UNDERSTANDING COLOMBIAN AMAZONIAN WHITE SAND FORESTS

Maria Cristina Peñuela Mora

The research presented in this thesis was carried out within the framework of the Plant Ecology and Biodiversity Group, Institute of Environmental Biology, Utrecht University and Ecology of Terrestrial Ecosystems Group, National University of Colombia.

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UNDERSTANDING COLOMBIAN AMAZONIAN WHITE SAND FORESTS

ECOLOGIE VAN WITZANDBOSSEN IN COLOMBIA

(met een samenvatting in het Nederlands)

ENTENDIENDO LOS BOSQUES DE ARENAS BLANCAS DE LA AMAZONIA COLOMBIANA

(con resumen en Español)

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To my son Luciano
and my mother Elvira

…and to my friends, women whose
hearts and minds battle between their
children, family and their studies.

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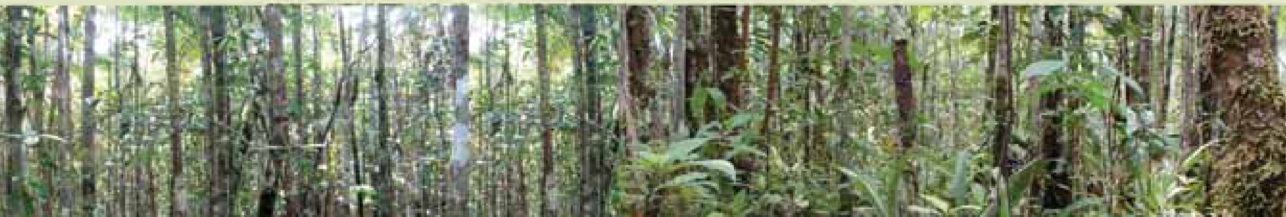

CHAPTER 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

The Amazon region covers an area of nearly six million square kilometres (Ramos da Silva et al. 2008) and harbours the richest assemblage of plant species on Earth (Gentry 1988, de Oliveira & Mori 1999, ter Steege et al. 2000a, Hoorn & Wesselingh 2010, ter Steege et al. 2013). The diversity of plant species is partly due to the fact that the different species are restricted to a subset of environmental conditions (Fine et al. 2006). In particular, the species are restricted by physical soil characteristics such as: the soil water holding capacity, drainage, soil structure and nutrients, factors that affect tree growth, mortality and the floristic composition of tropical forests worldwide (Ferry et al. 2010, Quesada et al. 2009b). Amazonian forests have long been grouped in three broad categories: flooded forests, non-flooded or terra firme forests and white sand forests.

White sand forests grow in large extensions in the Eastern Amazon and in Western Amazon they are located in small patches surrounded by terra firme forests that grow in different soils. Terra firme forests are found in clay soils and white sand forests grow in white sands or Podzols, which are also known as Spodozols or Arenosols (Quesada et al. 2011). Both types of soils are highly acidic, but terra firme soils have a higher cation exchange capacity and a higher amount of available total phosphorus. In general, white sand forests have extremely nutrient-poor soils that are strongly leached, and that are usually drained by black waters (Coomes & Grubb 1996, 1998a, Luizão et al. 2007, Quesada et al. 2009b, Quesada et al. 2011). In Podzols, complexes of aluminium, iron and organic compounds form a hardpan that impedes root penetration into deeper soil horizons (Schoenholtz et al. 2000) and causes waterlogging in the rainy season (Bongers et al. 1985, Medina et al. 1990, Quesada et al. 2011). In the dry season, the upper soil dries out due to the low water retention capacity (Duivenvoorden & Lips 1995, Williams et al. 2002), which increases mortality and decreases growth rates in tropical plants (Turner 1990, Condit et al. 1995, Veenendaal et al. 1995). Short periods of water stress are sufficient to cause important changes in the vegetation, not only in the floristic composition but also in the morphology and physiology of the plants (Franco & Dezzeo 1994, Hutyra et al. 2005, Walker et al. 2009).

Forest Structure and Composition of White Sand Forests

In general, white sand forest trees are of low stature, and have low average diameter and narrow crowns (Anderson 1981, Coomes & Grubb 1996). In Venezuela, the height of the trees was positively correlated with the depth of the aerated soil layer above the water table (Bongers et al. 1985). These forests have been given various names in different countries and the names can even vary among different regions in one country (Table 1).

Species richness in these forests is poor compared to other types of forests (Anderson 1981, ter Steege et al. 2000a, Duque et al. 2002, Duque et al. 2003, Fine et al. 2004, Fine et al. 2005, Fine et al. 2010, Stropp 2011) but they are rich in endemics (Prance & Schubart 1978, Anderson 1981, ter Steege et al. 2000a, ter Steege & Hammond 2001, Fine et al. 2006, Fine et al. 2010, Stropp 2011, Stropp et al. 2011, Pombo de Souza 2012). Because the diversity is low, these forests are commonly dominated by a few species (Anderson 1981, Klinge & Herrera 1983, Garcia Villacorta 2003, Fine et al. 2010).

In general, few families are dominant in these forests. In Western Amazonia, including the area examined in this study, Fabaceae, Clusiaceae and Malvaceae are the most common families and *Caraipa utilis, Dicymbe uaiparuensis* and *Pachira brevipes* are some of the common species (García Villacorta et al. 2003, Fine et al. 2010).

Tree species from white sands have traits that distinguish them from species growing in other types of forests, such as: thicker cuticles (Sobrado & Medina 1980, Fine et al. 2004, 2006), low specific leaf area (Turriago & Villanueva 2008) and higher wood density (Agudelo 2006, Patiño et al. 2009). They are also denser in terms of total root mass per unit of soil volume and finer roots (Jiménez et al. 2009).

Two main theories may explain the differences in the species composition of white sand forests and the traits of these species.

Table 1.
Names given to white sand forests on different Amazonian countries

Forest name	Country	Authors
Varillales altos and bajos	Peru	Revilla 1978
Varillal alto seco (high-dry-open white sand forest)		Garcia Villacorta et al. 2003
Varillal alto húmedo (high-wet-open white sand forest)		
Varillal bajo seco (low-dry-dense white sand forest)		
Varillal bajo húmedo (low-wet-open white sand forest)		
Chamizal (very low-wet-very dense white sand forest)		
Bosque de arenas blancas (White sand forest)	Colombia, Middle Caqueta, Guainia	Duivenvoorden & Lips 1995, Duque et al. 2002, Duque, Cárdenas et al. 2003, Cardenas 2007
Bosque mal drenado de terraza baja. Order Clusio spathulaefoliae -Rhodognaphalopsietalia brevipedis		Urrego 1997
Varillal	Leticia	This study
Bana = Low scrub on white sand, low woodland	Venezuela	Klinge & Herrera 1983
Amazon-caatinga		Medina & Cuevas 2011
Tall Amazon caatinga (Campinarana) and short Amazon caatinga (Campina) depending upon the average height of the trees	Brazil	Lisboa 1975,Coomes & Grubb 1996
Campinarana arbustiva (trees to 7m height)		
Campinarana arborizada (trees between 5-15 m)		Stropp et al. 2011
Campinarana florestada (20-30 m height)		Pombo de Souza 2012
Campinarana graminea lenhosa (herbs and bushes)		
Xeromorphic rain forest, woodland and scrub and Wallaba forest	Guyana	Granville 1988
Xeromorphic scrub =Muri		
Wallaba forest = Dry evergreen forest on withe sand soil = Xeromorphic rainforest		ter Steege et al. 1993

Resource Limitations

Several of the traits of white sand species are thought to be adaptations to the low resource availability of either nutrients or water.

Traditionally, low specific leaf area and high wood density are traits that have been associated with soils suffering from a water deficit, thus associated with drought. In very dry areas, plants do tend to have small sclerophyll, evergreen leaves that reduce transpiration rates (Turner 1994) and conserve water. Drought tolerant seedlings tend to have thinner and more compact conducting vessels that increase resistance to cavitation and xylem embolism (Hacke et al. 2001, Pedrol Bonjoch et al. 2003, Vilagrosa et al. 2003). Other species however, demonstrate that leaf shedding is a strategy to avoid water loss through transpiration, although it is at the expense of sustained growth (Poorter 1999, Poorter & Hayashida-Oliver 2000).

In addition, a dense root system improves water uptake and permits better rehydration after drought (Vilagrosa et al. 2003). In white sand forests, it is common to find a dense layer of absorbing fine roots near the soil surface (Cuevas & Medina 1986, Jiménez et al. 2009).

Species with high wood density show lower growth and mortality rates than species with lower wood densities (ter Steege et al. 2000b, Baker et al. 2004a, Lewis et al. 2004, ter Steege et al. 2006). The species with lower growth and mortality rates produce low values of aboveground biomass, basal area, net productivity (NP) (Aragão et al. 2009), and low turnover rates (Phillips & Gentry 1994, Malhi et al. 2004).

Resource availability theories suggest that if resources are scarce, trees grow slowly, conserve nutrients and avoid nutrient losses as much as possible with higher levels of defence (Coley 1983a, b).

The Trade-Off between Defence and Growth

More recently, leaf toughness and resource availability have been combined in a theory that indicates a trade-off between defence and growth. Thicker cuticles and low SLA are associated with mechanical defences, reducing herbivory (Fine et al. 2004, 2005). Reduction of herbivory enhances leaf longevity, decreases leaf loss, thereby reducing the demand for soil nutrients necessary to replace leaves and augment long term carbon gain in nutrient limited environments (Turner 1994, Cunningham et al. 1999). Thicker and smaller leaves are also associated with lower growth rates (Aerts 1989, Reich et al. 1992, Daws et al. 2005, Hikosaka 2005), as well as higher leaf toughness. Recently, Fine et al. (2004, 2006) found that white sand specialists have a higher overall defence investment than terra firme species. When manipulating the presence of hervibores in white sand and terra firme forests, they discovered that the impact of herbivory on growth and survival was much stronger in white sand forests. In the absence of herbivores, terra firme species examined in their study always outgrew white sand species. On richer soils, they were able to produce more biomass than the amount that was lost due to herbivores and on poor white sand soils with herbivores present they showed a very negative growth. Conversely, white sand species always grew slowly, being overtaken in terra firme forests but did not suffer losses due to herbivory in white sand forest where, despite their generally slow growth, white sand species showed positive increases in height and biomass. This confirmed the theoretical predictions that species in low resource habitats develop a higher optimal defence investment and that this trade-off might explain the major differences in composition between white sand and terra firme forests. Stropp et al. (2013), however, showed that if terra firme forests are also nutrient poor, as is the case in the upper Rio Negro, this mechanism may not be sufficient to explain the differences between white sand and terra firme forests.

Although progress has been made in studies on white sand forests in the Amazon, there is still a considerable gap in our knowledge of the unique species composition of white sand forests and their structure and dynamics, especially in Western Amazon. This thesis aims to fill this gap by addressing the following questions about white sand forests in Western Amazonia:

- Chapter 2: What is the species composition in white-sand forests in the Western Amazon? What is their geographic variation and how do they differ from other types of forests?

- Chapter 3: What are the dynamic rates (mortality, growth, recruitment) of a white sand forest in Colombia compared to other white sand forests in the Western Amazon and other forest types in the same region?

- Chapter 4: Do white sand tree seedlings differ in their growth, the production and loss of leaves, herbivory and mortality compared to terra firme seedlings and do they differ between the wet and dry season?

- Chapter 5: Under drought conditions, do white sand species perform better, in clay or sandy soils, than terra firme species? This chapter also aims to answer the question of whether species in white sands and terra firme forests grow, gain or lose leaves, suffer less or more herbivory and survive better in their own forest type, when subjected to drought.

CHAPTER 2

SPECIES COMPOSITION OF WHITE SAND FORESTS IN WESTERN AMAZON

With Eliana Jiménez, Rene Boot, Roel Brienen, Dairon Cardenas, Nallaret Davila, Alvaro Duque, Paul Fine, Euridice Honorio, Ana Catalina Londoño, Oliver Phillips, and Hans ter Steege.

ABSTRACT

White sand forests differ considerably from terra firme (clay or brown soil) forests in terms of composition, biomass and dynamics in different regions of the Amazon. White sand forests in the Western Amazon, Peru and Colombia usually occur in small patches, whereas these forests in Venezuela, Guyana and northern Brazil (Eastern Amazon) may cover large areas. Given that these forests grow in very nutrient poor soils, it has been suggested that only very few specialized species are able to inhabit them, and that these forests therefore would be relatively uniform in species composition. Amazon white sand forests have been poorly studied, especially in the Western Amazon region. Therefore, this study compares data from a set of 87 plots from the Western Amazon: 22 white sands, 32 terra firme, 20 igapo and 13 varzea forests. More species were found growing in white sand forests than varzea or igapo forests but Fisher's alpha was significantly lower in white sand forests compared to terra firme or varzea forests. All of the different types of forests contain species not found in other forest types, but white sand forests had proportionally more unique species than any other forest type; close to 29% of their species. Of these species, 44 were found to have significant indicator values and most of them belonged to the Fabaceae, Clusiaceae, Arecaceae and Apocynaceae families. Although these families are common in all white sand forests, no common species were found in all plots. An ordination analysis with 22 white sand plots showed that they split into three main groups that represent different regions: Peruvian plots, plots from Caquetá and Zafire in Middle Colombian Amazon and plots from Inirida in north-eastern Colombia.

INTRODUCTION

Amazon forests are of great interest, not only because of their diversity in plant and animal species, regional and global climate regulation, but also because they make up the largest continuous rainforest on Earth (Sioli 1984, Higgins et al. 2011). In the Amazon, three forest types are typically recognized:

1. Non-flooded or terra firme (TF) forests (Junk et al. 2011). These forests usually grow on clay or brown sandy soils that are never flooded. These forests are the dominant forest type covering ca. 80% of the Amazon.

2. Forests permanently or temporarily flooded by white or black water rivers cover ca. 10% of the Amazon basin. White-water rivers have their origin in the Andes and carry large amounts of nutrient-rich sediments; forests flooded by these waters are called varzea in the Amazon. Forests flooded by black water rivers are named igapó, their waters have a brownish-reddish-colour and contain low amounts of suspended matter but high amounts of humic acids and are therefore of low fertility.

3. Forests growing on white sands (Junk & Piedade 2010) cover nearly 5% of the Amazon basin. These white sand (WS) forests are drained by black waters and are characterized by trees of short stature, thin stems, and narrow crowns. They are often dominated by a few tree species (Macedo & Prance 1978, Anderson 1981, Medina et al. 1990, Duivenvoorden & Lips 1995, Coomes & Grubb 1996, 1998a, Banki 2010, Stropp 2011) and have an open canopy which allows more light to penetrate to the forest floor, compared to other Amazonian forests (Anderson 1981). These forests also lack large climbers (Coomes & Grubb 1996). Some WS forests can be exposed temporarily to waterlogging due to the presence of a hardpan at approximately one meter below the soil surface that also impedes root penetration to deeper soils and exposes these forests to drought due to their sandy soil texture (Bongers et al. 1985, Duivenvoorden & Lips 1995, Medina & Cuevas 2011).

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[1] Sandy plains (Pa), calculated from Sombroek 2000

Various names and classifications have been given to WS forests in the Amazon. In the North-eastern Amazon, WS forests cover extensive areas. In French Guiana and Suriname (approximately 26,000 ha)[1], two types of WS forests are distinguished: the Wallaba forest; a forest that is usually dominated by the genus *Eperua* and "xeromorphic rainforests, woodlands and scrub" (Granville 1988), grouped in "savanna forests" by Lindeman (1953).

Large areas of WS forests are also found along the upper Rio Negro in Venezuela (approximately 15,000 ha) and in the Rio Branco in Brazil (approximately 67,000 ha). These forests are similar in structure to the Wallaba forest and are named Tall white sand forests or Tall Amazon-caatinga (Coomes & Grubb 1996), Campina forest (Macedo & Prance 1978, Prance & Schubart 1978) Caatinga (Anderson 1981) and Amazon-caatinga (Medina & Cuevas 2011). Some of these forests are lower in height and are therefore called short Amazon caatinga or Bana (Bongers et al., 1985), located at lower topographic positions with a fluctuating ground water table at depths that are near the soil surface.

In the WS forests in Guyana and along the upper Rio Negro, Fabaceae are dominant (ter Steege 1993, ter Steege et al. 2000, Stropp 2011b) and the genus *Eperua* is the most abundant: *E. falcata* and *E. rubiginosa* in French Guiana (Granville, 1988), *E. falcata* and *E. grandiflora* in Guyana (ter Steege 1993, 1998) and *E. leucantha*, *E. purpurea* in the upper Rio Negro (Stropp 2011b, Stropp et al. 2011). Other abundant families are Sapotaceae, Malvaceae and Euphorbiaceae (Stropp 2011b) or Chrysobalanaceae, Malvaceae and Clusiaceae (Banki 2010).

In the Western Amazon, WS forests are located in small isolated patches scattered over the Colombian and northern Peruvian Amazon. In Peru, most of the WS forests are found in the Jenaro Herrera district or southwest of Iquitos and in the Allpahuayo-Mishana Reserve Zone (ZRAM) and cover nearly 570 km[2]. In Allpahuayo-Mishana, the white sands originate from the old-isolated meander of the Nanay River (Hoorn et al. 2010). In this region, WS forests are normally classified into two types that are based on drainage and canopy height; Varillales and Chamizales (Freitas 1996, Ahuite Reátegui et al. 2003, Honorio et al. 2008). Another classification of the Allpahuayo WS forests was made by García-Villacorta et al. (2003), which separated them into five types depending upon soil drainage and abundance and frequency of tree species.

In Venezuela and Colombia, WS forests grow on extremely oligotrophic, bleached white sand, frequently podsolized soils (Medina et al. 1990, Duivenvoorden & Lips 1995). In Colombia, WS forests have not been systematically studied or classified. Duivenvoorden & Lips (1995) found WS forests in the middle Caquetá region on different geomorphological units: sandstone plateaus, high terraces and the tertiary sedimentary plains and growing on podzolized soils that cover less than 5% of the uplands in this area. Podzolized soils occur at sites with a slightly concave topography where drainage is impeded due to the presence of an impermeable layer of tertiary clay close to the soil surface.

Fine et al. (2010) compared 16 Peruvian WS plots with published data from Duivenvoorden et al. (2001) in Colombia. They showed that Clusiaceae, Malvaceae, Fabaceae, Arecaceae are the most abundant families and *Pachira brevipes* and two species of *Caraipa* are the most abundant species in Peru and the middle Caquetá in Colombia.

Despite the studies conducted so far on WS forests, there is still a considerable lack of knowledge on the differences in species composition between these WS forests and the forests that surround them in the Western Amazon. Therefore, this chapter will describe the species composition of three new WS forest plots with the presence of a hardpan below the soil surface, and growing in different locations in the Western Amazon, close to the Andes in soils of the Pebas formation, and in soils of the Mariñame formation with the influence of the Guiana shield. The species composition of trees in the canopy (trees ≥ 10 cm DBH) and the understory (trees 2.5 cm < 10 cm DBH) will be described in this study. WS forests will be compared with other forest types studied in Peru and Colombia that are found in three regions: the Peruvian Amazon, the middle Colombian Amazon the Eastern Colombian Amazon and the Guiana shield. The following questions will be addressed: Are there floristic elements (plant families and species) that may serve as indicators of forests types in the Western Amazon? In addition, do WS forests have more unique species than other types of forests given the stressful conditions they face? This question is related to the fact that WS forests grow on very poor sandy soils, which implies a very low capacity to exchange and obtain nutrients, waterlogging in the rainy season and drought in the dry season.

Western TF forests are richer in species composition than those from the Eastern Amazon and WS forests in Western Amazon mostly occur in small patches that are embedded in a matrix of TF forests. However, there is a widespread perception of homogeneity in WS forests. Thus, the following questions will also be asked: Do WS forests differ in their species composition from the TF forest matrix that surrounds them in the Western Amazon? Are WS forests more homogeneous in composition than other types of forests?

METHODS

Study areas

Three plots of WS forests were established and sampled following standard methods (www.rainfor.org) in three different locations: one in Peru close to the Ucayali river in the Loreto department, district of Genaro Herrera, near the Centro de Investigaciones Jenaro Herrera (CIJH); one 27 km north of Leticia in the Amazonas department in Colombia close to the Zafire Biological Station (ZAF) in the National Forestry Natural Reserve; and one in Peña Roja (PR), an indigenous territory in the middle Caquetá river area in the north western part of the same Amazonas department (Fig. 1). Some characteristics of the sites are summarized in table 1.

Table 1. Main characteristics of the study sites, Centro de investigaciones Jenaro Herrera Peru (CIJH), Zafire biological station, near Leticia (ZAR) and Peña Roja (PR) in the middle Caquetá area.

Site	Location	Altitude m.a.s.l.	Rainfall mean annual	Temperature
CIJH	4°51'438'S73°37'129'' W	100	2,724 mm	Mean 26.9°C Mn 19.1 Max 33.3°C
ZAR	4°0'21''S69°53'55'' W	80	3,244 mm	Mean 26.0°C Mn 22.2 Max 28.7°C
PR	0°42'423''S72°03'477'' W	85	3,059 mm	Mean 25.7°C Mn 22.0 Max 30.9°C

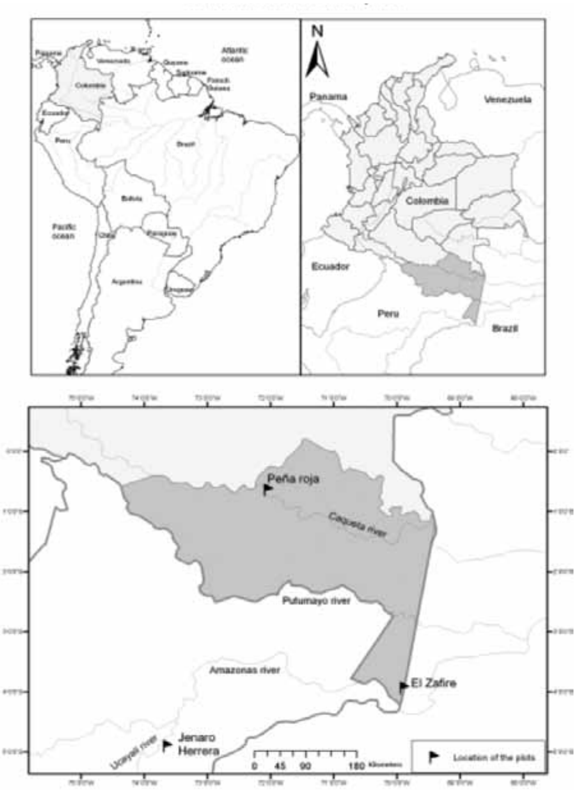

Figure 1. Location of the study sites.

All stems ≥ 10 cm in diameter, at breast height (DBH) were tagged and measured. In the middle of each plot an area that was two meters left and right of the main transect was delimited and all individuals ≥ 2.5 and < 10 cm DBH (0.1 Ha) (understory) were tagged and measured. In Peña Roja one subplot was randomly used to measure these small trees. Two DBH classes were distinguished; canopy ≥ 10 cm and understory ≥ 2.5 and < 10 cm DBH.

Botanical identification

Herbarium specimens of each tree species were collected using standard techniques. Palms and frequently occurring morpho-species were collected once or possibly more if there was sufficient doubt about the identity of the species. Vouchers were sent to the Jardin Botánico de Medellín Herbarium (JAUM) and Colombian Amazon Herbarium (COAH) in Bogotá for identification.

Samples of Ucayali were identified at the CIJH Herbarium at the Instituto de Investigaciones de la Amazonia Peruana IIAP, and later at the COAH herbarium. Fertile botanical samples were deposited at COAH and all vouchers (sterile and fertile) from CIJH and Zafire were deposited in the Laboratorio de Productos naturales y semillas of the Universidad Nacional de Colombia in Leticia.

Data set

In addition to the three new plots, 84 other plots from the ATDN (ter Steege et al. 2013) were used; 46 were located in Peru and 38 located in Colombia, which made a total of 87 plots for the analyses (Fig. 2). These plots were classified into four types of forests: 20 flooded by black waters forest plots - igapó (IG), 22 in white sand forests (WS), 32 in terra firme forests (TF) and 13 flooded by white water rivers forests -varzea (VA).

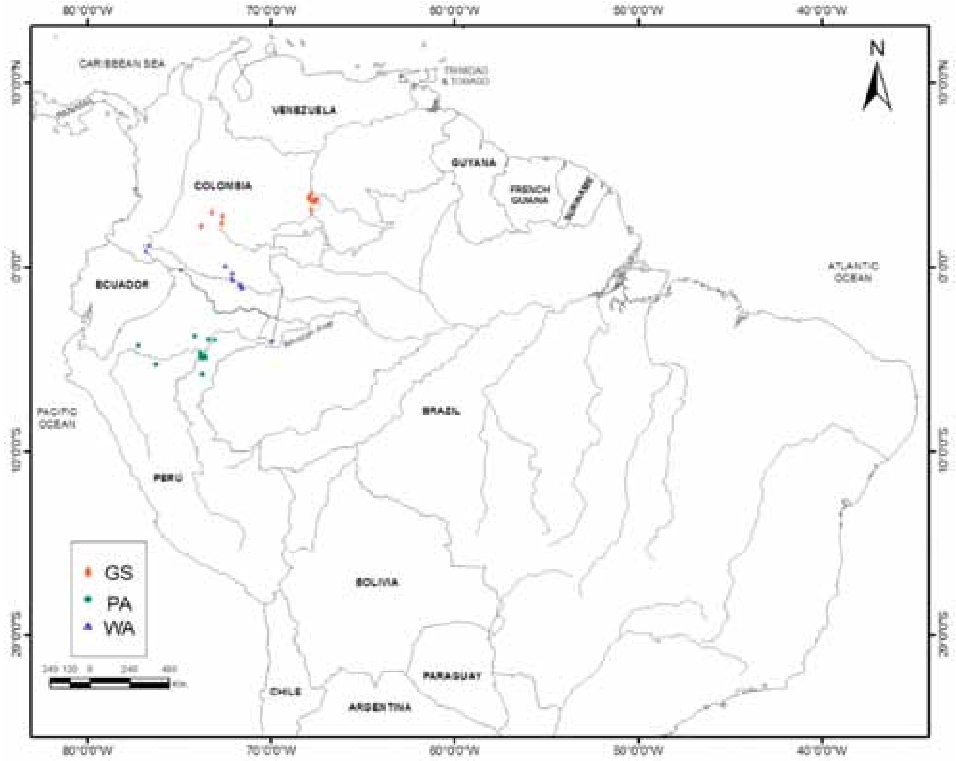

Figure 2. Location of 87 ATDN plots considered for comparisons; (GS) plots on the Guiana shield, (WA) plots in the Middle Colombian Amazon and (PA) Peruvian plots.

Data Analysis

The specificity of the species in relation to the forests groups was quantified by using indicator species analysis (IndVal) (Dufrene & Legendre 1997). Indicator values take into account the frequency (a measure of fidelity) and abundance (a measure of exclusivity) of the species among the groups of plots. Indicator species are defined as those that have a significant IndVal value and have more than 90% of their individuals in the forest for which they are an indicator.

Floristic patterns between all forests were explored by combining a PCA (Principal component analyses) with a DCA (Detrended Correspondence Analysis) in a DAPC Discriminant Analysis of Principal Components because it allows a complete graphic description of the samples, first joining characteristics in groups (PCA) and then separating them (DCA) (Guisande & Vaamonde 2012, Jombart et al. 2010). To observe floristic patterns within white sand forest plots, a DCA was used.

As a measure of diversity, and given the differences in plot size, Fisher's alpha of the plots was calculated because it is relatively independent of sample size (Fisher et al. 1943). Thereafter, the differences between forest types were tested using Kruskall-Wallis and then a Mann-Whitney test.

The analyses were conducted with the R environment for statistical computing (version 2.15.0), for the indicator species value –IndVal- analysis Dufrene & Legendre (1997) was used for the labdsv package.

RESULTS

Species Composition

In the three new plots 41 families were found; 36 families occurred in the understory and 37 in the canopy class, 78 genera and 186 (morpho-) species. Of these 186, 108 were identified at the species level (90.13% of the individuals), 49 were identified at the genus level, 21 at the family level and 10 remained unidentified. Ten families were common in the three plots: Fabaceae, Clusiaceae, Arecaceae, Malvaceae, Theaceae, Euphorbiaceae, Elaeocarpaceae, Burseraceae, Myristicaceae and Icacinaceae (Fig. 3).

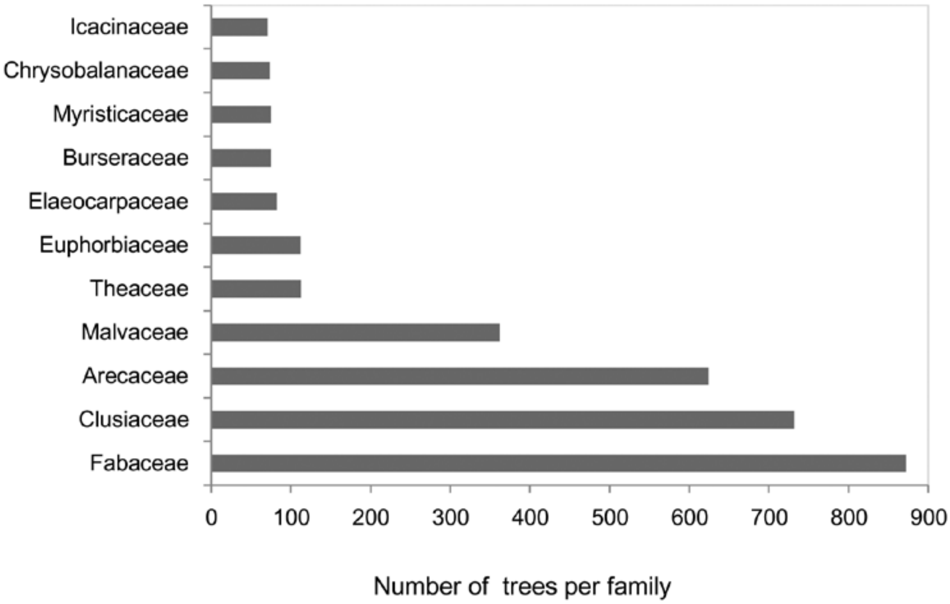

Figure 3. Most abundant families registered in three white sand plots: Peru: Centro de investigaciones Jenaro Herrera. Colombia: Zafire Biological Station and Peña Roja, middle Caquetá.

The most abundant families in both DBH classes were; Arecaceae and Clusiaceae, followed by Fabaceae and Malvaceae. Some families were present only in the canopy class and not in the understory, and were found with very low frequencies such as; Cecropiaceae, Chrysobalanaceae, Combretaceae, Lecythidaceae, Meliaceae, Ochnaceae and Tiliaceae. Other families were only found in the understorey such as Bignoniaceae, Rutaceae and Siparunaceae and were relatively frequent.

The plots from the ATDN database combined (including all types of forests) had 39,172 individuals and 1,859 morpho-species. The analysis used 439 genera that belong to 93 families and 1,583 fully identified species and found 531 of these in WS forests, 1,164 in the TF forest, 436 species in igapó (IG), and 479 in várzea (VA) (Table 2). It was found that the percentages of species found in one type of forest and not in others was; 49% of the terra firme species, 29% of the WS species, 17% of the species from IG and 15% from VA.

Table 2. Table 2. ATDN plots by forest type: white sand (WS), terra firme (TF), igapo (IG) and varzea (VA), total number of species, species unique for the type of forest.

Type of forest	WS	TF	IG	VA
Number of plots by forest	22	32	20	13
Area sampled by type of forest (ha)	11.3	26.7	11.4	11.4
Total number of species found by forest	531	1164	436	479
Species found only in that type of forest	157 (29%)	571 (49%)	73 (17%)	74 (15%)

When all types of forests were considered, 10 families comprised the 12 species that showed the highest indicator values (Table 3). Five of these 12 species were found in all types of forests: *Euterpe precatoria, Brosimum lactescens, Virola elongata, Minquartia guianensis and Micropholis guyanensis*. The varzea forests included all of these species.

Table 3. Families with the species that had the highest indicator values in all types of forests; white sand (WS), terra firme (TF), Igapo (IG) and varzea (VA).

Family	Species	WS	TF	IG	VA
Arecaceae	*Oenocarpus bataua*	x	x		x
Arecaceae	*Euterpe precatoria*	x	x	x	x
Euphorbiaceae	*Croton cuneatus*			x	x
Lecythidaceae	*Eschweilera parvifolia*		x	x	x
Moraceae	*Brosimum lactescens*	x	x	x	x
Moraceae	*Pseudolmedia laevis*		x		x
Myristicaceae	*Virola elongata*	x	x	x	x
Olacaceae	*Minquartia guianensis*	x	x	x	x
Polygonaceae	*Coccoloba densifrons*		x	x	x
Putranjivaceae	*Drypetes amazonica*			x	x
Sapotaceae	*Micropholis guyanensis*	x	x	x	x
Violaceae	*Leonia glycycarpa*		x	x	x

Of the 93 families in the ATDN data base, 22 had more than 15 species (Fig. 4): 12 families in WS, 22 in TF, 8 in IG and 10 in VA. These families accounted for 61.8%, 80.6%, 50% and 58% of the WS, TF, IG and VA forests species respectively. Within these families, those with the highest number of species present in all types of forests were Fabaceae, Annonaceae, Sapotaceae, Chrysobalanaceae and Moraceae (Fig. 4).

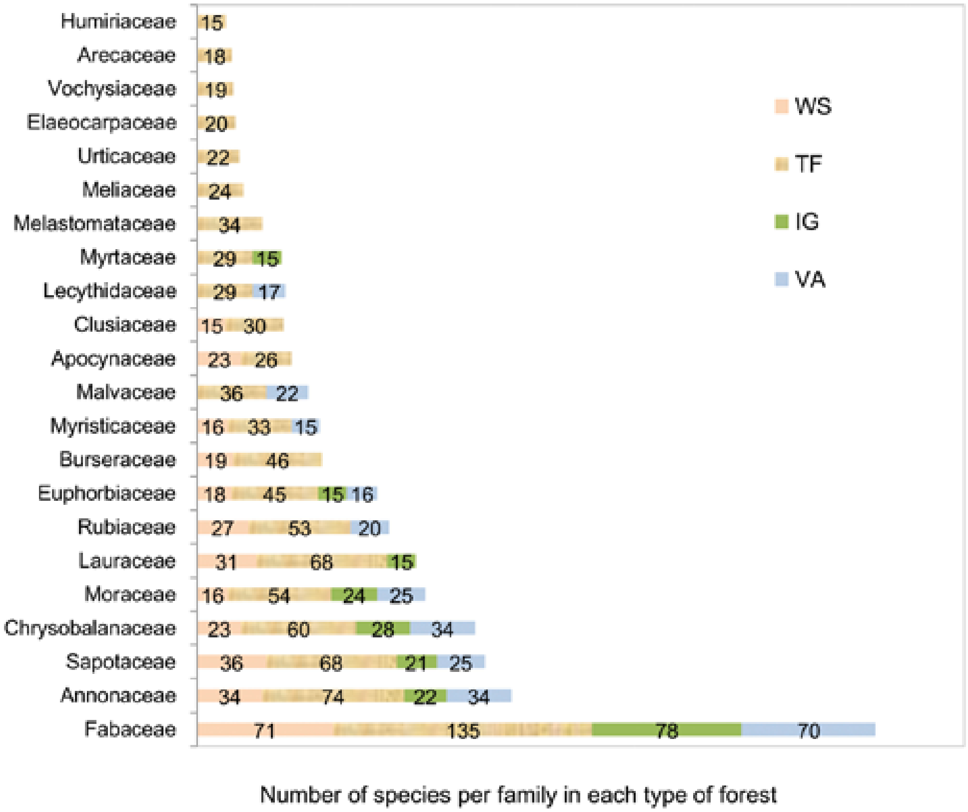

Figure 4. Families with ≥ 15 species per type of forest in the ATDN data base.

In the DAPC, the plots formed groups that were clearly defined by forest type. The first axis separated dry (WS and TF) and wet (VA and IG) forests, and the second axis separated TF from WS forests (Fig. 5).

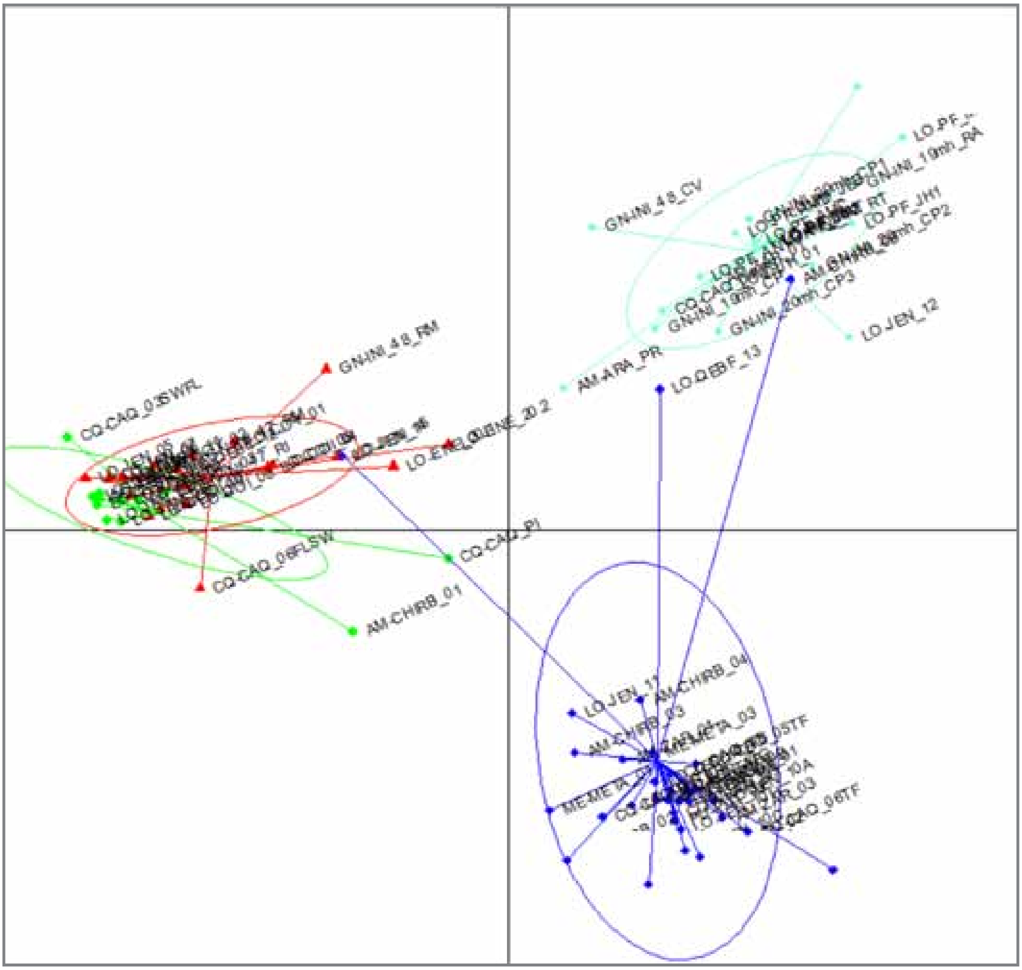

Figure 5. Bi-plot of a DAPC analysis of forest plots in the Western Amazon. Forest types are indicated by colours; White sand plots (Light blue), igapó (red), várzea (green) and terra firme (dark blue). For each group, a medium centre was plotted from which vectors are drawn to form a variability ellipsoid (95% of the plots of the group).

Fisher's alpha of the WS and the IG did not differ, but their values were significantly lower than those of the VA and TF (Mann-Whitney, $P< 0.0001$). No differences were found between Fisher's alpha of VA and TF plots (Fig. 6).

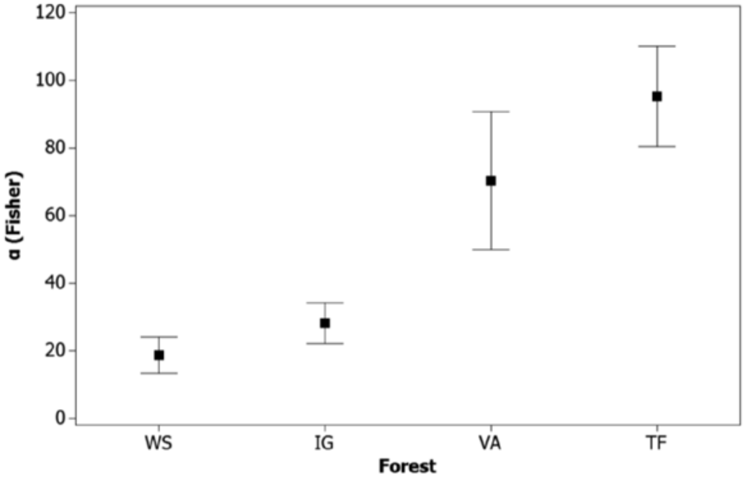

Figure 6. Fisher alpha by forest types: WS white sands, IG igapó, VA várzea and TF terra firme.

Fisher’s alpha did not show significant differences among forest types located in the Inirida, Guainia and Macarena regions, which are all remnants of the Guiana shield formation. In contrast, in the Peruvian Amazon, all forests types had a significantly different Fisher’s alpha; WS had the lowest followed by IG, VA and TF had the highest Fisher’s alpha. In the Middle Colombian Amazon the plots were separated by larger distances. Here TF and VA did not show significant differences, but both showed significant differences with WS, which had the highest variation in Middle Colombian Amazon (WA) (Fig.7).

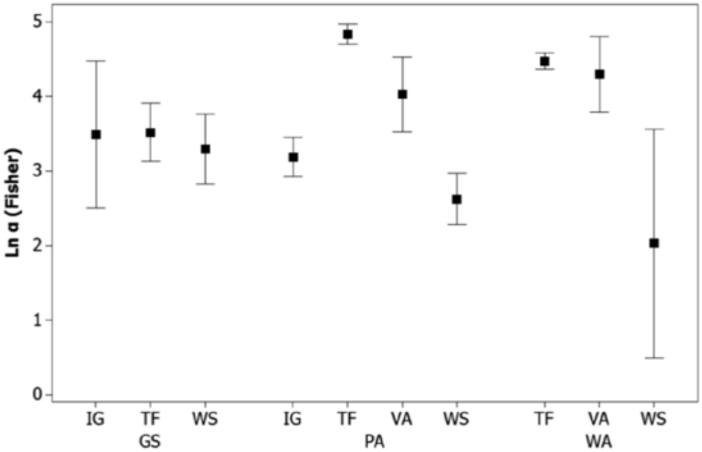

Figure 7. Fisher alpha by region Guiana shield (GS), Peruvian Amazon (PA) and middle Western Amazon (WA) for the forest types: IG igapó, TF terra firme, VA várzea and WS white sands.

White Sand Forests

White sand forests were separated into three main groups that corresponded with the regions that were sampled (Fig. 8). The first axis separated eastern plots located in the Guiana shield from western plots located in the Peruvian Amazon and the Middle Colombian Amazon. The second axis separated the Peruvian plots (including one of the new plots in this study (CIJH) from the plots in the Middle Colombian Amazon. This last region is represented in this study by three plots that were different enough to be separated from the other regions.

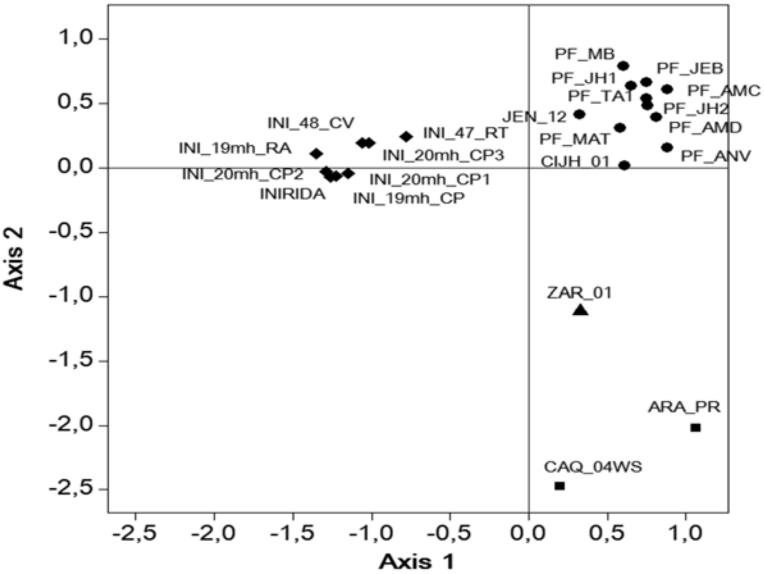

Figure 8. DCA of WS plots in the Western Amazon; three groups are clearly visible, Inirida (North eastern Colombian plots) ◆ Peruvian plots ● , middle-Colombian Amazon plots ■ with Zafire (southern Colombia) plot ▲

There were found 43 species as indicators of WS forests taking into account those with significant indicator values ($P< 0.05$) and found with more than 90% of their individuals in WS. The species belong to 36 genera and 22 families (Table 4). The family with the highest number of species was once again Fabaceae (nine species), followed by Clusiaceae (six species), Apocynaceae (five species) and Arecaceae (four species). Of these species, 30 were found exclusively in WS forests.

Four species were found in WS (Podzols) in the three regions: *Mauritia carana, Protium heptaphyllum, Haploclathra cordata* and *Xylopia benthamii.* Eleven species were found only in Podzols in the Peruvian Amazon and seven were found only in Podzols in Inirida; see Table 4. The other species were found between Inirida/Caquetá, Inirida/Zafire, Peruvian/Zafire or Caquetá/Zafire.

Table 4. Species of WS with significant indicator values (P < 0.05), species present only in Inirida(+) GS and only in Peru(**) in WA.

Family	Species	Family	Species
Annonaceae	*Xylopia benthamii*	Erythroxylaceae**	*Erythroxylum kapplerianum*
Apocynaceae	*Couma catingae*	Euphorbiaceae +	*Micrandra elata*
Apocynaceae	*Parahancornia surrogata*	Euphorbiaceae +	*Micrandra sprucei*
Apocynaceae **	*Aspidosperma pichonianum*	Fabaceae	*Dicymbe uaiparuensis*
Apocynaceae	*Aspidosperma spruceanum*	Fabaceae +	*Eperua leucantha*
Apocynaceae	*Neocouma ternstroemiacea*	Fabaceae**	*Hymenolobium nitidum*
Araliaceae	*Dendropanax palustris*	Fabaceae	*Hymenolobium velutinum*
Arecaceae	*Euterpe catinga*	Fabaceae	*Inga gracilior*
Arecaceae +	*Leopoldinia piassaba*	Fabaceae**	*Macrolobium bifolium*
Arecaceae	*Mauritia carana*	Fabaceae	*Macrolobium microcalyx*
Arecaceae	*Mauritiella armata*	Fabaceae	*Macrolobium suaveolens*
Bignoniaceae **	*Tabebuia serratifolia*	Fabaceae	*Tachigali rusbyi*
Burseraceae	*Protium heptaphyllum*	Icacinaceae	*Emmotum floribundum*
Caryocareaceae +	*Caryocar pallidum*	Malpighiaceae**	*Byrsonima stipulina*
Chrysobalanaceae	*Licania_intrapetiolaris*	Malvaceae	*Pachira brevipes*
Clusiaceae +	*Caraipa longipedicellata*	Myristicaceae**	*Marlierea caudata*
Clusiaceae	*Caraipa tereticaulis*	Ochnaceae +	*Lacunaria macrostachya*
Clusiaceae**	*Caraipa utilis*	Rubiaceae**	*Remijia pacimonica*
Clusiaceae	*Clusia magnifolia*	Sapindaceae**	*Cupania diphylla*
Clusiaceae	*Haploclathra cordata*	Theaceae	*Ternstroemia klugiana*
Clusiaceae**	*Tovomita calophyllophylla*	Vochysiaceae	*Ruizterania cassiquiarensis*
Elaeocarpaceae	*Sloanea robusta*		

DISCUSSION

New plots

Densities of trees in our study plots and generally on white sand forests are usually higher than in other types of forests. Table 5 shows data from terra firme or flooded forests that were located at the same sites of sampled white sands. The density of trees ≥ 10 cm DBH in the three new plots ranged from 632 to 984 trees per ha, and had a basal area that ranged from 18.79 to 23.05 m2/ha. These densities are within the range found by Duivenvoorden & Lips (1995) in the middle Caquetá (600-1140) and WS forests in the Western Amazon (Honorio et al. 2008), although the range for WS forests is very wide; ranging from 564 in Inirida (Cárdenas in ATDN) to 1270 in the middle Caquetá (Duque in ATDN).

Table 5. Density of trees by hectare in other forests close to the three new plots sampled.

Location	Author	Type of forest	No of trees
Middle Caquetá	Duivenvoorden 1996	Terra firme Floodplain	720±24
	Duque et al. 2002	Terra firme	790±14
		Floodplain	570±9
Perú	Honorio et al. 2008	Terra firme	517-617
		Flooded (igapó)	508-560
	Nebel et al. 2001	Flooded	417-737
Zafire	Peñuela et al.np	Terra firme	675
		Flooded (igapó)	664

In the understory, 423 to 600 individuals in 0.1 ha were found which is within the range found by Duque et al. (2002 in the middle Caquetá (309 - 733). Compared to flooded forests in Zafire (204 individuals) and Caquetá (273 ± 53, Duque et al. 2002), WS forests have double the number of individuals.

The families with a higher number of species in the new plots were Fabaceae, Burseraceae, Clusiaceae and Sapotaceae that were also important in other studies (Table 6). Fabaceae is the family with the highest number of species in Peru and middle Caqueta in Colombia (Table 6).

Table 6. Families with a higher number of species in this study compared with Fine et al. (2010) in WS in Peru and Duque et al. (2002) in the middle Caquetá.

Three new plots this study 2.4 ha		Fine et al. 2010 Peru ca.1.7 ha		Duque et al. 2002 Middle Caquetá 0.5 ha	
Fabaceae	(22)	Fabaceae	(30)	Fabaceae	(11)
Burseraceae	(11)	Lauraceae	(10)	Sapotaceae	(10)
Clusiaceae	(10)	Annonaceae	(14)	Annonaceae	(10)
Sapotaceae	(10)	Sapotaceae	(13)	Clusiaceae	(8)
Sapindaceae	(9)	Rubiaceae	(13)	Rubiaceae	(5)
Myrtaceae	(9)	Myrtaceae	(11)	Euphorbiaceae	(3)

In this study, Fabaceae was also the most common family (32.11% of all individuals) in CIJH due to *M. microcalyx* and *D. uaiparuensis* and 25% in ZAR mainly due to *Aldina* and *D. uaiparuensis*. The latter species is also common in Peru (García-Villacorta et al. 2003, Fine et al. 2010). The presence and abundance of *Dicymbe* is interesting, because the genus is endemic to the greater Guiana Shield region (Steyermark et al. 1998) and it is among the ten most abundant genera in that region (ter Steege et al. 2006a). In that area, some species may become monodominant: *D. corymbosa* by (Henkel 2003) with a basal area (BA) that was 70% of the total forest basal area or dominant *D. altsonii* (BA > 40%) (Zagt 1997). In the lowland tropical rainforest of Guyana, Banki (2010) found *D. corymbosa* to be an important species, but in the upper Rio Negro region, Stropp (2011) found only one individual of *D. parangiphila*. In all cases, it was shown that *Dicymbe* is a genus of white sands.

Clusiaceae is highly abundant in WS forests in Peru, with 24.5% of all trees larger than 10 cm DBH belonging to this family (Fine et al. 2010). In the plots for this study, *H. cordata* comprised 40% of all individuals of the ZAF plot, and *C. punctulata* was 35.2% in Peña Roja, although in CIJH only 9% belonged to this family.

Malvaceae (with the genus *Pachira*) is a dominant family in western WS forests. In Peruvian WS forests, it is one of the most common species (Fine et al. 2010). In Colombia, the species is common in the middle Caquetá (Duivenvoorden & Lips 1995, Urrego 1997, Duque et al. 2002) as well as in the plots from this study. *Pachira* has been reported to be restricted to periodically flooded habitats (Kubitzki 1987) and *P. brevipes* to poorly drained white sands (García Villacorta et al. 2003).

Arecaceae is among the most abundant families in the Western Amazon (ter Steege et al. 2006b, 2013) and it is not an exception in western WS forests together with the species *Euterpe catinga* and *Mauritiella armata*. *E. catinga* was abundant in the understory in the three plots from this study and it is already known to be a species that grows on sandy, poorly drained soils (Galeano & Bernal 2010). In WS forests in the Eastern Amazon, palms are not common.

Other families with species that are well represented in WS forests are; Euphorbiaceae with the genera *Micrandra* and *Hevea*; Araliaceae with the genus *Dendropanax* (Fine et al. 2010) in Peru and in Colombia (Duque et al. 2002) and also in the plots used in this study. Theaceae is also a well-represented family in Western Amazon WS forests with the genus *Ternstroemia; T. klugiana* was common in ZAF, and Fine et al. (2010) also found them to be endemic of Peruvian WS forests.

Low diversity and thus high dominance in WS forests could be the result of their scattered distribution in the Amazon basin and the small patches of white sands that they occupy (ter Steege et al. 2000a). Neutral dynamics and species (population) drift in each area may lead to any WS species becoming the dominant species, because re-migration between the patches is difficult. Other explanations of dominance are associated to mechanisms that are common although not exclusive of monodominant species (Peh et al. 2011). For example, associations with ectomycorrhizal (EM) fungi are found in *D. uaiparuensis* and *Aldina* sp. in ZAR (Vasco et al. 2014), in *D. corymbosa* in Guyana (Henkel 2003) and *Aldina heterophylla* in Reserva Biologica de Campina north of Manaus (Mardegan 2007). Such ectomycorrhizal associations allow plant species to exploit larger volumes of soil than those without such associations, giving them a competitive advantage over other species. However, these associations are not a sufficient explanation for monodominance (Torti & Coley 1999). Avoiding or reducing herbivory by investing in leaf defences is another adaptation to nutrient poor growing conditions. This thesis (chapter 4) and Fine et al. (2004, 2006) found that WS species have tougher leaves and suffer less herbivory. In addition, WS species have high wood density which reduces growth rates and turnover rates. Lower turnover rates in turn (see also chapter 3 of this thesis) have been postulated as one ecological factor that could explain monodominance (Peh et. al. 2011). None of these factors alone may sufficiently explain the dominance of tree species in WS forests, but as Peh et al. (2011) suggested, it is more likely that dominance is the result of multiple interacting factors.

Comparison using ATDN Data Base

In general, significant floristic differences were found between WS and TF or VA forests, but there were no significant differences with IG (Fig. 6). Among the various regions, no significant differences were found between IG from the Guiana shield and the Peruvian Amazon and the VA from the middle Colombian Amazon and the Peruvian plots. However, there were significant differences between TF and WS forests among regions. No significant differences in Fishers' alpha were found among forest types in the Guiana shield, but differences were clearly shown among forest types in the Peruvian Amazon and in the middle Colombian Amazon (Fig. 7), which suggests higher variability of environmental conditions in the Western Amazon and conversely, more homogeneous conditions in the Guiana shield.

More species were found in the WS forests (Table 2) than in the VA or IG, in a similarly sampled area (ca.11 ha). However, the Fisher's alpha was lower, which indicates that the WS forests are heterogeneous and that their species are not widely distributed among them, as had previously been thought.

In all forest types 26 families and 66 species were found: Fabaceae (10 species), Myristicaceae (7), Chrysobalanaceae (6) and Euphorbiaceae, Moraceae and Sapotaceae each had 4 species. These families also had the highest indicator values, except for Annonaceae, which had only one species common to all forest types.

Four of the species with the highest indicator values were among the most common species found for the Amazon basin (ter Steege et al. 2013): *Euterpe precatoria, Brosimum lactescens, Oenocarpus bataua* and *Pseuldolmedia laevis.*

In the Western Amazon, the number of tree species with DBH ≥10 cm in WS forests can reach 80 species per hectare, which shows that a considerable number of species are able to establish and survive in these very nutrient poor and sometimes waterlogged WS forests. In the white sands 43 abundant species were found with high indicator values that could serve as indicators of this type of forests (Table 4).

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CHAPTER 3

EIGHT YEARS OF FOREST DYNAMICS IN A WHITE SAND FOREST IN THE COLOMBIAN AMAZON – WITH REFERENCE TO WHITE SANDS AND TERRA FIRME CLAY FORESTS IN THE AMAZON

with Eliana Jiménez, Hans ter Steege and Rene Boot

ABSTRACT

White sand forests are found on poor, sandy soils and are generally dense with trees that are small in diameter and that have high wood density. These characteristics are usually associated with slow growing trees that have low mortality and recruitment rates. To determine the dynamics of white sand forests in a seasonally waterlogged soils of the Colombian Amazon we calculated tree mortality, modes of death, recruitment, turnover and growth rates of canopy trees that were greater than 10 cm DBH and understory trees more than 2.5 cm and less than 10 cm DBH. This was done by conducting 8 censuses during the period 2004 - 2012 in a 1-ha plot in South-eastern Colombia. Parameters such as mortality, recruitment and growth were also calculated for common tree species (≥ 15 stems in the plot). The average mortality rate was 1.31% yr^{-1} for trees with a DBH ≥ 10 cm and 1.59% yr^{-1} for trees < 10 cm DBH, and 0.18% yr^{-1} for common species that represented 84.97% of the tree population; 68% of the dead trees belonged to three of the most common species. Therefore the recruitment and mortality rate of common species determined the rates of the stand. Most trees died *standing* (81.93%), regardless of their size, followed by *broken* (9.69%) and *uprooted* (5.72%). The percentage of 'standing mortality' was very high compared to other Amazon forests. Annual recruitment rates were 1.49% yr^{-1} for trees ≥ 10 DBH and 2.30% yr^{-1} for the understory trees. Mortality and recruitment rates were highly variable but were within ranges reported in other forests on Spodozols in the Amazon. A high variation was also found when comparing white sand with terra firme forests, which indicates that there are greater differences between the two types of forests in Peru compared to the differences found between forests in the South-eastern Colombian Amazon or Rio Negro watershed. A slight increase in mortality relative to recruitment was observed for the most common species since 2008. This increase in mortality coincided with an overall decrease in growth except in palms where recruitment was higher, indicating that they responded differently to the causes of death. Based on the performance of common species, it is possible to predict the performance of white sand forests under different climate scenarios.

INTRODUCTION

The Amazon River basin contains a wide variety of different habitats which results in an extraordinary diversity in plant and animal species (Tuomisto et al. 2003). Western and Eastern Amazonian forests show differences in productivity, dynamics and diversity (Baker et al. 2003, Baker et al. 2004a, Lewis et al. 2004, Phillips et al. 2004, ter Steege et al. 2006, Stropp et al. 2009). These differences have been associated with precipitation, intensity and duration of the dry season and soil fertility and are reflected in the gradients of wood density, seed mass, and species diversity from East to West across the basin (ter Steege et al. 2006).

In addition, local variation exists in surface hydrology, soil properties and topography that influence functional forest properties such as biomass production rates, mortality and turnover rates that are difficult to analyze on broad spatial scales (Malhi et al. 2009, Stropp et al. 2009, Chave et al. 2010). White sand (WS) forests, a well-defined type of forest in the Amazon, grow on highly weathered, podzolized soils (Spodozols in US classification). In general, these soils are highly acidic and have high Aluminum concentrations (do Nascimento et al. 2004, Quesada et al. 2011), very low cation exchange capacity and the lowest Phosphorus concentrations compared with other Amazonian soils (Quesada et al. 2009a, Quesada et al. 2011).

WS forests are relatively low in tree diversity (< 100 species per hectare) (Anderson 1981, ter Steege 1993, Coomes & Grubb 1996, Prance 1996, García Villacorta et al. 2003, Fine et al. 2004, Stropp et al. 2009, Banki 2010, Stropp 2011) compared to other types of forests in the Amazon and show a lack of lianas and large trees (> 100 cm DBH) (Coomes & Grubb 1996). Tree species that grow on white sands are also characterized by high-density wood and xylem stems (Agudelo 2005, Patiño et al. 2009) and, in Peru, the trees have tough leaves that are more resistant to leaf herbivores than the species of a terra firme forest (Fine et al. 2004), but see Stropp et al. (2013).

Previous studies of forest dynamics discuss temporal changes in the structure and floristic composition of forests and they explain the factors that determine these changes (Terradas, 2005). These studies use re-measurements of permanent plots to determine growth, mortality, recruitment, turnover rates, and modes of death of populations of tree species.

Mortality depends on abiotic (e.g. nutrients, water availability) and biotic (e.g. genetics, wood density, pests, shading) conditions that affect trees (Putz 1984, Mori & Becker 1991, Condit et al. 1995, Gale & Barfod 1999, Arriaga 2000, Gale & Hall 2001, King et al. 2006). Forests with a high average wood density show lower mortality rates and lower species diversity than those with lower wood density (ter Steege & Hammond 2001, Parolin 2002, Baker et al. 2004a, Lewis et al. 2004, ter Steege et al. 2006).Changes in the abiotic conditions such as a typically long dry season or flooding can cause widespread tree mortality and a certain mode of death (Mori & Becker 1991, Condit et al. 1995). Different modes of tree death can create different types of canopy gaps (Gale & Hall 2001), which give rise to a diverse forest structure and dynamic characteristics which may indicate the most probable factors that influence tree mortality (Toledo et al. 2012).

Recruitment is related to tree growth and gap dynamics and refers to trees that appear in a given area, during a certain period of time or that are grown to a specific size class that has been established in the plot (Laurance et al. 2009, Prior et al. 2009).

Tree turnover, which is the mean of mortality and recruitment, has been shown to correlate positively with tree species richness (Phillips et al. 1994) and higher soil fertility (Phillips et al. 1994, Phillips et al. 2004), which can both drive forest productivity (Malhi et al. 2004).

Tree growth is related to site conditions such as climate, solar radiation, and soils (nutrient and water availability) but it also shows age and wood density (Worbes 1999, Baker et al. 2003, Feeley et al. 2007, Keeling et al. 2008).

This chapter will study the dynamics of a western Amazon WS forest by measuring growth, recruitment, turn over and the number of dead trees and the mode of death by examining 8 censuses that were carried out between 2004 and 2012. The censuses looked at canopy trees that had a DBH ≥ 10 cm and understory trees that were taller than 2.5 m and that had DBH < 10 cm, while focusing on the most common species in the plot (N > 15). Then the results from this study were compared with data from other forest types in the Western Amazon and WS forests from the Eastern Amazon. Based on the special characteristics of WS forests of low diversity, high wood and xylem density trees on very poor soils, we expected lower turnover rates, resulted in very low growth and recruitment rates compared to other type of forests.

Additionally, this study addressed the following questions: Are there marked differences between the dynamics of smaller trees and canopy trees? How WS forests trees die? Which species are more prone to die or recruit in the plot? And which of the species grow better? The answers to these questions may offer a better understanding of the forest dynamics of WS forests.

METHODS

A one hectare plot (250 m x 40 m) was established in September 2004 in a white sand forest at the Zafire biological Station (ZAF) (4°00’00” S, 69°53’57” W) in the Rio Calderon Forest Reserve (Fig. 1). We distinguished two tree DBH (Tree diameter at 1.3 m above the ground surface) classes: trees ≥ 10 cm DBH (canopy) and trees ≥ 2.5 m height and < 10 cm DBH (hereafter referred to as understory trees). To analyse the size at which trees die we further distinguished the following size categories based on height: 2.5 m < 5.0, 5.0 < 7.5, 7.5 < 10.0, ≥ 10 < 15 and ≥ 15 m. All canopy trees were numbered with aluminum tags and painted with a ring around the trunk (to mark the point of measurement) at DBH or higher when necessary due to irregularities of the trunk. In the understory, two 0.1 ha transects (250 m x 4 m) were established and all trees were painted and marked with a tag hanging on a wire to avoid trunk damage. Stem diameter, height, coordinates and other observations (e.g. any type of damage) of each tree in the plot were recorded for all individuals. Voucher specimens for herbarium identification were collected and were identified to species, when possible, at Herbario Amazonico Colombiano (COAH) and Herbario Nacional (COL) in Bogotá.

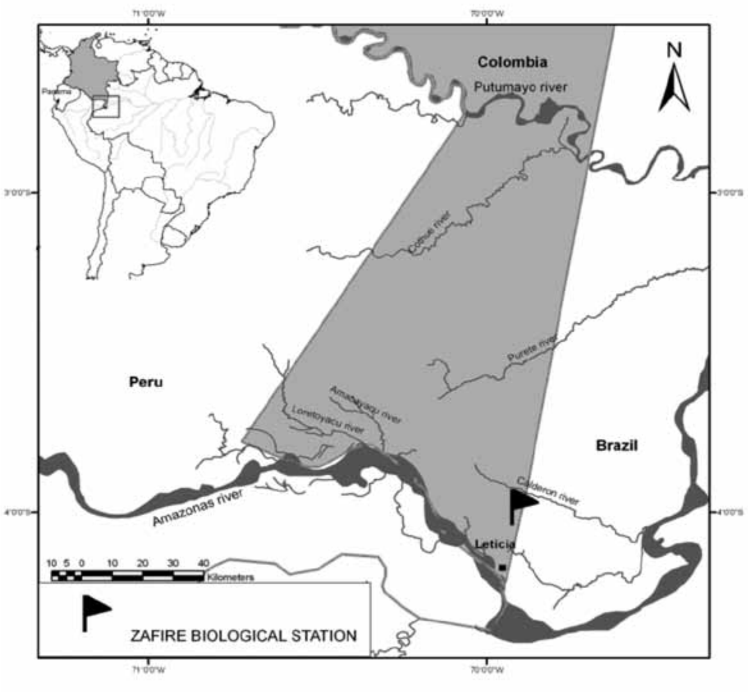


Figure 1. Study site, Zafire Biological Station, Colombian Amazon

Census intervals

The time interval between two measurements was approximately twelve months (with the exception of 2010-2012, when it was 20 months). This facilitated the estimation of annual growth, mortality and recruitment rates (Rolim et al. 1999, Lewis et al. 2004). All marked individuals were measured each year and since 2004, deaths and recruits have been registered. All rates were calculated for the common species that occur in these white sand forests (for the purposes of this study, 'common species' are those with more than 15 individuals in the plot).

Mortality

A dead tree was recorded when it had lost all of its leaves and/or its stem was dried out, or simply when the tree was not present during subsequent measurements. At each census, all dead trees were recorded and the mode of tree death: standing, broken, uprooted or missing (Clark 1990, Gale & Barfod 1999) was also noted.

Mortality rate was assessed at each census interval for both canopy and understory trees, including all stems, and also for the more common species ($N \geq 15$ live stems at the beginning of the census interval), with a commonly used formula (Phillips et al. 1994, Condit et al. 1995, Sheil & May 1996, Nebel et al. 2001):

$$r_m = \ln (N_0) - \ln (N_0 - N_m) / \Delta t$$

Where, N_0 is the number of stems at the beginning of the period, N_m is the individuals that died during the time period Δt.

The distribution of dead trees by DBH size at each group considering diameter and height was also reported.

Recruitment

Recruits, defined as plants that enter a size class of ≥ 2.5 cm DBH (understory) or ≥ 10 cm DBH (canopy), were recorded and tagged, mapped and measured as described above during each census. The mean annual rate of tree recruitment was calculated using a logarithmic model (Phillips et al. 1994) which followed the same criteria of analysis: first with all stems and then with only species with $N \geq 15$:

$$r_r = \ln ((N_0 - N_m - N_r)/ (N_0 - N_m))/t$$

Where N_0 is the number of trees at the beginning of the interval, N_m is the number of trees that died in the interval, Nr is the number of recruitments of the interval and t is the time elapsed.

Turnover

Turnover rates were calculated as the mean of recruitment and mortality rates (Phillips et al. 1994, Laurance et al. 2009).

$$T_r = (r_m + r_r) / 2$$

Growth

The diameter of each individual was carefully measured every year at the same location along the stem, marked with paint. Most individuals between ≥ 2.5 cm and <10 cm DBH were measured with calipers, except for those that were ≥ 7 cm, with irregularities or difficulties when measuring; in which case, tree diameter tapes were used. The tool used for measurement was noted for each tree. Stems with DBH ≥10 cm were measured with diameter tapes.

Understory and canopy growth were calculated for each year considering only living, standing trees that were identified and measured at the beginning and end of an interval. Palms were excluded from this calculation given that their growth is determined by apical extension and their heights were not measured accurately each year.

Annual diameter increment (cm yr^{-1}) was calculated as the difference between two measurements, divided by the time elapsed in years (Clark & Clark 1999):

$$G_r = (Diameter_t - Diameter_0) / t_2 - t_1$$

Because wood density plays an important role in forest dynamics (Chao et al. 2008), the common species were divided into four groups according to their wood density (Table 1): Group I: trees with wood density < 6.5 g/cm3; Group II: trees with wood density between 6.5-7.5 g/cm^3; Group III trees with wood density > 7.5 g/cm3 and palms constitute the Group IV.

Statistical analyses, computing and graphics were carried out in the R environment for statistical computing (version R 2.15).

RESULTS

In one ha of white sand forest, 2280 stems consisting of 1296 understory (smaller) trees and 984 canopy trees were marked and measured during 8 re-measurements. 16 common (≥ 15) species were found at the establishment of the plot that together corresponded to 84.97% of all individuals in the plot (Table 1).

Table 1. Common species with more than 15 stems found in a white sand forest plot at the Zafire Station at the moment of establishment.

Group	Species ≥ 15 stems	Abbr.	Wood density group
Fabaceae	*Dicymbe uaiparuensis* R.S. Cowan	Du	II
	Diplotropis martiusii Benth.	Dm	II
	Macrolobium gracile Spruce ex Benth.	Mg	II
	Macrolobium suaveolens Spruce ex Benth.	Ms	II
Palmae	*Euterpe catinga* Wallace	Ec	IV
	Mauritiella armata (Mart.) Burret	Ma	IV
Clusiaceae	*Haploclathra cordata* Vásquez	Hc	III
	Tovomita sp.	Tv	III
Euphorbiaceae	*Hevea nitida* Mart. ex Müll.Arg.	Hn	I
Humiriaceae	*Humiriastrum excelsum* (Ducke) Cuatrec.	He	III
Araliaceae	*Dendropanax palustris* (Ducke) Harms	Dp	I
Icacinaceae	*Emmotum floribundum* R.A.Howard	Ef	III
Myristicaceae	*Iryanthera obovat*a Ducke	Io	I
Malvaceae	*Pachira brevipes* (A. Robyns) W.S Alverson	Pb	I
Elaeocarpacee	*Sloanea parvifructa* J.A.Steyermark	Sp	III
Theaceae	*Ternstroemia cf. verticillata* Klotzsch ex Wawra	Tv	II

Haploclathra is in Callophylaceae in http://www.tropicos.org/, but Fine 2010 and Stropp 2011classified it in Clusiaceae thus we leave it in that family for comparisons.

Dynamics of the understorey

During the period from 2004 - 2012 (8 years) 136 dead trees (680 per hectare) were recorded. The number of dead trees varied from 65 - 140 per ha with an average of 97.14 ± 38.89 deaths yr^{-1}. Of the 86 species found in the understory, 26 species showed deaths. *E. catinga*, which is an important component in the understory, (see chapter 2), represented 36.76% of deaths, followed by *D. uaiparuensis* with 18.34% and *H. cordata* at 5.88%.

Mortality rates varied from 1.15 to 2.45% yr^{-1} over the 8 years, with an average of 1.59 ± 0.12% yr^{-1} (Fig. 2).

The total number of recruits in the understory was 1015 ha-1, belonging to 40 species in this DBH class. Of the species recorded in the establishment, 32 were found only in the understory and no recruitment was shown during the 8 year time period. The average of the annual recruits was 145 ± 53.30 individuals per hectare and varied from 60 to 210 recruits per census. During the period from 2008-2010, the highest number of recruits was recorded and during the period from 2006-2007 the lowest number was noted.

In the understory, annual recruitment rates varied from 0.98 to 3.40% yr^{-1} per year with an average of 2.31 ± 0.99% yr^{-1}. The turnover in the understory varied from 1.10 to 2.92% yr^{-1} with an average of 1.95 ± 0.43% yr^{-1}.

The understory growth increment varied between 0.048 to 0.11 cm yr^{-1}, with an average of 0.079 ± 0.077 cm yr^{-1} (Fig.2). Mortality and recruitment were synchronized which indicates a different behavior compared to canopy performance.

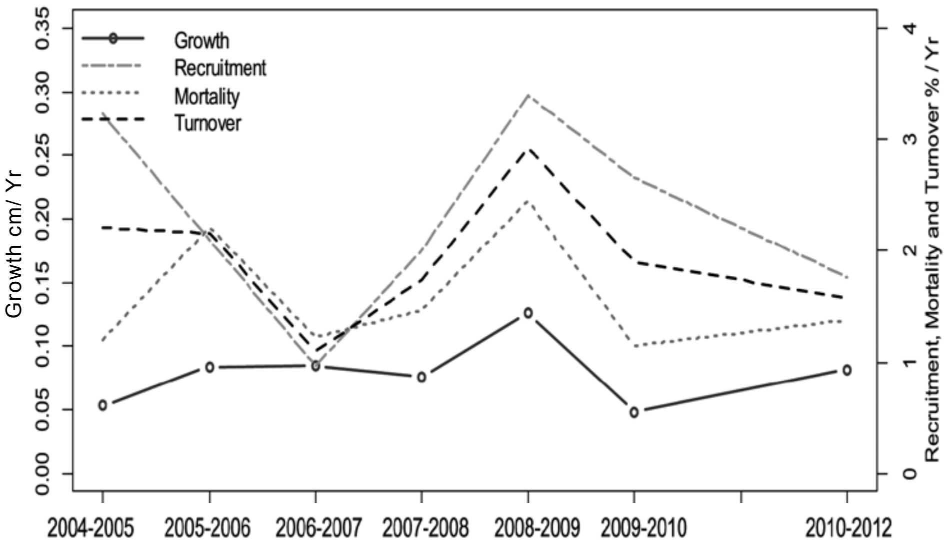


Figure 2. DBH growth, Mortality, recruitment and turnover rates in the understory, during the 2004-2012 time periods.

Dynamics in the canopy

During the 8 year time period, 91 stems ≥ 10 cm DBH died, with an annual variation that ranged between 1 and 25, and an average of 13 ± 16.97 trees per year. Of the 69 species found in this class, only 15 showed dead individuals; 51.65% belonged to *D. uaiparuensis*, followed by *H. cordata* 25.27% and D. *palustris*, *E. floribundum*, *P. brevipes* with 3.3%. The mortality rate was 1.31 ± 1.56% yr^{-1} and varied from 0.11 to 2.32% (Fig. 3).

The number of recruits was considerably lower for canopy trees than for understory trees; 94 individuals of 27 species presented recruits during the period from 2004-2012, with an average of 13.43 ± 3.54 individuals. The lowest number of recruits was registered in the year 2007-2008 and the highest number in 2008-2009. Annual recruitment rates varied from 0.69 to 3.64% in trees ≥ 10 cm DBH with an average of 1.41 ± 0.58%. Turnover rate varied from 0.51 to 2.28% yr^{-1}, with an average of 1.38 ± 1.07% yr^{-1}.

Differences in the growth of canopy trees ≥ 10 cm DBH were lower than in the understory, showing a range of 0.057 to 0.085 cm yr^{-1} and an average of 0.073 ± 0.065 cm yr^{-1}.

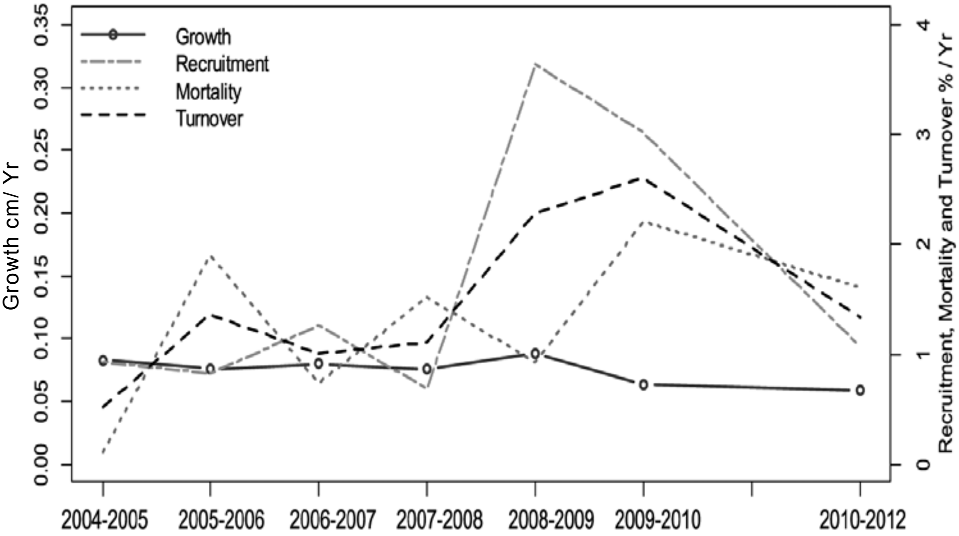


Figure 3. Annual mortality, recruitment and turnover rates in the Canopy and annual growth differences during the years from 2004-2012.

Deaths by Size Class

When separating all of the stems into smaller 'DBH' and 'Height' classes, it was observed that mortality was higher but not significant in the smaller DBH classes. In the diameter class from 5.0 to 7.5 cm, proportionally more dead trees were recorded (Table 2) than in the other classes.

In terms of height, it was found that most individuals died in the height class between 10 and 12.5 m, but differences were not statistically significant (Table 2).

Table 2. Percentage of dead stems in understory and canopy trees per DBH and Height classes.

Classes	I	II	III	IV	V	VI
DBH (cm)	2.5 < 5	5 < 7.5	7.5 < 10	10 < 15	15 < 20	≥ 20
% Understory	55.14	33.82	11.02	-	-	-
% Canopy	-	-	-	68.13	24.17	6.59
Total	33.04	20.26	6.60	27.75	9.69	2.64
HEIGHT (m)	> 5	5 < 7.5	7.5 < 10	10 < 12.5	12.5 < 15	≥ 15
% Understory	30.35	35.29	22.05	8.08	2.20	0.00
% Canopy	1.09	3.29	8.79	50.54	18.68	17.58
Total	19.82	22.49	16.74	25.11	8.81	7.05

No relationship between the different diameter classes and modes of death was found. However, it was observed that missing and uprooted trees were positively correlated to the smallest height class (Pearson’s Chi-squared test $P < 0.09$).

Dynamics of Common Species

For common species, which constituted 84.97% of all trees, the mortality rate was 1.60 ± 2.07% yr^{-1} and varied from 0.20% yr^{-1} in *H. nitida* and *I. obovata*, to 4.10% yr^{-1} in *D. uaiparuensis, E. catinga* and *Tovomita sp.*

The recruitment rate was much lower than the mortality rate and averaged 0.10 ± 0.48 yr^{-1} varying from 0.20 to 1.90% yr^{-1} during the measurement period. *M. gracile, Tovomita sp.* and *D. martiussi* always showed the highest recruitment rates and the turnover varied from 0.55 to 1.90% yr^{-1} and averaged 0.85 ± 0.55% yr^{-1}.

The average diameter increment in common species was 0.078 ± 0.032 cm yr^{-1} and varied from 0.037 to 0.163 cm yr^{-1}. The species with the highest diameter increment for all years was *D. uaiparuensis* at 0.163 ± 0.017 cm yr^{-1}, followed by *H. excelsum* 0.113 ± 0.023 cm yr^{-1}, *E. floribundum* 0.095 ± 0.024 cm yr^{-1},*T. verticillata* 0.092 ± 0.043cm yr^{-1}, *D. martiussii* 0.090 ± 0.015 cm yr^{-1}.

There were some other species not as abundant as the common species and not defined as specialist of WS that have a higher growth such as *Swartzia argentea* with 0.393 ± 0 cm yr^{-1}, Myrtaceae sp 1. (0.316 ± 0 cm yr^{-1}), Fabaceae sp.2 (0.303 ± 0 cm yr^{-1}), *Guatteria lesnieri* (0.226 ± 0 cm yr-^{1}), *Protium llanorum* (0.185 ± 0 cm yr^{-1}).

Dynamics and Wood Density

It was also found that dynamics rates increased with wood density, which is in contrast with findings from other forests. In all groups except palms, it was found that mortality rates were higher than recruitment rates in the period from 2008 to 2012, and especially in the periods from 2008-09 and 2009-10 (Fig. 4). In contrast, palms showed higher recruitment rates during all measurement periods except for the period from 2009-2010 when the ratio of recruits/dead reduced.

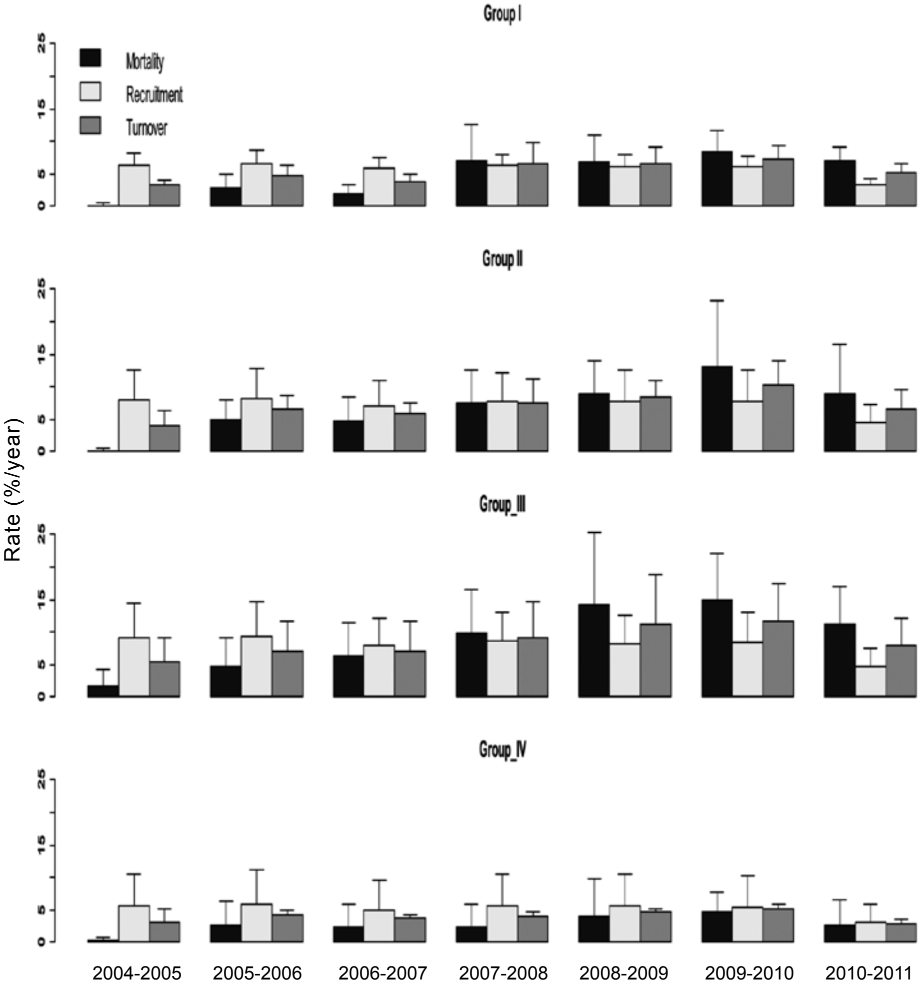


Figure 4. Mortality, recruitment and turnover rates by wood-density groups, from the 16 most common species. Group I (Dp, Hn, Io, Pb $< 6.5\ g/cm^3$), Group II (Dm, Du, Mg, Ms, Tv $\geq 6.6 < 7.5\ g/cm^3$), Group III (Emf, Hc, He, Sp,To $> 7.5\ g/cm^3$) and Group IV palms (Ma and Ec). Wood density in most cases was calculated for these species in the site by (Agudelo 2006).

Species and Death

Approximately 68% of dead trees belong to three of the most common species: *D. uaiparuensis* (31.72%), *E. catinga* (22.03%) y *H. cordata* (13.66%), and the number of dead trees per diameter class was proportionate to the number of individuals per class. For example, 53% of *D. uaiparuensis* deaths belong to height category IV (10-15 m), 74% of *E. catinga* deaths belong to categories II and III (< 7,5 m) and 80% of *H. cordata* deaths were trees that were more than 10 m tall and these belong to categories IV, V and VI (Fig. 5). In all cases, the main mode of death was standing which accounted for 84% of deaths in *D. uaiparuensis*, 78% in *Ec* and 100% in *Hc*. It is probable that in *Hc*, and even in *Du*, senescence, as well as wood density could have caused this mode of death, as has been suggested in the literature (Chao et al. 2008, Toledo et al. 2012) for Eastern Amazon tree deaths. However, the standing deaths in *E.catinga* must correspond with other causes that could be associated more with anchorage or desiccation, given that most deaths were found in the height classes I and II. This mode of death also helps to maintain the stability in species composition due to the gradual release of nutrients that increase growth rates of established plants (Martini et al. 2008).

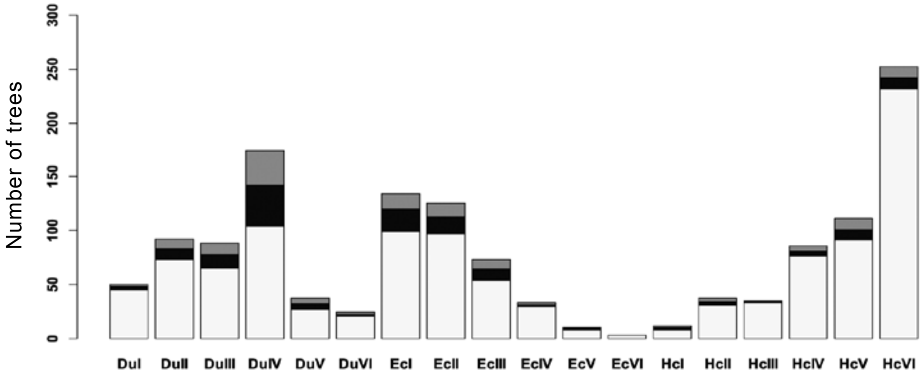


Figure 5. Number of trees per species (white) dead (black) and standing mode of death (grey) per height class (I, II, III, IV, V, VI) in the three most common species in the plot Du: *D.uaiparuensis*, Ec: *E.catinga* and Hc: *H.cordata*.

Modes of Death of White-sand Trees

Most individuals died standing (81.93%), followed by broken stem (9.69%), uprooted (5.72%) or missing (2.64%). However, proportionally more uprooted and broken trees were registered in the understory than in the canopy.

In the understory in 2005, uprooted and broken stems were more frequent and significant (Pearson's Chi-squared test $P < 0.05$) than in other years. No other modes of deaths were significantly different between or within years or in ≥ 10 cm DBH class.

DISCUSSION

Mortality and recruitment rates were different for understory and canopy trees, these rates were higher in the understory. The rates varied among different years and during the 2008-2009 and 2009-2010 periods showed a marked increase in mortality rates for some species, with the exception of palms. Recruitment rates of palms were always higher than their mortality rates, which suggests that monocots respond differently to environmental climatic conditions and that if these conditions persist for a long period of time, palms may become the dominant life form in the stand.

The mean of all recruitment, mortality and growth rates found in this study were similar to the rates reported for other Amazonian forests on Oxisols and other Spodozols (Table 3). Most trees died standing, regardless of their diameter and uprooted and missing modes of death were only present in smaller DBH trees. Other authors have also associated the missing mode of death with small trees (Holzwarth et al. 2013). And modes of death have been associated with topography, drought, or species (Gale & Hall 2001). Given that the plot is situated on level ground, the observations could respond more to soil conditions, drought and species traits, such as wood density, size of crown and root anchorage.

In general, average growth rates were similar for understory and canopy trees. In the period from 2008-2009, the average growth was higher than in the other years in both DBH classes, which could explain the higher recruitment and turnover rate in the same year.

Mortality

The average mortality rate (1.31% yr^{-1}) of trees ≥ 10 cm DBH was within the range of 1.0 - 2.0% that was reported for tropical forests growing on other Podzols (Spodozols) as shown by (Phillips et al. 2004, Table 3) and for forests in North-eastern Amazonia (Chao et al. 2008). Mortality rates in the plot were lower than for terra firme forests in the same location, although recruitment rates were higher as were turnover rates. These results were not expected given the better soil quality of terra firme forests (Alisol or Cambisol soils).

Tree mortality was variable during the period of measurement as has been found in other studies that examined tropical forests (Condit et al. 1992, Rolim et al. 1999, Rolim et al. 2005). In this case, mortality was measured on an annual basis which offers better insight into the factors that determine

Table 3. Mortality, recruitment and turnover in terra firme (TF) and white sand (WS) Amazonian forests.

Forest	Site	Code	Reference	Monit. period (years)	Soil type	R (%)	M (%)	Turnover	Diameter Growth (cm)
TF	Zafire altura	ZAF TF-Alt	Unpublished data	7	Alisol	0.53	1.56	1.04	0.17 ± 0.01
TF	Zafire Transición	ZAF TR	Unpublished data	8	Cambisol	0.83	1.69	1.26	0.15 ± 0.04
WS	Zafire varillal	ZAF WS	This study	8	Podzol	1.41	1.31	1.38	0.07 ± 0.06
TF	San Carlos	SCR-01	Uhl et al. 1988	10.71	Oxisol	1.73	1.38	1.56	
TF	Manaus		Vieira et al. 2004						0.17 ± 0.02
WS	San Carlos	SCR-02	Veillon 1985	4.01	Spodozol	0.83	0.49	0.66	
WS	San Carlos de Rio Negro, SC3	SCR-03	Heuveldop & Neumman 1983	4	Spodozol	1.72	1.82	1.77	
TF	Jenaro TF		Phillips et al. 2004b			1.14	1.14	1.14	
WS	Centro de Investigaciones Jenaro Herrera	CIJH	Unpublished data	1	Podzol	0.29	0.99	0.64	0.16 ± 0.25
TF	Allpahuayo A, poorly drained	ALP-11	Phillips et al. 2004	10.15	Ultisol	2.72	3.24	2.99	
TF	Allpahuayo A, well drained	ALP-12	Phillips et al. 2004	10.15	Entisol (psamment)	2.02	2.94	2.48	
TF	Allpahuayo B, sandy	ALP-21	Phillips et al. 2004	10.16	Entisol (psamment)	2.97	2.47	2.72	
TF	Allpahuayo B, clayey	ALP-22	Phillips et al. 2004	10.16	Ultisol	2.79	2.32	2.55	
WS	Mishana	MSH-01	Phillips et al. 2004	7.67	Spodozol	1.64	1.86	1.75	

R (%), M (%) and turnover interval corrected (percyr_1) an increase or decrease in mortality and recruitment, and that consequently allow better predictions to be made for the way in which these forests and their species respond to future climate events.

These differences in mortality rates over the years can be attributed to climatic events such as an interruption in the dry or rainy season and by the death of certain species (Lieberman & Lieberman 1987, Swaine et al. 1990, Rolim et al. 1999).

Conversely, annual precipitation trends (Fig. 6) indicate that in the periods from 2008-2009 and 2009-2010 there was an interruption of the dry season; In May 2008, when rainfall is usually low (Avg. 250 mm), rainfall was extremely high, reaching 500 mm and in August 2009, in the middle of the dry season, when rainfall rarely exceeds 110 mm, the precipitation was three times as high, 362 mm. Other authors (Chen et al. 2010, Marengo et al. 2012), also found that 2008 – 2009 was an extremely wet year. Although a very weak correlation (Spearman, 0.32) was found between annual rain and mortality it is believed that irregularities in the season could be a caused increased mortality. For instance, extreme rainfall in this white sand forest with a hardpan at 1 meter depth, causes waterlogging to affect monthly root production of the plot as was demonstrated in this forest by Jiménez et al. (2009). This could also have caused the decline in growth in the same time period.

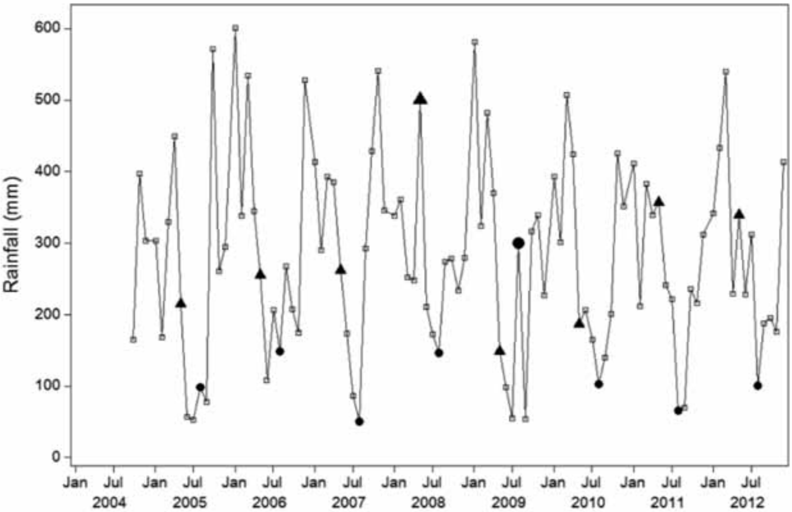


Figure 6. Monthly rainfall values at Leticia – IDEAM (Instituto de Hidrología, Meteorología y Estudios Ambientales de Colombia) - during the time period from Nov 2004-Dec 2012; ▲ May, ● August. The biggest triangle and the biggest circle show anomalous rainfall during those months that interrupted the dry season.

Recruitment

Recruitment rates in the understory are generally twice as high as those in the canopy. This was expected given the differences in the size of the trees, with the exception of 2008 - 2009 and 2009 - 2010 when recruitment rates were similar. This finding suggests that years with a shorter dry season negatively affect the recruitment and growth of trees of this forest especially those with smaller diameters. The number of species recruited was also higher than in the canopy, which indicates that many species are able to reach the 2.5 cm diameter threshold of the understory but fewer are able to reach the threshold of the canopy. This explains the relation of the numbers of dead trees in each category: 97.14 ± 38.89 deaths yr^{-1} in the understory compared to 13 ± 16.97 deaths yr^{-1} in the canopy per hectare.

Contrary to most terra firme forests, recruitment rates were higher than mortality rates, and the rate at Zafire was very high compared to the WS in the Centro de Investigaciones Jenaro Herrera (CIJH) which is located in the Peruvian Amazon. These results are difficult to explain based on diameter increase, because growth rates were very low compared to those in the terra firme and also to that which was found in CIJH.

Modes of death

In general, ‘standing’ may be the most common mode of death in Amazonian forests but it ranges from 13.5% (Chao et al. 2009) in western Amazon in Ecuador to 81% for ≥ 10 cm DBH in the study plot used for this thesis (Table 4). According to Carey et al. (1994), this mode of death suggest environmental stress and the very high percentage found in this study plot could be the result of waterlogging during the rainy season, lack of nutrients and drought in the dry season. However, in this study the most probable cause of the standing mode of death is senescence as has been found by other authors (Chao et al. 2008, Chao et al. 2009, Toledo et al. 2012). This is also in accordance with Toledo et al. (2012) who found that in terra firme tropical moist forests; there was a positive relation between standing mortality and sandy soils in valleys. In addition, Chao et al. (2009) reported that this mode of death was the most common form of mortality in the Eastern Amazon, where soils are generally sandier, poorer and drier than in the Western Amazon and where forests are dominated by hard-wood tree species, which tend to grow slower than species with softer wood. This mode of death is favorable for the growth of seedlings and saplings because the forest understory is less disturbed than when trees die by uprooting or breakage (Yamamoto, 2000). Additionally, this could be considered a strategy to gradually release and slowly bind nutrients of organic matter (Martini et al. 2008) which maintains the species composition of a site and relatively constant modes of deaths through time.

Table 4. Modes of death in terra firme and white sand Amazonian forests.

Reference	Location	Modes of death %		
		Standing	Broken	Uprooted
This study	ZAF/WSF (≥ 10 cm DBH)	81	9.5	5.7
Toledo et al. 2012	Manaus/TFF	54	26	14
Londoño 2011	Caqueta/TFF	28.6	59.3	10
	Caqueta/ Flooded	17.2	42.7	19.8
Ferry et al. 2010	French Guiana /TFF	48	52	
Chao et al. 2009	Venezuela/TFF	48	18	35
	Peru/WS/TFF	13.5	32.6	19.2
Gale & Barfod 1999	Ecuador /TFF	15	35	34

No relationship was found between year and mode of death which indicates that even if more trees died in the 2008 - 2010 period, the proportion of the different modes of death were the same. In contrast, the situation with understory trees showed more broken trees in 2005 which was the year that an extreme drought occurred in the Amazon (Phillips et al. 2009).

Mortality and mode of Death vs. Size Classes

It was found that the number of dead trees was not uniformly distributed among tree size classes nor in diameter or in height, which was most likely due to small numbers (Table 2), as was also found in other forests (Lieberman et al. 1985a, Lieberman et al. 1985b, Lieberman & Lieberman 1987).

Additionally, no relationship was observed between the mode of death and tree size for trees ≥ 10 cm DBH, contrary to reports from other forests (Korning & Balslev 1994, Rolim et al. 1999, Arriaga 2000). However, understory trees showed a positive relationship between lower height classes and the mode of death; smaller trees die more often which could be a response to a very weak or superficial anchorage that impedes proper absorption of water or stem stability.

The turnover rate of common species was lower than the average turnover rate of canopy and understory tree classes. This could be due to the fact that less common species have a constant recruitment but grow and die faster than common white sand forest species do.

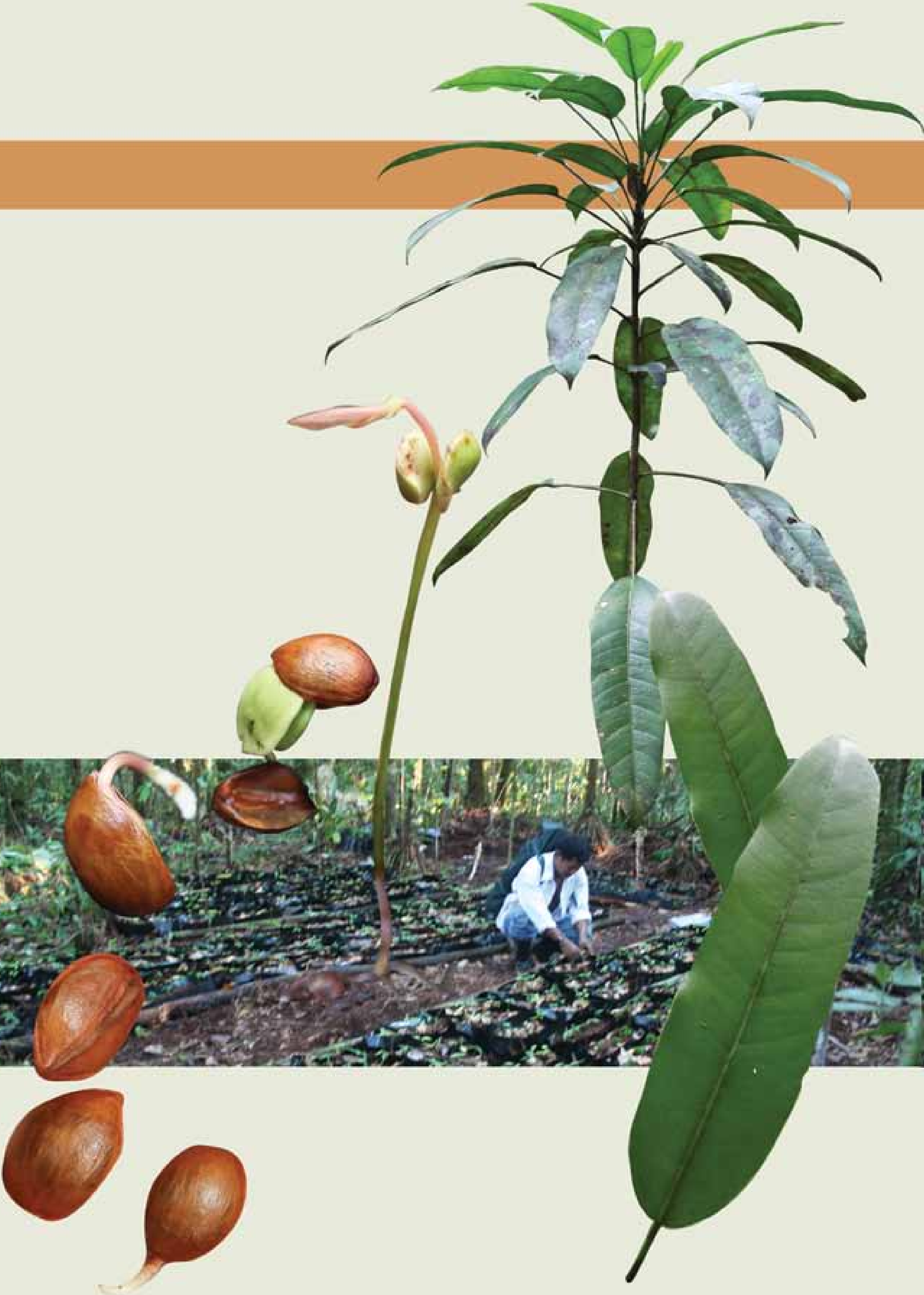
The results of this study show that few species occur in high numbers (are dominant) and therefore their mortality and in some cases recruitment rate determines the rates of the stand. Thus, biotic and abiotic impacts to any one of these species will most likely change the abundance of these species and the dynamics of this forest. In addition, most studies on growth and dynamics have emphasized the ecosystem or forest stand level of ≥ 10 cm DBH stems, instead of individual tree growth patterns. This work highlight the need to develop realistic forest dynamic models based on species as was suggested by Clark & Clark (1999) and da Silva et al. (2002).

These results also have implications for the potential impact of climate change on the tropical forest structure, dynamics and species composition. By using a regional model system to simulate the changes in climate while deforestation occurs, Ramos da Silva and co-authors (2008) predicted that with increases in the rate of deforestation, rainfall would gradually decrease, impacts of El Niño conditions would become more intense in western and southern regions which would lead to large areas with low precipitation and higher temperatures. Additionally, scientists have suggested that forests found in shallow or infertile soils, are more vulnerable to climate change (Malhi et al. 2009, Allen et al. 2010) and palms, particularly *E. catinga* and *M. armata,* growing in these soils could be particularly vulnerable as they may close the stomata and lower their productivity when soil water content drops, as has been shown for other palms (Renninger et al. 2010).

However, predicting changes in the dynamics of different forests types as a response to climate change should be done with care. It may be better to monitor trees that are smaller than 10 cm DBH to observe trends of the key variables that influence forest dynamics

ACKNOWLEDGMENTS

Many people have contributed to the re-census and maintenance of this plot. We especially appreciate the collaboration in the field of Ivan Niño, Adriana Aguilar, Angel Miguel Arcángel, Miguel García and Yessica Gómez. This study was financially supported by the National University of Colombia (2005 census), by RAINFOR group (2006 census) and by Nuffic grant (2007 to 2012 censuses).



CHAPTER 4

EFFECTS OF SOIL CONDITIONS ON THE PERFORMANCE OF TREE SEEDLINGS FROM TERRA FIRME AND WHITE SAND FORESTS – RESULTS OF AN IN SITU EXPERIMENT TRANSPLANTING SOILS AND SEEDLINGS

with Juan David Turriago, Rene Boot and Hans ter Steege

ABSTRACT

White sand forests called varillales in Western Amazon or Amazon caatingas in the Eastern Amazon cover 2.8% of the Amazon basin and 7.8% of Guianas. In the Western Amazon, white sand forests grow on sandy, shallow soils with very low cation exchange capacity, which exerts a triple stress on plants: water-logging during the rainy season, drought in the dry season, and a very low soil nutrient content. To understand how site conditions affect the growth, mortality, leaf dynamics and herbivory of seedlings from white sand forests and terra-firme-clay forests, an in situ experiment was developed near the Zafire Biological Station, Amazonas, Colombia (4º0'21"N y 69º53'55"W), with four replicates of pairs of soils per forest and seedlings from both types of forests. Six species were selected from a white sand forest and six from a terra-firme forest. Ten seedlings per species per replicate, totaling 1920 seedlings, were transplanted. To calculate the relative growth rate in height (RGRH), in foliar area (RGRLA), new leaves (NL) and leaves lost (LL), mortality and herbivory (HB) were measured over a 13 month period. The origin of species and soils were the main factors that affected seedling performance; RGRH was higher in white sand seedlings, independent of the season. RGRH was also higher in white sand seedlings in the dry season. In general, RGRLA was higher in terra firme seedlings and higher in clay compared to sand in the dry season. Terra firme seedlings suffered higher herbivory in any season or soil, and lost more leaves in the wet season. Leaf loss and proportional mortality of seedlings were considerably higher in clay soils during both seasons. Herbivory was higher in sandy soils. The results of this study show that soil type is an important factor that determines seedling performance and hence the species composition of these forests. The results also show that the dry season had a more negative effect on terra firme seedlings than those from the white sand forest. This suggests that white sand seedlings are more resistant to drought, which may be an advantage as the climate becomes drier in the future, as predicted by climate change scenarios.

INTRODUCTION

White sand (WS) forests in the Western Amazon (varillales) are often small areas of low, open scleromorphic vegetation. They generally contain trees of short stature that have thin stems with hard wood, narrow crowns and denser stands, and a few dominant tree species (Duivenvoorden & Lips 1995, Ahuite Reátegui et al. 2003, García-Villacorta et al. 2003, Fine et al. 2010) are imbedded in a matrix of taller, terra-firme forests. White sand forests also lack thick stemmed climbers (Coomes & Grubb 1996) and have an open canopy which allows more light to penetrate to the forest floor, in comparison to other Amazonian forests (Anderson 1981). Terra firme (TF) forests are found in clay soils or clay and brown sandy soils. They are highly diverse (>200 tree species on a 1-ha plot), with trees that can reach 150 cm DBH, and that form a closed canopy that can be up to 40 m tall and a stem density of 600 trees (DBH >10) per hectare that occupy multiple vertical strata (Duque et al. 2002).

White sand forests are usually drained by highly acidic black waters (Anderson 1981, Medina et al. 1990, Duivenvoorden & Lips 1995, Coomes & Grubb 1996, Fine et al. 2004). These forests grow on well-drained, albic arenosols in Guyana (Banki 2010) or on waterlogged quartzite sandy soils classified as Podzols (oxiaquic) (Quesada et al. 2009a, Quesada et al. 2009b, Quesada et al. 2011). During the formation of Podzols, Aluminum, Iron and organic matter transfers from the surface of the soil to greater depths to form chelates that together form a hardpan (Quesada et al. 2011), an impermeable layer of hard rock or hard ferric clay (Medina et al. 1990). This layer restricts drainage and limits root space, which exerts a major influence on plant growth and survival (Schoenholtz 2000).

Consequently, these forests may suffer nutrient stress due to the very low concentrations of minerals and the high acidity of the mineral horizons and, in rainy periods, from water stagnation, which maintains a water table near the surface (Duivenvoorden & Lips 1995, Ruokolainen & Tuomisto 1998). Flooding can lead to soil-anoxia, and when this occurs, the root system may be injured, reduced (Jiménez et al. 2009) or it may die due to starvation from a reduction of carbohydrate reserves induced by anaerobic respiration (Lüttge 2008). It has been shown that seedlings in flooded forests suffer higher mortality, leaf loss and insect herbivory (Mori & Becker 1991, Castaño 2005) although other authors (ter Steege 1994, Parolin et al. 2004, Parolin 2009) have shown that seedlings from species from a flooded forest perform better than those from a terra-firme forest in waterlogged conditions. In the dry season, drying due to the low water holding capacity of sandy soils may periodically result in a drop in the water table below the zone of seedling root penetration (Sombroek 1966, Medina et al. 1990), which increases mortality and decreases growth rates in these plants (Turner 1990, Condit et al. 1995, Veenendaal et al. 1995).

Terra-firme-clay soils are strongly acidic soils, but contrary to Podzols, they have higher cation exchange capacity due to the clays that accumulate in a subsurface horizon. In this area of study, terra firme soils are classified as Alisols (Ultisols in US Soil classification) (Quesada et al. 2011). The available total phosphorus of terra firme soils is high - 250 mg kg^{-1} compared to 25 mg kg-1 in Podzols (Quesada et al. 2010). The presence of a higher percentage of clay reduces percolation. Aluminum or iron chelates do not accumulate in the subsurface horizons, which allow root penetration to deeper soil horizons of 1.5 to 3.5 m (Quesada et al. 2011). These soils do not suffer from waterlogging.

In addition to differences in soil conditions, plant differences between these two forests are evident. Various species of WS species have leaves with abundant schlerenchymatic tissue, thick cuticles (Sobrado & Medina 1980), as well as leaf photo-protection (photo-inhibition by absorbing excess photo-energy under high irradiance stress, which protects photosystem 2) (Sobrado 2008, 2009). It has been observed that soil fertility and water availability strongly determine leaf morphology (Larcher 2003, Gil-Pelegrín et al. 2005). Plants that grow in soils with a certain degree of water deficit, have leaves with a thicker cuticle and foliar reduction, and a consequently low specific leaf area (SLA; ratio between leaf area and leaf mass (cm^2.g-^{1})) (Larcher 2000). A thicker epidermis may reduce herbivory (Fine et al. 2004), which would enhance leaf longevity, reducing leaf loss, thereby reducing the demand for soil nutrients required to replace leaves and increase long term carbon gain in nutrient limited environments (Turner 1994, Cunningham et al. 1999). Thicker leaves are usually smaller, which reduces growth rates (Aerts 1989, Reich et al. 1992, Daws et al. 2005, Hikosaka 2005). Some authors emphasize the role of these defences in the evolution of the white-sand specialist (Janzen 1974, Fine et al. 2004) rather than physiological tolerance to poor soils.

Finally, WS forests have higher light conditions that are thought to contribute to better seedling survival (Augspurger 1984a, 1984b, Palow & Oberbauer 2009), leaf production (Pompa & Bongers 1988, Aide & Zimmerman 1990) and growth (Montgomery & Chazdon 2002).

How soil, origin of species (which means clay or sand specialist following Fine et al. 2004, 2006) or herbivory combined determine the success of seedlings in WS or TF forests is unclear. Therefore, this study has examined the temporal patterns of seedling mortality, growth, herbivory and leaf dynamics in an in situ experiment with WS and TF seedlings in the southern Amazon of Colombia.

Based on the special characteristics of white sand forests species of higher wood and xylem density, higher fine root production and higher leaf toughness which are traits associated to a better tolerance to poorer soils, and also in the differences between clay and sandy soils, it is expected that the seedling survival and growth of white sand species will be higher than those of terra-firme species growing on sandy soils. This will also allow them to grow better than terra firme species when planted in clay soils in a WS forest. Tougher leaves of WS species will live longer no matter whether they grow in clay or sandy soils, and the same trait will offer them more protection from herbivores regardless of whether they are rooted in clay or sandy soils.

In order to test these hypotheses, a reciprocal transplant experiment was developed with species of white sand and terra firme forests.

METHODS

Study Site

The study was carried out at the Zafire biological station near the city of Leticia, State of Amazonas, Colombia 4º 0′ 21″N and 69º 53′ 55″ W. The station is located on the geological sand unit Mariñame in the formerly named Terciario Superior Amazonico (Tsa) (IGAC 1979, Hoorn 1994, Hoorn et al. 2010, IGAC-SINCHI-UM-IDEAM. 1997) which was formed by heavily leached and coarser textured soils that are composed mainly of quartz (Duivenvoorden & Lips 1995). Some authors

(Phillips 2009, Quesada et al. 2009a, Quesada et al. 2011) classified the soils based on the WS forest in which the species grow as Podzols (oxiaquic), and those in TF forests such as Alisol (Appendix 1). Those in TF forests contain more nutrients.

The mean annual rainfall is 3200 mm, the mean annual temperature is 27° C and the rainy season extends from December to May, with a mean monthly rainfall of 324 mm, and a dry season from July to beginning of October in which the mean monthly rainfall is 190 mm (Jiménez et al. 2009). November is a transition month; Relative humidity is high, with an annual average of 86% recorded for Leticia. Precipitation in the study site was recorded during the experiment (Fig.1) which shows that August 2009 was exceptionally wet, reaching 362 mm compared to an average of 107.87 mm (Instituto de Hidrología, Meteorología y Estudios Ambientales de Colombia –IDEAM-).

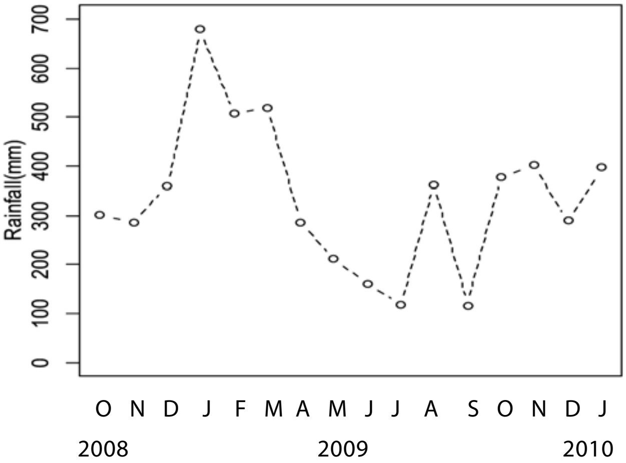


Figure 1. Mean monthly precipitation during the study period (October 2008-January 2010) from the meteorological station of the Vasquez Cobo airport, Leticia (Amazonas, Colombia) IDEAM.

Species selected

Twelve species were selected from two types of forest: a sand forest and a clay forest (Table 1). Species selection was based on work carried out for this thesis (Ch 2) and previously published work (Anderson 1981, Medina et al. 1990, Duivenvoorden and Lips 1995, Coomes and Grubb 1996, Cárdenas 1997, Coomes and Grubb 1998, Duque et al. 2001, Duque et al. 2002, Duque et al. 2003, Honorio et al. 2008, Fine et al. 2010, Stropp 2011), web herbaria (COAH, COL), plus the advice of local people who described such species as frequently found in white sand forest and no other places. In addition, seedling availability of the species at the time of fieldwork was a criterion.

Table 1. Species selected from white sand (WS) and terra firme (TF) forests at the Zafire biological station, Colombia.

Species	Family	Forest	Authors that associate the species with a type of forest
Dicymbe uaiparuensis R.S. Cowan	Fabaceae	WS	Gentry 1993, Garcia Villacorta et al. 2003, Fine et al. 2010
Pachira brevipes (A. Robyns) Alverson	Malvaceae	WS	Gentry 1993, Duivenvoorden & Lips 1995, Garcia Villacorta et al. 2003, Fine et al. 2010
Haploclathra cordata Vásquez	Euphorbiaceae	WS	Duque et al. 2002
Hevea nitida Mart. ex Müll.Arg.	Clusiaceae	WS	Gentry 1993, Garcia Villacorta et al. 2003, Fine et al. 2010, This species was not exclusive of white sands although in the area of study was only present in WS forests
Dendropanax palustris (Ducke) Harms	Icacinaceae	WS	Gentry 1993, Fine et al. 2010
Emmotum floribundum R. A. Howard	Araliaceae	WS	Duque et al. 2002, Fine et al. 2010
Couma macrocarpa Barb Rodr.	Apocynaceae	TF	Different types of forests
Hevea guianensis Aubl.	Euphorbiaceae	TF	Fine et al. 2010, although found in other types of forests
Eschweilera sp.	Lecythidaceae	TF	No Lecythidaceae in Duque et al. 2002 or Fine et al. 2010
Virola pavonis (A.D.C.) AC. SM	Myristicaceae	TF	Duivenvoorden & Lips 1995, Duque et al. 2002, Fine et al. 2010
Brosimum sp.	Moraceae	TF	No Moraceae found in Duque et al. 2002, and there is only one Ficus in Fine et al. 2010
Chrysobalanaceae sp.	Chrysobalanaceae	TF	No Chrysobalanaceae found in Duque et al. 2002 or Fine et al. 2010

Although some Lecythidaceae and Chrysobalanaceae are families associated with Brown sands in the Eastern Amazon, in the Western Amazon they have not been reported in WS forests; see Duque et al. 2002, Fine et al. 2010.

Experimental design

In order to determine the planting distance in the experiment, we measured rooting depth and crown width of 100 seedlings per species (height 10 - 30 cm).

A factorial design with five fixed factors was used: Forest, soil, origin of species, species and block. There were two forests (Terra-firme-T / White sand-W) used, two soils (Clay-C / Sand-S), two origins (Terra-firme-TF / White sand-WS), 12 species (6 from TF and 6 from WS) with ten replicates and 8 block levels (four in each forest type). In each forest, four sites were selected at random and were no more than 20 meters apart (Fig. 2 Top). Each site consisted of a pair of experimental plots of ca. 17 m2 separated from each other by approximately 5 m. In one plot, the area was marked out and the vegetation present was removed to prepare the plot for planting. In the other plot, the original soil up to a depth of 0.5 m was excavated and filled with soil of the contrasting soil type. Soils were carefully transported to maintain their relative position from top to bottom, including the litter. The bottom and sides of the experimental plots were covered with a finely perforated plastic to allow drainage but avoiding lateral in or outgrowth of plants, and the soils were allowed to rest for about 2 weeks before transplanting the seedlings The experimental plots were also covered with a 2 m high frame, to avoid damage from falling branches (Fig. 2 Right bottom). In each experimental plot, seedlings from both forests were transplanted. Seedlings were collected at the same time, taking care that seedlings of similar height for each species were kept together. All seedlings were gathered in black 15 x 8 cm bags 3 weeks prior to transplanting (Fig. 2 Left bottom). Then, ten seedlings per species were transplanted into each experimental site, resulting in 20 (10 and 10) per soil, 80 per forest and a total of 160 seedlings per species in both forests. Thus, at each forest there were four locations of pairs of soil types with seedlings from both types of forest that led to the following origin of species, type of soil, and type of forests seedlings-blocks:

(B1) TF species in clay soil in terra-firme forest (TF-C-T)
(B2) TF species in sandy soil in terra-firme forest (TF-S-T)
(B3) WS sand species in clay soil in terra-firme forest (WS-C-T)
(B4) WS species in sandy soil in terra-firme forest (WS-S-T)
(B5) TF species in clay in white-sand forest (TF-C-W)
(B6) TF species in sandy soil in white-sand forest (TF-S-W)
(B7) WS species in clay in white-sand forest (WS-C-W)
(B8) WS species in sandy soil in white-sand forest (WS-S-W)

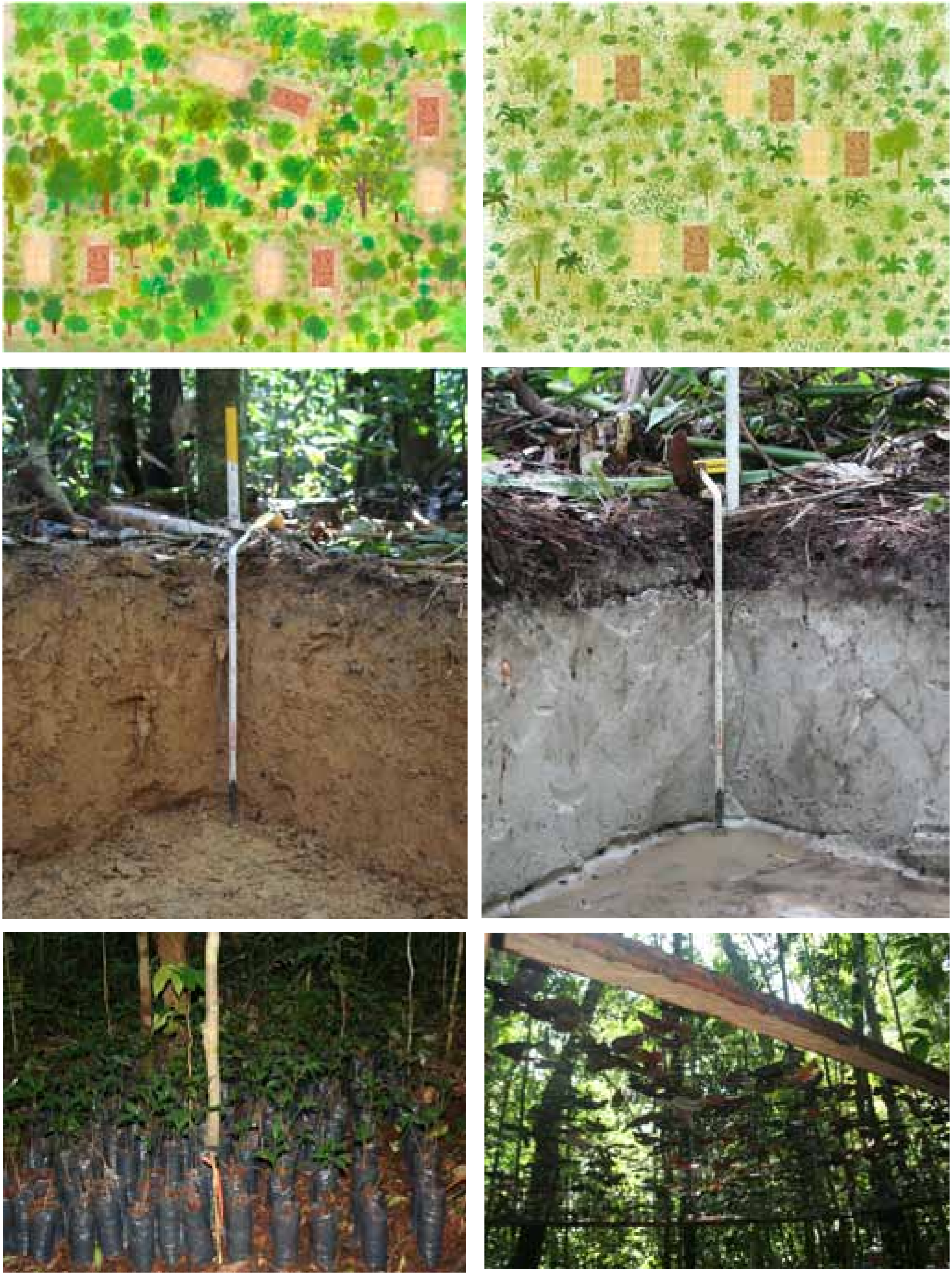


Figure 2. *In situ* experiment: Terra-firme (left) and white sand (right) forests and the four locations: dark squares represent clay soil plots (middle left) and clear squares white sand soil plots (middle right). Bottom left, seedlings collected, and bottom right, wire mesh covering each planting area.

Variables

Relative Growth Rate: The height of seedlings was measured on a monthly basis with a tape measure (± 1 mm). The relative height growth rate RGRH was calculated as:

$RGRH = (\log Ht_2 - \log Ht_1)/(t_2-t_1)$

Where Ht_1 = height measurement at t_1, Ht_2 = height measurement at t_2; t_1 = time of the first height measurement; and t_2 = time of the second height measurement (Benitez-Malvido & Kossmann-Ferraz 1999, Baraloto et al. 2005, Barberis & Tanner 2005).

Growth was also assessed by looking at the relative growth of leaf area RGRLA using $\ln LA2-\ln LA_1/T_2-T_1$ (Barberis & Tanner 2005). Leaf area was measured for all leaves and plants starting in April 2009 by using a Hand-Held Laser Leaf Area Meter CI- 203 (CID Bio-Science, Inc.).

Leaf dynamics (leaf loss and leaf gain): At the start of the experiment, all leaves were carefully marked on the underside with an ultra-fine point permanent marker (Sharpie) and newly produced leaves were marked each time in order to count new leaves produced, or lost. The rate of new leaves was calculated as:

NLR= *Number of leaves produced / Number of leaves* t_1 $(1/t_2 - t_1)$

And loss rate of leaves was assessed as:

LLossR= *Number of leaves lost / Number of leaves* $t_1(1/t_2 - t_1)$ (Shimizu et al. 2006).

Herbivory: Herbivory was estimated by evaluating the percentage of leaf area removed by herbivores or damaged by fungi. Each leaf from every seedling was assigned to one of the following categories of damage (Modified from Benitez-Malvido et al. 2005): 0= intact; 1= 0,1 - 5%; 2= 6 – 25%; 3= 26 - 50%; 4= 51 - 75%; 5= 76 - 100% and for fungus or other pathogens the categories were: A= 0 - 5%; B= 6 - 25%, C= 26 - 50%; D= 51 - 75%; E= 76 - 100% .

Seedling mortality: At every census, each seedling was examined for damage and was classified as dead or alive. A seedling was considered dead when it was completely dried out, when the stem was cut in two showing no signs of living green tissue, or when the whole seedling was missing (Alvarez-Clare & Kitajima 2009). The proportional mortality is the proportion of dead seedlings after the dry or wet season, compared to the number of seedlings alive at the beginning of the season.

Measurements of height, herbivory, leaf loss and leaf gain were taken monthly, for 13 months. Leaf area was measured from April 2009 to the end of the experiment.

The wet season ran from October to the end of May and the dry season from June to September. For the analysis by seasons (wet and dry) of relative leaf area growth and leaf turnover, four months for each season was considered with the wet season running from October to January and dry season from June to September.

Leaf toughness is, in terms of absolute strength, the force needed to puncture a seedling leaf per unit surface area (Edwards et al. 2000). Leaf toughness was calculated by collecting three leaves from 30 seedlings per species (n=1080), using the mean of 3 measurements on each leaf (Li et al. 2009) while care was taken to avoid measuring the major leaf veins. A digital force gauge "penetrometer" (Chatillo E-DFEseries -3lb capacity) was also used. The index is expressed in Newtons per mm^2.

Statistical analyses

Statistical analyses, computing and graphics were performed using the R environment for statistical computing (version 2.14.0) and Minitab® 16.2.3. © 2012 Minitab Inc. To determine the effect of blocks in the analysis, an analysis of the variance on each of the factors was calculated and no significant block effect was found. Therefore, all blocks were pooled together, which resulted in 480 seedlings per treatment.

In addition to analysing the effect of transplanted soils, which means clay soils in WS forests and sandy soil in terra firme forest vs. intact soils clay soil in terra firme forests and sandy soil in white sand forests, we develop an analysis of covariance (ANCOVA) for each of the variables, where the co-variable was the transplanted soil.

Growth data, as well as leaf area, loss and gain of leaves and herbivory at the end of the wet and dry seasons were analyzed by a multifactorial analysis of variance (ANOVA). Growth data was square transformed to improve homogeneity of variance.

Mortality was analyzed as the proportion of individuals that died in the wet and in the dry seasons, relative to the number of seedlings at the beginning and the end of each season, and by conducting an ANOVA analysis. Transformation of the data was required to achieve normality ($1 / X^2$) following (Guisande et al. 2011).

RESULTS

RGRH was considerably different between the two origins of species (Anova, $P< 0.01$), forests $P< 0.01$) and soils ($P< 0.05$). All the species grew better in height when planted in sandy soils in the terra firme forest ($P<0. 001$) (Fig. 3a). White sand seedling-species grew higher, independently of the treatment, than terra firme seedlings.

The RGRH was the only variable that showed a significant effect due to the co-variable transplanted soil ($P< 0.05$); the RGRH in transplanted sandy soils in the terra fime forest is the highest, but in the transplanted clay soils in the white sand forest the average of RGRH was the lowest.

Similar to RGRH the RGRLA was higher in all the species when planted in sandy soils compared to clay soil ($P< 0.001$) and in the terra firme forest ($P< 0.001$) (Fig. 3b right). When planted in clay, WS seedling-species grew slightly better than TF seedlings (Fig. 3b left). The performance of the WS seedling-species was higher in the dry season than in the wet season ($P< 0.05$). We found significant differences in origin in both seasons and lower significant differences between forests in dry ($P<0.01$) and in wet season ($P<0.5$).

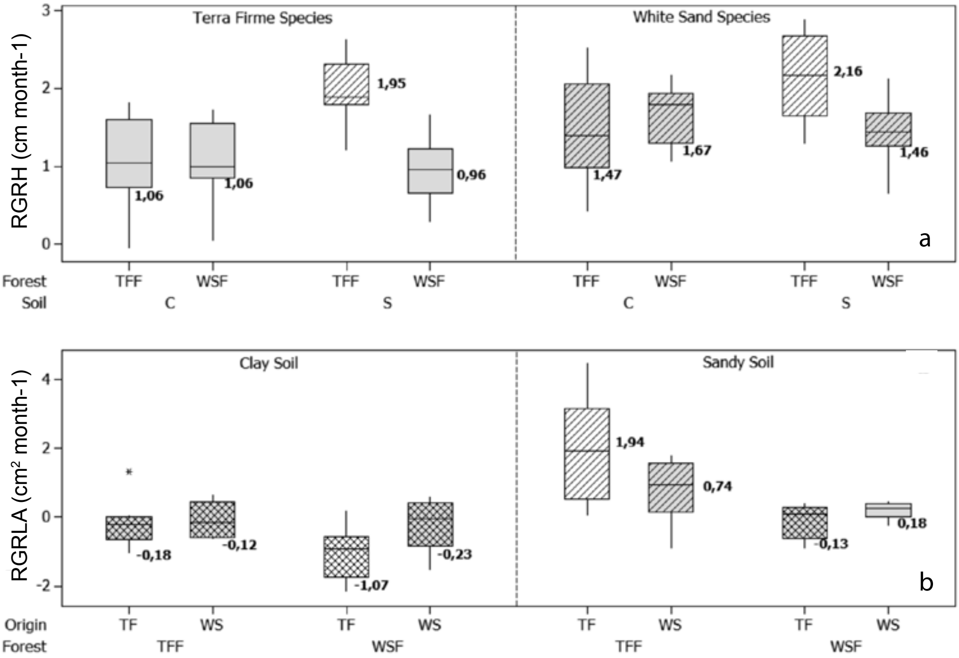


Figure 3. Performance of terra-firme (TF) and white sand (WS) seedling species: **a**) relative growth rate height RGRH and **b**) relative growth leaf area betweenTerra firme forests (TFF) and White sand forest (WSF) in clay (C) and sand (S). Box plots with different colour or hatching correspond to treatments with significant differences (P <0.05).

No significant differences were found in NLR between factors in any season. In contrast, leaf loss was higher in clay compared to sandy soils (P< 0.001) and in the wet season compared to the dry season (P< 0.05) (Fig. 4 top and middle), and between origins (P< 0.05) in the wet season (Fig. 4 bottom).

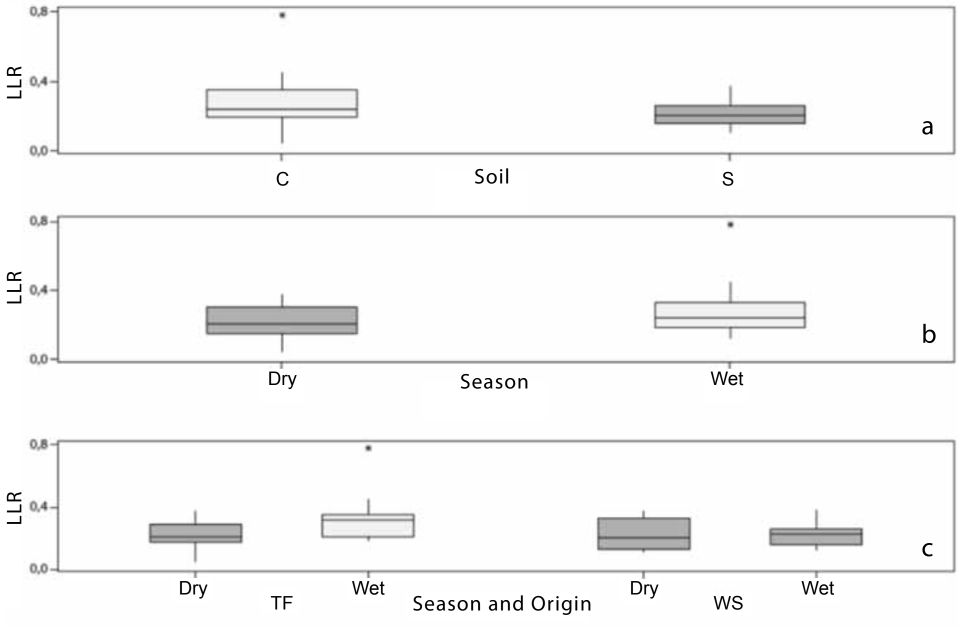


Figure 4. Seedling performance of terra-firme (TF) and white sand (WS) species: **a**) Leaf loss rate LLR in clay (C) and sand (S), **b**) in Dry and Wet season and **c**) the interaction season and origin.

Herbivory rates were significantly different between forest types and were found to be higher in the terra firme forest (Anova, $P< 0.001$) than in the white sand forest. Additionally, terra firme seedling-species suffered considerably more herbivory than WS species (origin factor $P< 0.001$), and the herbivory rate was higher in the wet season than in the dry season (Fig. 5). In relation to soils, herbivory was higher in sandy soils ($P< 0.01$) in the wet season (Fig. 5). Significant differences were found in the origin of species in both seasons, and lower differences between forests in dry ($P< 0.01$) and in wet season ($P< 0.5$).

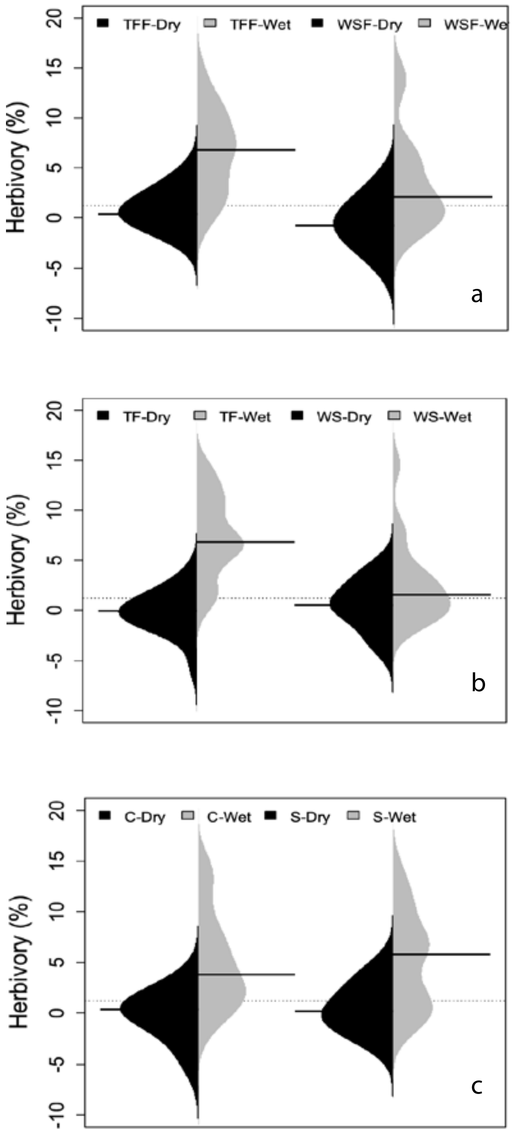


Figure 5. Differences in herbivory in the Dry (black) and Wet (grey) seasons between forest: **a**) Terra firme forest (TFF) and White sand forest (WSF); **b**) between seedlings origin from terra firme (TF) and white sand (WS) and **c**) between soils clay (C) and sand (S).

Seedling proportional mortality did not show differences between seasons, nor forests, or origin of species, although it showed differences between type of soils (Fig. 6). Proportional mortality was significantly higher on clay than on sandy soils (Anova, P<0.001).

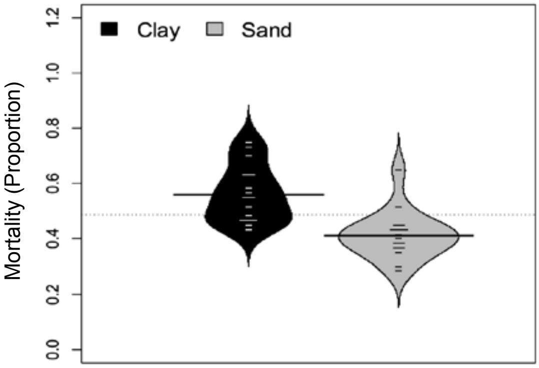


Figure 6. Proportional mortality of seedlings between types of soils clay (black) and sand (grey)

DISCUSSION

The origin of the species and the soil are the two main factors that explain the differences in performance between seedlings in the forests; soil affected seedling mortality, leaf area growth and loss of leaves independent of their origin. Similar results have been reported by other authors (Fine et al. 2004, Stropp 2011).

The results of this study showed a higher growth of white sand seedlings compared to terra firme seedlings regardless of whether they were growing in clay or sandy soils or in white sand or terra firme forests. And both terra firme and white sand seedlings grew better in sandy soil in the terra firme forest. These results were unexpected, given that the extra investment they make in leaf mass per unit area (leaf toughness) has been established as a trade-off between growth rate and defence investment and that Fine et al. (2004, 2006) and Baraloto et al. (2005, 2006) reported lower height growth rates in sandy soils than in clay soils, and clay specialists grew better in clay than in sandy soils, mainly when herbivores were excluded.

Similar to the results from the upper Rio Negro (Stropp 2011) RGRLA was comparable between seedlings' origins, which is a result that is not found in white sand forests in Peru (Fine et al. 2004), where growth rates of terra firme seedlings were higher than white sand seedlings. In addition, it was found that in the dry season, seedlings grew better in clay than in sand, which is similar to the results that Baraloto et al. (2006) and Fine et al. (2004) found in an experiment with contrasting soils. This difference is most likely the result of higher nutrient concentrations in clay soils.

RGRH was also higher in the dry season than in the wet season. This may be due to higher levels of irradiance which is the result of reduced cloudiness (Malhi et al. 2002) or a higher uptake of nutrients, due to increments in root growth during this season (Malhi et al. 2002, Jiménez et al. 2009). Therefore, lower RGRH and RGRLA in the wet season can be the consequence of stress that is imposed by flooding conditions and the lack of mechanisms for resistance to these conditions (Parolin 2001a, 2001b); Baraloto et al. (2005) and Myneni et al. (2007) also showed that the wet season negatively affected seedlings in both types of soils. In Venezuela, few species survived the long-term anoxia in waterlogged white sand soils (Coomes & Grubb 1996).

Given that the transplanted soil had opposite effects on RGRH when seedlings were planted in sandy soil in the terra firme forests compared to those planted in clay in white sand forest, it's difficult to discern if the effect is consequence of the particular combination of soil plus forest type. However, the effect of the soil movement was insignificant for the other variables.

Leaf toughness is associated with leaf production; the tougher the leaves, the higher the costs of production, thus plants with tougher leaves tend to keep them longer. It was found that this trait was significantly different and higher in white sand seedlings (Anova, $P< 0.001$) compared to terra firme seedlings, as was also observed by Fine and co-authors in WS seedlings in Peru (2004, 2006) in (Fig. 7). In this study, it was found that all species lost fewer leaves in sandy soils. As expected, plants growing in poor soil tended to keep their leaves longer than those growing in nutrient rich soil, due to the high cost of forming new ones (Engelbrecht & Kursar 2003, Eichhorn et al. 2010). Loss of leaves was higher in the wet season (waterlogging conditions), as has been reported by other authors (Parolin 2001b, 2009).

Higher leaf toughness is also related to lower growth rates (Fine et al. 2006). Seedlings that invest more in leaf toughness spend energy and nutrients that cannot be used for growth (Herms & Mattson 1992, Baraloto et al. 2006). RGRH was higher in these seedlings, however leaf toughness (sclerophylly) has been associated with oligotrophic soil and dry conditions; it reduces transpiration rates (Turner 1994), this could explain the higher leaf loss of terra firme seedlings.

Finally, leaf toughness is associated with a mechanism to avoid herbivores (Coley 1983, Baraloto et al. 2006, Fine et al. 2006). Thus, the observations made of lower rates of herbivory in WS seedlings are in agreement with observations from Fine et al. (2004). The data from this study differs from the study by Stropp et al. (2013) who found higher leaf toughness and similarities between terra firme and white sand seedlings in Içana, Rio Negro and no differences in herbivory rates, probably because leaf toughness in this case is a response to drought and not to herbivores in that region (Medina et al. 1978).

Herbivory is higher in the wet than in the dry season in both types of forests and both types of soils and is higher in terra firme than white sand seedlings. Therefore, in future climate scenarios that predict less rain, herbivory rates may decrease which would enhance growth in leaf area or height.

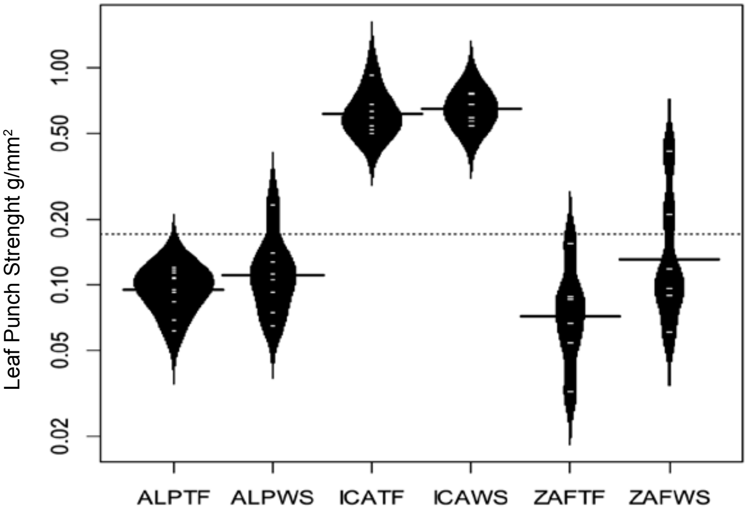


Figure 7. Leaf punch strength between types of soils in three different locations in the Amazon (TF=terra-firme seedlings, WS=white sand seedlings) ALP=Allpahuayo Mishana, Peruvian forest (Fine et al. 2004); ICA=Upper Rio Negro, Brazilian Upper Rio Negro forests (Stropp 2011) and ZAF=Zafire Colombia, this study)

Soil was an important factor in seedling mortality which was higher in clay than in sandy soils, and could be related to the higher leaf loss in clay soil. Although herbivory is often associated with mortality (Fine et al. 2004) no clear relationship was found between them. Herbivory was higher in sandy soils than clay soils but mortality showed the opposite result. Perhaps herbivory had less effect on the survival of species in this experiment than Stropp et al. (2013) found in upper Rio Negro, given that their toughness was very similar, as was also observed in seedlings in an experiment in flooded forests (Castaño 2005) in the Amazon.

ACKNOWLEDGMENTS

We would like to thank the field collaborators of the indigenous community of the *Kilómetro seis*, especially Sara Flores who helped us in the initial identification of the seedlings, to Edilberto Ribero and many other field assistants who dug pits and transported the soil between pits. We would also like to thank the assistants Magnolia Restrepo and Carolina Rivera for their collaboration with the planting at the beginning of the experiment. This study was supported by a Nuffic grant NPT-100 - and a supplemental research grant from Colciencias for young -researchers to J.D.Turriago.

Appendix 1

Soils data of the main chemical features in the White sand and terra-firme forest in the study site, adapted from Quesada et al. 2010.

Forest	Soils	POrg	PTotal	N	C	C:N	Ca	Mg	K
WS	PODZOLS	5.68	25.65	0.11	2.43	22.03	0.25	0.2	0.14
TF	ALISOLS	8.44	31.44	0.1	1.51	15.77	0.06	0.06	0.07

Forest	Soils	Na	Al	SB	IE	pH	sand	clay	silt
WS	PODZOLS	0.05	0.07	0.64	0.71	4.27	74.75	0.64	24.61
TF	ALISOLS	0.05	2.35	0.24	2.6	4.13	58.05	20.25	21.7

SB Sum of bases, IE cation exchange capacity.


5
4
20
21
6

CHAPTER 5

DROUGHT RESISTANCE OF RAINFOREST TREE SEEDLINGS FROM WHITE SAND AND TERRA FIRME FORESTS

with Juan David Turriago, Rene Boot and Hans ter Steege

ABSTRACT

White sands in the Amazon have been described as the most nutrient poor soils in the world. The vegetation growing in these soils is rich in endemics and many species have high leaf toughness and high xylem and wood density which are traits that have been associated with drought tolerance. During a 13 month study, an *ex-situ* experiment was used to examine the growth and mortality of seedlings from different forest origins. White sand and terra firme forests that had been exposed to drought conditions were compared to determine how their performance would differ under both drought and natural conditions. The experiment contained 5 beds filled with clay, 5 with sand, and 720 transplanted seedlings of 12 tree species, 6 from a terra firme forest and 6 from a white sand forest. The tree seedlings from white sand and terra firme forests reacted differently to drought, although they did not show significant differences in growth (height or leaf area) between origins. Leaf loss was higher in the white sand seedlings growing in clay compared to sand. Mortality was higher in terra firme seedlings when growing in clay under drought conditions. Performance between seedlings was very different under both conditions in all variables: growth, leaf area, stems volume and mortality. Under drought conditions, seedlings used the limited water supply to produce leaf area rather than height. Stem volume and mortality were affected by soil water content. White sand seedlings produced leaves and grew for longer periods, and had higher survival rates than terra firme seedlings. These findings suggest that white sand seedlings are more resistant to drought and that the growth of the tree species studied is highly affected by soil water content. Differences in the composition of white sand forests and terra firme forests can be explained in terms of drought resistance.

INTRODUCTION

Tropical rain forests generally have high amounts of precipitation throughout the year. However in most forests, there is a dry season with less rain which subsequently causes a decrease in soil water content that may negatively affect plant performance (Bonal et al. 2000, Harris et al. 2004, Kursar et al. 2005, Renninger & Phillips 2011).

Moisture availability in tropical forest soils is one of the main factors that influence plant growth (Parolin 2001b, Tyree et al. 2003) and mortality (Veenendaal et al. 1995, Whitmore 1998, Engelbrecht & Kursar 2003, Tyree et al. 2003, Daws et al. 2005, Poorter & Rose 2005, Slot & Poorter 2007). Substantial changes in soil water availability may exert significant effects on the vegetation, which would induce the presence of different species that are more resistant or adapted to particular soil conditions.

In the Amazon, plants respond to seasonality in precipitation, soil water content and irradiance (Myneni et al. 2007, Renninger et al. 2010). The length of the dry season can affect the successful regeneration of shallow rooted tree species as their seedlings are exceptionally vulnerable to drought (Poorter & Hayashida-Oliver 2000, Gilbert et al. 2001, Slot & Poorter 2007).

A period of ten consecutive days of drought in the wet season can cause a strong decline in pioneer species growing in natural canopy gaps (Bonal et al. 2000, Bonal & Guehl 2001) in deciduous and evergreen species. Parolin (2001b) observed a significant loss of leaves and only a limited production of new leaves, which indicates that drought can affect the establishment of seedlings in the dry season. Some seedlings have a high tolerance for drought events, and their mortality rates are not increased (Engelbrecht & Kursar 2003).

Seedling tolerance to drought has been associated with high wood density. Drought tolerant seedlings tend to have thinner and more compact conducting vessels that increase resistance to cavitation and xylem embolism (Hacke et al. 2001, Pedrol Bonjoch et al. 2003, Vilagrosa et al. 2003). A dense root system improves water uptake and permits better rehydration after drought (Vilagrosa et al. 2003). Leaf sclerophylly is another feature that is associated with leaf toughness and a low specific leaf area (SLA) (Medina et al. 1978). In very dry areas, plants do tend to have small sclerophyll evergreen leaves. These leaves reduce transpiration rates (Turner 1994) and conserve water. Leaf shedding is another strategy for avoiding water loss through transpiration; however this is at the expense of sustained growth (Poorter 1999, Poorter & Hayashida-Oliver 2000).

In the Amazon, a significant decrease in annual rainfall, larger inter-annual differences, a longer and more severe dry season and lower soil moisture are predicted to be the result of climate change (Hulme & Viner 1998, Whitmore 1998, Hulme et al. 1999, Timmerman et al. 1999, Phillips et al. 2004, Malhi et al. 2009). The changes in intensity and duration of the dry season will favour seasonal forests (Malhi et al. 2009). Thus, it is expected that species with traits that help them to tolerate desiccation are more likely to survive, or perform better than those lacking these traits.

White sand (WS) areas are arguably the most nutrient-poor soils in the world (Janzen 1974), and are associated with highly acidic black water rivers (Janzen 1974, Frasier et al. 2008). In the Western Amazon, the soils are frequently flooded, due to the presence of hardpans, or they dry out due to their low water retention capacity (Duivenvoorden & Lips 1995, Williams et al. 2002). The flora of the white sands is rich in endemics (Anderson 1981, Fine et al. 2004, Fine et al. 2010) and contains many species with high leaf toughness (Fine et al. 2006, This_study chapter 4). These forests also have species with dense wood and xylem (Agudelo 2006, Patiño et al. 2009) and low specific leaf area (Turriago & Villanueva 2008).

At this point, it is important to ask the question of whether species in WS and TF forests grow, gain or lose leaves, resist less or if they experience more herbivory and survive better in their own forest type, when subjected to drought. An *ex-situ* experiment was conducted with 10 blocks; five with clay soil and five with sandy soil and the 10 blocks contained 6 individuals of 12 species; six from a TF forest and six from a WS forest.

It was expected that the WS forest species would perform better under drought conditions given the characteristics associated with leaf toughness. It was also expected that plants would perform better in clay than in sand, given the capacity of clay soils to provide water for a longer period of time.

To evaluate differences between seedling performance under natural and experimental drought conditions, the following questions were asked: Are there differences in the relation between soil water content and seedling performance in two types of Amazon forest seedlings and soils, under natural and drought conditions? In addition, are there significant differences in growth and leaf dynamics under natural and drought conditions among seedlings from different forest types?

METHODS

Study site

The study was conducted in the Zafire Biological Station (04º01 26 S, 69º91 47 W) Fig.1. The area has a mean annual rainfall of approximately 3400 mm, with a dry season from June to September, and a wet season from the end of October to May.

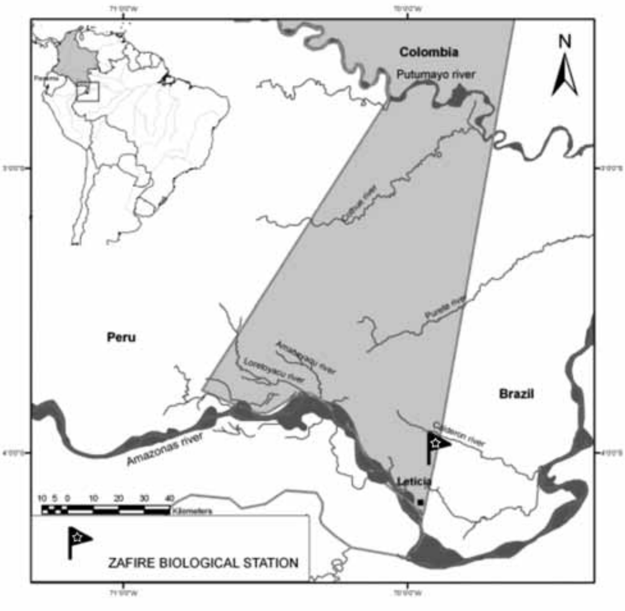


Figure 1. Location of the Zafire Biological Station

Study species

Twelve species were selected for the study; six from white sands (see chapter 2) and six non-specialists of white sands, common in terra firme clay-soil forests (Table 1).

Table 1. Species selected for the experiment, six from white sand and six from terra firme forest.

Species	Family	Forest
Dicymbe uaiparuensis R.S. Cowan	Fabaceae	WS
Pachira brevipes (A. Robyns) Alverson	Malvaceae	WS
Haploclathra cordata Vásquez	Euphorbiaceae	WS
Hevea nitida Mart. ex Müll.Arg.	Clusiaceae	WS
Dendropanax palustris (Ducke) Harms	Icacinaceae	WS
Emmotum floribundum R. A. Howard	Araliaceae	WS
Couma macrocarpa Barb Rodr.	Apocynaceae	TF
Hevea guianensis Aubl.	Euphorbiaceae	TF
Eschweilera sp.	Lecythidaceae	TF
Virola pavonis (A.D.C.) AC. SM	Myristicaceae	TF
Brosimum sp.	Moraceae	TF
Moraceae sp.	Moraceae	TF

Drought experiment

A factorial design with fixed factors was used: The factors were soil, origin of species, species and beds; two soils (Clay-C / Sand-S), two origins (Terra-firme-TF / White sand-WS), 12 species: (6 species from TF and 6 from WS) and ten replicates. Ten soil beds (dimension 3.5 x 0.5 x 0.5 m, and 0.5 m from the ground) were built in the open area of the Zafire Station. Five were filled with clay from a TF forest and five with sand from a WS forest. In each bed, six individuals per species were planted for a total of 72 seedlings per bed and 720 in the experiment. Beds were covered with a transparent plastic roof covered with palm leaves (Fig. 2).

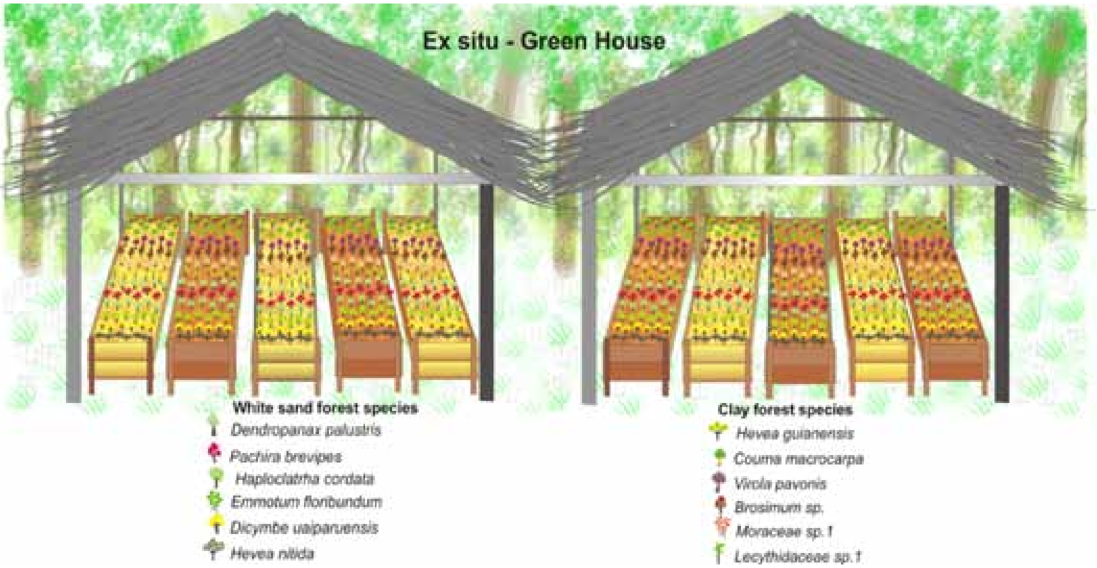


Figure 2. Drought experiment conducted at the Zafire Biological Station in Colombia. Five beds with clay-soil and five with sandy-soil; six individuals of 12 species, six from terra firme and six from white sands, in all beds.

Approximately 100 seedlings per species were collected and kept in bags with their own soil until the moment of transplanting and 60 of each species were planted (360 in sandy and 360 in clay soil). The experiment was initiated in November, 2008 which was a period of transition between the dry and the rainy season. After transplantation and during the first two months, the seedlings were watered and allowed to establish. Thereafter, they were no longer watered and monthly measurements of height, leaf area, leaf loss and survival were taken during a 13 month period. Leaf area was measured for a period of nine months starting in April, 2009.

Comparing Natural vs. Drought Conditions

To compare plant growth under natural and drought conditions, data from seedlings planted into their own soil origin was used; WS forest seedlings in sand and TF forest seedlings in clay. Thus eight plots contained seedlings in natural conditions: four blocks were in terra firme-clay soils, and four were in the white sand forests, thus in sandy soil. In each block, 40 seedlings of six species from each type of forest were transplanted into their own soil-forests for a total of 240 seedlings in each forest-soil type and a final total of 480 seedlings. These seedlings were compared to the 360 that were planted in the drought experiment, the 180 terra firme seedlings in clay soil (36 per bed) and the 180 white sand seedlings planted in sandy soil.

Variables

Soil volumetric water content (Θ)

Every two months, soil samples were collected from each plot and bed. These were undisturbed soil samples taken with an AMS soil Core Sampler that had a hammer attachment. The samples were in removable aluminum liners that were 2”Wx 4”L. The liners were packed in plastic zipper bags and transported to the Natural products Laboratory at the National University in Leticia where they were weighed fresh and oven dried at 105° C for 24 hours or more and then weighed once again when they were completely dried.

Thus, the water content was calculated to be Θm, with the mass of water expressed as a percentage of the mass of the solid phase, after being oven-dried.

$$\Theta m = \frac{\text{mass of water}}{\text{soil oven dry mass}} * 100$$

Then the volumetric water content (Θ) was calculated for which the bulk density (Bd = dry weight of soil per unit volume of soil (g/cm^3)) was calculated following the formula:

$$\Theta = \Theta m * \frac{\text{Bd}}{\text{density of water}} \quad \text{(Brady \& Weil 1999)}$$

Relative Growth Rate (RGR)

Plant height was measured monthly with a tape measure (± 1 mm). The RGR was calculated in height as:

$\mathrm{RGRH} = (\log Ht_2 - \log Ht_1)/(t_2 - t_1)$

Where Ht1 = height measurement at t_1, Ht_2 = height measurement at t_2; t_1 = time of the first height measurement; and t_2 = time of the second height measurement (Benitez-Malvido & Kossmann-Ferraz 1999, Baraloto et al. 2005, Barberis & Tanner 2005).

Growth was also assessed in relative increments of leaf area RGRLA:

$LA_2\text{-}LA_1/T_2\text{-}T_1$ (Barberis & Tanner 2005).

Leaf area was measured for all leaves and plants since April, 2009 by using a Hand-Held Laser Leaf Area Meter CI- 203 (CID Bio-Science, Inc.).

Leaf loss

At the start of the experiment, all leaves were carefully marked with an ultra fine point permanent marker (Sharpie). The rate of leaf loss was assessed as:

LLossR= *Number of leaves lost / Number of leaves* $t_1(1/t_2 - t_1)$ (Shimizu et al. 2006).

Seedling mortality

At every census, each seedling was examined for damage and classified as dead or alive. A seedling was considered dead when the stem was completely dried, and no new leaves were produced, or when the whole seedling was missing (Alvarez-Clare & Kitajima 2009).

Stem volume

The stem diameter was measured at the base (Db) and top (Dt) of the stem, and the stem volume was calculated by the formula:

$$V=\frac{\pi L}{12}\left(Dt^2+Dt * Db+Db^2\right) \text{ were L is the stem lenght (Poorter \& Markensteijn 2008)}$$

Statistical analyses, computing and graphics were carried out in the R environment for statistical computing (version R 2.15), with exception of graphics 3, 7 and 9 that were developed in Minitab 16.1. Differences in volumetric water content (θ) between drought and natural soils were analyzed with a paired t test. The relation between (θ) and mortality was assessed by means of simple regressions using relative mortality. In the drought experiment, water content (θ) showed a normal distribution, whereas in natural conditions they were transformed (x^2) to obtain normality.

To determine the effect of the blocks in the analysis, an analysis of variance was calculated for each of the factors and no significant block effect was found. Thus, all blocks were pooled together, which resulted in 180 seedlings under drought conditions and 240 in natural conditions.

To determine the differences of the parameters RGRH, RGRLA, Leaf loss for seedlings with a different origin and soil, under drought and also between treatments, a Mann-Whitney test was used. An ANOVA was used to test for the differences of herbivory for seedlings with a different origin and soil and also between treatments.

RESULTS

Volumetric water content (θ)

No significant differences in water content were found between clay and sand under natural conditions, but significant differences were found under drought conditions ($P= 0.000$; $\alpha = 0.05$), and between treatments. In clay soils, the highest values were found under natural conditions with a low variance (0.75 -0.82 g*cm^{3}), whereas in sandy soils the variance was higher (0.56 -0.95 g*cm^{3},) but most values were closer to the average.

The volume of water in soil consistently followed a cubic relation for the treatment in natural conditions and a negative linear decline under drought conditions (Fig. 3). The highest values of water content (θ) were found between August and September for sands in the WS forest and in October for clay in the TF forest. Thereafter, a drop off occurred, especially for the seedlings growing in sand. The negative regression was consistent throughout the year of the drought experiment (r = 0.95 for both soils) although in sandy soil the θ was 1 g*cm^{3} lower than in clay soil. In January 2010, the lowest θ values for clay soil (0.86 g*cm^{3}) was observed and in December 2009 the values were lower than 0 gr*cm^{3} for sandy soil.

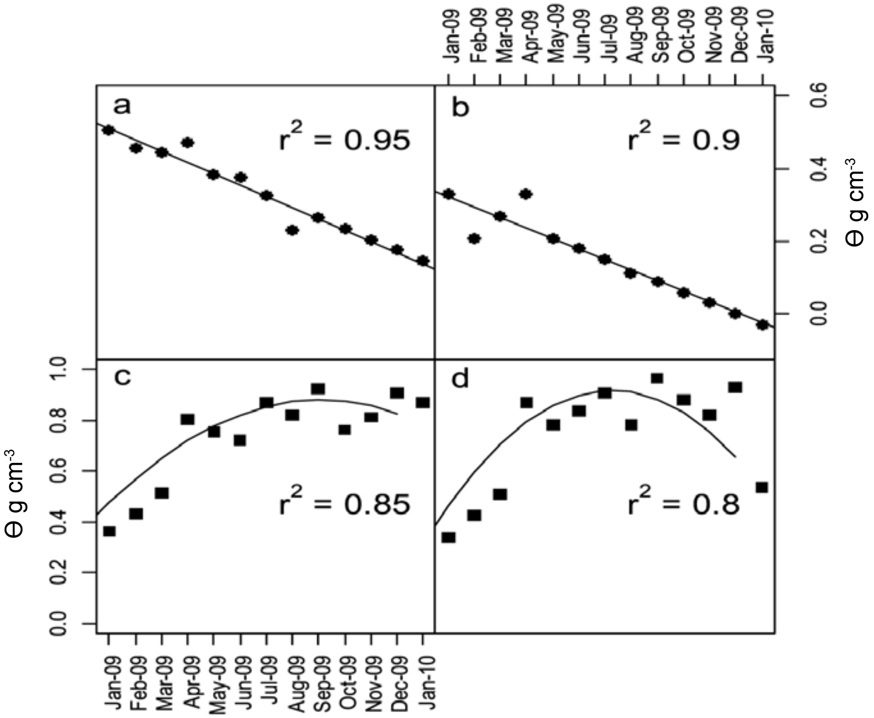


Figure 3. Soil volumetric water content (θ) in clay and sandy soils over time, under two different conditions: graphs **a** and **b** show clay and sandy soil under drought conditions respectively, **c** and **d** under natural conditions.

Natural vs. Drought Conditions

RGRH (Fig. 4a) was significantly lower in drought than in natural conditions (P< 0.005). Contrary to the growth in height, the relative growth rate in leaf area RGRLA (Fig. 4b) was significantly higher in drought than in natural conditions (P< 0.05).

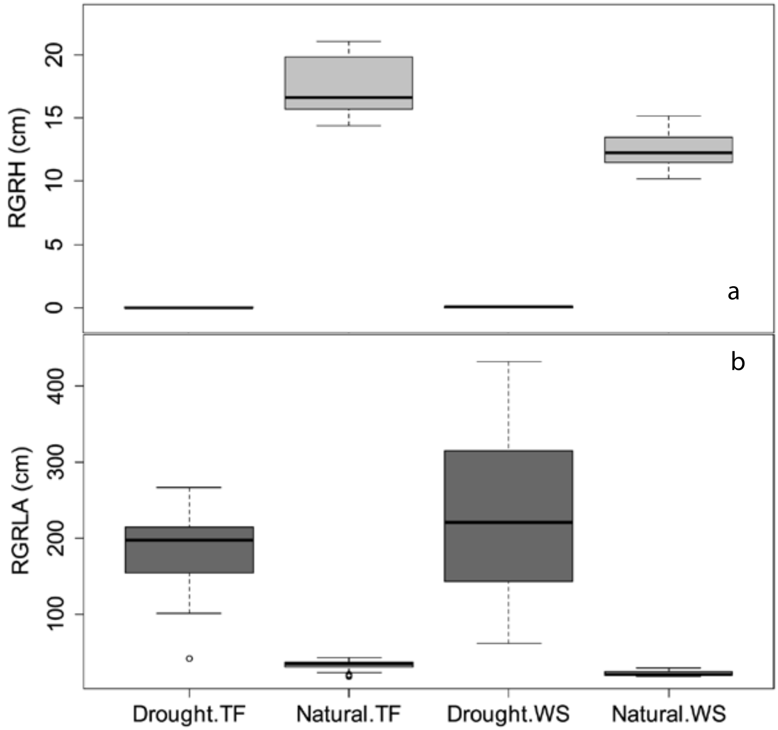


Figure 4. **a** Relative growth rate in height (RGRH) and **b** relative growth rate in leaf area (RGRLA) by origin terra firme (TF) and white sand (WS) seedlings in drought vs. natural conditions.

Stem volume was the highest under drought conditions for both seedling origins. In addition, significant differences were observed between seedling origins under drought conditions (vol = 45.41 cm^3 month^{-1}) and under natural conditions (vol = 18.52 cm^3 month^{-1}). Stem volume was the highest in terra firme forest seedlings regardless of the treatment (Fig. 5) (P< 0.05), mean = 139.63 cm^3 month^{-1} and 87.09 cm3 month-1 under drought and natural conditions respectively.

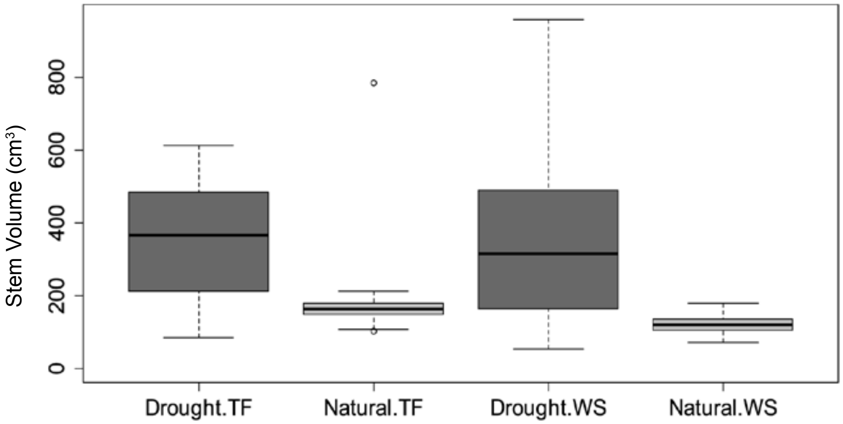


Figure 5. Stem volume by origin: terra firme (TF) and white sand (WS) seedlings, in drought vs. natural conditions.

Under drought conditions, the highest values in stem volume were observed in October for terra firme seedlings (193.601 cm*3* month-*1*) and for white sand seedlings (78.10 cm*3* month-*1*). In natural conditions, the maximum values were registered in August for both TF (97.93 cm3 month-1) and WS (25.03 cm*3* month-*1*) seedlings (Fig. 6).

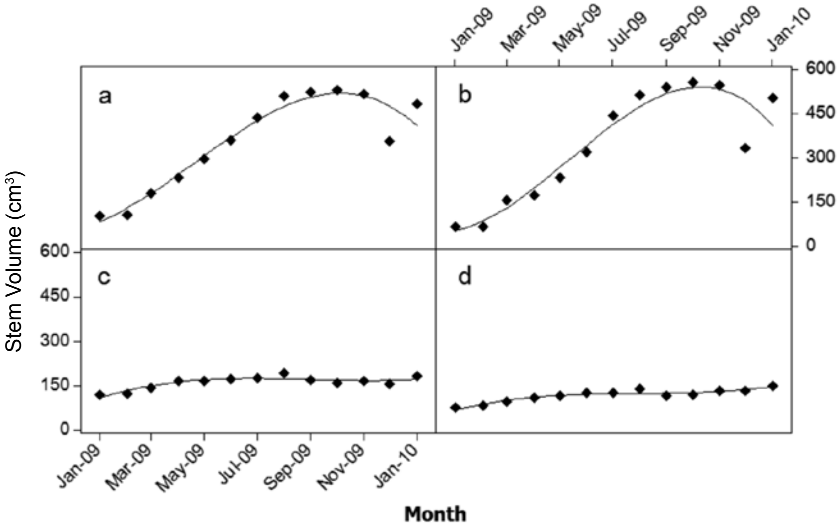


Figure 6. Stem Volume (cm^3) through time. Drought experiment (**a** and **b)** **a**. Terra firme seedlings in clay, **b**. White sand seedlings in sand; under natural conditions (**c** and **d)** **c.** Terra firme seedlings **d**. White sand seedlings.

Proportional mortality did not show statistical differences between TF seedlings or WS seedlings under different treatments (Fig. 7). As expected, dead seedlings had been accumulating over time, but near the end of the experiment, more dead seedlings were found under natural than under drought conditions.

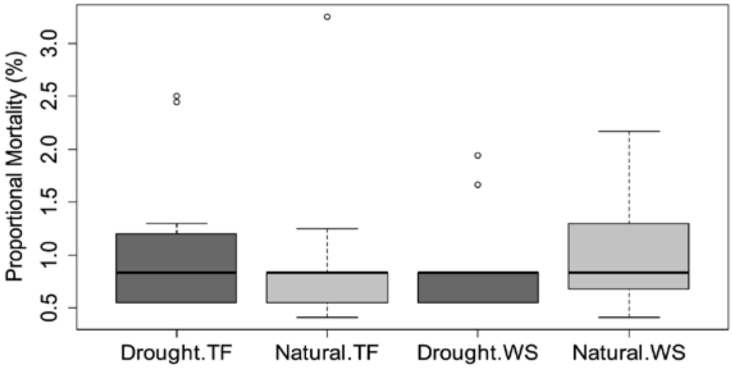


Figure 7. Proportional mortality in drought vs. natural conditions.

Over time, differences between treatments were also found, showing that in the drought experiment most deaths occurred at the beginning and at the end of the experiment, whereas in natural conditions it was relatively consistent (Fig. 8).

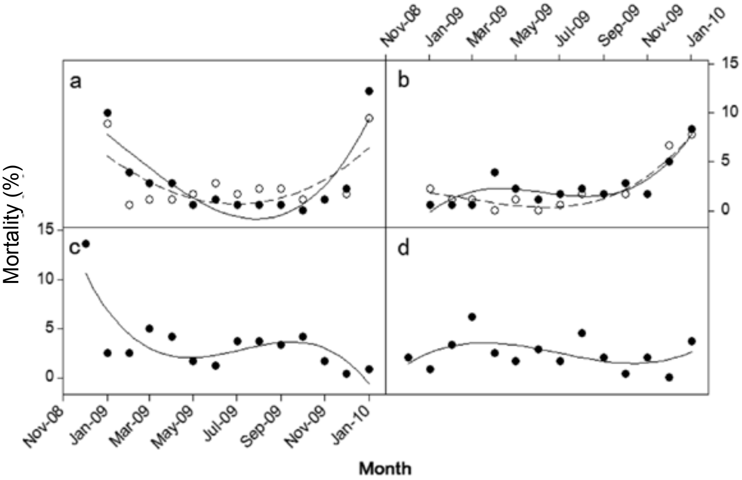


Figure 8. Mortality over time by treatments. Drought experiment (**a** and **b**), (**a**) shows TF seedlings planted in clay *block dots and solid line*, and in sand *circles and dotted line*. (**b**) shows WS seedlings in clay and sand, (**c** and **d**) In natural conditions TF seedlings in clay and WS seedlings in sand respectively.

A strong correlation was found between water content and mortality, with the highest mortality rates shown when soils had greater water saturation under natural conditions and also when soil water was very low under drought conditions.

Total herbivory was significantly higher ($P< 0.005$) under natural conditions for both types of seedlings (Fig. 9a), and also when considering soils. However, there were no significant differences in the herbivory by soil within each condition (Fig. 9b).

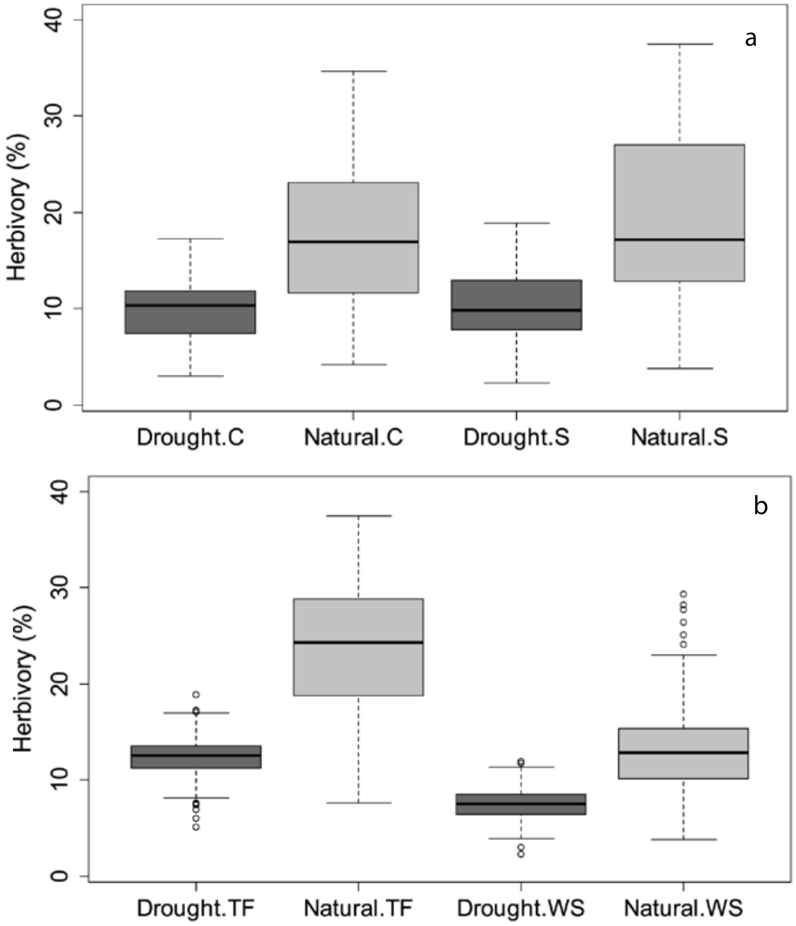


Figure 9. Herbivory of TF and WS seedlings **a** and in clay (C) or sandy (S) soils **b** in drought vs. natural conditions.

Within the Drought Experiment

Although the trends over time showed that seedling growth was different between origins, especially when growing in sand, RGRH did not show significant differences among TF species that were growing in sand or clay, nor in seedlings from the WS forest species that were growing in clay or sand (P> 0.05) (Fig. 10).

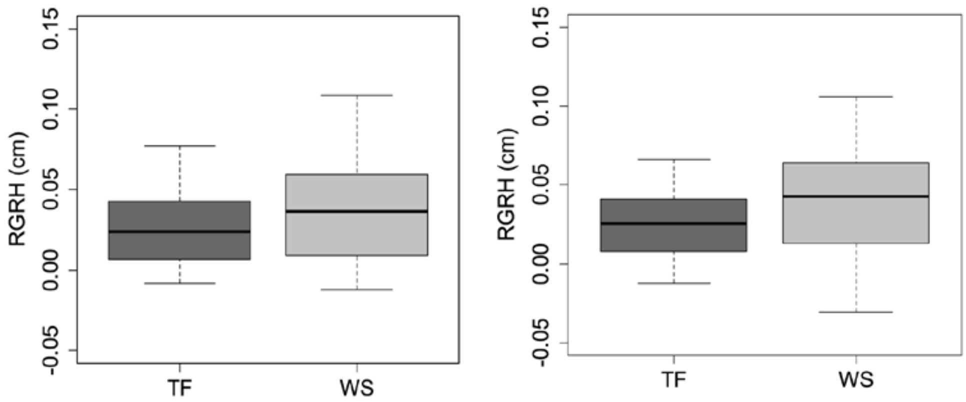


Figure 10. RGRH between origins when growing in clay (left) and sand (right).

RGRH was the highest at the beginning of the experiment from January to April; from that moment, growth rates declined rapidly (Fig.11 Left). RGRLA did not show significant differences between seedling origins, although TF seedlings grew better than WS seedlings when planted in clay, and WS seedlings grew better than TF seedlings when growing in sand (Fig.11 right). However, both TF and WS seedlings grew better in sand (Fig.11 c and d).

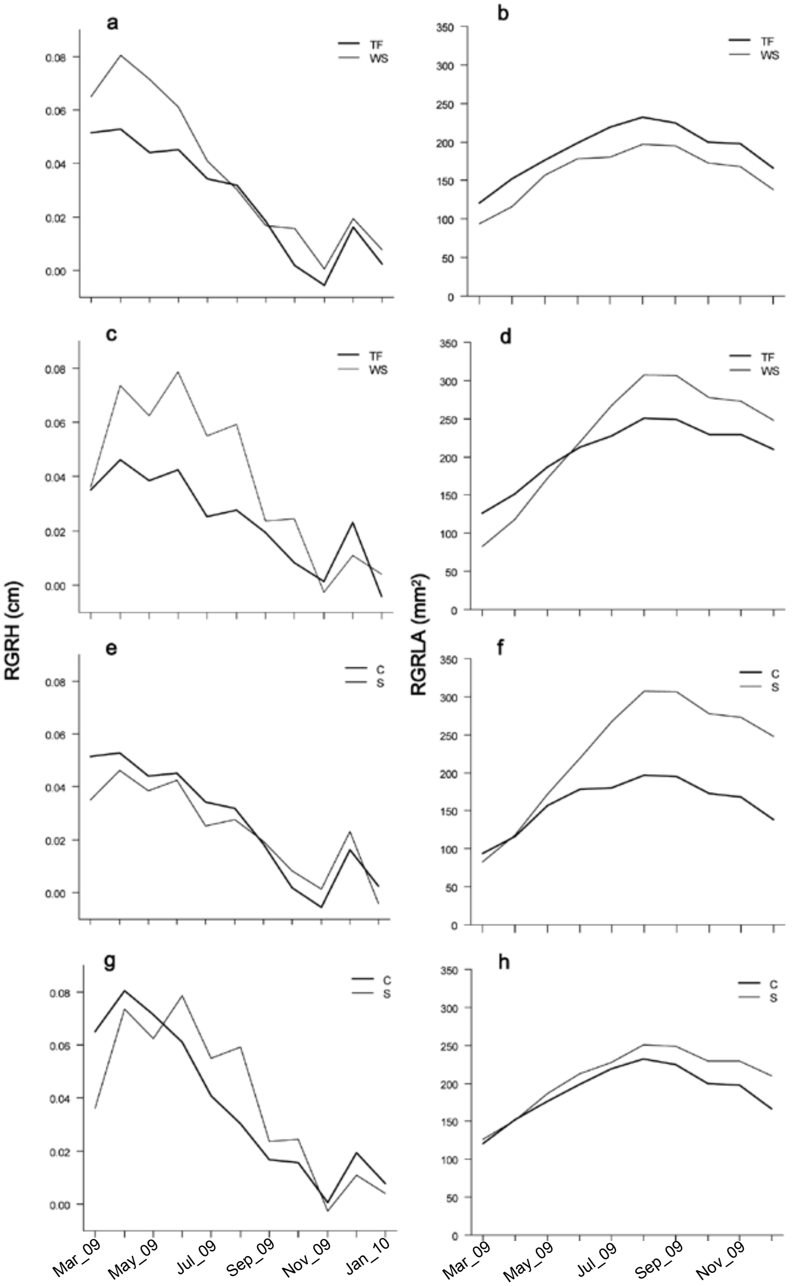


Figure 11. Trends over time for RGRH (left) and RGRLA (right) for TF and WS seedlings under drought conditions, growing in clay (**a** and **b**) and sandy (**c** and **d**) soils. Comparing the performance of TF seedlings (**e** and **f**) and WS seedlings (**g** and **h**) growing in both types of soils.

Differences observed in leaf loss showed that TF seedlings lose significantly more leaves than WS seedlings when growing in sand, but no differences were found when growing in clay. In turn, WS seedlings lose more leaves in clay soil compared to sand (P< 0.05) (Fig. 12).

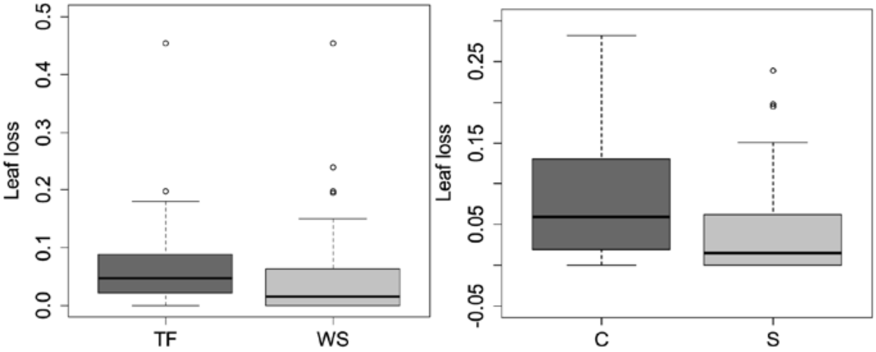


Figure 12. Leaf loss under drought experiment of TF and WS seedlings (Left), when growing in different soils (Right).

Proportional mortality showed that TF seedlings died significantly more than WS seedlings when growing in clay soils (P< 0.05).

Herbivory was significantly higher in TF seedlings compared to WS seedlings (P< 0.005) (Fig. 9 a, b) and no differences in TF seedlings were observed when rooted in sand or clay soil. A slight difference but not significant, was observed in WS seedlings when rooted in clay or sand, with the result being higher in clay.

DISCUSSION

The performance of seedlings, independent of origin or treatment, showed a significant relation to soil water content being in excess or in short supply. During the wet season, under natural conditions, sandy soils showed slightly higher water content than clay soils which was perhaps caused by impeded drainage; this also explains the drastic changes in water content during the experiment. Soil water volume in clay soil was relatively high over the year and certainly throughout the experiment.

In the drought experiment, the volumetric water content of both soils dropped consistently, the sandy soil was always drier, as was expected with the larger pores between sand particles compared to smaller clay particles and the pores between them.

The fact that under natural conditions, very high soil water content > 0.8 g*cm^3 negatively affected seedling mortality is perhaps a result of the lack of aeration in the soils which thereby limited root respiration and induced anaerobic respiration, which depleted carbohydrate reserves (Ferreira et al. 2009), nutrient acquisition and consequently plant growth.

Seedling mortality in response to drought is a common finding (Lichtenthaler 1996, Larcher 2000, Pedrol Bonjoch et al. 2003). The exponential increase in seedling mortality rates is similar to what others have found when rainfall decreases (Marod et al. 2004, Poorter & Rose 2005, Markesteijn & Poorter 2009), indicating that very low soil water content (0.0-03 g x cm^3) negatively affects these species but that WS seedlings resisted longer which suggests that they reach wilting point later.

Seedling specialization might be reflected in the loss of leaves; TF seedlings lose more leaves in sand and WS seedlings lose more in clay and in both cases, when more leaves were lost, less height growth was observed.

Although no significant differences were found between seedling origins for growth at the end of the experiment, significant differences were found over time, showing that WS seedlings grew more than TF species during at least five months, especially when growing in sand. WS seedlings produced new leaves until October, whereas no new leaves were produced by TF seedlings after August. In addition, after April, the relative growth rate in WS seedlings that were growing in clay decreased steadily but in sand they increased and then decreased which suggests a higher tolerance to drought.

The higher values of height growth at the beginning of the drought experiment, when soil water content was similar to the natural conditions, could be explained by the fact that WS seedlings had a greater net production of fine roots in the dry season. In the same forests, Jiménez et al. (2009) found that root biomass production is higher in sandy soils than in clay soils and closer to the soil surface (0 to 10 cm depth), more roots improve water absorption (Vilagrosa et al. 2003, Markesteijn & Poorter 2009). If water content drops and sends a signal of drought, plants possibly produce more roots allowing better performance while water is available, this reaction was also found for most of nine seedling species when growing in sand (Baraloto et al. 2005). The RGRLA in the drought experiment increased until September and at that moment the soil water content was lower than the lowest registered under natural conditions. This performance could be related to a strategy that has been mentioned in previous studies of certain plants that generate a denser crown to regulate transpiration and maintain a humid environment that surrounds the leaves and causes them to lose less water (Tausend et al. 2000; DaMatta 2004). However, once the soil water content is lower than in natural conditions, the foliar increment growth stops, which is a frequent response that plants have to water stress (Larcher 2003).

Herbivory was lower under drought conditions compared to natural conditions, probably due to the lack of natural herbivores in the experiment and also that drought does not favour the presence of herbivores as can also be seen by the differences found between wet and dry seasons (See chapter 4).

It is suggested that WS seedlings are less susceptible to drought because they have a higher wood density and high xylem density (Patiño et al. 2009), which results in higher cavitation resistance as found in plants in seasonal forests (Hacke et al. 2001, Markesteijn et al. 2011). Therefore, TF species are more prone to embolism, which reduces hydraulic conductivity in the xylem and then cannot supply their leaves with water (Vilagrosa et al. 2003). This could explain the higher and abrupt leaf loss of TF seedlings that were planted in sand compared to their performance in clay soil.

The results of this study highlight the influence of soil moisture on the dynamics of seedlings in that WS seedlings show a higher tolerance in the extremes of dry or wet soils. The Eastern Amazon is drier and more seasonal than the Western Amazon (Malhi et al. 2009) and therefore a higher tolerance to drought could be an additional explanation for the dominance of species with high wood density (ter Steege et al. 2006).

Some potential impacts of climate change in the Amazon are a decrease in annual rainfall, an increase in dry season length, greater inter-annual rainfall variability and an increase in atmospheric temperature that will enhance transpiration, and augment soil water deficits for the tropics (Markham 1996, Malhi et al. 2009). This may affect the floristic composition of forests that are subject to climatic changes.

Under a drought scenario in the Western Amazon, white sand families such as Fabaceae and Euphorbiaceae could become more common or even as dominant as they are in the Eastern Amazon. In contrast, families that can tolerate waterlogging, such as Clusiaceae with genera *Haploclathra* and *Caraipa* could diminish or disappear; as could families that are highly affected by the dry season such as Arecaceae. Renninger et al. (2010) showed in *I. deltoidea* that a greater vapor pressure deficit in the dry season caused by low soil water content caused stomatal closure, which limited carbon gain and lowered the productivity of these palms. .

ACKNOWLEDGMENTS

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CHAPTER 6

Discussion

White sand forests

White sand forests are areas with low, open, and scleromorphic vegetation in sandy soils that cover 2.8% of the Amazon basin and 7.9% of the Guianas (Prance & Schubart 1978, ter Steege et al. 2000a). In the northern Rio Negro, considerable extensions of white sand forests are called Amazonian caatingas, Amazonian campinas or campinaranas and these have been relatively well studied (Medina et al. 1978, Medina et al. 1990, Coomes & Grubb 1996, 1998a, b, Mardegan 2007, Sobrado 2009, Stropp et al. 2011). In the Peruvian and South Colombian Amazon, these forests occupy patches of a few hectares, generally surrounded by a tall rain forest (Prance & Schubart 1978, Borges 2004). Thus far, only a few studies have been conducted on the structure and composition of these white sand forests (García Villacorta et al. 2003, Fine et al. 2010).

Forests that grow in white sands are drained by black waters. They have low diversity, and typically have trees that are of short stature and that have thin stems, and narrow crowns. They are often dominated by a few tree species (Macedo & Prance 1978, Anderson 1981, Medina et al. 1990, Duivenvoorden & Lips 1995, Coomes & Grubb 1996, 1998, Banki 2010, Stropp 2011b). Some WS forests can be temporarily exposed to waterlogging due to the presence of a hardpan at approximately one meter below the soil surface. This hardpan also impedes root penetration to deeper soils and exposes the forest to drought due to the sandy soil texture during the dry season (Bongers et al. 1985, Duivenvoorden & Lips 1995, Medina & Cuevas 2011).

Tree species richness correlates positively with tree turnover (Phillips et al. 1994) which is the mean of mortality and recruitment and reflects the dynamics of forests, and higher soil fertility (Phillips et al. 1994, Phillips et al. 2004). Forests with a high average wood density show lower mortality rates and lower species diversity than those with lower wood density (ter Steege & Hammond 2001, Parolin 2002, Baker et al. 2004a, Lewis et al. 2004, ter Steege et al. 2006). Tree species growing on white sands are characterized as having high-density wood and xylem stems (Agudelo 2006, Turriago & Villanueva 2008, Patiño et al. 2009) and at least in Peru, they have tough leaves that are more resistant to leaf herbivores than the species of the terra firme forest (Fine et al. 2004).

Resource Limitations

Resource availability theories suggest that if resources are scarce, trees grow slowly, conserve nutrients and avoid nutrient losses as much as possible, usually with higher levels of chemical defence (Coley 1987). Lower growth and mortality rates produce low values of aboveground biomass, basal area, net productivity (NP) (Aragão et al. 2009), and low turnover rates (Phillips & Gentry 1994, Malhi et al. 2004). Thicker and smaller leaves are associated with lower growth rates (Aerts 1989, Reich et al. 1992, Daws et al. 2005, Hikosaka 2005), as well as with higher leaf toughness. Low specific leaf area and high wood density are traits that have been associated with soils suffering from a water deficit, thus associated to drought. Recently, Fine et al. (2004, 2006) found that WS specialists have a higher overall defence investment and when manipulating hervibores in WS and TF forests, found that the impact of herbivory on growth and survivorship was much stronger in WS forests which confirms the theoretical predictions that species in low resource habitats invest more in defence.

The Trade-off Between Defence and Growth

More recently, leaf defence and resource availability have been combined in a theory that indicates a trade-off between defence and growth. This theory predicts that species in low resource habitats evolve a higher optimal defence investment at the cost of being able to grow faster in richer environments and that this trade-off might explain the major differences in composition between white sand and terra firme forests.

Although progress has been made in studies on white sand forests in the Amazon, there is still a considerable gap in our knowledge about the unique species composition of WS forests and their structure and dynamics, especially in the Western Amazon. This thesis aimed to fill this gap by addressing a number of questions that pertain to composition (chapter 2), forest dynamics (chapter 3), and two tests of the interaction between soil and herbivory (the growth versus defense trade-off) in two experiments that first took place in a controlled field experiment (chapter 4) and second in a greenhouse experiment (chapter 5).

I established three new WS forest plots two in Colombia and one in Peru. In each plot, I tagged, measured and identified all trees ≥ 10 cm DBH (canopy) and trees between 2.5 and ≤ 10 cm DBH (understory). I compared these with 84 other plots from the ATDN (ter Steege et al. 2013); 46 of which were located in Peru and 38 that were located in Colombia and classified into four types of forests. 20 were in temporarily flooded forests or igapó forests (IG), 19 were in white sand forests (WS), 32 were in terra firme forests (TF) and 13 were in forests that were flooded by white water rivers or varzea forests (VA).

Second, in the WS forest in the Zafire Biological Station (ZAF) (4°00′00″ S, 69°53′57″ W), I measured the number of dead trees and the mode of death, recruitment, growth and turnover with 7 censuses that were conducted between 2004 and 2012, of 1296 canopy and 984 understory trees, focusing on the species with more than 15 individuals (common) in the plot. I related the mortality, recruitment, growth and mode of death with the climate and I separated the common species into wood density categories in order to compare their performance over the years.

Then, to test the effect of the seasons on seedling performance of WS and TF species I selected 12 species from these two types of forests and developed a reciprocal transplant ex-situ experiment In each forest, four sites were selected at random (Figure 2 chapter 4) and a pair of experimental plots of ca. 17 m2 separated from each other by approximately 5 m were established, one filled with clay and the other with sand. Thereafter, ten seedlings per species were transplanted in each experimental site, which resulted in 160 seedlings per species in both forests. Thus, in each type of forest there were four locations with pairs of soil types that contained 960 seedlings from both types of forest for a total of 1920 seedlings. For 13 months, I measured and compared the growth of seedlings in terms of height (RGRH) and leaf area (RGRLA), herbivory, leaf loss and leaf gain. In order to compare the seasons (wet and dry), we considered four months each with the wet season being from October to January and the dry season from June to September. I also measured Leaf toughness of the WS and TF species studied.

Finally, to determine how drought affects the seedlings of WS and TF species, I established an ex-situ experiment. Ten soil beds were built in the open area of the Zafire Biological Station (ZAF); five were filled with clay from a TF forest and five with sand from a WS forest. In each bed, six individuals per species per forest (the same species that we selected for the experiment in chapter 4) were planted for a total of 72 seedlings per bed and a total of 720 in the experiment. I compared the performance of the seedlings from different origins that were planted in different soils, and also compared the performance of seedlings that were planted in natural conditions (Drought vs. Natural). Then, for more than one year, I monthly measured the soil water content in both sites and in the different soils, and measured the same parameters that were used in the experiment in chapter 4: RGRH, RGRLA, herbivory, leaf loss and leaf gain, plus stem volume and water content.

Discussion of Main Findings

The 87 plots from the ATDN database, including white sands (WS), igapo (IG), varzea (VA) and terra firme (TF) together had 39,172 individuals and 1859 morpho-species that were from 439 genera and 93 families; 531 tree species out of 1583 fully identified species found in WS forests, 1164 in TF forests, 436 species in IG, and 479 in VA. Twenty-two of those families had more than 15 species and accounted for 61.8%, 80.6%, 50% and 58% of the WS, TF, IG and VA forests species respectively. Within these families, those with the highest number of species present in all types of forests were Fabaceae, Annonaceae, Sapotaceae, Chrysobalanaceae and Moraceae. Each of these families are among the most abundant and species rich families of the Amazon, with Fabaceae being the most abundant and diverse family in the Amazon (ter Steege et al. 2013).

Diversity was not significantly different among the WS and IG, or VA and TF. WS forests had significantly lower diversity than VA or TF forests. However, more species were found in white sand forests than in VA or IG forests.

The 22 white sand forest plots were separated into three main groups: the Peruvian Amazon, the middle Colombian Amazon and the Guiana shield formation. In the WS forest, we selected 43 species to be indicator species of these forests, with significant indicator values ($P < 0.05$) that occur in 90% of cases in WS and less than 10% in other types of forest. Of these species, four were found in Podzols in the three regions: *Mauritia carana, Protium heptaphyllum, Haploclathra cordata* and *Xylopia benthamii.*

The plant family with highest number of species in the WS forest was Fabaceae followed by Clusiaceae, Apocynaceae and Arecaceae.

Among the three regions, no significant differences were found in Fishers' alpha among forests types in the Guiana shield, but differences were clearly found among forests in the Peruvian Amazon and in the middle Colombian Amazon (Figure 7 chapter 2), which suggests a higher variability in forest conditions in the Western Amazon and conversely, more similar conditions in the region of the Guiana shield.

Dynamics of White Sands

During the eight censuses of the WS plot in the Zafire Station I found that mortality, recruitment and turnover rates varied greatly within the WS understory and canopy trees, and also at the yearly intervals. Among canopy trees, the mean values of each of these rates were similar to the rates reported for Amazonian forests on Oxisols, and other Spodozols (Table 3 chapter 3), but Podzols had the lowest rates; no comparisons were possible for understory trees. Thus, there is a substantial overlap of WS and TF forests with respect to their dynamic rates which makes it difficult to make generalizations about the differences in dynamic rates between different forest types. In this study, the recruitment rate in the WS forest was higher than the rate found in the surrounding TF forest. The palms *Euterpe catinga* and *Mauritiella armata*, had recruitment rates that were always higher than mortality rates which was the opposite of the rates for the other common species in the plot.

The periods from 2008-2009 and 2009-2010 showed an interruption in their dry season as well as a considerable increase in mortality rates in the most common species. There was also higher recruitment and consequently higher turnover in 2008-2009 for both understory and canopy trees which was caused by a higher average growth rate. This suggests that waterlogging negatively affects the performance of tree species in this forest as has been shown in the monthly root production (Jiménez et al. 2009). However, the increase in growth in 2008-2009, but not in 2009-2010 indicates that the interruption at the end of the dry season was most likely more harmful.

More than 80% of WS trees die standing and those trees exhibited a negative or zero growth increment for the years prior to their death. The other modes of death were broken, uprooted or missing. I found no relationship between the mode of death and tree size for trees ≥ 10 cm DBH, contrary to reports from other forests (Korning & Balslev 1994, Rolim et al. 1999, Arriaga 2000, Holzwarth et al. 2013). In addition, I found no relationship between the mode of death and the year. Understory trees showed contrasting results: uprooted and missing had modes of death that were only present in smaller DBH trees.

WS forests are dominated by just a few tree species and therefore the response of these species determines the mortality or recruitment rates of the stand and also the mode of death that characterizes the forest. Therefore, WS forests could be more vulnerable to climate change than TF forests because in these latter forests, high species diversity, to some extent, buffers changes in climate. Therefore, this work highlights the need to develop forest dynamic models that are based on species as suggested by Clark & Clark (1999), for trees that are smaller than 10 cm DBH as was suggested by da Silva et al. (2002), and long-time series, to avoid the effects of anomalous years.

Seedling Performance and Soils

I found significantly higher leaf toughness in WS seedlings compared to TF seedlings. After 13 months of observations, it was clear that all species lost fewer leaves in sandy soils than in clay soils. In addition, I found higher rates of herbivory in TF than in WS seedlings in both types of forests and soils. Herbivory was higher in the wet season than the dry season and during wet season, I also found a lower RGRH and RGRLA. Second, TF seedlings lost significantly more leaves than WS seedlings which similarly affected growth. I found RGRH to be higher in WS seedlings than in TF seedlings, which is most likely due to less herbivory and leaf loss.

Seedling mortality was higher in clay than in sandy soils, which is perhaps related to the higher leaf loss found in clay soil. Although herbivory is often associated with mortality (Fine et al. 2004), no clear relationship between them was found. Therefore, it appears that higher leaf toughness is an advantage for WS seedlings as their herbivory was reduced compared to TF seedlings. This finding supports the 'defence versus growth trade-off' in these forests. Conversely, the wet season negatively affects seedlings in both types of soils. Thus seedling performance in the forest is not only affected by the origin of the species and the type of soil but also by the season of the year.

Seedling Performance and Drought

I found sandy soils were always drier than clay soils. Under field natural conditions no differences in soil water content were found, except during the wet season when sandy soils showed slightly higher water content than clay soils which was caused by impeded drainage by the hardpan. Differences were also significant between treatments; natural vs. drought. Soil water content in clay under natural conditions was relatively high over the year throughout the experiment.

Soil water content and seedling mortality showed a strong correlation, with the highest mortality rates found when soils were saturated with water under natural conditions and also when soil water was very low under drought conditions. Proportional mortality did not show differences between the origins of seedlings (WS or TF) under different treatments. As expected, dead seedlings accumulated over time, but towards the end of the experiment, more dead seedlings were found under natural than under drought conditions. Within the drought conditions, TF seedlings died significantly more than WS seedlings when growing in clay soils. And WS seedlings died later than TF seedlings suggesting that they are more drought tolerant (Figure 11, chapter 5).

Relative growth rate in height was significantly lower in drought than in natural conditions. There were also differences in growth over time, which indicates that WS seedlings grew more than TF species during at least five months, especially when growing in sand. Although there were no significant differences shown for the total growth rates of the height or leaf area of seedlings from different origins, the seedlings grew better when planted in their own soil and lost more leaves when planted in the contrasting soil. Stem volume was highest in TF seedlings regardless of the treatment. Under drought conditions, stem volume and relative leaf area growth for all seedlings were higher than under natural conditions.

As mentioned earlier, future climate scenarios predict less rain. In these scenarios, It is plausible to think that herbivory rates may decrease which would favour growth in leaf area, but would most likelly affect growth in height for both TF and WS seedlings. However, considering the higher mortality of TF seedlings under drought conditions, WS seedlings could increase their density.

White Sand Forests Conservation in Colombia and Final Conclusions

The Colombian amazon region comprises ca. 41% of the national territory with 483,164 km2. The region is protected under different legal modalities such as indigenous reserves, forestry reserves and national parks. There are 17 national parks in the Colombian Amazon that cover close to 17% of the region and some overlap with indigenous reserves. The overlap between parks and reserves and the lack of a strategic research programme for understanding the conservation needs and priorities hamper the development of an effective management plan for the national parks in the Colombian Amazon. In addition, the absence of sustainable development projects or alternative sources of legal income generation for local people push individuals to explore illegal alternatives such as gold mining and coca production, threatening the biological and cultural diversity in some of these areas.

White sand forests are represented in Pure national park, that is located between the Caqueta and Putumayo rivers in the Amazon Colombian trapezoid, however, no inventories in the area have been taken to determine their size, structure and species composition. Such inventories are urgent, given the increase in illegal gold mining in the Park in recent years. It is also probable that the Yaigoje Apaporis National park contains WS, but no published data are known, and satellite images are not available to verify the presence of WS forests in this natural park. In addition, this park is also threatened by enterprises looking for gold (http://www.territorioindigenaygobernanza.com/col_14.html), which leaves the park in an uncertain state of conservation. In the middle of Caqueta there are some WS that were sampled by Duivenvoorden (1995, 1996), and by Duque et al. (2002). These patches are in the reserves of indigenous people, who traditionally do not use these forests for agriculture or any extractive activities. I have walked through other WS patches in the region between the Caqueta River and the Miriti River, as well as the region between La Chorrera in the Igara Parana River and El Encanto in the Caraparana River, both of which belong to the indigenous reserves. During these travels, it was clear that no inventories have been conducted.

Therefore, some WS are located in protected territories, but inventories are scarce to determine whether or not WS forests are well represented in the Colombian Amazon.

In addition, long term demographic studies will shed light on the effects of climate change on the species composition of the Amazonian forests, and thus the biodiversity, or the natural heritage of Colombia. Currently, the only WS plot being monitored over time is that which is located in the Zafire biological station.

Through the study we contributed to a better understanding of the diversity, dynamics and functioning of white sand forests in the Western Amazon, and the factors that could influence the distributions of plant species in different types of forests. We corroborated that just as in other countries; white sand forests in Colombia have a distinctive flora with few dominant tree species that determine the dynamics of the stand.

Our findings showed that waterlogging, the rainy season and also the interruption of the dry season can negatively influence the survival, herbivory and growth of white sand species. We also observed that the specificity of their species could be determined by sandy soils as well as by the resistance of the species to drought.

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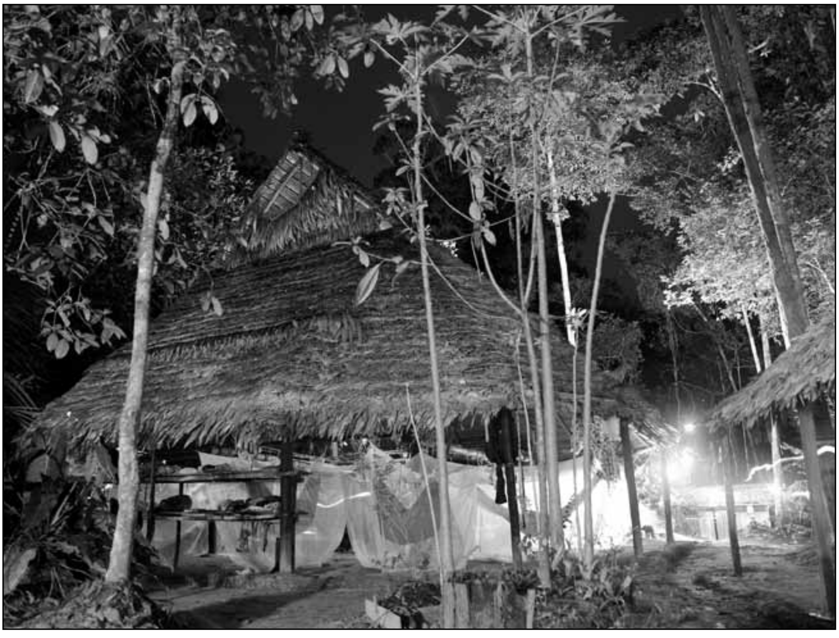

Resumen

En la Amazonia colombiana, los bosques de arenas blancas no han sido particularmente estudiados, probablemente debido a que se encuentran en pequeños parches en una matriz de bosques de tierra firme o porque no contienen especies de importancia económica.

Estos bosques se caracterizan por habitar suelos arenosos de extrema pobreza y en varios se observa la presencia de un durapan (capa impermeable) a uno o menos de un metro de profundidad. Estas condiciones del suelo ejercen tensiones sobre las plantas debido a su alto déficit de nutrientes, al alto contenido de agua (encharcamientos, en la época de lluvias), y a su baja retención de agua (en la época de sequía) (Anderson 1981).

Varias de las especies que habitan estos bosques son endémicas entre 52-61% (Fine et al. 2010) y poseen características que las diferencian de las especies de otros tipos de bosques, como por ejemplo: una alta densidad de madera (Agudelo 2006) y de xilema (Patiño et al. 2009), una baja área específica de hojas, (Turriago and Villanueva 2008) y alta dureza de hojas (Fine et al. 2006).

Esta tesis reporta por primera vez, una comparación de la estructura y composición florística de los bosques de arenas blancas de Colombia y el oeste amazónico (Cap. 2). Se establecieron tres parcelas en bosques de arenas blancas: en el Ucayali (en Perú), en Peña Roja (Medio Caquetá, Colombia) y en el trapecio amazónico (Estación Biológica El Zafire, Colombia) y se compararon con datos de otras 84 parcelas de la red ATDN: 46 localizadas en Perú y 38 localizadas en Colombia, unas en la región media Amazónica colombiana y otras en Inirida área de la región de la Guyana, para un total de 87 parcelas. Estas parcelas están clasificadas en cuatro tipos de bosques: 20 en bosques temporalmente inundados por aguas negras-igapó (IG), 19 en arenas blancas (WS), 32 en tierra firme (TF) and 13 en bosques inundados por aguas blancas o várzea (VA).

Se utilizaron 439 géneros de 93 familias y 1583 especies plenamente identificadas y reportamos 531 especies en bosques de arenas blancas, 1164 en TF, 436 en IG, y 479 en VA. De estas familias 22 tenían más de 15 especies y conformaban el 61.8%, 80.6%, 50% y 58% de las especies en bosques de WS, TF, IG y VA respectivamente. Entre estas familias las que contaron con mayor

número de especies y estuvieron en todos los tipos de bosque fueron Fabaceae, Annonaceae, Sapotaceae, Chrysobalanaceae y Moraceae.

Utilizando un análisis de ordenación observamos que las parcelas de arenas blancas se separaron en tres grupos cada uno representando una región geográfica específica: La Amazonia peruana, la media Amazonia Colombiana y las parcelas del área dela Guyana. En estos bosques seleccionamos 44 especies como indicadoras de arenas blancas por valores de significancia (P< 0.05) más su presencia en el 90% de los casos en bosques arenas blancas y menos de 10% en otro tipo de bosques. De estas, cuatro especies estuvieron en las tres regiones: *Mauritia carana, Protium heptaphyllum, Haploclathra cordata* and *Xylopia benthamii.*

Luego de estimar y comparar los alfa de Fishers entre bosques y regiones, observamos que no había diferencias significativas entre los diferentes tipos de bosques en la región de Guyana pero si hubo diferencias significativas entre los bosques de la Amazonia peruana y de la Amazonia media colombiana lo que sugiere una mayor variabilidad entre las condiciones de los bosques en el oeste amazónico y por el contrario condiciones más homogéneas en la región de la Guyana.

Adicionalmente observamos que, como ocurre en otros bosques con deficiencias de nutrientes, hay dominancia de solamente unas pocas especies. En nuestro estudio predominaron Macrolobium microcalyx en Perú, *H. cordata en el Zafire y Caraipa punctulata* en Peña Roja.

¿Es la dinámica de los bosques de arenas blancas tan distintiva como su estructura?

Se ha reportado que bosques con una alta densidad de madera, muestran menor diversidad y menores tasas de mortalidad que aquellos más diversos y con altas tasas de densidad de madera (ter Steege et al. 2000, Baker et al. 2004a, Lewis et al. 2004, ter Steege et al. 2006). En la parcela establecida en el trapecio amazónico (Estación Zafire) se encontró una alta densidad de madera (Agudelo 2006, Patiño et al. 2009. En esta parcela registramos el crecimiento, la mortalidad y el reclutamiento de los árboles durante un periodo de ocho años (2004-2012) y comparamos con otros bosques de arenas blancas y de tierra firme (Cap.3).

Monitoreamos un total de 2280 tallos divididos en dos categorías: sotobosque individuos de ≤ 10 cm DAP (1296) y de dosel con individuos ≥ 10 cm (984). Las 16 especies más comunes poseían 15 individuos o más; que unidas corresponden a cerca del 85% de todos los individuos en la parcela (Tabla 1 Cap3).

Las tasas de mortalidad y reclutamiento en el sotobosque y el dosel fueron significativamente diferentes. En el sotobosque se registró la mortalidad en 26 especies y el reclutamiento en 40 especies, mientras que en el dosel fueron 15 y 27 especies respectivamente. La tasa promedio de mortalidad fue de 1.59% en el sotobosque y de 1.31% en el dosel. En las dos categorías, las especies que presentaron mayor mortalidad fueron D. uaiparuensis y H. cordata. El reclutamiento fue de 2.31% y 1.41% respectivamente y, el crecimiento fue muy bajo en las dos categorías: 0.079 cm de diámetro promedio anual para sotobosque vs. 0.072 cm para el dosel. D. uaiparuensis es la especie con mayor crecimiento, no obstante tuvo un bajo reclutamiento.

Adicionalmente, observamos que la mayoría de los individuos que murieron lo hicieron en pie (82.38%), seguido de quebrados (9.69%) y caídos de raíz (5.72%). La muerte en pie es común para áreas con baja productividad y suelos pobres, y algunos autores atribuyen este modo de muerte a una estrategia para liberar gradual y lentamente nutrientes al suelo, lo que contribuye al mantenimiento de las mismas especies en el bosque (Martini et al. 2008). Este tipo de muerte también se atribuye a plantas con alta densidad de la madera (Arriaga 2000). Observamos que la muerte caída de raíz estuvo asociada a los individuos con menos altura, por lo que pudo haberse debido a un anclaje superficial que impidió una buena absorción de agua.

Nuestros resultados en general están entre los rangos de otros bosques amazónicos sobre suelos Podzoles u Oxisoles. Sin embargo, este bosque en el Zafire muestra un reclutamiento y una tasa de recambio mayor que los bosque de tierra firme contiguos, lo cual es inusual; esto puede deberse a que las pocas especies muy comunes están bastante adaptadas a las condiciones extremas y pueden permanecer por más tiempo en el bosque sin morir, pero además con las condiciones apropiadas para tener constantemente reclutas.

Por lo tanto, las generalizaciones acerca de la dinámica y tipos de bosque deben ser consideradas con cuidado, ya que no parecen ser indicadores de un tipo de bosque u otro. Es importante, además monitorear individuos de menor tamaño, es decir de sotobosque,en especial en este tipo de bosques, para observar con más claridad las tendencias a lo largo de los años y así quizás hacer mejores predicciones de las variables que influyen en la dinámica de bosques.

¿Son las condiciones del suelo realmente determinantes de la especialización de las especies comunes de arenas blancas?

Considerando que las plantas que crecen en el suelo de arenas blancas están sometidas a los extremos de sequía y encharcamiento, nuestra hipótesis fue que las plantas de bosques de arenas blancas crecerían y sobrevivirían más que las plantas de tierra firme que crecen en arcillas durante la época seca y la muy lluviosa. Además las plantas de arenas blancas tendrían hojas más duras que tendrían una mayor longevidad y una mayor protección contra los herbívoros. Para probar estas hipótesis (Cap 4.) desarrollamos un experimento de trasplante recíproco con cinco factores: origen de las plántulas de tierra firme o de arenas blancas, dos tipos de suelo: arcilla y arena, 8 bloques: 4 en el bosque de tierra firme y 4 en el de arenas blancas, con 12 especies 6 de arenas blancas y 6 de arcillas, y medimos durante 13 meses el crecimiento en altura y en área foliar, la ganancia o pérdida de hojas y la herbivoría cubriendo las dos estaciones: seca y lluviosa. Adicionalmente medimos la dureza de las hojas de las 12 especies estudiadas.

Encontramos que la dureza de las hojas de los bosques de arenas blancas fue mayor que la de las especies del bosque de tierra firme. Observamos además que el origen de las especies fue el principal factor afectando las variables estudiadas. El crecimiento relativo en altura fue mayor en plántulas de bosques de arenas blancas, independientemente de la estación. El crecimiento relativo en área foliar fue mayor en plántulas de tierra firme en la época de lluvias y éstas sufrieron una mayor herbivoría en cualquier estación y tipo de suelo. La pérdida de hojas y la mortalidad relativa no fueron significativamente diferentes entre origen y bosque, pero fue considerablemente mayor en los suelos arcillosos. El crecimiento en área foliar también fue mayor en suelos arcillosos y la herbivoría mayor en suelos arenosos.

Los resultados confirman que las especies de arenas blancas poseen características que las hacen más resistentes a los herbívoros y puede ser la dureza de hojas (Fine et al. 2004, Fine et al. 2006), aunque a diferencia de lo encontrado por estos autores las plántulas no sufrieron un detrimento del crecimiento en altura de las plántulas. Adicionalmente, en la época seca el crecimiento en área foliar de las especies de tierra firme se vio negativamente afectado y no así el de las especies de arenas blancas indicando cierta resistencia de estas especies a la sequía. Por lo tanto, el comportamiento de las plántulas en el bosque no solamente es afectado por el origen de las especies, por el tipo de suelo, sino además por la estación del año o condiciones de humedad del suelo.

¿Son las plántulas de especies de arenas blancas más resistentes a la sequía que las plántulas de especies de bosques de tierra firme?

Características como alta dureza de las hojas, y una alta densidad de madera y xilema encontradas en especies de bosques de arenas blancas también han sido asociadas a la tolerancia a la sequía (Vilagrosa et al. 2003). Por lo tanto nuestra hipótesis era que bajo condiciones de sequía las especies de arenas blancas tendrían mayores tasas de crecimiento y sobrevivencia que las de tierra firme. Para probar la hipótesis (Cap.5) establecimos un experimento ex-situ en un vivero que construimos en el área abierta de la estación biológica el Zafire con 10 camas: cinco llenas con arcilla del bosque de tierra firme y cinco llenas de arena proveniente del bosque de arenas blancas. Trasplantamos 720 plántulas de 12 especies, 6 especies de tierra firme y 6 de arenas blancas, las sembramos en los dos tipos de suelo y las dejamos de regar a los dos meses de establecidas. Medimos a lo largo de un año el contenido del agua en el suelo y medimos el crecimiento en altura, área foliar, volumen del tallo y la tasa de sobrevivencia de las plántulas de arenas blancas en comparación con las de tierra firme plantadas en los dos suelos de arenas y de arcillas, y a su vez las comparamos con las plántulas que crecieron bajo condiciones naturales (Cap. 4).

Los dos tipos de plántulas reaccionaron a la sequía, aunque no mostraron diferencias significativas entre orígenes en relación a la altura o al área foliar total. Sin embargo, la perdida de hojas si fue diferente en las plántulas de arenas blancas que crecieron en arcilla comparadas con las que crecieron en arena, perdiendo muchas más hojas en el suelo arcilloso. La mortalidad varió entre orígenes, pero solamente cuando las plántulas crecieron en arcillas y no en arenas.

Al comparar el experimento en condiciones de sequía y bajo condiciones naturales observamos que el volumen de agua disponible en el suelo a lo largo de los 13 meses de muestreo, describe una relación cubica para el tratamiento en condiciones naturales y una regresión lineal negativa para el tratamiento sequía. El comportamiento de las plántulas creciendo bajo las dos condiciones fue significativamente diferente en todas las variables. Bajo condiciones de sequía, el volumen del tallo fue mayor que bajo condiciones naturales, en todas las plántulas independientemente del origen, conservando, aparentemente, agua para ser utilizada en el crecimiento en área foliar de las plántulas. Observamos que el contenido del agua del suelo mostró una relación positiva con el volumen del tallo, y negativa con la mortalidad.

Las plántulas de arenas blancas sobrevivieron mejor, y produjeron hojas y crecieron por periodos más largos que las plántulas de tierra firme. Nuestros resultados por lo tanto sugieren que las plántulas de arenas blancas son más resistentes a la sequía y que en general las especies utilizadas son muy afectadas por el contenido de agua en el suelo. Consecuentemente es posible que la diferencia en la composición de especies entre los tipos de bosques pueda ser explicada por una combinación de factores como la resistencia a la sequía y a los herbívoros (Cap.4)

Estos hallazgos son muy interesantes a la luz de futuros escenarios de cambio climático que advierten una significativa disminución de las lluvias, sequias más largas y fuertes, y como consecuencia el contenido de agua en el suelo será aún menor que en las actuales épocas secas (Hulme and Viner 1998, Whitmore 1998, Hulme et al. 1999, Timmerman et al. 1999, Phillips et al. 2004, Malhi et al. 2009). También se pronostica que el régimen de lluvias cambie hacia un régimen más estacional favoreciendo los bosques estacionales (Malhi et al. 2009). Lo que podría indicar que bajo esas condiciones algunas de las especies de arenas blancas podrían tener ventajas competitivas frente a las de tierra firme cambiando la composición florística.

Por último queremos resaltar que los trabajos a largo plazo considerando aspectos ecológicos y fisiológicos son muy importantes para entender la dinámica y el comportamiento de los bosques, y que es necesario continuar realizando experimentos que nos ayuden a comprender la relación de costo-beneficio entre diferentes características de las plantas en medio de diversas condiciones medioambientales.

Summary

The Amazon region covers an area of nearly six million square kilometres (Ramos da Silva et al. 2008) and their forests have long been grouped in three broad categories: flooded forests, non-flooded or terra firme forests and white sand forests. White sand (WS) forests are areas of low, open, and scleromorphic vegetation on sandy soils that cover 2.8% of the Amazon basin and 7.9% of the Guianas (Prance and Schubart 1978, ter Steege et al. 2000a). In the Peruvian and south Colombian Amazon, these forests grow in patches of a few hectares, generally surrounded by tall rain forest (Prance and Schubart 1978, Borges 2004). Thus far, only a few studies have been conducted on the structure and species composition of these WS forests (García Villacorta et al. 2003, Fine et al. 2010) as well as the traits that make their species able to survive in the characteristically very poor sandy soils of these forests (Fine et al. 2004, 2006, Stropp 2011).

In order to answer the question that was posed in chapter 2 regarding the species composition of WS forests in the Western Amazon, their geographic variation and how they differ from other types of forests, I established three new WS forest plots, two in Colombia and one in Peru and compared them with 84 other plots from the ATDN (ter Steege et al. 2013): 20 in temporarily flooded forests or igapó forests (IG), 19 in WS forests (WS), 32 in terra firme forests (TF) and 13 in forests flooded by white water rivers or varzea forests (VA). Together these 87 plots had 39,172 individuals and 1859 morpho-species from 439 genera and 93 families; 531 tree species out of 1583 fully identified species growing in WS forests, 1164 in TF forests, 436 species in IG, and 479 in VA. Twenty-two of these families had more than 15 species and accounted for 61.8%, 80.6%, 50% and 58% of the WS, TF, IG and VA forest species respectively. Within these families, those with the highest number of species present in all types of forests were Fabaceae, Annonaceae, Sapotaceae, Chrysobalanaceae and Moraceae. Diversity was not significantly different between WS and IG, or VA and TF. WS forests had significantly lower diversity than VA or TF forests.

Among the regions, we did not find significant differences in Fishers' alpha among forest types in the Guiana shield, but differences were evident among forests in the Peruvian Amazon and in the Colombian Amazon, which suggests higher variability among forest conditions in the Western Amazon and

conversely more homogeneous conditions in the region of the Guiana shield. The 22 WS forest plots can be separated into three main groups; the Peruvian Amazon, the middle Colombian Amazon and the Guiana shield formation and only four species were found in the three regions; *Mauritia carana, Protium heptaphyllum, Haploclathra cordata* and *Xylopia benthamii.*

In chapter 3, I determined the dynamic rates (mortality, growth, recruitment) of a WS forest in Colombia compared to other WS forests in the Western Amazon and other forest types in the same region. I measured the number of dead trees and the mode of death, recruitment, growth and turnover of 7 censuses that were conducted between 2004 and 2012, in a WS plot in the Zafire biological station in Colombia (4°00′00″S, 69°53′57″W). I censused 1296 canopy (>10 cm DBH), and 984 (<10 cm DBH) understory trees, and focused the analysis on the species that had more than 15 individuals (common) in the plot. I found that mortality, recruitment and turnover rates highly varied within WS forest understory and canopy trees and among yearly intervals. Among canopy trees, the mean values of each of these rates were similar to the rates reported for Amazonian forests on Oxisols, and other Spodozols, but Podzols have the lowest rates. Thus, there is a substantial overlap between WS and TF forests with respect to their dynamic rates, which makes it difficult to form generalizations about the differences in dynamic rates between different forest types. I observed that the palms *Euterpe catinga* and *Mauritiella armata*, showed recruitment rates that were always higher than mortality rates, which was different from the other species in the plot.

I found that more than 80% of WS trees die standing and those trees exhibited a negative or zero growth increment for the years prior to their death. The other modes of death were broken, uprooted or missing. I found no relationship between the mode of death and tree size for canopy trees, which is contrary to reports from other forests (Korning & Balslev 1994, Rolim et al. 1999, Arriaga 2000, Holzwarth et al. 2013), nor did I find a relationship between mode of death and year. Understory trees showed contrasting results; uprooted and missing modes of death were present only in smaller DBH trees. We observed that in years when rains interrupted the dry season, the trees showed greater damage and there was an increase in mortality. WS forests are dominated by only a few tree species and therefore the response of these species determines the mortality or recruitment rates of the stand and it also determines the mode of death that characterizes the forest. Therefore, WS forests could be more vulnerable to climate change than TF forests because in these latter forests, high species diversity may buffer changes in climate to some extent.

In chapter 4, I tested to see whether soils are determinants of the specialization of WS species, so I developed a reciprocal transplant *ex-situ* experiment to answer the question of whether WS seedlings differ in the rate of survival, the production and loss of leaves and their growth and herbivory compared to TF seedlings. In addition, I looked to see whether the wet and dry season seasons showed any differences in these areas. To do so, I selected 12 species from these two types of forests, and measured and compared them for a period of 13 months, to determine the growth of seedlings in terms of height (RGRH) and leaf area (RGRLA), herbivory, leaf loss and leaf gain. For comparing the seasons (wet and dry) I considered the wet season to run from October to January and dry season from June to September. I also measured leaf toughness of the WS and TF species that were being studied. I found significantly higher leaf toughness in WS seedlings compared to TF seedlings. Seedling mortality was higher in clay than in sandy soils, which is perhaps related to the higher leaf loss found in clay soil for all seedlings, although TF seedlings lost significantly more leaves than WS seedlings, which similarly affected growth. Therefore, I found RGRH to be higher in WS seedlings than TF seedlings. I also found higher rates of herbivory in TF than WS seedlings in both types of forests and soils. Herbivory was higher in the wet season than the dry season and during the wet season I also found a lower RGRH and RGRLA.

Although herbivory is often associated with mortality (Fine et al. 2004), no clear relationship was found between them. Therefore, it appears that higher leaf toughness is an advantage for WS seedlings because their performance was better with less herbivory compared to TF seedlings, which confirms the defence/growth trade-off in this forest. Conversely, the wet season negatively affected the performance of seedlings in both types of soils. Thus, seedling performance in the forest is not only affected by the origin of the species and the type of soil but also by the season of the year.

Finally, in chapter 5 I determined whether WS species perform better under drought conditions, in clay or sandy soils, than TF species. I established an *ex-situ* experiment. Ten soil beds were built in an open area of the Zafire Biological Station; five were filled with clay from a TF forest and five with sand from a

WS forest. In each bed, six individuals per species, per forest were planted. I compared the performance of seedlings of different origins planted in different soils, and also compared the performance of seedlings with those that grew under natural conditions (drought vs. natural). For more than a year, I measured the soil water content on a monthly basis, in both sites and soils and measured RGRH, RGRLA, herbivory, leaf loss, leaf gain, stem volume and water content. I found that sandy soils were always drier than clay soils. Under field natural conditions, no differences in soil water content were found, except during the wet season when sandy soils showed slightly higher water content than clay soil which may have been caused by impeded drainage by the hardpan. Differences were also significant between treatments; natural vs. drought. Soil water content in clay under natural conditions was relatively high throughout the year and during the course of the experiment.

Soil water content and seedling mortality showed a strong correlation with each other and the highest mortality rates were found when soils were saturated with water under natural conditions and also when soil water was very low under drought conditions. Proportional mortality did not show significant differences between the origins of seedlings (WS or TF forests) under different treatments. As expected, dead seedlings accumulated over time, but towards the end of the experiment more dead seedlings were found under natural than under drought conditions. Within the drought conditions, TF seedlings died significantly more than WS seedlings when growing in clay soils. The fact that WS seedlings died later than TF seedlings, suggests that they are more drought tolerant.

RGRH was significantly lower in drought than in natural conditions. There were also differences in growth over time and we saw that WS seedlings grew more than TF seedlings during at least five months, especially when growing in sand. Although no significant differences were shown in total RGRH or leaf area between the origins of seedlings, it was clear that they grew better when planted in their own soil and lost more leaves when planted in the contrasting soil. Stem volume was highest in TF seedlings regardless of the treatment. Under drought conditions, stem volume and relative leaf area growth for all seedlings were higher than under natural conditions.

Our findings support the view that white sand forests have a distinctive flora with few dominant tree species that determine the dynamics of the stand. The uniqueness of their flora and the dominance of a few species could be caused by the poor sandy soils as well as by the resistance of the species to drought. Drought appears to affect herbivory. In the In situ experiment (chapter 4), we observed a higher herbivory in the dry than in the wet season, as well as under natural conditions compared to drought conditions for both types of seedlings (see chapter 5). No significant differences were found in the herbivory rates for seedlings planted in different soils and unlike other experiments with WS species (Fine et al. 2004), we did not find a clear relation between herbivory and mortality. It appears that herbivory has less of an effect on the survival of a species in the Colombian Amazon, as was found by Stropp et al. (2013) in upper Rio Negro.

Nederlandse Samenvatting

Het Amazonegebied heeft een oppervlakte van bijna zes miljoen vierkante kilometer (Ramos da Silva et al. 2008). De bossen in dit gebied worden vaak verdeeld in drie categorieën: overstromingsbossen, bossen op hoger gelegen gronden die niet overstromen en bossen op witte zanden. Wit zand (WS) bossen worden gekenmerkt door een lage, open en scleromorfe vegetatie. Ze komen voor op arme zandgronden die 2,8% van het Amazonegebied en 7,9% van de Guyana's beslaan (Prance en Schubart 1978, ter Steege et al. 2000a). In de Peruaanse en Zuid-Colombiaanse Amazone, groeien deze bossen in gebieden van een paar hectare, meestal omringd door bossen op bodems met meer klei (Prance en Schubart 1978, Borges 2004). Tot nu toe zijn slechts enkele studies in WS bossen uitgevoerd (García Villacorta et al. 2003, Fine et al. 2010). Ook is er nog weinig gekeken naar de eigenschappen waarmee de soorten kunnen overleven op de voor deze bossen karakteristieke zeer arme zandgronden (Fine et al. 2004, 2006, Stropp 2011).

In hoofdstuk 2 bespreek ik de soortensamenstelling van WS bossen in de Western Amazon, hun geografische variatie en hoe ze verschillen van andere soorten bossen. Hiervoor heb ik drie nieuwe bosinventarisatieplots in WS uitgezet, twee in Colombia en een in Peru en vergeleek ze met 84 andere plots uit de ATDN (ter Steege et al., 2013.): 20 in bossen die jaarlijks overstromen of of Igapó bossen (IG), 19 in WS bossen (WS), 32 in bossen op gronden die nooit overstromen, zogenaamde tierra firme bossen (TF) en 13 in bossen overspoeld door wit water rivieren of varzea bossen (VA). In deze 87 plots vonden we 39.172 individuen en 1.859 morpho-soorten uit 439 genera en 93 families; 531 boomsoorten uit 1583 volledig geïdentificeerde soorten groeien in WS bossen, 1.164 in TF bossen, 436 soorten in IG, en 479 in VA. Tweeëntwintig van deze families hadden meer dan 15 soorten en zijn goed voor 61,8%, 80,6%, 50% en 58% van de WS, TF, IG en VA bossoorten, respectievelijk. Van deze families, zijn de Fabaceae, Annonaceae, Sapotaceae, Chrysobalanaceae en Moraceae degenen met het hoogste aantal soorten in de verschillende bostypen. Diversiteit was niet significant verschillend tussen WS en IG, of VA en TF. WS bossen hadden een significant lagere diversiteit dan VA of TF-bossen.

Tussen de regio's, hebben we geen significante verschillen in Fishers alpha gevonden tussen de verschillende bostypen in het Guyana schild gevonden, maar er waren wel duidelijke verschillen tussen de bossen in de Peruaanse

Amazone en in de Colombiaanse Amazone, wat suggereert dat er meer variatie is in milieuomstandigheden in de Westelijke Amazone en meer homogene of vergelijkbare omstandigheden in de regio van het Guyana schild. De 22 WS bospercelen kunnen worden verdeeld in drie hoofdgroepen; de Peruaanse Amazone, het midden Colombiaanse Amazonegebied en de Guyana schild formatie en slechts vier soorten werden gevonden in alle drie de regio's: Mauritia carana, Protium heptaphyllum, Haploclathra cordata en Xylopia benthamii.

In hoofdstuk 3, stelde ik de dynamische ratio's (sterfte, groei, aanwas) vast van een WS bos in Colombia in vergelijking met andere WS bossen in het Westelijk Amazonegebied en andere bostypen in dezelfde regio. Ik registreerde het aantal dode bomen en de wijze van sterven, aanwas, groei en de omloopsnelheid in 7 metingen uitgevoerd tussen 2004 en 2012 in een WS plot in het Zafire biologisch station in Colombia (4 ° 00'00 "Z, 69 ° 53'57 "W). Ik registreerde 1296 bomen in de kroonlaag (> 10 cm DBH), en 984 (<10 cm DBH) bomen in de ondergroei van het bos, en richtte me op de analyse van soorten met meer dan 15 individuen in de plot. De mortaliteit, aanwas en omloopsnelheid varieerde sterk tussen de bomen in de ondergroei en kroonlaag van het WS bos en tussen de jaarlijkse intervallen. Bij de bomen in de kroonlaag waren de gemiddelde waarden van elk van deze demografische variabelen vergelijkbaar met de waarden die zijn gerapporteerd voor Amazone bossen op Oxisols, en andere Spodozols, maar podzolbodems hebben de laagste waarden. Er bestaat dus een aanzienlijke overlap tussen WS en TF bossen voor wat betreft hun dynamische variabelen, waardoor het moeilijk te generaliseren is over de verschillen in deze variabelen tussen verschillende bossen. Ik vond dat de aanwas van palmen Euterpe catinga en Mauritiella armata, altijd hoger waren dan de sterftecijfers, terwijl dit niet het geval was voor andere soorten in de plot.

Ik vond dat meer dan 80% van WS bomen sterven terwijl ze nog rechtop in het bos staan en die bomen vertoonden een negatieve of nulgroei in de jaren voorafgaand aan hun dood. Bomen sterven ook doordat de stam afbreekt, de boom wordt ontworteling of om een andere onduidelijke reden (ontbrekend). Ik vond geen relatie tussen de wijze van sterven en de grootte van de boom bij bomen in de kroonlaag, Dit is in tegenspraak met resultaten uit andere bossen (Korning en Balslev 1994, Rolim et al. 1999, Arriaga 2000, Holzwarth et al. 2013), noch vond ik een relatie tussen de wijze waarop bomen sterven en het jaar waarin ze sterven. Bomen in de ondergroei vertoonde tegengestelde resultaten; ontwortelde bomen en bomen waarvan de wijze waarop ze zijn gestorven onbekend is troffen we alleen aan tussen de kleine bomen in de ondergroei. We observeerden dat er in de jaren waarin het droge seizoen werd onderbroken door dagen met regenval, de bomen grotere schade vertoonden en er een toename in sterfte was. WS bossen worden gedomineerd door slechts enkele boomsoorten en dus de reactie van deze soorten bepaalt de mortaliteit of aanwas van de populaties van bomen en de wijze van sterven die het bos kenmerkt. Daarom kunnen WS bossen kwetsbaarder zijn voor klimaatverandering dan TF bossen, omdat in deze laatste, de hoge diversiteit aan soorten veranderingen in het klimaat tot op zekere hoogte kan bufferen.

In hoofdstuk 4, testte ik of de bodem bepalend is voor de specialisatie van WS soorten. Ik ontwikkelde daarvoor een ex-situ transplantatie experiment om na te gaan of WS zaailingen verschillen in de volgende variabelen: overleving, productie, verlies en groei van bladeren en herbivorie vergeleken met TF zaailingen. Bovendien, keek ik of er verschillen waren tussen de seizoenen. Om dit te bepalen, selecteerde ik 12 soorten uit bossen op wit zand en meer kleiige bodems en vergeleek hen gedurende 13 maanden, om de groei van zaailingen in de hoogte (RGRH) en bladoppervlak (RGRLA), herbivorie, bladverlies en aangroei vast te stellen. In deze vergelijking liep het droge seizoen van juni tot september en het natte seizoen van oktober tot januari. Ook heb ik de stugheid van bladeren van WS en TF soorten onderzocht. Ik vond dat WS zaailingen significant stuggere bladeren hadden dan TF zaailingen. De zaailingen sterfte was hoger in klei dan in zanderige bodems, wat misschien gerelateerd is aan het hogere bladverlies in kleigrond voor alle zaailingen, hoewel TF zaailingen significant meer bladeren verloren dan WS zaailingen. Dit beïnvloedde ook de groei. Vandaar dat RGRH hoger was in WS zaailingen dan in TF zaailingen. Ik vond ook hogere ratio’s voor herbivorie in TF dan in WS zaailingen in beide bosstypen en bodems. Herbivorie was hoger in het regen seizoen dan in het droge seizoen en tijdens het regen seizoen vond ik ook een lagere RGRH en RGRLA.

Hoewel herbivorie vaak is geassocieerd met sterfte (Fine et al. 2004), is er geen duidelijk verband tussen beide gevonden. Het lijkt er op dat stugge bladeren een voordeel opleveren voor WS zaailingen omdat ze minder last hebben van herbivorie in vergelijking met TF zaailingen. Dit resultaat bevestigt de ‘trade off’ tussen verdediging en groei. Omgekeerd beïnvloed het regenseizoen de prestaties van zaailingen in beide grondsoorten negatief. Dus de prestatie van zaailingen in het bos wordt niet alleen beïnvloed door de groeiplaats van de soort en het type bodem, maar ook door het seizoen.

In hoofdstuk 5 tenslotte stelde ik vast dat WS soorten het beter doen onder droge condities, in een klei- of zandbodem, dan TF soorten in een ex-situ experiment. Tien zelfgemaakte bedden met verschillende bodems werden aangelegd in een open gebied van het Zafire Biological Station; vijf werden gevuld met klei uit een TF bos en vijf met zand van een WS-bos. In elk bed werden zes individuen per soort en per bos geplant. Ik vergeleek de prestaties van geplante zaailingen van verschillende oorsprong in verschillende bodems, en vergeleek ook de prestaties van zaailingen met andere zaailingen die groeiden onder natuurlijke omstandigheden (droogte versus natuurlijk). Gedurende een periode van meer dan een jaar heb ik maandelijks het watergehalte op beide lokaties en bodems en gemeten. Daarnaast heb ik van de zaailingen de RGRH, RGRLA, herbivorie, bladverlies, blad aangroei, stengel volume en het watergehalte gemeten. Ik vond dat zandgronden altijd droger waren dan kleigronden. Onder natuurlijk omstandigheden werden geen verschillen in grondwatervolume gevonden. Alleen tijdens het natte seizoen vertoonden de zandgronden een iets hoger watergehalte dan de kleigrond, wat verklaard zou kunnen worden door slechte drainage door de harde ondergrond. Ook waren er significante verschillen tussen de behandelingen natuurlijk versus droog. Het bodemwatergehalte in klei onder natuurlijke omstandigheden was hoog gedurende het hele jaar en gedurende het experiment.

Bodemvochtgehalte en sterfte van zaailingen toonden een sterke correlatie met elkaar en de hoogste sterftecijfers werden gevonden toen de bodem onder natuurlijke omstandigheden met water verzadigd was en ook wanneer het bodemwater bij droogte zeer laag stond. Er werden geen significante verschillen gevonden in mortaliteit tussen zaailingen van verschillende groeiplaatsen (WS of TF bossen) en onder verschillende behandelingen. Zoals verwacht, nam het aantal dode zaailingen toe in de tijd maar deze toename was groter onder natuurlijke omstandigheden dan onder droge omstandigheden. Onder droge omstandigheden en groeiend op kleigrond stierven aanzienlijk meer TF zaailingen dan WS zaailingen. Het feit dat WS zaailingen later dan TF zaailingen stierven, suggereert dat ze meer droogte tolerant zijn.

RGRH was aanzienlijk lager onder droge dan onder natuurlijke omstandigheden. Er waren ook verschillen in de groei in de tijd en we zagen dat WS zaailingen meer groeide dan TF zaailingen gedurende een periode van ten minste vijf maanden, vooral wanneer ze groeiden op een zandige bodem. Hoewel we geen significante verschillen in de totale RGRH of bladoppervlak tussen de oorsprong van zaailingen vonden, bleek dat de zaailingen beter groeiden wanneer ze waren geplant in hun 'eigen' bodem, en meer bladeren verloren in de contrasterende bodem. TF zaailingen bleken meer stengelvolume te hebben dan andere zaailingen ongeacht de behandeling. Onder droge condities, stengel volume en de relatieve groei van het bladoppervlak waren voor alle zaailingen hoger dan onder natuurlijke omstandigheden.

Onze bevindingen ondersteunen de opvatting dat wit zand bossen een kenmerkende flora met enkele dominante boomsoorten hebben die de dynamiek van de standplaats bepalen. Droogte lijkt invloed te hebben op herbivorie. In het in situ experiment (hoofdstuk 4), zagen we een hogere mate van herbivorie in zowel het droge als het regenseizoen ook onder natuurlijke omstandigheden (zie hoofdstuk 5). Er werden geen significante verschillen gevonden in herbivorie bij zaailingen geplant in verschillende bodems. In tegenstelling tot andere experimenten met WS soorten (Fine et al. 2004), hebben we geen duidelijke relatie gevonden tussen herbivorie en mortaliteit. Het blijkt dat herbivorie minder effect heeft op de overleving van een soort in de Colombiaanse Amazone, zoals was gevonden door Stropp et al. (2013) in de bovenloop van de Rio Negro dan in de Peruaanse Amazone waar Fine zijn experimenten heeft uitgevoerd.

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I am very happy with what I have achieved during the development of this thesis, and especially for the multiple inquires that have now been coming in. The offer to develop a doctorate in 2006 came from NUFFIC, through a larger Project program that was established to support the development of the campus of the National University in Leticia. In 2004, I had created a research group and a biological station, therefore, when I accepted that offer, it served a dual purpose: to strengthen my research group, while developing my doctoral research.

Even though it sounded exciting, many things have been more difficult than I had originally anticipated. I never realized the effort, especially the *inner strength* that this project would require from my son and me. Long stays far apart, when I had to travel from one site to the other to work, that meant he had to move to new cities, enter new schools and make new friends. For that reason, the completion of this **doctorate is mainly thanks to him**.

As I mentioned, I was working in 2006 on strengthening the Zafire biological station, and I was working on a concomitant program to monitor four types of forests there. I have been working with students on topics related to the primary productivity and structure of those forests since then. One of the forests is a white sand forest that fascinated me in many ways; I have always seen them as remnants of the Guiana shield and I am still curious to know where these very specific species originate from, how they work and how they are different from the species of the forests that surround them. Therefore, I saw this doctorate as an opportunity to learn more about that type of forest.

I wanted to work in a research group where more students were learning about white sand forests, as a way to better understand these forests and also to extend the horizons of my research group. That was the main reason that I began to look at the Plant Ecology and Biodiversity group at Utrecht University, which meant that a change would have to be made to the initial terms of the grant and which took some time and effort to start.

During the transition process, I had the opportunity to meet René Boot, who offered to be my promoter and helped me join the Plant diversity group of Utrecht University. I sincerely thank him for his serenity and his ability to keep me on my feet. I enjoyed our discussions about academics and life and our common worries about ethics, education and conservation. At Utrecht University, Hans ter Steege agreed to be my co-promoter and I am extremely grateful to him. I have truly enjoyed our discussions about my experiments, and also the time we spent sharing many stories of life in the forests, his experiences about being a teacher in these times of easy-fast information and also his efforts to introduce me into "R"; Many thanks to him.

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I would also like to thank INRENA in Peru and Corpoamazonia in Colombia for processing the research licenses that were necessary to develop the work into the forest. In Corpoamazonia, I really thank the assistance of Alejandra Galindo.

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I would also like to give my heartfelt thanks to my sisters Esperanza and Claudia, and my niece Maria Camila for loving and taking care of my son when I was in Ucayali installing and re-censusing the plot, or looking for other white sand spots in the Rio Purité, or establishing the plot in Araracuara or in Utrecht during the short stays. Their love and help have been essential for the development of this thesis. I also would like to thank my father Héctor and my brothers Mauricio and Oscar and the rest of my family who despite being physically far away, sent me good wishes and thoughts, which were vital for my emotional well-being.

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Curriculum Vitae

Maria Cristina Peñuela Mora was born in Bogota. She received her BSc degree in Biology at the Los Andes University in 1989. She assisted and participated in various projects in the Colombian Amazon that gave her the opportunity to travel through many rivers and experience the great diversity of the Amazon. Walking through the Serrania Taraira and the Cerro Yupati in 1989 awakened her interests about their origin, and also about the origin of other remnants of the Guiana shield in Colombia. This encouraged her to contribute to building the Puerto Abeja biological station at Serrania del Chiribiquete in 1990, when she was working with the Puerto Rastrojo Foundation.

From 1989 to 1994, she worked on the plant characterization of Cahuinari and Chiribiquete National Parks. In 1991, she was awarded a WWF and British council grant, to compare botanical material from these parks in the Kew and New York Botanical Garden. In 1995, after travelling 4000 km from the Orinoco to the Amazon and Caquetá rivers, which brought her a more vivid experience of the structure, plant formations and people using these resources, she started her greatest adventure and the new project of being a mother.

She was hired by the National University of Colombia in Arauca in 1997 and in 1999 she was awarded a Fulbright scholarship and obtained her MSc degree in Forest Resources Management at the College of Environmental Sciences and Forestry at the State University of New York (SUNY-ESF) in August of 2001.

Public order problems in Arauca forced her to move to the University campus in Leticia in 2003. Her experience and interests in the Amazon, and a lingering dream that came from her field trips with Jaime Cavelier and “Caturo” Mejia from Los Andes University, inspired her to start a Biological station in that area in 2004 the Zafire Biological Station and the Laboratory of seeds and forestry at the University campus in Leticia which are both considered platforms for developing integrated research the components and functionality of the Amazon forests and, to train and learn from the local people and students. Her interest in studying Guayana remnants pushed her to work on white sand forests, part of which is detailed in her doctoral research.

Her main interests are to understand the dynamics and ecological functioning of Amazonian forests, to support research in that area, especially that which will help to develop ways of rational management and conservation of their species and ecosystems.

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