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DIPLOMARBEIT

Tree diversity and vegetation dynamics of a one hectare forest plot census in the lowland rain forests of the Piedras Blancas National Park ("Regenwald der Österreicher"), Costa Rica

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the Costa Rican staff of the Tropenstation La Gamba

Welfia regia (Arecaceae) on the Esquinas research plot

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1 Introduction

Tropical forests are systems with the highest diversity of the world. Those systems are in a permanent flow regarding abundance, local extinction and reimmigration. Changes are caused by exogenous (e.g. climatic, geological, anthropogenic) forces and endogenous ecological and evolutionary variation. The rates of change in space and time, the existence of regulation factors and responses of communities are very difficult to answer, especially in such complex systems like tropical forests (CONDIT et al. 1992, 2005).

Different studies have shown that some trends occured in the last years (PHILLIPS & GENTRY 1994; PHILLIPS 1996, 2004). E.g. turnover and biomass as well as rising dominance of fast growing species have increased in tropical forest census plots in the late twentieth century.

Tropical forests are an important part in the global carbon cycle. Over a third of the global carbon stock is retrieved in those ecosystems (DIXON et al. 1994). They contribute 30 % of terrestrial net primary production (FIELD et al. 1998). Athmospheric changes (e.g. increasing CO_2, increasing temperatures and nitrogen deposition) could possibly change environments or ecosystems. But to quantify answers of ecosystems to athmospheric changes is a difficult issue and could only be monitored by long term censuses (PHILLIPS et al. 2004).

Disturbance regimes are one of the basics of ecosystem progression. After disturbances several different phases of succession take place. Advantages and problems of each succession step (e.g. arrival, regeneration, establishment) take place (WHITMORE 1989). The presence and absence as well as spatial distribution will be influenced by physical and biotic conditions created in the different phases of succession (HERNANDEZ STEFANONI 2005). Both biotic and abiotic factors affect growth and survival, these factors are often autocorrelated (e.g. treefall gaps, soil nutrients) (URIARTE et al. 2004).

To validate reasons of changes due to athmospheric changing or responses to natural disturbances would be part of further studies.

To obtain such realizable results establishing forest census plots is essential. In this case assessment of biodiversity and comparative and absolute estimates of species diversity could be provided (CONDIT 1998).

Such study areas have been established in several tropical forests (CONDIT 1998, WHITMORE 1978; HUBBEL & FOSTER 1990; HARTSHORN 1980, 1990; DENSLOW & HARTSHORN 1994; LIEBERMANN & LIEBERMANN 1994; HUBER 1996; WEISSENHOFER 1996).

This thesis focuses on diversity and dynamic aspects of a one hectare plot on an inland slope in a primary tropical lowland wet forest in southern Costa Rica in the Piedras Blancas National Park (Esquinas forest).

2 Study area

The Piedras Blancas National Park, where the research plot is located, lies between 8°27'-8°41' North and 83°15'-83°45' West in the southern part of the Puntarenas province. The park has a size of 148 km² and a maximum level of 579 msm (WEISSENHOFER 2005).

The area is characterized by strong erosion processes which results in narrow ridges and steep slopes with dense drainage networks (HERRERA et al. 1997, MALZER et al. 2008). Such intensive removal of soil material due to a huge amount of streams inside the park occurs.

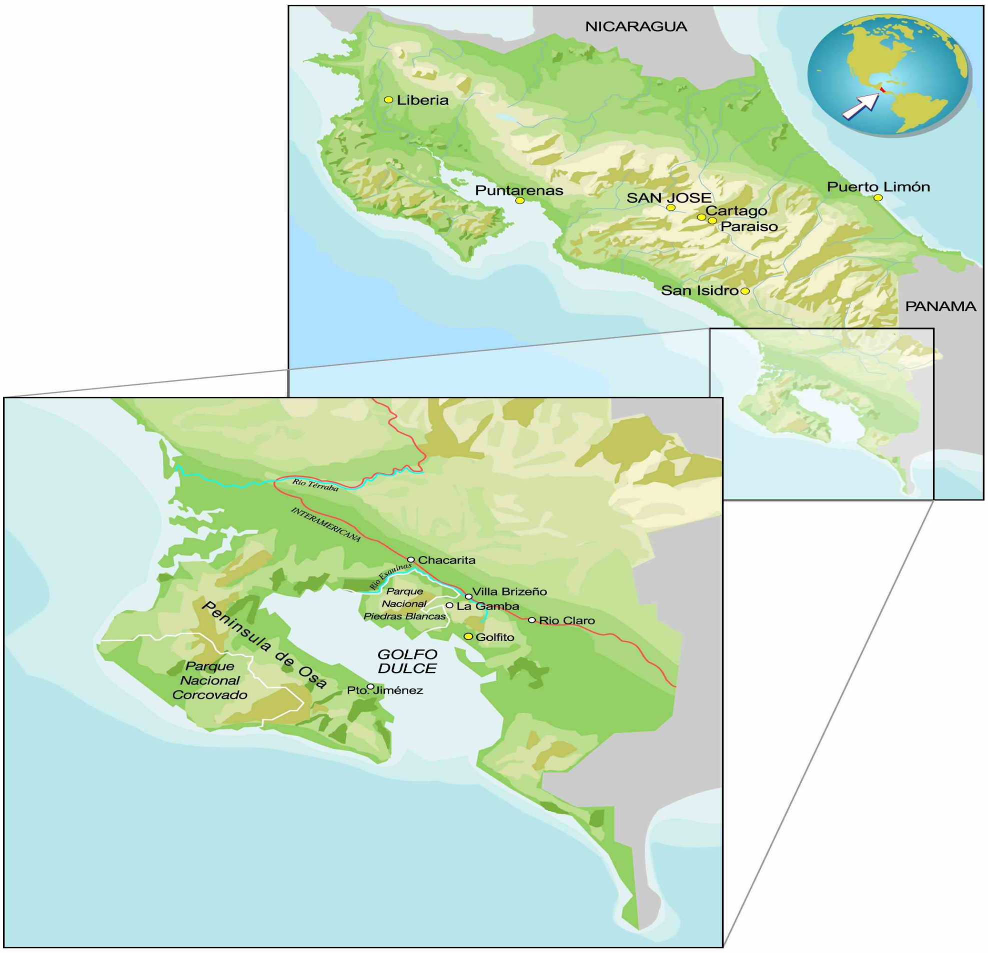

Fig. 2.1: The Golfo Dulce region (Corcovado and Piedras Blancas, from WEBER et al. 2001).

The primary forest remained nearly exclusively on slopes because lowlands are the most suitable areas for logging (WEISSENHOFER 2005). The plains consist mainly of secondary forests and farmland.

Costa Rica as one of the Central American countries is part of the isthmus between North and South America. This narrow stretch of land was formed at the end of the tertiary. Sedimentation and deposition of volcanic and volcanoclastic material endures until now (MALZER 2001 & 2008). Volcanism is induced by the motions of the lithosphere due to convergent plate boundaries. In Central America four tectonic plates are important, the North American plate, the Caribbean plate, the Cocos plate, and the Nazca plate. The Cocos plate is subducted under the North American and Caribbean plate and causes in this way the tectonical activities (MALZER 2008).

The soil formation in tropical forests is driven by the tropical climate. High temperature and precipitation all over the year lead to chemical weathering of rock and the soil (PAMPERL 2001). Local climate and microhabitat conditions cause different soil modifications and lead furthermore to different stands and ecological niches respectively (PAMPERL 2001). Relationships between plants and soils in tropical forests were described by RICHARDS (1961). Studies of correlations between soils and tree species distribution showed a connection between soils and their characteristics and plant species and their topographical location. Nutrient poor and acidic soils with a high aluminium saturation showed higher, nutrient rich soils lower diversity (PAMPERL 2001).

In the Piedras Blancas National park three soil types predominate: Ultisols, Inceptisols and Entisols (VASQUEZ 1989). Ultisols, the main type, are old soils which have been formed over a long period of undisturbed time. They are characterized as highly weathered, clayey, yellowish-red and high acidic thick layer. Due to the erosion effects steep slopes and lateral movements occur. Inceptisols can be found in ravines and flatter slopes. Those soils are younger and less weathered than Ultisols (PAMPERL 2001). Entisols are of less importance.

The Esquinas forest is one of the wettest lowland forests in Costa Rica and is influenced by the rain gradient caused by the mountains of the Fila Cruces range (WEISSENHOFER 2008b). Rainfall occurs nearly every day. A few days without rain can only be found in the dryer month January till March.

The average annual precipitation at the field station is about 6000 mm, with the highest monthly average in September (WEISSENHOFER 2008b).

The average yearly temperature is about 28°C, the average humidity about 88% on the open land (WEISSENHOFER 2001 & 2008b) and 98% in the forest (ASCHAN 1998).

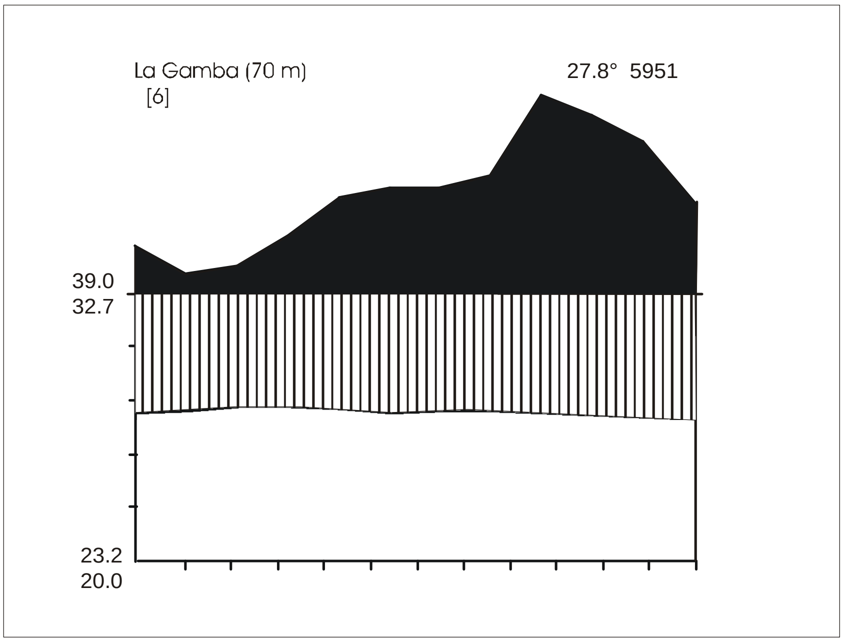

Fig. 2.2: Climatic diagram of the Tropenstation La Gamba, 70m (WEISSENHOFER 2001).

Several studies described the high diversity in tropical forests (KRICHER 1997, GENTRY 1988b). The Corcovado and Esquinas region additionally excels in the Neotropics despite their small geographic territory (VAUGHAN 1981). INBio counted nearly 2400 species out of nearly 1000 genera in over 180 families for the region. This region is described to have a strong relationship to South American tropical forests (GENTRY 1978 & 1982, STANDLEY 1937, HARTSHORN 1983, HARTSHORN & HAMMEL 1986, HUBER 1996a), to the Amazonian and Atlantic coastal rainforests (ALLEN 1956) and less affinity to the flora of Panama or Guanacaste (ALLEN 1956). This area was a refuge, cut off during glacial periods. Speciation was accelerated so many new species evolved in the fragmented forests (WEISSENHOFER 2005).

3 Methods

3.1 The Research Plot

The research on this plot started in 1993 by HUBER (1996) AND WEISSENHOFER (1996). It has following characteristics:
300-336 msm
south east exposed slope
well drained
average inclination of 27 (55) %
several gorges

The research plot is 1 hectare in size and is subdivided into 100 10 x 10 m subplots. For differentiation the subplots got identifications with ascending numbers down the slope (1 to 10) and parallel to slope with ascending letters (A to J).

3.2 Field work

The studies were performed from 2000 to 2001. Inside the plot all trees ≥ 2 cm up to 10 cm dbh were monitored. Hereby the exact location was plotted in a site map. Additional physical and physiological parameters were also collected.
Beside those data all individuals formerly monitored by HUBER & WEISSENHOFER (1993) with a dbh ≥ 10 cm were reevaluated and compared by means of data from 1993, all trees which survived, all which died in that period and all recruits that reached dbh ≥ 10 cm.

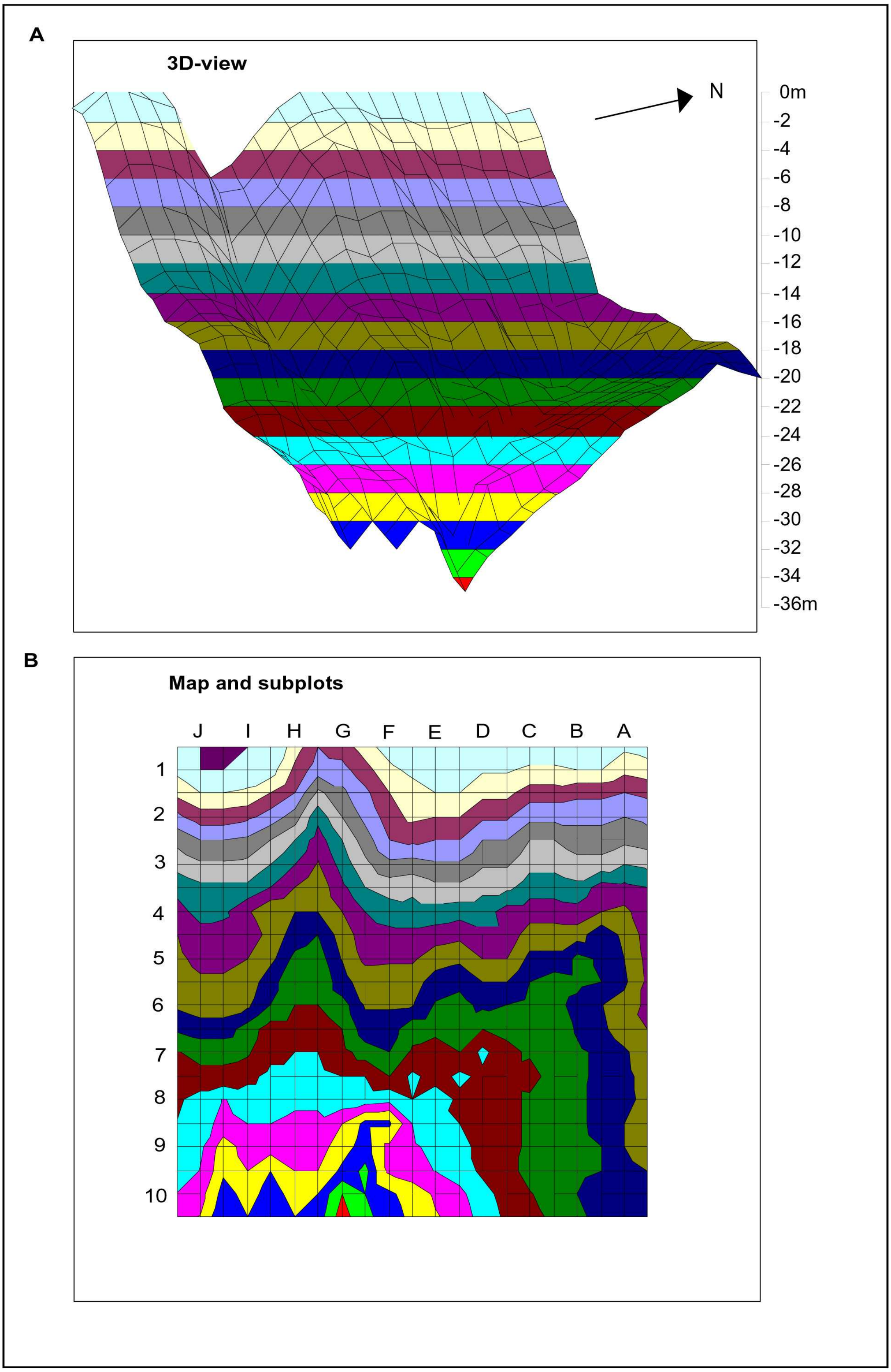

Fig. 3.1: Relief of the research plot. A. 3D view. B. Map and subplots. Colours represent elevation differences (WEISSENHOFER 1993).

It was important to collect relevant material for herbar issues. Due to high number of individuals it was not possible in logistics to collect parts from all trees. Species with high abundance and easy determination were not always collected.

Field work was performed with knives or stake saws for low plants. The parts from medium high trees were collected by self made collecting stakes (hoover tubes with pruning shears). The mature stand was determined by binocular and telescope, verified by the data from 1993.

Collections were done in 3 to 5 fold, depending on available tree material. As far as possible predetermination was performed on the study site.

Collected parts were numbered (subplot, individual number according to site plan).

Further tentative determination was performed in the research station by photo herbar and a Field Guide (GENTRY 1993). Final determination was carried out in the Museo Nacional de Costa Rica (San José) and the herbar of the University of Vienna.

Species difficult in determination were verified with specialists of the University of Vienna and the Instituto Nacional de Biodiversidad (INBio).

Following parameters were monitored:

- Dbh
- Height (if possible)
- Latex (color, taste, consistence, amount)
- Plants or fruits (if applicable)
- Other specifics (e.g. aromatics)
- Date

Illustration in the site map was verified by control survey of each fifth individual.

Diameter at breast height (dbh)

Dbh was measured at 1.3 m height above ground with a caliper, individuals with a higher dbh by a π-tape.

Trees with buttress or stilt roots were measured 30 cm above the roots.

In multiple stemmed plants each stem was measured.

Height

The height was measured in all small and medium heigh trees (dbh ≤ 10 cm). For those measurements the length of the collecting stakes were used for comparison.

Latex

Existing latex or resin were checked for colour and taste.

3.3 Basic forest structure

3.3.1 Size class distribution

Size classes were compiled in 5 cm steps. For comprehensive study sites (CONDIT et al. 1992; PHILLIPS et al. 2004) where greater research areas are established calculations with size classes in 10 cm steps were usually performed. Here a smaller resolution was selected to get more detailed information due to smaller sample pool.

3.3.2 Average dbh and BA

The **average dbh** was calculated via arithmetic mean value. A comparison with the data from HUBER & WEISSENHOFER (1993) was performed.

BA was calculated by following formula:

$$\mathrm{BA} = d^2 \times \pi / 4$$

with dbh for d or the diameter 30 cm above the roots in trees with buttress or stilt roots. The calculations were performed for individuals ≥ 10 cm dbh for comparability with the data from 1993 as well as with all individuals from 2 cm dbh up.

3.3.3 Biomass

Biomass was calculated according to a commonly used logarithmic regression model (CHAVE et al, 2001):

$$\ln(\mathrm{AGTB}) = \alpha + b \ln(D)$$

AGTB (aboveground dry biomass of a tree) is measured in kg, D is the measured dbh in cm, with 2.42 for b (the best-fit allometric exponent), and -2.00 +/- 0.27 for α.
This model is an estimation method specialized for a tropical lowland forest following the allometric relationship between biomass and dbh. The parameter tree height is not measured. This parameter is not necessary for calculation. Tree height is generally questionable to be a good estimator of the aboveground biomass due to the high variability of tree architectures in tropical forests (HALLE et al, 1978).

A comparison with the data from HUBER & WEISSENHOFER (1993) was performed. Therefore those data had been recalculated with this regression model.

Further NEP (net ecosystem production) and NPP (net primary production) were determined.
The calculations were performed for individuals $\geq$ 10 cm dbh for comparability with the data from 1993, as well as with all individuals from 2 cm dbh up.

3.3.4 Turnover and mortality

Mortality

$$m = \ln n_0 - \ln S_t / t$$

with the census interval be t, the population size at time zero be n_0, the number of survivors at time t be S_t.

Recruitment

$$r = \ln n_t - \ln S_t / t$$

with the population size at time t be n_t.

Population growth

$$\lambda = \ln n_t - \ln n_0 / t$$

Those standard methods were used in several former studies (e.g. CONDIT et al 1992).

The calculations were performed for trees dbh ≥ 10 cm for comparability with the data from 1993. No previous data from dbh 2 to 10 cm exist.

3.4 Floristic diversity

Diversity consists of two components, the variety and the relative abundance of species. So diversity can be measured by recording the number of species, by describing their relative abundances or by using a measure which combines the two components.

Diversity was calculated for individuals ≥ 10 cm dbh for comparability with the data from 1993 as well as with all individuals ≥ 2 cm dbh.

3.4.1 Species Density

Species density is a common species richness index and is defined as the measure of the number of species in a defined sampling unit. (MAGURRAN 1988)
It is used if the study area can be delimited in space and time and the constituent species can be enumerated and identified.
Species density describes the number of species per specified collection area (HURLBERT 1971), e.g. species / m^2. A density calculated via 1 hectare is common.

The following indices are based on the proportional abundances of species trying to combine richness and evenness in a single figure (MAGURRAN 1988).

3.4.2 Simpson´s Index

The Simpson index (SIMPSON 1949) takes the number of species present as well as the relative abundance of each species into account. It represents the probability that two randomly selected individuals in the area belong to the same species.

It´s a reciprocal index **1 / D**, or an index of diversity **1 – D**, where D is calculated by **D = 1/(Sum (p_i^2))** and further for a finite community as follows:

$$D = \text{sum } n \times (n-1) \ / \ \text{sum } N \times (N-1)$$

where n is the number of individuals of a specific species and N is the total number of individuals.

Due to the **reciprocal** character of that index 1/D, it starts with the value 1 (if only one species occurs) and raises up to the total number of species (if each individual belongs to a different species).

The index of diversity 1-D lies between 0 and 1.

3.4.3 Shannon Wiener/Weaver Diversity Index

The Shannon index (SHANNON & WEAVER 1949) assumes that individuals are randomly sampled or distributed from an indefinitely large population.

It is calculated from following equation:

$$H' = - \Sigma p_i \ln p_i$$

The quantity p_i is the proportion of individuals found in the i^{th} species.

Like Simpson´s reciprocal Index it ranges from 1 to the total number of species.

3.4.4 Shannon´s Evenness

Evenness shows how similar abundances of similar species are. It is derived from Shannon and is calculated as follows:

$$E = H/\ln(S)$$

with H as Shannon Index and S as total number of species.

3.4.5 Alpha index

Alpha index or log series or Fisher´s α (FISHER et al, 1943) is a common diversity index. It assumes that samples are reasonable fit to a log-series.

$$\alpha = N\,(1-x) / x$$

x is estimated from:

$$S / N = (1-x) / x\,[-\ln(1-x)]$$

with N for the total number of individuals and S for the total number of species (MAGURRAN 1988).

3.4.6 Importance Value Index

The IVI is an indicator for the importance of a species in a research area. It contains relative frequency, relative density and relative dominance.

The relative frequency is calculated by general dispersal of the species, based on its presence in the sample units.
The sum of all relative frequency values for all counted species in a plot will be 100%.

The relative density is the proportion of each individual of species in the subplot.
The sum of all relative density values for all counted species in a plot will be 100%.

The relative dominance is the proportion of the BA in m^2 of the total BA in a plot.
The sum of all relative dominance values for all counted species in a plot will be 100%.

3.4.7 Family Importance Value Index

FIVI shows the importance of the families in a research area. Calculation is similar to IVI but instead of relative diversity relative frequency is used (MORI 1983).

The relative diversity is the number of species of a family divided by total number of species.
The sum of all relative diversity values for all species of a family in a plot will be 100%.

The relative density is the total number of individuals of each family divided by the total number of individuals in a plot.
The sum of all relative density values for all counted individuals of each family in a plot will be 100%.

The relative dominance is the total amount of BA in m^2 covered by each family, divided by the total BA of the plot.
The sum of all relative dominance values for all families in a plot will be 100%.

4 Results

4.1 Basic Forest Structure

4.1.1 Size Class Distribution

The size class distributions were compiled in 5 cm steps in Table 4.1 and Fig. 4.1 and showed the anticipated J graph. Most individuals are in the dbh range of the smaller size classes.

Size classes [dbh]	***Individuals***	***%***
´2-4.9	1999	66,66
´5-9.9	544	18,14
´10-14.9	135	4,50
´15-19.9	108	3,60
´20-24.9	69	2,30
´25-29.9	31	1,03
´30-34.9	28	0,93
´35-39.9	13	0,43
´40-44.9	13	0,43
´45-49.9	12	0,40
´50-54.9	9	0,30
´55-59.9	7	0,23
´60-64.9	6	0,20
´65-69.9	2	0,07
´70-74.9	5	0,17
´75-79.9	2	0,07
´80-84.9	5	0,17
´85-89.9	3	0,10
´90-94.9	0	0,00
´95-99.9	3	0,10
´100-104.9	2	0,07
´105-109.9	0	0,00
´110-114.9	2	0,07
´115-119.9	0	0,00
´120-124.9	0	0,00
´125-129.9	1	0,03

Tab. 4.1. Size class distributions (total individuals & %).

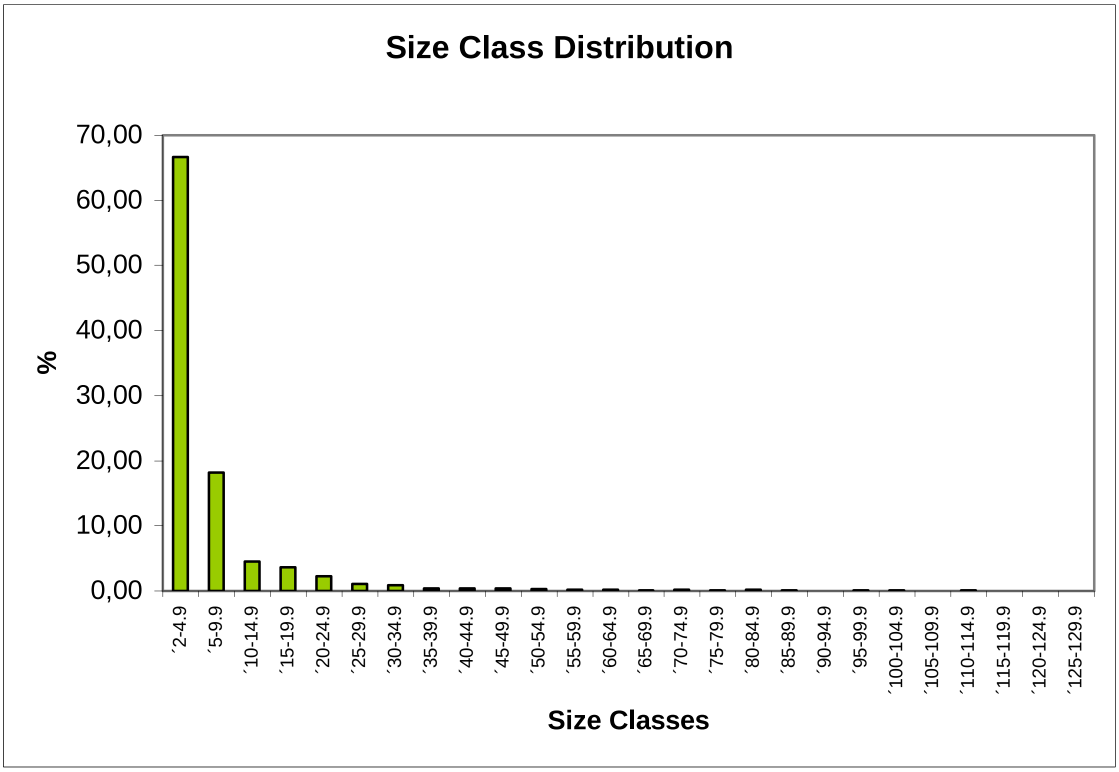

Fig. 4.1: Size class distributions (dbh in cm) of the plot in %

The most important class was 2 to 4.9 cm dbh. Here 1999 individuals (or 66.66 %) out of 190 species were found in this group. The dominant species was *Welfia regia* (Arecaceae) with 175 individuals. *Psychotria elata* (Rubiaceae) with 173 individuals and *Henriettea tuberculata* (Melastomataceae) with 106 individuals follow.

Carapa guianensis (Meliaceae) was the tree with the highest number of individuals (59).

The family with the highest abundance was the Rubiaceae with a total of 370 individuals, followed by the palms with 319, the Melastomataceae with 221 and the Euphorbiaceae with 175 individuals.

In size class dbh 5 to 9.9 cm 544 individuals (or 18.14 %) out of 109 species were found in this group.

The dominant species was *Iriartea deltoidea* (Arecaceae) with 46 individuals, *Henriettea tuberculata* (Melastomataceae) and *Welfia regia* (Arecaceae) follow with 37 individuals each.

Mabea occidentale (Euphorbiaceae) was the tree with the highest number of individuals (19), followed by *Brosimum alicastrum* (Moraceae) with 14 individuals. *Carapa guianensis* (Meliaceae) was found ten times in this class.

The dominant families were the Arecaceae with 136 individuals, the Melastomataceae with 44 and the Euphorbiaceae with 28 individuals. From the Rubiaceae remained only 27 individuals.

In size class dbh 10 to 14.9 cm 135 individuals (or 4.5 %) out of 50 species were found.

Iriartea deltoidea was the tree with the highest number of individuals (50), followed by *Socrathea exorrhiza* with 11 individuals.

The dominant tree species was *Carapa guianensis* (Meliaceae) with 5, followed by *Symphonia globulifera* (Clusiaceae) with 4 individuals.

The family with highest abundance was the palms with 67 individuals. Rubiaceae did not occur any more.

Climax families like Meliaceae or Moraceae remained in most bigger size classes.

4.1.2 Average dbh and BA

4.1.2.1 Individuals dbh ≥ 10 cm

The **average dbh** of all individuals ≥ 10 cm dbh in 1993 was 23.5 cm (WEISSENHOFER 1994).

In 2001 the average dbh of all remaining individuals ≥ 10 cm without recruits was 24.8 cm, including the recruits dbh was 25.9 cm.

In the size classes dbh ≥ 10 cm 128 individuals died with an average dbh of 19.5 cm, 43 individuals exceeded 10 cm dbh with an average dbh of 12 cm.

BA of all individuals ≥ 10 cm dbh in 1993 was 35.5 m² (WEISSENHOFER 1994).

In 2001 the BA of all individuals ≥ 10 cm was 35.9 m².

The size class with highest BA was 80-84.9 cm with a total amount of 7.26 % of the total BA.

The BA of all size classes was similar with a mean amount of 1.79 m² (SD 0.49).

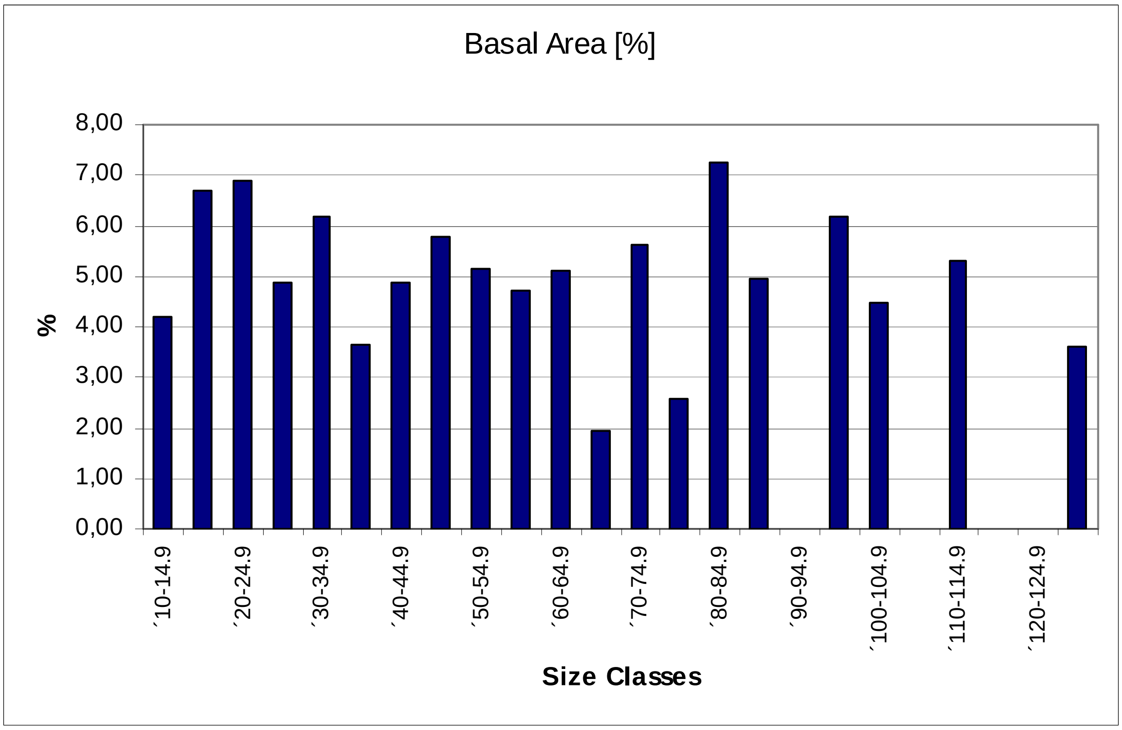

Fig. 4.2: BA, weighted for all plants dbh ≥10cm

4.1.2.2 Individuals dbh ≥ 2 cm

The **average dbh** of all individuals ≥ 2 cm was 7.0 cm.

The **BA** of all individuals dbh ≥ 2 cm was 38.7 m². This calculation also led to the most important size class 80-84.9 cm with a total amount of 6.73 % of the total BA. The size class up to 4.9 cm had an amount of 3.49 %, the class 5 to 9.9 cm 3.79 % of total BA.
In this case the mean BA of all size classes was 1.76 m² (SD 0.49).

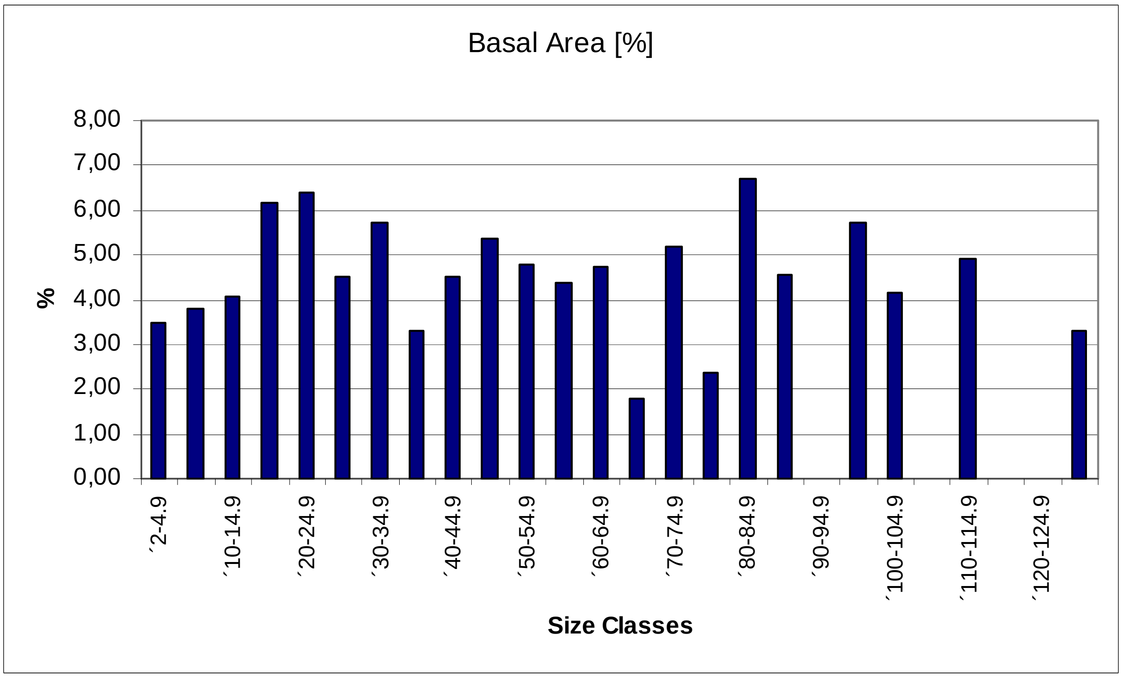

Fig. 4.3: BA, weighted for all plants dbh ≥ 2 cm

4.1.3 Biomass

4.1.3.1 Individuals dbh ≥ 10 cm

For trees dbh ≥ 10 cm the biomass was 330 Mg ha^{-1}.

Biomass of all individuals ≥ 10 cm dbh in 1993 was 315 Mg ha^{-1} (WEISSENHOFER 1994, recalculated with the formula from CHAVE et al, 2001).

Only 25 % of all trees were greater than 30 cm dbh, but they represented 85 % of the aboveground biomass and as much as 77 % of the BA.
The effect of larger trees on biomass was considerably more pronounced. Only 5 % of the trees were above dbh 70 cm, but 50 % of aboveground biomass and 40 % of the BA belonged to this size class.

The estimated biomass rose from 315 Mg ha^{-1} in 1993 to 330 Mg ha^{-1} in 2001. This meant a NEP of 1.9 Mg ha^{-1} y^{-1}.
The net loss due to mortality was 6.3 Mg ha^{-1} y^{-1}, and the increase due to recruits was 0.3 Mg ha^{-1} y^{-1}. Therefore the biomass accumulation (NPP) was 7.9 Mg ha^{-1} y^{-1}.

4.1.3.2 Individuals dbh ≥ 2 cm

For all trees dbh ≥ 2 cm the biomass was 339 Mg ha^{-1}. So all the plants smaller than 10 cm dbh contributed only 2,8 % (9 Mg ha^{-1}) to the whole aboveground biomass, although they represented 84 % of all individuals.

4.1.4 Growth and Mortality

Mortality was 3.54 % y^{-1} for all stems ≥ 10cm dbh. Recruitment was 1.29 % y^{-1}. Mortality mainly occured in the lowest size classes. Nearly 60 % of all dead individuals were below dbh 15 cm. 30 % of them belonged to the Arecaceae.
In larger size classes mortality was nearly constant or rose slightly with dbh.

There was a wide range of mortality and recruitment among the different species.
The palm *Iriartea deltoidea* for example had a mortality of 4.64 % y^{-1} and recruitment of 2.11 % y^{-1}.
Dendropanax arboreus (Araliaceae) had a mortality of 8.66 % y^{-1} and recruitment of 0 % y^{-1}.
Elaeoluma glabrescens (Sapotaceae) had recruitment and in this case a growth rate of 1.67 % y^{-1}. No individual died.
Carapa guianensis (Meliaceae) had a mortality of 2.79 % y^{-1} and recruitment of 4.35 % y^{-1}. Therefore a growth rate of 1.56 % y^{-1} occured.

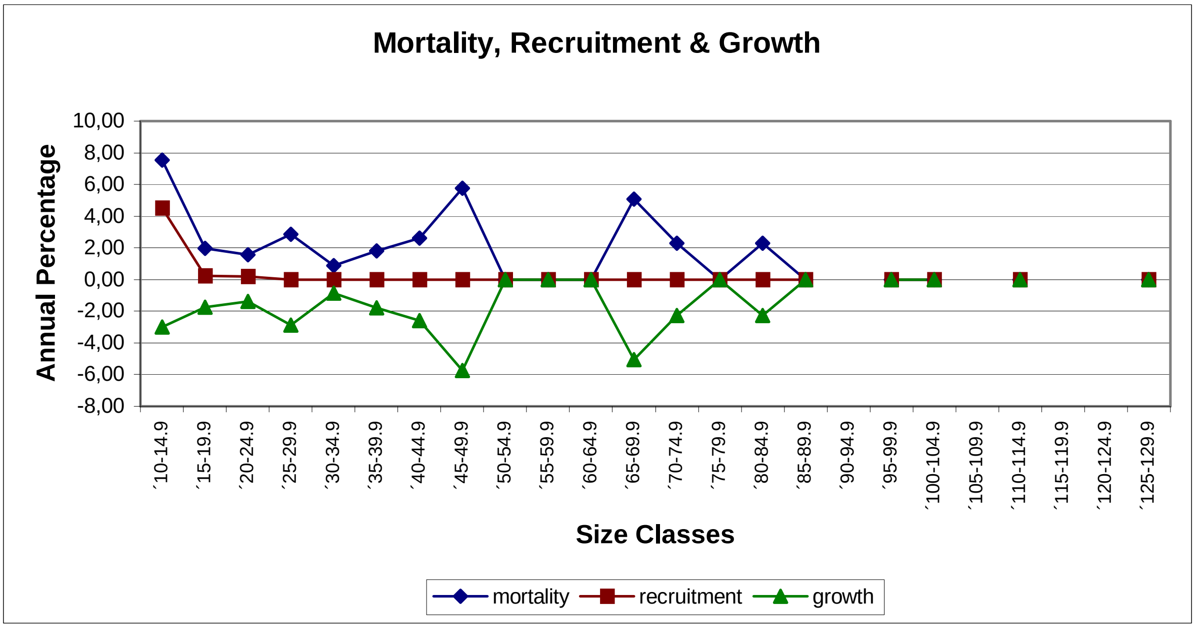

Fig. 4.4: Mortality, recruitment and growth rates including all individuals of all species. Points are placed above the midpoint of each size class.

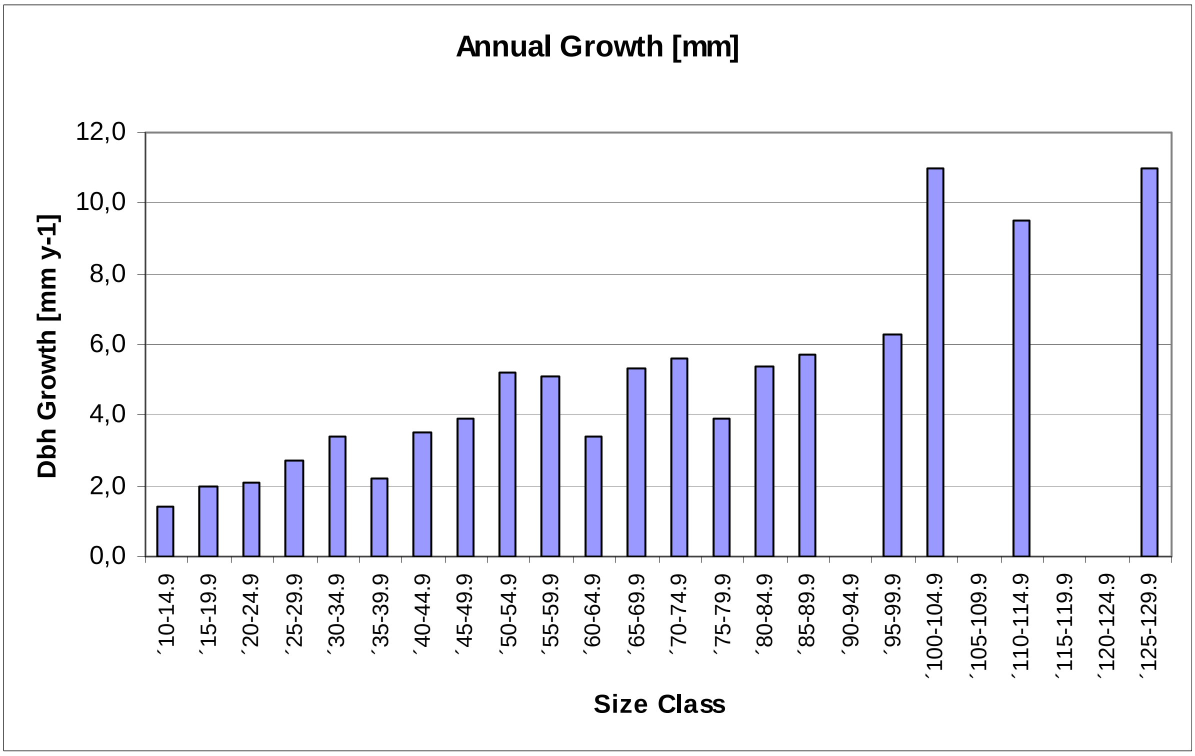

Fig. 4.5: Annual growth rates in mm y^{-1}, all individuals of all species included.

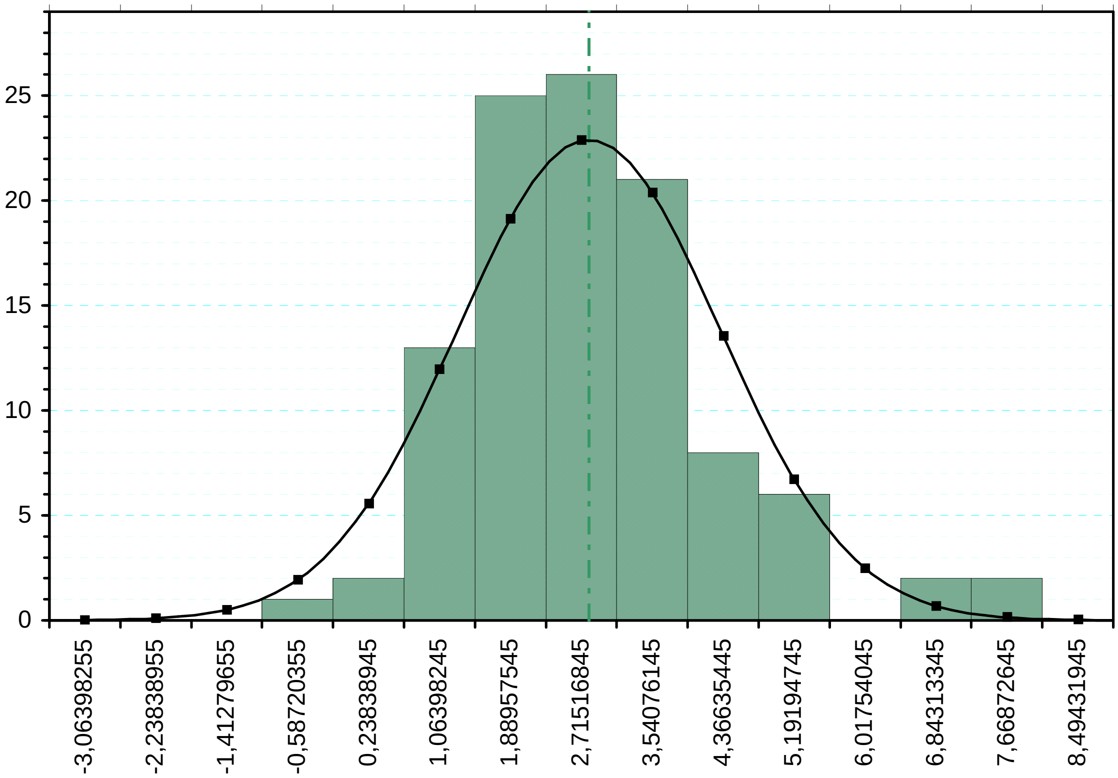

Fig. 4.6: Histogram of growth rate (mm y^{-1}), plotted against abundance

4.2 Floristic diversity

4.2.1 Species Density

The research plot comprised 527 individuals of 133 spp. in 1993 (HUBER 2005).
2001 there were 453 individuals dbh ≥ 10 cm out of 108 species and 43 families, including all the recruits.

Including all reported individuals dbh ≥ 2 cm 2849 individuals out of 232 species and 59 families were found.

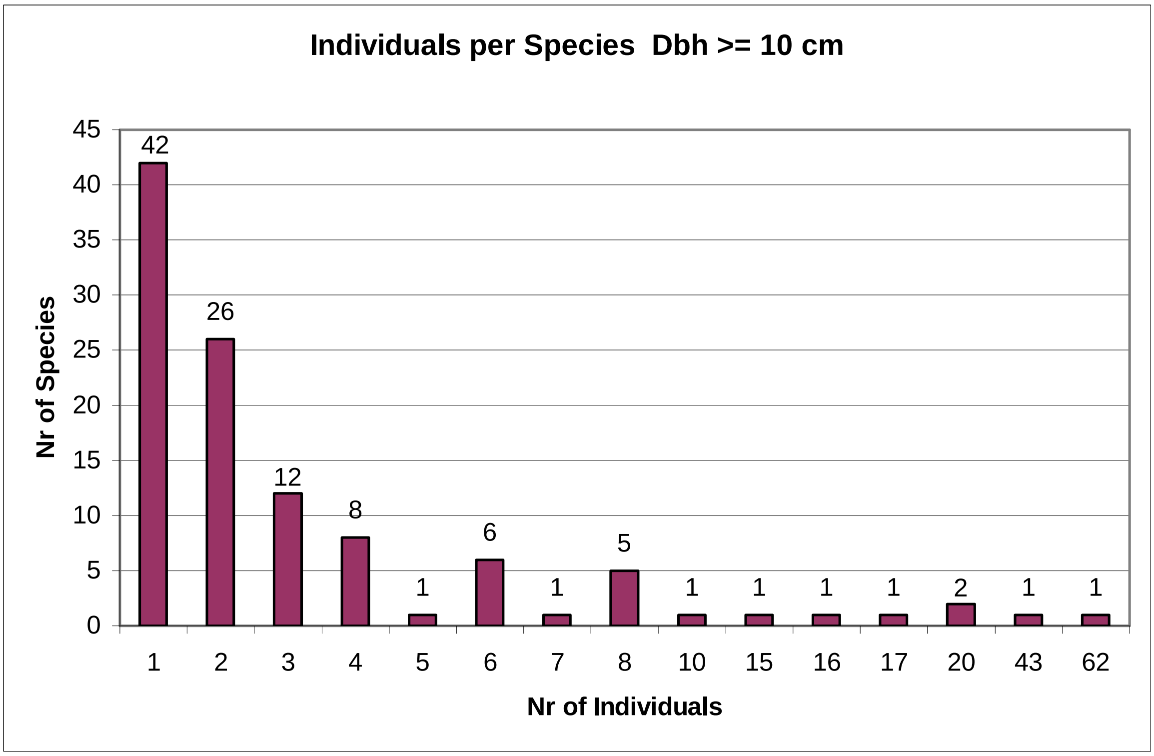

Fig. 4.7: Number of individuals per species of all individuals dbh ≥ 10 cm

The most frequent species of **all trees dbh ≥ 10 cm** were *Iriartea deltoidea* with 62, and *Welfia regia* (both Arecaceae) with 43 individuals. The Clusiaceae *Symphonia globulifera* and *Marila laxiflora* were presented with 20 individuals each. *Carapa guianensis* (Meliaceae) with 17, the palm *Socratea exorrhiza* with 16 and *Brosimum utile* (Moraceae) with 15 individuals also were frequent.
42 species were represented with only 1 individual (see Figure 4.7).

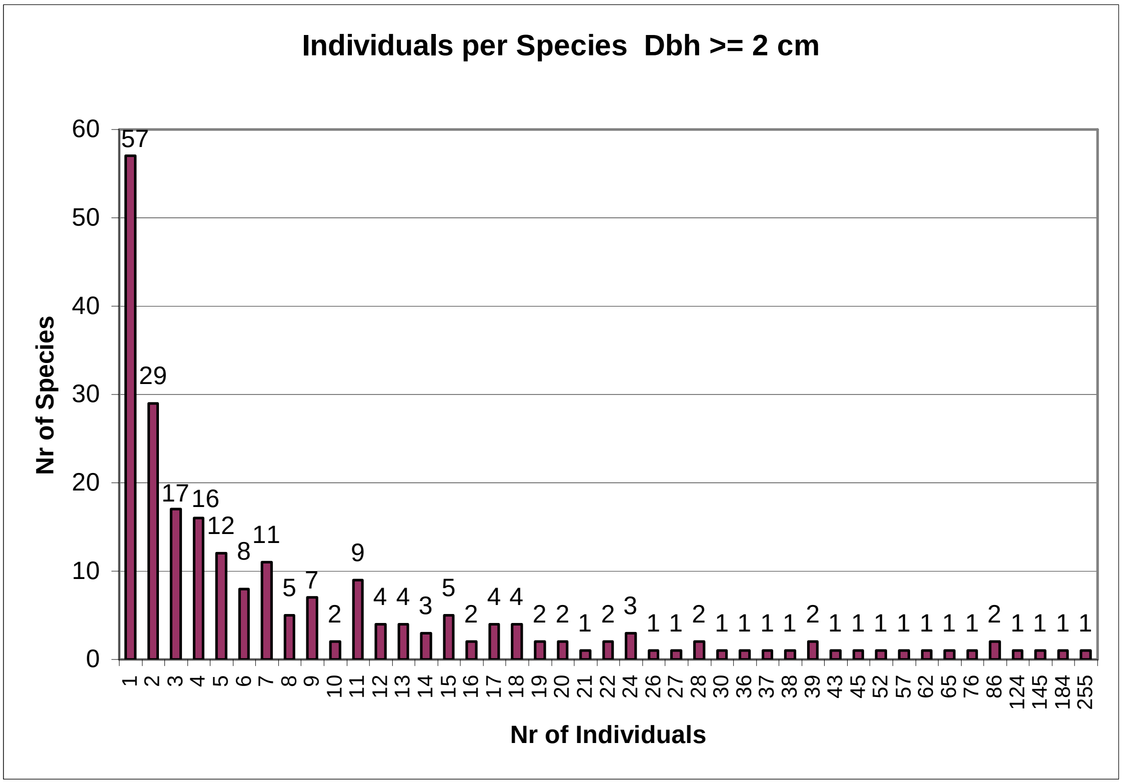

Fig. 4.8: Number of individuals per species of all individuals dbh ≥ 2 cm

The most abundant species of **all individuals dbh ≥ 2 cm** was the palm *Welfia regia* with 255 individuals. The understorey species *Psychotria elata* (Rubiaceae) with 184 and *Henriettea tuberculata* (Melastomataceae) with 145 plants were also very frequent. The palm *Iriartea deltoidea* with 124 and *Carapa guianensis* (Meliaceae) with 86 individuals followed up.

57 species were represented with only 1 individual (see Figure 4.8).

4.2.2 Simpson´s Index

The diversity measure according to Simpson´s index gave the value D = 0.039.

So the index of diversity was 1-D = 0.961 and the reciprocal index 1/D = 25.9 for **all individuals dbh ≥ 10 cm**.

In 1993 the diversity measure according to Simpson´s index gave the value D = 0.035, the index of diversity was 1-D = 0.965 and the reciprocal index 1/D = 28.6 for all individuals (HUBER 2005).

For **all individuals dbh ≥ 2 cm** Simpson´s index gave the value D = 0.024.
So the index of diversity 1-D = 0.976 and the reciprocal index 1/D = 41.3.

4.2.3 Shannon Wiener/Weaver Diversity Index

The Shannon-Weaver index gave the value H’ = 5.693 for **all individuals dbh ≥ 10 cm**.
In 1993 Shannon-Weaver index gave the value H’ = 4.119 (HUBER 2005).

For **all individuals dbh ≥ 2 cm** Shannon-Weaver index gave the value H’ = 6.427.

4.2.4 Shannon´s Evenness

The evenness index gave the value E = 1.21 for **all individuals dbh ≥ 10 cm**.
In 1993 the index gave 0.84 (HUBER 2005).

For **all individuals dbh ≥ 2 cm** evenness index was about 1.18.

4.2.5 Alpha index

Alpha index or log series or Fisher´s α gave the value α = 45.552 for **all individuals dbh ≥ 10 cm**.
In 1993 alpha index gave the value α = 57.953 (HUBER 2005).

For **all individuals dbh ≥ 2 cm** alpha index gave α = 59.699.

4.2.6 Importance Value Index

The IVI is an indicator for the importance of a species in a research area. It is the sum of relative frequency, relative density and relative dominance.

4.2.6.1 IVI dbh ≥ 10 cm

4.2.6.1.1 Relative Frequency

Species	**Family**	**Nr of Individuals**	**Nr of Subplots**	**Rel Frequency [%]**
Iriartea deltoidea	Arecaceae	62	40	**10,000**
Welfia regia	Arecaceae	43	34	**8,500**
Marila laxiflora	Clusiaceae	20	18	**4,500**
Symphonia globulifera	Clusiaceae	20	18	**4,500**
Carapa guianensis	Meliaceae	17	16	**4,000**
Socratea exorrhiza	Arecaceae	16	14	**3,500**
Brosimum utile	Moraceae	15	14	**3,500**
Mabea occidentale	Euphorbiaceae	10	9	**2,250**
Brosimum lactescens	Moraceae	8	8	**2,000**
Compsoneura sprucei	Myristicaceae	10	8	**2,000**
Otoba novogranatensis	Myristicaceae	8	8	**2,000**
Other Species		224		**53,250**
				100,000

Tab. 4.2: Relative Frequency for all individuals, dbh ≥ 10 cm

4.2.6.1.2 Relative Density

Species	**Family**	**Nr of Individuals**	**Relative Density [%]**
Iriartea deltoidea	Arecaceae	62	**13,687**
Welfia regia	Arecaceae	43	**9,492**
Marila laxiflora	Clusiaceae	20	**4,415**
Symphonia globulifera	Clusiaceae	20	**4,415**
Carapa guanensis	Meliaceae	17	**3,753**
Socratea exorrhiza	Arecaceae	16	**3,532**
Brosimum utile	Moraceae	15	**3,311**
Mabea occidentalis	Euphorbiaceae	10	**2,208**
Humiriastrum diguense	Humiriaceae	8	**1,766**
Brosimum lactescens	Moraceae	8	**1,766**
Compsoneura sprucei	Myristicaceae	8	**1,766**
Otoba novogranatensis	Myristicaceae	8	**1,766**
Elaeoluma glabrescens	Sapotaceae	8	**1,766**
Guarea grandifolia	Meliaceae	7	**1,545**
Other Species		203	**44,812**
			100,000

Tab. 4.3: Relative Density for all individuals, dbh ≥ 10 cm

4.2.6.1.3 Relative Dominance

Species	**Family**	**Basal Area [m²]**	**Nr of Individuals**	**Rel Dominance [%]**
Brosimum utile	Moraceae	5,10	15	**14,233**
Carapa guianensis	Meliaceae	3,77	17	**10,530**
Humiriastrum diguense	Humiriaceae	1,63	8	**4,548**
Vochysia megalophylla	Vochysiaceae	1,36	6	**3,796**
Elaeoluma glabrescens	Sapotaceae	1,24	8	**3,469**
Welfia regia	Arecaceae	1,23	43	**3,444**
Bombacopsis sessilis	Bombacaceae	1,19	6	**3,311**
Symphonia globulifera	Clusiaceae	1,12	20	**3,136**
Byrsonima crispa	Malpighiaceae	1,00	3	**2,803**
Marila laxiflora	Clusiaceae	0,96	20	**2,690**
Parkia pendula	Fabaceae-Mimos.	0,84	2	**2,351**
Iriartea deltoidea	Arecaceae	0,82	62	**2,284**
Otoba novogranatensis	Myristicaceae	0,77	8	**2,161**
Other Species		14,78	235	**41,245**
				100,000

Tab. 4.4: Relative Dominance for all individuals, dbh ≥ 10 cm

4.2.6.1.4 IVI dbh ≥ 10 cm

The IVI for all individuals **dbh ≥ 10 cm** is listed in Tab. 5.5.

Species	***Family***	**IVI**
Iriartea deltoidea	Arecaceae	**25,971**
Welfia regia	Arecaceae	**21,436**
Brosimum utile	Moraceae	**21,044**
Carapa guianensis	Meliaceae	**18,283**
Symphonia globulifera	Clusiaceae	**12,051**
Marila laxiflora	Clusiaceae	**11,605**
Humiriastrum diguense	Humiriaceae	**8,064**
Socratea exorrhiza	Arecaceae	**7,650**
Elaeoluma glabrescens	Sapotaceae	**6,985**
Vochysia megalophylla	Vochysiaceaeara	**6,371**
Bombacopsis sessilis	Bombacaceae	**6,135**
Otoba novogranatensis	Myristicaceae	**5,927**
Brosimum lactescens	Moraceae	**5,288**
Mabea occidentale	Euphorbiaceae	**5,259**
Compsoneura sprucei	Myristicaceae	**4,559**
Byrsonima crispa	Malpighiaceae	**4,215**
Guarea grandifolia	Meliaceae	**4,182**
Other Species		**124,977**
		300,000

Tab. 4.5: IVI for all individuals, dbh ≥ 10 cm

4.2.6.2 IVI dbh ≥ 2 cm

4.2.6.2.1 Relative Frequency

Species	**Family**	**Nr of Individuals**	**Nr of Subplots**	**Rel Frequency [%]**
Welfia regia	Arecaceae	255	84	**4,504**
Henriettea tuberculata	Melastomataceae	145	65	**3,485**
Psychotria elata	Rubiaceae	184	60	**3,217**
Iriartea deltoidea	Arecaceae	124	59	**3,164**
Carapa guianensis	Meliaceae	86	54	**2,895**
Mabea occidentale	Euphorbiaceae	76	49	**2,627**
Euphorbia elata	Euphorbiaceae	86	38	**2,038**
Socratea exorrhiza	Arecaceae	52	37	**1,984**
Marila laxiflora	Clusiaceae	43	36	**1,930**
Compsoneura sprucei	Myristicaceae	57	36	**1,930**
Brosimum utile	Moraceae	38	34	**1,823**
Faramea sessifolia	Rubiaceae	39	32	**1,716**
Symphonia globulifera	Clusiaceae	39	31	**1,662**
Protium aracouchini	Burseraceae	37	30	**1,609**
Other Species		1588		**65,416**
				100,000

Tab. 4.6: Relative Frequency for all individuals, dbh ≥ 2 cm

4.2.6.2.2 Relative Density

Species	**Family**	**Nr of Individuals**	**Relative Density [%]**
Welfia regia	Arecaceae	255	**8,951**
Psychotria elata	Rubiaceae	184	**6,458**
Henriettea tuberculata	Melastomataceae	145	**5,090**
Iriartea deltoidea	Arecaceae	124	**4,352**
Euphorbia elata	Euphorbiaceae	86	**3,019**
Carapa guianensis	Meliaceae	86	**3,019**
Mabea occidentale	Euphorbiaceae	76	**2,668**
Psychotria officinalis	Rubiaceae	65	**2,282**
Asterogyne martiana	Arecaceae	62	**2,176**
Compsoneura sprucei	Myristicaceae	57	**2,001**
Socratea exorrhiza	Arecaceae	52	**1,825**
Psychotria solitudinum	Rubiaceae	45	**1,580**
Marila laxiflora	Clusiaceae	43	**1,509**
Symphonia globulifera	Clusiaceae	39	**1,369**
Faramea sessifolia	Rubiaceae	39	**1,369**
Brosimum utile	Moraceae	38	**1,334**
Other Species		1453	**51,071**
			100,000

Tab. 4.7: Relative Density for all individuals, dbh ≥ 2 cm

4.2.6.2.3 Relative Dominance

Species	**Family**	**Basal Area [m²]**	**Nr of Individuals**	**Relative Dominance [%]**
Brosimum utile	Moraceae	5,14	38	**13,275**
Carapa guianensis	Meliaceae	3,84	86	**9,924**
Humiriastrum diguense	Humiriaceae	1,63	11	**4,219**
Welfia regia	Arecaceae	1,48	255	**3,822**
Vochysia megalophylla	Vochysiaceae	1,35	9	**3,480**
Elaeoluma glabrescens	Sapotaceae	1,26	18	**3,254**
Bombacopsis sessilis	Bombacaceae	1,19	11	**3,087**
Symphonia globulifera	Clusiaceae	1,17	39	**3,023**
Iriartea deltoidea	Arecaceae	1,04	124	**2,676**
Byrsonima crispa	Malpighiaceae	1,00	3	**2,595**
Marila laxiflora	Clusiaceae	0,99	43	**2,548**
Parkia pendula	Fabaceae-Mimos.	0,84	2	**2,177**
Otoba novogranatensis	Myristicaceae	0,78	15	**2,016**
Other Species		16,99	2195	**43,905**
				100,000

Tab. 4.8: Relative Dominance for all individuals, dbh ≥ 2 cm

4.2.6.2.4 IVI dbh ≥ 2 cm

The IVI for all plants **dbh ≥ 2 cm** is listed in Tab. 5.9.

Species	***Family***	**IVI**
Welfia regia	Arecaceae	**17,277**
Brosimum utile	Moraceae	**16,432**
Carapa guianensis	Meliaceae	**15,838**
Iriartea deltoidea	Arecaceae	**10,192**
Psychotria elata	Rubiaceae	**9,998**
Henriettea tuberculata	Melastomataceae	**9,080**
Mabea occidentale	Euphorbiaceae	**6,295**
Symphonia globulifera	Clusiaceae	**6,054**
Marila laxiflora	Clusiaceae	**5,988**
Euphorbia elata	Euphorbiaceae	**5,194**
Humiriastrum diguense	Humiriaceae	**5,141**
Compsoneura sprucei	Myristicaceae	**4,830**
Elaeoluma glabrescens	Sapotaceae	**4,637**
Socratea exorrhiza	Arecaceae	**4,573**
Vochysia megalophylla	Vochysiaceae	**4,171**
Bombacopsis sessilis	Bombacaceae	**4,063**
Asterogyne martiana	Arecaceae	**3,742**
Other Species		**166,566**
		300,000

Tab. 4.9: IVI for all individuals, dbh ≥ 2 cm

4.2.7 Family Importance Value Index

The FIVI shows the importance of families in a research area. It is the sum of relative diversity, relative density and relative dominance.

4.2.7.1 FIVI, dbh ≥ 10 cm

4.2.7.1.1 Relative Diversity

Family	Nr of Individuals	Nr of Species	Relative Diversity [%]
Moraceae	35	9	**8,333**
Clusiaceae	52	7	**6,481**
Sapotaceae	20	7	**6,481**
Fabaceae-Mimosoideae	8	6	**5,556**
Arecaceae	125	5	**4,630**
Myristicaceae	25	5	**4,630**
Annonaceae	4	4	**3,704**
Burseraceae	10	4	**3,704**
Chrysobalanaceae	9	4	**3,704**
Melastomataceae	9	4	**3,704**
Meliaceae	30	4	**3,704**
Fabaceae-Caesalpinioideae	4	3	**2,778**
Flacourtiaceae	4	3	**2,778**
Lauraceae	3	3	**2,778**
Sapindaceae	4	3	**2,778**
Other Families	111	37	**34,259**
			100,000

Tab. 4.10: Relative Diversity for all families, dbh ≥ 10 cm

4.2.7.1.2 Relative Density

Family	**Nr of Individuals**	**Nr of Species**	**Relative Density [%]**
Arecaceae	125	5	**27,594**
Clusiaceae	52	7	**11,479**
Moraceae	35	9	**7,726**
Meliaceae	30	4	**6,623**
Myristicaceae	25	5	**5,519**
Sapotaceae	20	7	**4,415**
Euphorbiaceae	13	2	**2,870**
Burseraceae	10	4	**2,208**
Chrysobalanaceae	9	4	**1,987**
Vochysiaceae	9	2	**1,987**
Melastomataceae	9	4	**1,987**
Myrsinaceae	9	2	**1,987**
Fabaceae-Mimosoideae	8	6	**1,766**
Humiriaceae	8	1	**1,766**
Violaceae	7	2	**1,545**
Other Families	84	44	**18,543**
			100,000

Tab. 4.11: Relative Density for all families, dbh ≥ 10 cm

4.2.7.1.3 Relative Dominance

Family	**Nr of Individuals**	**Nr of Species**	**BA [m²]**	**Relative Dominance [%]**
Moraceae	35	9	6,04	**16,865**
Meliaceae	30	4	4,68	**13,052**
Clusiaceae	52	7	2,59	**7,215**
Myristicaceae	25	5	2,37	**6,619**
Arecaceae	125	5	2,34	**6,525**
Sapotaceae	20	7	1,93	**5,381**
Humiriaceae	8	1	1,63	**4,548**
Vochysiaceae	9	2	1,60	**4,456**
Chrysobalanaceae	9	4	1,27	**3,538**
Fabaceae-Mimosoideae	8	6	1,23	**3,430**
Bombacaceae	6	1	1,19	**3,311**
Other Families	126	57	8,98	**25,059**
				100,000

Tab. 4.12: Relative Dominance for all families, dbh ≥ 10 cm

4.2.7.1.4 FIVI, dbh ≥ 10 cm

The FIVI for all plants **dbh ≥ 10 cm** is listed in Tab. 5.13.

Family	**Nr of Individuals**	**Nr of Species**	**FIVI**
Arecaceae	125	5	**38,749**
Moraceae	35	9	**32,925**
Clusiaceae	52	7	**25,175**
Meliaceae	30	4	**23,379**
Myristicaceae	25	5	**16,768**
Sapotaceae	20	7	**16,278**
Fabaceae-Mimosoideae	8	6	**10,752**
Chrysobalanaceae	9	4	**9,228**
Vochysiaceae	9	2	**8,295**
Burseraceae	10	4	**8,160**
Humiriaceae	8	1	**7,240**
Melastomataceae	9	4	**6,061**
Fabaceae-Caesalpinioideae	4	3	**5,918**
Euphorbiaceae	13	2	**5,744**
Annonaceae	4	4	**5,636**
Bombacaceae	6	1	**5,561**
Myrsinaceae	9	2	**4,409**
Malpighiaceae	3	1	**4,391**
Lauraceae	3	3	**4,200**
Sapindaceae	4	3	**4,199**
Olacaceae	4	2	**4,009**
Other Families	63	29	**52,924**
			300,000

Tab. 4.13: FIVI for all families, dbh ≥ 10 cm

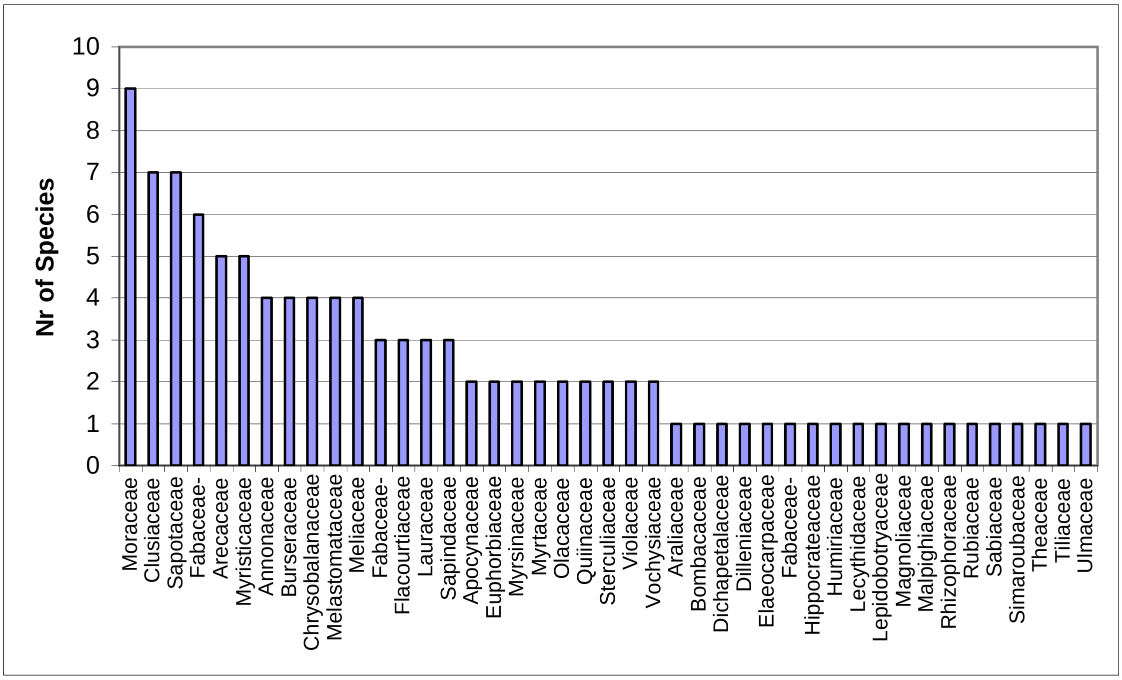

Fig. 4.9: Family Diversity for all individuals, dbh ≥ 10 cm

4.2.7.2 FIVI, dbh ≥ 2 cm

4.2.7.2.1 Relative Diversity

Family	Nr of Individuals	Nr of Species	Relative Diversity [%]
Rubiaceae	398	17	**7,328**
Fabaceae-Mimosoideae	58	16	**6,897**
Moraceae	120	15	**6,466**
Clusiaceae	170	14	**6,034**
Arecaceae	580	13	**5,603**
Melastomataceae	275	12	**5,172**
Sapotaceae	82	9	**3,879**
Annonaceae	44	8	**3,448**
Euphorbiaceae	217	8	**3,448**
Lauraceae	23	8	**3,448**
Burseraceae	78	7	**3,017**
Chrysobalanaceae	26	7	**3,017**
Flacourtiaceae	55	7	**3,017**
Meliaceae	115	6	**2,586**
Fabaceae-Caesalpinioideae	21	5	**2,155**
Myristicaceae	103	5	**2,155**
Sapindaceae	11	5	**2,155**
Vochysiaceae	39	5	**2,155**
Other Families	473	65	**28,017**
			100,000

Tab. 4.14: Relative Diversity for all families, dbh ≥ 2 cm

4.2.7.2.2 Relative Density

Family	Nr of Individuals	Nr of Species	Relative Density [%]
Arecaceae	580	13	**20,344**
Rubiaceae	398	17	**13,960**
Melastomataceae	275	12	**9,646**
Euphorbiaceae	217	8	**7,611**
Clusiaceae	170	14	**5,963**
Moraceae	120	15	**4,209**
Meliaceae	115	6	**4,034**
Myristicaceae	103	5	**3,613**
Sapotaceae	82	9	**2,876**
Burseraceae	78	7	**2,736**
Fabaceae-Mimosoideae	58	16	**2,034**
Violaceae	57	3	**1,999**
Flacourtiaceae	55	7	**1,929**
Annonaceae	44	8	**1,543**
Myrtaceae	42	4	**1,473**
Other Families	457	88	**16,029**
			100,000

Tab. 4.15: Relative Density for all families, dbh ≥ 2 cm

4.2.7.2.3 Relative Dominance

Family	Nr of Individuals	Nr of Species	BA [m²]	Relative Dominance [%]
Moraceae	120	15	6,18	**15,974**
Meliaceae	115	6	4,76	**12,309**
Arecaceae	580	13	3,06	**7,899**
Clusiaceae	170	14	2,74	**7,078**
Myristicaceae	103	5	2,46	**6,357**
Sapotaceae	82	9	2,03	**5,233**
Humiriaceae	11	1	1,63	**4,219**
Vochysiaceae	39	5	1,62	**4,178**
Chrysobalanaceae	26	7	1,30	**3,363**
Fabaceae-Mimosoideae	58	16	1,28	**3,309**
Bombacaceae	11	1	1,19	**3,087**
Other Families	1536	140	10,45	**26,995**
				100,000

Tab. 4.16: Relative Dominance for all families, dbh ≥ 2 cm

4.2.7.2.4 FIVI, dbh ≥ 2 cm

The family importance value index for all plants **dbh ≥ 2 cm** is listed in Tab. 5.17.

Family	**Nr of Individuals**	**Nr of Species**	**FIVI**
Arecaceae	580	13	**33,846**
Moraceae	120	15	**26,648**
Rubiaceae	398	17	**22,134**
Clusiaceae	170	14	**19,075**
Meliaceae	115	6	**18,929**
Melastomataceae	275	12	**15,847**
Euphorbiaceae	217	8	**12,572**
Fabaceae-Mimosoideae	58	16	**12,240**
Myristicaceae	103	5	**12,125**
Sapotaceae	82	9	**11,988**
Burseraceae	78	7	**8,039**
Vochysiaceae	39	5	**7,701**
Chrysobalanaceae	26	7	**7,292**
Annonaceae	44	8	**6,089**
Flacourtiaceae	55	7	**5,406**
Fabaceae-Caesalpinioideae	21	5	**5,055**
Lauraceae	23	8	**5,040**
Humiriaceae	11	1	**5,035**
Malpighiaceae	5	3	**4,065**
Violaceae	57	3	**3,928**
Bombacaceae	11	1	**3,904**
Other Families	363	62	**53,041**
			300,000

Tab. 4.17: FIVI for all families, dbh ≥ 2 cm

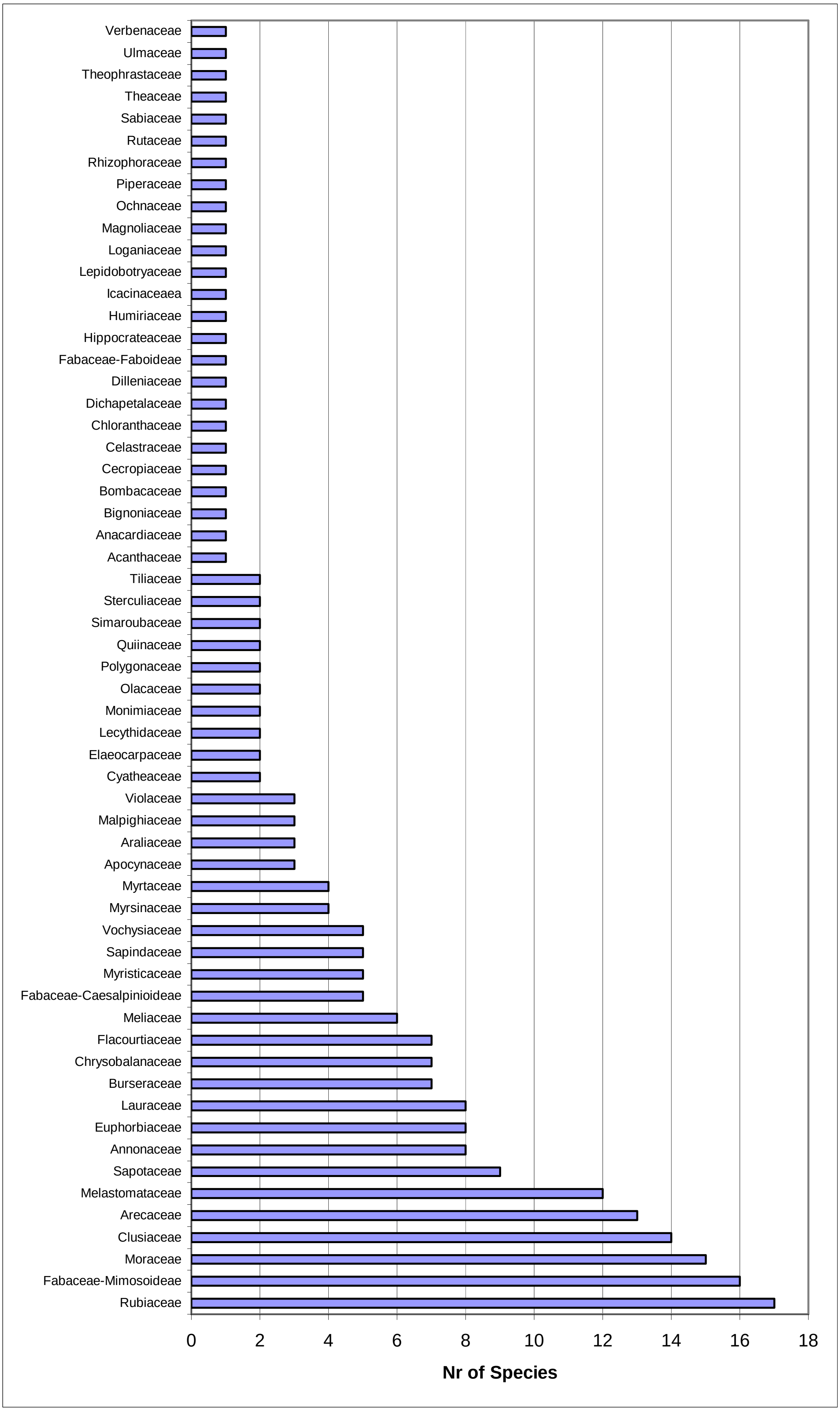

Fig. 4.10: Family Diversity for all individuals, dbh ≥ 2 cm

5 Discussion

5.1 Basic Forest Structure

5.1.1 Size Class Distribution

Forest research plots are periodically monitored using size classes for better description, presentation and visualization. Monitoring varies in scope. Several studies cover a range from dbh ≥ 10 cm, some contain individuals from dbh ≥ 1 cm or dbh ≥ 2 cm. The corresponding size classes are frequently stated in 10 cm intervals, smaller research plots occasionally in 5 cm steps.

Size classes usually give the base for parameters of structure, e. g. for BA, biomass and turnover variables and make them comparable with other forest sites and areas.

The distribution on the research plot showed the anticipated J graph. Most of the individuals were found in the smaller size classes, a common feature of primary forests (GENTRY & TERBORGH 1990, HUBBEL & FOSTER 1990, LIEBERMANN & LIEBERMANN 1994).

453 individuals dbh ≥ 10 cm out of 108 species were found on the research plot. In 1993 527 individuals out of 133 species were present (HUBER 2005). Many species are represented with very few individuals. For example, on this research plot 57 species had only one individual. If disturbances occur species with low density are more influenced than species with a higher number of individuals. Especially the lower size classes showed higher mortality and loss of those individual poor species. So a decrease of species richness at the moment of the inventory occurred.

With all plants dbh ≥ 2 cm there were 2849 individuals out of 232 species.

Compared with research areas in other neotropical regions that number of individuals was more or less average. E. g. Barro Colorado Island, Panama, had about 415 individuals dbh ≥ 10 cm per ha in a 50 ha plot (CONDIT 1995), Paracou, French Guiana about 615 individuals per ha in a 19 ha plot (FAVRICHON 1994). For further data see Tab. 6.2.

Density could be influenced by the dominant soil type. Hereby it is stated that highest density occured on depressions and floodplains on flatter areas (LIEBERMANN & LIEBERMANN 1985). DEWALT (2003) showed no significant differences in total number of trees on different soil types in La Selva, Costa Rica. WEISSENHOFER (2005) showed that the research areas with highest amount of individuals were on the poorest soils in Esquinas forest, Costa Rica.

Another alternative reason for reducing or limiting density was a higher number of taller trees. Those could reduce the number of smaller individuals by e. g. shadowing or killing in treefall events (LIEBERMANN & LIEBERMANN (1994). On the plot several larger trees were present.

Due to treefall of large trees in the recent years smaller individuals were killed and relative huge gap areas formed. So some plants which had reached a dbh ≥ 10 cm disappeared and less individuals could reach that border. Otherwise the high number of individuals in the lowest size classes were caused by the colonization of the gap areas by several species meanly of Rubiaceae (e.g. *Psychotria spp., Isertia laevis, Faramea sessiliflora*) and Arecaceae (*Iriartea deltoidea, Welfia regia*). The high density of palms causes difficulties for regeneration. First, large palm leaves reduce light transmission for smaller plants and second, dying and falling leaves could possibly kill most of the young regeneration standing below. Especially very large and heavy leaves like those of *Welfia regia* could cause such effects.

Location	Author	Density	Range (Dbh)
Costa Rica, Esquinas	Present Study	2849	2cm up
Costa Rica, La Selva	DEWALT 2003	3360	1cm up
Panama, BCI	DEWALT 2003	4910	1cm up
Peru, Cocha Cashu	DEWALT 2003	5377	1cm up
Brazil, KM41	DEWALT 2003	6150	1cm up
Ecuador, Yasuni	VALENCIA 2004	6094	1cm up
Malaysia, Pasoh	PLOTKIN 2002	6705	1cm up

Tab. 5.1: Comparison of tropical forests: Density

5.1.2 Basal area

The BA (dbh ≥ 10 cm with 35.9 m², dbh ≥ 2 cm with 38.7 m²) of the plot had an amount more or less found in similar studies in Latin American forests and was higher than the average respectively. DEWALT & CHAVÉ (2004) showed BA in four different forests in Brazil, Peru, Panama and Costa Rica, VALENCIA (2004) in an Ecuadorian forest (see Table 6.1). Here the nutrient poor Peruvian and Brazilian forests showed surprising high BA, whereas the Central American forests were comparatively low despite its relative high fertile soils. Usually the growth of trees is greater on soils with high nutrition status (GENTRY & TERBORGH 1990). Those nutrient poor south American forests showed a very high density of medium sized trees whereas the Central American forests showed a higher amount of trees with higher dbh.

The research plot suffered several severe disturbances in the past years with loss of many bigger trees. The remnants of the boulders could be seen for years on the plot. So a good part of the area showed gap phase characteristics with dense understorey, low dbh´s and few canopy trees. A loss of few plants with high dbh caused lower BAs.

Relief was deciding the amount of BA and therefore of growth. WEISSENHOFER (2005) showed highest BA on plots with higher slopes and on ridges (up to 43.5 m²). HARTSHORN (1983) confirmed this statement with BA of 45.8 m² on those stands and lower values on sites with lower gradients in the same area.
Low values on flat landscapes in La Selva, Costa Rica, were approved by HARTSHORN & HAMMEL (1994) and LIEBERMANN et al. (1996). BA varied between 23.5 and 27.1 m²/ha.

Location	Costa Rica Research Plot Esquinas	Costa Rica La Selva	Panama BCI	Peru Cocha Cashu	Brazil KM41	Ecuador Yasuni
Author	Present Study	DEWALT 2003	DEWALT 2003	DEWALT 2003	DEWALT 2003	VALENCIA 2004
Ind. Density	2849	3360	4910	5377	6150	6094
Basal Area (m²)	38.7	29.2	27.9	45.3	38.6	33.4
Range (Dbh)	2cm up	1cm up	1cm up	1cm up	1cm up	1cm up

Tab. 5.2: Comparison of Neotropical forests: Density and BA.

5.1.3 Biomass

Biomass strongly varies dependent on the way of calculation. Differences of two slightly different calculations may result in deviations caused by the square sum deviation of two measurement uncertainties. Due to great variations of the crown shape and the tree architecture in general exact calculations seem difficult (HALLE et al 1978). Also the height measurement of tropical trees has an error due to estimation differences which often ranges up to 10 m (CHAVÉ et al 2001). So a regression model excluding the height was chosen. A derivation of the formula was provided by CHAVE (2001). Those regression model is commonly used in biomass estimation nowadays (FEELEY et al 2007; DEWALT et al 2004; CHAVÉ et al 2001).

Previous studies on biomass resulted in a range from 148 Mg ha^{-1} up to 669 Mg ha^{-1} (KIRA 1971). The Esquinas research plot showed average biomass (339 Mg ha^{-1}) compared to other tropical forests. Biomass for about 300 Mg ha^{-1} are common in tropical forests (CHAVE et al, 2001).

CHAVE (2001) measured values from 309 up to 345 Mg ha^{-1} in French Guiana. FEELEY (2007) obtained data from 4 different research areas: BCI, Panama; Pasoh, Malaysia; Lambir, Malaysia; Huai Kha Khaeng, Thailand, with estimations of 301 Mg ha^{-1} for BCI, 326 Mg ha^{-1} for Pasoh, 490 Mg ha^{-1} for Lambir and 211 Mg ha^{-1} for Huai Kha Khaeng. CHAVE (2008) obtained data from the same research plots with 307 Mg ha^{-1} for BCI, 340 Mg ha^{-1} for Pasoh, 497 Mg ha^{-1} for Lambir and 211 Mg ha^{-1} for Huai Kha Khaeng.

The biomass accumulation (NPP) was high with 7.9 Mg ha^{-1} y^{-1}. Usually 2 to 4 Mg ha^{-1} y^{-1} were reported (BROWN 1990; LUGO 1992; CHAVE 2001).

The ingrowth rate (NEP or uptake of biomass minus losses through death) was with 1.9 Mg ha^{-1} y^{-1} in the usual range. Literature described values from 0.7 up to 1.9 Mg ha^{-1} y^{-1} (e. g. PHILLIPS et al 1998; CHAVE 2001).

The high NPP could be explained with the great gap-similar area in the lower part of the research plot. High NPP values are typical for secondary forests and primary forests with high areal amount of gaps.

The increase of biomass from 1993 to 2001 had an amount of 15 Mg ha^{-1}. This result complied with the increasing average dbh and BA. That increment corresponded with the assumption of increasing biomass in tropical forests in the late twentieth century (PHILLIPS & GENTRY 1994; PHILLIPS 1996). The root cause could not be detected. First, possibilities were disturbances and increment of fast growing species due to distinct gap formation, and second, athmospheric changes like increasing CO_2, increasing temperatures or nitrogen deposition. This thesis could not answer that question. It could be part of further analyses.

All the plants smaller than 10 cm dbh contributed only 2,8 % (9 Mg ha^{-1}) to the whole aboveground biomass, although they represented 84 % of all individuals. This corresponded with LESCURE (1983) who stated an amount of 2 to 4 % of the total biomass for such size classes.

Only 25 % of all trees were greater than dbh 30 cm, but they represented 85 % of the aboveground biomass and as much as 77 % of the BA. Larger tree affect on biomass was considerably more pronounced. Only 5 % of the trees were above dbh 70 cm, but 50 % of aboveground biomass and 40 % of the BA belonged to this class.
So a potential loss of only one greater individual reflected in a strong decrease in biomass.

5.1.4 Growth and mortality

Growth and mortality rates generally vary through ontogeny and therefore influence size distribution (WRIGHT et al 2003). Mortality generally declines with age or tree size (HARCOMBE 1987). This decline is highest for light demanding species because they are rare as seedlings and treelets due to their quick dying when shaded, or their rapid growing into higher size classes if high light levels remain high (WRIGHT et al 2003).
Shade tolerant species in contrast are very frequent as seedlings and treelets because of their persistence and slow growth behaviour (WRIGHT et al 2003).
Some species produce an ontogenetic shift, therefore they need high levels of light for establishment as seedling. When established they switch to a shade tolerant growth

(CLARK & CLARK 1992; DALLING et al 2001, WRIGHT et al 2003). But generally the mortality rates tend to be consistent across all juvenile stages (WRIGHT et al 2003).
Size distributions with many small individuals and rare large individuals characterize prevailing of shade tolerant species with lower fertility, slower growth in smaller size classes and lower mortality of seeds and seedlings (WRIGHT et al 2003).
Rates and therefore size class distribution varies in relation to disturbances (e.g. drought, pathogens, predation, windfall and others) (GILBERT et al 1994; CONDIT et al 1996).
Former studies showed different results. HARTSHORN (1980) showed a dominance of species with high light requirements with an amount of 71 % of all canopy tree species. At BCI, Panama, several studies demonstrated converse results with a dominace of over 80 % of species regenerated in the shaded understorey (HUBBELL & FOSTER 1986, CONDIT et al 1996).

Generally pioneer species show rapid growth and short longevity, subcanopy trees have slow growth and high longevity, and canopy and emergent species have moderate to high growth and high longevity (LAURANCE et al, 2003; KORNING & BALSLEV 1994; LIEBERMAN & LIEBERMAN 1987; CONDIT et al 1996).

Mortality was 3.54 % y^{-1} for all stems dbh ≥ 10 cm. Plants from 2 to < 10 cm could not be included because they were not evaluated in 1993 and therefore no comparison was possible.
LAURANCE (2003) calculated mortality rates of 0.86 % y^{-1} in a forest near Manaus, Central Amazonia. CONDIT (1995) found mortality rates in 2 censuses from 2.26 up to 2.66 % y^{-1} at BCI, Panama. PHILLIPS (2004) described nearly 100 research plots in Bolivia, Brazil, Ecuador, French Guiana, Peru and Venezuela and reported mortality rates from 0.44 up to 3.36 % y^{-1}. LEWIS et al (2004b) showed mortality rates of 0.86 % y^{-1} for seven stands in Panama, French Guiana, Australia, Brazil, Peru, Cameron and Malaysia.
Mortality rates are usually higher in pioneer species (CONDIT 1995). But this could not be verified with the Esquinas data. No absolute trend occurred which ecological group has high and which has low mortality. In contrary, the Esquinas data showed slightly higher mortality in the climax or canopy species. This corresponded with the conclusion

of CONDIT (1995) who recognized similar results in BCI, Panama, and WEISSENHOFER (2005) for four different Esquinas research plots, Costa Rica.

Iriartea deltoidea (Arecaceae), the most abundant species on the plot, had a mortality of 4.64 % y^{-1}, *Welfia regia* (Arecaceae), the second abundant species, 2.02 % y^{-1}, *Marila laxiflora* (Clusiaceae), the most abundant canopy species, 2.03 % y^{-1}.
Some species occurring in the Esquinas and BCI, Panama, showed very different mortality rates:
Beilschmiedia pendula (Lauraceae) for example had 8.66 % y^{-1}, in BCI 1.95 % y^{-1}.
Brosimum alicastrum (Moraceae) had 5.07 % y^{-1}, in BCI 1.85 % y^{-1}.
Protium panamense (Burseraceae) had 1.93 % y^{-1}, in BCI 9.00 % y^{-1}.
Symphonia globulifera (Clusiaceae) had 1.47 % y^{-1}, in BCI 10.39 % y^{-1}.
Virola sebifera (Myristicaceae) had 0 % y^{-1}, in BCI 3.27 % y^{-1}.

The reason of those differences might be different disturbances in the two forests, as well as different level of climatic influences, as well as the timing of the census. Generally understorey plants or plants of smaller size classes could be killed by other falling trees or parts of them (DENSLOW & HARTSHORN 1994). That could explain the higher mortality rates of the palms and Melastomataceae. Mortality occured mainly in the lowest size classes. Nearly 60 % of all dead individuals were below dbh 15 cm. 30 % were palms. Canopy plants could be eliminated by lightning, a very important mortality factor, windthrow or snapping.
Climatic influences are a widely discussed theme. Is global warming and additional carbon and nitrogen input responsible for accelerating growth rates? That could not be identified for sure. LEWIS (2004) could not certainly show an influence of warming on tropical growth. Events with a greater impact (e.g. ENSO, El Nino Southern Oscillation) certainly affect different growth and mortality rates, but those influences strongly vary depending on variables like region, year, species composition, slope. PHILLIPS (2004) could not exclude an influence of additional carbon input on accelerated growth rates. Further studies and simulations should take place.
The timing of the census could possibly affect the measured rates, because climate fluctuations could affect stem hydrations, growth rates and mortality probabilities (PHILLIPS et al 2004).

Another reason could be different soil fertilities. Recent studies showed a strong correlation between fertility, mortality and growth rates. Those rates are higher with increasing soil fertility (PHILLIPS et al 1994; MAHLI et al 2004; PHILLIPS et al 2004). Especially on pioneer species soil fertility has an enormous impact (CONDIT 1999). But that growth driver is generally too poorly characterized and too spatial localized.

Growth rates varied strong among species and among years. This corresponds with other publications (LAURANCE et al, 2003; CLARK & CLARK 1992; CLARK & CLARK 1994; DA SILVA et al 2002).

The growth rates in mm y^{-1} range from 0 up to 7.5. The dbh growth in mm y^{-1} was inclining with higher size classes. LAURANCE (2008) found growth rates of 0.25 up to 6.39 mm y^{-1}. Here pioneer species also had no higher growth than canopy species.

The weighted growth rate as a function of mortality and recruitment was negatively correlated (–2.35%) due to the higher mortality rate.

The relation between climate, soils and disturbances with growth are very complex. In La Selva, Costa Rica, dry years often tend to produce over averaged growth of canopy trees possibly due to higher availability of photosynthetically active radiation during years or periods with lesser cloud cover (CLARK & CLARK 1994).

5.2 Floristic diversity

5.2.1 Species Diversity

5.2.1.1 Species Density

Tropical forests are characterized for having hundreds of species per single hectare (CONDIT et al 2005). The research plot in the Esquinas belongs to one of the forests with highest species diversity in Central America (QUESADA & al 1997, WEBER & al. 2001, (HUBER 2008)). In Central America those forests are in the wet Pacific and Caribbean lowlands of Costa Rica.

Diversity can be measured generally on different levels ranging from genes to ecosystems (GASTON 2000). Most analyses measuring diversity are performed by observation of the number of species in a specific area (CONDIT et al 2005).
One of the primary purposes of tree censuses is to assess biodiversity with the intent of providing absolute and comparative estimates of species diversity (CONDIT et al 1998).
Terrestrial systems have a significant higher species richness in tropical forests than in temperate regions. While 200 or more species per hectare are no curiosity for tropical forests, temperate forests contain only more or less 10 species per hectare. The whole northern Europe has approximately 50 tree species.

In the research plot 108 species out of 43 families dbh ≥ 10 cm and 232 species out of 59 families dbh ≥ 2 cm respectively occurred.
The palms *Iriartea deltoidea* and *Welfia regia* as well as the Clusiaceae *Symphonia globulifera* and *Marila laxiflora* and *Carapa guianensis* (Meliaceae) were very common. Many understorey and disturbance species of the families Rubiaceae and Melastomataceae (eg. *Psychotria elata, Isertia laevis*) were also characterized by a very high abundance. Due to the high disturbance degree of the research plot palms were very frequent in succession, a characteristic where disturbances frequently occur and results in gaps or gap areas in the forests.

5.2.1.2 Diversity Indices

The best practice and measure respectively of diversity would be independent of frequency for comparing diversity of smaller with larger areas or plots. But species richness is clearly dependent on sample size. All indices usually increase with increasing sample size.

The **Simpson diversity index** (D) showed similar results within the censuses 1993 and 2001. 1-D lied between 0.965 and 0.961. Including all individuals dbh ≥ 2 cm the index was about 0.976. The reciprocal index 1/D lied between 25.9 and 28.6. Here including all individuals dbh ≥ 2 cm resulted in an index of about 41.3. These higher indices including the smaller plants were caused by higher species density (232 species per hectare and nearly 3000 individuals).

You should sometimes be careful using the Simpson index in tropical forests because it represents evenness but nearly no part of richness.

Shannon-Weaver diversity index (H') is usually the least variable and most stable index containing information about both richness and evenness.
The plot showed a H' index 5.693 and was slightly higher than in 1993 (H' = 4.119).
Including all individuals dbh ≥ 2 cm resulted in an index of H' = 6.427.

The **Evenness** E = 1.21 compared to 1993 with E = 0.84 and with all individuals dbh ≥ 2 cm E = 1.18.

Compared with other tropical forests these indices attest the Esquinas forest its high diversity. LIEBERMANN et al (1996) calculated indices from H' = 2.556 to H' = 4.508 and the Evenness (E) ranges from 0.759 to 0.901 for forests of the Carribean sites of Costa Rica. CONDIT et al (1998) showed indices for Pasoh, Malaysia, BCI, Panama and Mudumalai, India from H' = 1.3 up to H' = 1.6. LAFRANKIE (2006) calculated H' = 3.91 for Korup, Cameroon, H' = 3.65 for BCI, Panama, H' = 5.59 for Yasuni, Ecuador, H' = 5.39 for Lambir, Malaysia, H' = 5.28 for Pasoh, Malaysia and H' = 4.57 for Palanan, Philippines.

The **Alpha Index** gave the value α = 45.552. That index was lower than 1993 (α = 57.953) and lower than with all individuals dbh ≥ 2 cm (α = 59.699).
The range found in Fisher's α in the Esquinas forest (HUBER 2005) was from 38.82 (coastal slope) to 70.49 (ridge forest). CONDIT et al (1998) showed indices for Pasoh, Malaysia, BCI, Panama and Mudumalai, India with α = 125.2, α = 36.0 and α = 5.6. VALENCIA et al (1994) showed indices for the Ecuadorian Cuyabeno forests from α = 211.0 to α = 230.8. PHILLIPS et al (1994b) showed α = 221.1 for Yanamono, Peru, α = 87.3 for Tambopata, Peru and 52.5 for Sepilok, Malaysia. GENTRY (1982b) showed α = 146.9 for Manaus, Brazil. LAFRANKIE (2006) calculated α = 44.4 for Korup, Cameroon, α = 34.6 for BCI, Panama, α = 190.5 for Yasuni, Ecuador, α = 158.0 for Lambir, Malaysia, α = 120.0 for Pasoh, Malaysia and α = 47.7 for Palanan, Philippines.
Highest diversity was shown for Neotropical forests with a hot spot in the areas of Peru and Ecuador. But the tropical forests of Central America showed also high diversity, especially in the Esquinas forest.

5.2.1.3 Importance Value

This index is considerable important because it includes three calculations. It is the sum of relative frequency, relative density and relative dominance.

The species with the highest Importance Values were from the Arecaceae (*Iriartea deltoidea*, IV 25.971; *Welfia regia*, IV 21.436), the Clusiaceae (*Symphonia globulifera*, IV 12.051; *Marila laxiflora*, IV 11.605), the Meliaceae (*Carapa guianensis*, IV 18.283) and the Moraceae (*Brosimum utile*, IV 21.044). In 1993 Huber found the same species on top of the importance scale.

For all species (dbh ≥ 2 cm) the understorey species *Henriettea tuberculata* (Melastomataceae) and *Psychotria elata* (Rubiaceae) are additionally in the top ranking.

The three included indices showed the dominance of those species in all cases (but in various order). Merely the relative dominance (defined by BA) showed increasing relevance of the bigger canopy species like *Vochysia megalophylla* (Vochysiaceae), *Humiriastrum diguense* (Humiriaceae) and *Elaeoluma glabrescens* (Sapotaceae).

Palms are very abundant in Central American and northern South American tropical forests. Especially a few genera like *Welfia*, *Iriartea* and *Socratea* are typical. There is nothing equivalent found in lowland forests of Asia. There palms are abundant as caespitose understorey plants and especially climbers, a fact that is largely missing in America (LAFRANKIE 2006). Generally no absolute dominance of one species in whatever case could be recognized on the plot. On the contrary extreme non-dominance was given, no species had such occurrence that it could be designed as leading species, although palm species were frequent and a very high amount of understorey or pioneer trees (many Rubiaceae, Melastomataceae, Euphorbiaceae) were found on the large gap areas.

5.2.1.4 Family Importance Value

No family showed absolute dominance on the research area. On top of both (dbh ≥ 10 cm, dbh ≥ 2 cm) calculations were the palms. They were not very diverse and did not have highest BA but had the highest relative density (20 to 30 %). The Moraceae were second in both ways and had generally a high importance in the Esquinas forest (HUBER 2005). While Clusiaceae, Meliaceae, Myristicaceae and Sapotaceae were important in the greater size classes, the calculation including the smaller classes showed increasing dominance of families with a high amount of understorey species (e.g. Rubiaceae, Melastomataceae, Euphorbiaceae, Chrysobalanaceae).

The results showed that the Esquinas forest is one of the highest diverse tropical forests. The forest itself is very dynamic with high amounts of turnover rates. Due to this characteristics the stands are spatially divided in many microhabitats like a mosaique. So many species with very diverse ecological requirements could establish.

The forest is said to be in a “state of dynamic equilibrium” that may be subdivided into three phases: the gap phase, the building phase, and the mature phase. Gap phase has great importance for diversity, especially in the highly diverse tropical forests (WHITMORE 1978, HUBBELL & FOSTER 1986, HUBBELL & al. 1990). The Esquinas forest is very dynamic and therefore all phases between gap and climax were found in all plots.

6 Abstract

The Esquinas rainforest in Costa Rica is among the plant communities with the highest number of species in Central America (QUESADA et al 1997). The thesis describes the structure and the floristic diversity of a research plot of an undisturbed primary forest in the Piedras Blancas / Esquinas National Park ("Regenwald der Österreicher").

The data were collected between 2000 and 2001. Analyses were performed collecting and identifying woody plants of ≥ 10 cm and ≥ 2 cm dbh respectively. A detailed site map was generated, data were collected and calculated of each tree and the whole plot with individual number, diameter in breast height (dbh), tree height, basal area (BA), and biomass. Further growth and mortality rates were calculated. Furthermore species density, diversity indices (Simpson, Shannon-Wiener, Fisher´s α), Importance Value (IVI) and Family Importance Value (FIVI) were calculated.

All data were compared with former studies performed by HUBER (1996a, 2005) and WEISSENHOFER (1996, 2005)

In total 2849 individuals of 232 species ≥ 2 cm dbh and 453 individuals of 108 species ≥ 10 cm dbh were recorded. Palms were very abundant with the most frequent species *Iriartea deltoidea* (62 individuals) and *Welfia regia* (43 individuals) for all trees dbh ≥ 10 cm. In the lower size classes understorey species like *Henriettea tuberculata* (Melastomataceae) and *Psychotria elata* (Rubiaceae) were very frequent with 184 and 145 individuals respectively.

The graph of the size class distribution showed the anticipated J graph. The average dbh of all individuals ≥ 10 cm was 25.9 cm, in 1993 23.5 cm. The average dbh of all individuals ≥ 2 cm was 7.0 cm.

The BA was 35.9 m² (dbh ≥ 10 cm) and 38.7 m² (dbh ≥ 2 cm), an amount found on the lower range in similar studies in Latin American forests. Compared to WEISSENHOFER (2005) who calculated 35.5 m² in 1993 similar values could be reported. Root causes of lower BA were suffering several severe disturbances in the past years with loss of many

bigger trees. Also relief was deciding the amount of BA. WEISSENHOFER (2005) showed highest BA on plots with higher slopes and on ridges (up to 43.5 m²). HARTSHORN (1983) confirmed this statement with BA of 45.8 m² on those stands and lower values on sites with lower gradients in the same area.

The Esquinas research plot showed average biomass (339 Mg ha^{-1}) compared to other tropical forests. WEISSENHOFER calculated 315 Mg ha^{-1} in 1993. Biomass accumulation (net primary production NPP) was high with 7.9 Mg ha^{-1} y^{-1}. Ingrowth rate (net ecosystem production NEP or uptake of biomass minus losses through death) was with 1.9 Mg ha^{-1} y^{-1} in the range of comparable tropical forests. The high NPP could be explained with the great gap-similar area in the lower part of the research plot. High NPP values are typical for secondary forests and primary forests with high amount of gap areal.

The mortality rate was 3.54 % $y^{-1}$for all stems dbh ≥ 10 cm. The size class distribution for mortality was different. Lower size classes showed a higher rate. Nearly 60 % of all dead individuals were below dbh 15 cm. In the higher size classes mortality was nearly constant. Recruitment was 1.29 % y^{-1} for all stems dbh ≥ 10 cm.

In the research plot 232 species out of 59 families occurred. The palms *Iriartea deltoidea* and *Welfia regia* as well as the Clusiaceae *Symphonia globulifera* and *Marila laxiflora* as well as *Carapa guianensis* (Meliaceae) were very common. Many understorey and disturbance species of the families Rubiaceae and Melastomataceae (eg. *Psychotria elata, Isertia laevis, Henriettea tuberculata*) were also characterized by a very high abundance. Due to the high disturbance degree of the research plot palms were very frequent in different succession phases, a characteristic where disturbances frequently occur and results in gaps or gap areas in the forests.

57 ssp. were represented with only one individual.

The Shannon-Wiener index was H´= 6.427, Simpson index gave D = 0.035, Simpson index of diversity 1-D = 0.965 and Alpha index α = 59.699.

The families with the highest FIVI were the Arecaceae (33.846), Moraceae (26.648) Rubiaceae (22.134) and the Clusiaceae (19.075). The species with the highest IVI were

Welfia regia (Arecaceae; 17.277), *Brosimum utile* (Moraceae; 16.432), *Carapa guianensis* (Meliaceae; 15.838) and *Iriartea deltoidea* (Arecaceae; 10.192).

Probably due to the high precipitation, the missing dry season, the strong structured landscape and soil heterogeneity the Esquinas forest has a very high species diversity for a tropical forest.

7 Zusammenfassung

Der Esquinas Regenwald in Costa Rica gehört zu den artenreichsten Pflanzengesellschaften in Mittelamerika (QUESADA et al 1997). Diese Diplomarbeit beschreibt die Struktur und floristische Diversität eines Forschungsplots in einem Primärwald im Piedras Blancas Nationalpark (“Esquinas rainforest” oder "Regenwald der Österreicher"), welcher in einer Seehöhe von 300-336 msm und einer geographischen Lage von N 8°41’ und W 83°12’ auf einem gut drainagierten südwestlich exponierten Hangwald liegt. Der durchschnittliche jährliche Niederschlag liegt bei etwa 6000 mm, die jährliche Durchschnittstemperatur bei ca. 28°C. Diese Eigenschaften sowie die Abwesenheit einer ausgeprägten Trockenzeit führten zur Ausbildung eines „Perhumid tropical lowland wet forest“ gemäß HOLDRIDGE et al 1971.

Die Feldaufnahmen wurden zwischen 2000 und 2001 durchgeführt. Diese wurden in Form von Besammlungen und Bestimmungen von holzigen Pflanzen mit einem Brusthöhendurchmesser (dbh) ≥ 10 cm sowie ≥ 2 cm dbh durchgeführt. Ein detaillierter Lageplan wurde erstellt, Daten jedes einzelnen Individuums und der gesamten Untersuchungsfläche erhoben mit laufender Nummer, dbh, Baumhöhe, Bestandesgrundfläche und Biomasse. Weiters wurden Wachstums- und Mortalitätsraten sowie verschiedene Artendichte- und Diversitätsindices (Simpson, Shannon-Wiener, Fisher´s α), Importance Value (IVI) und Family Importance Value (FIVI) berechnet.

Alle Berechnungen wurden mit jenen aus früheren Studien von HUBER (1996a, 2005) und WEISSENHOFER (1996, 2005) verglichen.

Insgesamt 2849 Individuen aus 232 Arten ≥ 2 cm dbh sowie 453 Individuen aus 108 Arten ≥ 10 cm dbh wurden ermittelt. Palmen wiesen eine ausgesprochene Häufigkeit vor allem mit den Arten *Iriartea deltoidea* (62 Individuen) und *Welfia regia* (43 Individuen) für alle Individuen dbh ≥ 10 cm auf. Bei den niederen Größenklassen traten Unterbauarten wie *Henriettea tuberculata* (Melastomataceae) und *Psychotria elata* (Rubiaceae) sehr häufig auf (184 bzw. 145 Individuen).

Die graphische Darstellung der Größenklassenverteilung zeigt die typische reverse J-Kurve mit den meisten Individuen in den niederen Größenklassen. Der durchschnittliche dbh aller Individuen ≥ 10 cm betrug 25.9 cm, im Jahr 1993 23.5 cm. Der durchschnittliche dbh aller Individuen ≥ 2 cm betrug 7.0 cm.

Die Bestandesgrundfläche betrug 35.9 m² (dbh ≥ 10 cm) beziehungsweise 38.7 m² (dbh ≥ 2 cm). Dieses Ergebnis liegt im unteren Bereich verglichen mit ähnlich designten Studien in lateinamerikanischen Wäldern. Es wurde ein ähnliches Ergebnis wie bei WEISSENHOFER (2005) erzielt, welcher 35.5 m² in 1993 ermittelte. Hauptgrund einer niedrigeren Bestandesgrundfläche sind schwere Störungen in den vergangenen Jahren mit Ausfällen von Individuen mit höherem dbh. Das Relief ist ebenfalls ein für die Bestandesgrundfläche entscheidender Parameter. WEISSENHOFER (2005) zeigte höchste Bestandesgrundfläche auf steileren Untersuchungsflächen sowie auf Rücken (bis zu 43.5 m²). HARTSHORN (1983) ermittelte ebenfalls höhere Bestandesgrundflächen auf Steilhängen und Rücken (bis zu 45.8 m²), sowie niedrigere in flacheren Beständen desselben Areals.

Der Esquinas Forschungsplot weist mit 339 Mg ha^{-1} eine durchschnittliche Biomasse im Vergleich mit anderen tropischen Wäldern auf. WEISSENHOFER ermittelte 315 Mg ha^{-1} in 1993. Die Biomasseakkumulation (Nettoprimärproduktion) war mit 7.9 Mg ha^{-1} y^{-1} hoch. Die Zuwachsrate (Netto-Ökosystemproduktion oder Biomassezunahme abzüglich Verluste durch Absterben) lag mit 1.9 Mg ha^{-1} y^{-1} im typischen Bereich vergleichbarer tropischer Wälder. Die hohe Nettoprimärproduktion kann durch den hohen Anteil an gap-Fläche im unteren Bereich des Plots erklärt werden. Hohe Produktionswerte charakterisieren typische Sekundärwälder und Primärwälder mit einem höheren Anteil an gap-Areal.

Die Mortlitätsrate betrug 3.54 % y^{-1} für alle Individuen dbh ≥ 10 cm. Mortalität war ungleich über die Größenklassen verteilt. Höhere Raten traten in den niedrigeren Klassen auf. Beinahe 60 % aller ausgefallenen Individuen wiesen einen dbh unter 15 cm auf. Über die höheren Klassen verlief die Mortalität nahezu konstant. Die Einwuchsraten betrugen 1.29 % y^{-1} für alle Individuen dbh ≥ 10 cm.

Auf der Untersuchungsfläche wurden 232 Arten aus 59 Familien bestimmt. Die Palmen *Iriartea deltoidea* und *Welfia regia* wie auch die Clusiaceae *Symphonia globulifera* und *Marila laxiflora* sowie *Carapa guianensis* (Meliaceae) waren sehr häufig. Viele Unterwuchspflanzen sowie Besiedler von Störungsregimes, Arten der Familien Rubiaceae und Melastomataceae (eg. *Psychotria elata, Isertia laevis, Henriettea tuberculata*) traten ebenfalls ausgesprochen oft auf. Eine hohe Abundanz an Palmen ist charakteristisch für sehr humide Wälder sowie Bestände in denen Störungen häufig auftreten.

57 Arten traten nur mit einem Individuum auf.

Der Shannon-Wiener Index betrug H´= 6.427, Simpson Index ergab D = 0.035, der Simpson Diversitätsindex 1-D = 0.965 und Alpha Index betrug α = 59.699.

Die Familien mit dem höchsten FIVI waren die Arecaceae (33.846), Moraceae (26.648), Rubiaceae (22.134) und die Clusiaceae (19.075). Die Arten mit dem höchsten IVI waren *Welfia regia* (Arecaceae; 17.277), *Brosimum utile* (Moraceae; 16.432), *Carapa guianensis* (Meliaceae; 15.838) und *Iriartea deltoidea* (Arecaceae; 10.192).

Diese ausgesprochen hohe Diversität des Esquinas Regenwalds ist darauf zurückzuführen, dass hohe Niederschläge, keine ausgeprägte Trockenzeit, stark strukturierte Bestände sowie heterogene Böden dieses System charakterisieren.

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9 Appendices

Tab. 8.1. Number of Individuals per Species and Size Class

		´2-4.9	´5-9.9	´10-14.9	´15-19.9	´20-24.9	´25-29.9	´30-34.9	´35-39.9	´40-44.9	´45-49.9	´50-54.9	´55-59.9	´60-64.9	´65-69.9	´70-74.9	´75-79.9	´80-84.9	´85-89.9	´90-94.9	´95-99.9	´100-104.9	´105-109.9	´110-114.9	´115-119.9	´120-124.9	´125-129.9
Acanthaceae	*Aphelandra sp*	1																									
Anacardiaceae	*Tapirira myriantha*	12	2																								
Annonaceae	*Annona amazonica*			1																							
Annonaceae	*Cymbopetalum costaricense*	9	3																								
Annonaceae	*Guatteria amplifolia*	9	3				1																				
Annonaceae	*Guatteria chiriquiensis*				1																						
Annonaceae	*Guatteria recurvisepala*	3	3											1													
Annonaceae	*Rollinia pittieri*	6																									
Annonaceae	*Sp.1*	3																									
Annonaceae	*Unonopsis theobromifolia*		1																								
Apocynaceae	*Aspidosperma spruceanum*	14	4						1																		
Apocynaceae	*Lacmellea panamensis*				1	1																					
Apocynaceae	*Stemmadenia paulii*	18																									
Araliaceae	*Dendropanax arboreus*	15	7	1	2	1		2																			
Araliaceae	*Dendropanax caucanus*	1																									
Araliaceae	*Dendropanax cf. sessiliflorus*	1																									
Arecaceae	*Asterogyne ghiesbreghtiana*	1																									
Arecaceae	*Asterogyne maritiana*	47	15																								
Arecaceae	*Bactris hondurensis*	12	12																								
Arecaceae	*Calyptrogyne ghiesbreghtiana*	16																									
Arecaceae	*Chamaedorea matae*	1																									
Arecaceae	*Chrysophila guagara*		1																								
Arecaceae	*Euterpe macrospadix*	3																									
Arecaceae	*Euterpe precatoria*				2																						
Arecaceae	*Geonoma cuneata*	15																									
Arecaceae	*Iriartea deltoidea*	16	46	50	12																						
Arecaceae	*Oenocarpus mapora*	16	6	2																							
Arecaceae	*Socratea exorrhiza*	17	19	11	5																						
Arecaceae	*Welfia regia*	175	37	4	20	16	3																				
Bignoniaceae	*Amphitecna kennedyi*	7																									
Bombacaceae	*Bombacopsis sessilis*	4	1	1		1					1	2						1									
Burseraceae	*Protium aracouchini*	29	7		1																						
Burseraceae	*Protium costaricense*	5	4																								
Burseraceae	*Protium glabrum*	1																									
Burseraceae	*Protium panamense*	3	2		1	2	1				1		1														
Burseraceae	*Protium ravenii*	7	3	1																							
Burseraceae	*Tetragastris panamensis*	6	1																								
Burseraceae	*Trattinickia aspera*					1					1																
Caesalpiniaceae	*Copaifera camibar*	1	2									1				1											
Caesalpiniaceae	*Cynometra retusa*	3	1																								
Caesalpiniaceae	*Macrolobium hartshornii*	6	1									1															
Caesalpiniaceae	*Peltogyne purpurea*					1																					
Caesalpiniaceae	*Swartzia myrtifolia*	3																									
Cecropiaceae	*Cecropia obtusifolia*	9	2																								
Celastraceae	*Perottetia sessiliflora*	7																									
Chloranthaceae	*Hedyosmum scaberrimum*	6	1																								
Chrysobalanaceae	*Hirtella americana*	1																									
Chrysobalanaceae	*Hirtella lemsii*	3																									
Chrysobalanaceae	*Hirtella triandra*	2	1	2																							
Chrysobalanaceae	*Licania hypoleuca*	1	1																								
Chrysobalanaceae	*Licania operculipetala*	2	2	1																							
Chrysobalanaceae	*Licania sparsipilis*	4									1					1											
Chrysobalanaceae	*Licania Sp.*					1						3															
Clusiaceae	*Calophyllum longifolium*	15	2																								
Clusiaceae	*Calophyllum Sp.1*	1																									
Clusiaceae	*Chrysochlamis allenii*					4																					
Clusiaceae	*Chrysochlamis grandifolia*	15	1																								
Clusiaceae	*Clusia Sp.1*			1																							

Clusiaceae	*Clusia valerii*			1																							
Clusiaceae	*Garcinia intermedia*	1																									
Clusiaceae	*Garcinia madruno*	8	3	1	1		2																				
Clusiaceae	*Marila laxiflora*	20	3	2	6	3	2	5	2																		
Clusiaceae	*Symphonia globulifera*	10	9	4	5	2	1	5		1	2																
Clusiaceae	*Tovomita longifolia*	4	1				1			1																	
Clusiaceae	*Tovomita stylosa*	7	4																								
Clusiaceae	*Tovomita weddeliana*	9	2																								
Clusiaceae	*Tovomitopsis myrcioides*	2																									
Cyatheaceae	*Alsophila firma*	2	6																								
Cyatheaceae	*Cyathea delgadii*	4	5																								
Dichapetalaceae	*Stephanopodium costaricense*	6	2											1													
Dilleniaceae	*Doliocarpus hispidus*			1																							
Elaeocarpaceae	*Sloanea guianensis*	2	3																								
Elaeocarpaceae	*Sloanea sp.1*	3	1	1	2																						
Euphorbiaceae	*Croton schideanus*	29	7																								
Euphorbiaceae	*Drypetes standleyi*		1																								
Euphorbiaceae	*Euphorbia elata*	86																									
Euphorbiaceae	*Hyeronima sp.*	3																									
Euphorbiaceae	*Mabea occidentalis*	47	19	2	4	3	1																				
Euphorbiaceae	*Pausandra trianae*	10			3																						
Euphorbiaceae	*Richeria obovata*		1																								
Fabaceae	*Dussia discolor*				1													1									
Flacourtiaceae	*Carpotroche platyptera*	7	4																								
Flacourtiaceae	*Casearia arborea*	5																									
Flacourtiaceae	*Casearia sylvestris*	7	2																								
Flacourtiaceae	*Laetia procera*	2	1																								
Flacourtiaceae	*Pleuranthodendron lindenii*			1				1																			
Flacourtiaceae	*Tetrathylacium macrophyllum*	18	3	1																							
Hippocrateaceae	*Sp.1*			1																							
Humiriaceae	*Humiriastrum diguense*	3			3				1		1			1		1			1								
Icacinaceaea	*Discophora guianense*	3	2																								
Lacistemataceae	*Lacistema aggregatum*	1			1																						
Lauraceae	*Beilschmiedea pendula*	3					1																				
Lauraceae	*Nectandra umbrosa*	2	3																								
Lauraceae	*Ocotea insularis*	1																									
Lauraceae	*Ocotea nicaraguensis*	3	1																								
Lauraceae	*Ocotea rivularis*		1																								
Lauraceae	*Pleurothyrium golfodulcensis*	2			1																						
Lauraceae	*Pleurothyrum trianae*	1									1																
Lauraceae	*Sp.1*	3																									
Lecythidaceae	*Eschweilera integrifolia*	1																									
Lecythidaceae	*Grias cauliflora*	2					1	1																			
Lepidobotryaceae	*Ruptiliocarpon caracolito*	1							1	1				1													
Loganiaceae	*Strychnos peckii*	7																									
Magnoliaceae	*Talauma gloriensis*	2			2																						
Malphigiaceae	*Bunchosia corniflia*	1																									
Malphigiaceae	*Bunchosia macrophylla*	1																									
Malphigiaceae	*Byrsonima crispa*						1								1				1								
Melastomataceae	*Clidemia densiflora*	13																									
Melastomataceae	*Henriettea odorata*	14	4																								
Melastomataceae	*Henriettea Sp.1*			1	2	1																					
Melastomataceae	*Henriettea tuberculata*	106	37	2																							
Melastomataceae	*Leandra granatensis*	23	1																								
Melastomataceae	*Miconia centrodesma*	30																									
Melastomataceae	*Miconia cf argenata*	13																									
Melastomataceae	*Miconia Sp.1*	16	1																								
Melastomataceae	*Miconia Sp.2*	3																									
Melastomataceae	*Miconia sp.3*	1																									
Melastomataceae	*Miconia trinerva*	1		1																							
Melastomataceae	*Mouriri gleasoniana*	1	1	1																							
Meliaceae	*Carapa guanensis*	59	10	5	1	2		2		1			1	1				1	1		1			1			
Meliaceae	*Guarea grandifolia*	5		1	3	1	1			1																	
Meliaceae	*Guarea kunthiana*	2																									
Meliaceae	*Sp.1*	2	1																								
Meliaceae	*Trichilia martiana*									1						1											
Meliaceae	*Trichilia septentrionalis*	3	3	2	2																						
Mimosaceae	*Acacia allenii*	3	2	1																							
Mimosaceae	*Inga acuminata*	1																									
Mimosaceae	*Inga cf alba*	1																									
Mimosaceae	*Inga densiflora*	4	1																								
Mimosaceae	*Inga goldmannii*	1																									
Mimosaceae	*Inga marginata*	2																									
Mimosaceae	*Inga pezizifera*	1																									
Mimosaceae	*Inga polita*	1																									
Mimosaceae	*Inga sapindoides*	1						1																			
Mimosaceae	*Inga thibaudiana*	10	4																								
Mimosaceae	*Inga umbellifera*					1																					
Mimosaceae	*Inga venusta*	14	3																								
Mimosaceae	*Inga verrucosa*	1																									
Mimosaceae	*Inga Sp.1*						1																				
Mimosaceae	*Parkia pendula*				1																	1					
Mimosaceae	*Pithecellobium macradenium*				1						1																
Monimiaceae	*Mollinedia costaricensis*	1																									
Monimiaceae	*Siparuna pauciflora*	1																									
Moraceae	*Brosimum alicastrum*	12	14	1		1																					
Moraceae	*Brosimum costaricanum*	2																									

Moraceae	*Brosimum guianense*	4				3	1																				
Moraceae	*Brosimum lactescens*		1	1	2	2	1			1			1														
Moraceae	*Brosimum utile*	16	7	2		2	1	1	1	1	1		1				1				1	1		1			1
Moraceae	*Castilla tunu*				1																						
Moraceae	*Ficus nymphaeifolia*	1																									
Moraceae	*Ficus tonduzii*	1						1																			
Moraceae	*Maquira costaricana*	1	1																								
Moraceae	*Naucleopsis ulei*	13	1	1																							
Moraceae	*Perebea angustifolia*	3	1																								
Moraceae	*Perebea hispidula*	2		1	1																						
Moraceae	*Perebea xanthochyma*	2																									
Moraceae	*Sorocea affinis*		1			1																					
Moraceae	*Sorocea pubivena*	2																									
Myristicaceae	*Compsoneura sprucei*	36	13	1	2	3	1	1																			
Myristicaceae	*Otoba novogranatensis*	6	1	1	2	1	1				2		1														
Myristicaceae	*Virola guatemalensis*	1			1		1	1									1										
Myristicaceae	*Virola koschnii*	9	3						1			1															
Myristicaceae	*Virola sebifera*	9		1			1							1													
Myrsinaceae	*Ardisia compressa*	1			1	2																					
Myrsinaceae	*Ardisia dodgei*	7	5																								
Myrsinaceae	*Ardisia pittieri*	2																									
Myrsinaceae	*Parathesis aeruginosa*	10	2	5			1																				
Myrtaceae	*Calyptranthes chytraculia*	15	3		1	1																					
Myrtaceae	*Calyptranthes Sp. 1*	1																									
Myrtaceae	*Eugenia sp.*	12	7	1																							
Myrtaceae	*Myrcia Sp.*	1																									
Ochnaceae	*Ouratea lucens*	3																									
Olacaceae	*Chaunochiton kappleri*												1														
Olacaceae	*Minquartia guianensis*	2	1		1	1				1																	
Piperaceae	*Piper auritum*	7																									
Polygonaceae	*Coccoloba stanleyana*	1																									
Polygonaceae	*Cocoloba cf. acuminata*	1	1																								
Quiinaceae	*Lacunaria panamensis*			1																							
Quiinaceae	*Quiina schippii*	7	6		2	1																					
Rhizophoraceae	*Cassipourea elliptica*	7	5	1	1					1																	
Rubiaceae	*Boroja panamensis*	1																									
Rubiaceae	*Boroja patinoi*	3	1																								
Rubiaceae	*Chimarris latifolia*				1																						
Rubiaceae	*Chione silvicola*		1																								
Rubiaceae	*Duroja costaricensis*	17	1																								
Rubiaceae	*Faramea sessiflia*	35	4																								
Rubiaceae	*Gonzalagunia Sp.1*	1																									
Rubiaceae	*Isertia laevis*	3	2																								
Rubiaceae	*Pentagonia tinajita*	7																									
Rubiaceae	*Psychotria borucana*	10																									
Rubiaceae	*Psychotria capitata*	7	1																								
Rubiaceae	*Psychotria compressa*	3																									
Rubiaceae	*Psychotria elata*	173	11																								
Rubiaceae	*Psychotria officinalis*	62	3																								
Rubiaceae	*Psychotria poeppigiana*	2																									
Rubiaceae	*Psychotria solitudinum*	44	1																								
Rubiaceae	*Randia gentryi*	2	2																								
Rutaceae	*Zanthoxylum juniperinum*	1																									
Sabiaceae	*Meliosma grandiflora*	1		1		1	1		2																		
Sapindaceae	*Dilodendron Sp.1*	1																									
Sapindaceae	*Matayba ingifolia*	4		1																							
Sapindaceae	*Matayba oppositifolia*	2																									
Sapindaceae	*Talisia nervosa*					1			1																		
Sapindaceae	*Vouarana guianensis*					1																					
Sapotaceae	*Chrysophyllum colombianum*	2	2					2																			
Sapotaceae	*Elaeoluma glabrescens*	7	3	2	1	1		1		1		1									1						
Sapotaceae	*Micropholis melinoniana*	3	2		1	1	2																				
Sapotaceae	*Pouteria dasyadena*	1	3																								
Sapotaceae	*Pouteria durlandii*	12	7	1	1																						
Sapotaceae	*Pouteria foevolata*	3	3																								
Sapotaceae	*Pouteria laevigata*					1																					
Sapotaceae	*Pouteria reticulata*						1																				
Sapotaceae	*Pouteria torta*	11	4						1	1																	
Simaroubaceae	*Simaba cedron*	2																									
Simaroubaceae	*Simarouba amara*						1						1														
Sterculiaceae	*Sterculia recordiana*	4	1	1		2																					
Sterculiaceae	*Theobroma simiarum*	1			1	1																					
Theaceae	*Ternstroemia multiovulata*																	1									
Theophrastaceae	*Clavija costaricana*	1																									
Tiliaceae	*Apeiba membranacea*							1																			
Tiliaceae	*Apeiba tibourbou*	6	1																								
Ulmaceae	*Ampelocera macrocarpa*				1			1		1																	
Verbenaceae	*Tectoma grandis*	3																									
Violaceae	*Gloeospermum diversipetalum*	26		1																							
Violaceae	*Rinorea crenata*	3	1																								
Violaceae	*Rinorea dasyadena*	17	3	1	3	1		1																			
Vochysiaceae	*Qualea paraensis*	4	2																								
Vochysiaceae	*Vochysia ferruginea*	16	3				1	1	1																		
Vochysiaceae	*Vochysia guatemalensis*	1																									
Vochysiaceae	*Vochysia megalophylla*	3		2					1						1	1		1									
Vochysiaceae	*Vochysia Sp.1*		1																								

Tab. 11.2. Number of Individuals per Family and Size Class

	´2-4.9	´5-9.9	´10-14.9	´15-19.9	´20-24.9	´25-29.9	´30-34.9	´35-39.9	´40-44.9	´45-49.9	´50-54.9	´55-59.9	´60-64.9	´65-69.9	´70-74.9	´75-79.9	´80-84.9	´85-89.9	´90-94.9	´95-99.9	´100-104.9	´105-109.9	´110-114.9	´115-119.9	´120-124.9	´125-129.9
Acanthaceae	1																									
Anacardiaceae	12	2																								
Annonaceae	30	10	1	1		1							1													
Apocynaceae	32	4		1	1			1																		
Araliaceae	17	7	1	2	1		2																			
Arecaceae	319	136	67	39	16	3																				
Bignoniaceae	7																									
Bombacaceae	4	1	1		1					1	2						1									
Burseraceae	51	17	1	2	3	1				2		1														
Caesalpiniaceae	13	4			1						2				1											
Cecropiaceae	9	2																								
Celastraceae	7																									
Chloranthaceae	6	1																								
Chrysobalanaceae	13	4	3		1					1	3				1											
Clusiaceae	92	25	9	12	9	6	10	2	2	2																
Cyatheaceae	6	11																								
Dichapetalaceae	6	2											1													
Dilleniaceae			1																							
Elaeocarpaceae	5	4	1	2																						
Euphorbiaceae	175	28	2	7	3	1																				
Fabaceae				1													1									
Flacourtiaceae	39	10	2	1			1																			
Hippocrateaceae			1																							
Humiriaceae	3			3				1		1			1		1			1								
Icacinaceaea	3	2																								
Lacistemataceae	1																									
Lauraceae	15	5		1		1				1																
Lecythidaceae	3					1	1																			
Lepidobotryaceae	1							1	1				1													
Loganiaceae	7																									
Magnoliaceae	2			2																						
Malphigiaceae	2					1								1				1								
Melastomataceae	221	44	6	2	1																					
Meliaceae	71	14	8	6	3	1	2		3			1	1		1		1	1		1			1			
Mimosaceae	40	10	1	2	1	1	1			1											1					
Monimiaceae	2																									
Moraceae	59	26	6	4	9	3	2	1	2	1		2				1				1	1		1			1
Myristicaceae	61	17	3	5	4	4	2	1		2	1	1	1			1										
Myrsinaceae	20	7	5	1	2	1																				
Myrtaceae	29	10	1	1	1																					
Ochnaceae	3																									
Olacaceae	2	1		1	1				1			1														
Piperaceae	7																									
Polygonaceae	2	1																								
Quiinaceae	7	6	1	2	1																					
Rhizophoraceae	7	5	1	1					1																	
Rubiaceae	370	27		1																						
Rutaceae	1																									
Sabiaceae	1		1		1	1		2																		
Sapindaceae	7		1		2			1																		
Sapotaceae	39	24	3	3	3	3	3	1	2		1									1						
Simaroubaceae	2					1						1														
Sterculiaceae	5	1	1	1	3																					
Theaceae																	1									
Theophrastaceae	1																									
Tiliaceae	6	1					1																			
Ulmaceae				1			1		1																	
Verbenaceae	3																									
Violaceae	46	4	2	3	1		1																			
Vochysiaceae	24	6	2			1	1	2						1	1		1									

Tab. 11.3. Indices and Number of Diversity

	Dbh ≥ 2 cm 2001	**Dbh ≥ 10 cm 2001**	**Dbh ≥ 10 cm 1993**
Total Nr of Species	232	108	133
Total Nr of Families	59	43	50
Total Nr of Individuals	2849	453	527
Average dbh	7.0	24.8	23.5
Basal Area	38.7	35.9	35.5
Biomass	339	330	315
Shannon H´	6.427	5.693	4.119
Shannon J´ or Eveness (E)	1.18	1.21	0.84
Simpsons Diversity (D)	0.024	0.039	0.035
Simpsons Diversity (1/D)	41.3	25.9	28.6
Simpsons Diversity (1-D)	0.976	0.961	0.965
Alpha-Index	59.699	45.552	57.953
Mean Individuals per Species	12.28	4.19	3.93
Mean Species per Family	3.93	2.51	2.68
Nr of only one Individual per Species	57	42	66
Nr of Individuals of the most represented Species	255	62	71

10 Curriculum Vitae

Name: Wolfgang Prader

Date of birth: 27th of September 1973

Place of birth: Pinggau / Styria

Parents: Ilsa and Albrecht Prader

Education:

1980-1984	Pinggau, Primary school
1984-1988	Oberschützen, Secondary school
1988-1989	Oberschützen, High school
1989-1994	HTBLA Bruck/Mur (Höhere Bundeslehranstalt für Forstwirtschaft, Bruck/Mur), Technical High school
1998-2008	University of Vienna, Biology, Master degree (Mag.)
since 2003	Employment at Baxter AG