Master Thesis

‘From a pasture to rainforest’

Performance of native tree species in ecological restoration of tropical lowland rainforest, Costa Rica

(Case study)

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Abstract

Recreating high-diversity tropical rainforests through reforestation is challenging because suitable seed or seedling material is difficult to obtain, and because the performance of many tree species is little known. In 2010/11, nearly 4500 seedlings of 81 rainforest species had been planted on c. 4.8 ha of abandoned pasture in La Gamba, SW Costa Rica. Plants had been obtained from a nearby rainforest as seeds or seedlings and pre-grown in a nursery over several months. About one year after planting we evaluated survival and growth of seedlings of 31 species to identify environmental conditions that affect seedling performance and differences among species. Overall mean height was 1.4 m, ranging from 0.5 m (when plants may not have grown in height at all) to 8.0 m (*Ochroma pyramidale*). Total mortality was low (16%, range: 5 – 42%), >80% of the surviving plants appeared healthy, and herbivory affected only a few pioneer species (*Ochroma, Inga, Vochysia*). Conditions that fostered seedling survival and growth differed among species, but generally favourable were location in a flat area or on lower slopes, and with intermediate levels of light (i.e., moderate shading by surrounding plants). For the various topographic positions (flat terrain, lower-, middle- and upper slopes, ridges/hilltops) at different levels of light, an assortment of species was recommended for reforestation, depending on the most favourable conditions for growth. Of all trees planted at La Bolsa, 89% belonged to 31 species, and many of the abundant species found in local natural forests were lacking. The resulting species diversity was therefore not as high as in forests, but the reforestation plot is likely to provide a framework for the invasion of additional species from the adjacent forest. These first data can serve as a baseline to monitor trees over the following years, and provide useful information on suitable species and site selection.

Zusammenfassung

Die Wiederherstellung eines artenreichen tropischen Regenwaldes stellt eine Herausforderung dar, weil passende Samen und Setzlinge schwer erhältlich sind und die Eignung vieler Baumarten für die Wiederbewaldung bislang unzureichend erforscht ist. 2010/11 wurden in La Gamba, SW Costa Rica, ca. 4500 Setzlinge von 81 Baumarten auf ca. 4,8 ha aufgelassener Weidefläche gepflanzt. Das Pflanzmaterial stammte großteils aus dem umliegenden Regenwald und wurde in einer Baumschule einige Monate lang vorgezogen. Etwa ein Jahr nach der Auspflanzung wurden Überleben und Wachstum von 31 Arten unter den unterschiedlichen vorherrschenden Umweltbedingungen evaluiert. Die Baumhöhe variierte zwischen 0,5 und 8,0 m, der Durchschnitt betrug 1,4 m. Die Gesamtmortalität lag bei 16% (artspezifisch verschieden, von 5 – 42%), mehr als 80% der überlebenden Pflanzen waren gesund. Von Herbivorie waren nur wenige Pionierarten betroffen (*Ochroma, Inga, Vochysia*). Je nach Baumart wurden unterschiedliche Umweltfaktoren als begünstigend für das Wachstum festgestellt, allgemein waren Standorte im flachen Gelände oder Unterhang sowie mittlere Lichtintensität besonders günstig für viele Baumarten. Für die verschiedenen Standorte im Gelände (Ebene, Unter-, Mittel-, Oberhang, Kamm), kombiniert mit unterschiedlichen Lichtintensitäten, wurde eine Auswahl an Arten präsentiert, die sich für die Wiederbewaldung jeweils besonders gut eignen. Die gepflanzten Bäume setzten sich zu 89% aus 31 Arten zusammen, während viele der besonders häufigen Arten der lokalen Waldgesellschaften fehlten. Dennoch bietet die Fläche wahrscheinlich eine ausreichende Grundstruktur für die Einwanderung weiterer autochthoner Baumarten aus den angrenzenden Waldflächen. Diese erste Erhebung kann als Grundlage sowohl für weiteres Monitoring in den folgenden Jahren, als auch für eine passende Arten- und Standortauswahl bei künftigen Wiederbewaldungsprojekten dienen.

Content

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1 INTRODUCTION

1.1 Current Issues in Reforestation

The worldwide primary forest loss of approximately 0.4% per year, especially of tropical rainforests, has been on-going for decades (FAO, 2010). Large areas of primary forest have been lost due to the conversion of forest into other forms of land use, illegal logging, the massive economic interests of the timber processing industries and the resource extraction (e.g. Bauxite). Unsustainable use of deforested lands leads to degradation of soils and often results in abandoned pastures. Thus, further use of the remaining land is limited, leaving reforestation a reasonable option. Within the reforestation efforts, different goals can be distinguished. Establishing plantations with fast growing timber species is by far the most economic and popular solution. This lead to a situation in which by now about 42% of worldwide plantations consist of the few genera *Tectona, Eucalyptus, Pinus, Hevea and Acacia* (FAO, 2000). For reforestation with ecological objectives, financial incentives are necessary.

As the primary rainforest decreases, the ecological functions of secondary forests become more important (Chazdon et al., 2009). Therefore, reforestation efforts should meet more requirements than fast timber production (e.g. Breugel et al., 2011, Hall et al., 2011). Some projects aim at the recovery of biodiversity by re-establishing forest cover (e.g. Lamb et al., 2005, Benayas et al., 2009). Others are trying to restore the high-diversity native tropical forest (e.g. Rodrigues et al., 2009, Wishnie et al., 2007) or to improve connectivity in rural landscapes (e.g. DeClerck et al., 2010). Another objective is to enhance carbon sequestration for climate change mitigation (e.g. Silver et al., 2004, Lal, 2008). It can be also an important aspect to support resident native communities in a sustainable way by reforestation with an adapted species mix (Montagnini and Jordan, 2005).

Lamb (2011:136ff) differentiates three approaches: “Reclamation” means to overcome extremely degraded site conditions by planting few suitable species (often exotic) to stop the degradation process. (This can also result in monocultures or mixed timber plantations). Secondly, “rehabilitation” is the approach to use a mixture of native and exotic species being either economically or ecologically necessary to create a secondary forest cover. The most complex goal is probably to restore a deforested area to its presumed original conditions called “ecological restoration” (Lamb, 2011); see also Chazdon (2008, restoration staircase). When the ecosystem´s natural recovery from disturbances will be much retarded or fail, different restoration strategies and techniques can be applied to accelerate succession and biodiversity (Rodrigues et al., 2009, Holl et al., 2000).

In the past decades, theory and techniques of ecological restoration have changed fundamentally in the course of increasing experience and ecological knowledge. At the beginning (1980s), restoration projects intended to ‘copy’ natural forests, but this turned out to be a costly practice. The main focus has become to restore the basic ecological processes of the forest by the stimulation and acceleration of natural succession, aiming at recovering the forest´s ability to self-maintain. Thus, restoration is now understood as a non-deterministic process influenced by stochastic events with no guarantee to lead to any single pre-defined climax (Rodrigues et al., 2009). Concepts of native forest cover restoration now try to integrate “conceptual community assembly rules” as guidelines (Breugel et al., 2011, Lamb, 2011, e.g. SER – Society for Ecological Restoration International Science & Policy Working Group, 2004). There are numerous challenges in the field of ecological restoration. Most secondary forest systems need very much time to become similar to a primary forest ecosystem. Some of the species that inhabit particular sites are quite rare in terms of the number of individuals (widespread or even locally endemic). Many species also have a highly specialized ecology that is very difficult to restore (Lamb, 2011) (such as unique mycorrhizal associations (Urgiles et al., 2009) or specialized animal depending pollination or seed dispersal mechanisms). In practice, impaired natural succession can make re-establishing woody species on degraded pasture lands a slow process (e.g. Griscom and Ashton, 2011). Challenges are dominating invasive plants (such as grasses, e.g. Hooper et al., 2004, Jones et al., 2004), lack of seed dispersal without adjacent forest, as well as poor microsite conditions for seed germination (e.g. Holl et al., 2000). Although ecological restoration is difficult, considering the rapid loss of biodiversity and forest cover, it has to be regarded an important objective (Lamb, 2011).

A crucial point for all reforestation efforts is species selection. To avoid expensive trial and error methods in reforestation projects, detailed knowledge about species performance is needed. There is already well-founded information available for species of silvicultural interest, especially for few largely used exotic genera, as well as some fast growing Mesoamerican species (e.g. *Terminalia amazonia, Vochysia spp., Calophyllum brasiliense*). The vast diversity of native tree species has come into focus due to the growing ecological interest (e.g. Montagnini et al., 2005, Lamb, 2011, Hall et al., 2011, Haggar et al., 1998, as well as Diemont et al., 2011 who focussed on Mayan traditional agroforestry knowledge). Especially for reforestation methods aiming at acceleration of biodiversity, the use of native species is essential. The performance and growth preferences of neotropical tree species are in the course of evaluation in Central and South America (e.g. in Panama since 2003 by the course of the PRORENA trials of the Smithsonian Tropical Research Institute and Yale School of

Forestry and Environmental Studies), (see also Breugel et al., 2011, Wishnie et al., 2007, Piotto, 2007, Piotto et al., 2004b).

Despite these efforts, the knowledge about native species is still limited, and the usefulness of many species for reforestation remains to be investigated. In addition, it is difficult to predict species performance for a specific site because of the varying conditions in the complex tropical ecosystems. Thus, different (local) experiences are important and need to be examined to support successful reforestation practice.

1.2 Relevance of Reforestation for Costa Rica

In Costa Rica especially in the 1960s to the 1970s, the areas covered with forest ecosystems greatly decreased. In 1977, 42% of the national territory was covered with forests, but by 1987, the forest area was reduced to 25% (Vargas, 1993, in: Morera and Romero, 2008). This was a result of the above mentioned motives (Rosero-Bixby and Palloni, 1998, Lutz et al., 1993, Sader and Joyce, 1988). Meanwhile, the country counteracts the Mesoamerican trend to forest loss with a growth of 0.9% per year in the decade 2000-2010 (FAO, 2011). Clear cutting was prohibited by the forest law of Costa Rica (Weissenhofer et al., 2008a) and also reforestation programs and incentives contributed to this development (Piotto et al., 2003b, Montagnini et al., 2005). Today, the major part of the remaining forest area is protected by National parks.

In Costa Rica, the creation of national parks has basically been an effective conservation tool (DeClerck et al., 2010, Arturo Sánchez-Azofeifa et al., 2003). However, the current biodiversity research emphasizes the necessity of spatial links between protected areas to guarantee dispersal and genetic exchange (Bennett, 2003, Harvey et al., 2008). Therefore, initiatives to create biological corridors were launched. One result is the “Mesoamerican Biological Corridor” (MBC) project (Garcia, 2008, Morera and Romero, 2008, Diemont et al., 2011), aiming at the spatial connection of protected areas throughout whole Mesoamerica (Costa Rican areas included). In this regard, reforestation contributes to connectivity of biological corridors, even though there are also many other objectives as above mentioned.

1.3 Biological Corridor and Reforestation in La Gamba

Referring to the MBC, connectivity and reforestation is also discussed on the regional and local scale. This study focuses on the local level, around the small village La Gamba, located in the Golfo Dulce region, approximately 8 km NNW of the small harbour town Golfito at the Pacific Coast. The village has about 700 inhabitants and still no paved street leads there. It is

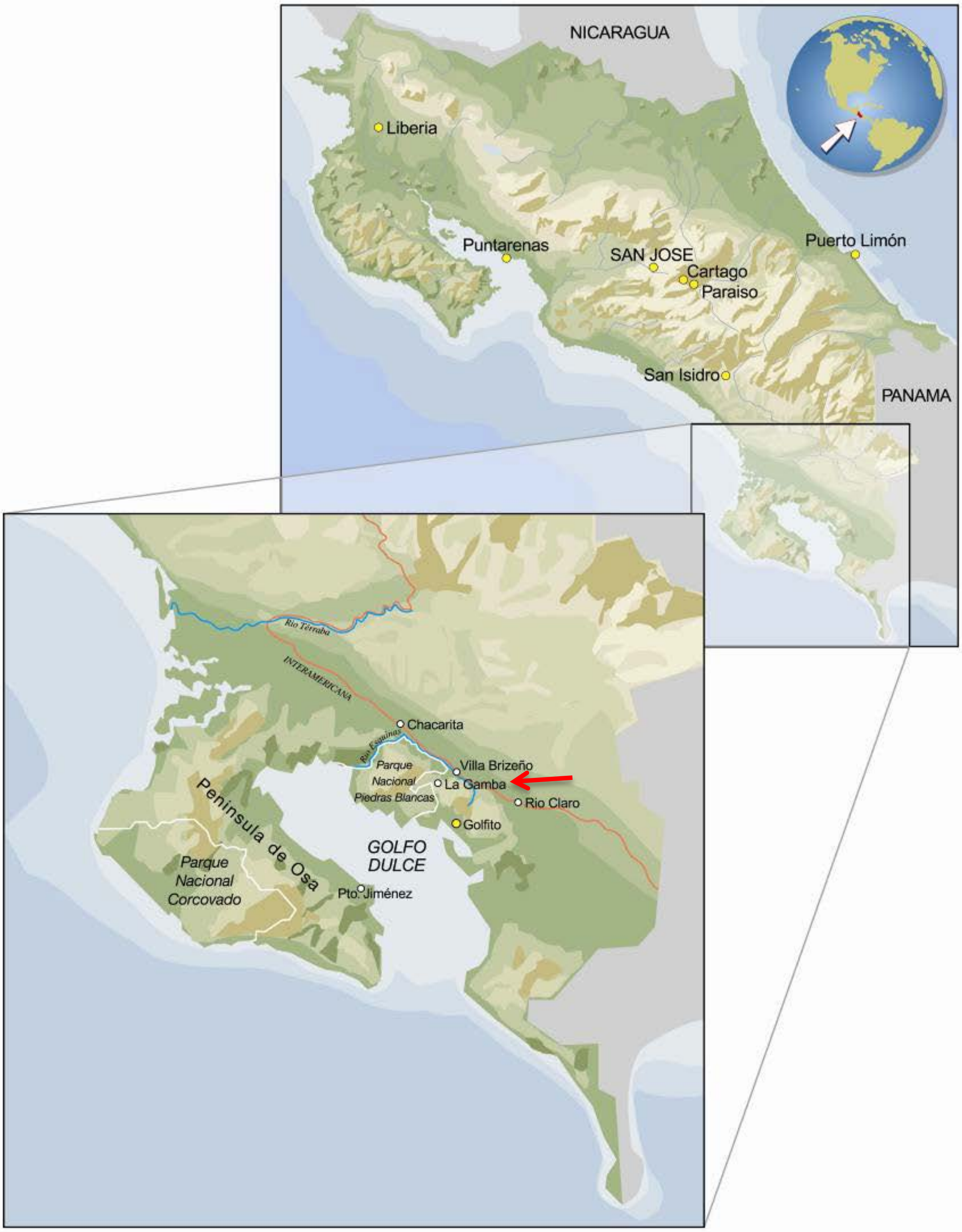


Fig. 1: Map of Costa Rica and the Golfo Dulce region in detailed view. The study area is located in La Gamba (arrow), (Weissenhofer et al., 2008c, modified).

surrounded by pastures and some oil palm plantations. The slopes of the nearby hills are covered with the Esquinas Rainforest (which has a total extension of c. 142 km^2). Parts of the Esquinas Rainforest belong to the Piedras Blancas National Park (NP), which covers approximately 150 km^2. It is known as one of the species-richest forests in Central and South America, with up to 180 tree species per hectare (Weissenhofer et al., 2008b).

At the Tropical Station next to La Gamba, reforestation projects have also become one focus of research (Weissenhofer et al., 2008a). By the use of aerial photos, forest cover of the whole Piedras Blancas NP forest was examined. It appeared to be coherent in the centre, but in the "Bosque Esquinas"-part, the periphery is interspersed with agricultural fields. To improve the coherence of the "Bosque Esquinas", reforestation projects were initiated by the association "Rainforest of the Austrians" and put into practice in cooperation with the Tropical Station. In this context, the "Biological Corridor La Gamba" -Project (COBIGA – Corredor Biologica La Gamba) was launched to deal with single reforestation areas comprehensively within a superordinate project. The aim of COBIGA is to link the Piedras Blancas NP with the unprotected mountain rainforest of the Fila Cal. COBIGA itself forms part of the larger Amistad-Osa Biological Corridor (AMISTOSA) that connects the Piedras Blancas NP with Corcovado NP on peninsula Osa and the La Amistad International Park (PILA) in the Cordillera de Talamanca. The main idea is to enhance genetic exchange between lowland and montane rainforest and enlarge the separated forest patches in between these areas (Weissenhofer et al., 2013).

1.3.1 Land uses around La Gamba

The flat surroundings of the village were affected by clear cutting in the 1950s, when United Fruit Company (UFCO) entered the region for banana cultivation. When UFCO left the region in 1986, plantations were converted into pastures and rice fields. Several sites fell into disuse (Weissenhofer et al., 2008b). The production of the African oil palm (*Elaeis guineensis Jacq.,* Arecaceae) has been rising steadily since its introduction into the Golfo Dulce region during the 1950s. On former pastures, palm plantations were created. By 2008, it had already become the second most land use type. This new cash crop development profoundly affects the economic situation of the local community as well as it alters the landscape structure. Despite an arboreal vegetation, African oil palm plantations can neither offer the same habitat and functions as a rainforest nor serve as biological corridors connecting forest patches. The forest patches have been affected by a decrease of connectivity owing to this land use conversion (Höbinger, 2010). Thus, reforestation, along with enrichment plantings in agro-silvicultural systems, represents an important step to increase the connectivity of the forest, but competes with the expansion of oil palm plantations.

1.3.2 Reforestation sites in La Gamba

The Tropical Station La Gamba is trying to integrate the local community into the COBIGA-project by supporting them to make use of national reforestation incentives. Until 2012, several farms ("fincas") of different sizes (in total approximately 30 ha) have been integrated into the project and reforested with the aid of a local forest engineer (Weissenhofer et al., 2013). One of these fincas has been “La Bolsa”. Originally, the approximately 13 ha big area was purchased by the Association for the Conservation and Protection of the Esquinas Rainforest in Costa Rica (“Regenwald der Österreicher”). Between May and November of 2010, saplings from around 80 species have been planted on about 4.8 ha that were used as a cattle pasture before (Jenking, pers. comment). As the site is very heterogeneous, seedlings were planted over a wide range of microsites and ecological conditions.

1.3.3 Objectives of this thesis

The aim of this thesis is the evaluation of species performance on the finca La Bolsa and to estimate the reforestation success in the initial phase (first 2 years). Survival and condition of the trees per species will be examined to figure out if they were appropriate for the site. Further consideration will be given to the intensity of herbivory on the different species, as well as to the impact of competitive ferns and grasses on tree growth. Additionally, the species mix will be compared with reference ecosystems to figure out whether main elements of the references are included or not. Issues of the applied reforestation strategy will be examined in the light of current reforestation theory and methods.

The final goal is to assess which species are suitable for reforestation in the area of La Gamba as accurately as possible. and to determine the conditions that may support or reduce seedling survival. Consideration will be given to factors which potentially affect growth, especially light availability and topography. Thereby it will be discerned, which of the planted species are more sensitive to special site conditions in terms of light and morphology of the terrain and which are less “specialized”. The findings of this study can serve for further reforestation projects where these species could be planted.

2 STUDY AREA

La Bolsa lies approximately 2 kilometres outside the village of La Gamba, at the very end of the cultivated part of „Quebrada Bolsa“, where a small river flows. The plot is borders to secondary forest; the other surrounding areas are characterised by pastures, oil palm- and teak plantations (Fig. 2).

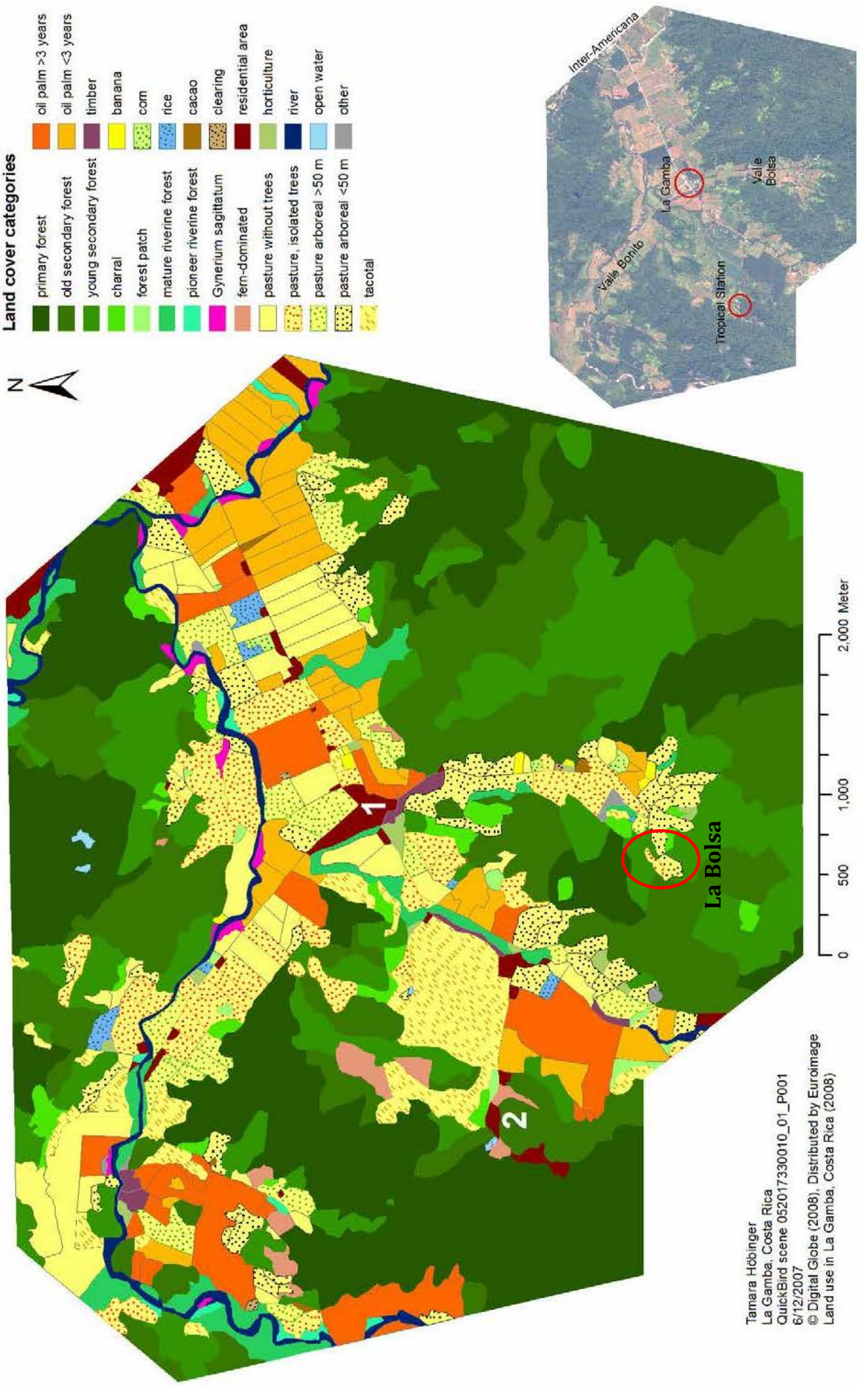


Fig. 2: Land cover map of La Gamba (2008). Village (1), Tropical Station (2), (Höbinger, 2010, modified).

2.1 Climate

Costa Rica lies within the intertropical convergence zone (ITCZ) which is a major factor for precipitation levels and wet and dry seasons in the tropics. Subsequent climate data is cited from Weissenhofer and Huber (2008), who describe the Piedras Blancas rainforest as one of the wettest lowland forests in Costa Rica and the whole of Central America. Extremely high precipitation is typical for the region of Golfito due to nearby mountain ranges (Cordillera de Talamanca, Fila Cruces). To highlight climatic particularities, I refer to data collected at the Tropical Station La Gamba from the period 1999 – 2007 (Weissenhofer and Huber, 2008): Average annual precipitation was 5836 mm, within 246 – 302 rainy days (per year). It rained most from August to November, while the dryer season ranged from January to March (still >100 mm monthly precipitation). Then there is also a period with less rain in July called “Veranillo” (“little summer”).

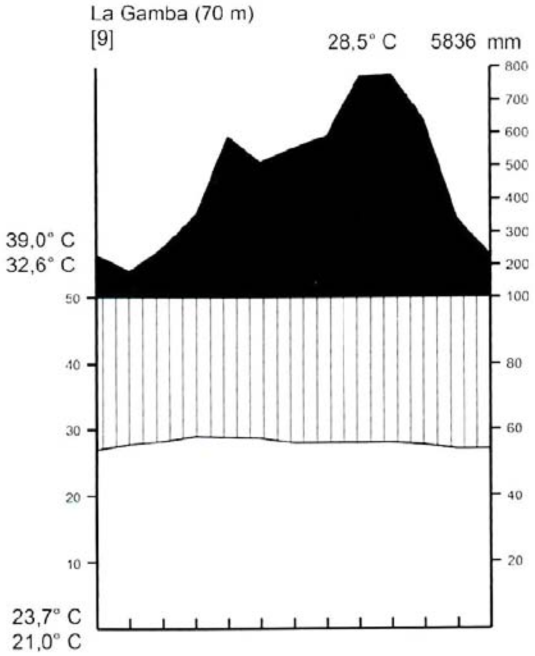


Fig. 3: Climate diagram, Tropenstation La Gamba, 70 m above the sea level (Weissenhofer and Huber, 2008).

Relative humidity was continually high, ranging from 80% in semi-open areas (measured at La Gamba) to 97.7% in the closed forest (measured by Aschan, 1998). The average yearly temperature was 28.5 degrees and monthly temperatures were fairly even which is typical for lowland equatorial climate. In April and May, the highest monthly temperatures occurred with 29.1° C, while lowest average temperatures were measured in December (27.3° C). Changes of daily temperature (based on monthly averages) in the rainy season were low, but during the dry season it varied from 10 to 15 degrees. Maximum temperature within a day was 39° C. Especially in January, February, March, September and December diurnal temperatures varied most.

2.2 **Soil**

For an introduction to the rainforest soils from the Golfo Dulce region can be referred to Pamperl (2001a): The tropical climate is the most important factor for pedogenesis in the Golfo Dulce region, characterised by deep-reaching chemical weathering of the original rock and the soil itself. The high precipitation is still shaping the topography: fine soil material is eroded from the surface and washed away creating steep slopes that are typical for the region (inclinations up to 60% and more). The upper soil layers of the slopes are highly dynamic, so lateral soil movement in many places results in a "staircase relief". Pedological conditions vary across relatively short distances in steeply dissected areas. Predominant soil orders of the Golfo Dulce region are Ultisols, Inceptisols and Entisols (the latter will not be explained any further because it does not occur at La Bolsa), (Vasquez Morera, 1989 in: Pamperl 2001a). Ultisols are most common wherever cretaceous volcanic rock is present as parent material and the terrain is heterogeneous. This soil order contains old, highly weathered, clayey soils with characteristic yellowish-red colour. The subsoils of Ultisols are strongly acidic. The main fraction of the soil body consists of the clay mineral Kaolinit, which has a low nutrient retention capacity (CEC), but a nutrient supply being slightly higher in the surface horizon due to decomposition of leaf litter.

On very steep slopes and ravines, soils of yellowish-brown colour prevail. These soils are categorised as Inceptisols which are of younger age and therefore, less weathered. Inceptisols contain weatherable clay minerals with a nutrient retention capacity moderate to high. A more detailed analysis of local soils was carried out by Pamperl (2001), as referred to in chapter 5.4.1.

At La Bolsa, two predominant soil types were identified by Chacón and Jenking Aguilera (2010). To investigate soil properties for reforestation, 22 samples were taken within a grid of approximately 3 ha. As a result, Andic dystrudept (Fig. 4) was found to cover 29% and Typic hapludult (Fig. 5) 71% of the sampled area (Fig. 6).

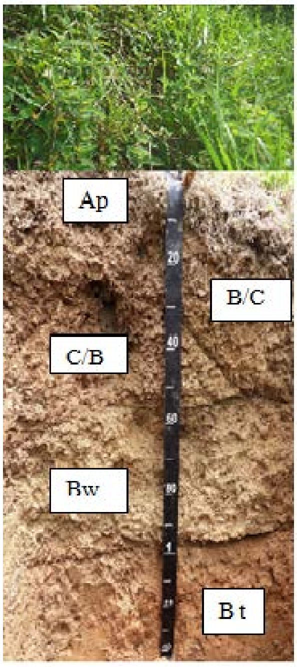
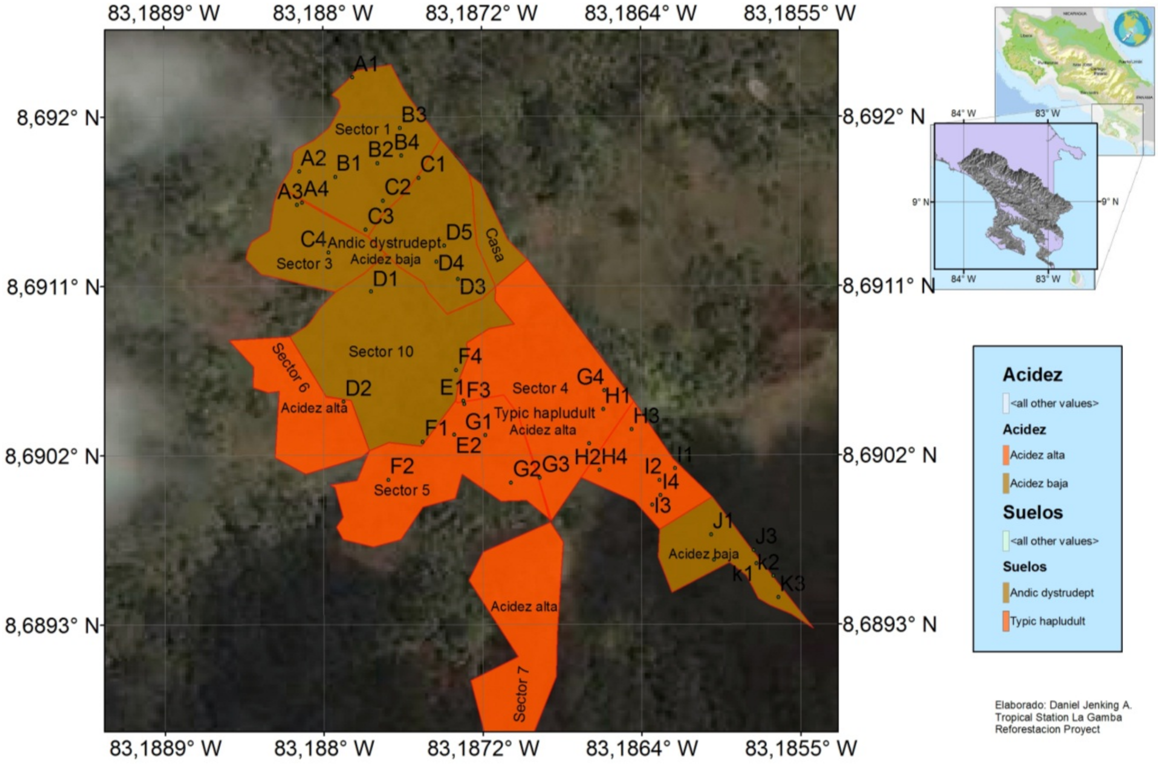


Fig. 4: Andic dystrudept. Profile n°3 in area 1, 22.05.2010. Hilly terrain, slope aspect SO, inclination 75%, horizons Ap, B/C, C/B, Bw, (Chacón and Jenking Aguilera, 2010).

Fig. 5: Typic hapludult. Profile n°2, in area 3, 22.05.2010. Hilly terrain, slope aspect SO, inclination 50%, horizons Ap, Bt1, Bt1/Ct1, Bt/Ct2, (Chacón and Jenking Aguilera, 2010).



Elaborado: Daniel Jenking A.
Tropical Station La Gamba
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Fig. 6: Soil map. Brown = Andic dystrudept, orange = Typic hapludult, (Chacón and Jenking Aguilera, 2010).

Within the classification “Keys to Soil Taxonomy” (Soil-Survey-Staff, 2010), Andic dystrudept belongs to suborder Andepts of the order Inceptisols. “Andic” means that the soil properties are influenced by the volcanic origin of the parental materials. A dystrophic character indicates low inherent fertility and/or a strongly weathered profile. The portion of organic carbon within Andic dystrudept is below 25% of its weight. Subsequently, only the soil properties of the horizons that are in reach for tree roots (in this case: Ap, B/C and C/B) are summarised from the study of Chacón & Jenking Aguilera (2010): The soil horizons consisted of 54 – 57% sand, 21 – 28% clay and 16 – 24% silt with the subsoils more clayey. The horizons were easily penetrable for plant roots (72 – 85% penetrable) and had good drainage properties. The pH-value was 4.1 – 4.4. Basically, nutrients for plant growth were available but washed out easily. Chemical analysis indicated that the average content of bases (Ca, Mg, K, Na cations) per horizon was 21.8 cmol (+)/kg. For the Ap-horizon, the Phosphorus content (2 mg/l) was very low, but Fe (116 mg/l) and Mn (64 mg/l) occurred in a very high concentration (limiting plants growth. The content of organic matter within the Ap-horizon was high (>7.2%) and approximately 1.4% in the other horizons. The described soil was classified as VI within the Costa Rican categories for agricultural use (clases de uso de Tierra, decreto ejecutivo n° 20501-MAG-MIRENEM, 1991, in: (Decreto-Nº23.214/MAG/MIRENEM)). This category means that the soil is suitable for silvicultural use or permanent cultures such as coffee and fruits, but intensive care is inevitable. Chacón and Jenking Aguilera (2010) considered land use at La Bolsa to be further limited because of the steep relief and the climatic conditions. Still, they recommended planting woody species which require better soil conditions (nutrients, drainage) on this soil type than on the subsequently described one.

The second soil type encountered at La Bolsa was Typic hapludult. It belongs to the group of Udults which again form a suborder of Ultisols. Typic hapludult is only described as fulfilling none of the criteria for other Udult-subgroups (Soil-Survey-Staff, 2010), what makes a precise characterisation difficult. In the similar Australian Soil Classification, “haplic” means “the major part of the upper 0.5 m of the soil profile is whole coloured” glossary (DEPI, 2013). For la Bolsa, Chacón & Jenking Aguilera (2010) presented the following details: Typic hapludult contained 45% clay in the subsoil (higher than for the previous described type). Only the Ap-horizon had a higher content of sand (60%, clay 28%, silt 12%). This soil type had poorer drainage properties and was little less penetrable by plant roots (67 – 77%) compared to the other type. A small buffering capacity of the soil was indicated by a pH-value between 4.0 – 4.3, and the content of bases was very low (average per horizon was 2.7 cmol (+)/kg), especially the underlying horizons were extremely washed out. The Phosphorus content in the soil solution was very low too (1 mg/l). Organic matter within the Ap-horizon amounted to 9.4% and 1.8% for the lower horizons. The high content of Fe (206 mg/l in the Ap-horizon) was visible by the red colour of the soil what pointed to strong leaching and weathering processes. Aluminium was not measured, but as the predominant mineral was Kaolinit (CEC 1:1), high concentrations were assumed for the local conditions. Therefore, the conditions for plant growth were considered to be less favourable than for Andic dystrudept. For this soil type, pasture- or silvicultural use was found to be suitable (clase V de uso de Tierra, decreto ejecutivo n° 20501-MAG-MIRENEM, 1991, in: Decreto-Nº23.214/MAG/MIRENEM).

The largest flat area at La Bolsa (sector 10) probably had divergent soil conditions because it was crossed by two creeks that had caused alluvial horizons and also soil compaction occurred in some parts (Jenking, pers. comment).

2.3 Characteristic vegetation assemblages and forest structure

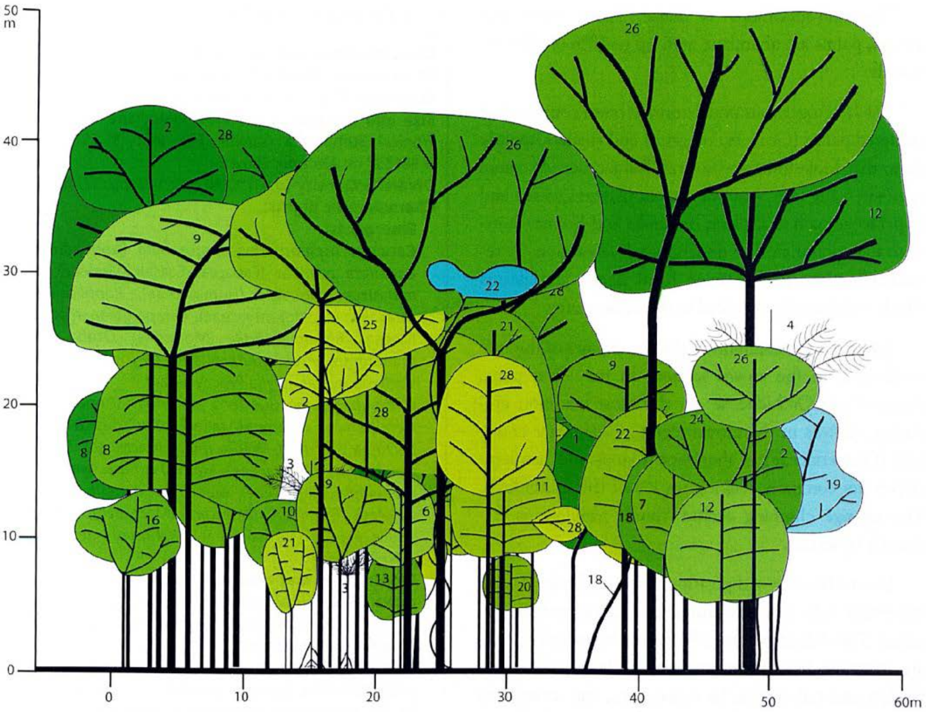
The extraordinary high biodiversity of the Costa Rican Neotropical forests was described by many authors (see Huber et al., 2008, Montagnini and Jordan, 2005, Whitmore et al., 1985). Especially the tropical wet lowland forests of the Golfo Dulce area have outstanding species richness (e.g. Allen, 1956, Weber et al., 2001). Within this relatively small region, over 700 tree species were counted, what is considered the greatest diversity of tree species in all of Central America (Quesada et al., 1997 in: Huber 2005). Gentry (1982) proofed floristic affinities between the Golfo Dulce area and the South American tropical forests. The ACOSA area (Osa Conservation Area, www.costarica-nationalparks.com) shares approximately 80% of its approximately 2662 vascular plant species with Panama, 36% with the Chocó region and 47% with Ecuador (Huber et al., 2008). Of the species found by Huber (2005) in the Esquinas Rainforest, 161 (=51%) are widespread in South and Central America. The absolute species richness of the region (gamma-diversity), as well as beta-diversity (the species number which accumulates over larger landscape scales), is high (Huber, 2005). He assumed that this is caused by the high habitat heterogeneity at the regional and local scale. Floristically rich areas as the Pacific Coast or the Chocó region are associated with steep topographical gradients (elevation) and diverse geological, edaphic, and climatic conditions (precipitation levels) that are considered to be the most important factors shaping species composition and supporting high beta-diversity (Condit et al., 2002, Duivenvoorden et al., 2002, Tuomisto et al., 2003). Furthermore, the Golfo Dulce region constituted a natural refuge in glacial periods without connection to the mainland. This is believed to be an additional cause for accelerated speciation and endemism (Huber, 2005).

For this thesis, the floristic composition of the Esquinas Rainforest in the nearness of the study site is of interest. Weissenhofer et al. (2008b) investigated ecosystem diversity for the whole of the Piedras Blancas National Park as well as the Esquinas Rainforest. They distinguished 28 vegetation assemblages ranging from primary rainforests through riverine vegetation, mangroves, coastal and beach vegetation to secondary and anthropogenic vegetation. Characteristic vegetation assemblages nearby La Bolsa (that will be referred to later), are “primary forest on hilltops and ridges” (2.3.1), “forest on inland* slopes” (2.3.2) and “secondary forests” (2.3.3). The following descriptions summarise these type definitions of Weissenhofer et al. (2008b). (*in contrast to coastal slopes)

2.3.1 Primary forest on hilltops and ridges

For ridges at 200 m altitude or higher with dry climatic conditions, a vegetation type referred to as “primary forest on hilltops and ridges”, is common (Weissenhofer et al., 2008b), Fig. 7. It is described to be well structured, up to 50 m tall and is considered to be the most species- and individual-rich forest type found in the region. 179 different tree species and 847 individuals (diameter in breast height (d.b.h) >10 cm) were counted at a 10 x 50 m plot next to the Fila trail (Huber, 2005, Weissenhofer, 2005). Palms were abundant with up to 10% of all individuals (*Welfia regia, Oenocarpus mapora, Socratea exhorriza*, mostly in the mid-subcanopy). During the dry season, some of the species even drop their leaves. Tree-fall-gaps due to the wind- and rain-exposed ridge position are common and support a highly dynamic forest ecosystem.

In a large enough natural forest gap, conditions (sunlight, temperatures, humidity) come close to those of open clearings so that species with high light requirements can establish (e.g. *Cecropia* species – Urticaceae). Also palms of the mid-subcanopy (e.g. *Socratea exhorriza* and *Welfia regia* – Arecaceae) are very common in gaps, as well as long-lived pioneer species (e.g. *Aspidosperma spruceanum* – Apocynaceae) that are able to survive several stages of succession until a mature forest state. The understory is described as diverse and dominated by fast-growing giant herbs, palms and natural regeneration of tree species. Ferns appear frequently at highly dynamic forest sites (e.g. *Metaxya rostrata* – Metaxyaceae, *Nephrolepis pectinata* – Oleandraceae and *Polybotrya cervina* – Polybotryaceae are mentioned as abundant fern species at ridges).



Profile diagram 1: Forest on hill tops and ridges. Fila trail, near Esquinas Rainforest Lodge. E 256932 m, N 962246 m. Altitude: 230 m. The strip is 50 m long and 10 m wide. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Tapirira myriantha* (Anacardiaceae), **2**. *Aspidosperma spruceanum* (Apocynaceae), **3**. *Socratea exorrhiza* (Arecaceae), **4**. *Welfia regia* (Arecaceae), **5**. *Bombacopsis sessilis* (Malvaceae), **6**. *Protium costaricense* (Burseraceae), **7**. *Protium tenuifolium* (Burseraceae), **8**. *Licania sparsipilis* (Chrysobalanaceae), **9**. *Calophyllum brasiliense* (Clusiaceae), **10**. *Marila laxiflora* (Clusiaceae), **11**. *Symphonia globulifera* (Clusiaceae), **12**. *Sloanea brachytepala* (Elaeocarpaceae), **13**. *Sloanea guianensis* (Elaeocarpaceae), **14**. *Peltogyne purpurea* (Fabaceae-Caesalpinioideae), **15**. *Talauma gloriensis* (Magnoliaceae), **16**. *Henriettea succosa* (Melastomataceae), **17**. *Guarea grandifolia* (Meliaceae), **18**. *Brosimum guianense* (Moraceae), **19**. *Ficus bullenei* (Moraceae), **20**. *Virola guatemalensis* (Myristicaceae), **21**. *Calyptrantes pallens* (Myrtaceae), **22**. cf. *Heisteria scandens* (Olacaceae), **23**. *Panopsis suaveolens* (Proteaceae), **24**. *Elaeoluma glabrescens* (Sapotaceae), **25**. *Sterculia recordiana* (Malvaceae), **26**. *Qualea polychroma* (Vochysiaceae), **27**. *Vochysia ferruginea* (Vochysiaceae), **28**. *Vochysia megalophylla* (Vochysiaceae).

Fig. 7: Forest on hilltops and ridges, (Weissenhofer et al., 2008b:69).

2.3.2 Primary forest on inland slopes

Primary forest on steep slopes is characterised as little less species-rich and moister than the previous described forest type, well-structured and up to 50 m tall (Weissenhofer et al., 2008b). Fig. 8: *Brosimum utile (Moraceae)* and *Carapa guianensis (Meliaceae*) belong to the most abundant tree species (dominant) in the canopy layer, but also *Copaifera cambiar* and *Schizolobium parahyba* (Fabaceae-Cesalpinioideae) are common in some areas.

Profile diagram 2: Forest on inland slopes. Near Tropical Station La Gamba, Fila trail. E 257235 m, N 961337 m. Altitude: 266 m. The strip is 50 m long and 10 m wide. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Ardisia compressa* (Myrsinaceae), **2.** *Bombacopsis sessilis* (Malvaceae), **3.** *Brosimum alicastrum* (Moraceae), **4.** *Brosimum lactescens* (Moraceae), **5.** *Brosimum utile* (Moraceae), **6**. *Byrsonima crispa* (Malpighiaceae), **7**. *Compsoneura excelsa* (Myristicaceae), **8.** *Hirtella triandra* (Chrysobalanaceae), **9**. *Licania sp.* (Chrysobalanaceae), **10.** *Marila laxiflora* (Clusiaceae), **11.** *Micropholis melinoniana* (Sapotaceae), **12.** *Pithecelobium macradenium* (Fabaceae-Mimosoideae), **13**. *Pouteria sp.* (Sapotaceae), **14.** *Pouteria* sp.1 (Sapotaceae), **15.** *Protium* sp. (Burseraceae), **16.** *Protium tenuifolium* (Burseraceae), **17.** *Protium ravenii* (Burseraceae), **18.** *Rinorea dasyadena* (Violaceae), **19.** *Ruptiliocarpon caracolito* (Lepidobotryaceae), **20**. *Symphonia globulifera* (Clusiaceae), **21.** *Virola sebifera* (Myristicaceae), **22.** *Welfia regia* (Arecaceae).

Fig. 8: Forest on inland slopes, (Weissenhofer et al., 2008b:70).

The mid-subcanopy often has gaps and consists of many species from different families, but there is no obvious dominance of any species. In the sub-canopy layer, palms comprise up to 25% of the tree individuals (with d.b.h. ≥10 cm, especially *Iriartea deltoidea*, *Socratea exhorriza*, *Welfia regia*). The understory and forest floor are rather bare, except for dwarf-palms that are abundant (*Asterogyne martiana*, *Calyptrogyne ghiesbreghtiana*, *Geonoma cuneata*). This is believed to be caused by the steepness of the slopes and seeds and seedlings washed out by the rain.

2.3.3 Secondary forest

Secondary forests are mostly defined as vegetation assemblies that can evolve after different kinds of disturbances, either natural (e.g. storms, fire) or anthropogenic (e.g. agriculture). Succession within a primary forest will eventually lead to a more or less similar structure and species composition, whereas after long-lasting anthropogenic disturbances, new secondary vegetation assemblies develop (Ghazoul and Sheil, 2010, Chazdon, 2003, Turner et al., 1998). Chazdon et al. (2010) compared mature forest to secondary forest plots of anthropogenic origin in the lowland wet forests of Costa Rica. They designated 5 plant functional types based on growth rates of 293 tree species. Their results indicated that secondary forests are dominated by fast-growing canopy and sub-canopy species during the first 20 years of succession. In contrast, old-growth forests have a higher relative abundance of understorey trees and slow-growing canopy/emergent trees than secondary forests of c. 40 years.

Weissenhofer et al. (2008b) reported that structure and species composition of secondary forests varied strongly from site to site for the Piedras Blancas National Park, thus a detailed floristic description was difficult. They only distinguished young and old secondary forest: sensu Weissenhofer et al. (2008b), a "young secondary forest" with a canopy up to 15 m comprises several fast growing pioneer species (*Guatteria amplifolia* – Annonaceae; *Trattinickia aspera* – Burseraceae; *Vismia baccifera* – Clusiaceae; *Cecropia spp*. – Urticaceae; *Vochysia allenii*, V. *ferruginea* – Vochysiaceae). The ground layer is covered with various growth forms, particularly ferns and vines. Common families are Melastomataceae, Piperaceae, Rubiaceae, and Heliconiaceae. "Old secondary forest") was found on lateritic soils on ridges and slopes. This forest type is little structured, but dense in terms of individuals. Species of the canopy (up to 30 m tall) are *Jacaranda copaia* (Bignoniaceae), *Carapa guianensis*, *Guarea grandifolia* (Meliaceae) and especially *Vochysia spp*. (Vochysiaceae) which often dominate secondary forest sites. The mid-subcanopy is also species-poor and consists mainly of natural regeneration of the mentioned canopy species and other fast growing pioneers. The understory and ground layer are species-rich comprising many growth forms (ferns, herbs, vines etc.) and tree seedlings of advanced successional stages (e.g. *Aspidosperma spruceanum* – Apocynaceae; *Calophyllum longifolium, Symphonia globulifera* – Clusiaceae; *Ruptiliocarpon caracolito* – Lepidobotryaceae). Palms, epiphytes, hemi epiphytes and large lianas are rare in older secondary forests.

3 METHODS

This chapter contains a brief description of the plot, followed by some background information about the project realisation. Then, some pictures from field work allow a closer view at La Bolsa and its microsites. Subsequently, the method of data acquisition is explained.

3.1 Morphology of the terrain at La Bolsa

The reforestation area is mainly a basin-shaped valley, with extremely heterogeneous terrain. It changes over short distances from flat areas to steep slopes and hilltops with inclinations ranging from zero to approximately 60 degrees (Fig. 9, 10)

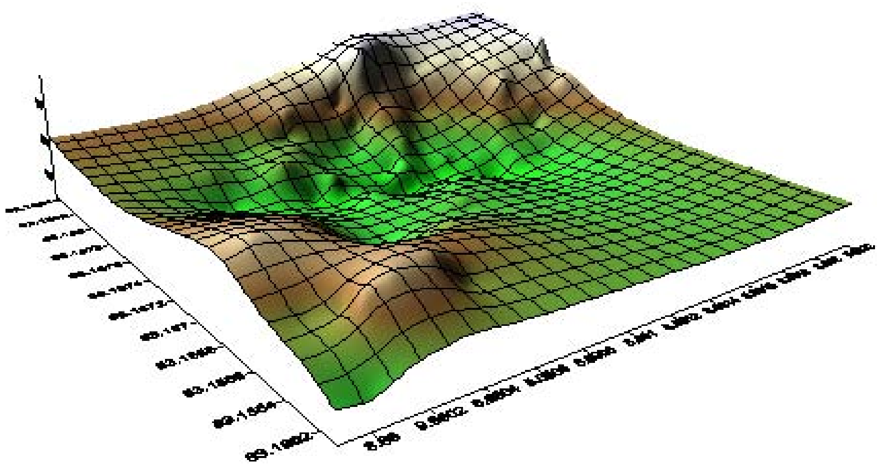


Fig. 9: Model of the terrain at La Bolsa (Chacón and Jenking Aguilera, 2010).

The area was used as a pasture for 30 years. After three months without any use, the trees were planted (Jenking, pers. comment). Grazing cattle and dynamics in the upper soil layers formed a stairway-pattern on the slopes, small terraces in horizontal lines, which were used to plant trees.

In the flat part of the basin, two creeks flow. To one side the area borders on a pasture, separated by a row of trees (mostly Eucalyptus), at the other sides the reforestation area is intermixed with adjacent secondary forest, and appears to be quite close even to primary forest (at least on one side). In general, the topography, inclination, exposition, soil conditions, and adjacent vegetation are very heterogeneous.

Fig. 10: Morphology of the terrain, draft based on personal GPS data and the soil map of Chacón and Jenking Aguilera (2010).

3.2 **Project Realisation**

To reforest La Bolsa, several steps were necessary: acquisition of seeds and trees, fertilizing, planting, maintenance. Daniel Jenking was the responsible agronomist for the realisation of the La Bolsa reforestation project. The main goal of the project was to cover the area completely with native tree species. Initially, a total amount of 6000 trees was estimated to be necessary for the task, but then the area turned out to be smaller than expected. Further goals were to use rare and endangered species and (since no information was available beforehand) to observe their performance in order to see if they were appropriate for the site (Jenking, pers. comment).

Seeds and seedlings were mainly collected on the trails nearby the tropical station (Fila trail, Bird trail) – from primary and secondary rainforest. Then they were sown in germination beds and later transplanted into black plastic nursery bags. In addition to these seedlings, raised in the nursery „Finca Modelo“ (which belongs to the Tropical Station La Gamba), many saplings of most commonly used species (e.g. *Carapa guinensis, Terminalia amazonia, Aspidosperma spruceanum, Schizolobium parahyba)* were purchased from a second nursery in San Miguel. These seeds had been obtained from the surroundings of the village San Miguel, which is situated higher in altitude and c. 127 km away from La Gamba. Therefore, the germination conditions for the saplings used on La Bolsa were probably different and could have influenced performance of trees. Some species turned out to be difficult to grow in the nursery, which reduced the variety of those planted at La Bolsa. Others were not difficult to germinate, but sensitive to transport (e.g. *Schizolobium parahyba*) (Jenking, pers. comment). In the nursery, Fertilisers were used at first to enhance root development („TECAMIN RAIZ“, composed of algae extracts, organic). When planted, each tree was supplied with 500 ml organic fertilizer (compost) as well as macronutrients (Nitrogen, Phosphorus, Potassium in relation 10:30:10). Foliar application of micronutrients was given to all planted seedlings once. Soil has not been treated any further. Some trees in bad condition were fertilized additionally at the beginning of the rainy season as a head start on succession (Jenking, pers. comment). To better organise reforestation, the area was divided into sectors of different sizes (Fig. 11). The sectors' numbers were changed during the course of the project, and I here use the new labels (1; 2 ; 2b; 2c; 2-1; 5; 6a; 6b; 7; 8; 9; 10; former names in Table 42, Appendix). Saplings at La Bolsa were planted in regular rows more or less horizontally following the contour lines with a distance between the rows of c. 3.5 m. Distance between trees within a line was c. 3 m. An exception was made in the flat area of sector 10 where 48 trees were planted in groups of 3 (*Terminalia amazonia, Carapa guianensis, Schizolobium parahyba – one individual per species*) with c. 1 m distance between the trees.

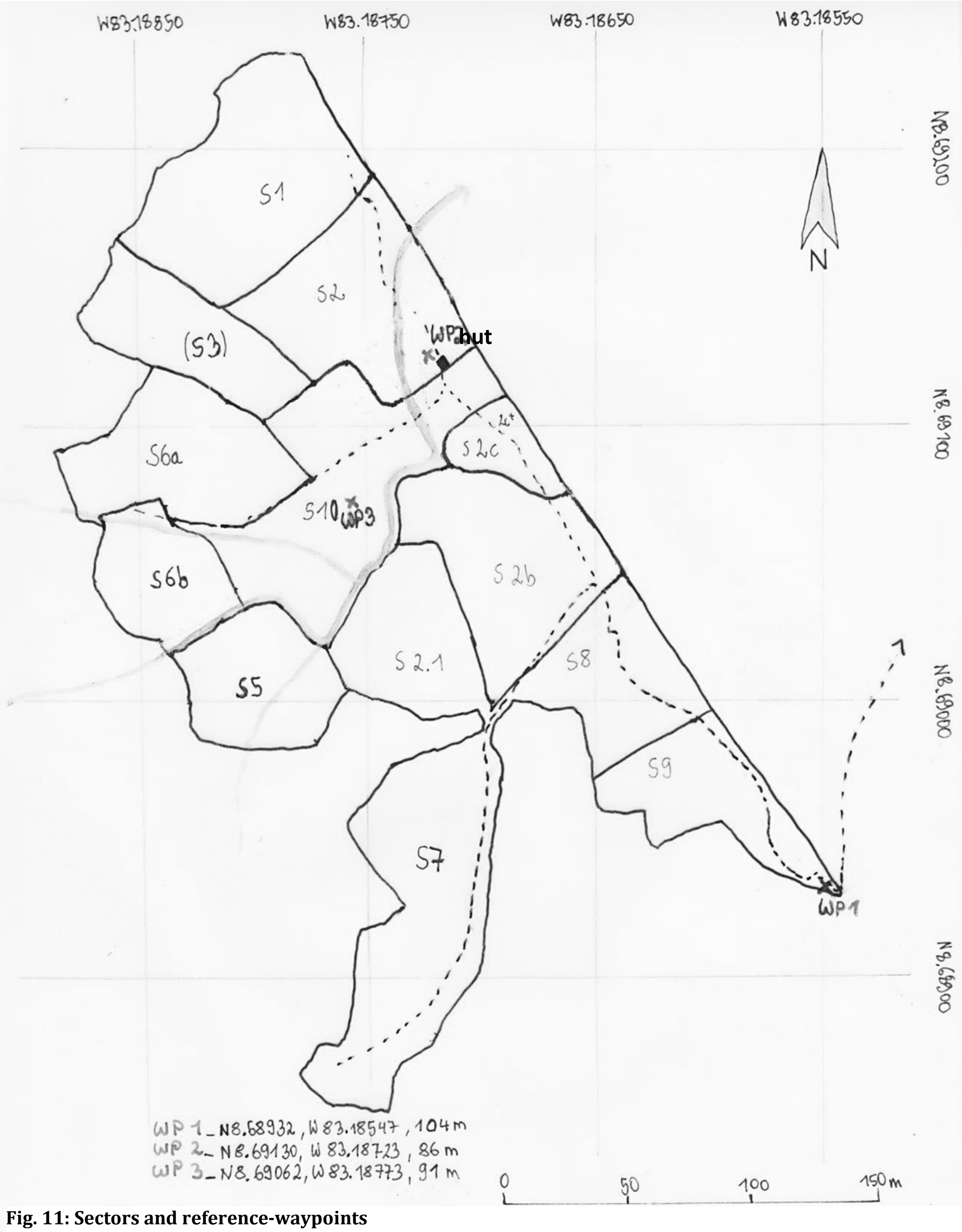


Fig. 11: Sectors and reference-waypoints

Fig. 12: Sector 1 during planting (Jenking, blog).

Fig. 13: Various trees before planting (Jenking, blog).

All trees were planted between May and November 2010. It is not documented accurately, in which order (sector sequence) the planting was carried out (Fig. 12). By the time of planting, the age of the saplings was not identical and seedling size varied between c. 20 and 60 cm, mainly because of differences in growth rates and to a lower extent because of different times in the nursery (Fig. 13). One year after planting, a total of 200 dead saplings were replaced, but species and location were not documented. During April – June 2012 naturally growing vegetation was cut back and saplings were cut free from creepers, ferns and grasses in sectors 1; 5; 6a; 7; 9; 10; 2_1; 2b; 2a. In total, all sectors were cut free two to three times since planting.

3.3 Detailed site description and vegetation at La Bolsa

The next section contains a description of the structures and vegetation encountered at the area during field work. La Bolsa borders to the forest edge, one long side adjoins to a pasture (Fig. 14, 15). Parts of La Bolsa may have been quite similar to this pasture before reforestation. La Bolsa is dissected by morphology of the terrain into several microsites: There are 3 larger flat areas (in sectors 5, 9 and 10) with parts in full sunlight as well as little to completely shaded and moist parts. The other microsites were mainly slopes with different inclination and exposition, fully or partially exposed to sunlight. Slopes in dark shade only occurred where the reforestation area merged with the adjacent forest. At the ridges/hilltops, there was hardly any shadow at all. Also, soil appeared to be drier than elsewhere (mainly in sectors 7, 9, 6a).

In the flat areas, some bigger trees grew that belonged to the old stand which contributed much to the shady conditions (Fig. 16). Many of these trees remained from former use, e.g.

Coconut palms, many Cacao trees, Guajava trees, Lime trees, *Pterocarpus officinalis, Artocarpus altissima,* Rose apple (*Syzygium malaccense*) and Cashew nut trees.

Natural succession/regeneration and planted trees already covered the former open pasture area, forming a dense thicket. Some of the planted trees stuck out remarkably high (e.g. highest individuals 16 m, *Ochroma pyramidale* next to the hut, Fig. 17). The denseness was mainly a result of the rapid natural succession between the planted rows (Fig. 18) where naturally regenerated plants overtopped most planted trees. In some sectors, different shrubs, herbs and creepers even overgrew the saplings, thus maintenance was indispensable. On the other hand, these plants had also the effect of providing shadow for the saplings.

In the flat areas, the ground was completely covered with grasses and herbs (Fig. 16), while steep slopes for most parts had less ground cover, with sometimes even the bare ground visible. An exception were slopes and hilltops with the ground affected by erosion and fully exposed to direct sunlight. These areas were covered to a large extent by clubmosses and a competitive fern species, probably *Dicranopteris pectinata* (Gleicheniaceae). (Fig. 20). It formed very dense thickets and overgrew slow growing species (Fig. 21). Similarly, breast-high competitive grasses* were overgrowing many planted trees on slopes (Fig. 22). (*different to the species in flat terrain)

Commonly observed species of spontaneous vegetation on La Bolsa were *Clidernia dentata, Clidernia capitelata, Conostegia subcrustulata* (Melastomataceae), *Piper aduncum, Piper auritum, Piper friedrichsthalii* (Piperaceae), *Vismia baccifera* (Clusiaceae), *Vernonia patens* (Asteraceae*), Cecropia obtusifolia* (Ceropiaceae), *Gliricidia sepium* (Fabaceae), *Lantana camara* (Verbenaceae).

The border of the reforestation area was not easy to define (Fig. 23). In some parts (especially sector 5, 6b), the rows ended inside the adjacent forest, what made it difficult to distinguish between planted trees and natural regeneration. In these parts, forest floor was mostly covered with litter, which in other parts was almost absent.

Fig. 14: Pasture adjoining to La Bolsa (direction NO).

Fig. 15: View across La Bolsa towards sector 1

Fig. 16: Shady part of sector 10.

Fig. 17: *Ochroma pyramidale,* hut

*in the front are planted trees, in the background, some emerging canopy trees shape the adjacent secondary forest

Fig. 18: Spontaneous vegetation at both sides of the planting row

Fig. 19: Erosion and ferns on slope in sector 2_1

Fig. 20: Ridge with clubmosses and ferns

Fig. 21: Fern, overgrowing *Peltogyne purpurea*-sapling

Fig. 22: Competetive grass species, sector 2

Fig. 23: View into adjacent forest from sector 8/9

3.4 Data Acquisition

About two years after planting, survival rates, growth and quality for the most used species were documented. Field work was conducted from April – June 2012. By means of planting lists from the sectors and some small marks at the beginning of some rows it was possible to identify the planted trees and to distinguish them from natural regenerating trees. All trees were identified, generally to the species. The height of every tree was measured from the ground to the top of the dominant apical shoot with a stick, with markings in 10 cm distances. In cases where height exceeded five meters, a laser rangefinder was used, the accuracy of which was generally >10 cm. Stem diameter was measured at a height of 50 cm and 130 cm with a calliper. Some species had a variable shape resulting in irregular measurements (e.g. the conical stem of *Pseudobombax septenatum*, or a thicker internode at the end of the highest apical shoot which constituted the thick base of the top pinnate leaf, e.g. *Carapa guianensis*).

The following qualitative or semi-quantitative parameters were also recorded:

Q = Quality: This category reflects seedling survival and a general impression of physical condition. Seedling survival was checked by comparing the existing plants to planting lists. As every three meters a tree should have been planted, obvious gaps (often with remnants of the seedling) were interpreted as missing tree. Physical condition was estimated by ramification, leaf-colour and -size as well as the occurrence of insect or fungal damage. View examples in Appendix, Fig. 45 – 56.

S = Light: This category reflects a qualitative measure of canopy density and light conditions for the seedlings. Canopy density was estimated by use of an index from 1 to 4, with 1 indicating no or little canopy space filled with leaves, while 4 indicates a filled canopy space (see Table 1; canopy closure pictures were taken to document the levels, Fig. 57 – 60, Appendix).

T = Topography: Six different positions were distinguished to describe the tree positions within the reforestation area, not in a larger landscape context.

I = Inclination of slope: To specify topography for each tree, inclination was roughly estimated in four levels.

H = Herbivory: Five levels were used to document herbivory for the majority of leaves on a tree. Leaf pictures were taken to document them (Fig. 61 – 66, Appendix).

Covered with other plants: Was annotated, when creepers, ferns, grasses, clubmosses were winding around the saplings or overgrowing them. While data was collected, parts of the area were cleared from overgrowing plants.

Table 1: Levels of the recorded factors.

Category	Description	Referred to as
Quality level of tree		
Q1	Well-ramified, normal leaf size	Very good condition (quality)
Q2	Yellow/fewer/small leaves	Good to average condition
Q3	Sparse habitus, showed problems such as die back, few (yellow) leaves, major insect or fungal damage	Poor condition, appeared to be dying
Q0	No leaves, dead stem (or missing stem)	Dead
Light level (canopy closure = canopy space filled with leaves)		
S1 <10%	No/very little shadow (high solar radiation).	Full sunlight
S2 <30%	Partially shaded by other plants, but still high direct solar radiation.	Intermediate sunlight
S3 <70%	Shaded by other plants, but canopy is permeable for light	Low sunlight
S4 >70%	Dense and dark canopy, no direct solar radiation	Strong shade
Topography level (tree is situated in ~)		
T1	Ditch (small scale)	~
T2	Flat area/terrain	~
T3	Base of the slope	~
T4	Middle slope	~
T5	Upper slope	~
T6	Hilltop/ridge	~
Inclination level (tree is situated in ~)		
I1 <4%	Plain	~
I2 <10%	Intermediate slopes	~
I3 <35%	Steep slopes	~
I4 >35%	Very steep slopes, difficult to access	~
Herbivory level (leaves affected by ~)		
H0 <2%	No herbivory	~
H1 <5%	Little herbivory	~
H2 <10%	Intermediate herbivory	~
H3 <20%	Increased herbivory	~
H4 <50%	Strong herbivory	~
H5 >50%	Extreme herbivory	~

Content of the Dataset

The dataset contains 4345 (+137 unidentified) observations of planted trees for 83 species, but less data was appropriate for use in statistical analysis. For the complete species list c.f.

Appendix, table 38. For analysis on the species level, sufficient individuals were necessary: Out of the total recorded species, only 31 contained more than 19 observations of still-living trees (with quality levels ranging from Q1 – Q3) and had sufficient height growth*. Hence species-level analysis was limited to these 31 species with a total of 3693 records. Out of these, 571 recordings (dead trees, Q0) were only used to calculate to mortality. (*For trees that had not reached 50 cm, diameter was not measured. These trees were excluded from analysis at the species level – particularly so for *Astronium graveolens, Caryodaphnopsis burgueri, Elaeoluma glabrescens, Tabebuia guayacan and Trichospermum grewifolium*.

Data that was not considered in statistical analysis:

200 trees that had died were replaced after one year. Since it is not documented which individuals were replaced, some uncertainty remains as up to 200 trees may be younger than the others. Additionally, 245 trees that could not be located or were not accessible were assigned Q0+ ("probably dead"). Palms *(Cryosphila, Asterogyne)* were too few individuals per species and do not show growth in girth (basal stem thickness). 137 trees could not be identified and therefore were not considered at all (with the majority in very good condition).

3.5 Statistical Analysis

MS Excel was used to create to summarise data by Pivot-tables and for some plots. Analyses were done in R version 2.15.2 (R-Development Core Team, 2012). One-way ANOVAs were conducted to test the influence of factors on height and diameter of trees. Graphical displays in the form of boxplots were constructed using seedling survival and seedling height as dependent variables (y-axis) and all other variables, as independent variables (x-axis) to identify trends. To obtain more balanced results, all one-way ANOVAs were conducted without *Ochroma pyramidale.* Because of its extraordinary fast growth rate, it would have imbalanced mean values for height and diameter of all species.

ANOVA-significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 (p-value ≤0.5 = significant). All summary tables (mean, SD) show all levels of the factor.

4 FINDINGS

In the subsequent sections species mix and results of tree mortality, quality and size are presented. Furthermore, the effects of light, topography and inclination on species performance are explained. Finally, herbivory and competition by other plants are considered.

4.1 Species composition

In this section, the number of trees per species in relation to the total amount of planted trees is presented. These calculations do not reflect the real distribution of individuals from a species per ha as trees were not homogeneously spread at La Bolsa.

Table 2: Selection of the 10 most abundant species.

Species portions – individuals of total	Trees alive	Per cent of planted trees alive (n=3431)	Ind. per ha
Terminalia amazonia	505	14.72%	39
Carapa guianensis	282	8.22%	22
Aspidosperma spruceanum	224	6.53%	17
Brosimum utile	197	5.74%	15
*Platymiscium spp.**	179	5.22%	14
Vochysia allenii	173	5.04%	13
Vochysia ferruginea	157	4.58%	12
*Inga spp.**	128	3.73%	10
Peltogyne purpurea	109	3.18%	8
Vitex cooperi	102	2.97%	5

**Platymiscium curuense* and maybe some individuals of *Platymiscium pinnatum; *Inga multiflora and others;*

10 species had at least 5 individuals per ha, while the others were less abundant. 15 species were represented only by one tree. For the complete species list, see Table 31 and Fig. 24 and Fig. 40 (Part II), Appendix.

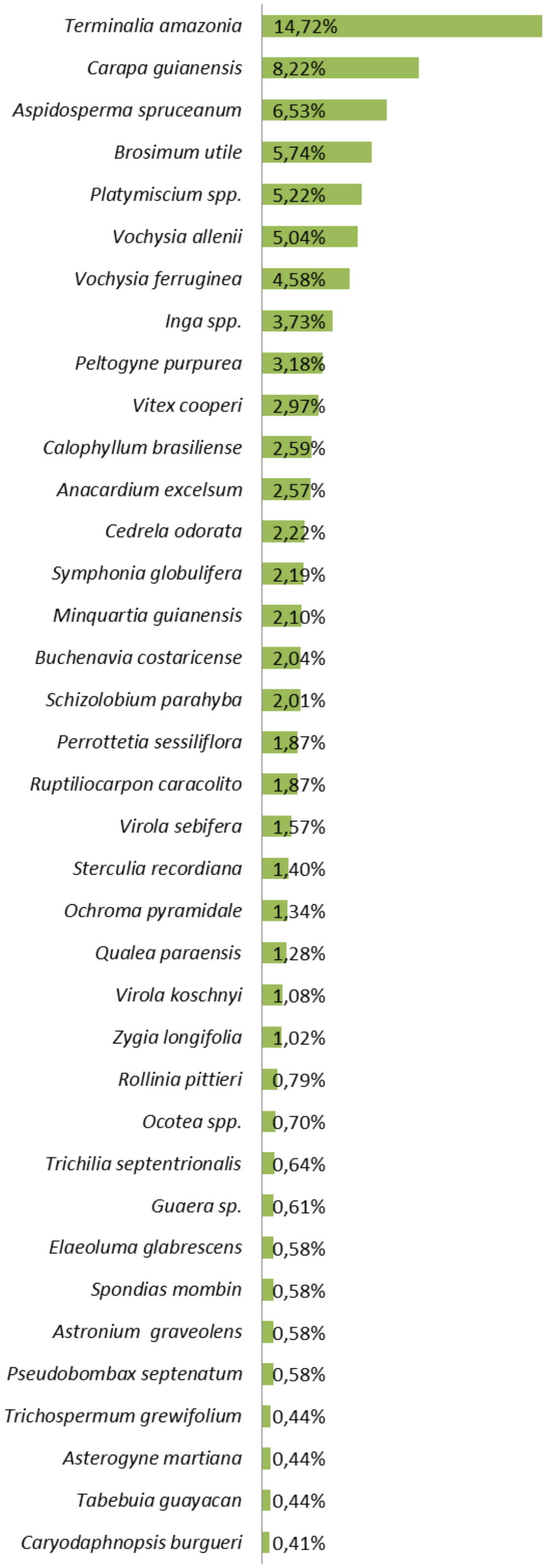


Fig. 24: Portion of trees alive per species.

4.2 Tree mortality and quality

Table 3: Number of recorded trees per quality level.

	Quality level				
	Very good c. (Q1)	Good cond. (Q2)	Poor cond. (Q3)	Dead (Q0)	N
Trees (all sp.)	2649	584	198	671	4102
Per cent	**65%**	**14%**	**5%**	**16%**	**100%**
*Trees (31 sp. with >19 individuals)	2405	536	181	572	3694
Per cent	65%	15%	5%	15%	100%
Trees (50 sp. with <20 individuals	244	48	17	99	408
Per cent	60%	12%	4%	25%	100%

Dead trees included. (*used for further analysis)

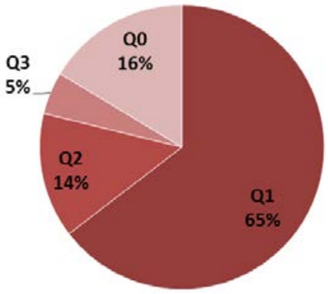


Fig. 25: Trees per level, all sp.

Most trees (considering all recorded species) were in very good condition (Q1=65%), while 14% were in good to average condition (Q2). Individuals in poor condition (Q3) amounted to 5% and 16% of all planted trees had died (Q0). For the 31 species that were selected for further analysis, the percentage of trees within the quality levels was comparable, while for the excluded 50 species, mortality was higher (25%).

Species with many individuals in good or very good condition (Q1, Q2) with also low mortality (<10% dead trees) were *Pseudobombax septenatum, Zygia longifolia, Ochroma pyramidale, Anacardium excelsum, Terminalia amazonia* and *Inga spp*. Species with an accelerated percentage of trees in poor condition (Q3 ≥7%) and mortality ranging from 16 – 27% were *Trichilia septentrionalis*, *Perrottetia sessiliflora*, *Sterculia recordiana, Spondias mombin*, *Buchenavia costaricense* and *Brosimum utile*.

Highest mortality (dead trees exceeded 29%) was shown by *Caryodaphnopsis burgueri, Schizolobium parahyba, Virola sebifera, Trichospermum grewifolium, Elaeoluma glabrescens, Tabebuia guayacan, Qualea paraensis, Minquartia guianensis* and *Virola koschnyi* (Fig. 26).

Note that species survival could not be calculated per year, because the planting at La Bolsa was carried out over six months and exact dates were not known. From the 31 selected species, 19 had an average of (82%) or even above-average survival (Table 32, Appendix).

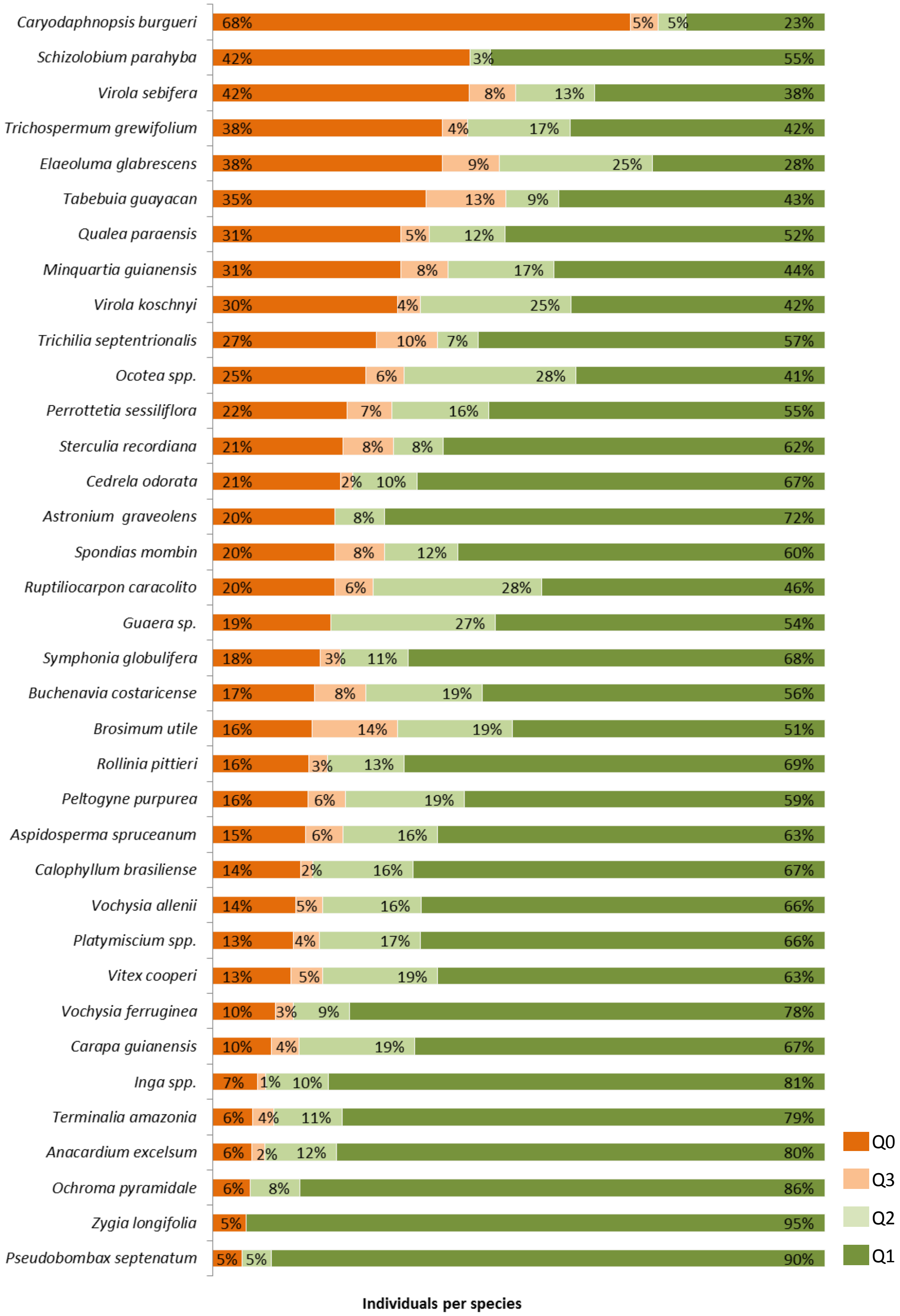


Fig. 26: Dead trees (Q0 = red) and condition (dark green = very good) of all species with ≥19 observations (n=36).From these, *Astronium graveolens, Caryodaphnopsis burgueri, Elaeoluma glabrescens, Tabebuia guayacan and Trichospermum grewifolium* were excluded from further analysis (<20 surviving individuals or no data for diameter at 50 cm). See Table 32, Appendix for details.

Table 4: Diameter at 50 cm by quality levels, n=31 species (dead trees excluded)

	Mean D50 [mm] ± SD	n
Q1	13.2 ± 12.92	2369
Q2	5.2 ± 4.97	535
Q3	3.0 ± 3.97	184

Table 5: Height by quality levels, n=31 species (dead trees excluded)

	Mean height [cm] ± SD	n
Q1	156.0 ± 116.15	2372
Q2	76.2 ± 47.89	540
Q3	54.9 ± 42.86	183

Mean tree diameter at 50 cm and stem height was variable for the quality levels. For trees with very good quality, mean diameter and height was more than twice as large as for the other levels. Trees in poor condition had the smallest mean size. Species-specific means of diameter and height for the quality levels are shown in Fig. 27.

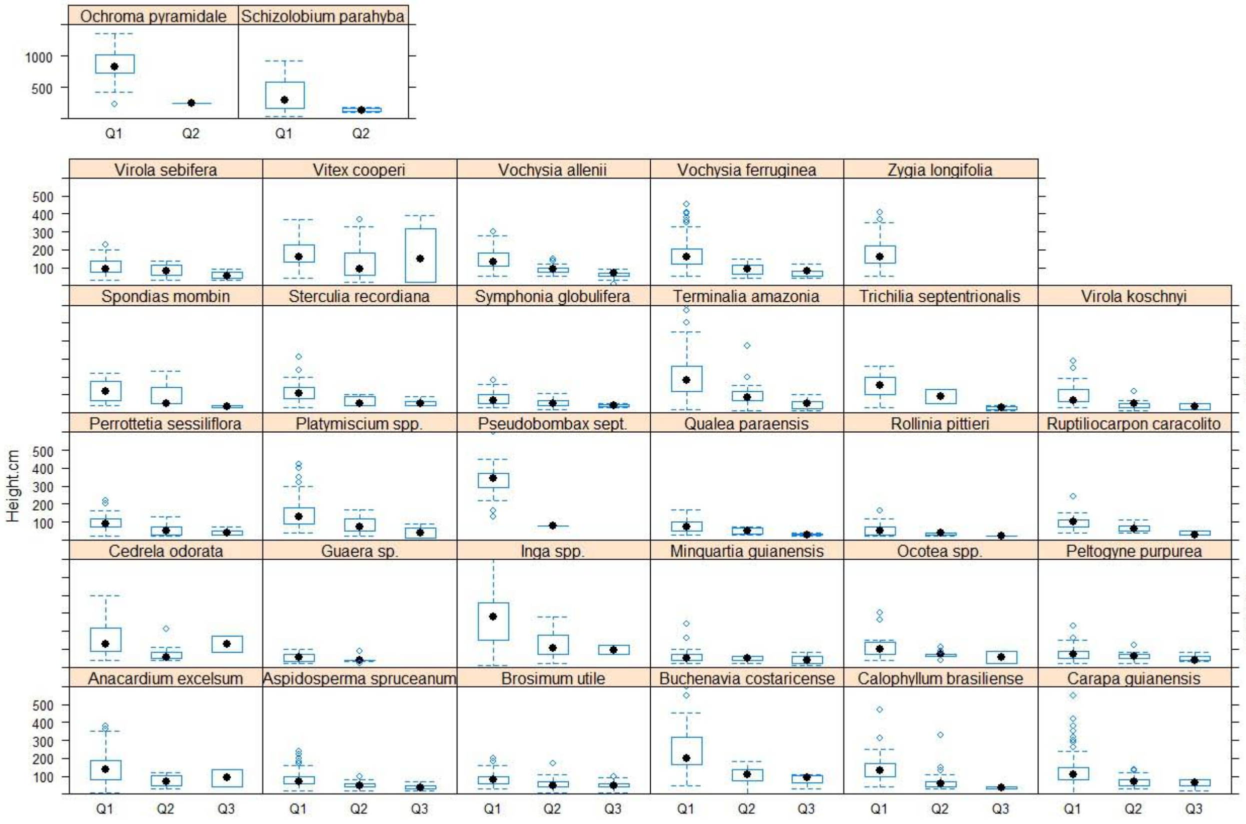


Fig. 27: Boxplots, height by quality levels for 31 species. Levels that do not contain any values are not displayed.

Generally, trees of high quality were taller than other trees, particularly so for *Vochyisa ferruginea, Terminalia amazonia, Trichilia septentrionalis, Schizolobium parahyba, Inga spp.* and *Buchenavia costraricense.* Exceptions were *Vitex cooperi* and *Cedrela odorata*. *Vitex cooperi* is deciduous in the dry season and some individuals may have been recorded incorrectly (as Q3) because they had shed their leaves. Tree species and quality had a significant effect on height (p <0.001, Table 6).

Table 6: ANOVA testing for the effect of quality on height

	Df	Sum Sq	Mean Sq	F value	p-value
Species (Sp)	30	12638962	421299	58.373	< 2e-16 ***
Quality levels* (Q)	2	2209208	1104604	153.049	< 2e-16 ***
Sp:Q	55	1093418	19880	2.755	1.29e-10 ***
Residuals	3007	21702550	7217		

*Dead trees excluded (no height values)

4.3 Tree size

The range of mean heights was 0.5 – 8.0 m, while mean diameter were 3 – 63 mm at 50 cm and at 130 cm, 1 – 6 mm.

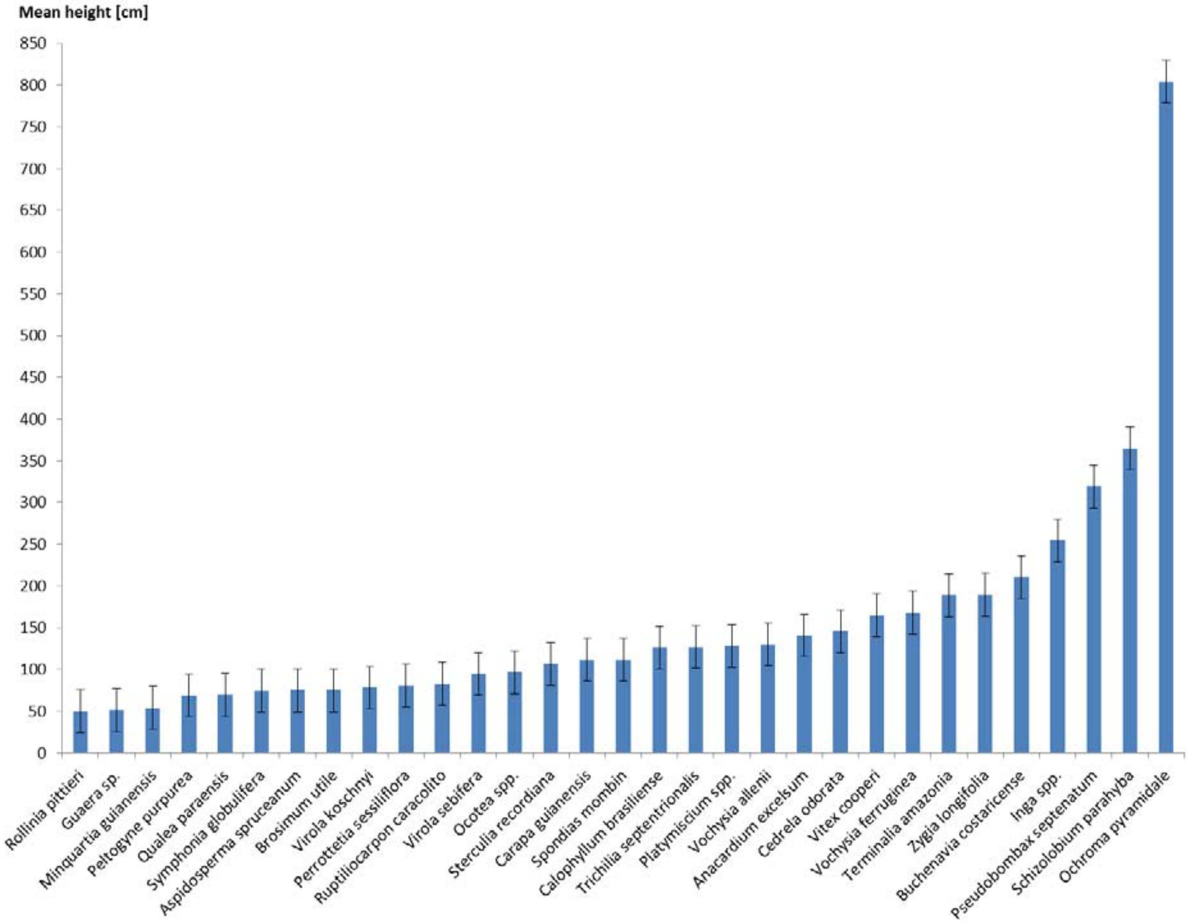


Fig. 28: Mean tree height per species (detailed numbers in Table 33, Appendix).

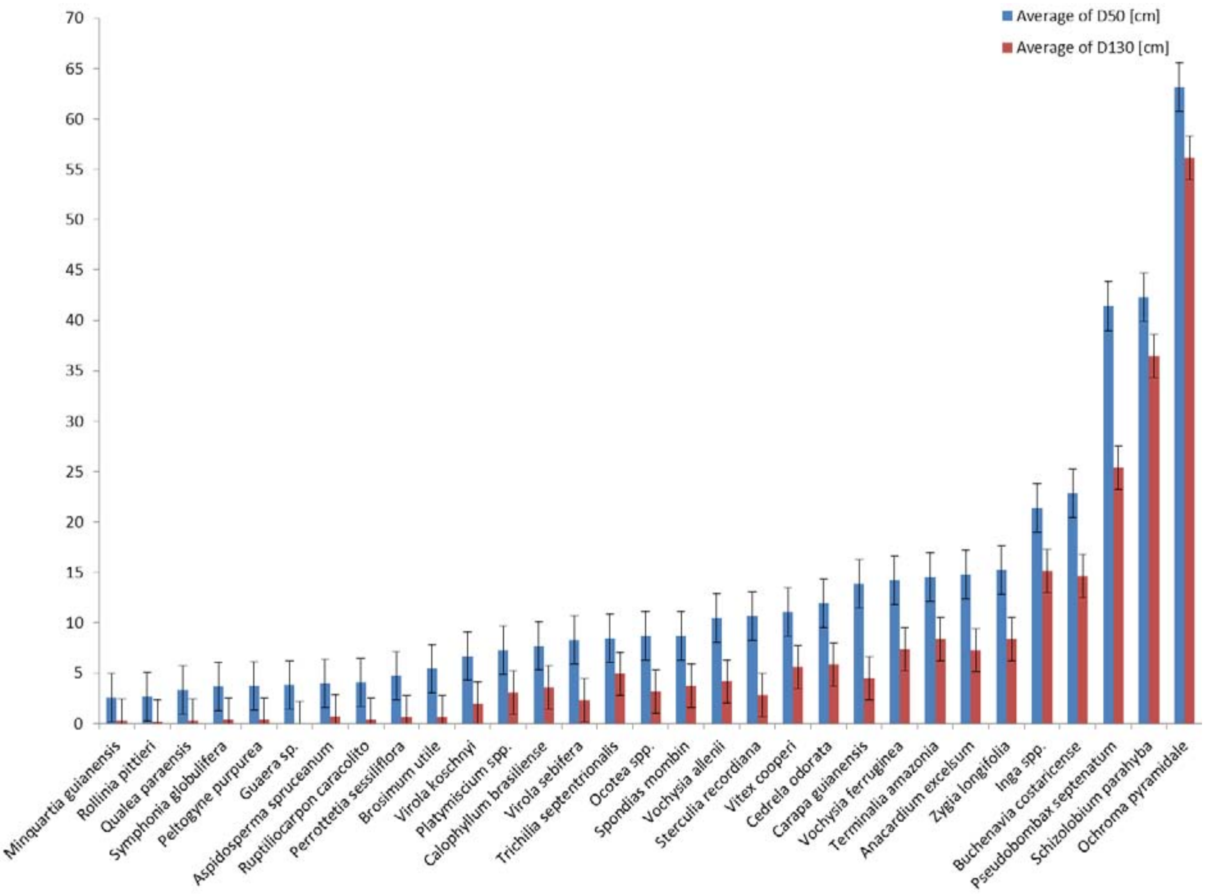


Fig. 29: Mean tree diameter at 50 cm and 130 cm per species (detailed numbers in Table 33, Appendix).

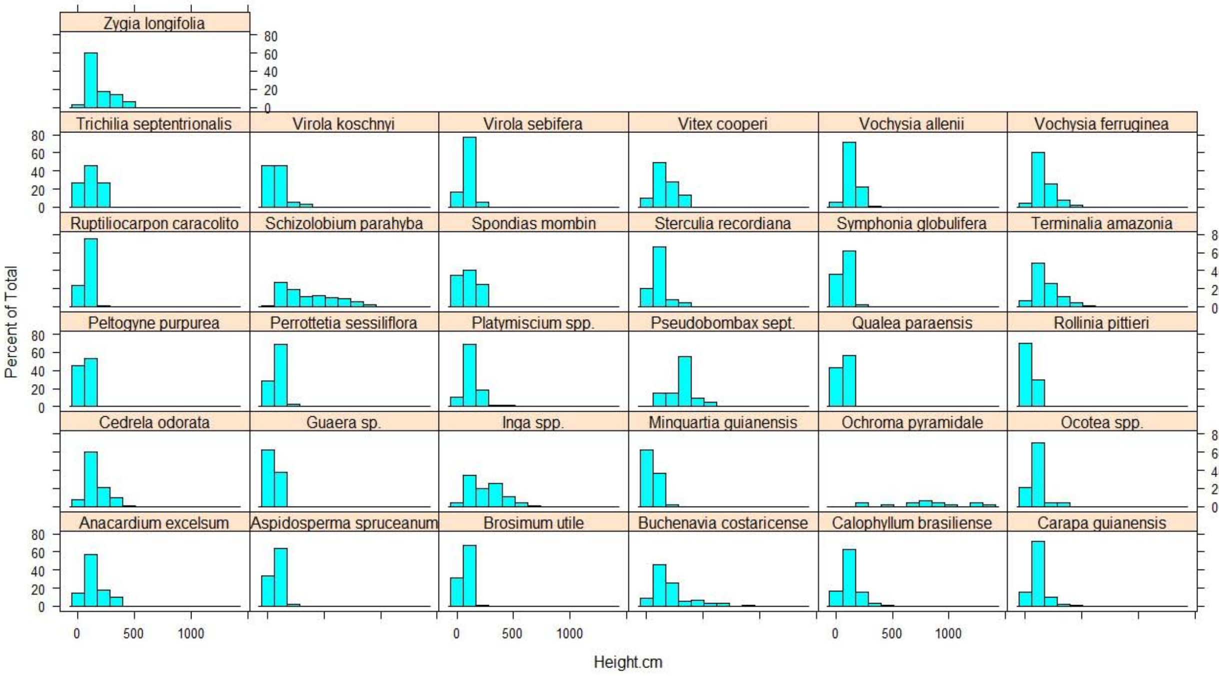


Fig. 30: Distribution of height classes per species, n=31species.

The majority of the species had not reached more than 3 m, with most individuals in the 1 – 3 m height classes.

Species were grouped by mean height into 4 classes of “very fast”, “fast” “intermediate” and “slow” growers:

Very fast “IV” (≥2 m): *Buchenavia costaricense, Inga spp., Pseudobombax septenatum, Schizolobium parahyba, Ochroma pyramidale*

Fast “III” (1.5 – 1.99 m): *Cedrela odorata, Vitex cooperi, Vochysia ferruginea, Terminalia amazonia, Zygia longifolia*

Intermediate “II” (1.0 – 1.49 m): *Anacardium excelsum, Calophyllum brasiliense, Carapa guianensis, Ocotea spp., Platymiscium spp., Spondias mombin, Sterculia recordiana, Trichilia septentrionalis, Vochysia allenii,*

Slow “I” (0.5 – 0.99 m): *Aspidosperma spruceanum, Brosimum utile, Guarea sp., Minquartia guianensis, Peltogyne purpurea, Perrottetia sessiliflora, Qualea parahyba, Rollinia pittieri, Ruptiliocarpon caracolito, Symphonia globulifera, Virola koschnyi, Virola sebifera*

Two thirds of the analysed species had slow and intermediate initial growth and one third grew fast to very fast.

4.4 **Functional traits**

Faster growing species had slightly higher survival, but the correlation to mean height was not significant (R^2=0.075, p=0.14). Furthermore, mean height was neither correlated with leaf mass per area (LMA, p=0.08405, R^2=0.1028, n=26), nor with Nitrogen content in leaves (p=0.2611, R^2=0.04487, n=21). The correlation of wood density* with tree height was not significant either (p=0.3422, R^2=0.03227, n=28; *understood as biomass invested per unit wood volume).

4.5 Light levels

Table 7: Number of recorded trees growing at different light levels

	Light level:				
	Full sunlight (S1)	Inter mediate s. (S2)	Low sunlight (S3)	Strong shade (S4)	n
Trees (All sp.)	1365	1363	1138	153	4019
Per cent	34%	34%	28%	4%	100%
*Trees (31 sp.)	1260	1238	999	126	3623
Per cent	**35%**	**34%**	**28%**	**3%**	**100%**

Dead trees included. (*used for statistical analysis)

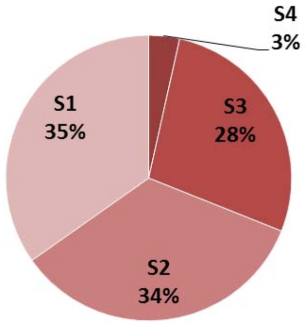


Fig. 31: *Trees per level, 31 sp.

Similar percentages of trees were recorded in full (S1), intermediate (S2) and low sunlight (S3) with fewer at the lowest light level (strong shade, S4).

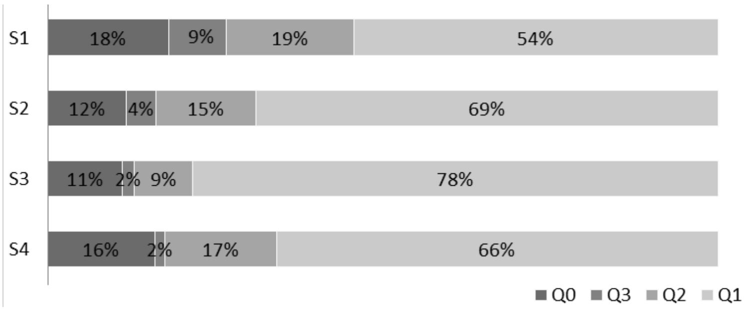


Fig. 32: Quality within the light levels

Trees that were either fully exposed to sun (S1) or growing with least light (S4) had the highest mortality (18% and 16% respectively). The highest percentage of trees in poor condition (Q3) was also recorded in full sunlight (9%). In contrast, in intermediate and low sunlight the largest proportion of trees was found in very good condition (Q1, 69% and 78% respectively).

Table 8: Diameter at 50cm by light levels, n=31 species (dead trees excluded).

	Mean D50 [mm] ± SD	n
S1	13.2 ± 15.48	991
S2	11.4 ± 10.62	1097
S3	9.3 ± 9.13	891
S4	7.0 ± 8.53	109

Table 9: Height by light levels, n=31 species (dead trees excluded).

	Mean height [cm] ± SD	n
S1	140.9 ± 123.95	991
S2	139.7 ± 10.72	1100
S3	130.3 ± 100.06	895
S4	103.8 ± 78.19	109

While mortality was high at full sunlight, mean height and diameter of all trees was also highest in full and intermediate sunlight (Tables 8 and 9). However, mean size was strongly influenced by few very rapidly growing species and species-specific mean heights varied a lot across the light gradient as presented in the following Fig. 33 as well as Table 35 (Appendix).

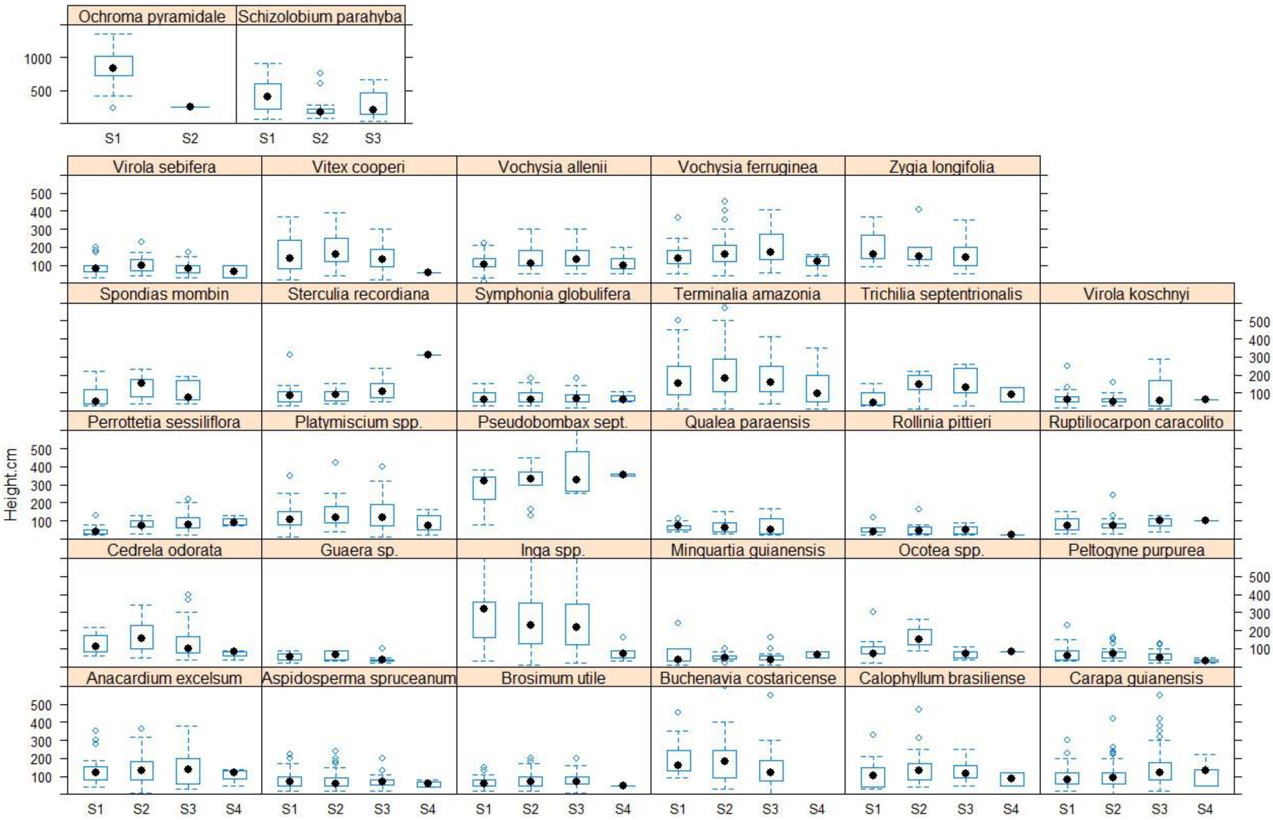


Fig. 33: Boxplots, height by light levels. Levels that do not contain any values are not displayed *(Ochroma pyramidale, Schizolobium parahyba).* The number of individuals per level differed for the species; see Tables 10 and 35 in Appendix).

Species-specific response to light was variable. For easier comparison, species were grouped in Table 10 by the light levels at which they had reached relative mean height >100% (marked green; relative mortality per level is marked grey; low height is red). *Guaera sp., Pseudobombax septenatum, Spondias mombin* had less than 30 individuals in total and therefore were excluded from Table 10, while *Ocotea spp., Rollinia pittieri, Trichilia septentrionalis* and *Ochroma pyramidale* were not considered because they had <8 individuals at 2 or more levels.

Table 10: Height (relative to species mean) and mortality depending on light conditions for trees.

	Light level					Mean height [cm]	Block	Growth class	p-value for height	p-value for D50
	Full sunlight (S1)	Inter-mediate (S2)	Low light (S3)	Dark Shade (S4)	n					
Per cent of mean height										
Mortality *					M. **					
n										
S. parahyba	**114.8%**	63.8%	83.9%		100.0%	365	S1	IV	*	**
	27.7%	54.1%	61.5%		42.0%					
	65	38	13		127					
Inga spp.	**111.3%**	99.8%	98.4%	30.8%	100.0%	254	S1	IV	*	***
	2.3%	2.0%	0.0%	33.3%	7.2%					
	43	49	32	10	142					
B. costaricense	**110.1%**	99.0%	78.2%	0.0%	100.0%	210	S1	IV		
	15.6%	8.6%	21.4%	100.0%	16.7%					
	32	35	14	1	92					
Z. longifolia	**107.3%**	104.5%	84.5%		100.0%	189	S1-S2	III		
	0.0%	0.0%	9.1%		5.4%					
	15	10	11		38					
V. sebifera	100.0%	**109.7%**	91.1%	68.7%	100.0%	95	S1-S2	I		
	50.0%	32.3%	23.8%	50.0%	41.9%					
	30	31	21	4	93					
A. spruceanum	**103.8%**	101.2%	96.4%	78.1%	100.0%	75	S1-S2	I		
	16.7%	12.5%	11.1%	14.3%	15.2%					
	84	96	75	7	279					
P. purpurea	104.4%	**115.5%**	85.8%	48.3%	100.0%	69	S1-S2	I	*	*
	18.6%	19.0%	2.6%	25.0%	15.5%					
	43	42	38	5	138					
V. koschnyi	101.1%	83.4%	**122.5%**	76.6%	100.0%	78	S1-S3	I		
	27.8%	23.5%	23.1%	50.0%	30.2%					
	18	18	13	2	58					
M. guianensis	**123.7%**	99.5%	91.0%	120.0%	100.0%	54	S1-S3	I		
	58.3%	18.4%	19.4%	0.0%	30.8%					
	24	40	36	2	109					
T. amazonia	92.5%	**112.2%**	99.0%	68.7%	100.0%	189	S2	III	**	***
	8.0%	5.9%	4.0%	0.0%	6.5%					
	177	189	149	26	572					
V. cooperi	98.1%	**110.9%**	86.6%	36.4%	100.0%	165	S2	III		
	8.9%	11.4%	19.2%	0.0%	12.8%					
	46	45	26	1	124					
C. odorata	85.2%	**117.3%**	94.0%	48.0%	100.0%	146	S2	III		**
	36.8%	3.2%	24.4%	25.0%	20.8%					
	19	31	41	4	102					
V. ferruginea	87.9%	104.0%	**120.7%**	67.9%	100.0%	168	S2-S3	III	**	
	4.5%	7.0%	16.7%	16.7%	10.3%					
	69	58	42	6	186					

A. excelsum	95.9%	100.1%	**105.8%**	73.4%	100.0%	141	S2-S3	II		
	4.0%	8.8%	6.3%	0.0%	6.4%					
	25	35	32	3	97					
V. allenii	87.9%	107.3%	**108.3%**	85.4%	100.0%	130	S2-S3	II	*	*
	23.9%	10.2%	5.3%	0.0%	13.5%					
	71	62	57	15	216					
Platymiscium spp.	92.3%	**107.8%**	105.2%	67.9%	100.0%	128	S2-S3	II		.
	12.3%	9.6%	11.5%	0.0%	13.1%					
	65	74	52	11	217					
C. brasiliense	85.4%	**112.4%**	101.1%	67.2%	100.0%	126	S2-S3	II		
	14.3%	13.3%	14.3%	33.3%	14.4%					
	35	45	21	3	105					
B. utile	88.0%	103.4%	**109.2%**	66.6%	100.0%	75	S2-S3	I	*	
	21.1%	13.2%	8.2%	33.3%	16.2%					
	76	93	61	3	248					
S. globulifera	98.1%	**100.9%**	100.4%	98.4%	100.0%	75	S2-S3	I		
	23.8%	15.6%	12.1%	25.0%	17.6%					
	21	32	33	4	97					
C. guianensis	83.8%	90.7%	**131.1%**	107.7%	100.0%	111	S3-S4	II	***	**
	10.1%	4.8%	8.1%	45.5%	9.6%					
	109	106	86	11	334					
S. recordiana	91.4%	80.6%	**110.2%**	290.6%	100.0%	107	S3-S4	II	**	*
	42.9%	11.8%	4.8%	0.0%	21.3%					
	21	17	21	1	61					
R. caracolito	97.1%	97.6%	**107.8%**	120.8%	100.0%	83	S3-S4	I		
	16.7%	20.0%	12.5%	0.0%	20.0%					
	30	31	16	1	86					
P. sessiliflora	61.0%	95.3%	**111.2%**	120.1%	100.0%	80	S3-S4	I	*	**
	52.2%	7.7%	11.6%	0.0%	22.0%					
	23	13	43	4	85					
Q. paraensis	95.9%	98.2%	**108.1%**		100.0%	70	S3-S4	I	***	***
	51.9%	9.1%	8.3%		31.3%					
	27	22	12		67					

* Mortality (in % of individuals planted per level); ** Mortality in % of all planted individuals

Significance codes: 0='***'; 0.001='**'; 0.01='*'; 0.05= '.' C.f. values in Table 37, Appendix. Grey area indicates less than 8 individuals per level, thus mortality and relative height values are not confidable in these cases. Red - blue areas indicate slow - fast growth.

<u>Six blocks could be distinguished</u> (separated with black horizontal lines), shorter horizontal lines indicate species within a block that had a different mortality-pattern (e.g. *Zygia longifolia*). Species that had relative mean height >100% in

- full sunlight and reached >2 m **= block S1**
- full and intermediate sunlight and reached <2 m **= block S1 – S2**
- different light levels and reached <0.8 m **= block S1 – S3**

- intermediate sunlight and reached <2 m **= block S2**
- intermediate and low sunlight and reached <1.7 m **= block S2 – S3**
- low light or dark shade and reached <1.2 m **= block S3 – S4**

Among all species, *Schizolobium parahyba* showed the highest relative growth in full sunlight. Nevertheless 27.7% of the planted individuals died in full sunlight and also at low light levels, this species had the highest mortality compared to the others. The second strongest increase of height growth in full sunlight was reached by *Minquartia guianensis*, despite highest mortality. In contrast, those species with lowest growth (and high mortality) at that level were *Perrottetia sessiliflora* and *Carapa guianensis*.

At low sunlight conditions, the strongest growth (relative height >111.2%) was shown by *Carapa guianensis, Vochysia ferruginea, Trichilia septentrionalis* and *Perrottetia sessiliflora.* These species had good survival in low light conditions, except for *Vochysia ferruginea*. The opposite case – lowest growth – was observed for *Buchenavi costaricense, Zygia longifolia* and *Ocotea spp.* which all had high mortality (except for *Ocotea spp.).*

At the dark shade level, *Carapa guianensis* was the species with highest relative mean height, but also highest mortality (45.5%). *Vochysia allenii* had the best survival (100%) among the species with sufficient data available and still achieved 85% relative mean height in dark shade. Other species with low mortality in dark shade were *Platymiscium spp*. and *Terminalia amazonia*, but growth decreased down to 67.9%. *Inga spp*. had worst growth (30.8%) and highest mortality (33.3%) in dark shade. Tree performance in dark shade cannot be described for the other species, because data was insufficient.

Most species had accelerated relative mean height in more than one level: e.g. *Zygia longifolia, Peltogyne purpurea* in full and intermediate sunlight (block S1 – S2) or *Brosimum utile, Calophyllum brasiliense, Anacardium excelsum* in intermediate as well as low sunlight (S2 – S3).

Similar relative mean height across the entire light gradient was shown by *Minquartia guianensis, Symphonia globulifera, Ruptiliocarpon caracolito* and *Qualea paraensis*. These slower growing species (mean heights 50 – 83 cm) only had decreased survival in full or intermediate sunlight. Other species that maintained at least >90% relative mean height at each level (except for dark shade) were *Inga spp., Virola sebifera, Rollinia pittieri, Terminalia amazonia, Anacardium excelsum* and *Platymiscium spp.* Mortality was <15.6% for these species in full sunlight with exception of *Virola sebifera* (50%).

Light conditions had a highly significant effect on diameter ($p < 0.001$) and height ($p < 0.001$) and light intensity affected species differently (species x light interaction, Tables 11,12):

Table 11: ANOVA testing for the effect of light conditions on diameter at 50 cm height

	Df	Sum Sq	Mean Sq	F value	p-value
Species (Sp)	30	170830	5694	65.299	< 2e-16 ***
Light (S)	3	3285	1095	12.555	3.72e-08 ***
Sp:S	85	19550	230	2.637	8.57e-14 ***
Residuals	2969	258910	87		

Table 12: ANOVA testing for the effect of light conditions on tree height

	Df	Sum Sq	Mean Sq	F value	p-value
Species (Sp)	30	12638962	421299	53.552	< 2e-16 ***
Light (S)	3	195871	65290	8.299	1.70e-05 ***
Sp:S	85	1396944	16435	2.089	3.51e-08 ***
Residuals	2976	23412361	7867		

For 12 species, the light levels were significant for height and/or diameter at 50 cm when testing light as a single factor, while when conducting a multi-factor Anova containing also the factor topography, the result was significant only for 7 species (*Schizolobium parahyba, Inga spp., Peltogyne purpurea, Teminalia amazonia, Sterculia recordiana, Perrottetia sessiliflora, Qualea paraensis;* c.f. Table 37 in Appendix).

4.6 Topography levels

Table 13: Number of recorded trees growing at different topographic positions

	Topography level						
	Ditch (T1)	Flat terrain (T2)	Base of the slope (T3)	Middle slope (T4)	Upper slope (T5)	Ridge (T6)	n
Trees (All sp.)	61	612	1167	942	1063	256	4101
Per cent	1%	15%	28%	23%	26%	6%	100%
*Trees (31 sp.)	54	503	1022	861	1005	248	3693
Per cent	**1%**	**14%**	**28%**	**23%**	**27%**	**7%**	**100%**

Dead trees included. (*used for statistical analysis)

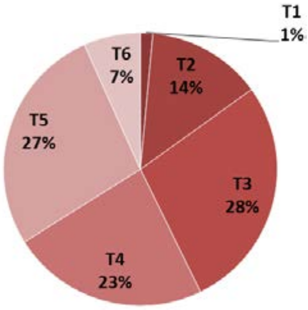


Fig. 34: *Trees per level, 31 sp.

Similar percentages of trees from the 31 analysed species were recorded at the base of the slope (28%) and upper slope (27%) and less in middle slope (23%). Only 14% of the recorded trees grew in flat terrain, while 7% were found on the hilltops and very few (1%) in the ditch. The latter were not considered at the species level (insufficient n).

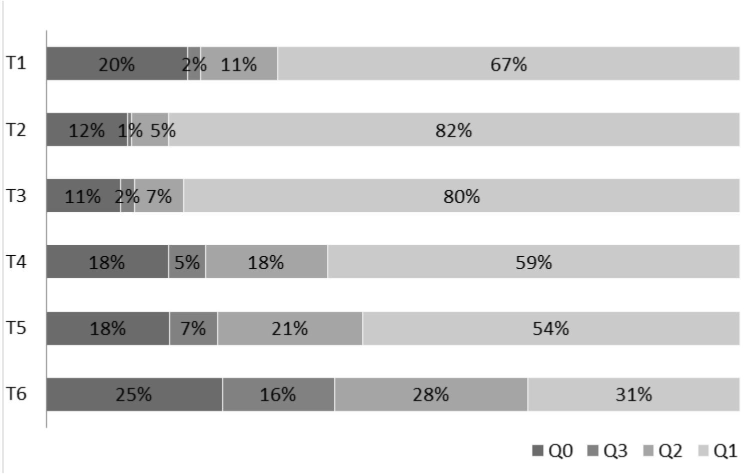


Fig. 35: Quality within the topography levels

The highest proportion of trees had died on ridges (25%) and in ditches (31%). The highest percentage of trees in poor condition was also found in ridge positions (16%) as well as upper slope (7%). In flat areas and at the base of the slope, most trees in were in very good condition (82% and 80%, respectively).

Table 14: Diameter at 50 cm by topography levels, n=31 species (dead trees excluded).

	Mean D50[mm] ± SD	N
T1	10.1 ± 12.82	44
T2	15.2 ± 17.92	446
T3	11.1 ± 12.49	921
T4	11.0 ± 10.13	708
T5	10.2 ± 9.27	790
T6	6.9 ± 6.30	179

Table 15: Height by topography levels, n=31 species (dead trees excluded).

	Mean height [cm] ± SD	N
T1	141.8 ± 142.44	44
T2	176.0 ± 159.49	447
T3	140.1 ± 108.65	921
T4	135.1 ± 98.15	713
T5	120.8 ± 85.88	791
T6	85.9 ± 53.73	179

Mean tree height and diameter at 50 cm was highest for flat terrain. For base of the slope and middle slope it was almost equal, while it was lowest for upper slope, ridge and ditch positions.

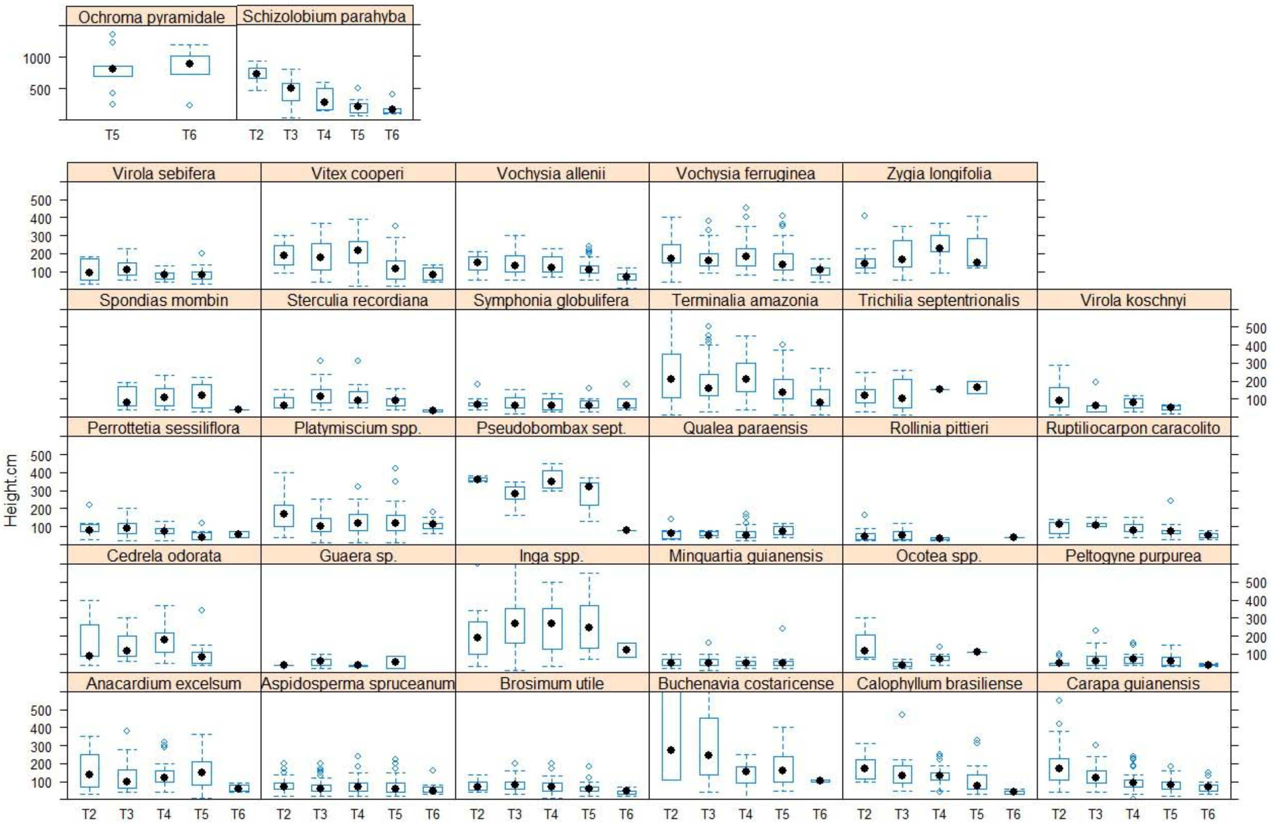


Fig. 36: Tree height at different topographies. *Ochroma pyramidale*: levels that do not contain any values are not displayed). The number of individuals per level varied for the species; see Table 10 and 36 in Appendix).

Species-specific height differed for the topographic positions. Hence a comparison of relative mean height and assortment to blocks was carried out similar to Table 10. Species with <8 individuals for 3 or more levels were excluded from the table (*Ocotea spp., Rollinia pittieri, Zygia longifolia, Trichilia septentrionalis* and *Ochroma pyramidale*).

Table 16: Height (relative to species mean) and mortality depending on the topographic position of trees.

	Topography level										
	Flat terrain (T2)	Base of the slope (T3)	Middle slope (T4)	Upper slope (T5)	Ridge, hilltop (T6)	n	Mean height [cm]	Block	Growth -class	p-value for height	p-value for D50
Per cent of mean height											
Mortality*						M. **					
n											
V. koschnyi	**153.1%**	94.4%	96.6%	62.0%	0.0%	100.0%	78	T2-T3	I	*	.
	15.4%	44.4%	12.5%	33.3%	100.0%	30.2%					
	16	10	8	22	2	58					
S. parahyba	**200.8%**	117.8%	88.0%	57.1%	48.0%	100.0%	365	T2-T3	IV	***	***
	0.0%	26.9%	61.5%	51.2%	38.5%	42.0%					
	13	26	27	42	13	127					
B. costaricense	**168.0%**	148.9%	67.2%	86.2%	49.9%	100.0%	210	T2-T3	IV	**	**
	40.0%	5.9%	11.1%	12.0%	60.0%	16.7%					
	13	18	28	26	5	92					
C. guianensis	**167.3%**	116.4%	85.1%	70.6%	62.8%	100.0%	111	T2-T3	II	***	***
	10.0%	10.3%	7.1%	9.1%	8.0%	9.6%					
	54	82	57	102	25	334					
V. sebifera	111.0%	**127.7%**	85.2%	90.4%	0.0%	100.0%	95	T2-T3	I		
	27.3%	36.8%	44.4%	43.8%	100.0%	41.9%					
	11	19	27	32	3	93					
P. sessiliflora	111.8%	**118.1%**	93.6%	64.4%	68.3%	100.0%	80	T2-T3	I	.	*
	13.3%	4.3%	28.6%	26.7%	71.4%	22.0%					
	16	24	21	15	7	85					
C. brasiliense	**141.3%**	114.6%	105.3%	87.0%	32.8%	100.0%	126	T2-T4	II	**	**
	22.2%	10.0%	4.2%	25.0%	12.5%	22.0%					
	7	27	23	24	7	89					
T. amazonia	**132.0%**	100.3%	117.3%	83.6%	54.2%	100.0%	189	T2-T4	III	***	***
	1.1%	3.7%	7.2%	9.5%	10.7%	6.5%					
	103	165	87	144	57	572					
R. caracolito	116.2%	**135.8%**	109.6%	92.7%	60.4%	100.0%	83	T2-T4	I	**	
	11.1%	11.1%	35.0%	19.4%	10.0%	20.0%					
	11	9	20	32	11	86					
B. utile	104.6%	**113.2%**	100.7%	81.5%	57.8%	100.0%	75	T2-T4	I	**	*
	25.9%	5.5%	9.7%	28.3%	40.0%	109.4%					
	28	75	65	63	10	248					
V. allenii	106.5%	**110.8%**	102.0%	88.3%	51.7%	100.0%	130	T2-T4	II	**	.
	5.6%	6.5%	16.7%	16.9%	46.2%	13.5%					
	22	82	32	63	13	216					
S. recordiana	77.7%	**119.3%**	106.7%	81.7%	32.8%	100.0%	107	T2-T4	II		
	0.0%	0.0%	7.1%	53.3%	60.0%	21.3%					
	7	18	14	15	5	61					
V. cooperi	117.2%	114.1%	**128.4%**	74.2%	51.5%	100.0%	165	T2-T4	III	***	**
	0.0%	27.3%	10.0%	4.5%	33.3%	12.8%					
	4	22	43	46	6	124					
V. ferruginea	117.5%	105.9%	**117.7%**	93.6%	64.0%	100.0%	168	T2-T4	III	**	*

	10.0%	23.1%	5.9%	5.0%	5.0%	10.3%					
	20	40	36	63	21	186					
C. odorata	110.5%	97.4%	**118.7%**	70.7%	0.0%	100.0%	146	T2-T4	III		
	30.8%	24.4%	9.1%	0.0%	100.0%						
	13	46	23	13	4	102					
Platymiscium spp.	**132.3%**	90.0%	104.2%	102.4%	85.9%	100.0%	128	T2-T5	II	.	.
	5.6%	8.2%	19.1%	14.5%	25.0%	20.8%					
	20	62	47	65	12	217					
A. spruceanum	**114.6%**	98.8%	101.7%	100.2%	78.2%	100.0%	75	T2-T5	I		
	14.8%	11.8%	14.5%	21.1%	18.8%	15.2%					
	29	86	79	59	16	279					
A. excelsum	**114.4%**	89.6%	100.6%	110.8%	44.4%	100.0%	141	T2-T5	II		
	9.5%	4.2%	6.3%	0.0%	0.0%	6.4%					
	21	24	33	10	4	97					
M. guianensis	101.5%	106.8%	88.9%	**109.5%**	0.0%	100.0%	54	T2-T5	I		
	25.0%	11.5%	30.8%	40.0%	100.0%	30.8%					
	9	26	42	25	4	109					
Inga spp.	88.1%	**106.1%**	98.8%	100.8%	47.2%	100.0%	254	TX	IV		
	10.5%	8.8%	7.1%	2.7%	33.3%	7.2%					
	20	35	43	37	3	142					
P. purpurea	81.2%	100.0%	**111.1%**	102.9%	58.0%	100.0%	69	TX	I		
	28.6%	4.8%	22.6%	13.9%	40.0%	15.5%					
	15	45	32	36	5	138					
Q. paraensis	92.1%	86.0%	95.3%	**109.9%**		100.0%	70	TX	I		
	0.0%	22.2%	43.3%	29.4%		31.3%					
	7	9	30	18		67					
S. globulifera	100.9%	100.4%	92.0%	101.6%	**111.8%**	100.0%	75	TX	I		
	8.7%	12.9%	22.2%	36.4%	25.0%	17.6%					
	25	32	18	11	8	97					

* Mortality (in % of individuals planted per level); ** Mortality in % of all planted individuals

Significance codes: 0='***'; 0.001='**'; 0.01='*'; 0.05= '.'.(c.f. values in Table 37, Appendix). Grey writing indicates less than 8 individuals per level, thus mortality and relative height values were not confidable in these cases. Red - blue areas indicate slow - fast growth.

Four blocks were distinguished: species that had relative mean height >100% in

- flat terrain and/or at the base of the slope **= T2 – T3**
- flat terrain, base of the slope or middle slope position **= T2 – T4**
- almost all considered levels except for ridge positions**= T2 – T5 .**

Species that could not be sorted to the other blocks, because of a different range **= TX** (4 species). Exceptions were *Sterculia recordiana, Cedrela odorata*, *Inga spp.*, *Qualea paraensis* were sorted to blocks because of the highest relative growth at the same position as the other species, despite a deviating range.

Most species (16) had highest growth in flat terrain and at the base of the slope. From block T2 – T3, especially *Schizolobium parahyba and Buchenavia costaricense* grew much higher at these levels. Highest mortality (40%) despite best growth in flat terrain was remarkable for *Buchenavia costaricense*. This was also the case for *Carapa guianensis* as well as *Anacardium excelsum,* but to a lower extent.

Block T2 – T4 is subdivided into 3 parts: 2 species had highest growth in respect to the other levels in flat terrain (*Calophyllum brasiliense* and *Terminalia amazonia*), some at the base of the slope (*Ruptiliocarpon caracolito, Brosimum utile, Vochysia allenii,* and *Sterculia recordiana*) and the others in middle slope position (*Vitex cooperi, Vochysia ferruginea* and *Cedrela odorata*).

In Block T2 – T5, all species had highest growth in flat terrain, with exception of *Minquartia guianensis* that grew higher in upper slope conditions, where it had highest mortality. The only species within this range (T2 – T5) that had >100% relative height in upper slope position as well as low mortality were *Anacardium excelsum* and *Inga spp.*

The majority of species with high growth in upper slope and/or ridge position suffered from accelerated mortality (*Platymiscium spp., Aspidosperma spruceanum, Minquartia guianensis, Peltogyne purpurea, Qualea paraensis, Symphonia globulifera*). *Symphonia globulifera* was the only species with highest growth in ridge conditions respect to the other levels. Topography had a significant effect on tree height and diameter for all species (Tables 17, 18), and for 12 single species (c.f. Table 37, Appendix).

Table 17: ANOVA testing for the effect of topography conditions on diameter at 50 cm height (*ditch excluded)

	Df	Sum Sq	Mean Sq	F value	p-value
Species (Sp)	30	166455	5549	74.118	<2e-16 ***
Topography* (T)	4	14493	3623	48.401	<2e-16 ***
Sp:T	108	47332	438	5.854	<2e-16 ***
Residuals	2901	217170	75		

Table 18: ANOVA testing for the effect of topography conditions on height (*ditch excluded)

	Df	Sum Sq	Mean Sq	F value	p-value
Species (Sp)	30	12268960	408965	61.277	<2e-16 ***
Topography* (T)	4	1840391	460098	68.938	<2e-16 ***
Sp:T	108	3252756	30118	4.513	<2e-16 ***
Residuals	2908	19408138	6674		

4.7 **Inclination**

Table 19: Number of recorded trees growing at different inclinations.

	Inclination level				
	Plain (I1)	Intermediate slope (I2)	Steep slope (I3)	Very steep slope (I4)	n
Trees (all sp.)	857	616	1733	892	4098
Per cent	21%	15%	42%	22%	100%
*Trees (31 sp.)	548	724	1596	825	3693
Per cent	**15%**	**20%**	**43%**	**22%**	**100%**

Dead trees included. (*used for statistical analysis)

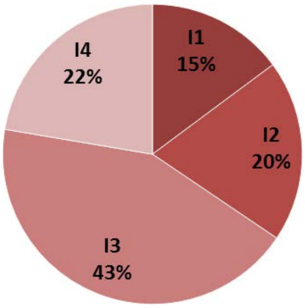


Fig. 37: *Trees per level, 31 sp.

The majority of trees were recorded at steep slopes, while at intermediate and very steep slope an almost equal number of trees were found. The lowest percentage of trees grew in flat terrain.

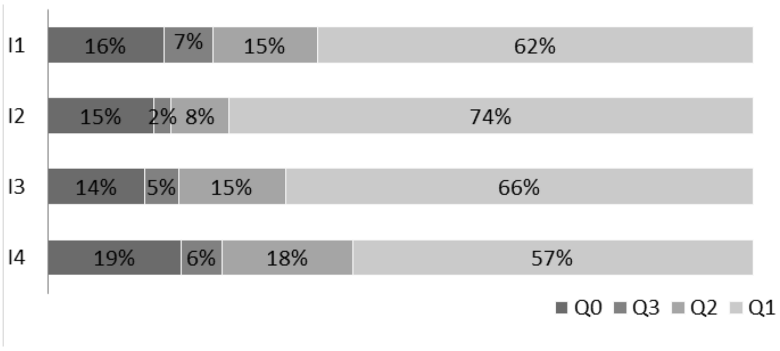


Fig. 38: Quality within the inclination levels

At very steep slopes, mortality was higher than for the other inclinations (Q0=19%). Most trees in very good condition grew in intermediate slope (74%) and at steep slopes (66%).

Table 20: Diameter at 50 cm by inclination, n=31 species (dead trees excluded).

	Mean D50[mm] ± SD	N
I1	10.0 ± 12.23	448
I2	13.2 ± 16.04	622
I3	11.5 ± 11.323	1352
I4	9.4 ± 8.38	666

Table 21: Height by inclination, n=31 species (dead trees excluded).

	Mean height [cm] ± SD	n
I1	122.3 ± 104.68	451
I2	159.2 ± 146.94	623
I3	137.6 ± 100.99	1354
I4	120.7 ± 85.78	667

Mean height for all species was highest at intermediate and steep slopes, while trees were smaller on very steep slopes as well as in plain. The most single species did not show remarkable differences of height growth for the inclination levels (Boxplot: Fig. 43 in

Appendix). Exceptions were fast growing species such as *Schizolobium parahyba, Buchenavia costaricense* and *Terminalia amazonia* that had maximum growth at intermediate slopes (I2), while *Inga spp.* had accelerated growth in steep and very steep terrain.

Inclination had a highly significant (p <0.001) effect on size with strong species x inclination interactions.

Table 22: ANOVA testing for the effect of inclination on diameter at 50 cm height

	Df	Sum Sq	Mean Sq	F value	p-value
Species	30	170830	5694	66.95	< 2e-16 ***
Inclination (I)	3	4950	1650	19.40	1.87e-12 ***
Sp:I	88	24545	279	3.28	< 2e-16 ***
Residuals	2966	252249	85		

Table 23: ANOVA testing for the effect of inclination on height

	Df	Sum Sq	Mean Sq	F value	p-value
Species	30	12638962	421299	54.725	< 2e-16 ***
Inclination (I)	3	514520	171507	22.278	2.91e-14 ***
Sp:I	88	1603030	18216	2.366	3.20e-11 ***
Residuals	2973	22887626	7698		

Only for 6 species, inclination had a significant effect on height (Table 37 in Appendix).

4.8 Comparison of factors light, topography and inclination

To compare the influence of the factors on species height, multi-factor ANOVA was applied.

Table 24: Multi-factor ANOVA testing topography, inclination and light on height of 31 sp.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Topography (T)	5	1365687	273137	42.972	< 2e-16 ***
Species (Sp)	30	13112677	437089	68.767	< 2e-16 ***
Inclination (I)	3	48926	16309	2.566	0.0529 .
Light (S)	3	568997	189666	29.840	< 2e-16 ***
T:Sp	131	3388710	25868	4.070	< 2e-16 ***
Sp:I	85	336700	3961	0.623	0.9972
Sp:S	85	1330428	15652	2.463	7.05e-12 ***
Residuals	2752	17492012	6356		

When testing the effect of the factors light, inclination and topography on height, topography and light were highly significant (p <0.001) and therefore were considered most important for species growth. Inclination was marginally significant (p=0.053) in the multi-factor ANOVA, though as a single factor, it was high (Tables 22, 23).

When the factors light and topography were tested for single species, in total 20 species showed significant effects (Tables 10, 17 and Table 37, Appendix). From these, both factors had a significant effect on growth of *Carapa guianenis, Schizolobium parahyba, Terminalia amazonia, Vochysia allenii, Vochysia ferruginea*. From all 3 factors, solely topography was significant for *Buchenavia costaricense, Calophyllum brasiliense, Pseudobombax septenatum, Ruptiliocarpon caracolito, Virola koschnyi, Vitex cooperii*, while light as the only factor for *Cedrela odorata, Inga spp., Peltogyne purpurea, Qualea paraensis, Sterculia recordiana*.

4.9 **Herbivory**

It was not possible to discern a significant effect of herbivory on seedling growth. For the majority of species and individuals, leaf area was not or only little affected: 59% of all trees had lost <2% of leaf area, 10% lost only a small leaf area (2–5%), while 7% were affected by intermediate herbivory (5 – 10% lost leaf area). Only 2% of all trees lost 10 – 20% or more of their leaf area. Hence, herbivory was generally low and turned out to be very species-specific:

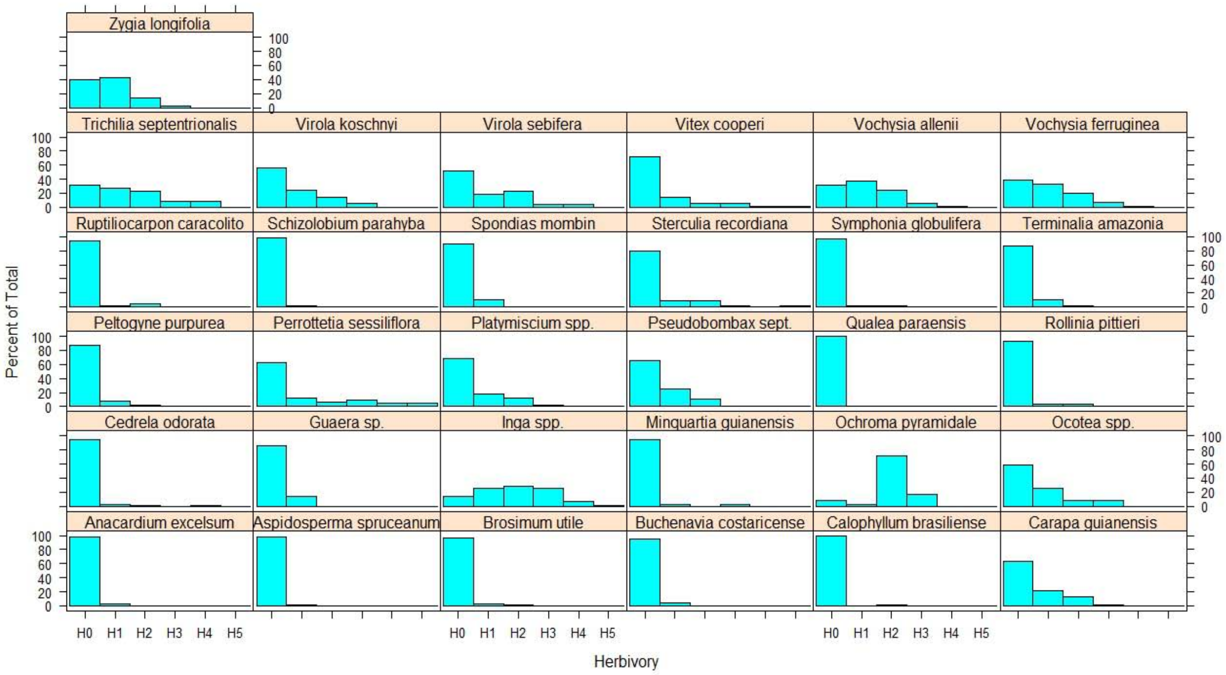


Fig. 39: Intensity of herbivory per species (explanation of levels in Table 1)

Most of the species that were affected by herbivory had fast growth and low mortality (*Ochroma pyramidale, Inga spp., Vochysia allenii, Vochysia ferruginea, Zygia longifolia, Vitex cooperi*).

4.10 Competition with other plants

Of all trees, individuals overgrown by ferns or grasses amounted to 7.8% and 10.8%, respectively. The average height per species was lower in most cases when ferns and grass were present (Table 25) though this may be due to shading by other plants or also the effect of topography as the growth of ferns and grasses was particularly high at positions where trees grew often poorly (middle and upper slope and especially ridge positions and in full sun). Significance of ferns on tree height could only be tested for few species (n ≥19):

Table 25: ANOVA testing for the effect of ferns, topography and light as factors on tree height

					Multi-factor ANOVA(height)		
Species	n ferns	Mean height (ferns) [cm]	Mean height (no ferns) [cm]	Ferns tested as single factor	p-value (ferns)	p-value (topography)	p-value (light)
C. guianensis	27	72	116	0.00194 **	0.000306 ***	1.05e-13 ***	3.79e-07 ***
Platymiscium s.	25	122	129	0.647	0.642	0.140	0.115
T. amazonia	39	144	192	0.0166 *	0.009066 **	3.75e-16 ***	0.000511 ***
V. allenii	21	96	135	0.00197 **	0.00109 **	0.00748 **	0.01688 *
V. ferruginea	19	142	171	0.129	0.09861 .	0.01235 *	0.00339 **

The factor ferns had a significant effect on tree height for *Carapa guianensis, Terminalia amazonia and Vochysia ferruginea*. As topography and light were also (highly) significant for these species, factor effects on growth are difficult to separate.

Table 26: ANOVA testing for the effect of grass, topography and light as factors on tree height

					Multi-factor ANOVA (height)		
Species	n grass	Mean height (grass) [cm]	Mean height (no grass) [cm]	Grass tested as single factor	p-value (grass)	p-value (topography)	p-value (light)
A. spruceanum	29	92	72	0.00868 **	0.00657 **	0.07180 .	0.76571
C. guianensis	30	94	113	0.159	0.0953 .	8.98e-15 ***	1.03e-07 ***
Inga sp.	31	223	264	0.176	0.15040	0.25609	0.00569 **
P. purpurea	19	60	71	0.227	0.2168	0.4318	0.0115 *
T. amazonia	41	161	191	0.135	0.100292	< 2e-16 ***	0.000685 ***

Aspidosperma spruceanum was the only species with a significant result for the factor grass.

Table 27: ANOVA testing for the effect of coverage by other plants, topography and light as factors on tree height

Species	N	Mean height (covered trees) [cm]	Mean height [cm]	covered with plants tested as single factor	Multi-factor ANOVA (height) p-value (covered)	p-value (topography)	p-value (light)
A. spruceanum	21	83	74	0.29	0.288	0.209	0.680
C. guianensis	33	80	116	0.00552 **	0.00112 **	4.71e-14 ***	2.67e-07 **
Platymiscium	23	110	131	0.194	0.188	0.135	0.114
T. amazonia	51	193	188	0.802	0.781078	< 2e-16 ***	0.000582 ***
V. allenii	26	100	135	0.00221 **	0.00113 **	0.00864 **	0.02567 *
V. ferruginea	21	160	169	0.653	0.63249	0.01052 *	0.00273 **

Species overgrown by other plants such as Melastomataceae, creepers and clubmosses had lower mean height except for *Terminalia amazoni* (higher). For the considered species coverage by other plants was only significant for *Carapa guinanensis* and *Vochysia allenii*. For these two species topography or light levels also had a significant effect on height growth. Hence the variation of mean heights for the selected species was stronger related to these conditions and do not reflect an effect of coverage by other plants.

Only 44 individuals of different species grew at sites that were affected by erosion, therefore its impact on growth could not be tested for any single species.

5 DISCUSSION

In the following section, mean species survival and height are compared with reference trials. After a short view of functional traits, light requirements of species are discussed. Then the influence of topography on species performance and its implications for species composition in an old-growth forest are examined. Finally, species mix used at La Bolsa and the reforestation method applied are considered.

5.1 Species performance

Out of all planted trees at La Bolsa, 65% had very good quality, while only 14% were in average condition. Total mortality was 16%, but an additional 5% of the trees appeared to be dying (Table 3). The already replaced individuals (c. 200) are included in these numbers. Because detailed documentation on the species level was lacking for La Bolsa, it was impossible to distinguish between those trees planted at the beginning and those replaced (slightly influencing results for growth and mortality) and to discern which of the already replaced individuals died in the meantime. When the replaced individuals are added to total mortality, it amounts to 20% (plus those not found and considered as probably dead: even 24%). Apart from the different factors that will be discussed, insect damage (except for herbivory) and fungal damage may have contributed to mortality, but will not be considered in detail. Of the analysed 31 species, almost two thirds had survival equal or superior to the average of 82%, only six species had survival ≤70%. Average height for all species was 1.4 m.

Mean species survival at La Bolsa can be considered (very good, at least) consistent with other studies in the humid tropics of native trees plantations in Central America (Breugel et al., 2011, Haggar et al., 1998). Some studies investigated the same species as were planted at La Bolsa, but in different site conditions (e.g. Piotto et al., 2004b in the dry tropics). Other studies in the humid tropics focused predominantly on other species or silvicultural aspects (e.g. Petit and Montagnini, 2006, Piotto et al., 2003a, Montagnini et al., 2003). Little data is suitable for comparison of the species level for La Bolsa: Butterfield (1995) was amongst the first to compare native species in the humid tropics for timber production at the La Selva Biological Station (Puerto Viejo de Sarapiqui, Costa Rica). Based on that data, Haggar et al. (1998) evaluated the same plots again under different influences. The 4 plots had been established on abandoned pastures, mainly in slope positions on clayey soils (Typic tropohumult with high Al-saturation), mostly in full sun. Mean annual precipitation was 3991 mm. After 6 years, a secondary forest had developed with recognisable canopy- and understorey layer. Height and survival data is from 3 years after planting (see also Butterfield, 1993). All species had better survival at La Bolsa except for *Vochysia ferruginea* and *Ocotea spp*. For the comparison of numbers, see Table 41, Appendix.

Breugel et al. (2011) conducted a large species selection trial in Panama at 4 distant sites on a precipitation gradient to find out whether precipitation or soil fertility is crucial for initial growth. They planted 180 individuals each for 49 species with spacing of 3 x 3 m. Seedling size was variable, depending on the species-specific process of germination until acclimation to full sun conditions prior to transplantation (2 – 8 months). After 2 years, seedling survival, height and basal diameter (50 mm above the soil surface) were measured. Breugel (2011) used data from the two sites Soberania and Rio Hato from a similar study by Wishnie et al. (2007).

One site (Las Lajas) allowed comparison to La Bolsa (mean annual rainfall 4610 mm, hilly terrain, former land use as a cattle pasture and clayey soils with low fertility – details in Table 47, Appendix). In contrast, the Soberania-site had less precipitation, was more fertile and not used for agriculture in the preceding ten years and completely covered with the exotic grass *Saccharum spontaneum L*. Across all sites compared in the trial more than 50% of the species had a mean survival equal or superior to 85%. Mean survival at all four plots was 78%, which was less than at La Bolsa and neither associated to soil fertility, nor to rainfall. The comparison of results showed that survival of the species at La Bolsa differed considerably from the Las Lajas-plot, but was surprisingly more similar to Soberania (numbers in Tables 38, 39, Appendix). Basically, most of the species had superior survival and mean height at La Bolsa (e.g. *Calophyllum brasiliense, Peltogyne purpurea*, *Vochysia ferruginea*, but the comparison of mean heights needs to be treated with caution as the age of the saplings at planting was heterogeneous at La Bolsa as well as in the Panamanian trial). Species that had a mean survival of ≥ 80% at all four plots of the Panamanian trial were *Inga sp*. (75.8%), *Ochroma pyramidale* (82.6%), *Spondias mombin* (98.5%) and *Terminalia amazonia* (83.8%). As these (commonly used and widely spread) species tolerated all site conditions in Panama as well as at La Bolsa, they can be considered as very robust. Additional species that performed very well in the Panamanian trial, but had insufficient sample size at la Bolsa (Table 40, Appendix) were *Astronium graveolens* (91.4% survival), *Cassia grandis* (90.8%), *Diphysa americana* (97.5%), *Erythrina fusca* (91.4%), *Gliricidia sepium* (99.3%), *Luehea seemannii* (86.9%), *Samanea saman* (97.4%) and *Tabebuia guayacan* (90.6%). These species appear to be robust and could be taken into account for further reforestation plantings in La Gamba at least from the survival point of view. Species that had better survival at la Bolsa than in Panama were *Calophyllum brasiliense, Cedrela odorata, Peltogyne purpurea, Vochysia ferruginea* and *Zygia longifolia* (Table 38, Appendix).

There are various factors that have an impact on tree growth and mortality. Functional traits (see subsequent chapter), which are strongest related to tree growth, are wood density and maximum height (Rüger et al., 2012). With regard to site conditions, nutrient-, water- and light availability are among the crucial factors for variations in species-specific performances (apart from inherent growth characteristics, see sections 5.3 and 5.4). In a large comparative study, Poorter et al. (2008) mentioned that taller species had increased growth (to reach higher adult stature) and decreased mortality. In a study that focussed on determinants of mortality across a tropical rainforest community, Rüger et al. (2011b) found that diameter had the biggest impact on mortality, while past growth and light availability were less important, respectively. For the majority of the 284 investigated species, mortality was observed to decrease remarkably with increasing diameter, but levelled off or even increased slightly at maximum diameter.

Breugel et al. (2011) also investigated the relation of survival with diameter and height growth after two years and found a correlation for all sites of their trial. Survival among faster-growing species was both higher and less variable than among those with slow growth. At La Bolsa, for the single species tree height and survival were not correlated. It is possible that the result of Breugel et al. (2011) is also valid for the species at La Bolsa, but could not be detected because of a smaller sample size and very heterogeneous conditions.

Compared to the other reforestation projects, performance at La Bolsa appeared to be quite satisfying for most species. Breugel et al. (2011) emphasised that early growth and initial mortality of rainforest species at open reforestation sites should be investigated before using them in reforestation projects to avoid poor performance in large-scale plantings. Breugel et al. (2011) also reminded that a final species choice should be adapted always to the many different objectives and conditions of each reforestation project. As growth and survival within the first two years represents only a short section in tree lifespans, data is not necessarily representative for further performance of a species. Clark and Clark (2001) reported that there was variable growth for the different size classes of species. Especially some slower growing species showed accelerated growth rates over time, whereas initially fast growing species tended to have slower growth with increasing age. Thus a generalisation of the results is limited and only continuous monitoring can show if a species meets the requirements of reforestation on the long term.

5.2 **Functional traits**

Functional traits are plant species attributes that influence survival, growth and reproduction (Ghazoul and Sheil, 2010). Maximum height, leaf area, seed mass, leaf mass per area, and wood density are considered as key traits that represent major aspects of tree anatomy and physiology. For instance, Poorter et al. (2008) found that seed size, specific leaf area (SLA, which is the inverse of leaf mass per area, LMA), wood density and plant height at maturity correlated significantly with relative growth rate and/or mortality rates at four different sites. Species with high SLA tend to have high Nitrogen concentrations and high photosynthetic and respiration rates (many pioneer species, Wright et al., 2004). Leaves of pioneer trees have rapid growth, short lifespan and are frequently affected by herbivores. Leaves with low SLA are typically thick, tough, and chemically well defended and belong to shade tolerant climax species. Seedlings with high SLA tend to have high growth rates (Wright and Westoby, 1999). High growth rates are typical for pioneer species and achieved by sacrificing structural robustness in the production of low density wood (Chave et al., 2009). In contrast, many climax species show lower growth rates, but have stable, high density wood. Thus, trade-offs in leaf- and wood economics are related to plant strategies in the competition for resources, persistence under resource shortage (e.g. shade tolerance), dispersal and resistance to pests or mechanical damage (Rüger et al., 2012). Plant strategies are also indicated by different average and potential demographic rates in combination with the mentioned trade-offs in resource use and functional constraints (Poorter et al., 2010). Species performance in different site conditions will be determined to a certain extent by these strategies. For example, many pioneer species require high light conditions and only germinate in gaps, while the majority of climax species germinates and establishes below canopy shade. Most climax species can persist for many years in the shaded understory forming seedling banks to have an advantage over pioneer species that germinate from dispersed or dormant seeds (Ghazoul and Sheil, 2010).

Apart from the basic differentiation between climax and pioneer species, other classification systems and models for rainforest tree species exist (Chazdon et al., 2010). For instance, species can also be grouped by stem diameter growth rate and canopy stratum (Finegan et al., 1999). Canopy development is based on height growth and longevity of the species and forms a most important structural aspect of the ecosystem which should be also considered when the species mix for reforestation is calculated (Lamb, 2011); see section 5.7. For this reason, it would be of interest if initial growth is related to functional traits (similar to plant height at maturity, Poorter (2008) and can indicate future tree performance.

Accordingly, for a selection of species at La Bolsa with relevant data available (Table 34, Appendix), the correlations of wood density, Nitrogen content in per cent of leaf-dry weight and leaf mass per area (LMA) with mean height per species were tested. None of these traits were significantly correlated to height as was expected with regard to literature. Small sample sizes may have contributed to deviant results. Also, heterogeneous site conditions at La Bolsa influenced tree height for some species remarkably (see subsequent paragraphs).

Furthermore, functional trait data was collected at different plots from trees of variable size, also possibly distorting the results. Apart from these restrictions, it may be concluded that differences of mean height from the various species are less distinct in the initial growth phase than for trees at maturity. This is not to be confused with ontogenetically changing growth rates (Clark and Clark, 2001, Herault et al., 2011).

5.3 Species performance in variable light conditions (light requirements)

Two years after planting, 18% of the trees in full sunlight and 16% of the trees in strong shade had died while mortality in intermediate and low sunlight was reduced (12% and 11% for S2 and S3, respectively, Fig. 32). Light levels also had a significant influence on mean height and diameter at 50 cm for all species (Tables 8, 9), whereas for single species, this was not always the case (significance for 14 from 31 species, Table 10). Six categories of species response to light could be distinguished, represented by the blocks in Table 10. Some species showed similar relative mean heights for the entire light gradient while others were restricted to a specific light spectrum, indicated by higher mortality in the remaining levels.

Trade-offs between growth and survival mostly occurred at the full sunlight level when relative mean height was still ≥100%, but mortality was accelerated compared to the intermediate light level (*Virola sebifera*, *Aspidosperma spruceanum*, *Virola koschnyi*, *Minquartia guianensis, Rollinia pittieri, Terminalia amazonia, Cedrela odorata,* and *Ocotea spp.*). To draw conclusions for species-specific trade-offs at the strong shade level, data was insufficient except for *Carapa guianensis* (relative mean height was 107.7%, but mortality 45.5%).

As many studies point out, light is a key resource and environmental factor for growth and survival of trees in the subcanopy of tropical wet forests (Sheil et al., 2006, Poorter et al., 2003). The ability to cope with different light conditions is an important factor of species coexistence and niche partitioning (Poorter and Arets, 2003, Clark et al., 1993, Clark and Clark, 1992), which even occurs in low light conditions as investigated by Montgomery and Chazdon (2002).

It is generally confirmed that growth of rainforest tree saplings varies significantly with light availability (e.g. Clark et al., 1993, Balderrama and Chazdon, 2005, Montgomery and Chazdon, 2002). Rüger et al. (2011b) tried to quantify the impact on light availability on tree size and past growth on mortality for a large number of species. Light availability for the single trees was estimated based on vegetation density. They figured out that 78% of all species from the assessed forest community had increasing mortality with increasing light, while only for 29 single species response to light was significant (increasing mortality at high light). As diameter turned out to have the biggest impact on mortality in the course of the study, they recommended considering species-specific size effects when investigating the impact of environmental conditions on mortality.

As species-specific references are rare, I have focused on Balderrama and Chazdon (2005) who evaluated the dependence of tree seedling survival and growth on light availability for *Dipteryx panamensis, Hyeronima alchorneoides, Virola koschnyi and Vochysia guatemalensis* in north-eastern Costa Rica in a 15-month-trial. They observed generally increased survival and growth with increasing light availability, but different species-specific responses in survival in shaded microsites (6 – 20% light transmittance) and in growth increments (measured in above-ground biomass and leaf mass per area) per light increase. In their trial, *Virola koschnyi* tolerated low light conditions very well, but showed a trade-off between survival and growth responses to increasing light. In contrast, *Vochysia ferruginea* could maintain high rates of growth and survival in different light conditions. At La Bolsa, *Virola koschnyi* had the strongest increase of relative mean height at the low light level and slightly decreased mortality. In full sunlight, relative mean height was still 101.1%, but mortality was accelerated respect to the other levels, which points to a trade-off between survival and growth similar to the result of Balderrama and Chazdon (2005). *Vochysia ferruginea* had the strongest growth in low light conditions and decreased growth in full sunlight, whereas mortality was highest in shade and lowest in full sunlight. As average mortality of *Vochysia ferruginea* was low, this contrast points towards a generally robust species with a broad spectrum, but unfavourable soil- or other conditions at la Bolsa.

In several studies focussing on practical aspects of reforestation, rainforest species were tested in direct sunlight (as mentioned in chapter reforestation strategy). Another possibility to discern species ability to tolerate specific light conditions is to investigate related functional traits such as wood and leaf traits. Morphological and physiological reasons for variable species performance were examined e.g. by Hérault et al. (2011) and Rüger et al. (2012). The latter tested wood density and adult stature among other traits in order to discern the response of growth to light and adult stature (tree size) for 171 neotropical tree species. The most important trait that determined average and/or potential growth rates was wood density, while intrinsic growth rates were additionally strongly related to adult stature. Wood density is linked to the ability of tree species to react to temporal changes in light availability: Species with low wood density are able to exploit temporary favourable growth conditions better than slow growing species with higher wood density. For taller species, which potentially reach over the main canopy (max. 25 m), there was no relationship between maximum height and intrinsic growth rate observed. They also have a stronger response to higher light because they can possibly reach the canopy. Small-statured species, which are likely to remain in shaded understorey conditions, need different survival strategies. Mostly they have a lower sensitivity of growth with respect to light, slower intrinsic growth rates and higher shade tolerance which was interpreted as a conservative resource use strategy by Rüger et al. (2012). Baltzer and Thomas defined shade tolerance as "the ability to survive and grow under low light". Poorter (2005) annotated that seedling responses to light differ from post-seedling stages, because the majority of species follows the vertical light profile in the forest canopy. Initially shade tolerant species (growing in low light conditions as juveniles) have to cope with high light in adulthood.

To explore the significance of light availability for seedling performance La Bolsa, the different light levels were estimated (not measured). Because of this restriction, a fine-scaled differentiation between light levels was not possible and niche-partitioning in low-light conditions is probably not sufficiently represented in the results, as Montgomery and Chazdon (2002) criticism for some studies that used highly contrasting discrete light levels. Also, other supplementary measures of growth such as increase in aboveground biomass or Nitrogen content in leaves could not applied at La Bolsa because of practical reasons.

Furthermore, there is evidence that light availability should not be overestimated for its impact on tree growth. Rüger et al. (2011a) found that for 274 woody species on Barro Colorado Island, Panama, light availability and tree diameter together only explained on average 12% of the variation in growth rates. Hence much of the variation is related to other factors such as ontogenetic development as well as other environmental conditions (e.g. soil, herbivory).

5.4 Influence of topography and inclination on species performance

Tree survival differed related to the morphology of the terrain. After 2 years, the highest percentage of trees that had died was found at ridges and hilltops (25%). Best survival and quality results were observed in flat terrain (82%) and at slope bases (80%) (Fig. 35). The means of height and diameter at 50 cm (of all species) varied significantly for the topography levels (Tables 17, 18). Growth was highest in flat terrain and similar for slope bases and middle slope. On upper slopes and hilltops, tree growth was generally reduced respect to the other topographic positions (Tables 14, 15).

For 13 (single) species, topography levels proved to have a significant effect on growth (Table 16). The variable species-specific response to the topographic positions is highlighted by the 4 blocks in Table 16. These blocks mainly indicate how wide the range of favourable positions of the contained species was. Those species with relative mean ≥100% in 3 topographic positions can be considered tolerant to a broad range of conditions (Table 16; all species from blocks T2 – T4, T2 – T5, TX except for *Sterculia recordiana, Cedrela odorata*, *Inga spp.*, *Qualea paraensis*). From these tolerant species, some could be defined even as indifferent (*Calophyllum brasiliense, Terminalia amazonia, Anacardium excelsum, Inga spp., Vochysia allenii, Platymiscium spp* (mortality <20% for all positions within their blocks). Remarkable* discrepancies between growth and survival within a level were observed for *Buchenavia costaricense, Ruptiliocarpon caracolito, Brosimum utile, Vitex cooperi, Vochysia ferruginea, Cedrela odorata, Aspidosperma spruceanum, Minquartia guianensis* (*relative mean height >100% and mortality >20%). 15 of 23 species showed highest growth in flat terrain and 7 species at the base of the slope (also with moderate inclination) suggesting that the associated conditions were most suitable for the majority of the analysed species. In middle to upper slope positions only 5 and on ridges only 1 species *(Symphonia globulifera)* had highest growth indicating that (the conditions in) these topographic positions were less favourable.

The results for inclination showed that growth was highest on slopes with intermediate inclination (4 – 10%), while it was lowest in very steep slopes and reduced in plain. As steep inclinations occurred mostly in upper slope positions, this is coherent with the result for topography. In contrast, reduced growth for the lowest inclination level is contradictive to highest mean height for the topographic position "flat terrain". Hence results for topography and inclination are not congruent, probably because the designation of the inclination level per tree was focussed on a smaller area. As inclination was found to have less impact (less significant effect) on tree height than topographic position, this inclination will not be discussed any further.

Tree growth and soil properties

The influence of specific topographic positions on growth of neotropical rainforest tree species is rarely evaluated – and comparability of results is mostly restricted due to the scale dependence of the phenomenon (Guisan et al., 1999). More research has been done focussing on the influence of variable edaphic factors that determine plant growth, but are often closely interrelated to topography (especially drainage and fertility (Pélissier et al., 2002). Species-specific variations of growth for distinct edaphic conditions for high numbers of species were investigated by e.g. Butterfield (1995) and Haggar et al. (1998) in Costa Rica as well as Russo et al. (2005, in Indonesia). Calvo-Alvarado et al. (2007, in Costa Rica) and Breugel et al. (2011, in Panama) also factored in climatic gradients and more than one eco-region to differentiate between the effects of precipitation and fertility on growth. Breugel et al. (2011) reported that 30% of their screened species grew significantly better at the high-fertility sites than at the low-fertility sites despite different precipitation levels. On the other hand, 65% of the species did not show variations of growth for different fertility or humidity levels. (Results for species height from different sites compared to La Bolsa in Table 38, Appendix.). An interesting aspect was found by Russo et al. (2005) who suggested that to achieve high abundance in different conditions, some species have different demographic responses to variations in soil resources. On low-fertility soils, low mortality and growth is required, while on fertile soils, high growth rates (at higher mortality costs) are relatively more important to achieve high abundance.

In the Esquinas Rainforest, steeper slopes are mostly more strongly affected by erosion, which leads to increased leaching of humus and nutrients from the upper horizons and stronger weathering effects of the soil (section 2.2). Hence, soil conditions can be strongly altered in areas affected by erosion and differ greatly from flat areas or ravines where organic material and nutrients can accumulate. As a consequence, edaphic conditions vary with the morphology of the terrain affecting tree growth. At La Bolsa, at least two soil types with distinct chemical and physical properties were predominant (Andic dystrudept and Typic hapludult). As sufficient data was lacking, it was impossible to discern, which individuals of a species grew exactly on each soil type. Hence it could not be distinguished and tested, if and to what extent variations in tree growth reflect species-specific response on changes to the soil type itself or within a single soil type, different conditions related to the topographic position.

Tree growth and drainage

Topography and inclination influences the magnitude of drainage effects. For example, surface- and percolating water flows downhill from hilltops and upper slopes, causing drier conditions than at slope base or ravines where water arrives or can accumulate over an impermeable soil layer. Hence tree growth can be affected by different humidity conditions in relation to the morphology of the terrain (Pélissier et al., 2002, Sabatier et al., 1997). Furthermore, the availability of water for trees depends largely on influencing variables related to soil properties (such as field capacity of the horizons penetrable by roots). For example, Sabatier et al (1997) found that vegetation assemblages are different for soils with deep vertical drainage and such with superficial lateral drainage. In addition, slope inclination angle, elevation, slope aspect, plants coverage and albedo of the surfaces are factors that determine how much the soil surface experiences drought by exposition to the sun. The higher temperatures and evaporation from the topsoil become, the stronger the effects of drought can be in the uppermost soil layer. Steeper sun exposed slopes are likely to experience stronger effects than flatter areas, but threshold inclinations have not been measured at La Bolsa. To sum up, the reason for variable growth in different topographic positions cannot be traced back to a single factor, as the effects of position, soil type and light levels are interrelated. Therefore it is likely that the combination of direct sunlight and high temperatures at ridge- and upper slope positions caused drought in the uppermost soil layer causing reduced growth, quality and survival of many species, but chemical soil conditions may have also contributed to that (e.g. low fertility and Aluminium toxicity, compare to subsequent results for dry ridges of Pamperl, 2001). More data would have been necessary for further examination to differentiate these aspects at La Bolsa.

From the 23 analysed species planted at la Bolsa, 16 spanned 3 – 4 topography levels. The wide range of these species probably reflects that growth was not (closely) related to any topographic position. On the other hand, this result could also be due to some extent to the arbitrary definition/zoning of the topography levels in the terrain (which was inevitable due to practical reasons): In some areas, similar conditions might have occurred within 2 adjoining levels, distorting the results for factor effects on tree growth.

5.4.1 Species distribution related to topography

As species-specific responses to soil variables (including soil hydrology) exist, these are likely to be reflected in species spatial distributions on different scales – at the meso- and landscape scale (Clark et al., 1999, Tuomisto et al., 2003, Potts et al., 2002, Pyke et al., 2001) as well as in the local terrain (Russo et al., 2005, Pélissier et al., 2002, Sabatier et al., 1997, Steege et al., 1993, Herrera and Finegan, 1997). John et al. (2007) investigated three neotropical sites (Columbia – La Planada, Ecuador – Yasuni, Panama – Barro Colorado Island) and observed that 36 – 51% of the local distributions from 1400 different tree species were associated with soil nutrient distributions. Clark et al. (1999) estimated that approximately 30% of the species from their trial were distributed in relation to edaphic factors. He also found that within a predominant soil type, 13 of 110 species were associated with one or more topographic positions. Homeier et al. (2010) stressed that forest structure of highly diverse montane rainforest in southern Ecuador changes along topographical gradients, similar to those along elevational gradients. These gradients correlate with many interrelated environmental factors that are difficult to disentangle (e.g. soil hydrology, temperature regimes, fertility etc.). Pélissier et al. (2002) studied soil hydrology and species composition in French Guiana and found water excess to be a main factor determining species composition and floristic singularity of extreme positions in tropical forests. Especially upper slopes and hilltops with well drained soils, species diversity was higher.

In a recent study of factors affecting the spatial distribution of tree species by Kübler et al. (2012), species-specific distribution models were computed for 16 species on a montane rainforest plot in southern Ecuador, based on elevation models (and distribution data from the plots). For these models, topography related environmental parameters were ranked by their impact on species distribution: elevation turned out to be most important, followed by the Topography Position Index (see also Weiss, 2001). Then wetness index and slope aspect followed (in this order). Two groups of species were generated: some were distributed according to higher elevation, ridge positions and generally dry sites. The other group of species occurred on sites with lower elevation and wetter conditions. These results resemble results from the Esquinas Rainforest (subsequently explained) and also support the previous reflections concerning the importance of drainage effects related to topography.

Topography-related species distributions, investigated in the Esquinas Rainforest

In the Esquinas Rainforest, the association of species distributions to different topographic positions was examined by Pamperl (2001), Table 28. Species diversity and abundance of trees were compared for the topographic positions dry ridge, wet ridge, slope and ravine at 3 old-grown forest plots in the vicinity of La Bolsa: For dry ridges, only 20 species were site-specific. Soils at ridges were the most weathered of all positions and characterised by very acid pH (average 4.5), very low nutrient availability and high aluminium saturation frequently accompanied by water stress in the topsoils. Pamperl (2001) concluded that the selective effect of the predominant edaphic conditions led to a reduction of tree diversity and density at dry ridges. In contrast, on wet ridges, the highest diversity of site-specific tree species occurred from all examined plots (59 spp.). The topsoils of wet ridges were only occasionally affected by water stress and had a good supply of plant-available Ca and Mg, whereas the subsoils had lower pH and nutrient availability, as well as high aluminium content. It was assumed that the species richness of that topographic entity was not only due to its edaphic conditions. On slopes, less site-specific species were counted than for ridges in total (61 spp.) The soils were found to have very acid pH, moderate to low nutrient availability, a tendency to aluminium-toxicity and a big fraction of pedogenic oxides. The edaphic conditions of slopes basically resembled those of ridge positions and therefore, could not explain the higher number of slope-specific species. The diversity of tree species in ravines (56) was lowest compared to the other topographic positions. Soils in ravines had good nutrient retention capacity despite average pH of 5.6 in top-and subsoils, no aluminium-toxicity and optimal hydrological conditions. Although the edaphic conditions appeared to be relatively favourable for plants, they were not believed to foster species richness.

Table 28: Tree species at different topographies with b.h.d. >10cm. 313 tree species within 3 plots of 1ha size. Source: Tables 5 and 6 from Pamperl (2001), modified

Plot	Species total	Number of Individuals (alive)	Site specific species, (by topography level)	Site specific species, in % of species of the whole forest
Ravine	118	481	56	17.9
Slope	140	563	61	19.5
Only wet ridge:		610	59	
Only dry ridge:		237	20	
Wet and dry r.:			11	
Ridge total	188	847	90	28.8
Total	313		207	66.2

Pamperl (2001) suggested that the following limiting factors have main influence on the species composition at the Esquinas Rainforest plots: the generally small soil nutrient budget of Ultisols, a high amount of iron oxide leading to phosphorus fixation and local occurrence of phytotoxic Aluminium concentrations in the soil solution when pH is <5.5. Her results show that the morphology of the terrain at La Bolsa is related to the composition of species. Hence reduced performance of the most species when planted at ridge positions at La Bolsa could indicate that they were not suitable for that position as it did not correspond to their natural habitat.

This leads to the question, if species performance in different positions on the reforestation plot can also reflect their preferred habitat in natural forests, in which case their natural distribution could serve as a guide for which microsites they are suitable for. Performance of species planted at La Bolsa that were found by Huber (2005) and Weissenhofer et al. (2008b) to be common for the investigated topographic positions (see section 5.6) will be subsequently compared.

<u>Typical species for ridges* and slopes; in brackets: relative density (r.d.) in a 1 ha-mature forest plot):</u>

For <u>*Vochysia ferruginea*</u>*, topography had a significant effect on growth and showed with over-average performance from flat terrain to middle slope positions (block T2 – T4) with highest growth for the latter. Mortality (relative) was highest at the base of the slope while it was low on upper slopes and ridges (5.0%). These outcomes weakly point towards the fact that this species is normally most abundant at ridges (r.d. 4.48%), but at least indicate that it is capable of growing there. <u>*Symphonia globulifera*</u>* (r.d. 2.83%) was the species with the widest range at La Bolsa, and the only species that had highest growth at ridges (despite high mortality). Topography as a factor was not significant for growth. This species was also considered to be characteristic for slopes (with r.d. 3.42%) in the Esquinas Rainforest (Huber, 2005). Results from La Bolsa reveal its preferred positions and the fact that it is a tolerant (generalist) species (Weber et al., 2001, Jiménez, 2002). For <u>*Calophyllum brasiliense*</u>* (r.d <2.24%), topography was significant as a factor for growth, which was highest from flat terrain to middle slope positions. At upper hill and ridge positions, growth and survival was reduced. These results do not suggest its common occurrence at slope and ridge positions – Jiménez (2002) reported that the species has usually reduced growth in flat terrain. <u>*Peltogyne purpurea*</u>* (r.d. <2.24%) showed highest growth at middle to upper slope positions, while in flat terrain, most trees died. As the result for ridge was not representative, only a tendency to higher growth in slope positions is recognisable from the results, but it points at least weakly towards its preferred habitat: Jiménez (2002) stated that *Peltogyne purpurea* normally grows in well drained areas and hills on poor reddish clay soils with high aluminium and iron contents. *Aspidosperma spruceanum** was considered typical for ridges (despite low relative density <2.24%) as well as for slopes. At La Bolsa, the factor topography was not significant for growth and the species showed a wide range (block T2 – T5). *Aspidosperma spruceanum* had highest growth in flat terrain, but also good growth performance in middle to upper slope conditions, despite accelerated mortality. At ridges, relative mean height and survival were reduced with respect to the other levels. Therefore the results from La Bolsa do not clearly indicate any preferred habitat, but emphasize that this species tolerates a wider range of conditions. Huber (2005) highlighted that *Qualea paraensis** is the most characteristic species for ridges in the mature forest plots (r.d. 5.90%). At La Bolsa, Qualea paraensis showed a clear tendency for higher growth at upper slopes, while very high mortality was observed for middle slopes. No results were available for ridges as it has not been planted there. Topography was not significant for growth and the outcomes were not sufficient to discern any preferred position. According to Jiménez (2002), *Qualea paraensis* prefers hills and well drained sites and is capable to regenerate in sunny areas. *Brosimum utile* is a quite frequent species on slopes (r.d 3.30%). Topography was a significant and best growth performance was observed in flat terrain and at the base of the slope. Surprisingly, mortality was accelerated for flat terrain, but lowest for base of the slope and middle slope. Hence the result for *Brosimum utile* is (at least) not contradictive to the species natural habitat (Jiménez, 2002). *Carapa guianensis* is also a common species on slopes (r.d. 2.85%). *Carapa guianensis* had highest growth as well as mortality in flat terrain and at the base of the slope, while for middle and upper slope, mortality was lowest. Topography was significant, but the results from La Bolsa do not clearly suggest most suitable conditions at well drained slopes for Carapa guianensis (see also Jiménez, 2002). *Ruptiliocarpon caracolito* developed best within the range flat terrain to middle slopes, with highest growth at the base of slope. The results do not point to slope positions as a habitat of that species, but topography was significant.

To sum up, species response to the topographic positions reflects the common habitat of *Symphonia globulifera* clearly, but for *Vochysia ferruginea, Qualea paraensis* and *Brosimum utile* only weakly. For *Calophyllum brasiliense, Peltogyne purpurea, Aspidosperma spruceanum, Carapa guianensis, Ruptiliocarpon caracolito,* results were either inconclusive or variable from their natural habitat. Deviating outcomes at La Bolsa are probably due to its previous use as a pasture what may have altered soil conditions and the lack of a coherent canopy.

A restriction of this comparison is that at La Bolsa, species have been planted in flat terrain where perhaps some of them naturally would not occur. Another aspect of this comparison is that most of the considered characteristic species were found to have low abundance in the natural forest plots investigated by Huber (2005) and also, data from flat terrain was lacking. Hence it also remains unclear if there are further topographic positions where these species are common as well. As the outcomes from this evaluation reflect the most suitable positions for growth and survival in a reforestation area, distinct topographic positions then in the natural forest should be chosen for planting of several species. To simply copy species composition from a natural forest plot could easily result in decreased reforestation success, as conditions in an open pasture are too different from a mature forest. Specifically highly specialised species (e.g. mycorrhiza) and those very sensitive to direct sunlight presumably will have reduced performance at the topographic positions they are common to in the natural forest. As a conclusion, the knowledge of a species natural habitat at best can point to suitable conditions for reforestation in the case soil conditions are not strongly altered, but will be insufficient for clear predictions as sensitivity to other limiting factors requires examination.

5.5 Synopsis of light and topography results from La Bolsa and species-specific recommendations for reforestation use

For reforestation areas with climatic and edaphic conditions comparable to La Bolsa, the species-specific outcomes can be used to find suitable species for reforestation. Further aspects to consider when defining a suitable species mix and reforestation strategies to apply will be discussed in the subsequent chapters. The following proposals are based on the assumption that a species is most suitable to conditions in which they have shown good* performance at La Bolsa which can be referred to in Tables 10 and 16. (*Understood as relative mean height ≥100% combined with mortality <30% within the concerned topography/light levels.) For a few species, results for mortality were contradictive to relative mean height within single levels of a factor (e.g. growth and mortality were highest in flat terrain for *Buchenavia costaricense* or at upper slopes for *Minquartia guianensis*). As far as results for mortality seemed to be outliers, they were considered less important, while obvious trade-offs should be taken into account when calculating tree numbers.

The most suitable species for specific topography and light conditions of a reforestation area can be found in two steps: First, the species with corresponding topography range need to be chosen from Table 16. Secondly* light requirements of these species (Table 10) have to be checked (*or in the inverse order). Species with mortality exceeding 30% should be excluded in each step. Subsequently, the species most appropriate to plant in specific conditions are listed in the boxes 1-12 in Table 29:

Table 29: Optimal environmental conditions per species.

	Species with *relative mean height ≥100% and mortality <30% in >>			Full sunlight (F)	Intermediate sunlight (I)	Shade
<< Species with relative mean height ≥100% and mortality <30% at				***B. costaricense***		
				Inga spp.		
				S. parahyba		
				A. spruceanum	*A. spruceanum*	
				Z. longifolia	*Z. longifolia*	
				P. purpurea	***P. purpurea***	
					C. odorata,	
					T. amazonia (+F)	
					V. cooperi (+F)	
					S. globulifera (+F)	*S. globulifera*
					Platymiscium (+F)	*Platymiscium spp.*
					C. brasiliense	*C. brasiliense*
				V. koschnyi		***V. koschnyi***
					A. excelsum (+F)	***A. excelsum***
					B. utile	***B.utile***
					V. allenii	***V. allenii***
					V. ferruginea	***V. ferruginea***
						Q. paraensis (+I)
						P. sessiliflora (+I),
						R. caracolito (+I)
						C. guianensis
						S. recordiana
Ridge	***S. globulifera***			1	2 *S. globulifera (+F)*	3 *S. globulifera*
Upper slope	*A. excelsum,* *A. spruceanum,* *P. purpurea,* *Platymiscium*	*Inga spp. (+M)*	***Q. paraensis***	4 *A. spruceanum,* *Inga spp. (+M),* *P. purpurea*	5 *A. excelsum (+F),* *A. spruceanum,* *P. purpurea,* *Platymiscium (+F)*	6 *A. excelsum* *Platymiscium,* *Q. paraensis (+I)*
Middle slope (M)	*A. excelsum,* *A. spruceanum,* ***P. purpurea**,* *Platymiscium*	*C. brasiliense,* *B. utile,* *S. recordiana,* *T. amazonia,* ***V. cooperi,*** *V. allenii,* ***V. ferruginea***		7 *A. spruceanum,* *P. purpurea*	8 *A. excelsum (+F),* *A. spruceanum,* *B. utile,* *C. brasiliense,* *P. purpurea,* *V. cooperi (+F),* *Platymiscium (+F),* *T. amazonia (+F),* *V. allenii,* *V. ferruginea*	9 *A. excelsum,* *B. utile,* *C. brasiliense,* *Platymiscium,* *S. recordiana,* *V. allenii,* *V. ferruginea*

Base of the slope + flat terrain	***A. excelsum,*** ***A. spruceanum,*** *P. purpurea,* ***Platymiscium,*** *S. globulifera (+M)*	***C. brasiliense,*** ***B. utile,*** ***Inga spp.,*** ***S. recordiana,*** ***T. amazonia,*** *V. cooperi,* ***V. allenii,*** *V. ferruginea*	***C. guianensis,*** ***C. odorata, B. costaricense,*** ***M. guianensis,*** ***P. sessiliflora,*** ***R. caracolito,*** ***S. parahyba,*** ***V. koschnyi,*** ***V. sebifera***	10 *A. spruceanum,* *B. costaricense,* *Inga spp.,* *P. purpurea* *S. parahyba,* *V. koschnyi*	11 *A. excelsum (+F),* *A. spruceanum,* *B. utile,* *C. brasiliense,* *C. odorata,* *P. purpurea,* *Platymiscium (+F),* *S. globulifera (+F, M),* *T. amazonia (+F),* *V. cooperi (+F),* *V. allenii,* *V. ferruginea*	12 *A. excelsum,* *B. utile,* *C. brasiliense,* *C. guianensis,* *P. sessiliflora (+I),* *R. caracolito (+I),* *Platymiscium,* *S. recordiana,* *S. globulifera (+M),* *V. koschnyi,* *V. allenii,* *V. ferruginea*

*Species that fullfil this criterion are listed for every category and are marked ***bold,*** where relative growth was highest. (+F) means 90 – 99% rel. growth in full sunlight; (+I) means 90 – 99% rel. growth in intermediate sunlight; (+M) means 90 – 99% rel. growth at middle slope → species can be planted with almost optimal performance in these conditions, but is not listed in the corresponding category. Blue areas highlight species that grow within a broad(er) range of topographic positions.

For example, for a reforestation area without an existing stock of shading trees, species from the category full sunlight should be chosen *(Aspidosperma spruceanum, Buchenavia costaricense, Inga spp., Schizolobium parahyba, Peltogyne purpurea, Virola koschnyi, Zygia longifolia).* Additionally, some species with highest growth at the intermediate sunlight level that still had 90 – 99% relative mean height in full sun *(Anacardium excelsum (+I), Platymiscium spp. (+I), Symphonia globulifera (+I), Terminalia amazonia (+I), Vitex cooperi (+I))* can be selected to enlarge the assortment, but slightly reduced performance has to be taken into account. For upper slope positions, *Anacardium excelsum, Aspidosperma spruceanum, Inga spp., Peltogyne purpurea, Platymiscium spp.* and *Qualea paraensis* are recommendable. After merging these groups, 3 species turn out to be most suitable (optimal growth) at **upper slopes in full sun:** (box 4) - *Aspidosperma spruceanum, Inga spp.,* and *Peltogyne purpurea,* while *Anacardium excelsum (F)* and *Platymiscium spp. (F)* (box 5) could be planted as well, but will have lower growth. Also, *Symphonia globulifera* is supposed to have optimal growth, but with slightly higher mortality, Table 16). No species had optimal growth in **ridge positions in full sun** (box 1). The most suitable species for reforestation would be *Symphonia globulifera, Aspidosperma spruceanum, Inga spp,. Peltogyne purpurea, Anacardium excelsum and Platymiscium spp. (box 2, 4, 5*; but reduced performance has to be taken into account. Further species that had at least low relative mortality (<11%) at ridges and hilltops were *Vochysia ferruginea, Ruptiliocarpon caracolito, Terminalia amazonia* and *Carapa guianensis* (Table 16; less healthy and growth much reduced). *Ochroma pyramidale* grew very well at ridges and upper slopes too (Fig. 36), including natural regeneration. These 5 species would be appropriate for upper slopes in full sun as well. From the usable species, especially those with generally faster growth *(Ochroma pyramidale, Terminalia amazonia, Vochysia ferruginea, Platymiscium spp., Anacardium excelsum)* could serve as nurse trees, i.e. to provide shadow for other species that can be inter-planted later on (compare section 5.7). In the case an **upper slope or ridge** is already **shaded** (box 3, 6) by trees, *Anacardium excelsum, Platymiscium spp. Qualea paraensis* and *Symphonia globulifera* will have optimal conditions for growth.

Species found to be most suitable for **middle slope in full sun** (box 7) were *Aspidosperma spruceanum* and *Peltogyne purpurea*, while *Terminalia amazonia (I), Vitex cooperi* (*I), Platymiscium spp. (I), Anacardium excelsum (I)* can be recommended as well (from box 8; also with reduced growth). Species that should have optimal growth in **shaded conditions at middle slopes** (box 9) are *Anacardium excelsum, Brosimum utile, Calophyllum brasiliense, Platymiscium sp., Sterculia recordiana, Vochysia allenii, Vochysia ferruginea.* Some of those species tolerate a broad range of light conditions and also have optimal growth at **intermediate sunlight** (box 8).

When a reforestation area includes **flat terrain/slope base in full sun** (box 10), *Aspidosperma spruceanum, Buchenavia costaricense, Inga spp., Peltogyne purpurea, Schizolobium parahyba, V. koschnyi* are likely to have very good performance, whereas *Anacardium excelsum (I), Platymiscium spp. (I), Symphonia globulifera (I), Terminalia amazonia (I), Vitex cooperi (I),* can be planted as well (reduced growth). In **flat terrain/slope base and shade** (box 12), some slightly more sensitive species (*Carapa guianensis, Perrottetia sessiliflora, Ruptiliocarpon caracolito, Sterculia recordiana)* meet optimal conditions for highest growth performance (e.g. when planted under nurse trees/as enrichment planting). Also *Anacardium excelsum, Brosimum utile, Calophyllum brasiliense, Platymiscium spp., Symphonia globulifera, Virola koschnyi, Vochysia allenii* and *Vochysia ferruginea* are supposed to have optimal growth. Repeatedly listed species are perfectly suited for **different combinations,** especially so for *Anacardium excelsum, Aspidosperma spruceanum*, *Peltogyne purpurea*, *Platymiscium spp., Symphonia globulifera*. Other species may be still robust enough for reforestation at various conditions, but excluded from some boxes because low growth (Tables 10, 16). If certain species are considered for planting despite unfavourable conditions, the reforestation strategy needs to be adapted (e.g. plant a higher number and/or nurse trees, fertilisation).

Some species are excluded from table 29 (despite good results in single levels of Tables 10, 16), either because levels could not be compared (*Ochroma pyramidale, Ocotea spp., Rollinia pittieri*, *Trichilia septentrionalis, Zygia longifolia*) or mortality for the levels with highest growth exceeded 30% (e.g. *Virola sebifera* (50% in full sunlight), *Minquartia guianensis* (58.3% in full sunlight). Results for dark shade are insufficient for the most species or point to high trade-offs (e.g. *Carapa guianensis* had over-average growth, but mortality was 45.5%). As such conditions will rarely be faced in reforestation projects, combinations with topographic positions are useless (and recommendations impossible too).

5.6 **Species mix**

While the success of establishing a tree plantation can be quantified via survival and growth rates, the purpose of reforestation is to restore an ecosystem similar to the natural forest, which means that the species mix should include more than the species easiest to grow. A common approach to discuss species mix for an ecological restoration project is to compare it with a reference-ecosystem:

"A reference ecosystem can serve as the model for planning an ecological restoration project, and later serve in the evaluation of that project. (…) In other words, the restored ecosystem is eventually expected to emulate the attributes of the reference, and project goals and strategies are developed in light of that expectation. (…) Restoration attempts to return an ecosystem to its historic trajectory. Historic conditions are therefore the ideal starting point for restoration design. The restored ecosystem will not necessarily recover its former state, since contemporary constraints and conditions may cause it to develop along an altered trajectory." (SER – Society for Ecological Restoration International Science & Policy Working Group, 2004:2)

In brief, if the historic conditions of the restoration area are assumed to be similar to a nearby natural forest, this ecosystem would be the reference. On an open reforestation site, a secondary forest will develop, but its species composition will differ from the reference for a longer period of time until species invade and conditions become more similar to the reference.

The vegetation study of Weissenhofer et al. (2008b), mentions two vegetation assemblies of the region that also match with the morphology of the terrain at La Bolsa and therefore are suitable as a reference: "Primary forest on hilltops and ridges" and "Primary forest on inland slopes" (section 2.3). Diversity, abundance and spatial distribution of species in different topography conditions of that vegetation assemblies in the Esquinas Rainforest were examined in detail by Huber (2005, at the same 1 ha-plots). He calculated the relative density which represents the proportion of individuals per species within a subplot.

Subsequently, all species used at La Bolsa will be compared to the characteristic species of the references, including those with few planted individuals. Understorey species (Weissenhofer et al., 2008b:68) were not specifically considered during fieldwork and therefore are mentioned here only in few cases. Relative density (r.d.) was not available for all species, written in brackets.

Out of the most abundant canopy*/mid-subcanopy species found on ridges, were planted at La Bolsa (sensu Huber, 2005:Table 3.22.):

> **Vochysia ferruginea* (4.48%, Vochysiaceae), **Symphonia globulifera* (2.83%, Clusiaceae), **Calophyllum brasiliense* (r.d. <2.24%, Clusiaceae), **Peltogyne purpurea* (r.d. <2.24%, Fabaceae-Caesalpinioideae)*, *Aspidosperma spruceanum* (r.d. <2.24%, Apocynaceae*)*

Missing:

> **Qualea paraensis* (5.90%, Vochysiaceae), *Welfia regia* (5.78%, Arecaceae), **Vochysia megalophylla* (4.13%, Vochysiaceae), *Brosimum guianense* (3.30%, Moraceae), *Croton schiedeanus* (2.95%, Euphorbiaceae), *Pausandra trianae* (2.36%, Euphorbiaceae), *Socratea exhorriza* (2.36%, Arecaceae), *Marila laxiflora* (2.24%, Clusiaceae)

Further missing species according to (sensu Weissenhofer et al., 2008b:68):

> **Calophyllum longifolium* (Clusiaceae), **Macrolobium hartshornii* (Fabaceae-Caesalpinioideae), **Parkira pendula* (Fabaceae-Mimosoideae), **Couratari guianensis* (Lecythidaceae), **Humirastrum diguense* (Humiriaceae), **Qualea polychrome* (Vochysiaceae).

The most abundant canopy species on the ridge, *Qualea paraensis* (5.90), was not planted. In total, only 5 of the 13 characteristic canopy* species are present at La Bolsa. Furthermore, none of the 8 subcanopy-species were planted. Notably palms are completely missing (*Welfia regia, Oenocarpus mapora, Socratea exhorriza),* which usually are very abundant in natural forests (c. 10% of all individuals at ridges; Huber 2005).

Out of the most abundant canopy*/mid-subcanopy species found on inland slopes were planted at La Bolsa (sensu Huber, 2005, Table 3.31.):

> *Iriartea deltoidea* (r.d 13.47%, Arecaceae), *Symphonia globulifera* (r.d. 3.42%, Cusiaceae), **Brosimum utile* (r.d. 2.85%, Moraceae), **Carapa guianensis* (r.d. 2.85%, Meliaceae)*;* (According to Weissenhofer et al. (2008b) plus: **Aspidosperma spruceanum* (Apocynaceae), **Ruptiliocarpon caracolito* (Lepidobotryaceae)

Missing:

> *Welfia regia* (8.92, Arecaceae), *Marila laxiflora* (3.80, Clusiaceae), *Socratea exhorriza* (3.23, Arecaceae), *Mabea occidentalis* (2.47, Euphorbiaceae), *Dendropanax arboureus* (2.28, Araliaceae), *Brosimum lactescens* (2.09, Moraceae), **Humiriastrum diguense* (Humiriaceae)

Further missing species according to Weissenhofer et al. (2008b:70):

**Copaifera cambiar* (Fabaceae-Cesalpinioideae), **Otoba novogranatensis* (Myristicaceae), **Vochysia megalophylla* (Vochysiaceae), **Virola guatemalensis* (Vochysiaceae), *Guatteria amplifolia* (Annonaceae), *Protium tenuifolium* (Burseraceae), *Compsoneura excelsa* (Myristicaceae), *Parathesis aeruginosa* (Myrsinaceae)

Out of 8, only 4 characteristic canopy species were planted. Only 2 subcanopy species out of 12 were present at La Bolsa (*Symphonia globulifera* plus one individual of *Iriartea deltoidea*). Again, palm species were under-represented in the species mix (normally c. 27% of all individuals at slopes). One typical understory palm species, *Asterogyne martiana*, was planted (normally also abundant: *Calyptrogyne ghiesbreghtiana, Geonoma cuneata*).

To resume, most of the abundant species found at the natural forest plots were lacking at La Bolsa. Thus primary forest's vegetation assemblies were not very well represented by the initially planted species mix at La Bolsa. Except for *Terminalia amazonia* (not mentioned in the references), those species planted in high numbers constitute at least important elements of the natural vegetation assemblies in the proximity of the reforestation plot. For example, *Vochysia ferrugina* is typical for naturally regenerating young secondary forests of the Golfo Dulce region (Weissenhofer et al., 2008b) and was planted to a large extent. Many of the used species have wide native ranges (in brackets) and are commonly used for reforestation in Costa Rica, (Piotto et al., 2004a, Jiménez, 2002) e.g.: *Terminalia amazonia* (Mexico to tropic South America), *Vochysia guatemalensis* (Mexico to Panama), *V. ferruginea* (Nicaragua to tropic South America), *Virola koschnyi* (Belize to Ecuador), *Cedrela odorata* (Mexico to northern Argentina), *Calophyllum brasiliense* (Mexico to South America), *Symphonia globulifera* (Mesoamerica, the Caribbean, South America, tropical Africa). The mix was also constrained by practical reasons, because many species were not available in large numbers within the project time (Jenking, pers. comment).

<u>Limitations of the reference-approach</u>

One important point is that species have different spatial distribution patterns. For example, species can be restricted only to slopes (e.g. *Memora cladotricha)*, or aggregated (e.g. *Rinorea viridifolia*), while others are wide spread (e.g. *Iriartea deltoidea*), (Ghazoul and Sheil, 2010). The references have been defined based on 1 ha-plots, but these may not sufficiently represent these distribution effects. Also with regard to the great landscape heterogeneity of the region, vegetation assemblies deviating from the 1 ha-plots studied by Huber (2005) cannot be excluded: Even in similar topographic positions, edaphic conditions may vary because of diverse parent material in the region (Pamperl, 2001). Thus it is difficult to scale-up stand-level patterns of species compositions to a higher landscape-level (Chazdon, 2003).

Furthermore rare species are not considered in the references which are restricted to the most abundant species of a plot. Nevertheless, these species constitute important elements of Neotropical rainforests and should be included in a species mix (despite practical problems in obtaining or reproducing them).

Another important point to mention is that rainforest ecosystems are highly dynamic and species composition in an early successional stage naturally differs from an old-growth forest composition such as was used as a reference (Weissenhofer et al., 2008b, Chazdon et al., 2010). For that reason the question arises, whether all species of the reference ecosystem need to be comprised in the initial mix or if a basic framework of common species would be sufficient. Lamb (2011) recommended high species diversity at least when the distance to a diverse forest is considerable. When a higher degree of disturbance alters edaphic and microclimatic conditions, characteristic later-successional species may not be suitable, at least not for the conditions in an early successional state (Lamb 2011). If these species are not comprised in the initial mix for such reasons, this again alters the trajectory of succession. This raises the question, if an alternative reference should be chosen. The Society for Ecological Restoration International Science & Policy Working Group (SER 2004) only suggested defining the species mix for reforestation based on any potential stage along the trajectory of succession from the ecosystem. But species compositions of earlier successional stages are highly variable and depend on many interacting site-specific factors and the influence of the former land use. This renders predictions of successional trajectories extremely difficult (Guariguata and Ostertag, 2001).

Therefore primary or secondary old-growth forest may still be the most precise reference. It can serve at least as a basic guideline, but reforestation strategy (next chapter) needs to be adapted. Lamb (2011) suggested the use of fast growing but short-lived species to ensure that canopy closure is rapid and weeds are excluded. By this means, suitable conditions are created for long-lived-pioneers and finally for the shade-tolerant (climax-) species. Chazdon et al. (2010) found that 40% of the species only start to invade a secondary forest stand after the canopy is closed. When it is not likely for typical species to invade by themselves, a succession process could be initiated by planting them, though it is not necessary to mimic all successional stages (Lamb 2011). For example, experiences at La Gamba with *Brosimum utile* showed that it easily becomes burnt in the direct sunlight in open conditions. Thus *Brosimum utile* would be a species to interplant when sufficient shade is provided, as it is an important species of the reference.

5.6.1 How likely is it that species will invade into La Bolsa?

Generally, the main factors that are considered to determine species invasion and succession are: the surroundings of an area on a local and landscape level, as well as the scale, duration and intensity of disturbances affecting the site conditions (Chazdon, 2003, Turner et al., 1998). The proximity of disturbed areas to remnant forest patches is crucial for recovery and species composition. When the area is embedded in a structurally and compositionally intact forest on the landscape level, recovery will be faster and more likely than within other surroundings (e.g. degraded agricultural land, Hooper et al., 2005).

Namely the availability of seeds in combination with the microsite conditions affects species composition (Dalling and Hubbell, 2002). Adjacent and remnant vegetation is important as it promotes increases in species richness, tree density and aboveground biomass Guariguata and Ostertag (2001). It causes seed rain and influences microclimate and attractiveness for dispersal agents (e.g. perch trees and fodder for mammals, birds, bats, see Holl et al., 2000, Jones et al., 2004). Spatial patterns and reproductive traits of tree species (e.g. seed size, seed production at the species level and dispersal mechanisms) in the proximity of the area are documented to alter species composition (Guariguata and A. Pinard, 1998, Franklin and Rey, 2007). Furthermore, the rate of successional recovery is very much based on edaphic conditions such as soil type, fertility, and erosion. Severely degraded soils will recover slower or can be stabilized and fertilized before restoration attempts, depending on the restoration strategy (Lamb, 2011, Carpenter et al., 2001).

Lamb (2011) and other authors underscored that succession on a former pasture area will evolve differently than at a recently logged forest site. Especially factors such as seedling competition with pasture grasses, high light intensity (Hooper et al., 2004, Hooper et al., 2002, Celis and Jose, 2011), lack of dispersal of forest seeds, high seed predation, low seed germination, lack of nutrients and herbivory were found to be accountable in retarding or even inhibiting succession on abandoned pasture lands (Holl et al., 2000, Wijdeven and Kuzee, 2000).

Chazdon (2003) emphasized in a meta-analysis of forest recovery that duration of recovery processes is extremely variable. Some processes such as aboveground biomass accumulation, forest structure and recovery of soil fertility can occur within decades whereas species number and especially species composition often remains different for longer periods, even centuries (Guariguata and Ostertag, 2001, Turner et al., 1997). For example, Spiotta et al. (2007) compared secondary forests at Puerto Rico (established 10 to 80 years ago on former pasture lands) to primary forests with regard to species composition and aboveground biomass accumulation in a chronosequence study. They found out that tree species composition in all secondary forests was different from that of primary forests, but species richness was similar. The 80 year-old secondary forests had even greater biomass than the primary forests because of more woody species instead of palms. Guariguata et al. (1997) compared the structure and floristics of secondary and old-growth forest stands in lowland Costa Rica: 15 – 20 year old secondary forests had substantially lower species richness than old-growth forests. The understorey regeneration (saplings) of the secondary forest contained a higher percentage of the species typical for the old growth forest than the canopy layer. Some studies attribute divergent species composition of young secondary forests to dispersal limitations of late-successional trees, especially when they have large seeds (Dalling and Hubbell, 2002, Ingle, 2003). Chazdon (2003) remarked that post-agricultural succession is discussed in some chronosequence studies, but long term studies on the same monitored plots are rare.

With regard to species invasion at La Bolsa, no species-specific predictions can be made as no detailed investigations of the adjacent flora nor of the soil seed bank potential are available. According to Dalling and Denslow (1998), the former use as a pasture for 30 years is probably less influential than the composition of the vegetation in the proximity of La Bolsa, which borders on old secondary forest. They found that species richness and density of the soil seed bank were not directly related to duration since abandonment of the site, but to the presence of seed-bank-forming species in the adjacent vegetation. As La Bolsa borders on two sides to apparently well-structured old-growth secondary forest (primary forest is believed to be within 500 meters behind), the dispersal of seeds from there can be generally considered as likely: according to Rodrigues et al. (2009) at least in the adjacent parts <100 m afar the forest edge. During Fieldwork, I encountered manifold insects, birds and mammals at La Bolsa: e.g. the Central American squirrel monkey *(Saimiri oerstedii)* and White-nosed Coati *(Nasua narica))*, the monkeys obviously attracted by the old-stand trees and the banana plants (*Musa sp.,* Musaceae) that were planted as fodder for potential seed dispersers.

Natural understorey regeneration was not investigated during field work. Some studies found that understorey regeneration in the most cases is supported by reforestation with native or exotic timber species (Carnevale and Montagnini, 2002, Haggar et al., 1997). Cusack and Montagnini (2004) compared plantations with control plots on abandoned pasture lands and found that understorey woody species diversity was significantly accelerated at plantations and varied depending on the planted species. Experimental plantations showed that especially *Virola guatemalensis* and *Calophyllum brasiliense* were successful at recruiting understorey regeneration. Light intensity also played a major role: very high as well as very low percentages of canopy openness reduced understorey regeneration abundance. Naturally, these results do not consider all species and growth forms. For example, as mentioned by

Weissenhofer et al. (2008b) palms are rare in old secondary forests (with canopy height c. 30 m) indicating invasion of palm species is slow or not very likely. Also Spiotta et al. (2007) confirmed that old secondary forests contain more woody species instead of palms. Taking into account that they occur in high abundance and thus constitute one of the most important structural elements in the reference ecosystem (section 2.3), palms might deserve to be planted more frequently. As they are often encountered in gaps under high light conditions (Weissenhofer et al., 2008b) they probably would prosper well at La Bolsa. From the other mentioned factors that can impede invasion of species, some were present at the plot: pasture grasses, ferns and other competitive vegetation can delay succession processes at least in some parts of La Bolsa as long it is not shaded out by the planted trees. The high light intensity supported the competitive vegetation and challenged even some planted species. The germination of seeds was possibly reduced in these overgrown parts. Herbivory did not compromise reforestation success until 2012. Furthermore, the soil was severely eroded at least where the landslides occurred. Herbaceous vegetation was lacking there (except ferns and clubmosses). Otherwise soil fertility was considered sufficient (section 2.2 for present soil conditions). Litter had rarely accumulated since the plantation of trees.

For monitoring purposes, (comparison with) stages of natural succession might be of interest (observing the trajectory succession follows at La Bolsa). Some of the species mentioned by Weissenhofer et al. (2008b:85) for „Succession after logging“ (intact soil) appeared as spontaneous vegetation (*Ochroma pyramidale, Senna sp., Cecropia sp.*) or were planted (*Brosimum utile, Carapa guinanensis, Vochysia spp., Ochroma pyramidale*). Further species typical for "Old secondary forest" (section 2.3) are also present at La Bolsa (*Guarea grandifolia*, *Calophyllum longifolium, Symphonia globulifera*, *Ruptiliocarpon caracolito*). Monitoring for a longer period of time can show, if species composition accelerates and succession develops towards the expected state as expressed in the references and ecosystem functions are fulfilled.

5.7 **Reforestation strategy**

According to a review of reforestation approaches and efforts from the past 30 years in the Brazilian part of the Amazonian region by Rodriges et al. (2009), the planting of many native species from different functional groups is currently the most common reforestation strategy in the Atlantic Forest (Brazil). Many other promising techniques have been developed as well (e.g. seed rain management or promotion of natural regeneration, section 5.7.3). Lamb (2011:340ff) generally distinguished three methods of ecological restoration: nurse-tree method, framework species method and maximum diversity method. In most projects combinations or adapted versions of these methods are used. To compare their major elements with the reforestation method at La Bolsa, the explanations of Lamb (2011) are summarised subsequently:

On severely degraded sites the use of nurse tree species (native or exotic) is recommended. One or a few of easy to raise and fast growing species, able to tolerate and mitigate the local conditions, have to be planted in order to exclude weeds and improve environmental conditions. This method works only close to an existing forest, otherwise not enough species will invade to create a self-sustaining ecosystem. To provide sufficient space for colonists to grow later on, the nurse trees must be thinned, girdled or can be harvested.

The framework species method is also a nurse tree technique, but uses more species (20 – 30) to initiate succession and provide a framework for further species invasion. This method is again limited to sites close to existing natural forest. Species composition is important: a good solution is to use quickly growing species for canopy closure, as well as rare and endangered species from the start. About 30% of the initially planted, fast growing pioneers should be short-lived to guarantee the creation of gaps for subsequent colonists. Additionally, fruit reward and perch trees to attract seed dispersers are very important as an initial structure. For planting density, 2500 – 3000 tph (tree stocking per ha) are considered an adequate number.

For the maximum diversity method a larger number of species is essential. Depending on possibilities and the need for rapid establishment of biodiversity, approximately 80 – 100 species are necessary. This method was suggested for sites distant to natural forests, when natural species invasion is limited. All trees would be planted at the same time. Species mix should be composed of 90% belonging to later successional stages. Especially important are species with large seeds, as well as poorly dispersed, endangered and vulnerable ones. Regarding planting density, 20 – 30 individuals of each species per ha can be taken as a guideline to ensure that sufficient trees of each survive. Species that are known to be functionally important or slow to reproduce might be represented in greater numbers within the species mix.

Reforestation strategy applied at La Bolsa

At La Bolsa, species diversity ranges between the mentioned numbers of framework- and maximum diversity method. 89% of all planted trees belonged to 31 species, but only 2 species had more than 20 tph. The other 52 species were planted only in small numbers. The 10 most abundant species may be considered as the framework species – for example, a considerable number of *Terminalia amazonia* trees were planted (14.7% of all individuals, 39 tph). It is well known as a suitable species for reforestation that tolerates most site conditions (see below, Carpenter et al., 2004a), which are useful properties for a framework species. The main (practical) reason for planting *Terminalia amazonia* has been the easy availability of the saplings, while other seeds and saplings were more difficult to obtain. Time and money needed for the acquisition of even more species would have been missing later on for maintenance (Jenking, pers. comment). Slower growing species such as *Brosimum utile* and *Carapa guianensis* also belong to the 10 most frequently planted species representing the shade-tolerant and long-lived elements of the framework.

Rodrigues et al. (2009) emphasized that in a number of projects the use of more than 50 species was most efficient in establishing more permanent forests, although the reason for this is still unclear. They assumed that higher species diversity inserted higher functional diversity influencing long term forest functioning (e.g. keystone species, ecological engineers). On the other hand side, they discussed the possibility that particular species combinations are more important than the number of species itself, what could reduce costs (see Mansourian et al., 2005). In the light of these results species diversity at La Bolsa can be considered sufficient as a basis for the development in a relatively species-rich secondary forest. The low number of individuals per species (except for the 10 abundant and common "framework species" (Table 2) can in all probability be compensated by the likeliness of future species invasion.

In the next section, the 4 growth classes are used for an estimation of the distribution of fast and slow growing trees at La Bolsa:

Table 30: Trees per growth class per ha.

Growth Class	Trees alive (4.8 ha)	Trees alive (% of total)	Trees alive (per ha)	Planted* (4.8 ha)	Planted (% of total)	Planted (per ha)
"Very fast" (5 sp.)	333	10%	69	411	10%	88
"Fast" (5 sp.)	875	26%	182	965	24%	201
"Intermediate" (9 sp.)	925	27%	193	1064	26%	222
"Slow "(12 sp.)	989	29%	206	1254	31%	261
Subtotal (from 31 sp.)	3122	91%	650	3694	90%	770
Trees of the other 52 species	309	9%	64	408	10%	85
Trees total (from 83 sp.)	3431	100%	715	4102	100%	855

*(incl. dead individuals); species in growth classes are listed in section 4.3 tree size

From the calculated 855 tph (including all 83 species), 715 tph had survived. These numbers are low number compared to those suggested by Lamb (2011) for the framework species method. Most of the analysed species belonged to the growth classes "intermediate" and "slow", with also the largest percentage of individuals alive (27% and 29%, respectively). "Very fast" growing tree species were represented by the lowest number of trees alive (10%), while "fast"-growing trees were abundant (26%). It has to be mentioned that the growth classes were arbitrarily defined (section 4.3 tree size) and initial growth is not a sufficient determination of further species performance (section 5.1). Nevertheless these results may help to gain at least a rough idea of (future) canopy development at La Bolsa: Those 10% “very fast” growing trees belong* to short-lived pioneer species (*Buchenavia costaricense, Inga spp., Ochroma pyramidale, Pseudobombax septenatum, Schizolobium parahyba)* will contribute to the development of gaps. Species considered* long-lived pioneers (*Terminalia amazonia, Cedrela odorata, Vochysia guatemalensis* can grow rapidly and quickly develop a relatively closed and stable canopy, while some “Climax'' hardwood species such as *Calophyllum brasiliense* that are contained in the growth classes intermediate and slow will form the most persistent canopy elements with time *(Carpenter et al., 2004b, Calvo-Alvarado et al., 2007, Jiménez, 2002).

5.7.1 Functional important and endangered species

As mentioned before, the planting of functional important* species can support restoration and accelerate species diversity. (*in the sense of ecological functions that underlie/support the development of further, more complex ecological functions within the ecosystem; species can fulfil many functions). Some species attributed to be functionally important were also present at La Bolsa (in brackets). For example, in the case of a severely degraded site, Nitrogen-fixing species can be planted for nutrient accumulation (e.g. *Inga spp*., *Platymiscium spp*., *Schizolobium parahyba, Zygia longifolia)*, while others contribute to soil stabilisation, enhanced nutrient cycling and improved microclimatic conditions, such as e.g. *Vochysia ferruginea*, *Terminalia amazonia, Vochysia allenii, Anacardium excelsum, Ochroma pyramidale, Spondias mombin, Zygia longifolia* (Carpenter et al., 2004a, Jiménez, 2002). To foster natural regeneration, tree species that provide fodder and nesting opportunities for potential seed dispersers (animals) can help to enhance species diversity on a succession area, e.g. *Anacardium excelsum, Brosimum utile, Calophyllum longifolium, Carapa nicaraguensis, Inga spp., Minquartia guianensis, Ochroma pyramidale, Platymiscium curuense, Samanea saman, Schizolobium parahyba, Spondias mombin, Virola koschnyi, Vitex cooperi, Zygia longifolia* (Wunderle Jr, 1997, Tucker and Murphy, 1997, Jiménez, 2002).

An important goal of reforestation efforts is to maintain species diversity. For that reason the planting of endangered species should be aimed at. From the species planted at La Bolsa, only few have yet been assessed for the global IUCN Red List, but it cannot be excluded that some of the others are threatened as well. For 5 species, the IUCN Red List status was available: *Cedrela odorata* (Vulnerable, IUCN, 2013b), *Vitex cooperi* (Endangered, IUCN, 2013a), *Cryosophila guagara* (Lower risk/near threatened; IUCN, 2013b), *Minquartia guianensis* (Lower risk/near threatened (IUCN, 2013b), *Cecropia obtusifolia* (Lower Risk/least concern; IUCN, 2013b). Further data from the IUCN National Red Lists could be used, but for Costa Rica no current list was available. Some species planted at La Bolsa were included in the current

Columbian National Red List (IUCN, 2013c): *Anacardium excelsum* (assessed 2005, least concern/near threatened), *Podocarpus guatemalensis* (assessed 2006, vulnerable; but global IUCN status is least concern), *Perrottetia sessiliflora* (assessed 2003, near threatened).

For Costa Rica (C.R.), Jiménez (2002) also assessed *Cedrela odorata* and *Minquartia guianensis* to be rare species because of exploitation for timber. In contrast to the IUCN red list, he considered *Vitex cooperi* and *Perrottetia sessiliflora* (grows occasionally outside the forest) common species for C.R., while he considered *Peltogyne purpurea* (occurrs only in Panama and on the Costa Rican Pacific slope) to be highly endangered with very low regeneration in the forest (see also Jiménez, 1995). Further species that Jiménez (2002, 1995) found to be endangered or very rare are *Platymiscium curuense* (only on the Pacific slope of C.R., endangered, low regeneration), *Platymiscium pinnatum* (Guatemala to Colombia, drier forests, endangered in C.R.), *Minquartia guianensis* (widespread species from Nicaragua to Brazil; endangered, in C.R. regeneration is rare in the forest), *Ceiba pentandra* (widespread, but very rare in C.R.), *Humiriastrum diguense* (C.R. to Colombia, very rare, little regeneration), *Hymenaea courbaril (*widespread, but in C.R. very rare in the forest, little regeneration), *Elaeoluma glabrescens* (widespread species, in C.R. rarely encountered in undisturbed primary forests, little regeneration), *Hyeronima alchorneoides* (widespread, in C.R. adult trees and regeneration are rare, grows sometimes in abandoned pasture lands), *Qualea paraensis* (widespread, Meso- and South America, endangered in C.R.), *Caryodaphnopsis burgeri* (endemic to the pacific coast of C.R.; at the risk of extinction), *Tabebuia guayacan* (Mexico-Colombia, endangered in C.R.).

Hence, a handful of endangered species have been planted at La Bolsa as well, but mostly in low numbers. Even though performance was not very good for all of them, endangered and rare species should generally be included in the species mix. For some of the species, sufficient data was lacking, so specific recommendations for reforestation are difficult and performance should be documented in further reforestation projects, especially *Caryodaphnopsis burgeri, Tabebuia guayacan, Hyeronima alchorneoides, Elaeoluma glabrescens, Hymenaea courbaril, Humiriastrum diguense, Ceiba pentandra, Podocarpus guatemalensis, Cryosophila guagara* (and also for those trees with the precise species unknown – *Ocotea spp., Guaera sp., Inga spp.).*

5.7.2 Reforestation sites difficult to restore and weeds

Areas that are more difficult to reforest (such as ridges/hilltops and steep slopes affected by erosion at La Bolsa) may require adapted methods in further projects. Taking into account the unfavourable conditions on ridges and upper slope sites, a higher planting density is recommendable. This could reduce the necessity of seedling replacement and thus render plantings more efficient. With regard to the species choice and soil fertility, a trial of Carpenter et al. (2004b) is of interest. They tested *Terminalia amazonia* in catalysing reforestation: Good results were achieved on areas that were not too severely eroded, especially when legumes were interplanted. The effects of different legumes (*Inga edulis, Gliricidia* and herbaceous legumes) at enhancing soil fertility fostering growth of *T. amazonia*, were compared and *I. edulis* showed the best results. *I. edulis* also improved growth of *T. amazonia* on the long run in contrast to initial use of chemical fertilisers. For the goal of re-establishing a variety of native species, Carpenter et al. (2004b) stated that the soil must not be degraded too much. They proposed to plant a combination of *Vochysia guatemalensis*, *Terminalia amazonia*, *Calophyllum brasiliense* and maybe *Cedrela odorata* when a remnant B horizon exists at the site, before interplanting more shade-loving species. At La Bolsa, similar species (*Terminalia amazonia, Vochysia* ferruginea as well as nitrogen fixers *Inga spp., Platymiscium spp.*) were planted in positions difficult to reforest with acceptable results while *Calophyllum brasiliense* cannot be confirmed to be useable as it grew least in steep and sunny terrain.

For some species, competitive weeds, grasses and ferns were found to reduce tree growth at La Bolsa. As fern-dominated vegetation is considered typical for gaps in old growth forests and on succession areas, it can be tolerated, but problems arise, when ferns cover large areas and start to form impenetrable thickets. *Dicranopteris pectinata (Gleicheniaceae)* and *Nephrolepis multiflora* (Oleandraceae) are very common on eroded soil and after clear cuts. Referring to Weissenhofer et al. (2008b), only few species which are mostly bird- or wind dispersed have a chance to colonise such fern thickets which can persist up to 20 years until the first species invade. Naturally, these ferns die rapidly when shaded. Similar observations for competitive grasses were made by Kim et al. (2008). Several studies address possible methods to reduce influence of weeds on tree performance and succession (e.g. Hooper et al., 2002). An attempt to limit ferns growth can be to interplant robust and competitive tree seedlings, for example from the genera *Inga* or *Vochysia* (Jones et al., 2004, see also Otsamo et al., 1997). However, in the area of La Gamba, strategies to avoid weeds have to be applied and maintenance needs to be calculated in reforestation projects as much reduced tree performance on ridges and steep slopes with competitive vegetation were proofed. Not only Rodrigues et al. (2009) considers the need for maintenance of a restored area – at least during the first two years – to be the key lesson for restoration, also Holl et al. (2000) emphasize that the control of weeds is particularly important to make sure that reforestation processes will not be seriously compromised.

5.7.3 Further aspects of the planting scheme at La Bolsa

In most parts of La Bolsa, species were placed at random. There was no experimental concept that would allow drawing conclusions about favourable species combinations. Furthermore, in some sectors, the planted rows ended inside the adjoining forest or old cacao stands. It remains unclear, whether this was meant as "enrichment planting" or had other reasons. Rodrigues et al. (2009) found some aspects that can serve as a guideline for further projects: They emphasized that a close distance to forest fragments (distances <100 m) greatly affects the speed and trajectory of forest recovery, as well as the reestablishment of critical ecological interactions. To strengthen the self-recovery potential of the forest, they suggest the use of alternative or complementary strategies to tree planting, if the self-recovery potential of the area is sufficient (Morrison and Lindell, 2011, Holl and Aide, 2011). In this context, stimulation of pre-existing advanced regeneration (seedlings and/or tree sprouts protection and conduction), management of seed dispersal (e.g. artificial perches), and enrichment through soil seed bank, seed rain (Cole et al., 2010), seedling transference as well as topsoil transposition (Viani et al., 2007), nucleation techniques (Holl et al., 2011) and direct seeding (Cole et al., 2011) were mentioned. For other reforestation areas similar to La Bolsa can be concluded that planting trees is dispensable within distances less than 100 m to existing forest, if competitive exotic weeds are absent and shadow is provided.

5.8 **Summary**

Species performance: Of the analysed 31 species, almost two thirds had survival equal or superior to the average of 82%, only six species had survival ≤70%. Average height for all species was 1.4 m. Mean species survival (performance) at La Bolsa can be considered (very good, at least) consistent with other studies in the humid tropics of native trees plantations in Central America (Breugel et al., 2011, Haggar et al., 1998).

Functional traits such as seed size, specific leaf area (SLA, which is the inverse of leaf mass per area, LMA), wood density and plant height at maturity are often correlated with relative growth rate and/or mortality rates (Poorter et al., 2008). For a selection of species at La Bolsa with relevant data available (Table 34, Appendix), the correlations of wood density, Nitrogen content in per cent of leaf-dry weight and leaf mass per area (LMA) with mean height per species were tested, but none of these traits were significantly correlated to height as was expected with regard to literature.

Light levels had a significant influence on mean height and diameter at 50 cm for 14 of 31 species. Some species showed similar relative mean heights for the entire light gradient while others were restricted to a specific light spectrum, indicated by higher mortality in the remaining levels (for detailed results in Table 10). Generally, for the majority of the species, intermediate levels of light were favourable (i.e., moderate shading by surrounding plants). Trade-offs between growth and survival mostly occurred at the full sunlight level when relative mean height was still ≥100%, but mortality was accelerated compared to the intermediate light level (*Virola sebifera*, *Aspidosperma spruceanum*, *Virola koschnyi*, *Minquartia guianensis, Rollinia pittieri, Terminalia amazonia, Cedrela odorata,* and *Ocotea spp.*).

For 13 single species, <u>topography levels</u> proved to have a significant effect on growth. The species-specific response to the topographic positions is presented in detail in Table 16. 15 of 23 species showed highest growth in flat terrain and 7 species at the base of the slope (also with moderate inclination) suggesting that the associated conditions were most suitable for the majority of the analysed species. In middle to upper slope positions only 5 and on ridges only 1 species *(Symphonia globulifera)* had highest growth indicating that (the conditions in) these topographic positions were less favourable.

<u>Though species distributions</u> are often related to topography in the natural forest, the knowledge of a species natural habitat is not necessarily helpful for reforestation. The comparison of a species natural habitat to the conditions at which it had optimal performance at La Bolsa showed, that the natural habitat can at best point to suitable conditions for reforestation in the case soil conditions are not strongly altered, but will be insufficient for clear predictions as sensitivity to other limiting factors requires examination.

<u>Recommendations for reforestation – species use:</u> For the various topographic positions (flat terrain, lower-, middle- and upper slopes, ridges/hilltops) at different levels of light, an assortment of species can be recommended for reforestation, depending on the most favourable conditions for growth (for complete list see boxes 1 – 12 in Table 29). No species will have optimal growth in ridge positions in full sun (box 1). The most suitable species to plant at ridges* would be *Symphonia globulifera, Aspidosperma spruceanum, Inga spp,. Peltogyne purpurea, Anacardium excelsum and Platymiscium spp. (box 2, 4, 5*; but reduced performance has to be taken into account. These species can be recommended also for all other topographic positions within a broad range of light conditions, except for *Inga spp.*)

Further species that had at least low relative mortality (<11%) at ridges and hilltops were *Vochysia ferruginea, Ruptiliocarpon caracolito, Terminalia amazonia* and *Carapa guianensis* (Table 16; but less healthy and with much reduced growth). *Ochroma pyramidale* grew very well at ridges and upper slopes too (Fig. 36), including natural regeneration. These 5 species would be appropriate for upper slopes in full sun as well. From the usable species, especially those with generally faster growth *(Ochroma pyramidale, Terminalia amazonia, Vochysia ferruginea, Platymiscium spp., Anacardium excelsum)* could serve as nurse trees, i.e. to provide shadow for other species that can be inter-planted later on (compare section 5.7).

For optimal performance in reforestation, the majority of the investigated species require canopy shade (i.e. below nurse trees), especially so for *Brosimum utile, Carapa guinanensis,* *Qualea paraensis, Perrottetia sessiliflora, Ruptiliocarpon caracolito, Sterculia recordiana* (see Table 29).

Species mix: Most of the abundant species found at the natural forest plots were lacking at La Bolsa. Thus primary forest's vegetation assemblies were not very well represented by the initially planted species mix. With regard to species invasion, no species-specific predictions can be made, but as La Bolsa borders on two sides to apparently well-structured old-growth secondary forest (primary forest is believed to be within 500 meters behind), the dispersal of seeds from there can be considered as likely. According to Rodrigues et al. (2009), at least in the adjacent parts <100 m afar the forest edge, species will can invade easily. Only monitoring for a longer period of time can show, if species composition accelerates and succession develops towards the expected state as defined in the reference ecosystems (primary forest on inland slopes/primary forest on ridges and hilltops - sensu Weissenhofer et al., 2008b) and ecosystem functions are fulfilled.

Reforestation strategy: At La Bolsa, species diversity lies between the numbers for the framework- and maximum diversity method defined by Lamb (2005). 89% of all planted trees belonged to 31 species, but only 2 species had more than 20 tph. The other 52 species were planted only in small numbers. The 10 most abundant species may be considered as the framework species – for example, a considerable number of *Terminalia amazonia* trees were planted (14.7% of all individuals, 39 tph). Those 10% "very fast" growing trees belong* to short-lived pioneer species (*Buchenavia costaricense, Inga spp., Ochroma pyramidale, Pseudobombax septenatum, Schizolobium parahyba)* will contribute to the development of gaps. Species considered* long-lived pioneers (*Terminalia amazonia, Cedrela odorata, Vochysia guatemalensis* can grow rapidly and quickly develop a relatively closed and stable canopy, while some "Climax" hardwood species such as *Calophyllum brasiliense* that are contained in the growth classes intermediate and slow will form the most persistent canopy elements with time *(Carpenter et al., 2004b, Calvo-Alvarado et al., 2007, Jiménez, 2002).

Some species attributed to be functionally important were also present at La Bolsa (Nitrogen-fixing, e.g. *Inga spp.*, *Platymiscium spp.*, *Schizolobium parahyba, Zygia longifolia;* soil stabilisation, enhanced nutrient cycling and improved microclimatic conditions, e.g. *Vochysia ferruginea*, *Terminalia amazonia;* fodder and nesting opportunities for potential seed dispersers (animals), e.g. *Anacardium excelsum, Brosimum utile, Calophyllum longifolium, Carapa nicaraguensis).* A handful of endangered species have been planted at La Bolsa as well, but mostly in low numbers. Even though performance was not very good for all of them, endangered and rare species should generally be included in the species mix. For some of the species, sufficient data was lacking, so specific recommendations for reforestation are difficult and performance should be documented in further reforestation projects, especially

Caryodaphnopsis burgeri, Tabebuia guayacan, Hyeronima alchorneoides, Elaeoluma glabrescens, Hymenaea courbaril, Humiriastrum diguense, Ceiba pentandra, Podocarpus guatemalensis, Cryosophila guagara (and also for those trees with the precise species unknown – *Ocotea spp., Guaera sp., Inga spp.).*

Reforestation sites difficult to restore and weeds: Areas that are more difficult to reforest (such as ridges/hilltops and steep slopes affected by erosion at La Bolsa) may require adapted methods in further projects. Taking into account the unfavourable conditions on ridges and upper slope sites, a higher planting density is recommendable. This could reduce the necessity of seedling replacement and thus render plantings more efficient. The effect of the surrounding vegetation was often inconclusive, but plants growing next to grasses, clubmosses or ferns often had lower survival rates, especially when associated with direct solar radiation on hilltops. An attempt to limit ferns growth can be to interplant robust and competitive tree seedlings to shade out weeds, for example from the genera *Inga* or *Vochysia* (Jones et al., 2004, see also Otsamo et al., 1997). Hence, maintenance needs to be calculated in reforestation projects – at least during the first two years.

6 APPENDIX I

6.1 References

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6.2 Abbreviations

°	Degree
°C	Degree Celsius
c.	circa
C.R	Costa Rica
Fig.	Figure
ha	Hectare
ind.	Individual
km^2	Square kilometre
m	Meter
mm	Millimetre
no°	Number
NP	National Park
sp.	Species
spp.	Different species of a genus
tph	Trees per hectare
r.d.	Relative density
MIRENEM = MINAET	Ministerio de Ambiente, Energía y Telecomunicaciones

6.3 **Tables**

6.4 **Table of Figures**

7 APPENDIX II

7.1 Tables (supplementary data)

Table 31: All recorded species

	n per quality level				**Total**
Species	**0**	**3**	**2**	**1**	
Abaracema adenophora				1	1
Accacia allenii				1	1
Anacardium excelsum	6	2	11	75	94
Andira inermis	3			4	7
Apeiba tibourbou	1			3	4
Araliaceae				5	5
Artocapus altilis	1			11	12
Aspidosperma spruceanum	40	16	41	167	264
Asterogyne martiana	1	1	1	13	16
Astronium graveolens	5		2	18	25
Billia colombiana	2		4	4	10
Brosimum utile	*38*	*33*	*44*	*120*	*235*
Buchenavia costaricense	14	7	16	47	84
Bursera simaruba				1	1
Byrsonima crispa	1			2	3
Calophyllum brasiliense	15	2	17	70	104
Calophyllum longifolium			1	2	3
Carapa guianensis	30	14	59	209	312
Caryodaphnopsis burgueri	30	2	2	10	44
Cassia grandes				1	1
Castilla tunu	1			3	4
Cecropia sp.				2	2
Cedrela odorata	20	2	10	64	96
Cedro amargo				1	1
Ceiba petandra				1	1
Chrysophyllum sp.				4	4
Cojoba arborea			1	10	11
Come negro	1			8	9
Croton schiedeanus	1		1	12	14
Cryosophila guagara	2		3	8	13
Diphysa americana	2	1		9	12
Dussia grandifolia				3	3
Elaeoluma glabrescens	12	3	8	9	32
Erythrina fusca	2				2
Ficus spp.	1	1	1	8	11
Garcinia madruno			1	9	10

Portion of trees alive per sp. (II).

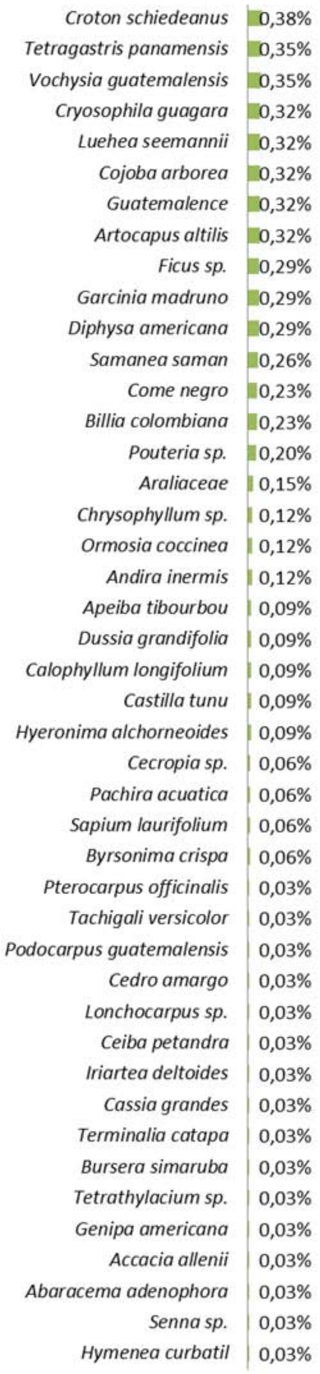

Fig. 40: Portion of trees alive per species, part II.

Genipa americana				1	1
Gliricidia sepium	1				1
Guaera sp.	5		7	14	26
Guatemalence	1	2	3	6	12
Hyeronima alchorneoides		1		2	3
Hymenea curbatil				1	1
Inga spp.	10	2	14	112	138
Iriartea deltoidea				1	1
Lonchocarpus sp.				1	1
Luehea seemannii			4	7	11
Minquartia guianensis	32	8	18	46	104
Ochroma pyramidale	3		4	42	49
Ocotea spp.	8	2	9	13	32
Ormosia coccinea	4	1		3	8
Pachira acuatica	2			2	4
Peltogyne purpurea	20	8	25	76	129
Perrottetia sessiliflora	18	6	13	45	82
Platymiscium pinnatum (sp.)	27	9	34	136	206
Podocarpus guatemalensis				1	1
Pouteria sp.	2	1	1	5	9
Pseudobombax septenatum	1		1	19	21
Pterocarpus officinalis				1	1
Qualea paraensis	20	3	8	34	65
Rollinia pittieri	5	1	4	22	32
Ruptiliocarpon caracolito	16	5	22	37	80
Samanea saman			3	6	9
Sapium laurifolium	1			2	3
Schizolobium parahyba	50		4	65	119
Senna sp.				1	1
Spondias mombin	5	2	3	15	25
Sterculia recordiana	13	5	5	38	61
Symphonia globulifera	16	3	10	62	91
Tabebuia guayacan	8	3	2	10	23
Tachigali versicolor				1	1
Terminalia amazonia	35	19	60	426	540
Terminalia catapa	1		1		2
Tetragastris panamensis			3	9	12
Tetrathylacium sp.	4		1		5
Trichilia septentrionalis	8	3	2	17	30
Trichospermum grewifolium	9	1	4	10	24
Virola koschnyi	16	2	13	22	53
Virola sebifera	39	7	12	35	93
Vitex cooperi	15	6	22	74	117
Vochysia allenii	27	9	32	132	200

Vochysia ferruginea	18	5	16	136	175
Vochysia guatemalensis			1	11	12
Zygia longifolia	2			35	37
Total	**671**	**198**	**584**	**2649**	**4102**

Quality levels

Table 32: Mortality and quality per species, sorted by Q0, n=36 species with ≥ 19 Individuals

Species	Quality-level					n				
	0	3	2	1	≙ Survival	0	3	2	1	Total
Caryodaphnopsis burgueri	68%	5%	5%	23%	32%	30	2	2	10	44
Schizolobium parahyba	42%	0%	3%	55%	58%	50	0	4	65	119
Virola sebifera	42%	8%	13%	38%	58%	39	7	12	35	93
Elaeoluma glabrescens	38%	9%	25%	28%	62%	12	3	8	9	32
Trichospermum grewifolium	38%	4%	17%	42%	62%	9	1	4	10	24
Tabebuia guayacan	35%	13%	9%	43%	65%	8	3	2	10	23
Minquartia guianensis	31%	8%	17%	44%	69%	32	8	18	46	104
Qualea paraensis	31%	5%	12%	52%	69%	20	3	8	34	65
Virola koschnyi	30%	4%	25%	42%	70%	16	2	13	22	53
Trichilia septentrionalis	27%	10%	7%	57%	73%	8	3	2	17	30
Ocotea spp.	25%	6%	28%	41%	75%	8	2	9	13	32
Perrottetia sessiliflora	22%	7%	16%	55%	78%	18	6	13	45	82
Sterculia recordiana	21%	8%	8%	62%	79%	13	5	5	38	61
Cedrela odorata	21%	2%	10%	67%	79%	20	2	10	64	96
Ruptiliocarpon caracolito	20%	6%	28%	46%	80%	16	5	22	37	80
Spondias mombin	20%	8%	12%	60%	80%	5	2	3	15	25
Astronium graveolens	20%	0%	8%	72%	80%	5	0	2	18	25
Guaera sp.	19%	0%	27%	54%	81%	5	0	7	14	26
Symphonia globulifera	18%	3%	11%	68%	82%	13	5	5	38	61
Buchenavia costaricense	17%	8%	19%	56%	83%	14	7	16	47	84
Brosimum utile	16%	14%	19%	51%	84%	38	33	44	120	235
Rollinia pittieri	16%	3%	13%	69%	84%	5	1	4	22	32
Peltogyne purpurea	16%	6%	19%	59%	84%	20	8	25	76	129
Aspidosperma spruceanum	15%	6%	16%	63%	85%	40	16	41	167	264
Calophyllum brasiliense	14%	2%	16%	67%	86%	15	2	17	70	104
Vochysia allenii	14%	5%	16%	66%	86%	27	9	32	132	200
Platymiscium spp.	13%	4%	17%	66%	87%	27	9	34	136	206
Vitex cooperi	13%	5%	19%	63%	87%	15	6	22	74	117
Vochysia ferruginea	10%	3%	9%	78%	90%	18	5	16	136	175
Carapa guianensis	10%	4%	19%	67%	90%	30	14	59	209	312
Inga spp.	7%	1%	10%	81%	93%	10	2	14	112	138
Terminalia amazonia	6%	4%	11%	79%	94%	35	19	60	426	540
Anacardium excelsum	6%	2%	12%	80%	94%	6	2	11	75	94
Ochroma pyramidale	6%	0%	8%	86%	94%	3	0	4	42	49

Zygia longifolia	5%	0%	0%	95%	95%	2	0	0	35	37
Pseudobombax septenatum	5%	0%	5%	90%	95%	1	0	1	19	21

Underlined = Not included in further analysis (living individuals <19 or mean tree height <0.5 m)

Tree size

Table 33: Means and standard deviations for tree size, n=31 species

Species	Mean diameter at 50 cm [mm] + SD	Mean diameter at 130 [mm] + SD	Mean height [m] + SD
Anacardium excelsum	15 ± 10	7 ± 9	1.4 ± 0.9
Aspidosperma spruceanum	4 ± 3	1 ± 2	0.7 ± 0.4
Brosimum utile	5 ± 3	1 ± 2	0.8 ± 0.3
Buchenavia costaricense	23 ± 23	15 ± 20	2.1 ± 1.6
Calophyllum brasiliense	8 ± 5	4 ± 5	1.3 ± 0.8
Carapa guianensis	14 ± 10	5 ± 9	1.1 ± 0.7
Cedrela odorata	12 ± 8	6 ± 8	1.5 ± 0.9
Guaera sp.	4 ± 4	0 ± 0	0.5 ± 0.3
Inga spp.	21 ± 14	15 ± 13	2.5 ± 1.5
Minquartia guianensis	3 ± 4	0 ± 2	0.5 ± 0.3
Ochroma pyramidale	63 ± 20	56 ± 20	8.0 ± 3.4
Ocotea spp.	9 ± 11	3 ± 9	1.0 ± 0.7
Peltogyne purpurea	4 ± 4	0 ± 1	0.7 ± 0.4
Perrottetia sessiliflora	5 ± 4	1 ± 2	0.8 ± 0.4
Platymiscium spp.	7 ± 5	3 ± 4	1.3 ± 0.7
Pseudobombax septenatum	41 ± 18	25 ± 12	3.2 ± 1.2
Qualea paraensis	4 ± 5	1 ± 3	0.8 ± 0.6
Rollinia pittieri	3 ± 4	0 ± 1	0.5 ± 0.3
Ruptiliocarpon caracolito	4 ± 3	0 ± 1	0.8 ± 0.4
Schizolobium parahyba	42 ± 29	36 ± 30	3.6 ± 2.4
Spondias mombin	9 ± 7	4 ± 5	1.1 ± 0.7
Sterculia recordiana	11 ± 8	3 ± 6	1.1 ± 0.6
Symphonia globulifera	4 ± 3	0 ± 1	0.7 ± 0.3
Terminalia amazonia	15 ± 11	8 ± 11	1.9 ± 1.2
Trichilia septentrionalis	9 ± 7	5 ± 6	1.3 ± 0.8
Virola koschnyi	7 ± 7	2 ± 5	0.8 ± 0.6
Virola sebifera	8 ± 6	2 ± 5	0.9 ± 0.5
Vitex cooperi	11 ± 8	6 ± 6	1.6 ± 0.9
Vochysia allenii	11 ± 6	4 ± 5	1.3 ± 0.5
Vochysia ferruginea	14 ± 9	7 ± 8	1.7 ± 0.8
Zygia longifolia	15 ± 10	8 ± 8	1.9 ± 1.0
Total	12 ± 14	6 ± 13	1.4± 1.2

Functional traits

Table 34: Correlation height with wood density*/leaf.N*/leaf*mass per area (LMA)

Species	**mean height**	**wood density**	**leaf.N**	**(LMA)**
	[m]	g/cm3	% dry wt	g /m^2
Anacardium excelsum	1.41	0.42	1.59	67.06
Aspidosperma spruceanum	0.75	0.77	1.54	117.00
Brosimum utile	0.75	0.51	2.35	71.40
Buchenavia costaricense	2.13	0.75	-	-
Calophyllum brasiliense	1.26	0.50	1.09	148.60
Carapa guianensis	1.12	0.48	-	96.45
Cedrela odorata	1.46	0.48	3.67	42.90
Guaera sp.	0.51	0.58	3.32	72.32
Inga spp.	2.54	0.57	2.91	65.81
Minquartia guianensis	0.54	0.79	-	69.00
Ochroma pyramidale	8.04	0.19	2.32	-
Ocotea spp.	0.96	-	-	-
Peltogyne purpurea	0.69	0.88	-	69.50
Perrottetia sessiliflora	0.80	-	-	70.97
Platymiscium spp.	1.28	0.76	3.50	43.10
Pseudobombax septenatum	3.19	0.30	1.93	43.52
Qualea paraensis	0.76	0.56	1.51	71.29
Rollinia pittieri	0.50	0.27	-	-
Ruptiliocarpon caracolito	0.83	-	-	-
Schizolobium parahyba	3.65	0.49	3.85	48.69
Spondias mombin	1.12	0.42	1.80	57.15
Sterculia recordiana	1.07	0.49	2.48	78.20
Symphonia globulifera	0.75	0.54	-	64.03
Terminalia amazonia	1.89	0.67	2.18	60.46
Trichilia septentrionalis	1.27	0.65	2.12	70.44
Virola koschnyi	0.78	0.39	2.02	59.49
Virola sebifera	0.95	0.45	2.71	75.65
Terminalia amazonia	1.89	0.67	2.18	60.46
Vitex cooperi	1.65	0.56	3.34	91.50
Vochysia allenii	1.30	0.25	1.83	68.40
Vochysia ferruginea	1.68	0.39	1.83	68.40
Zygia longifolia	1.89	0.69	-	92.60
Total	**1.40**	**0.53**	**2.37**	**72.46**

*Data source: Univ.Prof. Mag.rer.nat. Dr.rer.nat. Peter Hietz

Light levels

Table 35: Mean height per light levels

Mean height [cm]	**Light level**					**n**				
Species	**1**	**2**	**3**	**4**	**Total**	**1**	**2**	**3**	**4**	**Total**
Anacardium excelsum	135	141	149	103	**141**	24	31	30	3	88
Aspidosperma spruceanum	78	76	72	58	**75**	69	84	63	6	222
Brosimum utile	66	78	82	50	**75**	60	79	56	2	197
Buchenavia costaricense	231	208	165		**210**	27	32	10		69
Calophyllum brasiliense	108	142	128	85	**126**	30	39	18	2	89
Carapa guianensis	93	101	146	120	**111**	98	99	79	6	282
Cedrela odorata	124	171	137	70	**146**	12	30	30	3	75
Guaera sp.	55	63	41		**51**	6	6	9		21
Inga spp.	283	254	250	78	**254**	42	48	32	6	128
Minquartia guianensis	67	54	49	65	**54**	10	30	29	2	71
Ochroma pyramidale	847	250			**804**	45	1			46
Ocotea spp.	96	167	69	80	**96**	13	3	7	1	24
Peltogyne purpurea	72	80	59	33	**69**	35	33	37	3	108
Perrottetia sessiliflora	49	77	89	97	**80**	11	12	38	3	64
Platymiscium pinnatum (sp.)	118	138	135	87	**128**	57	65	46	10	178
Pseudobombax septenatum	268	314	375	355	**319**	5	9	4	2	20
Qualea paraensis	67	69	75		**70**	13	20	11		44
Rollinia pittieri	56	56	51	20	**50**	5	8	10	3	26
Ruptiliocarpon caracolito	80	81	89	100	**83**	25	24	14	1	64
Schizolobium parahyba	419	233	306		**365**	47	17	5		69
Spondias mombin	92	133	105		**112**	5	7	8		20
Sterculia recordiana	98	86	118	310	**107**	12	15	20	1	48
Symphonia globulifera	73	75	75	73	**75**	16	27	29	3	75
Terminalia amazonia	175	212	187	130	**189**	160	176	143	26	505
Trichilia septentrionalis	68	140	150	90	**127**	4	6	10	2	22
Virola koschnyi	79	65	96	60	**78**	13	13	10	1	37
Virola sebifera	95	104	86	65	**95**	15	21	16	2	54
Vitex cooperi	162	183	143	60	**165**	41	39	21	1	102
Vochysia allenii	114	139	141	111	**130**	54	53	54	12	173
Vochysia ferruginea	148	175	203	114	**168**	64	53	35	5	157
Zygia longifolia	203	198	160		**189**	15	10	10		35
Total	141	140	131	105	**137**	**1033**	**1090**	**884**	**107**	**3114**

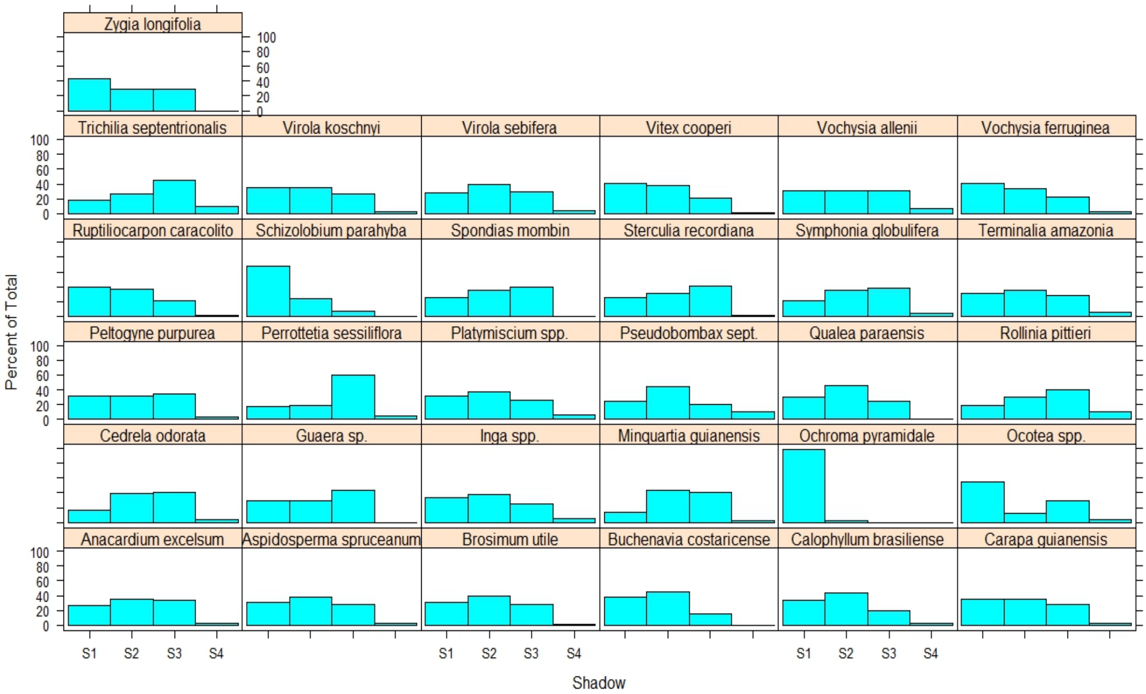

Fig. 41: Distribution of trees on light levels

Topography levels

Table 36: Mean height per topography level

Mean height [cm]								**n**						
Species	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**Total**	**T1**	**T2**	**T3**	**T4**	**T5**	**T6**	**Total**
A. excelsum	185	161	126	142	156	63	**141**	2	19	23	30	10	4	**88**
A. spruceanum	53	86	74	76	75	58	**75**	3	23	75	65	45	13	**224**
B. utile	77	79	85	76	61	43	**75**	3	20	69	56	43	6	**197**
B. costaricense		353	313	141	181	105	**210**		6	16	24	22	2	**70**
C. brasiliense	100	179	145	133	110	41	**126**	1	7	27	23	24	7	**89**
C. guianensis	165	186	130	95	79	70	**111**	2	45	70	52	90	23	**282**
C. odorata		161	142	173	103		**146**		9	34	20	13		**76**
Guaera sp.		40	58	36	55		**51**		1	13	5	2		**21**
Inga spp.	373	224	270	251	256	120	**254**	3	17	31	39	36	2	**128**
M. guianensis	50	55	58	48	59		**54**	1	6	23	27	15		**72**
O. pyramidale					800	812	**804**					9	5	**14**
Ocotea spp.	40	148	43	77	110		**96**	1	8	3	11	1		**24**
P.e purpurea	40	56	69	77	71	40	**69**	1	10	40	24	31	3	**109**
P. sessiliflora	80	90	95	75	52	55	**80**	1	13	22	15	11	2	**64**
Platymiscium spp.	95	169	115	133	131	110	**128**	6	17	55	38	53	9	**178**
P. septenatum	510	363	272	363	276	80	**319**	2	3	5	4	5	1	**20**

Q. paraensis	150	64	60	66	77		**70**	1	7	7	17	12		**44**
R.pittieri	20	55	55	33		40	**50**	1	10	11	4		1	**27**
R. caracolito	80	96	113	91	77	50	**83**	1	8	8	13	25	9	**64**
S. parahyba	170	733	430	321	209	175	**365**	1	11	19	10	20	8	**69**
S. mombin			110	117	120	40	**112**			7	7	5	1	**20**
S.recordiana	90	83	127	114	87	35	**107**	1	7	18	13	7	2	**48**
S. globulifera		75	75	69	76	83	**75**		21	27	14	7	6	**75**
T. amazonia	166	249	189	221	158	102	**189**	5	94	155	77	124	50	**505**
T. septentrionalis	40	125	127	150	165		**127**	1	11	7	1	2		**22**
V. koschnyi		120	74	76	49		**78**		11	5	7	14		**37**
V. sebifera	70	105	121	81	86		**95**	1	8	12	15	18		**54**
V. cooperi	130	193	188	212	122	85	**165**	1	3	16	36	42	4	**102**
V. allenii	117	138	144	132	115	67	**130**	3	17	72	25	49	7	**173**
V. ferruginea	160	197	178	198	157	107	**168**	1	18	30	32	57	19	**157**
Z. longifolia		165	191	240	208		**189**		14	12	5	4		**35**
Total	**142**	**176**	**140**	**135**	**129**	**106**	**139**	**44**	**447**	**921**	**713**	**800**	**184**	**3109**

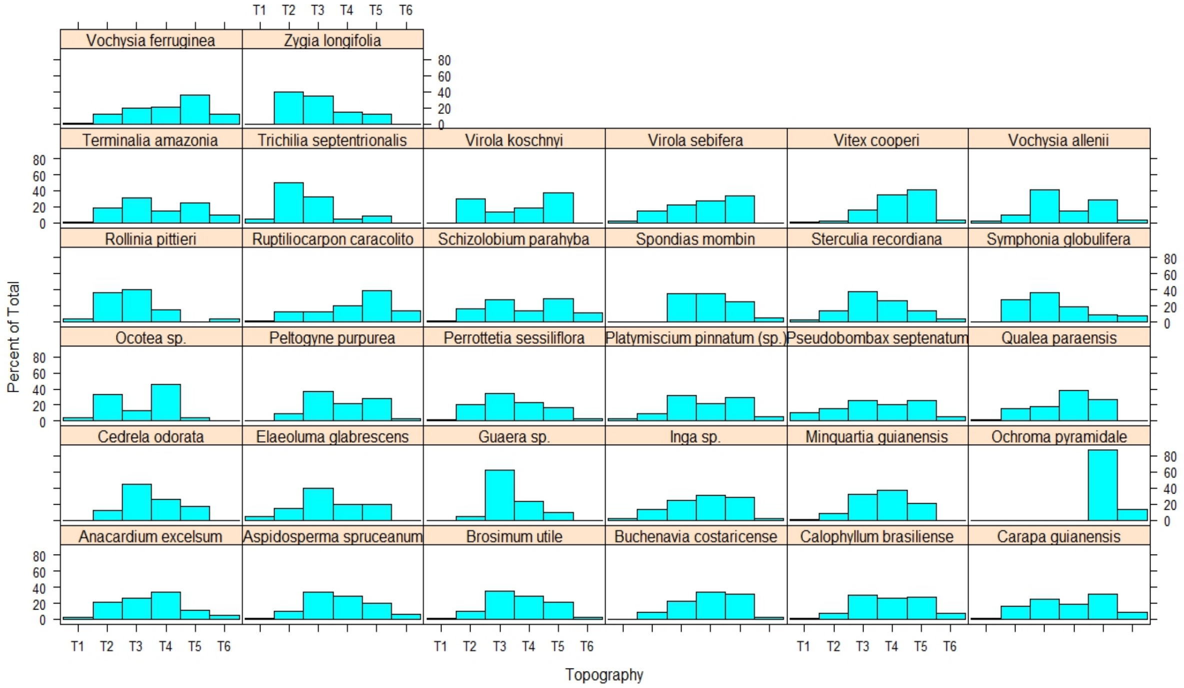

Fig. 42: Distribution of trees on topography levels

Inclination levels

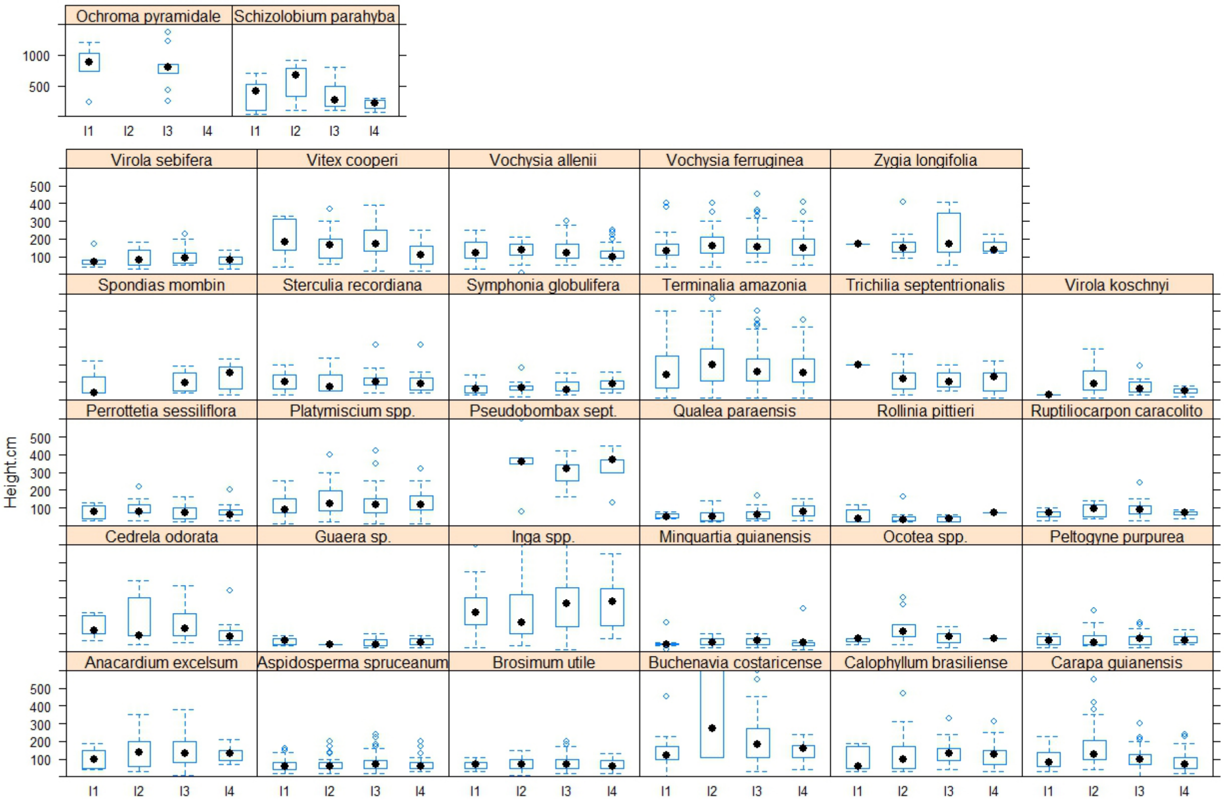

Fig. 43: Boxplots, height per inclination levels.

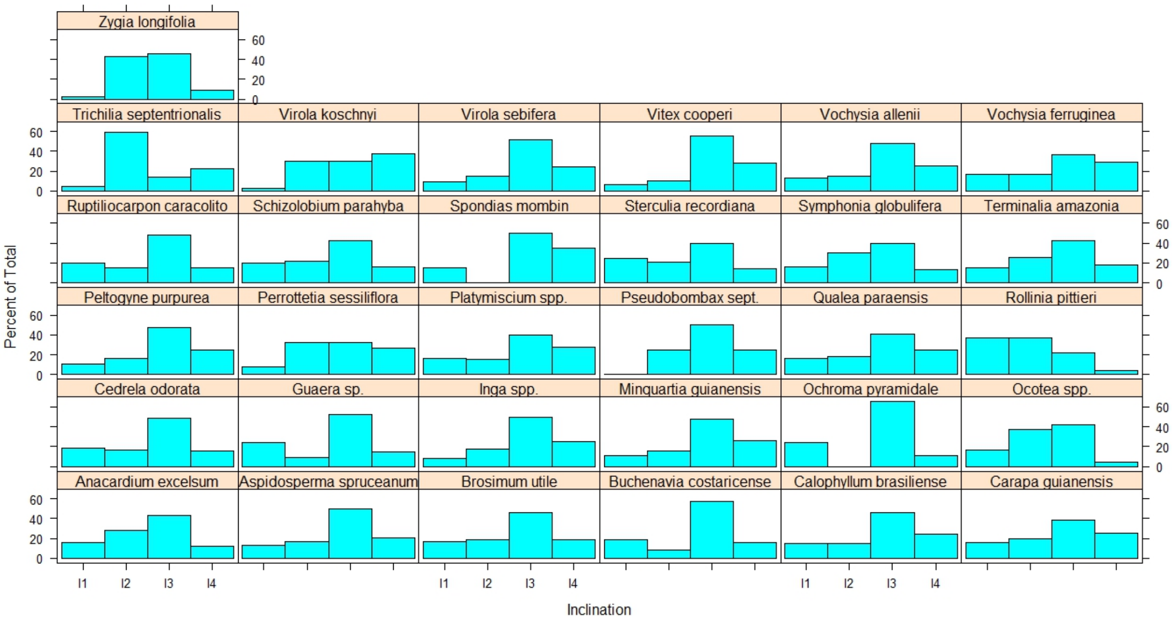

Fig. 44: Distribution of trees on inclination levels

ANOVA per species

Table 37: ANOVA per species, testing for the effect of topography/light/inclination on height and diameter at 50 cm.

		Topography (T) (inc. levels T1 – T6)			Light (S)			Inclination	
Species	n	P D50 (singly)	P Height (singly)	P Height (T:S)	P D50 (singly)	P Height (singly)	P Height (T:S)	p D50 singly	P Height (singly)
A. excelsum	94	0.197	0.336	0.378	0.686	0.824	0.872	0.176	0.233
A. spruceanum	264	0.126	0.411	0.413	0.3	0.623	0.293	0.137	0.415
B. utile	235	0.0186 *	0.00179 **	0.00177 **	0.189	0.0416 *	0.27302	0.116	0.0971 .
B. costaricense	84	0.00167 **	0.00123 **	0.000679 ***	0.339	0.528	0.027633 *	0.132	0.0315 *
C. brasiliense	104	0.00803 **	0.0084 **	0.00934 **	0.38	0.271	0.37878	0.493	0.56
C. guianensis	312	<2e-16 ***	<2e-16 ***	< 2e-16 ***	0.00153 **	2.02e-06 ***	0.37375	2.48e-10 ***	4.17e-10 ***
C. odorata	96	0.206	0.13	0.1284	0.00294 **	0.107	0.0731 .	0.208	0.251
Guaera sp.	26	0.0724 .	0.428	0.444	0.26	0.234	0.492	0.388	0.869
Inga spp.	138	0.565	0.457	0.43233	0.000229 ***	0.015 *	0.00746 **	0.117	0.879
M. guianensis	104	0.609	0.824	0.829	0.196	0.511	0.440	0.403	0.926
O. pyramidale	49	0.814	0.952	0.9483	0.0238 *	0.0896 .	0.0992 .	0.238	0.952
Ocotea sp.	32	0.115	0.051 .	0.0652 .	0.511	0.184	0.2890	0.198	0.14
P. purpurea	129	0.396	0.395	0.3594	0.0133 *	0.0248 *	0.0368 *	0.551	0.75
P. sessiliflora	82	0.0334 *	0.074 .	0.107	0.00616 **	0.028 *	0.484	0.846	0.608
Platymiscium	206	0.132	0.0846 .	0.0894 .	0.0522 .	0.108	0.1982	0.63	0.21
P. septenatum	21	0.273	0.00724 **	0.0276 *	0.8	0.583	0.4843	0.89	0.705
Q. paraensis	65	0.25	0.463	0.126	1.5e-07 ***	9.07e-08 ***	9.96e-07 ***	0.673	0.545
R. pittieri	32	0.597	0.689	0.738	0.652	0.449	0.493	0.775	0.735
R. caracolito	80	0.281	0.0064 **	0.00583 **	0.868	0.846	0.43452	0.215	0.0811 .
S. parahyba	119	8.94e-10 ***	5e-12 ***	1.85e-14 ***	0.00338 **	0.0173 *	3.93e-05 ***	0.000153 ***	0.00012 ***
S. mombin	25	0.551	0.773	0.784	0.771	0.578	0.528	0.819	0.73
S. recordiana	61	0.332	0.274	0.10636	0.0161 *	0.0027 **	0.00133 **	0.632	0.952
S. globulifera	91	0.973	0.94	0.9329	0.527	0.998	0.9882	0.234	0.328
T. amazonia	540	5.58e-09 ***	1.16e-12 ***	1.60e-13 ***	0.000595 ***	0.0022 **	2.27e-08 ***	0.00561 **	0.00101 **
T.septentrional	30	0.555	0.798	0.836	0.176	0.284	0.443	0.962	0.791
V. koschnyi	53	0.0915 .	0.0351 *	0.043 *	0.754	0.71	0.463	0.148	0.0303 *
V. sebifera	93	0.616	0.136	0.1220	0.106	0.528	0.0511 .	0.743	0.7
V. cooperi	117	0.00943 **	0.000121 ***	6.87e-05 ***	0.135	0.253	0.1572	0.00378 **	0.00558 **

V. allenii	200	0.0989 .	0.00176 **	0.00163 **	0.0422 *	0.0202 *	0.06271 .	0.0811 .	0.641
V. ferruginea	175	0.0398 *	0.00132 **	0.00127 **	0.101	0.0034 **	0.03675 *	0.298	0.812
Z. longifolia	37	0.123	0.511	0.480	0.198	0.532	0.593	0.486	0.536

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1 ;

Comparison of La Bolsa to the Panamanian plots Las Lajas and Soberania

Table 38: Comparison of mean survival at La Bolsa, with two plots in Panama (in per cent).

Site:	La Bolsa	Las Lajas*	Soberania*
Soil conditions:	(wet, mostly low fertility)	(„wet, low fertility“)	(„wet, fertile“)
Soil properties (mean values per site + SD	P 1 - 2 mg/l Bases (Na, Ca, Mg, K) 2.7 – 21.8 mol (+)/kg C 1.4 – 1.8%	N (%) 0.2±0.0 C (%) 2.5±0.7 P (ppm) 2.6±1.5 K (ppm) 58.1±53.1 Ca (ppm) 185.6±207.2 Mg (ppm) 89.3±64	N (%) 0.2±0.1 C (%) 3.0±1.0 P (ppm) 12.0±12.5 K (ppm) 496.6±391.2 Ca (ppm) 3873.3±2186.5 Mg (ppm) 1158.4±348.2
Precipitation mean [mm/year]:	5836	4610± 99	2239±146
Lower survival at La Bolsa:			
Spondias mombin	80.0	97.2	100
Terminalia amazonia	93.5	98.3	94.4
Equal/superior survival at La Bolsa:			
Calophyllum brasiliense	85.6	41.7	76.1
Cedrela odorata	79.2	61.7	94.4
Inga spp.	92.8	80.6	85.6
Ochroma pyramidale	93.9	77.8	90
Peltogyne purpurea	84.5	46.1	14.4
Vochysia ferruginea	89.7	16.7	33.3
Zygia longifolia	94.6	78.3	80.6
Mean for selected species:	90.8	66.4	74.3
Mean (all species planted at the site)	82.3	76.6	77.1

*Data source: Breugel et al. 2011

Table 39: Comparison of mean tree height

Site:	La Bolsa [m]	Las Lajas [m]	Soberania [m]
Lower mean height at La Bolsa:			
Spondias mombin	1.1	1.6	4.2
Terminalia amazonia	1.9	3.1	3.8
Equal or superior mean height at La Bolsa:			
Calophyllum brasiliense	1.3	1.1	1.2
Cedrela odorata	1.5	1.3	2.4
Inga spp.	2.5	1.2	1.4
Ochroma pyramidale	8	4.1	7
Peltogyne purpurea	0.7	0.4	0.3
Vochysia ferruginea	1.7	1.1	1.2

Zygia longifolia	1.9	1.2	1.5
Mean for the selected species:	2.3	1.7	2.6
Mean (all species of the plot)	1.4	1.9	2.7

*Data source: Breugel et al. 2011

Table 40: Mean survival rates of additional species from the Panamanian plots

Species	Las Lajas*	Soberania*	Bolsa (trees alive/ total)
Astromium graveolens	88.3	91.1	20/25
Cassia grandis	94.4	93.9	1/1
Diphysa americana	96.1	95.6	10/12
Erythrina fusca	84.4	91.4	0/2
Gliricidia sepium	100.0	98.3	0/1
Luehea seemannii	95.0	95.6	11/11
Samanea saman	92.8	97.8	9/9
Tabebuia guayacan	86.7	97.2	13/13

*Data source: Breugel et al. 2011

Table 41: Data from Haggar et al. 1998

Species	Survival*	Height*
Ochroma pyramidale	46%	15.2 m
Vochysia ferruginea	94%	11.2 m
Vochysia allenii	14%	11.7 m
Terminalia amazonia	53%	13.9 m
Ocotea spp.	33%	8.2 m
Carapa guianensis	74%	10.8 m
Pseudobombax septenatum	88%	8.4 m
Calophyllum brasiliense	77%	7.5 m
Cedrela odorata	10%	4.9 m
Vitex cooperi	64%	6.5 m
Virola koschnyi	58%	5.3 m
Brosimum utile	24%	5.7 m
Minquartia guianensis	20%	3.1 m
Inga edulis/ coruscans	54% /78%;	9.5 /13.2 m

*after 3 years; [*Gliricidia sepium* (42%, 3 m), *Tabebuia guayacan* (72%, 5.2 m), *Genipa americana* (58%, 5.9 m), *Pouteria sp*. (15%, 5.5 m), *Vochysia guatemalensis* (96%, 12.6 m)].

Table 42: changed sector names (see also soil map of Chacón and Jenking Aquilera 2010)

Former label	New label	Former label	New label
4	2a	6	6b
4	2b	3a	7
4	2c	4a	8
5	2-1	4b	9
7	5	10	10
6	6a	S1,S2,S3	unchanged

7.1 Categories (pictures)

Quality levels

Fig. 45: ***Carapa guianensis*** **Q1**

Fig. 46: ***Calophyllum brasiliense*****Q1**

Fig. 47: ***Brosimum utile*** **Q1**

Fig. 48: ***Peltogyne purpurea*** **Q1**

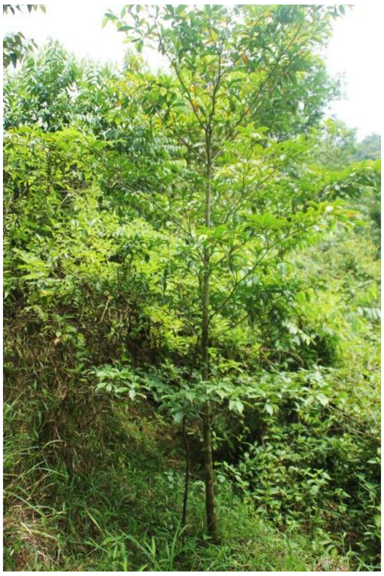

Fig. 49: ***Terminalia amazonia*** **Q1**

Fig. 50: ***Schizolobium parahyba*** **Q1**

Fig. 51: ***Terminalia amazonia*** **Q2**

Fig. 52: ***Calophyllum brasiliense*****Q2**

Fig. 53: ***Symphonia globulifera*** **Q2**

Fig. 54: ***Aspidosperma spruceanum*** **Q3**

Fig. 55: ***Carapa guianensis*** **Q3**

Fig. 56: ***Brosimum utile*** **Q3**

Light levels (canopy closure)

Fig. 57: Light level S1 (0 – 10%)

Fig. 58: Light level S2 (10 – 30%)

Fig. 59: Light level S3 (30 – 70%)

Fig. 60: Light level S4 (70 – 100%)

Herbivory levels

Fig. 61: H0 (<2%)

Fig. 62: H1 (2 – 5%)

Fig. 63: H2 (5 – 10%)

Fig. 64: H3 (10 – 20%)

Fig. 65: H4 (20 – 50%)

Fig. 66: H5 (50 – 100%)

Curriculum vitae – Nina Schnetzer

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Education:

09. 2009 – 02. 2014	University of Natural Resources and Life Sciences, Vienna, Master programme: Landscape Architecture and Landscape Planning, with focus on landscape preservation
03. 2007 – 08. 2009	University of Natural Resources and Life Sciences, Vienna, Bachelor: Landscape Architecture and Landscape Planning, co-registered at Vienna University of Technology (urban planning)
10. 2005 – 02. 2007	Technische Universität Berlin: study of Landscape planning (continued as Bachelor programme in Vienna)
10. 2004 – 07. 2005	Humboldt Universität zu Berlin: study of agriculture sciences

Work experience:

02. 2012 – 07. 2012	EU-Leader project „Lebendiger Noplerberg-Biri“, community Stoob, Austria: vegetation mapping and database design (self-employed)
09. 2011 – 06. 2012	Environmental education project with focus on amphibians in the course of the „Sparkling Science“ incentive programme of the Federal Ministry of Science and Research Austria (self-employed)
07. 2010 – 09. 2010	National park Hohe Tauern, community Matrei, Osttirol: GIS-works, reports, visitor support (internship)
09. 2008 – 02. 2009	Studio Land Milano, Italy: Landscape planning and Landscape architecture projects and competitions (internship)

Visits abroad:

04. 2013 – 07. 2013	Costa Rica, La Gamba (Fieldwork for Master Thesis), Panama
08. 2012 – 10. 2012	China - Tibet - Nepal - India (independent travel)
08. 2008 – 09. 2008	Padua, Italy: scholarship for Italian (before internship in Milano)

Languages:	German (mother tongue), English (good), Italian, Spanish: basic
Computer skills:	MS Office (Word, Excel, Powerpoint, Access), ArcGIS, R, Adobe (Photoshop, Indesign, Illustrator), AutoCAD