
| 81 | Pakitsa1 | PK1 | Peru | Manu | * | | |
| 82 | Pasoh | PA | Malaysia | | * | | |
| 83 | SucusariC | SU3 | Peru | Loreto | * | | |
| 84 | SucusariD | SU4 | Peru | Loreto | * | | |
| 85 | SucusariE | SU5 | Peru | Loreto | * | | |
| 86 | 1101 | BD101 | Brazil | Amazonas | * | * | |
| 87 | 1102 | BD102 | Brazil | Amazonas | * | * | |
| 88 | 1103 | BD103 | Brazil | Amazonas | * | * | |
| 89 | 1109 | BD109 | Brazil | Amazonas | * | * | |
| 90 | 1113 | BD113 | Brazil | Amazonas | * | * | |
| 91 | 3304(8) | BD338 | Brazil | Amazonas | * | * | |
| 92 | 3304(9) | BD339 | Brazil | Amazonas | * | * | |
| | **TOTAL** | | | | **91** | **68** | **40** |

# Appendix 2

Lists of the selection of plots from the Biological Dynamics of Forest Fragments (BDFFP) used for the present work. The code associated to each plot can be read as it follows: a. first number = location (1= Fazenda Esteio, 2=Fazenda Dimona, 3=Fazenda Porto Alegre, 4=Fazenda Agroman). See map in Fig. 1. b. second number = dimensional class of forest fragment (1=1ha, 2= 10ha, 3=100 ha, 4=1000 ha, 5= control). C. third and fourth numbers= number of replica.

| Plot | Location | area tot (ha) | first census | last census |
|---|---|---|---|---|
| 1101 | Gaviao | 1 | 81 | 99 |
| 1102 | Gaviao | 1 | 81 | 99 |
| 1103 | Gaviao | 1 | 81 | 99 |
| 1109 | Gaviao | 1 | 81 | 99 |
| 1113 | Florestal | 1 | 87 | 97 |
| 1201.1 | Gaviao | 3 | 81 | 99 |
| 1201.2 | Gaviao | | 81 | 99 |
| 1201.3 | Gaviao | | 81 | 99 |
| 1301.1 | Florestal | 6 | 83 | 97 |
| 1301.4 | Florestal | | 83 | 97 |
| 1301.5 | Florestal | | 83 | 97 |
| 1301.6 | Florestal | | 83 | 97 |
| 1301.7 | Florestal | | 83 | 97 |
| 1301.8 | Florestal | | 83 | 97 |
| 2303.5 | Fazenda Dimona | 2 | 85 | 97 |
| 2303.6 | Fazenda Dimona | | 85 | 97 |
| 3304.8 | Porto Alegre | 2 | 84 | 98 |
| 3304.9 | Porto Alegre | | 84 | 98 |
| 3402.1 | Cabo Frio | 9 | 85 | 98 |
| 3402.2 | Cabo Frio | | 85 | 98 |
| 3402.3 | Cabo Frio | | 85 | 98 |
| 3402.4 | Cabo Frio | | 85 | 98 |
| 3402.5 | Cabo Frio | | 85 | 98 |
| 3402.6 | Cabo Frio | | 85 | 98 |
| 3402.7 | Cabo Frio | | 85 | 98 |
| 3402.8 | Cabo Frio | | 85 | 98 |
| 3402.9 | Cabo Frio | | 85 | 98 |
| TOTAL | | 27 | | |

## Appendix 3

List of pioneers species, compiled merging three lists from the Central Amazon (Manaus), South Peru (Tambopata) and French Guiana (Paracou-Nourages).

| Family | Genus | Species |
|---|---|---|
| Anacardiaceae | Tapirira | guianensis |
| Anacardiaceae | Tapirira | peckoltiana |
| Annonaceae | Annona | hypoglauca |
| Annonaceae | Guatteria | citriodora |
| Annonaceae | Guatteria | guentheri |
| Annonaceae | Rollinia | exsucca |
| Annonaceae | Rollinia | pittieri |
| Annonaceae | Urera | caracasana |
| Annonaceae | Xylopia | nitida |
| Annonaceae | Xylopia | pulcherrima |
| Annonaceae | Xylopia | surinamensis |
| Apocynaceae | Himatanthus | articulatus |
| Apocynaceae | Himatanthus | sucuuba |
| Apocynaceae | Rauvolfia | praecox |
| Apocynaceae | Rauvolfia | sprucei |
| Apocynaceae | Tabernaemontana | arcuata |
| Apocynaceae | Tabernaemontana | sananho |
| Araliaceae | Dendropanax | arboreus |
| Araliaceae | Didymopanax | morototonii |
| Araliaceae | Schefflera | decaphylla |
| Araliaceae | Schefflera | morototoni |
| Bignoniaceae | Jacaranda | copaia |
| Bignoniaceae | Jacaranda | copaia subsp.copaia |
| Bixaceae | Bixa | arborea |
| Bixaceae | Bixa | orellana |
| Boraginaceae | Cordia | alliodora |
| Boraginaceae | Cordia | exaltata |
| Boraginaceae | Cordia | nodosa |
| Boraginaceae | Cordia | sellowiana |
| Burseraceae | Trattinnickia | rhoifolia |
| Caricaceae | Jacaratia | digitata |
| Cecropiaceae | Cecropia | concolor ssp. engleriana |
| Cecropiaceae | Cecropia | distachya |
| Cecropiaceae | Cecropia | engleriana |
| Cecropiaceae | Cecropia | ficifolia |
| Cecropiaceae | Cecropia | membranacea |
| Cecropiaceae | Cecropia | obtusa |
| Cecropiaceae | Cecropia | purpurascens |
| Cecropiaceae | Cecropia | sciadophylla |
| Cecropiaceae | Pourouma | bicolor |
| Cecropiaceae | Pourouma | bicolor ssp. bicolor |
| Cecropiaceae | Pourouma | bicolor ssp. scobina |
| Cecropiaceae | Pourouma | cecropiifolia |
| Cecropiaceae | Pourouma | guianensis |
| Cecropiaceae | Pourouma | guianensis subsp.guianensis |
| Cecropiaceae | Pourouma | minor |
| Cecropiaceae | Pourouma | palmata |

Pioneer sp. *(Continued)*

| Family | Genus | Species |
|---|---|---|
| Cecropiaceae | Pourouma | substrigosa |
| Cecropiaceae | Pourouma | tessmannii |
| Celastraceae | Goupia | glabra |
| Clusiaceae | Chrysochlamys | ulei |
| Clusiaceae | Chrysochlamys | weberbaueri |
| Clusiaceae | Symphonia | globulifera |
| Clusiaceae | Vismia | cayennensis |
| Clusiaceae | Vismia | guianensis |
| Clusiaceae | Vismia | japurensis |
| Clusiaceae | Vismia | latifolia |
| Clusiaceae | Vismia | sessilifolia |
| Clusiaceae | Vismia | cayennensis |
| Dilleniaceae | Pinzona | coriacea |
| Dilleniaceae | Tetracera | parviflora |
| Elaeocarpaceae | Muntingia | calabura |
| Elaeocarpaceae | Sloanea | fragrans |
| Euphorbiaceae | Acalypha | diversifolia |
| Euphorbiaceae | Acalypha | mapirensis |
| Euphorbiaceae | Alchornea | triplinervia |
| Euphorbiaceae | Alchorneopsis | floribunda |
| Euphorbiaceae | Conceveiba | guianensis |
| Euphorbiaceae | Conceveiba | rhytidocarpa |
| Euphorbiaceae | Croton | palanostigma |
| Euphorbiaceae | Hura | crepitans |
| Euphorbiaceae | Hyeronima | oblonga |
| Euphorbiaceae | Margaritaria | nobilis |
| Euphorbiaceae | Pogonophora | schomburgkiana |
| Euphorbiaceae | Sapium | glandulosum |
| Euphorbiaceae | Sapium | marmieri |
| Flacourtiaceae | Casearia | arboria |
| Flacourtiaceae | Casearia | commersoniana |
| Flacourtiaceae | Casearia | javitensis |
| Flacourtiaceae | Casearia | pitumba |
| Flacourtiaceae | Casearia | sylvestris var.sylvestris |
| Flacourtiaceae | Hasseltia | floribunda |
| Flacourtiaceae | Homalium | racemosum |
| Flacourtiaceae | Laetia | corymbosa |
| Flacourtiaceae | Laetia | corymbulosa |
| Flacourtiaceae | Laetia | procera |
| Flacourtiaceae | Lindackeria | paludosa |
| Flacourtiaceae | Lunania | parviflora |
| Flacourtiaceae | Lunania | parvifolia |
| Flacourtiaceae | Tetracylacium | macrophyllum |
| Hippocrateaceae | Cheiloclinium | cognatum |
| Hippocrateaceae | Hippocratea | volubilis |
| Lacistemataceae | Lacistema | aggregatum |
| Lacistemataceae | Lacistema | grandifolium |
| Lauraceae | Ocotea | oblonga |
| Lauraceae | Pleurothyrium | intermedium |
| Lecythidaceae | Bertholletia | excelsa |
| Lecythidaceae | Gustavia | hexapetala |
| Leguminosae Caesalpinaceae | Bauhinia | tarapotensis |
| Leguminosae Caesalpinaceae | Dialium | guianense |
| Leguminosae Caesalpinaceae | Schizolobium | parahybum |

Pioneer sp. *(Continued)*

| Family | Genus | Species |
|---|---|---|
| Leguminosae Caesalpinaceae | Sclerolobium | bracteosum |
| Leguminosae Caesalpinaceae | Sclerolobium | rugosum |
| Leguminosae Caesalpinaceae | Sclerolobium | vasquezii |
| Leguminosae Caesalpinaceae | Tachigali | bracteosa |
| Leguminosae Caesalpinaceae | Tachigali | cavipes |
| Leguminosae Caesalpinaceae | Tachigali | chrysophylla |
| Leguminosae Caesalpinaceae | Tachigali | guianensis |
| Leguminosae Caesalpinaceae | Tachigali | melinonii |
| Leguminosae Caesalpinaceae | Tachigali | paniculata |
| Leguminosae Caesalpinaceae | Tachigali | poeppigiana |
| Leguminosae Caesalpinaceae | Tachigali | polyphylla |
| Leguminosae Caesalpinaceae | Tachigali | ptychophysca |
| Leguminosae Caesalpinaceae | Tachigali | rugosum |
| Leguminosae Caesalpinaceae | Tachigali | rusbyi |
| Leguminosae Caesalpinaceae | Tachigali | tessmannii |
| Leguminosae Mimosaceae | Abarema | jupunba |
| Leguminosae Mimosaceae | Acacia | loretensis |
| Leguminosae Mimosaceae | Balizia | pedicellaris |
| Leguminosae Mimosaceae | Cassia | sylvestris |
| Leguminosae Mimosaceae | Dinizia | excelsa |
| Leguminosae Mimosaceae | Entada | polystachya |
| Leguminosae Mimosaceae | Inga | acreana |
| Leguminosae Mimosaceae | Inga | alba |
| Leguminosae Mimosaceae | Inga | auristellae |
| Leguminosae Mimosaceae | Inga | capitata |
| Leguminosae Mimosaceae | Inga | cayennensis |
| Leguminosae Mimosaceae | Inga | chartacea |
| Leguminosae Mimosaceae | Inga | coruscans |
| Leguminosae Mimosaceae | Inga | edulis |
| Leguminosae Mimosaceae | Inga | fagifolia |
| Leguminosae Mimosaceae | Inga | marginata |
| Leguminosae Mimosaceae | Inga | nobilis |
| Leguminosae Mimosaceae | Inga | pezizifera |
| Leguminosae Mimosaceae | Inga | pruriens |
| Leguminosae Mimosaceae | Inga | quaternata |
| Leguminosae Mimosaceae | Inga | semialata |
| Leguminosae Mimosaceae | Inga | stipularis |
| Leguminosae Mimosaceae | Inga | tenuistipula |
| Leguminosae Mimosaceae | Inga | thibaudiana |
| Leguminosae Mimosaceae | Inga | thibaudiana subsp. peltadenia |
| Leguminosae Mimosaceae | Inga | tocacheana |
| Leguminosae Mimosaceae | Inga | umbellifera |
| Leguminosae Mimosaceae | Marmaroxylon | basijugum |
| Leguminosae Mimosaceae | Marmaroxylon | ramiflorum |
| Leguminosae Mimosaceae | Mimosa | pigra |
| Leguminosae Mimosaceae | Newtonia | suaveolens |
| Leguminosae Mimosaceae | Parkia | decussata |
| Leguminosae Mimosaceae | Piptadenia | communis |
| Leguminosae Mimosaceae | Piptadenia | suaveolens |
| Leguminosae Mimosaceae | Pithecellobium | latifolium |
| Leguminosae Mimosaceae | Stryphnodendron | pulcherrimum |
| Leguminosae Papilionaceae | Andira | inermis |
| Leguminosae Papilionaceae | Dalbergia | frutescens |

Pioneer sp. *(Continued)*

| Family | Genus | Species |
|---|---|---|
| Leguminosae Papilionaceae | Dalbergia | inundata |
| Leguminosae Papilionaceae | Dalbergia | monetaria |
| Leguminosae Papilionaceae | Dalbergia | monetaria var. monetaria |
| Leguminosae Papilionaceae | Desmodium | adscendens |
| Leguminosae Papilionaceae | Erythrina | poeppigiana |
| Leguminosae Papilionaceae | Lonchocarpus | spiciflorus |
| Leguminosae Papilionaceae | Swartzia | cardiosperma |
| Leguminosae Papilionaceae | Swartzia | myrtifolia |
| Malpighiaceae | Byrsonima | aerugo |
| Malpighiaceae | Byrsonima | arthropoda |
| Malpighiaceae | Byrsonima | densa |
| Melastomataceae | Bellucia | grossularioides |
| Melastomataceae | Bellucia | pentamera |
| Melastomataceae | Clidemia | capitellata |
| Melastomataceae | Henriettea | succosa |
| Melastomataceae | Loreya | arborescens |
| Melastomataceae | Loreya | mespiloides |
| Melastomataceae | Miconia | acuminata |
| Melastomataceae | Miconia | argyrophylla |
| Melastomataceae | Miconia | bubalina |
| Melastomataceae | Miconia | burchellii |
| Melastomataceae | Miconia | calvescens |
| Melastomataceae | Miconia | eriodonta |
| Melastomataceae | Miconia | fragilis |
| Melastomataceae | Miconia | minutiflora |
| Melastomataceae | Miconia | nervosa |
| Melastomataceae | Miconia | pilgeriana |
| Melastomataceae | Miconia | plukenetii |
| Melastomataceae | Miconia | poeppigii |
| Melastomataceae | Miconia | prasina |
| Melastomataceae | Miconia | tomentosa |
| Melastomataceae | Miconia | triplinervis |
| Melastomataceae | Miconia | tschudyoides |
| Melastomataceae | Tococa | guianensis |
| Meliaceae | Cabralea | canjerana ssp. canjerana |
| Meliaceae | Guarea | guidonia |
| Menispermaceae | Cissampelos | indet |
| Menispermaceae | Sciadotenia | toxifera |
| Monimiaceae | Siparuna | bifida |
| Monimiaceae | Siparuna | cervicornis |
| Monimiaceae | Siparuna | cristata |
| Monimiaceae | Siparuna | cuspidata |
| Monimiaceae | Siparuna | guianensis |
| Moraceae | Bagassa | guianensis |
| Moraceae | Brosimum | guianense |
| Moraceae | Brosimum | lactescens |
| Moraceae | Brosimum | potabile |
| Moraceae | Brosimum | utile |
| Moraceae | Castilla | ulei |
| Moraceae | Clarisia | biflora |
| Moraceae | Clarisia | racemosa |
| Moraceae | Ficus | citrifolia |
| Moraceae | Ficus | insipida |
| Moraceae | Ficus | insipida subsp. Insipida |

Pioneer sp. *(Continued)*

| Family | Genus | Species |
|---|---|---|
| Moraceae | Ficus | juruensis |
| Moraceae | Ficus | krukovii |
| Moraceae | Ficus | maxima |
| Moraceae | Ficus | nymphaeifolia |
| Moraceae | Ficus | paraensis |
| Moraceae | Ficus | pertusa |
| Moraceae | Ficus | schultesii |
| Moraceae | Ficus | trigona |
| Moraceae | Helicostylis | elegans |
| Moraceae | Maquira | coriacea |
| Moraceae | Naucleopsis | ulei |
| Moraceae | Perebea | tessmannii |
| Moraceae | Perebea | xanthochyma |
| Moraceae | Sorocea | hirtella |
| Moraceae | Trymatococcus | amazonicus |
| Myristicaceae | Otoba | glicycarpa |
| Myristicaceae | Virola | calophylla |
| Myristicaceae | Virola | flexuosa |
| Myristicaceae | Virola | mollissima |
| Myristicaceae | Virola | sebifera |
| Myrtaceae | Calyptranthes | longifolia |
| Myrtaceae | Eugenia | riparia |
| Myrtaceae | Myrciaria | floribunda |
| Myrtaceae | Psidium | acutangulum |
| Myrtaceae | Psidium | coriaceous |
| Myrtaceae | Psidium | guajava |
| Ochnaceae | Cespedesia | spathulata |
| Ochnaceae | Ouratea | iquitosensis |
| Palmae | Bactris | gasipaes |
| Palmae | Socratea | exorrhiza |
| Piperaceae | Piper | arboreum |
| Piperaceae | Piper | pseudoarboreum |
| Piperaceae | Piper | tuberculatum |
| Polygonaceae | Coccoloba | lehmannii |
| Polygonaceae | Triplaris | americana |
| Polygonaceae | Triplaris | peruviana |
| Polygonaceae | Triplaris | poeppigiana |
| Proteaceae | Roupala | montana |
| Rhamnaceae | Gouania | lupuloides |
| Rubiaceae | Calycophyllum | megistocaulum |
| Rubiaceae | Genipa | americana |
| Rubiaceae | Isertia | coccinea |
| Rubiaceae | Isertia | hypoleuca |
| Rubiaceae | Isertia | spiciformis |
| Rubiaceae | Palicourea | grandiflora |
| Rubiaceae | Palicourea | guianensis |
| Rubiaceae | Palicourea | nigricans |
| Rubiaceae | Palicourea | punicea |
| Rubiaceae | Palicourea | quadrifolia |
| Rubiaceae | Uncaria | guianensis |
| Rubiaceae | Warscewiczia | coccinea |
| Rutaceae | Zanthoxylum | djalmabatistae |
| Sapindaceae | Cupania | hirsuta |

Pioneer sp. *(Continued)*

| Family | Genus | Species |
|---|---|---|
| Sapindaceae | Paullinia | alata |
| Sapindaceae | Cupania | scrobiculata |
| Sapindaceae | Talisia | mollis |
| Simaroubaceae | Simarouba | amara |
| Staphyleaceae | Huertea | glandulosa |
| Staphyleaceae | Turpinia | occidentalis |
| Sterculiaceae | Byttneria | aculeata |
| Sterculiaceae | Guazuma | crinita |
| Sterculiaceae | Guazuma | ulmifolia |
| Sterculiaceae | Sterculia | apeibophylla |
| Sterculiaceae | Theobroma | cacao |
| Tiliaceae | Apeiba | aspera |
| Tiliaceae | Apeiba | glabra |
| Tiliaceae | Apeiba | membranacea |
| Tiliaceae | Apeiba | membranacea subsp. membranacea |
| Tiliaceae | Apeiba | petoumo |
| Tiliaceae | Apeiba | tibourbou |
| Tiliaceae | Heliocarpus | americanum |
| Tiliaceae | Triumfetta | indet |
| Ulmaceae | Celtis | iguanea |
| Ulmaceae | Celtis | schippii |
| Ulmaceae | Trema | integerrima |
| Ulmaceae | Trema | micrantha |
| Urticaceae | Myriocarpa | stipitata |
| Urticaceae | Urera | baccifera |
| Urticaceae | Urera | capitata |
| Urticaceae | Urera | caracasana |
| Verbenaceae | Aegiphila | glabra |
| Verbenaceae | Aegiphila | integrifolia |
| Verbenaceae | Citharexylum | poeppigii |
| Verbenaceae | Petrea | maynensis |
| Vitaceae | Cissus | neei |
| Vitaceae | Cissus | sicyoides |
| Vochysiaceae | Vochysia | guianensis |