Structure and Dynamics of semi-evergreen and deciduous lowland forest in Bolivia

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Abstract

According to the Bolivian forestry law, Bolivian forests should be managed in a sustainable way. Yet, Bolivia is a country with four very diverse ecoregions and corresponding forest types. To fine tune forest management plans to local site conditions we should know how local environmental conditions affect forest structure and dynamics.

In this study I have compared the environmental conditions, forest structure and forest dynamics of two ecological regions in lowland Bolivia that are important for timber production; the dry Chiquitano forest, and the moist Transitional forest. Using a simplified path model, I have compared the effect of rainfall, soil texture and soil fertility on forest structure (basal area, tree height, stem density and crown exposure) and dynamics (increment, mortality and recruitment) for 20 1 ha plots.

The “moist” Transitional ecoregion and the “dry” Chiquitano ecoregion differed in annual rainfall, soil texture and soil fertility. The Transitional ecoregion had a higher annual rainfall, coarser texture and lower soil fertility. However these differences did not result in a large difference in structure or dynamics. The Chiquitano ecoregion had a higher basal area and higher fraction of emergent trees then in the Transitional ecoregion. The Transitional ecoregion had a higher diameter growth rate, but did not differ in mortality and recruitment rate. High variation within each ecoregion seemed to be the reason for this lack of significant difference.

A path analysis was carried out to evaluate how rainfall and soil characteristics influence each other, and how they influence forest structure and dynamics. To this end the soil characteristics were summarized using a principal component analysis. Rainfall had a negative effect on soil fertility, because high rainfall leads to more sandy soils due to runoff and infiltration, and lower soil fertility due to leaching. Forest structure was not affected by rainfall. Average tree height was the only forest structural variable that was affected by soils. A higher clay and silt content had a positive effect on tree height, and soil fertility had, unexpectedly a negative effect on tree height. Recruitment rate and diameter growth rate were positively affected by annual rainfall and soil fertility. Natural mortality was only positively affected by soil fertility.

In general, forest structure does not seem to be influenced by abiotic factors but could be the result of differences in species composition and long-term forest dynamics. Forest dynamics was positively influenced by rainfall and soil fertility. Higher dynamics leads to higher turnover and affects the forest structure over time. The negative effect of rainfall on soil fertility reduces the positive effect of rainfall on forest dynamics. Abundant rainfall could reduce dynamics as soon as soil fertility is too low for regeneration or growth.

Introduction

Bad forest management can lead to degradation of tropical forests. Bolivia implemented a forestry law in 1996 to prevent deforestation and serious degradation (Frederickson, 2003). According to this forestry law cutting cycles for all of Bolivia where set on a minimum of 20 years, because detailed data on tree growth rates were not available. Yet, Bolivia is a country with diverse ecoregions and forest types. Four ecological regions were distinguished on basis of maps of climates and vegetation; The Amazonian forest, Pre-Andean forest, Transition forest and Chiquitano dry forest (Killeen et al.1993, Navarro & Maldonado 2004). Most management plans promised to calculate cutting cycles for each ecoregion once data became available (Frederickson 2003). The aim of this study was to provide knowledge on forest structure and dynamics in different ecoregions to adapt forest management plans to local site conditions. To be able to do this we need to know how local environmental conditions affect forest structure and dynamics. According to Mahli et al. (2002) the three most important factors that determine forest productivity and dynamics are: 1. rainfall 2. light and 3. soil fertility.

Hall & Swaine (1981) state: “the distribution of forest types is largely determined by a complex of interacting environmental factors of which climate, geology and soils are the most important”.

In this study a comparison of structure and dynamics was made between two ecoregions with different rainfall and soil conditions in Bolivia, the dry Chiquitano forest, and the moist Transitional forest, that are important for timber production. The effect of rainfall, soil texture and fertility on forest structure (mean basal area, mean canopy height, mean stem density and average crown exposure) and dynamics (increment, mortality and recruitment) will be studied.

To do so the analysis was split up in three parts, in the first part the averages of structure, dynamics, and rainfall and soil fertility per ecoregion were determined. . The second part tested how rainfall affected soil texture and fertility as well as how soil texture affected soil fertility using summarized abiotic conditions. The third part analyzed how the summarized abiotic conditions (rainfall, soil texture and soil fertility) affect the structure and dynamics using a flow-diagram and looking at whether or not the results matched the hypotheses or gave answers to the formulated questions. By looking at the three parts I concluded how rainfall can affect soil and how these abiotic conditions can affect the structure and dynamics of Bolivian lowland forests

1. Theoretical Background

In this study two forest types were compared in which way they differed in forest structure and dynamics. Forest structure was characterized by average tree canopy height, tree density, and basal area and crown exposure on stand level and forest dynamics by the annual mortality, recruitment and increment rate. In the proposed model structure and dynamics are influenced only by rainfall, soil texture and soil fertility. In this section first the effect of rainfall on structure and dynamics and then the effect of soil fertility on structure and dynamics will be discussed. Finally, I will discuss the relation between the environmental factors; rainfall and soil fertility, and how these affect structure and dynamics

1.1. The effect of rainfall on forest structure and dynamics

Structure

In the tropics, water availability is the most important environmental factor that determines forest structure (Mahli et al. 2002). Water availability is determined by the amount of rainfall (mean annual rainfall), how it is distributed through time (duration of the dry period) and the water retaining capacity of soils.

The importance of rainfall for forest structure will decrease along the rainfall gradient, from being the limiting factor in the driest regions, towards a non-limiting factor in the wettest regions. In Ghana, basal area and height increase with an increasing precipitation (Swaine et al. 1990). Halfway the rain gradient, sufficient rainfall and high soil fertility resulted in the highest basal area and forest height (Hall & Swaine 1981). When rainfall becomes a non-limiting factor and soil fertility is low, stem density increases and height declines along the increasing rainfall as found in Colombia. (Faber-Langendoen & Gentry 1991).

The length of the dry season has a negative effect on water availability. Accordingly, the duration of the dry period has a negative effect on stem density in the Brazilian Amazon forest. (Vieira et al. 2004). The effect of water availability has two sides. When water availability increases, height and stem density increases. When water availability becomes abundant other environmental factors become limiting and forest height decreases. Stem density tends to increase which leads to a more closed canopy and therefore a low average crown exposure. Overall when rainfall, and hence, water availability, is the limiting factor then it tends to have a positive effect on forest height, stem density and basal area.

Dynamics

The direct effect of rainfall on forest growth has not been studied often (Schuur et al. 2001). In Ghana, low rainfall in dry forest resulted in similar tree diameter growth, mortality and recruitment rates as high rainfall in rain forest, probably because of higher soil fertility in dry areas (Swaine et al.1990). On the other hand, in Bolivia and Panama, forest dynamics increase with the increase of rainfall, as higher rainfall tends to lead to higher mortality, recruitment and growth (Dauber 2003, Condit et al. 2004, Dauber et al. 2005).

When the forest has a closed canopy, no light passes to the lower forest strata, which results in lower increment rate, mortality and recruitment, as found for pre-Andean forest in Bolivia (Dauber et al. 2005). Rain has a negative indirect effect on forest dynamics, through leaching rainfall lowers soil fertility, and hence, forest productivity. Highest values for dynamics in Bolivia have therefore been found half way the rain gradient in the Transitional forest (Dauber et al. 2005).This is in correspondence with what has been found for other tropical forests. In montane forest, on Hawaii, aboveground net primary productivity decreased with an increased mean annual precipitation (Schuur et al.

2001). This was because these forest were found in the wetter part of the rainfall gradient (2000-5000mm), where water availability is not limiting anywhere.

The influence of water availability on dynamics is positive (Figure 1: Flowchart with the effects of rainfall, soil texture and soil fertility on forest structure and dynamics. The upper boxes represent the abiotic characteristics. The lower on the left represent the structural characteristics and on the right the dynamics). Dynamics increases with increasing water availability, except for forest with a closed canopy. Those forests will have a low mean increment, mortality and recruitment rate, because light availability becomes a limiting factor.

1.2. The effect of soil fertility on forest structure and dynamics

Structure

Mahli et al. (2004) expect in absence of climatic constrains, that fertile soils will have higher productivity then poor soils. However, they did not have clear data to support those predictions. A study in Brazil pointed out a positive effect of soil fertility, especially nitrogen, on above ground biomass (Laurence et al.1999)

Also a wide spread study in the Neotropics found a positive relation between fertility and stem density and basal area of the different sites (DeWalt 2004)

In contrary to these findings, a study on rich volcanic soils in Costa Rica showed no clear effect of higher soil fertility on above ground biomass (Clark & Clark 2000) However amount of stems per ha decreased and with an equal basal area per ha it shows a shift from a lot relative thin trees o a few of thick trees. This could be a result of abundant nutrients.

Higher nutrient levels tend to expresses in higher stem densities (Swaine et al. 1990, Mahli et al. 2002). Overall soil fertility tends to have a positive effect on forest structure especially on stem density and average tree height (Figure 1).

Dynamics

Unfortunately, very little is known of the direct effect of soil fertility on forest dynamics. Phillips et al. (2004) found a clear positive relation between soil fertility, recruitment and mortality rates.

1.3. Interaction between rainfall and soil fertility

Hall & Swaine (1981) state: “the distribution of forest types is largely determined by a complex of interacting environmental factors of which climate, geology and soils are the most important”. They also mention an indirect effect of rainfall on soil nutrient levels. Variation in rainfall has an effect on pattern of primary production and nutrient cycles (Schuur et al. 2001). More rain leads to more leaching which leads to poorer and more acidic soils.

Leaching occurs when excessive rainfall can not be totally absorbed by soil and vegetation (Radulovich and Sollins 1991).The flow of the water drains to depths unreachable for the vegetation. Leached cations (from water-soluble nutrients) are replaced by H^+ which lowers the pH of soils. Most soils in the wet tropics are therefore more acidic. The reduced soil nutrient level partly will lead to a reduction in the growth of trees, and therefore also changes in structure and dynamics of a forest.

Structure

Combinations of rainfall and soil fertility determine forest structure as well. We expect to find the highest forest and basal area halfway the rain gradient. In Ghana the dry forests have low rainfall and high soil fertility, and a low canopy height (Swaine et al. 1990).

As earlier stated rainfall has a positive effect on forest height but due to excessive rainfall, leaching of soils occurs and less soil fertility suppresses forest height and basal area. (Hall & Swaine 1981). In Brazil, the site with the highest rainfall had the densest stand with a canopy of relatively the same height. Light penetration is therefore lower which had a negative effect on the understory growth (Viera et al. 2004) and therefore fewer understory trees.

Dynamics

Dry forests in of Ghana were found to have the same dynamics (mortality, recruitment, and tree diameter growth) as in wetter rain forests (Swaine et al. 1990). These dry forests had relatively high nutrient rich soils and higher stem density and short stature. Baker et al. (2003) evaluated the growth of two tree species in moist seasonal evergreen forest and moist semi-deciduous forest. They found a higher growth in the semi deciduous forest, because of higher soil fertility.

Apparently lower water availability had less effect on the growth of the semi-deciduous forest then lower nutrient availability had on the evergreen forest (Baker et al. 2003). Mahli et al (2002) expects that water availability is the first factor, in determining forest productivity and dynamics with radiation levels being the second factor and soil fertility as the third factor. Looking at the effect of rainfall on soil fertility is important to be able to see if rainfall has an even stronger effect on forest structure and dynamics. In the warm humid tropics, the high rainfall and high temperatures lead to rapid decomposition, and therefore leaching of nutrients from soils (Radulovich & Sollins 1991). This could be a reason why, in Ghana, basal area and stem size is highest halfway along the rainfall gradient and could be an explanation for the higher soil fertility in those relative dry forests than in areas where rainfall is even more abundant (Hall & Swaine 1981). In Columbia the soils with the highest rainfall also had the lowest soil fertility and showed higher dynamics and stem density (Faber-Langendoen & Gentry 1991).

Most forests with low mean annual rainfall have higher soil fertility (Swaine et al. 1990, Mahli et al. 2002) and forests with higher rainfall tend to have lower soil fertility levels (Baker et al. 2003) Since higher dynamics are found in areas with lower soil fertility and higher rainfall (Faber-Langendoen & Gentry 1991) and water is the most important abiotic factor influencing the growth and development (Mahli et al 2002) one could say that the established trees (trees in the canopy) have less problems coping with the low soil nutrient levels whereas most dynamics is originated from the trees beneath the canopy, with smaller root systems and less radiation due to the canopy

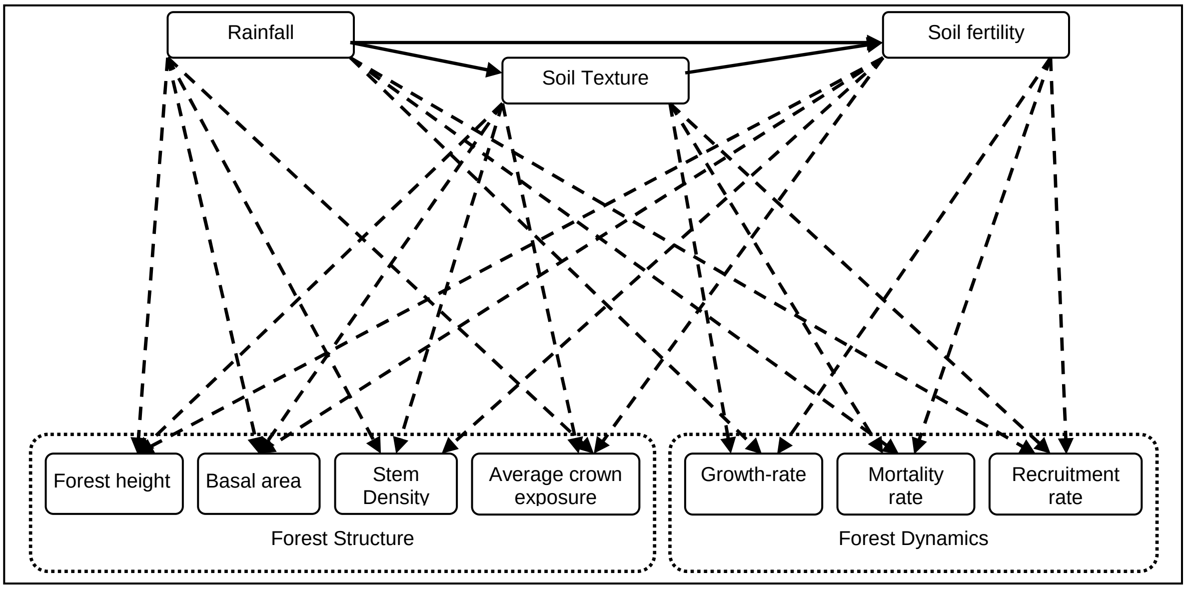

Figure 1: Flowchart with the effects of rainfall, soil texture and soil fertility on forest structure and dynamics. The upper boxes represent the abiotic characteristics. The lower on the left represent the structural characteristics and on the right the dynamics

1.4. Research questions and hypotheses

To fine tune a country wide management system to local site conditions, one needs to understand how forest structure and dynamics vary between ecological regions.

The main objective of this thesis was: To find out how Bolivian Transitional and Chiquitano forests differ in forest structure and dynamics and how annual rainfall and soil fertility determine these differences over a gradient, as shown in a simplified model (Figure 1).

The following questions have been formulated:

Q1: How do the two forest types differ in their abiotic conditions (rainfall, soil fertility)?
Q2: Do the two forest types differ in their structure in terms of canopy height, stem density, basal area and average crown exposure?
Q3 Do the two forest types differ in their dynamics in terms of growth-, mortality- and recruitment-rate?
Q4 What environmental variables are the best predictors of structure and dynamics?
Q5 Looking at rainfall as a gradient, how does this gradient influence the soil texture and soil fertility?
Q6 Is it possible to show the effects of abiotic factors on structure and dynamics simplified in a flowchart model and quantify these effects?

The first three questions have the following corresponding hypotheses:

H 1: Transitional forest will have a higher rainfall and shorter dry season because the position is closer to the equator. The Transitional forest will have lower soil fertility because of the high rainfall leads to an increased leaching of nutrients.

H 2: In the Transitional forest stem density will be higher because of more rainfall and a shorter dry period. Water availability will be higher and saplings will not have a lot of water stress, leading to a higher survival and tree density. Canopy height and basal area will be lower in the Transitional forest because of lower soil fertility.

H 3: In the Transitional forest there will be higher increment than in the Chiquitano forest. Higher rainfall increases stem density and hence the average crown exposure will be higher than in the Chiquitano forest, leading to reduced growth per stem but higher growth per ha. Because of higher rainfall there will be higher recruitment rates. Because of higher recruitment rates there will be more small stems, self thinning and therefore higher mortality rates.

2. Methodology

2.1. Study area

For this study a total of 20 permanent samples plots in six different forestry concessions located in two different Bolivian ecoregions in were measured and analyzed. Twelve of the plots were located in the Transitional Amazonian-Chiquitano region and 8 plots were located in the Chiquitano ecoregion (Figure 2). Location coordinates were documented in UTM coordinates retrieved with a GPS receiver (Table 1).

All plots lie in a seasonal climate with a dry, relative cold, period, and a wet and hot period. Dry periods are defined as amount of months with < 100mm rainfall per month. The Transitional ecoregion lies in the north east of the department of Santa Cruz between the wet Amazonian ecoregion and the dry Chiquitano ecoregion. It has an annual rainfall of 1200-1800 mm, a dry period of 3-5 months and an average temperature of 25 degrees C. The Chiquitano ecoregion is located in the south of the Department of Santa Cruz and has an annual rainfall of 1000-1500 mm, a dry period of 2-4 months, with an average temperature of 23 degrees C. The altitudes of the different plots lie between 200-400 m and 300-500 m respectively for the Transitional and Chiquitano ecoregions.

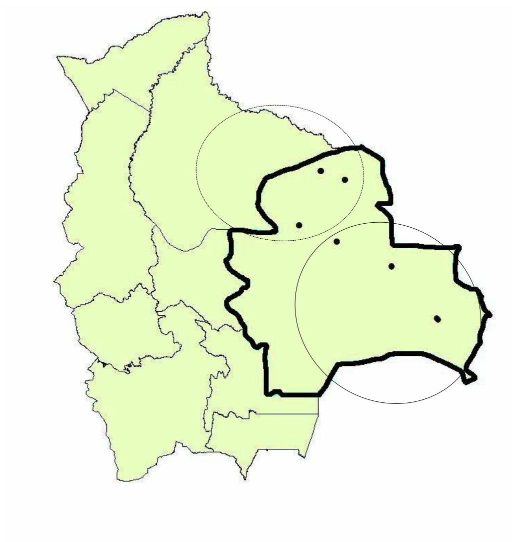

Figure 2: Location plots within Bolivia, thick black line is border of department of Santa Cruz, dashed circle: Transitional ecoregion and full circle Chiquitano ecoregion

The different plots lie on three different geological substrates. Lago Rey and Cibapa, both in the Transitional region are located on the Planycies north of the Brazilian shield. Cimal Velasco and Inpa, both Chiquitano ecoregion and La Chonta transitional ecoregion, on the Brazilian shield. Suto is situated on Cordilheiras de Chiquitano. The soils of the different plots have been classified (www.agteca.org) according to the FOA soil classification. Soils in Cibapa, Lago Rey and La Chonta are mainly Ortic ferrasols. Inpa and Cimal Velasco have mainly Ortic luvisols and Suto has Lithosols.

Table 1: Plot information, interval lengths are for all plots within each concession

Concession	GPS (UTM)		First measurement	First interval	Second interval	Third interval	Geological substrate	Soils (FOA)
	North	East		Years	Years	Years		
Cibapa	661258	8406160	03-12-2004	1,00	0,87		North of Brazilian shield	Ortic ferrasols
Cimal Velasco	798140	8137149	14-06-1998	2,10	1,97		Brazilian shield	Ortic luvisols
Inpa	636604	8214600	16-03-2003	1,02	1,01		Brazilian shield	Ortic luvisols
La Chonta	522887	8265427	15-02-2001	1,15	1,06	1,96	Brazilian shield	Ortic ferrasols
Lago Rey	589135	8435520	10-01-2005	1,75			North of Brazilian shield	Ortic ferrasols
Suto	295309	7973933	14-05-1999	4,43			Cordilheiras de Chiquitana.	Lithosols

2.2. Data gathering

In Bolivia the Bolivian Institute for Forestry Research (IBIF, Instituto Boliviano de Investigación Forestal) is the organization responsible for the monitoring the permanent sample plots of most Bolivian forest concessions. Most plots are established by the forestry companies themselves and now re-measured and maintained by IBIF.

Within the framework of this thesis 6 forest concessions were visited to re-measure permanent sample plots, 3 concessions per ecoregion. In the Chiquitano ecoregion eight one-hectare plots were re-measured in Suto (2 plots), Cimal Velasco (2 plots) and INPA (4 plot). In the Transitional ecoregion 12 plots were re-measured in concessions called: Cibapa (4 plots), La Chonta (4 plots) and Lago Rey (4 plots).

Two different kinds of permanent sample plots were used (experimental plots and conventional plots). The experimental plots are located in Inpa, La Chonta and Cibapa. These plots are between 20 and 27 ha and form part of the Long Term Silvicultural Research Project (LTSRP). Of these plots only the 1ha subplots from the "normal treatment" (conventional logging) were used. Both types of plots, conventional and experimental were 100 meters by 100 meters and were subdivided in subplots a grid of 20 meters by 20 meters (Table 3). At the intersection of the border of the plot and the subplots plastic tubes are placed to mark the border of the plot. Each subplot is given a coordinate code which is the same as the pole located in the south west of the subplot. In the (0,0) point a metal pin is placed in the ground to flag the plot for future measurements in case all other tubes/poles get lost. Experimental subplots have similar design as the conventional plots. The first measurement is carried out before logging. After logging plots are re-measured.

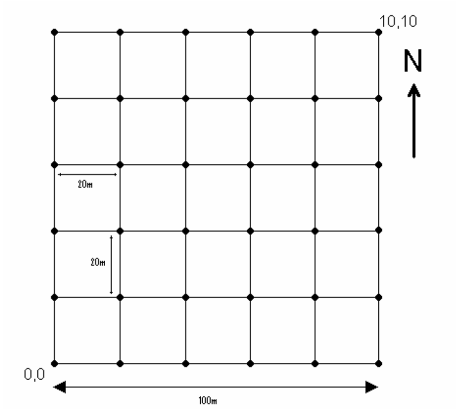

Figure 3: Technical drawing of conventional and experimental (1ha subplots) plots

Re-measurements of the plots have been done with a field team from IBIF. All measurement methods are extensively described in the National Network of permanent Plots working Protocol (Toledo et al. 2005).

The establishment and re-measurements within each concession are all done in the same season and year. At each measurement the date is recorded.

Tree measurements:

All trees ≥10 cm diameter in each plot have previously been mapped, measured, tagged and identified. Position of the tree within the plot has been estimated by giving it an x and y coordinate on a (100, 100) grid of 100 by 100 meters. Diameter at breast height (dbh) is measured with a diameter tape. In case of irregularities and/or buttresses the dbh is estimated at 3 meter above ground. For each tree the crown position is estimated. One should note that the rank number is the inverse of the Dawkins Index (Table 2) (Dawkins & field 1978). Height has been estimated from bottom to top of the crown in meters. Each tree has been recorded with a category code, to be able to see what has happened or in what state the tree was when measured (Table 3).

Table 2: Description crown exposure index

Inverse Dawkins code	Description crown exposure
1	Emergent: Crown is fully exposed to vertical light and free from lateral competition within a 90º inverted cone with the vertex at the base of the crown.
2	Full overhead light: the top part of the crown is fully exposed to vertical light but within the 90º inverted cone other crowns shade the crown.
3	Some overhead light: top part of the crown is only exposed to vertical light or some parts are shaded by other crowns.
4	Some lateral light. The top part of the crown is fully shaded and is located beneath the canopy crown but gets some lateral light due to gaps or edges in the canopy crown.
5	No light: tree is completely shaded by other tree crowns, no vertical or lateral light

Table 3: Codes describing state of recorded tree.

Code	Description
1	Living tree
2	Recruited tree
3	Tree has died due to natural causes
4	Tree has been logged
5	Tree has died due to logging
6	Tree cut down for other reason
7	Live but girdled tree
8	Tree that has disappeared
9	Tree forgotten during previous measurements
10	Tree that died due to girdling

Soil sampling and analysis:

Per plot 20 soil samples have been systematically collected using a soil drill colleting the upper 30 cm. Each plot has been divided in 25 subplots of 20 meters by 20 meters. In each line (five in total) of these subplots, soil has been taken in the middle of 4 out of the 5 subplots (Figure 3). Samples are taken without the litter layer. The 5 samples per plot were mixed and about one kilo of sub-sample was taken. 500 gram was used for the analysis; the remainder was stored in case a reanalysis was necessary. In some cases collecting soils in the middle of each subplot was not possible because of dense vegetation or fallen trees. In that case another point within the subplot was chosen, taking into account that the distance between the different soil sample points was as far as possible.

Soil samples have been analyzed by the Centro de Investigación Agrícola Tropical (CIAT-Santa Cruz). Soil samples were analyzed for the chemical soil characteristics; pH, organic matter content, N, P, exchangeable K, Na, Ca and Mg, electric conductivity and total nitrogen (N) content. The total exchangeable bases (TEB) were calculated as the sum of all exchangeable bases, Ca, Na, K and Mg. Also Cation exchange capacity (CEC) was measured, which is the total amount of positive cations held by the soil. This is the sum of the TEB and other positive charged cations (H^+, Al^{3+}). The CEC indicates the capacity of the soil to hold plant nutrient. From these figures the % base saturation was calculated as the fraction of TEB in CEC, i.e., the fraction of nutrients over the whole amount of cations. Acidity is the absolute difference between CEC and TEB giving the amount of acid cations bound to the soil. The C:N ratio was calculated from these data as the carbon content (C) divided by the recorded amount of nitrogen. The carbon content was estimated as the organic matter content divided by two. The texture of each soil sample was recorded as percentage of sand content (particles 2.0 to 0.05 mm), silt content (0.05 to 0.002mm) and clay content (particles < 0.002mm).

Data on soil substrate have been gathered from agrotechnologica amazonica (www.agteca.com). This organization provides soil and substrate data from the Amazon region. The provided shape files were combined with the plot shape file.

Climate data:

Climate data was obtained from a couple of sources. First the interpolated climate maps of Worldclim (www.worldclim.org) were used. This organization provides climatic data files and Arcgis shape files of the whole world combining climatic data from as many weather stations as possible and calculated averages for the 1960-90 period. However these interpolation maps were not accurate whereas big outliers in annual precipitation were presented. For example La Chonta, a wet concession with evergreen forest, came out as the driest site of all used concession this was probably because of recorded low rainfall. After examining the yearly data of the weather station Guarayos, a station not far from the La Chonta concession. For this station interpolation values were wrong, in the year 1970 the precipitation rose instantaneously from 900 mm in the sixties to 1500 mm in the seventies. Maybe the measurement equipment had been changed position or replaced.

To be able to have reliable climatic data (especially precipitation) other sources have been used. The institute agrotechnologica amazonica, (www.agteca.com) offers compiled data gathered by the NOAA satellite and information service. The NOAA satellite and information service gives the annual precipitation of weather stations in Bolivia, Brazil, Peru and Paraguay (Figure 4).

With the program Arcgis 9.1 an interpolation map was made. The interpolation method used was kringing with a first factor equation, which can be found in the Geo-statistical analyst toolbox in the program Arcgis 9.1. Further more all default settings have been used. For this thesis report I used the interpolated precipitation levels (Figure 5). Further fine tuning the interpolation maps would have required lots of expertise and time. However for the purpose of this study a general spread of the rainfall gradient was sufficient.

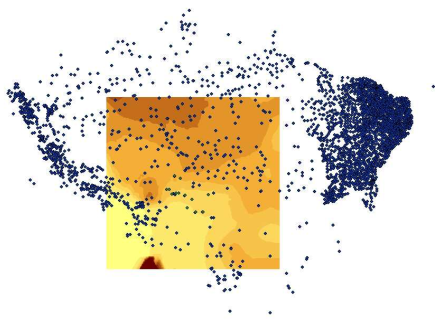

Figure 4: All weather stations from Bolivia, Peru and Brazil, Stations within the square were used for kringing interpolation

Worldclim could not be used to determine rainfall data for this study because of unreliable data. Originally not only rainfall but also temperature, length dry of season, rain deficit and perhumidity index were supposed to be used in the analysis. However because these data were also derived from Worldclim they were not used in this thesis. For future research it is recommended that the following climatic data be used instead of only annual rainfall.

Temperature: Mean maximum temperature, mean minimum temperature and diurnal temperature range could be gathered using interpolation maps.

Dry period: Dry period can be derived as the duration of the dry period in months per year. Months are regarded dry if the precipitation per months is less then twice the average temperature of that month.

Rain deficit: The rain deficit could be used to quantify the strength of the dry period and is calculated by summarizing the rain deficits (R-2T<0) of all months. Climatic diagrams can be made for each concession to visualize the rain and temperature differences per month.

Perhumidity index: To summarize the effect of dry and wet periods in the tropics Walsh (1996) has developed a Perhumidity index. It is calculated by giving each month a simple score depending on the mean monthly rainfall. Drought months (<50mm) get a -2 score, a dry month (50-99mm) gets a -1. All wet months (100-199 mm) get a 1 and very wet month (>200) get a 2. The first dry or drought months after a wet or very wet month get respectively -0,5 or -1,5 instead of -1 or -2. This way the different effect of two short dry periods or one strong dry period is put into account.

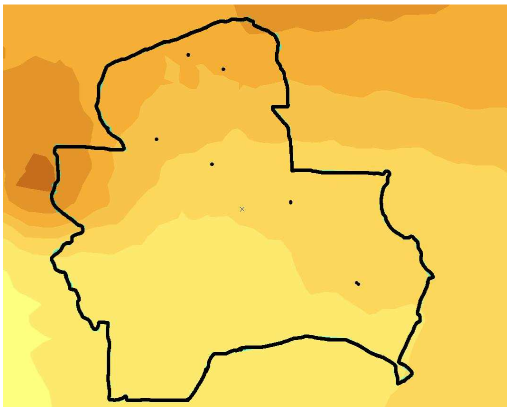

Figure 5: Map of department of Santa Cruz with the 6 concessions plotted from north to south: Lago Rey, Cibapa, La Chonta, INPA, Cimal Velasco, and Suto. Kringing interpolation with colour classes, with

2.3. Data analysis

The software packages Microsoft Excel and SPSS 12.0.1 were used for data analysis. Arcgis 9.0 has been used to make interpolation maps.

Structural variables

Structural characteristics were calculated from the first measurement, when plots were installed before cutting. For Cimal Velasco the second measurement was taken, because of the around 80 trees in each plot were forgotten with the first measurement (cat=9)

The population structure has been summarized as the slope of log number of trees per diameter class, versus the average diameter of that size class. Each diameter class contained all trees within a 10 cm diameter interval. (0-9 cm,10-19 cm, etc), plotted on a logarithmic scale.

Stem density is the amount of trees within each plot at the installation of the plot before logging. Tree height (HT) per plots is the average height of all trees at the installation of the plot. For each canopy position group the average height has been calculated. Also the fraction of all trees within each of the canopy position group ($HTCP_1$, $HTCP_2$, etc.) has been calculated. With the diameter at breast height (dbh) of each tree the basal area of each plot at every measurement has been calculated, as well the basal area for each tree class category.

Dynamics variables

Natural mortality rate (M_{nat}) is expressed as the fraction of trees lost per year and is calculated by the following formula (Sheil, 1995):

$$m = 1-(1- (N_0 -N_1)/N_0)1/t$$

With m= mortality rate in fraction per year, N_1= amount of trees after an interval, the maximum interval, N_0= the amount of tree at installation. t= interval length in years. (N_0 - N_1) can also be seen as amount of trees lost within the interval. Interval time was calculated per plot by calculating the number of days between two measurements and divide by 365 to gain an interval time in years.

For each plot N_0 is determined as all trees recorded with category 1 from the first measurement adding all trees that had been forgotten and were recorded in the second measurement with a category 9. For (N_0 -N_1) all trees recorded with category 3 (trees that have died due to natural causes) has been used. The different plots were measured with different frequencies and dates. To be able to compare the different dynamical characteristics of the different plots the total interval length between the first measurement and last measurement has been maximized, although some plots had longer measurement history (Table 1). Mortality and recruitment rates tend to become lower with longer intervals. (Sheil 1995).

Logging mortality rate (M_{log}) has been calculated using the formula for the natural mortality rate, but instead of (N_0 -N_1) now the amount of trees lost due to logging were used. All logged and extracted trees have been recorded with category 4, all trees that have died due to logging or management practice , like girdling have been recorded with category 5, 6, 10. The recruitment rate (K_{rec}) of the different plots has been calculated like mortality, with k for recruitment instead of m. For (N_0 -N_1) now all trees recorder with category 3, recruited trees, have been used.

Increment rate have been calculated in two ways; basal area growth (m^2/ha/year) and annual diameter growth (cm/year). Average diameter increment rate cm/year ($Incr_{cm}$) is the average increase of diameter per tree in cm per stand. This has been determined by plotting a line through the measured diameters per tree per year for each individual tree. The slope determines the average growth per year and averaging it for all measured trees calculates the average increment (cm/year). The increment in basal area ($Incr_{bas}$) has been calculated by subtracting the basal area of all trees not logged but which died due to logging trees or disappeared trees (cat. 4, 5, 6, 8,) of the first measurement by the last measurement and dividing it by the measurement interval.

Statistical analysis

A t-test was used to evaluate how the two ecoregions differed in climate and soil fertility, structure and dynamics, using the 20 1 ha plots as data points. Of each t-test a table was made with averages, standard errors and significance of climate and soil fertility variables per ecoregion. To evaluate the strength of the response, I calculated the ratio between the average values for the Chiquitano and Transitional ecological regions.

Soil and climatic variables were summarized using Principal Component Analysis (PCA). For the soil variables two PCA's were run, one on the chemical characteristics and one on the texture characteristics. For the PCA on the chemical characteristics TEB, C:N ratio and base saturation were not included, because these values were calculated from measured values of the soil samples. This way I prevented to use the same variables twice in the analysis. (TEB as a summarizing value of Na, Mg, Ca and K, C:N ratio calculated from organic mater content and nitrogen content and base saturation as the fraction value of the Cation Exchange Capacity.) By using a principal component analysis soil characteristics were summarized in 4 axes, Nutrient axis 1 (Nutr. 1), Nutrient axis 2 (Nutr. 2), Texture axis 1 and Texture axis 2.

The results of these two PCA's have been put into graphs. For each PCA an axis loading plot and an axis score plot has been made. In the axis loading plot (Figure 6 a,b) the different variables used to compose the axis were plotted against the summarized axes in order to see how the variables were associated amongst each other. To determine relations and influence of rainfall on the soil characteristics correlations were carried out between the different soil characteristics as well as between the soil axis and rainfall. Pearson correlations of each environmental variable (soil, rainfall, PCA axes) and the structure and dynamic variables were calculated. These are placed and shortly described into appendix 1 to provide more background information.

Forest structure and dynamics

In the appendix correlations on all variables are shown (Appendix 1, Table 2) and carried out to be able to determine and quantify the influence of structure and dynamics on each other. Scatter plots show the correlation between the different variables (Appendix 1).

Multiple Regression analysis (forward) was carried out on all soil and climatic characteristics for each variable to determine which characteristic(s) could explain the variation within variables and show which variable is the most important. This was also done on the six axes which summarize the abiotic characteristics to determine which of the axis and thus major group of abiotic factors could determine structure or dynamics.

By comparing the regressions it was possible to determine if summarizing the characteristics in the six axes with the PCA's brought out the same most influencing factors.

Path analysis

A path analysis was done by determining the regression values for each relation within the flowchart, presenting the simplified forest model on stand level. This was done by doing a multiple regression analyses (enter) on each structural and dynamical variable. The significant relations between rainfall and the summarized soil texture and soil fertility characteristics will be shown in the flow chart (Figure 1). The completed flowchart shows which and how strong the relations are between the abiotic characteristics and the forest structure and dynamics.

3. Results

3.1. Difference between ecoregions in abiotic conditions

Table 4: Abiotic characteristics: rainfall, textural and nutrient soil characteristics (mean ±se) of Transitional (n=12) and Chiquitano (n=8) forest plots. The ratio between Chiquitano and Transitional (C/T), as well as the significance (P) level of a t- test are given. * = p≤0.05, ** = p≤0.01, *** = p≤0.001, ns = non significant

	Transitional		Chiquitano			
	Mean	**se**	**Mean**	**se**	**C/T**	**p**
Rainfall (mm/year)	1603	14.71	1169	26.03	0.7	***
pH -	5.28	0.31	6.05	0.22	1.1	ns
Electronic Conductivity (µS cm-1)	70.8	7.06	87.1	13.05	1.2	ns
Ca (cmol kg -1)	2.83	0.78	8.00	1.64	2.8	*
Mg (cmol kg -1)	1.26	0.24	2.89	0.32	2.3	***
Na (cmol kg -1)	0.19	0.08	0.12	0.01	0.6	ns
K (cmol kg -1)	0.25	0.02	0.53	0.02	2.1	***
TEB (cmol kg -1)	4.4	1.02	10.8	1.81	2.4	**
CEC (cmol kg -1)	4.9	0.95	11.0	1.80	2.2	*
Base Saturation (%)	82.3	3.98	98.0	0.33	1.1	**
Acidity (cmol kg -1)	0.51	0.11	0.19	0.01	0.3	*
Al(cmol kg -1)	0.02	0.02	0.00	0.00	-	ns
P(mg Kg -1)	3.58	0.57	2.75	0.41	0.7	ns
OM (%)	2.53	0.15	4.20	0.22	1.6	***
N total (%)	0.21	0.02	0.28	0.02	1.3	**
C:N ratio	6.40	0.40	7.57	0.38	0.8	*
Sand (%)	61.7	3.38	49.5	2.71	0.8	**
Silt (%)	14.9	2.62	23.5	2.07	1.5	*
Clay (%)	24.3	2.70	27.0	1.20	1.1	ns

Rainfall differed significantly between the ecoregions; the Transitional ecoregion had significantly more rain then the Chiquitano ecoregion. Transitional and Chiquitano forest differ significantly in 12 out of 18 evaluated soil characteristics (Table 4). The Chiquitano forest had significantly higher Ca concentrations (2.8x), TEB (2.4x) Mg (2.3x) and CEC (2.2x). Transitional forest had a significantly higher acidity and percentage of sand. Silt content was lower in the Transitional forest. The two forest regions had a statistically similar pH, electric conductivity and phosphorus content. Exchangeable aluminum has only been found in one sample of the Transitional forest.

Summary of soil characteristics

To evaluate how soil variables are associated and to summarize them in fewer variables, two principle component analyses were done; one with soil chemical variables and one with soil texture variables (Table 5). Cation exchange capacity, acidity and C:N ratios were not included in this analysis, because fertility was already described by the cations, Mg, Na, K and Ca. All variables used for this PCA were actual measurements. C:N ratios are rough estimate which has been calculated based on the organic matter and nitrogen content, which both are already taken into account in the PCA and both are significant and very closely related to the first PCA axis.

To evaluate how soil characteristics are related with rainfall, rainfall is plotted afterwards into the loading plots of both nutrient and textural PCA

Table 5: Component matrix of chemical and textural soil characteristics. Correlations of the different soil variables and rainfall with the chemical and textural axis. Rainfall was not used in calculating the component matrix but added later.

Nutrient	Component	
	1	2
pH	0,859	0,338
E.C.	0,738	0,192
Ca	0,920	0,045
Mg	0,883	-0,140
Na	0,410	0,600
K	0,825	-0,524
P	0,448	0,753
OM %	0,744	-0,541
N total %	0,854	-0,115
Rainfall	-0,768	0,514

Texture	Component	
	1	2
Sand (%)	-1.00	0.01
Silt (%)	0.75	-0.65
Clay (%)	0.68	0.73
Rainfall	-0,57	0,36

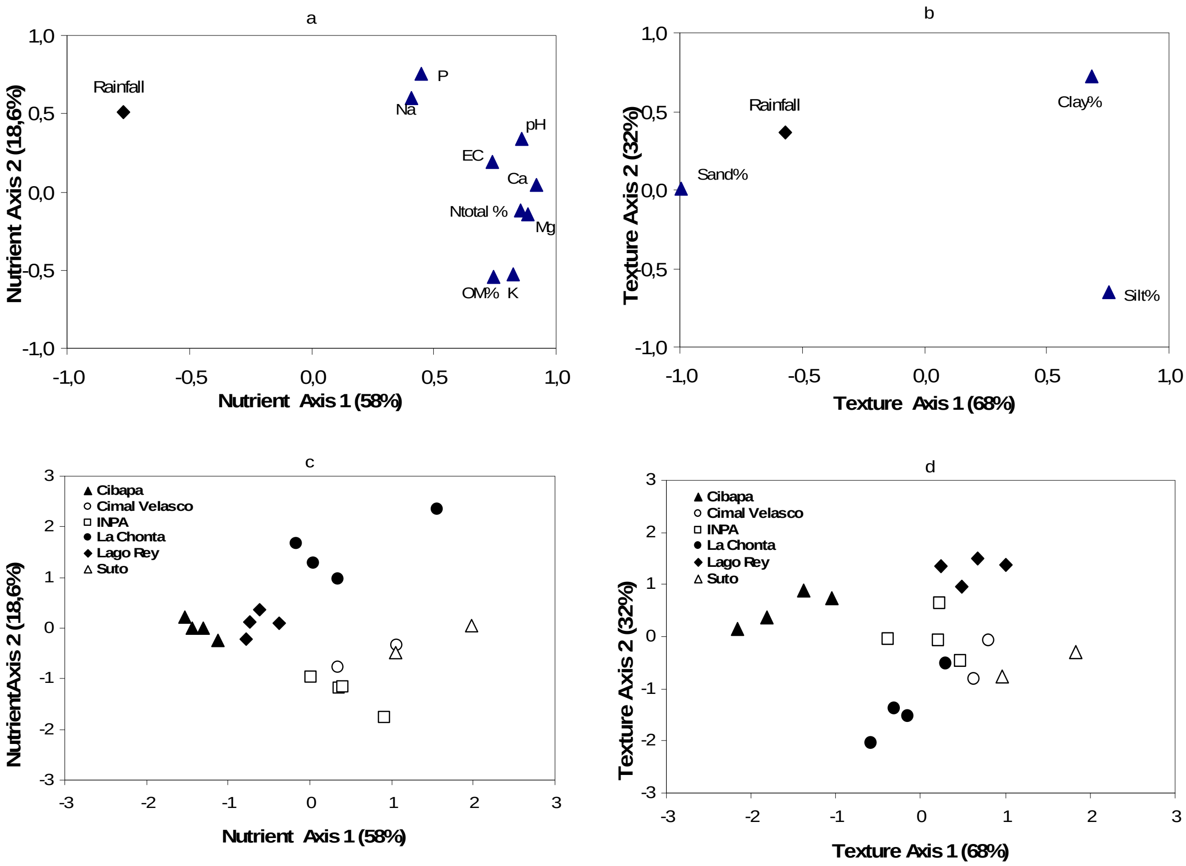

Figure 6: Results of PCA analysis: a) Axis-loading plot of chemical characteristics b) Axis-loading plot of textural characteristics. c) Axis-scores of sites plotted along the nutrient-axis; d) Axis-scores of sites plotted along the textural axis. Plot in the Transitional ecoregion are indicated with filled symbols, plots from the Chiquitano ecoregion with open symbols. Rainfall was not included in the analysis but plotted afterwards in the Axis-loading plots of both soil characteristics.

The PCA of the chemical soil characteristics resulted in two gradients. The first axis described 58% of the total variation, and correlated strongly and positively with Ca and N total %. The second axis described 15% of the variation and correlated positively with P and Na content, and negatively with OM and K (Figure 6,Table 5).

The PCA of textural characteristics produced 2 gradients. The first texture axis accounted for 68% of the variation and correlated negatively with percentage of sand. The second axis accounted for 32% of the variation and correlated positively with clay and negatively with silt (Figure 6b). The group with bigger cations like Na, P, and Mg are located on the right in the PCA space; acidity is located opposite of pH, indicating that there is a negative relation between acidity and the presence of cations.

Plots that belong to the same concession are more or less closely together in the PCA space. Transitional and Chiquitano forests occupy different positions in the chemical PCA space, with the Transitional forests having soils with higher acidity and the Chiquitano forests having soils with a higher fertility. Within the Transitional ecoregion La Chonta is an exception, having soils with high Na and P content.

Transitional and Chiquitano forests differ less clearly in textural characteristics. Transitional forests showed a large variation in soil texture characteristics, whereas Chiquitano forests were characterized by a low percentage of sand.

3.2. Difference in structure between in Chiquitano and Transitional forests

Table 6: Structural characteristics (mean ±SE) of Transitional (n=12) and Chiquitano (n=8) forest plots. The ratio between Chiquitano and Transitional (C/T), as well as the significance level (P) of a t-test are given. * p≤0.05, ** p≤0.01, *** p≤0.001, ns = non significant.

	Transitional		Chiquitano		T/C	P
	Mean	Se	Mean	se		
Basal Area (m^2 /ha)	17.0	0.76	19.7	0.76	0.86	*
Stem density (#/ha)	381.9	17.7	363.3	34.9	1.05	ns
Height (m)	12.4	0.49	13.4	0.37	0.93	ns
Slope (#/cm)	-0.018	0.002	-0.020	0.002	0.88	ns
$HeightCP_1$ (m)	18.4	0.65	18.8	0.54	0.98	ns
$HeightCP_2$ (m)	14.4	0.64	16.2	0.71	0.89	ns
CP_1 (%)	9.3	1.16	19.9	4.27	0.47	*
CP_2 (%)	21.3	2.84	15.4	1.27	1.39	ns
CP_3 (%)	33.9	3.74	24.2	2.29	1.40	ns
CP_4 (%)	23.2	1.84	21.8	5.86	1.07	ns
CP_5 (%)	7.12	2.19	5.82	1.75	1.22	ns
$CP_{average}$ (-)	2.98	0.07	2.70	0.19	1.10	ns

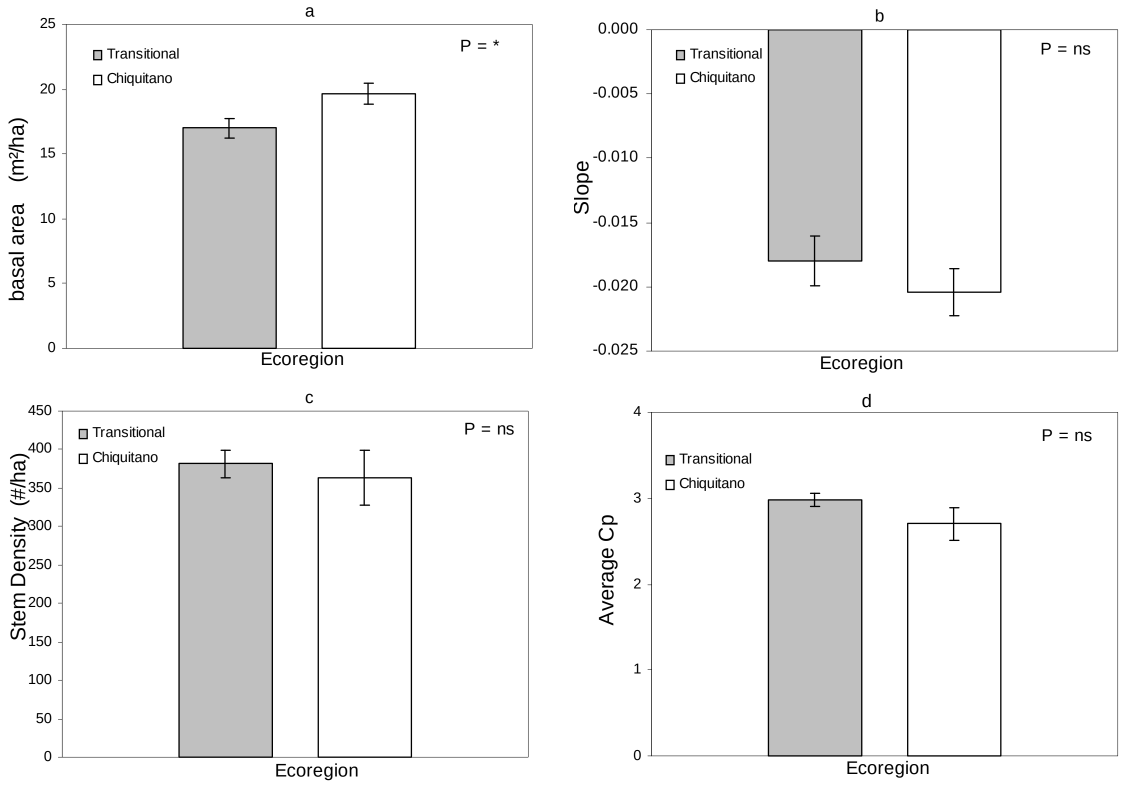

Figure 7: Bar graphs of structural characteristics (mean ±SE) of Transitional (n=12) and Chiquitano (n=8) forest plots. a) Basal area b) Slope c) Stem density d) Average CP.

Chiquitano forests have a significantly higher basal area and percentage of trees with crown position one (Table 6). The two ecoregions did not differ significantly in any of the other structure variables. The Transitional and Chiquitano forests had statistically similar stem densities, but especially the Chiquitano forest showed a large variation in these densities

3.3. Difference in dynamics between in Chiquitano and Transitional forests

Table 7: Dynamical characteristics (mean ±SE) of Transitional (n=12) and Chiquitano (n=8) forest plots. The ratio between Chiquitano and Transitional (C/T), as well as the significance level of a t-test are given. * p≤0.05, ** p≤0.01, *** p≤0.001, ns = non significant

	Transitional		Chiquitano		C/T	P
	Mean	**se**	**Mean**	**se**		
Mortality rate (natural) (% / year)	3.6	0.9	3.4	0.7	0.92	ns
Mortality rate (logging) (% / year)	1.4	0.7	0.7	0.3	0.52	ns
Recruitment rate (% / year)	1.4	1.0	0.5	0.4	0.33	ns
Increment (cm/year)	**0.397**	**0.021**	**0.176**	**0.019**	**0.44**	*******
Increment (m²/ha/year)	0.658	0.457	0.545	0.210	0.83	ns

Overall the Transitional forests had higher average values for the dynamical variables, although this was not significant. Due to high variation within each ecoregion significant differences didn't come out. Only the diameter increment rate was significantly different between the two ecoregions and higher for the Transitional region. The mean recruitment rate of the Transitional ecoregion was 3 times higher then the Chiquitano but not significant. There was not one single recruitment tree recorded in Lago Rey. This is probably a mistake.

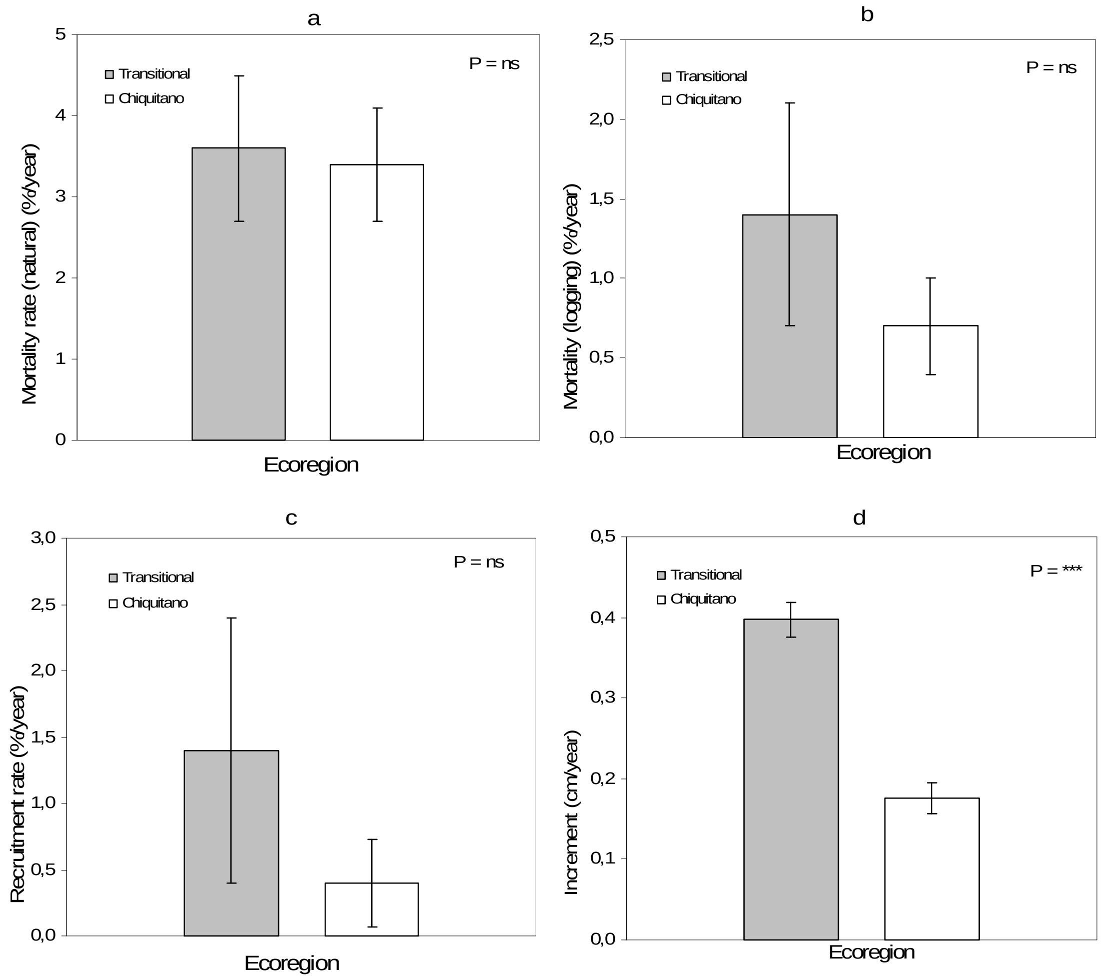

Figure 8: Bar graphs of forest dynamics (mean ±SE) of Transitional (n=12) and Chiquitano (n=8) forest plots. a) Natural mortality rate b) Logging related mortality rate c) Recruitment rate d) Basal area increment

3.4. What environmental variables are the best predictors of structure and dynamics analysis?

Table 8: Multiple forward regressions of structural and dynamical variables on soil and climatic variables. In each column the significant variables are given in the order in which they were included in the model. For each variable the regression coefficient (B), p-value and r^2 of the model are provided. * p≤0.05, ** p≤0.01, *** p≤0.001

Variables	First			Second			Third			r²	P
	Var 1	B	P	Var 2	B	P	Var 3	B	P		
Basal area (m²/ha)	K	10.15	**							0.33	**
Stem density (#/ha)	Ca	-15,88	***	N tot	684,54	*				0.49	**
Height (m)	Clay	0.14	***							0.49	***
Slope (#/cm)											
Height$_{CP1}$ (m)	P	-0.76	***							0.44	***
Height$_{CP2}$ (m)	Clay	0.18	**							0.36	**
Height$_{CP3}$ (m)	Clay	0.10	*							0.28	*
Height$_{CP4}$ (m)											
Height$_{CP5}$ (m)											
CP 1 (%)	TEB	3.01	***	EC	-0.169	*				0.79	***
CP 2 (%)											
CP 3 (%)	Base Sat.	-0.076	**	CEC	1.80	***	pH	-7.04	*	0.82	***
CP 4 (%)											
CP 5 (%)	Na	23.15	***							0.51	***
CP$_{avarage}$	CEC	-0.08	***	Na	0.80	*	N tot	2.97	*	0.64	***
Mortality (fraction /year) (natural)[1]	Base Sat.	2.09	***	Rainfall	0.84	**				0.56	***
Mortality (fraction /year) (logging)[1]	Mg	-7.22	***	N %	79,43	*				0.48	**
Recruitment (fraction /year)	P	5.72	**							0.50	***
Increment (cm/ha/year)	Rainfall	0.001	**	TEB	0.021	***	K	-0.473	*	0.88	***
Increment (m²/ha/year)[2]	Al	13.83	*							0.24	*

[1] Rates times 1000
[2] Regression without Al gives no model

A multiple forward regression was carried out in which structural and dynamical variables were regressed against all environmental characteristics. Structural variables were mostly affected by a combination of soil characteristics. Basal area was related with potassium within a model explaining 33 percent of the variation. Stem density showed a negative relation with calcium and positive relation with nitrogen. The vertical structure was mainly related to the clay content effecting height. Height of the canopy (Height, $HtCP_2$, $HtCP_3$) seem to be affected by clay content in the soil. The average height of the emergent trees (CP_1) were mostly explained by phosphorus.

The dynamical variables were influenced by a combination of rainfall and soil characteristics. The regression of diameter increment (m2/ha/year) was positively related with Al. This however is not a reliable result as only one of the twenty plots contained Al.

The model of recruitment explained 50% with only phosphorus as a variable. However, as stated earlier in one concession no recruitment had been measured.

The dynamical variables were predicted by very different variables. Only rainfall describes two dynamical variable, natural mortality and increment (cm/ha/year). Natural mortality was predicted by base saturation and rainfall explaining 56 % of the variation. Phosphorus had a positive relation on recruitment and explained 50 % of the variation. Increment (cm/ha/year) tends to increase with increasing rainfall and TEB and decrease with potassium content in the soil. 88% of the variation found in increment (cm/ha/year) was explained by these three variables (Table 8).

3.5. Path analysis

Table 9: Multiple enter regressions of structural and dynamical variables on soil and climatic variables. In each column the determining variables with decreasing explaining ability of the model. For each variable the regression coefficient, p value and r2 of the model are provided. * p≤0.05, ** p≤0.01, *** p≤0.001

Variables	Rainfall		Nutrient 1		Texture 1		r^2	P
	B	P	B	P	B	P		
Basal area (m^2/ha)	-0.52	ns	-0.26	ns	0.30	ns	0.30	ns
Stem density (#/ha)	0.11	ns	-0.36	ns	0.25	ns	0.11	ns
Height (m)	-0.48	ns	***-0.96***	**	***0.86***	**	***0.49***	*
Slope (#/cm)	0.63	ns	0.61	ns	0.08	ns	0.20	ns
HeightCP$_1$ (m)	-0.47	ns	-0.947	ns	0.44	ns	0.28	ns
HeightCP$_2$ (m)	-0.46	ns	***0.70***	*	***-0.81***	*	0.35	ns
HeightCP$_3$ (m)	-0.27	ns	-0.65	ns	***0.71***	*	0.29	ns
HeightCP$_4$ (m)	-0.18	ns	-0.47	ns	0.34	ns	0.08	ns
HeightCP$_5$ (m)	-0.54	ns	0.17	ns	-0.23	ns	0.23	ns
CP$_1$ (%)	***-0.60***	*	0.17	ns	0.84	ns	***0.59***	**
CP$_2$ (%)	0.28	ns	-0.38	ns	0.28	ns	0.22	ns
CP$_3$ (%)	-0.12	ns	-0.73	ns	0.11	ns	0.33	ns
CP$_4$ (%)	0.61	ns	0.62	ns	0.47	ns	0.06	ns
CP$_5$ (%)	0.52	ns	***1.01***	*	-0.52	ns	0.32	ns
CP$_{avarage}$	0.52	ns	0.40	ns	-0.40	ns	0.28	ns
Mortality (fraction /year) (natural)	0.52	ns	***0.86***	*	-0.21	ns	0.24	ns
Mortality(fraction /year) (logging)[1]	0.54	ns	0.27	ns	-0.26	ns	0.27	ns
Recruitment (fraction /year)	***0.63***	*	***1.24***	**	-0.49	ns	***0.47***	*
Increment (cm/ha/year)	***1.25***	***	***0.68***	**	-0.07	ns	***0.76***	***
Increment (m^2/ha/year)	-0.23	ns	-0.39	ns	0.07	ns	0.09	ns
Soil texture (texture axis 1) [2]	***-0.57***	**					***0.32***	**
Soil nutrients (nutrient axis 1) [3]	***-0.55***	**			***0.39***	*	***0.69***	***

[1] rates times 1000

[2] Regression analysis (enter) with Rainfall only

[3] Regression analysis (enter) with Rainfall and Soil texture (Text 1.)

No relations were found between basal area, stem density and the different axes. The effect of clay on the height of the canopy and other strata showed the average height had positive relations with texture axis 1 (Table 9, Appendix 1 Table 2). However the multiple regression also gave a negative relation between average height and nutrient axis 1.

This is opposite from the relation found from the height of trees located in the canopy (HtCP$_2$). Nutrients have a positive and texture axis one a negative influence on the height of the canopy trees. However this model is not significant as the model for the average height (including all measured trees) is significant. The height of the trees in the sub-canopy (HtCP$_3$) had a negative relation with silt content (Appendix 1 Table 2, Table 9).

The fraction of emergent trees (CP$_1$) is negatively affected by rainfall like also seen from the correlations (Appendix 1 Table 2, Table 9). The fraction of trees totally covered by the canopy (%CP$_5$) is strong positively influenced by nutrient axis 1.

Mortality (natural) is positively related by the nutrient levels in the soil.

Recruitment rate and increment (cm/ha/year) are positively influenced by rainfall and nutrient axis 1. Recruitment rates are most influenced by nutrient axis 1 and growth rate by rainfall (Table 9, Figure 9).

Soil texture is significantly predicted by rainfall. Soil nutrient content is predicted significantly with a model in which rainfall has a negative coefficient and soil texture (axis1) has a positive coefficient. (Table 9, Figure 9)

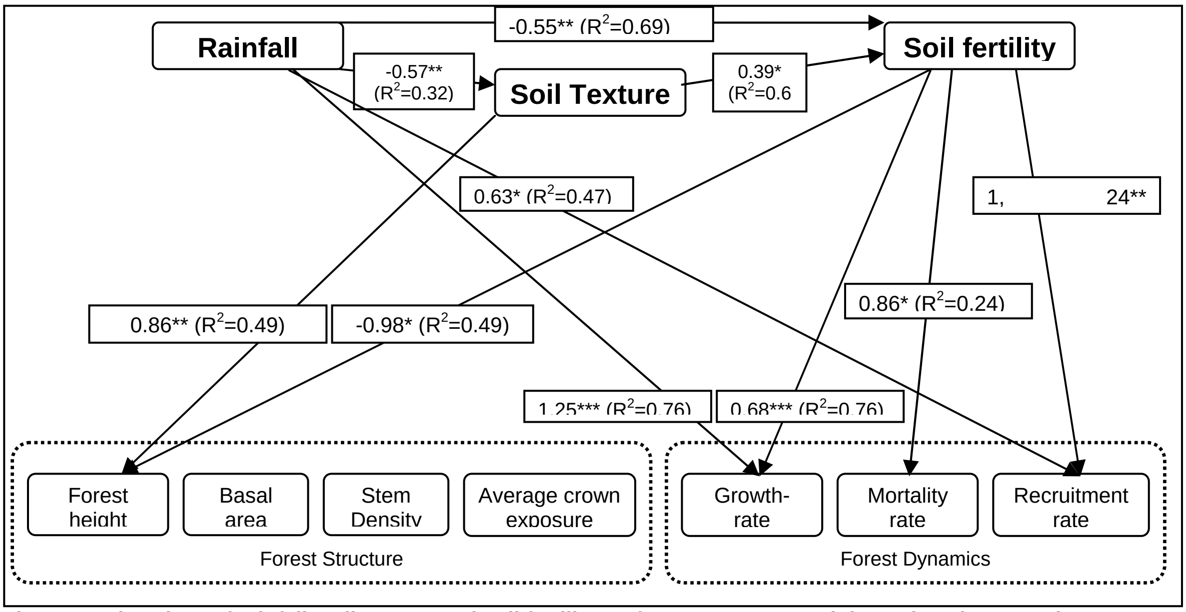

Figure 9: Flowchart of rainfall, soil texture and soil fertility on forest structure and dynamics The upper boxes represent the abiotic characteristics, The lower on the left represent the structural characteristics and on the right the dynamical characteristics of the forest. Each arrow represents the effect of each characteristic on the other. Within the boxes each significant variable the regression coefficient and R2 of the model are provided. * p≤0.05, ** p≤0.01, *** p≤0.001 (n=20)

4. Discussion

This discussion will address the answers to the 6 questions stated in the introduction. First I will discuss the differences found in rainfall, soil characteristics and forest structure and dynamics between the two ecoregions. Then what combination of abiotic variables can predict forest structure and dynamics. Finally, if and how the summarized abiotic factors influence one another and determine the structural and dynamical components of the forests. In the end the limitations of this study will be discussed and some recommendations will be given. In the discussion I will use the term "ecoregion" and "forest" interchangeably.

4.1. How do two forest types differ in their abiotic conditions (rainfall, soil texture, soil fertility)?

Difference in Rainfall between Transitional and Chiquitano forest

The two ecoregions differed significantly in rainfall. Higher rainfall was recorded in the Transitional ecoregion (Table 4). This was in accordance to the hypothesis, as the Transitional ecoregion lies more north and thus closer to the equator. This was also in correspondence with the rainfall map (Rafiqpoor, D. 2003). Although the two ecoregions differed in the total rainfall data for other important climatic characteristics such as distribution of rainfall throughout the year, were not available. Length and severity of the dry season are for example known to have a large influence on forest structure and dynamics (Takyu et al. 2005).

Difference in soil characteristics between Transitional and Chiquitano forests

I expected more coarse soil texture and lower soil fertility in the Transitional forest due to higher rainfall, and hence, nutrient and particle leaching. As predicted the Transitional forests had lower pH and soil nutrient levels (Ca, K, and Mg) and CEC but similar sodium content (Table 4). Gerold (2003) compared average soil characteristics over two regions with different rainfall in Bolivia and found lower pH and CEC for the wetter region as well.

Most studies found a positive relation between soil fertility and clay content (Gerold 2003, Laurence et al. 1999, Silver 2000). However, despite strong differences in soil fertility, the two forests did not differ significantly in clay content (Table 4). For soil texture the difference between the two types of forest lies in the silt and sand content. The Chiquitano forests had higher silt contents and the Transitional forests had higher sand contents.

In Brazil Silver et al. (2000) found a relationship between the texture of soils and the fertility of soils in terms of C, N, P and organic mater. Sandy soils tended to have more extractable phosphorus then clay soils which were in compliance with the soil averages of the Transitional and Chiquitano forest. In the Chiquitano forest higher organic mater content was found and thus higher C:N ratios. Together with less coarse soil texture (less sand, more silt and clay). Research done regarding the effect of acidification of soils found there was a decrease in Ca, Mg and K with increasing acidity (Tomlinson 2003). This was in correspondence with the difference between the two forest types. Overall one could say the soils in the Chiquitano ecoregion have higher fertility and the texture is finer then in the Transitional ecoregion (Table 4).

Gerold (2003) found ferrasols in the humid to semi-humid areas of eastern Bolivia. Similarly in the semi-humid to semi-arid Transitional region found Luvisols, Cambisols ad Nitrosols. This was in correspondence with the plots in the Transitional forests and in a large extent with the Chiquitano forests except Suto which lies geographically speaking the furthest south and on a different soil substrate (www.agteca.com).

Summarizing soil characteristics

I summarized the soil characteristics using a PCA. In the chemical PCA the plots of the different concessions were located close to each other and the Transitional and Chiquitano ecoregion were clearly separated in the PCA space (Figure 6a).

Within the Transitional ecoregion la Chonta is an exception because it is more fertile and it contained more sodium and phosphorus (Table 4). A large part (15%) of the soil in La Chonta has been classified as black soil (terra preta) (Peňa Claros et al. unpublished.). These soils contain more phosphorus and calcium, which is in compliance with the found values that I found in La Chonta (Figure 6a). The two ecological ecoregions were not clearly separated in the PCA space for soil texture. There was especially a lot of variation in the texture in the Transitional ecoregion, with higher sand content for Cipaba, higher clay content for Lago Rey and higher silt content for La Chonta. There was no clear explanation why these soil textures differ so much.

4.2. Do the two forest types differ in their structure in terms of canopy height, stem density, basal area and average crown position?

The structural differences between the two ecoregions were not as big as expected. The forest differed only significantly in their basal area and fraction of emergent trees which were higher for the Chiquitano forests (Table 6, Figure 7).

I expected a higher basal area in the Chiquitano ecoregion because this region had a higher soil fertility (Table 4). This hypothesis was indeed confirmed. Similarly in Brazil the above ground biomass increased with higher soil fertility, especially nitrogen (Laurence et al. 1999). Basal area was mainly determined by trees with big diameters and therefore strongly affected by the amount of emergent trees. The higher basal area in the Chiquitano region was in correspondence with the higher fraction of emergent trees in this region (Table 6). Mainly the fraction of emergent trees responds positively to an increase in soil fertility (Appendix 1, Table 2).

I expected more exposed crowns in the Chiquitano ecoregion, because a stronger dry season would lead to a low stem density and hence more exposed crowns in this region.

However the two ecoregions did not differ significantly in stem density nor crown position index. The Chiquitano ecoregion did have a higher proportion of emergent trees with a crown position score of one. This could be because the high soil fertility of the Chiquitano region gives rise to more emergent trees (see above), or because it is easier to estimate the crown position score in more open and deciduous forest. Tall trees in the Chiquitano appear to be emergent because it is easy to see the top of their deciduous crown, and therefore they receive a crown position score of 1, whereas tall trees in the Transitional ecoregion appear to be part of the canopy and not emergent, because people see only the bottom of the green crown, and therefore these receive a crown position score of 2.

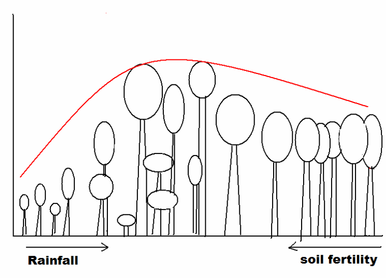

Figure 10: Negative effect of rainfall on soil fertility. Resulting in an increase and when abundant in a decline of stem density and height

I expected a lower average tree height and a lower canopy height in the Transitional forest, because of the lower soil fertility in this ecoregion (Hall & Swaine 1990, Faber Langendoen & Gentry 1991). However no significant height difference has been found.

Apparently the two ecoregions do not differ sufficiently in soil fertility to have a marked impact on tree height.

It could also be that the higher rainfall compensates for the lower soil fertility; If forest height showed a unimodal response to the combined rainfall/nutrient gradient then it could be that the Transitional and the Chiquitano ecoregion have the same height because the Chiquitano ecoregion could lie just left from the rainfall optimum and the Transitional ecoregion just to the right, resulting in the same tree height (Figure 7, Figure 10).

Another reason might be that systematic errors have been made in the estimates of tree height, because estimates were made in the dry season when the two forests differ in foliage cover. Due to foliage the presence of the trees in the evergreen Transitional ecoregion were underestimated because it is difficult to look through the foliage. In contrast most trees in the Chiquitano forest lost their foliage, so their height could be estimated correctly.

I expected higher tree densities in the Transitional ecoregion, because less water stress and shorter dry season would give saplings a better chance to survive, resulting in higher stem densities (Faber Langendoen & Gentry 1991). However the average amount of stems per ha were not significantly different. Apparently the two ecoregions and there different average rainfall were too similar to each other in terms of water availability.

4.3. Do the two forest types differ in their dynamics in terms of growth, mortality and recruitment rate?

I expected a higher natural mortality rate in the Transitional forest, because higher rainfall would lead to higher stem densities and lower soil fertility. More individual trees compete for fewer nutrients and shade each other. This will lead to higher mortality. However the two ecoregions did not differ significantly in their natural mortality rate. Stem densities were not significantly higher (Table 6) but soil fertility was lower in the Transitional ecoregion (Table 4). It could also be that the mortality rates do not differ, because in the Chiquitano forest drought or water stress could induce mortality as much as nutrient and light competition do in the Transitional ecoregion. I expected a higher recruitment rate in the Transitional ecoregion, because higher rainfall and shorter and less strong dry period would enhance the survival possibilities of saplings. However the recruitment rate did not differ significantly between ecoregions, one reason could be an error in the database. Lago Rey, one of the concessions located in the in the Transitional ecoregion, did not have one single recruited tree recorded. This must be a mistake in the data and it resulted in a large standard error for the recruitment estimate for the Transitional ecoregion (Table 7).

Mortality and recruitment were closely related, as higher mortality creates more gaps ideal for regeneration and therefore recruitment (Brokaw 1995, Baker et al. 2003). However, it is not possible to test for a direct effect by correlating both rates in this study. Time interval in which the recruitment rate was measured was short with a maximum of 4.4 years (Table 1). The time it takes for regeneration to become a part of the canopy in such a gap and taken into account as recruitment exceeds the time interval.

I expected lower diameter increment in the Transitional ecoregion because of canopy closure and less soil fertility. However, diameter increment rate was higher in the Transitional ecoregion (Table 7), probably because the shorter dry season in the Transitional ecoregion results in a longer growing period then in the Chiquitano ecoregion. Dauber et al. (2005) found higher increment levels in the Transitional ecoregion. Baker et al. (2003) studied the growth of two species in evergreen and semi-deciduous tropical forests in Ghana and found higher growth on the more fertile soil in semi-deciduous forest. They state that growing rates are also influenced by the tree species specialty in handling with environmental conditions. However, in this study there has been looked at growth at stand level. Species composition has not been taken into account.

I also expected higher growth expressed in basal area increment however, the increment rate in basal area (m2/ha/year) was not significantly different between the two ecoregions. Swaine et al. (1990) study comparing wet and dry forests in Ghana had similar results as to this study; both studies did not find higher tree increments in wetter forests. The reason why the increment rates in the two ecoregions were not significant in comparison to the significant higher diameter increment in the Transitional ecoregion could be caused by the significant higher proportion of emergent trees in the Chiquitano forest (Table 6). Basal area is comparatively formed by thicker trees. So even with a stronger growth in the Transitional ecoregion over all tree classes the growth expressed in basal area increment will show no significant difference. In short measurement periods, like in this study (Table 1), diameter increment rate measurements are more sensitive because the growth of the smaller classes is mainly in diameter and thicker trees show less diameter increment.

4.4. What environmental variables are the best predictors of structure and dynamics?

Structure

I used a multiple regression analysis to relate forest structure and dynamics to environmental variables (Table 8). Of the 15 structural variables, 10 variables were significantly related to soil characteristics, which explained between 28-82% of the variation in structure. Although it was expected that rainfall would influence structure positively, like higher basal area, stem density, height and crown position (cf. Hall & Swaine 1981, Swaine et al. 1990, Faber-Langendoen & Gentry 1991, Radulovich & Sollins 1991), none of the variables were explained by rainfall (Table 8).

Forest structure variables were related by a variety of soil characteristics. If a soil characteristic was related significant for several variables, then these were often related variables. For example, clay content was significantly related to several aspects of height (Average tree height, $HeightCP_2$, $HeightCP_3$. In Bolivia a positive relationship between height and clay content was found (Table 8). In contrast, Herrera et al. (1999) found in Costa Rica, using a correlation and forward multiple regression, a negative influence of clay content on the emergent trees of Vochysia ferruginea.

The fractions of each crown exposure class were mostly influenced by the abundance of cations (e.g. relations with TEB, CEC, base saturation and sodium). Basal area was related positively with potassium which was surprising. It was not expected that one single micronutrient would be related with basal area. However, in the Chiquitano region, more emergent trees and higher concentrations of potassium were found (Table 4, Table 6).

Stem density was related negatively with calcium and positive with nitrogen. Which is strange as it was expected that higher amount of nutrients would lead to higher stem densities (Swaine et al. 1990, Mahli et al. 2002, Dewalt et al. 2004)

Height of emergent trees, HtCP1, was related negatively with phosphorus (Table 8). The plots were located in two ecoregions, an evergreen and semi-deciduous one. As stated earlier, it could be that height has been under estimated in the evergreen plots due to foliage. Also species composition could have an influence in the height of the emergent trees.

Overall one could make the generalization, that soil “fertility” in general affects forest structure and most of the time positively. Forest height was affected by soil texture as well (Table 8). It could be that not the total amount of annual rainfall, but rather the duration and the strength of the dry season are causing the differences in forest dynamics and structure. Therefore rainfall is not significant but the spread throughout the year could be. Duration and severity of dry season have influences on sapling growth and therefore species composition. Species react differently on drought so the dry period influences structure as well (Poorter et al. 2000, Bunker et al. 2005).

Dynamics

Overall it can be concluded that rainfall and soil fertility together influence forest dynamics. The multiple regression analysis showed that all five dynamical variables were significantly related to environmental factors. The fitted models explained 24 to 88 % of the variance.

In contrast to forest structure, forest dynamics was often related with rainfall (Table 8). As expected annual rainfall and soil fertility had a positive influence on forest dynamics. Higher growth rates lead to dense and more closed vegetation, which lead to higher competition and mortality. Higher mortality leads to more gaps which create places for regeneration, and therefore lead to a higher recruitment rate. Again as expected more rainfall and higher soil fertility increase growth. Diameter Increment showed a positive effect of total cations (TEB) and rainfall but also a negative relation with the cation potassium. This could be a case of collinearity as potassium is included in TEB. So the model corrects a too strong relation of TEB with a negative coefficient for potassium (Table 6).

According to the multiple regression, increment rate in basal area was influenced positively by the aluminum content in the soil. However, there was only one plot with aluminum. If any, I would expect a negative influence of aluminum on increment, because of aluminum toxicity (Sanchez 1976). When aluminum was excluded from the regression analysis no significant model was found. It could be that the measurement interval was too short to be able to see significant differences in increment among these sites. Basal area increment could also be small because big trees tend to allocate their resources first to crown expansion, (in order to close the logging gap) and then in basal area growth. Therefore diameter increment, largely determined by the trees below the canopy could have been significant and basal area increment was not.

Natural mortality was positively related to base saturation and rainfall (Table 8). Rainfall had a positive influence on mortality, which showed that mortality from drought was a less important factor then the increase of dynamics leading to higher competition and therefore mortality. Both a higher rainfall and the fact that plots were harvested could lead to destabilization of trees and soil which leads to higher wind throw.

Recruitment rates were positive with phosphorus, this was as expected, because nutrient abundance is important for trees to be able to grow fast and rapidly recruit into larger diameter classes and phosphorus is often the limiting factor in tropical soils (Raaimakers et al. 1995).

Logging mortality was determined by human activity, but this human activity concentrates on trees that are harvestable. Apparently trees that have been harvested mostly were located on soils with less Mg and more nitrogen (Table 8). The more nitrogen in the soil, the faster trees grow and more growth means more harvestable trees.

4.5. Looking at rainfall as a gradient, how does this rainfall gradient influence soil texture and soil fertility?

An enter regression analysis was used to see how rainfall would relate and influence soil texture and soil fertility and how soil texture would relate to soil fertility. The regression analysis showed a significant negative relation, explaining between rainfall and soil texture, which was as expected; a higher rainfall leads to more coarse texture (Table 9), because small particle are washed away through runoff or infiltrated (Chow et al. 1995). Apparently the runoff and infiltration of smaller particles goes quicker then the weathering of the soil. Both rainfall and soil texture affected the amount of soil nutrients and explained 69% of the variation

Soil nutrient levels were negatively influenced by rainfall (-0.55**) and positively influenced by soil texture (0.39*). Soil fertility was more determined by rainfall then soil texture, as indicated by the standardized regression coefficients (Table 9).

4.6. Is it possible to show the effects of abiotic factors on structure and dynamics simplified in a flowchart model and quantify these effects?

Structure

I summarized many environmental variables with 3 PCA axes (rainfall, soil texture, soil fertility) and analyzed their effect on forest structure and dynamics using a simplified path model (Figure 9) According to the path analysis rainfall did not have any influence on forest structure. Forest height is the only structural variable that was significantly affected by soil texture and soil fertility according to the multiple regression (Figure 9, Table 9). Positive relations were expected. Soil texture had a positive relation indicating higher average tree height on soils containing more silt and clay. However, soil fertility had a negative (-0.98*) direct effect on forest height. This was in contrast with the prediction of a positive effect of soil fertility on average tree height (Hall & Swaine 1981). It is not really explainable how the negative effect of soil fertility on average tree height came out. The hypothesis was focused on the canopy height instead of average tree height. However the average tree height was used for the regression analysis. The average height per tree is influenced by a great amount of lower trees (CP_3, CP_4, CP_5) and does not indicated the height of the canopy. However we found a positive influence of soil nutrients on the height of trees that had their crowns in the canopy (CP_2) (Table 9).

However other structural variables (basal are, stem density, average crown position) were not explained by the models constructed by the three abiotic variables. It could be that disturbances have a great influence on the current forest structure and overrule the more subtle effects of rain and soils. Or the difference in rainfall, soil texture and soil fertility between the twenty plots is not large enough to have a significant effect on forest structure. In this study species composition was not looked at. However this could determine structure as well. The plots located in the “wet” Transitional ecoregions palm species were more abundant then in the “dry” Chiquitano. Palms do not have large basal area and therefore suppress the basal area per stand.

Dynamics

I expected a positive effect of rainfall and soil fertility on the forest dynamics of the plots. Higher fertility and rainfall should increase growth and therefore competition for light. Life cycles of trees should be shorter, leading to higher mortality, higher gap creation and regeneration.

The strongest relation of rainfall and soil fertility with a dynamical variable was with growth rate. I have used diameter increment for growth rate, which has a stronger relation with the trees in the lower strata and shows therefore a clearer image of the growth of the whole tree population. The model explained 76 % of the variation of growth rates found between the 20 plots. Rainfall had a stronger relation with tree growth than nutrients and were both positive (Table 9).

It seems logical that nutrients and rainfall have a positive effect on the growth. As these abiotic growing conditions are with light the most limiting factors for tree growth (Mahli et al. 2002). Mortality showed a positive relation with nutrients. At very low nutrient availability one would expect more mortality because nutrient starved trees can not survive. However in the study areas the nutrient levels were not that low and more nutrients lead to higher growth, faster completion of lifespan and therefore faster turnover. The mortality could increase with nutrient availability because fast growth leads to more recruitment (this can also be seen from the strong relation nutrient availability has with recruitment rate (Table 9)) and more trees leads to a denser stand (This is also shown by the positive regression coefficient between nutrient availability and percentage of trees below the canopy (CP_5)). This leads to thinning mortality due to competition. This competition gets even stronger when more trees are able to survive the sapling stage and reach the critical 10 cm dbh stage.

In comparison with the effect of rainfall nutrients and texture, dynamics responded more as expected. This is not strange as forest dynamics are directly influenced by the environmental variables which are measured over the same time period as the dynamics (Table 1). Forest structure is more directly influenced by forest dynamics and thus indirectly affected by the measured abiotic factors. Forest structure is a result of dynamics throughout the years, environmental and human influences.

4.7. Limitations

This study has several limitations. The plots are not equally divided over the two ecoregions ($n_{transitional}$=12 and $n_{chiquitano}$=8) and the total amount of plots is small and could lead to misleading estimates of averages forest conditions in the regions.

Three of the 6 forestry concessions contain experimental plots; the remainders contain conventional logging plots. The four plots used from each one of these concessions lie within a square of 500 by 500 meter. So Twelve out of the 20 plots are located within experimental plots and because of the low resolution (5 min) of the rainfall interpolation map, the rainfall data are exactly the same for each concessions, which reduced the total amount of plots that can be compared to six concessions. There has to be stated that in this study only rainfall as climatic variable has been used. Temperature, radiation, spread of rain throughout the year are important as well but could unfortunately but not included due to the lack of reliable data. Rainfall data has been acquired by making an interpolation map from a climatic data base. This interpolation has been done without the exact knowledge of making interpolation maps. The rainfall data was gathered by using interpolated climatic maps using data from metrological stations. This could give a wrong image of the actual climate within the forests as interpolations are statistical methods that do not take into account local variables.

Data collection was done by different persons for different plots which can lead to structural estimate errors. The tree heights tend to be underestimated, because they were not measured but estimated by eye. Another confounding factor was that plot measurements are made in the dry season, when it was possible to enter the forest. In the dry season the canopy in the Chiquitano ecoregion is deciduous because of the long and severe dry season. Therefore difference between estimates of height and canopy crown position of the evergreen Transitional plots and Chiquitano plots may occur, because height and crown position of trees without leaves easily can be overestimated in comparison to trees with there foliage.

5. Conclusion

The two ecoregions differ from each other in abiotic factors, rainfall and soil fertility, which were all found to be higher in the Transitional forests. Also the soil structure differed as the soil in the Transitional forest contained more sand in comparison to the soils in the Chiquitano forest. Although these differences were found in abiotic factors the comparison of the two forests on structure and dynamics did not show many differences. Structure basal area and average height of the crown ($HtCP_2$) were found to be higher in the Chiquitano forest. For dynamics only diameter increment was different between the two ecoregions.

The strong negative impact of rainfall on the soil texture implies that more rain washes away the smaller soil particles. However, percentage of clay in the soil was not affected. Nutrient level tends to be higher in soils with more silt then sand which shows the indirect effect of rainfall on soil fertility.

By looking at the plots as a gradient instead of averages of ecoregions showed there was quite a large influence of rainfall on soil fertility and soil texture. These factors together explained to a large extent the dynamics within each forest. Forest structure could not be explained satisfactorily through the found rainfall and soil characteristics. Soil fertility and rainfall have a bigger influence on forest dynamics then forest structure. Overall dynamics increased with more available nutrients and rainfall. In order to get better insight in this matter, more plots over a wider gradient should be used. To be able to see how abiotic factors influence forest it is important to include more climatic variables, such as seasonality and temperatures. It would also be interesting to examine how species composition influences forest structure and dynamics as many species are specialized to be able benefit optimal from the abiotic conditions in their region.

This study was too small to be able to tell something about the length of sustainable cutting cycles. However in the forest I have seen the removal of the commercial species leaving almost no trees for the next cutting cycles. Either more species should be used for commercial purposes or else cutting yields will drop.

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