

# Investigations on tree species suitable for the recultivation of degraded land areas in Central Amazonia

(SHIFT project BMBF 0339638A / CNPq ENV 42-2)

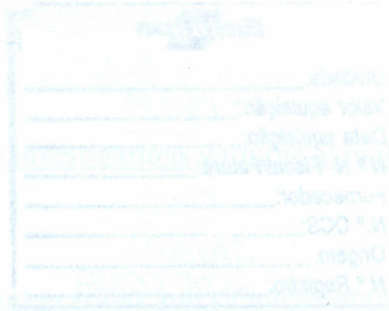
From May 1, 1998 to April 30, 2001

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## Annual Report 1999

(From January 1, 1999 to December 31, 1999)

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## **1. Introduction and approach of the second phase of the project**

Due to the strong demand for sustainable wood production in the Amazon, since 1995 investigations on suitable tree species for wood production in plantations on the „terra firme“ of the Central Amazon are carried out within the SHIFT project 0339638 A/ENV 42. The study is carried out at the experimental site of EMBRAPA Amazonia Ocidental, located 29 km out of the city of Manaus.

In this study the site conditions (nutrient supply of the soil, water supply of the trees, light) of a traditional monoculture plantation are compared with the site conditions of mixed plantations. The study is carried out from the period of site preparation until an age of 8 years.

As to determine the site demands of eight important native tree species of the Amazon (*Swietenia macrophylla*, *Carapa guianensis*, *Cedrela odorata*, *Dipteryx odorata*, *Hymenaea courbaril*, *Ceiba pentandra*, *Virola surinamensis*, *Tabebuia heptaphylla*) the influence of light, the water supply and the nutrient supply of the soil on the growth dynamics of the trees is studied.

The results obtained during the first phase of the project were published in 1999 in 9 individual contributions within the series „Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft“, Hamburg (comp. chapter 5).

As to get stronger correlations between the site conditions and the growth of the plantation grown trees, during the second phase of the project (since May 1998) the investigations were extended to the subsequent aspects:

- (1) The significance of exogenous factors for the plant metabolism and with that for wood formation and wood quality. For this purpose in 1999 the **water and carbohydrate** supply of the trees was studied in more detail. As to prove the results obtained in the field, supplementary experiments were carried out under controlled conditions in the greenhouse and in growth chambers (comp. 2.1).
- (2) Besides exogenous factors genetic (endogenous) factors influence tree growth, wood formation, and with that wood quality. Therefore in the second phase of the project comparative studies on the relationship of exogenous input and tree growth were carried with different **seed provenances**.

The concept of the project ENV 42 is part of the interdisciplinary research program SHIFT (Studies on human impact on forests and floodplains in the tropics) at the EMBRAPA Amazonia Ocidental in Manaus. There are tight links to ENV 23 (comp. Schmidt et al. 1999, Preisinger et al. 1999), ENV 45 (comp. Dünisch et al. 1999) and ENV 52 (comp. chapter 5).

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## 2. Investigations carried out in 1999 and scientific results

### 2.3. Overview over the project activities in 1999

*Water supply of the trees:* Besides the quantification of water fluxes in the plantations (comp. Dünisch et al 1999a) studies on the relationship between the water potential of the soil, the stem and leaf of the trees and the atmosphere are of main interest as to study in how far the investigated tree species are adapted to drier periods. For this purpose in 1999 xylem water flux measurements of *Swietenia macrophylla*, *Carapa guianensis* and *Cedrela odorata* and meteorological measurements at the leaf-atmosphere interface of the trees were intensified (6 months research stay of Thorsten Eilers in Manaus). As to study the water potential of the leaves, pressure bomb measurements were carried during wet and dry periods.

In December 1999 Ronaldo Marais extended these studies to *Dipteryx odorata* and *Bertholletia excelsa* (PhD thesis INPA, Manaus, financial support: PhD grant CNPq, Brasilia and BMBF, Bonn, cooperation: EMBRAPA, Manaus, INPA, Manaus, University of Hamburg).

*Carbohydrate supply of the trees:* In 1999 the seasonal variation of the reserve carbohydrate content of *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea*, the content of soluble sugar (glucose, fructose, sucrose, raffinose, stachyose) and starch of the leaves, the phloem of the stem, the xylem of the stem and of the roots was monthly quantified. Sample collection was carried out from 1998 until September 1999. Sample preparation and carbohydrate analyses are carried out in cooperation with the Institute of Wood Chemistry, Federal Research Center for Forestry and Forest Products, Hamburg (results will be presented on the workshop in September 2000 in Hamburg).

The relationship between the light intensity and the net photosynthesis of selected species is studied under growth chamber conditions in cooperation with the Institute of World Forestry in Hamburg. As to get some information on the photosynthetic activity of the trees under field conditions, besides the water and element supply of the trees, the light intensity is registered in the plantation systems (results will be presented on the workshop in September 2000 in Hamburg).

*Seed provenances:* As to study the influence of genetic factors on the growth dynamics of *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea*, seed provenances were sampled in the state of Amazonas, Para, Roraima, and Mato Grosso. Germination was carried out in the greenhouse of the EMBRAPA in Manaus. 25 plants of each provenance were planted in April/May 1999 at the experimental site of the EMBRAPA in Manaus and a more fertile site in Mato Grosso (exploited area in a primary forest near the city of Aripuana). The water and nutrient content as well as the content of reserve carbohydrates of the plants is monitored during a wet and a dry period. In addition the height and diameter increment of the plants are measured

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twice a year (first results will be presented on the workshop in September 2000 in Hamburg).

*Wood quality:* For the study of wood properties of plantation grown trees a case study on the anatomical structure and mechanical properties of *Hymenaea* was carried out by Claudene Atayde (Maestrado thesis INPA, Manaus, will be finished in March 2000). In addition the heartwood formation and the durability of the wood of plantation grown *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea* was studied (ongoing, results will be presented at the workshop in September 2000 in Hamburg).

## **2.2. Scientific results**

After five years of experiments the investigations on (1) the biomass production and nutrition of 5 plantation grown tree species, (2) the comparison of nutrient fluxes and growth dynamics of *Carapa guianensis* grown in monoculture and enrichment plantations, and (3) the study of cambial growth dynamics of 3 selected *Meliaceae* were terminated. In 1999 the data evaluation was carried out and the main aspects are summarized below.

### **2.2.1. Biomass, nutrient stocks, and nutrient fluxes in monoculture plots of 5 plantation grown tree species for wood production**

#### **Introduction**

In urban areas of the Central Amazon, an increasing demand for wood for the local market and for the export of timber products is obvious (BENCHIMOL, 1996). This increasing demand for wood is exclusively satisfied from primary forests, which frequently leads to exploitation of high quality species (comp. GOTTWALD, 1961; WAGENFÜHR and SCHEIBER, 1985; DAHMS, 1989; RIZZINI, 1990). As a rule, the negative development is associated with serious negative affects on the ecosystem "tropical forest" (LAMPRECHT, 1986). The restricted availability of high quality timber for Amazonia may even lead to the import of wood to some extent (BENCHIMOL, 1996).

During the last decades intensive research on timber production in plantation systems of the tropics was carried out as to counteract this tendency (LAMPRECHT, 1986; WHITMORE, 1995; BRÜNIG, 1996). Nevertheless the knowledge about the site demands of commercial timber tree species, which is the basis for sustainable tree growth, is still restricted in the Amazon.

In tropical rain forests of the Central Amazon, tree growth is especially limited by the restricted mineral element supply of the soils (KLINGE, 1976; DRECHSEL and ZECH, 1991; BRÜNIG, 1996). Furthermore, the traditional slash and burn management of the vegetation for agriculture and the exploitation of high quality timber trees out of the primary forests lead to a further degradation and to a strong

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reduction of the element stocks of the soil in this region (FEARNSIDE, 1995; FERNANDES et al., 1997).

With regard to tree growth and wood formation, the macronutrients are of main importance due to their significance for enzyme reactions, the turgor of the cells (BAUCH, 1993; MARSCHNER, 1995; DÜNISCH et al., 1998), the stabilisation of cell membranes, the formation of the cell wall (WARDROP, 1981; WESTERMARK, 1982), and for the photosynthesis of the trees (KÜPPERS et al., 1985).

Due to the significant alterations in tree growth and nutrition, long lived timber plantations pass through different growth phases from site preparation to the phase of growth stagnation. Therefore time series analyses are an urgent need for the selection of well adapted tree species for plantations for high quality wood production (comp. SCHROTH et al. 1995), the evaluation of the sustainability of growth (BRÜNIG 1971), and the appropriate management of the plantations (SANCHEZ 1976).

Therefore, in this study, the biomass, the nutrient stocks, and the nutrient fluxes (N, P, S, K, Ca, and Mg) of a high quality timber plantation near Manaus, Brazil, were investigated from the period of the site preparation until an age of 7 years. As to prove the suitability of different tree species for sustainable timber production and for the stabilisation of the nutrient supply in plantations comparative investigations were carried out in experimental plots of *Swietenia macrophylla* King., *Carapa guianensis* Aubl., *Cedrela odorata* L., *Dipteryx odorata* (Aubl.) Willd., and *Hymenaea courbaril* L. (comp. DAHMS, 1989; GOTTWALD, 1961; WAGENFÜHR and SCHEIBER, 1985).

## Materials and Methods

### Study site and experimental plots

The experimental plots are located at the EMBRAPA Amazônia Ocidental, 24 km out of the city of Manaus, 3°8' S, 59°52' W. The area is located at approximately 50 m above sea level with an annual precipitation of about 2,500 mm (Min. 110 mm/Max. 295 mm per month) and a mean temperature of 26.4° C (Min. 20.3° C/Max. 34.1° C). According to categorisation, the soil is a poor yellow latosol with a reduced cation exchange capacity (ZECH et al. 1998, DÜNISCH et al., 1999). The investigations on the N, P, S, K, Ca, and Mg supply and the biomass production of *Swietenia macrophylla* Aubl., *Carapa guianensis* King, *Cedrela odorata* L., *Dipteryx odorata* (Aubl.) Willd., and *Hymenaea courbaril* L. were carried out in the experimental plots, which are used for interdisciplinary research projects within the Brazilian-German cooperation program "SHIFT" (comp. BAUCH et al., 1999).

For the experimental plots an abandoned rubber plantation (*Hevea brasiliensis* (H. B. K.) Muell. Arg.) with a dense secondary vegetation, which was clear cut in 1991, was selected. After 5 months of site preparation the 25 plants (4 to 6 months old) per plot were planted with a spacing of 3 x 3 m in January 1992. Every plant was fertilised with 150 g superphosphate. The spontaneous vegetation of the plantation was dominated by the cover crops *Pueraria phaseoloides* (Rosed.) Benth and *Homolepis*

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*aturensis* (H.B.K.), which were chased and cut by field workers twice a year. The experiment was carried out with 4 replicates.

### **Biomass of the plantation**

For the quantification of the biomass of the plantation, the breast height diameter, the tree height, the height of the crown, the diameter, and the density of the crown of all trees of the experimental plots ( $n = 43\text{--}95$  per species) were studied annually. Based on these dendrometric data, four trees with an age of 5, 39, 47, 59, and 83 months of each species were selected for felling and the oven dry biomass ( $105^\circ\text{C}$ ) of 9 to 17 plant fractions (e.g. fine roots, main roots, stem xylem, stem phloem, leaves etc.) was quantified.

The biomass of the spontaneous vegetation of an area of 4 m x 4 m was quantified annually in all experimental plots by destructive harvesting. For comparison the biomass of the secondary vegetation, which covered the experimental plots before planting, was quantified at an corresponding area of 10 m x 10 m.

### **Nutrient stocks of the soil and the vegetation**

The N, P, S, K, Ca, and Mg stocks of the soil and the vegetation were quantified before and after site preparation and for the plantation at an age of 5, 39, 47, 59, and 83 months (data for the nutrient stocks before and after site preparation are obtained from a corresponding 10 m x 10 m plot). The nutrient stocks of the plantation were calculated for an area of 10 m<sup>2</sup> and a soil depth of 80 cm, approximately representing the growth compartment of a single tree within the plantation (AZEVEDO et al. 1999).

As to calculate the nutrient stocks of the soil, 30 soil samples each were collected in all experimental plots to a soil depth of 90 cm. The N content of the soil was determined by a C-H-N Analyzer (Heraeus Vario). The P, S, K, Ca, and Mg content of the soil was determined after HF treatment by optical emission spectroscopy with an inductively coupled plasma flame (ICP-OES). The exchangeable K, Ca, and Mg content of the soil was quantified after a percolation of the soil samples with NH<sub>4</sub>Cl (1 N), according to KÖNIG and FORTMANN (1996). The nutrient stocks of the soil were calculated from the element content and the density of the soil samples.

The element analyses of biomass samples were carried out for 9 to 17 fractions of the felled trees to get an insight in the nutrient status of the trees. As to study the variation of the nutrient status of the tree individuals, mature leaves of all trees were collected for element analyses (MARSCHNER 1995, HÜTTL 1992). After preparation according to RADEMACHER et al. (1992), the N content of the samples was analysed by a C-H-N Analyzer (Heraeus Vario) whereas the P, S, K, Ca, and Mg contents were determined by optical emission spectroscopy with an inductively coupled plasma flame (ICP-OES, comp. BERNEIKE et al., 1985). The nutrient stocks of the vegetation were calculated from the element contents and the biomass of the vegetation.

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## Nutrient fluxes within the plantation

The nutrient fluxes within the plantation were calculated for one-year-intervals. The study was carried out for the period before site preparation, the period of site preparation, the period from the start of the site preparation to a tree age of 5 months as well as the period of a tree age of 27 to 39 months, 39 to 51 months, 47 to 59 months, and 71 to 83 months (for the period of site preparation the calculation of the nutrient fluxes for a one-year interval is based on a 7-months experimental period).

As to quantify the nutrient input into the soil during the experimental period, the quantity and the element content of the precipitation, the throughfall, and the stemflow were quantified in one-month-intervals (sample collection was carried out weekly). The rain collectors were installed in a distance of 50 cm and 150 cm from the trunk of three trees of each plot. Stemflow collectors were installed at four trees of each species.

The nutrient input into the plantation caused by litterfall and litter decomposition was calculated from the weekly litterfall (collectors 3 m x 3 m in each plot) and two litter decomposition experiments carried out in 1995 and 1999 (litterbags 40 cm x 40 cm, mesh width 1 mm x 1 mm, 4 repeats, sample collection after 1, 2, 3, 6, and 12 months). The samples were also analysed by optical emission spectroscopy with an inductively coupled plasma flame (ICP-OES). The nutrient input into the soil due to litter decomposition was calculated from the mass loss and the element concentration of the litter bags.

The net element uptake per year of the vegetation was calculated from the biomass of the felled trees and the element analyses of the biomass samples.

According to a methodical approach of BREDEMEIER (1987) the leaching of the macronutrients out of the soil was quantified from water flux measurements and the chemical analyses of the soil solution in different soil depths. The water flux in the soil was quantified from weekly tensiometer measurements (T 3 UMS Umweltanalytische Meßsysteme, München) and the pF relationship of the soil determined for soil depths of 0-15 cm, 15-30 cm, 30-45 cm, 45-60 cm, 60-75 cm, and 75-90cm; RICHARDS 1949). The tensiometers were installed in 5 cm, 15 cm, 35 cm, 65 cm, and 125 cm depth. The element content of the soil solution was quantified in one-week-intervals in soil depths of 10, 20, 60 cm and 120 cm. The tensiometers and the suction cups (P80, UMS Umweltanalytische Meßsysteme, München) were installed in a distance of 1 and 2 m from the trunk of the center tree of all plots.

## Statistical analyses

As to evaluate the statistical significance of the study the Gauß' error of the biomass, the nutrient stock (biomass determination x element content x variation of the soil x accuracy of element analyses), and the nutrient flux (nutrient stock determination x variation of throughfall and stemflow x accuracy suction cups) determination was quantified. The absorbance curves of the suction cups were simulated in the laboratory for one-year-water fluxes.



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Data were examined by analysis of variance (ANOVA) using tree species and age of the plantation as treatment factors in a completely randomized design. The significance of the results was tested for  $P < 0.05$  (Fisher's F-test).

## Results

### Biomass of the plantation

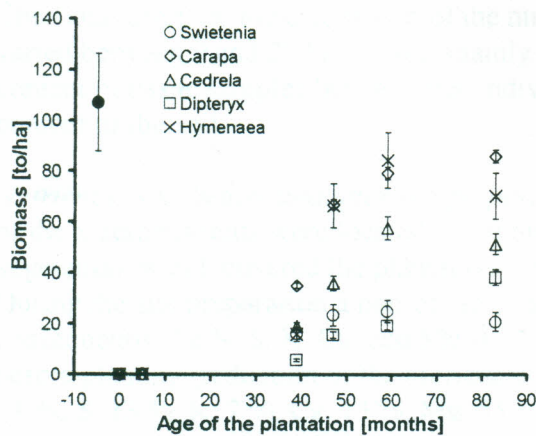
The Gauß' error of the biomass calculation for an area of one hectare based on dendrometric data and the biomass of the felled trees varied between 3 % and 18 %. The high error of 18 % for the biomass calculation of the *Swietenia* plots was caused by the attack of *Hypsipyla grandella*, which had a strong impact on the relationship between dendrometric data and the biomass of the trees.

Already after an experimental period of 39 months, significant differences were found between the biomass production of the species (Fig. 1). At the initial phase of the plantation, *Carapa* showed the highest biomass production compared to *Swietenia*, *Cedrela*, *Dipteryx* and *Hymenaea*. After 39 months of growth the biomass production of *Carapa* already reached 37 to/ha, which is 35 % of the biomass of the former 20-year old secondary vegetation (107 to/ha). After 59 months growth the biomass production of *Carapa* was strongly reduced and only a slight increase of the biomass was detected between 59<sup>th</sup> and 83<sup>th</sup> month of growth.

Corresponding to that also the *Hymenaea* and *Cedrela* plot entered the phase of growth stagnation after a period of approximately 5 years. After 83 months the biomass of *Hymenaea* was only 78 to/ha and of *Cedrela* only 52 to/ha compared to 90 to/ha of *Carapa* (Fig. 1).

Due to a high mortality and a stagnation of growth already after 47 months, after 83 months the lowest biomass stocks resulted in the *Swietenia* plot (20 to/ha, Fig. 1), indicating a low adaptation of *Swietenia* to the site conditions.

During the first 59 months the biomass production of *Dipteryx* was significantly reduced compared to the other species, but even after 83 months *Dipteryx* showed sustainable biomass production (40 to/ha, Fig. 1).



**Fig. 1:** Biomass [to/ha] of the *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea* plots during the 83 months experimental period. Comparative data are presented for the secondary vegetation before planting (•)

The results on the biomass production of the plantations showed that expressed in terms of ecological aspects *Carapa* is better adapted to the site conditions of the experimental area compared to the other species. On the other hand the results showed that with an average of 23 % only a small portion of the biomass is fixed in the stem of *Carapa*, while 28 % was taken from the roots and 33 % was covered by the leaves (Table 1). In contrast to that a high biomass portion of the stem was found for *Swietenia* (48 %), *Dipteryx* (64 %), and *Hymenaea* (43 %).

**Table 1:** Biomass portion [%] of leaves, branches, stem, and roots of 83-months old *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea*.

Biomass fraction	Swietenia	Carapa	Cedrela	Dipteryx	Hymenaea
Leaves	9	33	12	11	17
Branches [%]	24	28	18	10	24
Stem [%]	48	23	34	64	43
Roots [%]	19	16	36	15	16

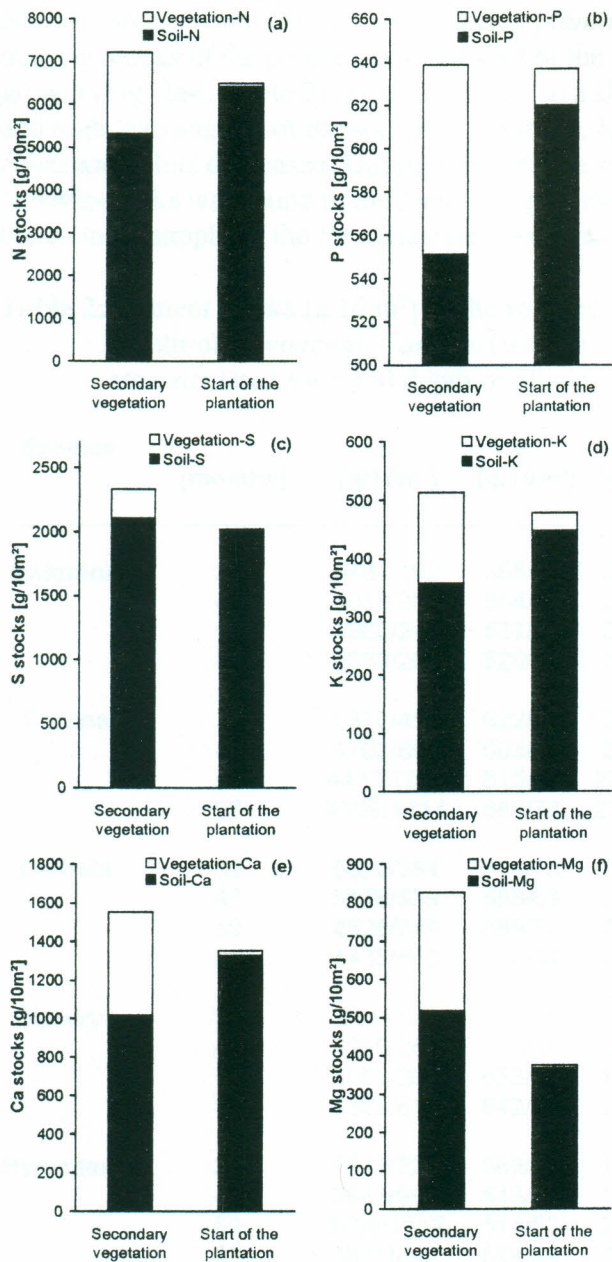
### Nutrient stocks before and after site preparation and during plantation growth

The data on the biomass of the plantation showed that even after 83 months growth (besides in the *Carapa* plots) the biomass of the plantation is significantly less than the biomass of the former secondary vegetation. As to study the relationship between the biomass production and the fixation of mineral elements in the plantation the nutrient stocks were studied before and after site preparation and at a plantation age of 39, 47, 59, and 83 months, respectively.

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The Gauß' error for the calculation of the nutrient stocks of the soil and the vegetation varied between 9 and 25 % and was mainly caused by a high variation of the element content of tissue samples between tree individuals and the heterogeneity of the element content of the soil.

*Nutrient stocks before and after site preparation:* Between 10 % (S) and 37 % (Mg) of the macronutrients were located in the biomass of the 20-year-old secondary vegetation, which covered the plantation before the site preparation (Fig. 2a-f). During the site preparation a part of the organic material was removed and consequently the N, S, K, Ca, and Mg stocks of the area were significantly reduced before planting (reduction of the nutrient stocks during site preparation: N: 10 %, P: <1 %, S: 13 %, K: 7 %, Ca: 13 %, Mg: 55 %). A part of the N, P, K, and Ca content of the slashed biomass, which remained in the plots was transferred to the soil. S and Mg, which were mainly located in the leaves of the slashed vegetation might be lost to a certain amount by wind. The analysis of the soil solution showed that a high amount of Mg was leached out of the soil during the period of the site preparation (Fig. 2f), which is a further reason for the strong reduction of the Mg stocks of the area of 55 %. A significant uptake of K and P by the spontaneous vegetation (cover crop *Pueraria phaseoloides*) was found during the 5 months period of site preparation, indicating a high absorbance capacity of *Pueraria phaseoloides* for these two elements. These results showed that due to the common site preparation technique used for the plantation, the nutrient stocks of the experimental plots were already reduced before planting. Especially the further reduction of the low K- and Mg-stocks contributed to a further reduction in fertility of the area. Besides low K- and Mg-stocks of the experimental area, this study also revealed low P stocks of the soil.



**Fig. 2a-f:** N, P, S, K, Ca, and Mg stocks [ $\text{g}/10\text{m}^2$ ] of the soil/vegetation of the experimental plots before site preparation (secondary vegetation) and before planting (data are calculated for a soil depth of 80 cm). Maximum standard deviation: 37 % of mean value.

*Nutrient stocks within 39 and 83 months of plantation growth:* A comparison of the nutrient stocks of the plantation at the start of the plantation and after 39 months of growth (Fig. 2a-f, Table 2) showed that due to a slow growth (comp. Fig. 1, Fig. 4d) and high leaching out of the soil (Fig. 4c) the N, K, and Ca stocks of the *Dipteryx* and *Hymenaea* plots decreased. During this period a significant decrease of the K-, Ca-, and Mg-stocks was found in the *Swietenia* plot indicating that also after 39 months the element supply of the *Swietenia* plot was not balanced.

**Table 2:** Element stocks [g/10 m<sup>2</sup>] of the soil/vegetation of the 39-, 47-, 59-, and 83-month-old *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea* plots (data are calculated for a soil depth of 80 cm).

Species	[months]	N [g/10m <sup>2</sup> ]	P [g/10m <sup>2</sup> ]	S [g/10m <sup>2</sup> ]	K [g/10m <sup>2</sup> ]	Ca [g/10m <sup>2</sup> ]	Mg [g/10m <sup>2</sup> ]
<b>Swietenia</b>	39	5481/192	565/12	2205/12	295/112	625/193	259/15
	47	5038/281	554/17	2520/17	126/165	439/284	265/22
	59	4962/249	537/16	2997/13	8/154	569/172	244/21
	83	4960/207	529/13	2917/11	24/134	567/143	248/18
<b>Carapa</b>	39	5377/455	622/30	2466/45	221/203	1091/411	280/57
	47	4703/869	603/56	2633/85	137/289	612/786	198/110
	59	4473/1024	615/67	2264/133	109/312	862/950	274/139
	83	4999/1114	683/73	2340/144	52/404	767/1029	308/151
<b>Cedrela</b>	39	5629/284	544/28	2488/28	229/192	1003/214	284/58
	47	5176/539	588/53	2757/54	65/364	765/407	199/112
	59	4528/749	589/50	2345/72	30/472	630/447	224/151
	83	4433/666	552/44	2509/63	78/446	689/397	228/134
<b>Dipteryx</b>	39	5316/95	627/3	2203/3	364/15	974/18	381/3
	47	4955/265	610/8	2199/8	156/42	675/49	357/9
	59	4901/306	633/10	1290/11	119/37	667/44	360/11
	83	4302/611	642/18	2395/22	30/74	638/87	330/22
<b>Hymenaea</b>	39	4978/223	582/10	1999/12	241/80	686/81	387/15
	47	3883/931	543/44	1966/51	70/377	460/338	363/48
	59	3799/1012	514/53	2216/59	62/397	413/364	418/58
	83	3831/843	594/44	2313/49	43/325	486/303	379/49

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In the subsequent 44 months of experiments a significant decrease of 61 % and 73 % of the K stocks of the *Swietenia* and *Dipteryx* plots, respectively, was monitored (Table 2), whereas the K stocks of the *Carapa*, *Cedrela*, and *Hymenaea* plots were already stabilised. Nevertheless a strong reduction of the K stocks of the soil were found in all plots due to the transfer of large quantities of K from the soil to the trees (Table 2). After 83 months growth only 11 % (*Carapa* plantation) to 29 % (*Dipteryx* plantation) of the total K stocks of the plantation are located in the soil, whereas the predominant part of K is located in the biomass (Table 2). The strong reduction of the K content of the soil during the 44 months became also obvious by a significant decrease of the K content of the soil solution.

Although a significant transfer of N, P, S, Ca, and Mg from the soil to the plant was found during the experimental period, after 7 years growth the N, P, S, Ca, and Mg stocks of the soil were still high compared to the N, P, S, Ca, and Mg stocks located in the biomass (Table 2).

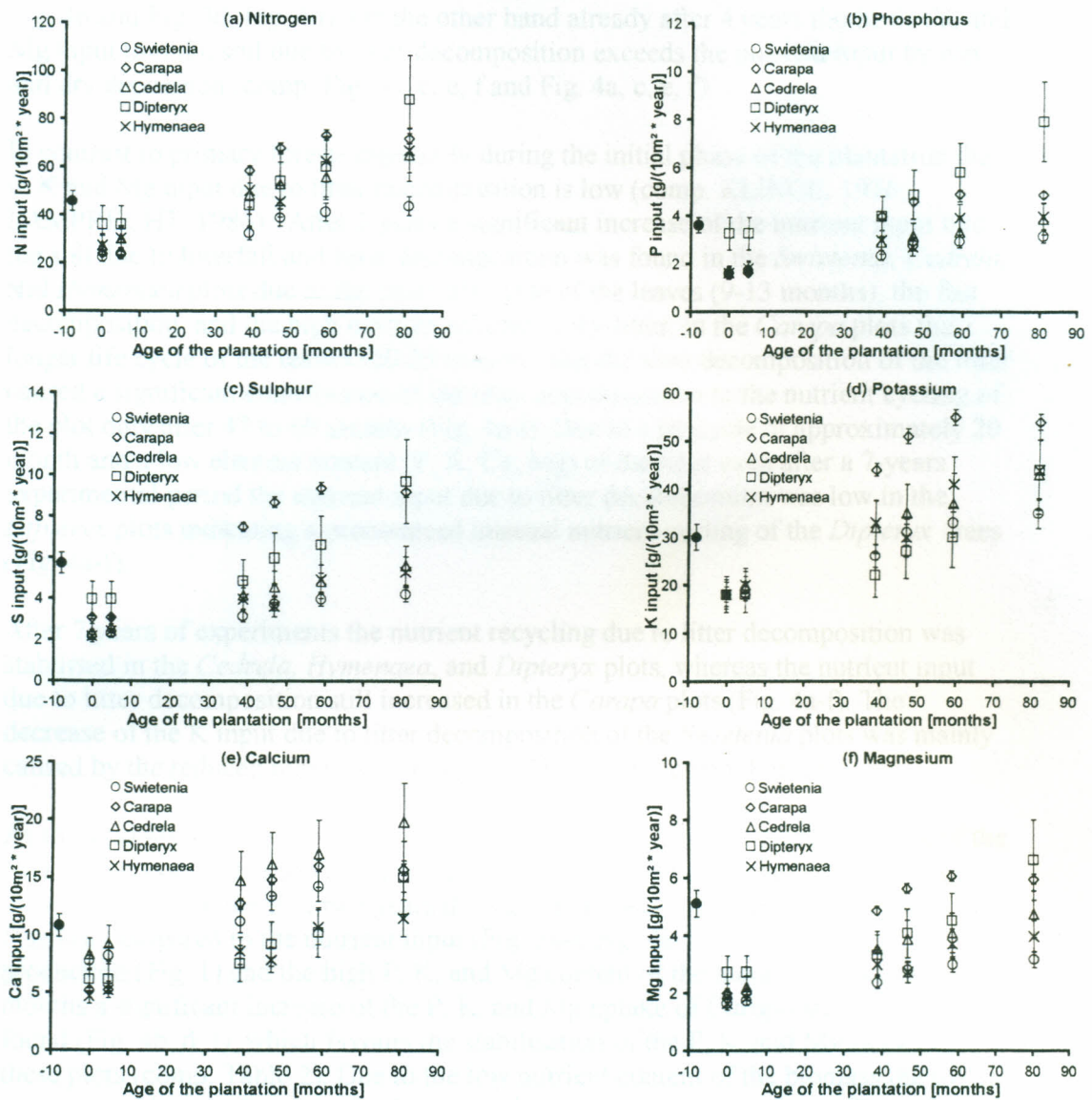
The results on the nutrient stocks of the soil and the vegetation before and after planting and throughout the 83 months of plantation growth showed that the stabilisation of the N, P, S, K, Ca, and Mg stocks of the plantation is more favoured by *Carapa* and *Cedrela*, whereas during the initial phase the N, K, Ca, and Mg stocks of *Swietenia*, *Dipteryx*, and *Hymenaea* plots are not stabilised. A comparison of the results with the biomass production of the species showed a strong relationship between the biomass production of *Swietenia*, *Carapa*, *Cedrela*, and *Hymenaea* and the K stocks of the experimental plots (comp. Fig. 1), but no significant relationship was found between the reduced K supply of the soil and the biomass production of *Dipteryx*.

### **Nutrient fluxes of the plantation**

In addition to the calculation of nutrient stocks, nutrient fluxes expressed in terms of nutrient input into the soil by rain, throughfall and stemflow (Fig. 3a-f), by litter decomposition (Fig. 4a-f), the nutrient output out of the soil due to the nutrient uptake of the vegetation (Fig. 5a-fd) as well as by leaching (Fig. 6a-f) were calculated. The Gauß' error of the calculation of the nutrient fluxes in the plantation varied between 13 and 39 %. For this study the number of throughfall and stemflow collectors as well as the accuracy of suction cups for the analyses of the soil solution were the main source of error. Due to the low P-, K-, and Mg- stocks of the plantation the study was carried out with special regard to these elements (Table 2).

Only a small amount of P, S, K, Ca, and Mg reached the plants via precipitation due to the low element content of the rain water in the Manaus region (Fig. 3a-f). Due to a strong leaching of mineral elements from the leaves the N, K, Ca, and Mg content of the throughfall of the *Swietenia*, *Carapa*, *Cedrela*, and *Hymenaea* plots was significantly higher compared to the element content of the precipitation. No leaching out of the leaves of *Dipteryx* was found indicating a morphological and anatomical adaptation of this species to avoid element loss due to leaching. The extremely high element content of the stemflow, which exceeds the element content of the





**Fig. 3a-f:** (a) N, (b) P, (c) S, (d) K, (e) Ca, and (f) Mg input [g/(10 m<sup>2</sup> x year)] by rain, throughfall, stemflow into the soil of the *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea* plots during the 83 months of experiments. Comparative data are presented for the secondary vegetation before planting (•). Data points are set at the end of the 12-months experimental periods.

Because of the low nutrient input by wet and dry deposition on this forest site, the nutrient recycling due to litterfall and litter decomposition is of main interest for the study of the nutrient supply of the plantation. A comparison of the nutrient input due to wet and dry deposition and litter decomposition showed that after 7 years of experiments the P and K input into the soil due to litter decomposition is still low compared to the P and K input due to rain, throughfall and stemflow (comp. Fig. 3b,



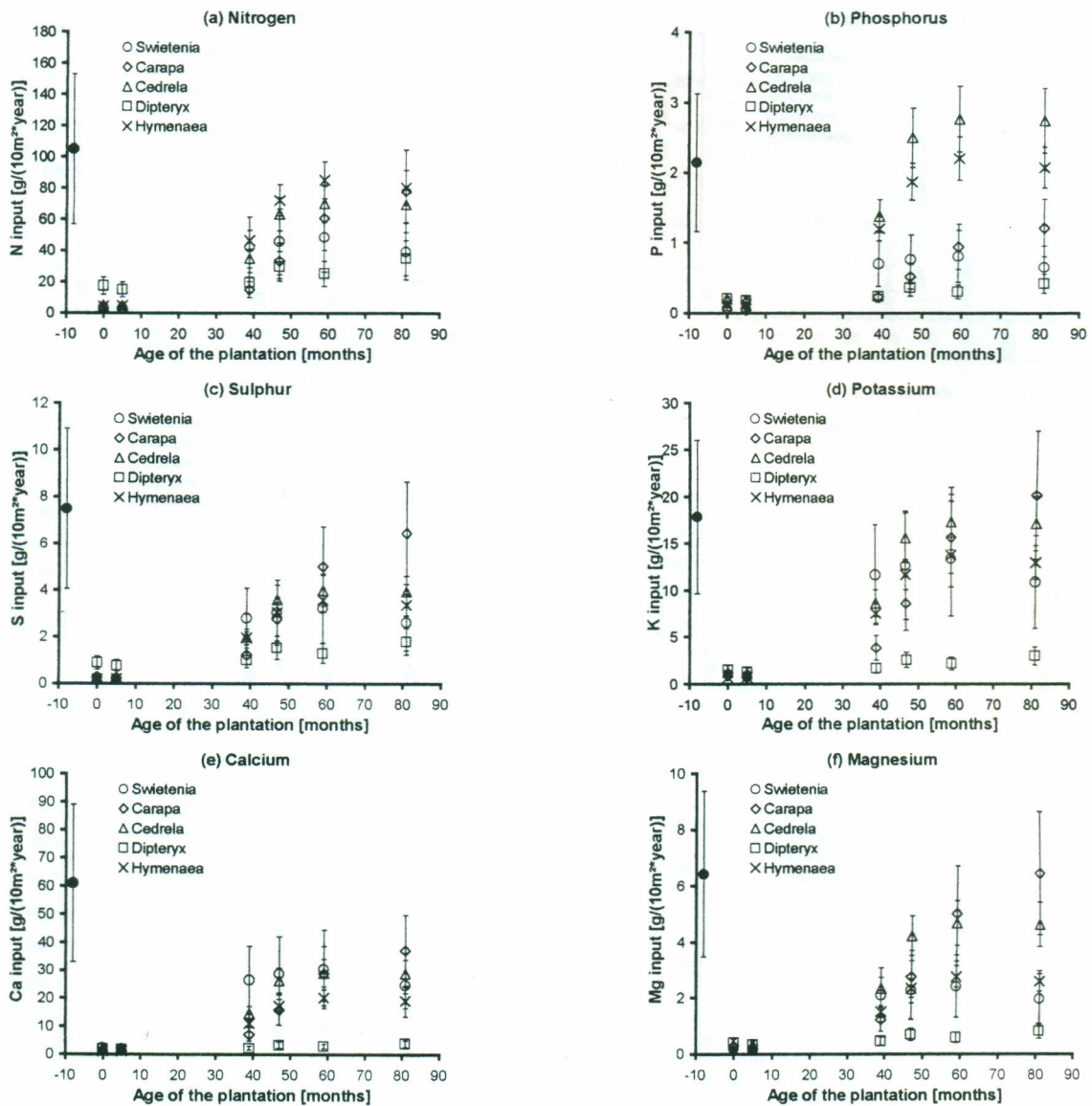
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Fig. 4b and Fig. 3d, Fig. 4d). On the other hand already after 4 years the N, S, Ca, and Mg input into the soil due to litter decomposition exceeds the nutrient input by wet and dry deposition (comp. Fig. 3a, c, e, f and Fig. 4a, c, e, f).

In contrast to primary forests especially during the initial phase of the plantation the P, K and Mg input due to litter decomposition is low (comp. KLINGE, 1976; LAMPRECHT, 1986). After 3 years a significant increase of the nutrient input into the soil due to litterfall and litter decomposition was found in the *Swietenia*, *Cedrela*, and *Hymenaea* plots due to the short life cycle of the leaves (9-13 months), the fast decomposition, and the high nutrient content of the litter. In the *Carapa* plots the longer life cycle of the leaves (20-25 months) and the slow decomposition of the litter caused a significant contribution of the litter decomposition to the nutrient cycling of the plot only after 47 to 60 months (Fig. 4a-f). Due to a lifecycle of approximately 20 month and a low element content (P, K, Ca, Mg) of the litter even after a 7-years experimental period the nutrient input due to litter decomposition was low in the *Dipteryx* plots indicating a pronounced internal nutrient cycling of the *Dipteryx* trees (Fig. 4a-f).

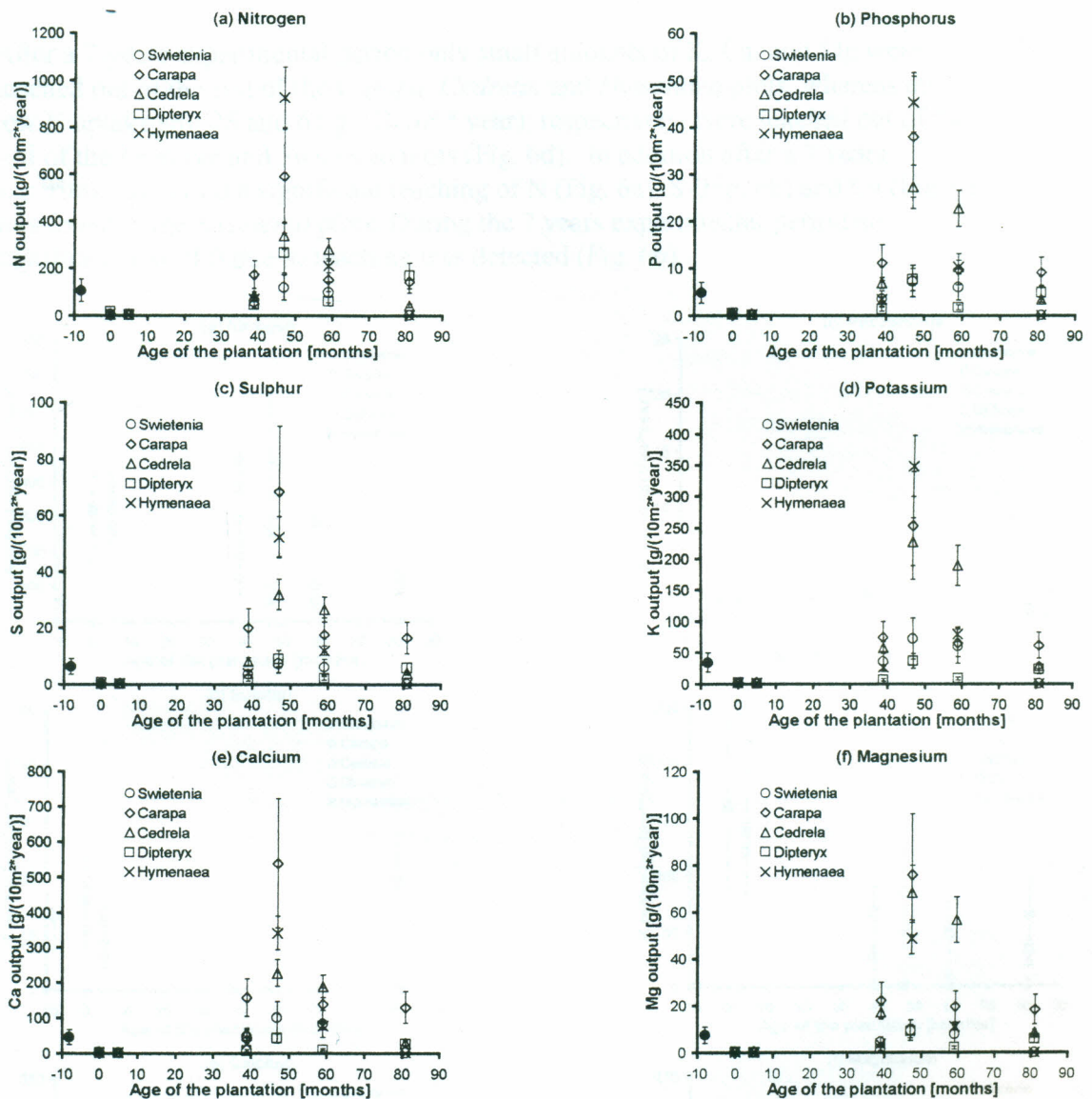
After 7 years of experiments the nutrient recycling due to litter decomposition was stabilised in the *Cedrela*, *Hymenaea*, and *Dipteryx* plots, whereas the nutrient input due to litter decomposition still increased in the *Carapa* plots (Fig. 4a-f). The decrease of the K input due to litter decomposition of the *Swietenia* plots was mainly caused by the reduced biomass production of *Swietenia* (comp. Fig. 1).

As to avoid high nutrient loss due to leaching out of the soil, the nutrient uptake of the vegetation is of main importance for the stabilisation of the nutrient supply of the plantation. During the first two years the nutrient uptake of the planted trees (Fig. 5a-f) is low compared to the nutrient input (Fig. 3a-f, Fig. 4a-f). Due to the high biomass production (Fig. 1) and the high P, K, and Mg content of the biomass, after 39 months a significant increase of the P, K, and Mg uptake of *Carapa* and *Cedrela* was found (Fig. 4b, d, f), which favours the stabilisation of the P, K, and Mg stocks of these plots (comp. Table 2). Due to the low nutrient content of the biomass the lowest nutrient uptake was found in the *Dipteryx* plot indicating a low nutrient (P, S, K, Ca, Mg) demand for tree growth of this species.



**Fig. 4a-f:** (a) N, (b) P, (c) S, (d) K, (e) Ca, and (f) Mg input [g/(10 m<sup>2</sup> × year)] by litterfall and litter decomposition into the soil of the *Swietenia*, *Carapa*, *Cedreia*, *Dipteryx*, and *Hymenaea* plots during the 83 months of experiments. Comparative data are presented for the secondary vegetation before planting (•). Data points are set at the end of the 12-months experimental periods.

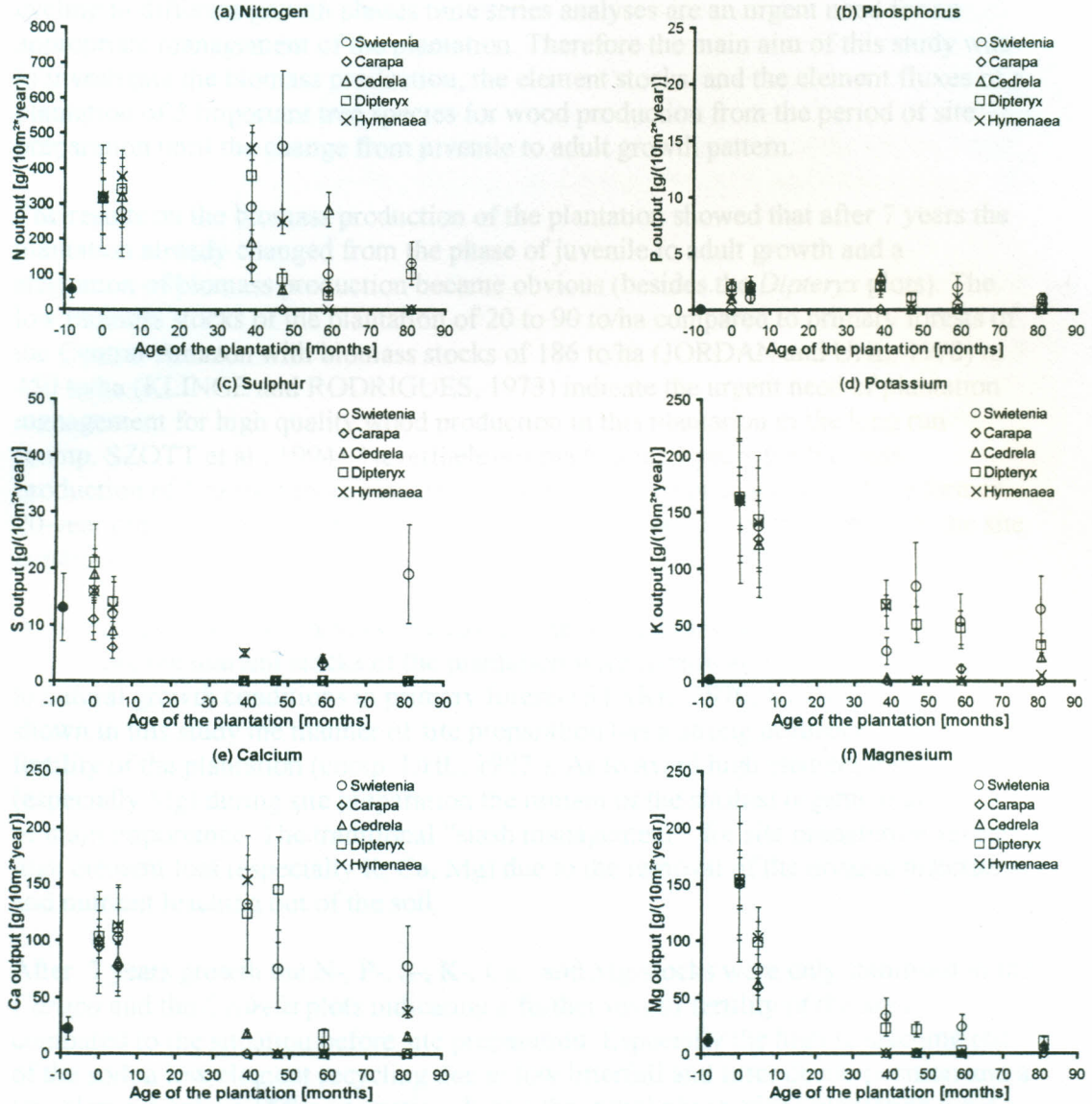
In general the course of the K uptake of the trees followed the course of the biomass production curve with maximum values at an tree age of 40 to 60 months (Fig. 5a-f, Fig. 1), but it has to be pointed out that until a tree age of approximately 5 years the mean N, S, K, and Mg content per kg dry mass diminished with increasing tree age indicating the change from juvenile to adult growth pattern. Besides *Cedreia* the mean P and Mg content of the tree species was already stabilised at an tree age of 39 months.



**Fig. 5a-f:** (a) N, (b) P, (c) S, (d) K, (e) Ca, and (f) Mg output [ $\text{g}/(10\text{m}^2 \times \text{year})$ ] by element uptake of the vegetation out of the soil of the *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea* plots during the 83 months of experiments. Comparative data are presented for the secondary vegetation before planting ( $\bullet$ ). Data points are set at the end of the 12-months experimental periods.

Due to the high amount of precipitation and a low cation absorbance capacity of the soil nutrient leaching out of the soil was studied in more detail. During the first three years N, K, Ca, and Mg loss due to leaching out of the soil (N: 118-320, K: 20-63, Ca: 3-114, Mg: 4-31  $\text{g}/(10\text{m}^2 \cdot \text{year})$ , Fig. 6a, d, e, f) exceeded the N, K, Ca, and Mg input due to rain, throughfall, stemflow, and litter decomposition into the soil (comp. Fig. 4a-f). Due to a reduced growth rate (Fig. 1) and low nutrient uptake during this period highest N, K, Ca, and Mg leaching rates were found in the *Dipteryx* and *Hymenaea* plots.

After a 7-years experimental period only small amounts of K, Ca, and Mg were leached out of the soil of the *Carapa*, *Cedrela*, and *Hymenaea* plots, whereas due to low K uptake still 28 and 61 g / 10 m<sup>2</sup> \* year), respectively, were leached out of the soil of the *Dipteryx* and *Swietenia* plots (Fig. 6d). In addition after a 7 years experimental period a significant leaching of N (Fig. 6a), S (Fig. 6b) and Ca (Fig. 6e) was found in the *Swietenia* plots. During the 7 years experimental period no significant loss of P due to leaching was detected (Fig. 6b).



**Fig. 6a-f:** (a) N, (b) P, (c) S, (d) K, (e) Ca, and (f) Mg output [g/(10 m<sup>2</sup> x year)] by leaching out of the soil of the *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea* plots during the 83 months of experiments. Comparative data are presented for the secondary vegetation before planting ( • ). Data points are set at the end of the 12-months experimental periods.

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## Discussion

With regard to the sustainability of plantation systems of the Central Amazon the nutrient supply of the plantation (e. g. K, Mg, P) is of main interest (KLINGE, 1976; JORDAN, 1982; SANCHEZ et al., 1982; SZOTT and PALM, 1996 ). With regard to the stabilisation of the nutrient cycling of plantation systems especially the role of the selected tree species and the plantation management is emphasised in many field studies (SZOTT et al. 1991; WHITMORE, 1995; FERNANDES et al., 1997). Due to the non-linear growth of long-lived trees and significant alterations of the nutrient cycling in different growth phases time series analyses are an urgent need for an appropriate management of the plantation. Therefore the main aim of this study was to investigate the biomass production, the element stocks, and the element fluxes of a plantation of 5 important tree species for wood production from the period of site preparation until the change from juvenile to adult growth pattern.

The results on the biomass production of the plantation showed that after 7 years the plantation already changed from the phase of juvenile to adult growth and a stagnation of biomass production became obvious (besides the *Dipteryx* plots). The low biomass stocks of the plantation of 20 to 90 to/ha compared to primary forests of the Central Amazon with biomass stocks of 186 to/ha (JORDAN and UHL, 1978) to 450 to/ha (KLINGE and RODRIGUES, 1973) indicate the urgent need of plantation management for high quality wood production in this plantation in the long run (comp. SZOTT et al., 1994). Nevertheless already after 7 years the biomass production of *Carapa* plots approximately reached the biomass stocks of the former 20-year old secondary vegetation indicating a fast adaptation of this species to the site conditions.

As a consequence of the history, the low biomass stocks and the low diversity of the plantation, the nutrient stocks of the plantation were significantly reduced compared to natural growth conditions in primary forests (STARK, 1970; KLINGE, 1976). As shown in this study the manner of site preparation has a strong influence on the soil fertility of the plantation (comp. UHL, 1987 ). As to avoid high element loss (especially Mg) during site preparation the remain of the slashed organic material is of main importance. The traditional "slash management" for site preparation favours high element loss (especially K, Ca, Mg) due to the removal of the organic material and nutrient leaching out of the soil.

After 7 years growth the N-, P-, S-, K-, Ca-, and Mg-stocks were only stabilised in the *Carapa* and the *Cedrela* plots indicating a further loss of fertility of the area compared to the situation before site preparation. Especially the high K leaching out of the soil, a low element recycling due to low litterfall and litter decomposition and a low element uptake of the vegetation during the initial phase of the plantation were responsible for the slight (*Carapa*, *Cedrela*) to strong (*Dipteryx*, *Swietenia*) decrease in fertility of the experimental plots. After 4 years the major part of K was transferred from the soil to the planted trees indicating a demand for K fertilisation already in this period.

Although the results on nutrient stocks and nutrient fluxes of the plantation indicate a limitation of tree growth on this forest site by a restricted K and Mg supply, the

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results of the soil analyses proved that the soil of the study site also exhibit an extreme lack of P. With regard to the availability of nutrients (especially P and S), sample fractioning might be an appropriate tool for further information and should be studied in more detail (comp. TIESSEN et al., 1984).

Although after 7 years an acceptable stabilisation of the element fluxes was only detected in the *Carapa* and *Cedrela* plots, no conclusions on the adaptation of the tree species to the site conditions can be drawn from the results on nutrient stocks and nutrient fluxes. Due to the low P, K, and Mg demand of *Dipteryx* and *Hymenaea* compared to *Swietenia*, *Carapa*, and *Cedrela* a sustainable growth of these two species was still possible in soils with extremely low element concentrations (K). Comparing the nutrient stocks and fluxes with the biomass production of the trees, according to a concept on nutrient uptake and plant growth proposed by INGESTAD (1987), sustainable growth of *Swietenia* is possible at a K content of the soil >17 ppm, of *Carapa* >10 ppm, of *Cedrela* >13 ppm, of *Dipteryx* >5 ppm, and of *Hymenaea* >8 ppm.

With regard to the nutrient supply of plantations these investigations pointed out that *Carapa* and *Cedrela* are suitable tree species for the stabilisation of the nutrient stocks and the nutrient supply of plantations of the Amazon. On the other hand *Dipteryx* and *Hymenaea* are well adapted to low fertile soils of the Central Amazon, but under monoculture conditions these species are not suitable for the stabilisation of the element supply during the initial phase of the plantation. Consequently, these two species are recommended for reforestation together with plants, which stabilise the element stocks of the soil (comp. FEARNSIDE, 1995; SCHROTH et al. 1995). The high quality timber species *Swietenia* has a very high K and Mg demand and did not stabilise the nutrient fluxes of the monoculture plots. This indicates that sustainable timber production of *Swietenia* is only possible in stabilised plantations, which take the low ecological amplitude of this species into account (MAYHEW and NEWTON, 1998).

From these results it can be concluded that with regard to nutrient supply time series analyses on nutrient supply-tree growth relationships are the basis for the establishment of sustainable plantations for wood production in the Central Amazon. Especially plantation systems, such as mixed systems and enrichment systems (LAMPRECHT, 1986; DÜNISCH et al., 1999), which take the site demands of different species into account and include the existing vegetation might be helpful for the stabilisation of the mineral element supply of the trees.

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### **2.2.1. Comparative study on the nutrient fluxes and the growth dynamics of *Carapa guianensis* Aubl. in a monoculture and an enrichment plantation**

#### **Introduction**

In the Central Amazon the demand for wood for the local market and for export is exclusively satisfied from primary forests, which leads to strong exploitation especially of high quality species (comp. LOUREIRO et al. 1979; RIZZINI, 1990; FEARNside and FERRAZ 1995). In addition, logging in primary forests is often associated with serious negative affects on the ecosystem "tropical forest" (LAMPRECHT, 1986; BRÜNIG, 1996) and with a degradation of the soil (FERNANDES et al., 1997). As to counteract this tendency during the last years in the Central Amazon special attend was given to the cultivation of tree species for high quality timber production in plantation systems (LAMPRECHT, 1986; WHITMORE, 1995; BRÜNIG, 1996; BAUCH et al. 1999). Nevertheless the knowledge about the site demands of native timber tree species and the appropriate management of timber plantations is still restricted in the Amazon.

Beside genetic factors tree growth depends on a sufficient light, water, and mineral element supply of the trees (KOZLOWSKI et al. 1991; LARSON 1995). In large areas of the Central Amazon, tree growth is limited by the restricted mineral element supply of the soils (KLINGE, 1976; DRECHSEL and ZECH, 1991). Recent field studies exhibited especially a strong lack of K, Mg, and P on "terra firme" sites of this region (JORDAN 1982; FERNANDES et al., 1997; DÜNISCH et al., 1999 a; SCHROTH et al., in press).

As a rule, traditional monoculture plantations cause nutrient imbalance and strong nutrient loss of the soil, due to the "slash and burn" management for site preparation (HÖLSCHER et al., 1997) and the low nutrient fixation in the biomass (DÜNISCH and SCHWARZ, in press). This often leads to low productivity of monoculture plantations in the long run (WILLIAMS and MELACK, 1997). As to counteract these problems enrichment plantation systems in existing primary or secondary vegetation are discussed as an alternative for sustainable wood production in plantations of the tropics (LAMPRECHT, 1986). However, the native vegetation of enrichment plantations is a strong competitor for the planted trees (AZEVEDO et al., 1999), which might lead to a strong reduction in productivity of the planted trees in enrichment plantations compared to monoculture plantation systems.

In this comparative study, the K, Mg, and P fluxes as well as the growth dynamics of a 7 years old enrichment plantation and a traditional monoculture plantation of the high quality timber tree *Carapa guianensis* Aubl. (GOTTWALD, 1961; WAGENFÜHR and SCHEIBER, 1985, BAUCH and DÜNISCH, in press) were investigated. Special regard was given to the stabilisation of the nutrient balance of the plantation and the sustainability of wood production.

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## Material and Methods

### Study site and plantation systems

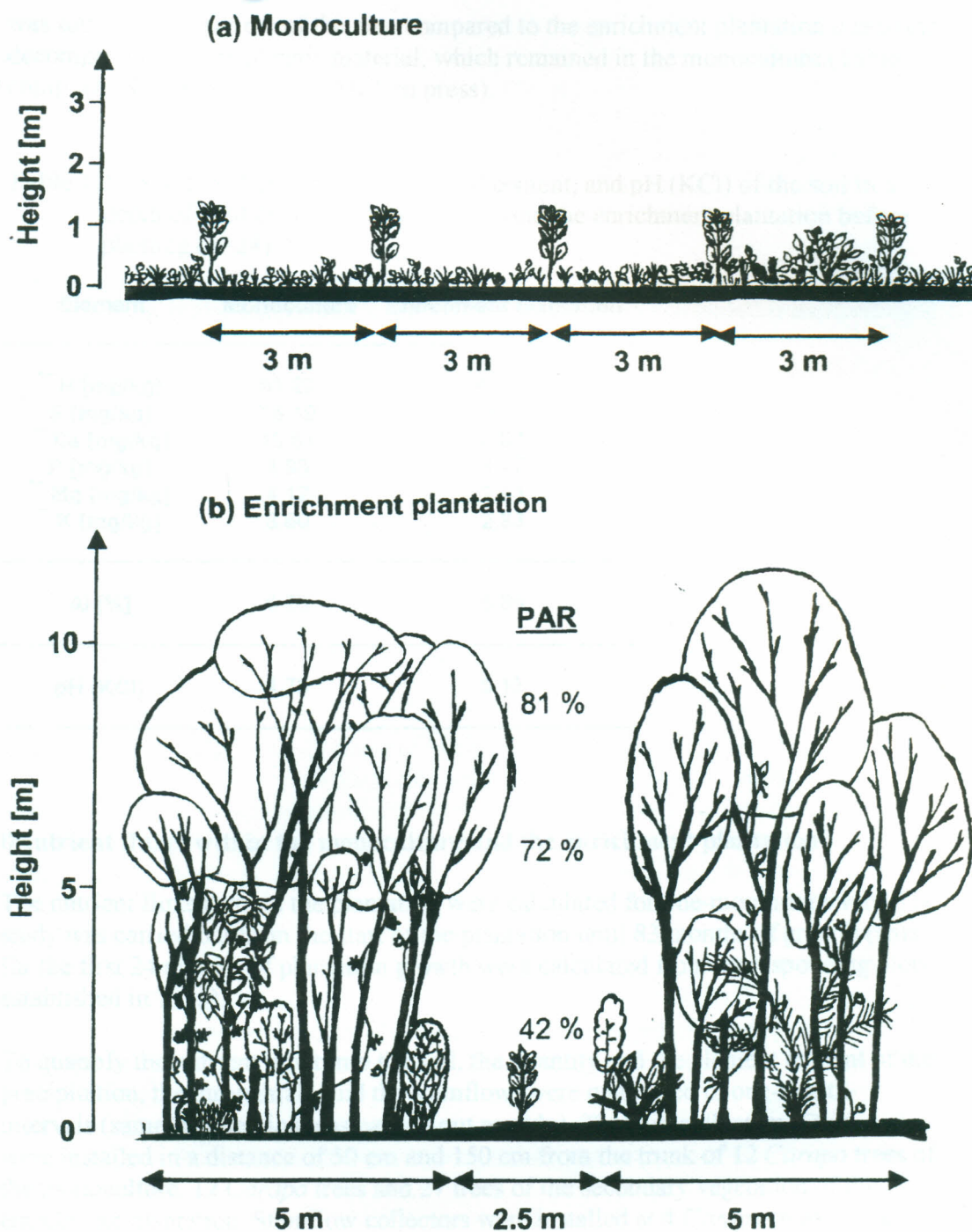
The study was carried out on the research station of the EMBRAPA Amazônia Ocidental, 24 km out of the city of Manaus, 3°8' S, 59°52' W. The area is located at approximately 50 m above sea level with an annual precipitation of about 2,500 mm (Min. 110 mm (August) / Max. 295 mm (February) per month), a mean air temperature of 26.4° C, and a mean humidity of the air of 87 %. According to categorisation, the soil is a poor xanthic Ferralsol (FAO, 1990; comp. Table 1) with a low cation exchange capacity (ZECH et al., 1998; DÜNISCH et al., 1999 a; SCHROTH et al., in press). The investigations were carried out on a study site which is used for interdisciplinary research projects within the Brazilian-German cooperation program "SHIFT" (comp. BAUCH et al., 1999).

The study site was cleared from primary forest in 1980 by slash and burn treatment, as to install a rubber plantation (*Hevea brasiliensis* (H. B. K.) Muell. Arg.) After a two years experimental period the rubber plantation was abandoned and during the subsequent 10 years covered with a dense diverse secondary vegetation of approximately 78 different species (comp. PREISINGER et al. 1994).

For the installation of the monoculture plantation the secondary vegetation was clear cut without burning in 1991. After 5 months of site preparation 100 plants (4 to 6 months old) of *Carapa guianensis* were planted with a spacing of 3 x 3 m in January 1992 in 4 experimental plots of 25 plants each (Fig. 1a). Every plant was fertilised with 150 g superphosphate. The spontaneous vegetation of the plantation was dominated by the cover crops *Pueraria phaseoloides* (Rosed.) Benth and *Homolepis aturensis* (H.B.K.), which were chased and cut by field workers twice a year.

For the enrichment plantation lines of 30 m x 2.5 m of the same secondary vegetation were clear cut in 1991 (Fig. 1b). Between these lines 5 m of the fallow vegetation remained untouched. In each line 10 plants (4 to 6 months old) of *Carapa guianensis* were planted with a spacing of 3 m in January 1992. According to the treatment in the monoculture every plant was fertilised with 150 g superphosphate. The spontaneous vegetation of the cleared lines was cut by field workers twice a year. Corresponding to the monoculture the enrichment plantation was installed with 4 repeats.

30 m      2.5 m



**Fig. 1a/b:** Scheme of (a) the monoculture and (b) the enrichment plantation at the start of the experiment in 1992. The reduction [%] of the photo active radiation (PAR) within the enrichment plantation compared to the monoculture is presented for 1m, 5m, and 8m height.

Soil analysis carried out in the two plantations before planting indicated low K, Mg, and P contents and high Al contents of the soil (Table 1) of the experimental site. A significant increase of the N, Ca, K, and Mg content of the soil of the monoculture

was found after clear cut of the area compared to the enrichment plantation due to the decomposition of the organic material, which remained in the monoculture (Table 1, comp. DÜNISCH and SCHWARZ, in press).

**Table 1:** N, S, Ca, K, Mg, P [mg/kg], Al [%] content, and pH (KCl) of the soil in a depth of 0-20 cm of the monoculture and the enrichment plantation before planting (n=24).

Element	Monoculture	Enrichment plantation
*** N [mg/kg]	51.23	42.54
S [mg/kg]	16.19	16.91
*** Ca [mg/kg]	10.61	8.07
P [mg/kg]	4.93	4.47
*** Mg [mg/kg]	4.12	2.93
** K [mg/kg]	3.60	2.93
Al [%]	6.26	5.85
pH (KCl)	4.73	5.13

### 0Nutrient fluxes within the monoculture and the enrichment plantation

The nutrient fluxes within the plantation were calculated for one-month-intervals. The study was carried out from the start of the plantation until 83 months of growth (data for the first 24 months of plantation growth were calculated from corresponding plots established in 1995).

To quantify the nutrient input into the soil, the quantity and the element content of the precipitation, the throughfall, and the stemflow were quantified in one-month-intervals (sample collection was carried out weekly). The rain collectors (Ø 15 cm) were installed in a distance of 50 cm and 150 cm from the trunk of 12 *Carapa* trees of the monoculture, 12 *Carapa* trees and 27 trees of the secondary vegetation of the enrichment plantation. Stemflow collectors were installed at 4 *Carapa* trees of the monoculture, 4 *Carapa* trees and 9 trees of the secondary vegetation of the enrichment plantation. The K, Mg, and P contents of the solutions were analysed monthly (mixed samples of weekly sample collections) by optical emission spectroscopy with an inductively coupled plasma flame (ICP-OES; BERNEIKE et al. 1985).

The nutrient input into the soil caused by litterfall and litter decomposition was calculated from weekly litterfall collections (collectors 3 m x 3 m, 4 collectors in the monoculture, 6 collectors in the enrichment plantation) and two litter decomposition experiments carried out in 1995 and 1999 with litter of *Carapa*, of the cover crops

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*Pueraria phaseoloides* (Rosed.) Benth and *Homolepis aturensis* (H.B.K.), and of mixed litter of 78 species of the secondary vegetation of the enrichment plantation (litterbags 40 cm x 40 cm, mesh width 1 mm x 1 mm, 4 repeats, sample collection after 1, 2, 3, 6, and 12 months). After acid digestion (67 % HNO<sub>3</sub>) according to RADEMACHER (1986) the samples were analysed by optical emission spectroscopy with an inductively coupled plasma flame (ICP-OES). The nutrient input into the soil by litter decomposition was calculated from the mass loss and the element concentration of the litterbags.

The net K, Mg, and P uptake per year by the vegetation was calculated from the biomass of the trees and the K, Mg, and P analyses of the biomass samples carried out according to RADEMACHER (1986). For the quantification of the biomass of the plantations, the survival rate, the breast height diameter, the tree height, the height of the crown, the diameter, and the density of the crown of all *Carapa* trees and of 78 species of the secondary vegetation were studied annually. As to prove the significance of the selected dendrometric parameters for the biomass calculation, 4 *Carapa* trees of the monoculture and the enrichment system with an age of 5, 39, 47, 59, and 83 months were felled and the oven dry biomass (105° C) of 9 to 17 plant fractions (e.g. fine roots, main roots, stem xylem, stem phloem, leaves etc.) was quantified. Corresponding to that the biomass of the secondary vegetation of the enrichment plantation was quantified at an corresponding area of 10 m x 10 m at the beginning of the experiment.

According to a methodical approach of BREDEMEIER (1987) the leaching of K, Mg, and P out of the soil was quantified from water flux measurements and the chemical analyses of the soil solution in different soil depths. The water flux in the soil was quantified by weekly tensiometer measurements (T 3 UMS Umweltanalytische Meßsysteme, München). The soil hydraulic properties were determined from the pF relationship investigated for soil depths of 0-15 cm, 15-30 cm, 30-45 cm, 45-60 cm, 60-75 cm, and 75-90cm (RICHARDS 1949). The tensiometers were installed at 5 cm, 15 cm, 35 cm, 65 cm, and 125 cm depths. The element content of the soil solution was quantified in one-week-intervals at soil depths of 10, 20, 60 cm and 120 cm. The tensiometers and the suction cups (P80, UMS Umweltanalytische Meßsysteme, München) were installed in a distance of 1 and 2 m from the trunk of 4 *Carapa* trees of the monoculture, 4 *Carapa* trees of the enrichment plantation, and at 6 places within the secondary vegetation of the enrichment plantation. The soil solution was sampled with a vacuum of -700 hPa. of the suction cups.

The K, Mg, and P balance of the soil of the two plantations was calculated for monthly intervals for the 83 months of plantation growth as the sum of nutrient input minus the sum of nutrient output. Water surface runoff was neglected in this calculation (declination of the study site less than 3 %).

### **Growth dynamics of the monoculture and the enrichment plantation**

The biomass of the 2 plantations was quantified at 5, 39, 47, 59, and 83 months age. Based on the breast height diameter, the tree height, the height of the crown, the diameter, and the density of the crown of all *Carapa* trees of the monoculture and the

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enrichment plantation 4 *Carapa* trees of the monoculture and the enrichment plantation were selected for excavation and the oven dry biomass (105° C) of the trees was quantified. The significance of the relationship of the dendrometric parameters and the biomass of the trees varied between 84 % and 97 %.

The spontaneous vegetation of the cover crops in the monoculture was also quantified at 5, 39, 47, 59, and 83 months age by destructive harvesting of an area of 4 m x 4 m. The biomass of the secondary vegetation of the enrichment plantation was quantified by means of destructive harvesting of an area of 10 m x 10 m at the beginning of the experiment and dendrometric measurements (breast height diameter, tree height, height of the crown, diameter and density of the crown) carried out at 5, 39, 47, 59, and 83 months age in 4 fallow lines of the enrichment plantation according to DÜNISCH and SCHWARZ (in press).

The tree height of 8 *Carapa* trees of the monoculture and 8 *Carapa* trees of the enrichment plantation was quantified in monthly intervals. The significance of the result was cross checked by tree height measurements of all trees carried out at an age of 5, 39, 47, 59, and 83 months age.

The radius increment of 3 trees of the monoculture and 3 trees of the enrichment plantation was quantified in monthly intervals by repeated wounding of the cambium (1 to 12 months and 36 to 83 months old plants). The cambium was wounded with a scalpel according to KURODA and SHIMAJI (1984). Fixation of the samples was carried out with ethanol (70%) and the radius increment was studied by light microscopy according to DÜNISCH et al. (1999 b). In addition the radius increment of 8 trees each of the monoculture and the enrichment plantation was quantified by dendrometer measurements (4 points of measurements per tree) according to VOGEL (1994).

### **Statistical analyses**

As to evaluate the statistical significance of the study the Gauß' error of the investigation (biomass determination x nutrient flux determination) was quantified (comp. DÜNISCH and SCHWARZ, in press).

Data were examined by analysis of variance (ANOVA) using age of the plantation and the plantation system (monoculture, enrichment plantation) as treatment factors in a completely randomized design. The significance of the results was tested for  $P < 0.05$ ,  $P < 0.01$ , and  $P < 0.001$  (Fisher's F-test).

### **Results**

#### **K, Mg, P fluxes and balances of the monoculture and the enrichment plantation**

The K, Mg, and P balance of the soil (Fig. 6a-c) of the monoculture and the enrichment plantation was calculated for monthly intervals from the nutrient input by rain, throughfall and stemflow (Fig. 2a-c), and by litter decomposition (Fig. 3a-c),

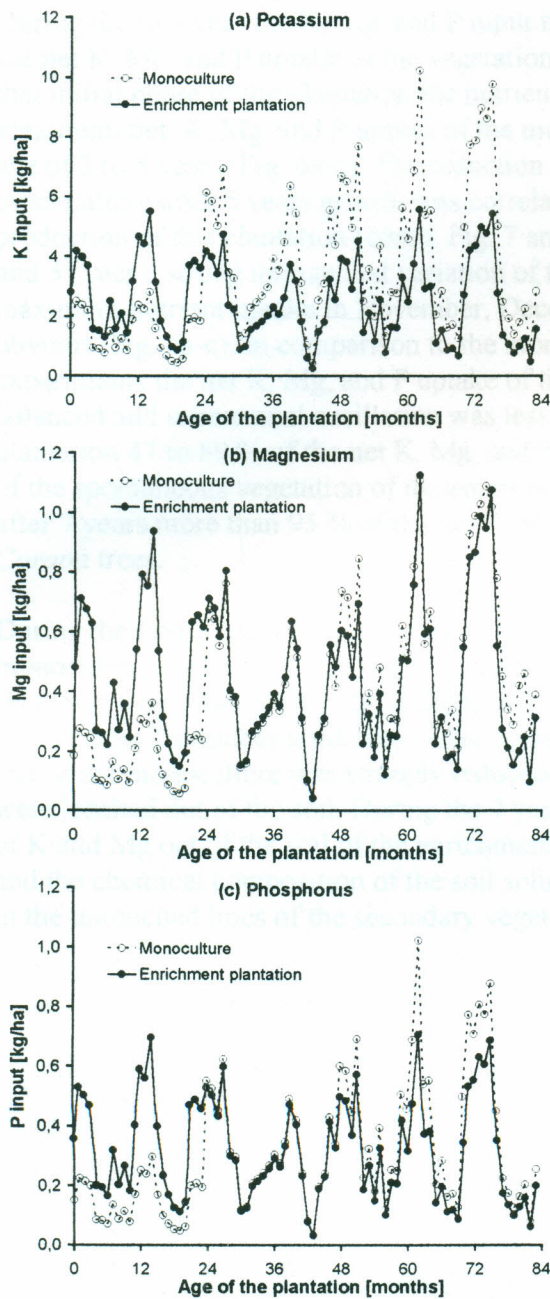
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from the nutrient output by nutrient uptake of the vegetation (Fig. 4a-c) as well as by leaching of nutrients out of the soil (Fig. 5a-c). The Gauß' error of the calculation of the nutrient fluxes in the plantation varied between 24 and 46 %.

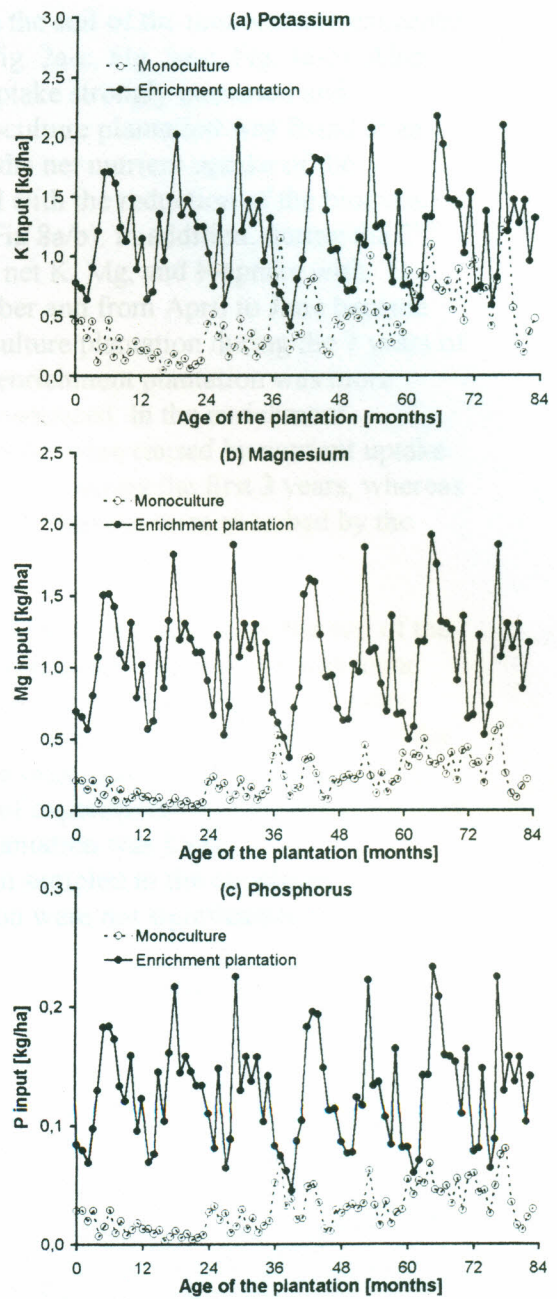
The K input into the soil of the plantations by precipitation, throughfall, and stemflow was high compared to the Mg, and P input (Fig. 2a-c). In addition, a strong seasonal variation of the nutrient input was found, which was correlated with the seasonal variation of the precipitation. Consequently highest K, Mg, and P input was found during the period from November until May. Due to the high K, Mg, and P content of *Carapa* leaves (comp. DÜNISCH et al., 1999 a) the nutrient input to soil in the monoculture increased with increasing age of the plantation. After 2 years of plantation growth the K input by precipitation and leaching from the crown of the trees in the monoculture exceeded the corresponding data of the enrichment plantation. The seasonal oscillation of the K input was higher in the monoculture plantation than in the enrichment plantation.

The K and P input into the soil of the 2 plantations by litterfall and litter decomposition was low compared to the K and P input due to precipitation, throughfall and stemflow (Fig. 2a and c, Fig. 3a and c), whereas litter decomposition was of main importance for the Mg supply of the plantations (Fig. 3b). Maximum nutrient input into the soil by litter decomposition was found from May until July, approximately 1 to 2 months after a significant increase of the microbial activity of the soil. As a rule, a higher K, Mg, and P input into the soil by litter decomposition was found in the enrichment plantation compared to the monoculture (Fig. 3a-c). Due to a life cycle of the *Carapa* leaves of 20 to 25 months only litter from the cover crops *Pueraria* and *Homolepis* were available for decomposition in the monoculture during the first 2 years of plantation growth. During the subsequent 5 years only a slow increase of litter decomposition was found in the monoculture, whereas nutrient cycling by litter decomposition remained on a high level in the enrichment plantation.





**Fig. 2a-c:** Monthly (a) K, (b) Mg, and (c) P input [kg/ha] by rain, throughfall, and stemflow into the soil of the monoculture and the enrichment plantation during the 84 months of experiments (December 1991 until November 1998).



**Fig. 3a-c:** Monthly (a) K, (b) Mg, and (c) P input [kg/ha] by litterfall and litter decomposition into the soil of the monoculture and the enrichment plantation during the 84 months of experiments (December 1991 until November 1998).

During the first year the K, Mg, and P input into the soil of the monoculture exceeded the net K, Mg, and P uptake of the vegetation (Fig. 2a-c, Fig. 3a-c, Fig. 4a-c). After that initial phase of the plantation the nutrient uptake strongly increased and maximum net K, Mg, and P uptake of the monoculture plantation was found at an age of 3 to 5 years (Fig. 4a-c). The reduction of the net nutrient uptake of the monoculture after 5 years growth was correlated with the reduction of the biomass production of this plantation (comp. Fig. 7 and Fig 8a/b). In addition, during the 2<sup>nd</sup> and 5<sup>th</sup> year a strong intraannual variation of the net K, Mg, and P uptake with maximum nutrient uptake in November, December and from April to June became obvious (Fig. 4a-c). In comparison to the monoculture plantation during the 7 years of experiments the net K, Mg, and P uptake of the enrichment plantation was more balanced and intraannual oscillation was less pronounced. In the enrichment plantation 47 to 89 % of the net K, Mg, and P uptake were caused by nutrient uptake of the spontaneous vegetation of the enrichment lines during the first 3 years, whereas after 7 years more than 95 % of the net K, Mg, and P uptake were absorbed by the *Carapa* trees.

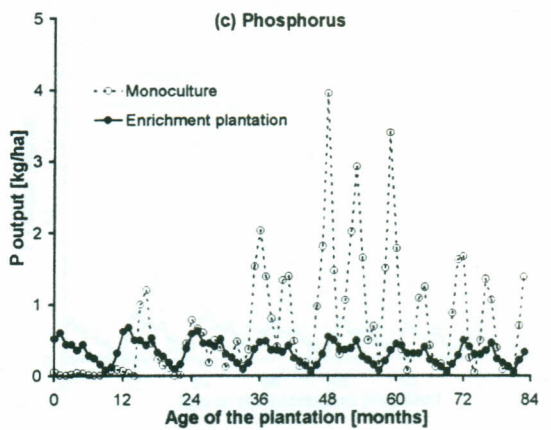
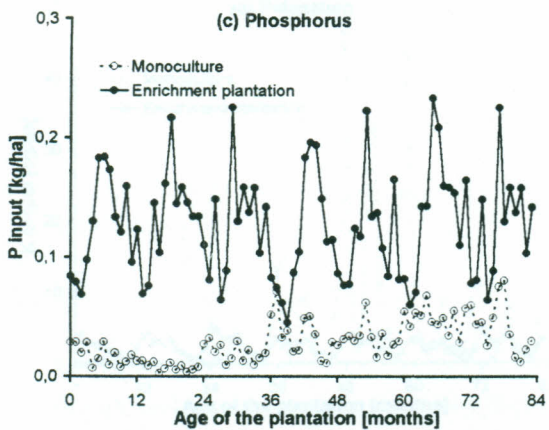
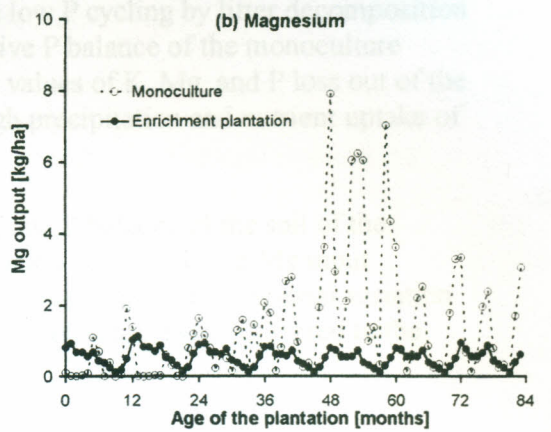
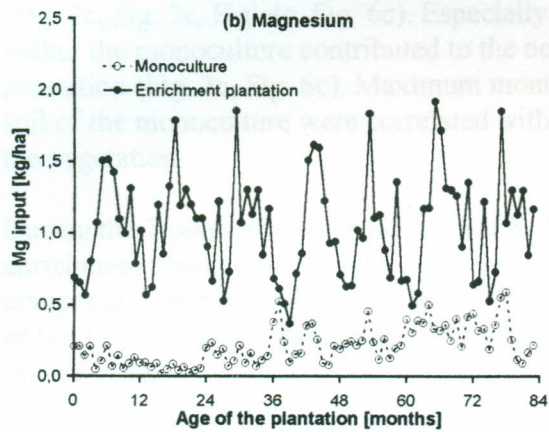
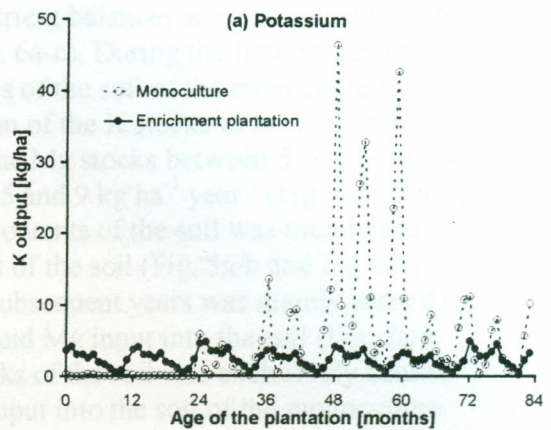
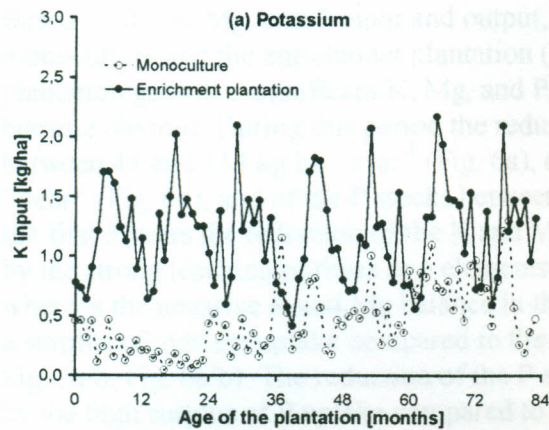
During the first 3 years high amounts of K and Mg were leached out of the soil of the monoculture plantation (Fig. 5a/b), whereas no significant leaching of P was found (Fig. 5c). Maximum K and Mg leaching out of the soil was found during the rainy season from December until May. After 3 years growth K and Mg leaching out of the soil of the monoculture was strongly reduced and only small amounts of K and Mg were leached out of the soil. During the 7 years of experiments no significant leaching of K and Mg out of the soil of the enrichment plantation was found. The water fluxes and the chemical composition of the soil solution sampled in the enrichment lines and in the untouched lines of the secondary vegetation were not significantly different.



Fig. 4a-c) Monthly (a) K, (b) Mg, and (c) P output (g ha<sup>-1</sup>) by net element uptake of the vegetation out of the soil of the monoculture and the enrichment plantation during the 7 months of experiments (December 1991 until November 1998).



Fig. 5a-c) Monthly (a) K, (b) Mg, and (c) P output flux (kg ha<sup>-1</sup>) from the soil of the monoculture and the enrichment plantation during the rainy season (December 1991 until November 1998).

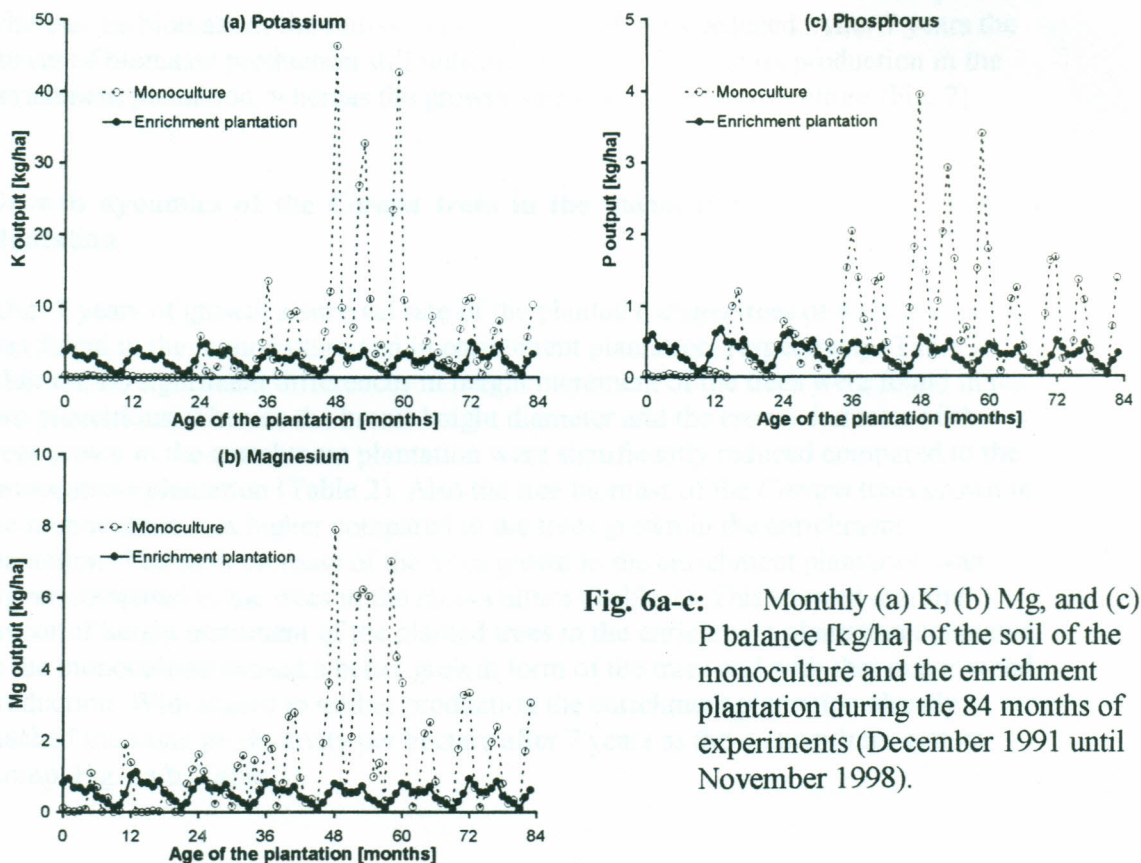


**Fig. 4a-c:** Monthly (a) K, (b) Mg, and (c) P output [kg/ha] by net element uptake of the vegetation out of the soil of the monoculture and the enrichment plantation during the 84 months of experiments (December 1991 until November 1998).

**Fig. 5a-c:** Monthly (a) K, (b) Mg, and (c) P output [kg/ha] by leaching out of the soil of the monoculture and the enrichment plantation during the 84 months of experiments (December 1991 until November 1998).

Based on the K, Mg, and P input and output, nutrient balances were calculated for the monoculture and the enrichment plantation (Fig. 6a-c). During the first 5 years of plantation growth a significant K, Mg, and P loss of the soil of the monoculture became obvious. During this period the reduction of the K stocks of the soil varied between 44 and 114 kg ha<sup>-1</sup> year<sup>-1</sup> (Fig. 6a), of the Mg stocks between 5 and 11 kg ha<sup>-1</sup> year<sup>-1</sup> (Fig. 6b), and of the P stocks between 0.5 and 9 kg ha<sup>-1</sup> year<sup>-1</sup> (Fig. 6c). During the first 3 years the reduction of the K and Mg contents of the soil was mainly caused by the strong leaching of these two elements out of the soil (Fig. 5a/b and Fig. 6a/b), whereas the negative K and Mg balance in the subsequent years was mainly caused by a surplus of nutrient uptake compared to the K and Mg input into the soil (Fig. 2a/b, Fig. 3a/b, Fig. 6a/b). The reduction of the P stocks of the soil was exclusively caused by the high surplus of P uptake compared to P input into the soil of the monoculture (Fig. 2c, Fig. 3c, Fig. 4c, Fig. 6c). Especially the low P cycling by litter decomposition within the monoculture contributed to the negative P balance of the monoculture plantation (Fig. 3c, Fig. 6c). Maximum monthly values of K, Mg, and P loss out of the soil of the monoculture were correlated with high precipitation and nutrient uptake of the vegetation.

During the 7 years of the experiment the K, Mg, and P balance of the soil of the enrichment plantation was stabilised (Fig. 6a-c) and a low surplus of Mg input compared to nutrient output was detected (Fig. 6b). In addition the seasonal variation of the K, Mg, and P balance was less in the enrichment plantation compared to the monoculture.



**Fig. 6a-c:** Monthly (a) K, (b) Mg, and (c) P balance [kg/ha] of the soil of the monoculture and the enrichment plantation during the 84 months of experiments (December 1991 until November 1998).

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## **Biomass production of the monoculture and the enrichment plantation**

The Gauß' error of the biomass calculation of the 2 plantations for an area of one hectare was 3 % for the monoculture and 21 % for the enrichment plantation, respectively.

The biomass production of the *Carapa* monoculture strongly increased during the first 4 years of growth (Fig. 7). Due to the strong competition with the *Carapa* trees the cover crops disappeared already after 3 years of growth and as a consequence the litter layer of the soil exclusively consisted of the slow decomposing litter of *Carapa* (comp. Fig. 3a-c). After 59 months growth the biomass production of the *Carapa* monoculture was strongly reduced and only a slight increase of the biomass was detected from the 59<sup>th</sup> to the 83<sup>rd</sup> month of growth.

Due to the moderate silvicultural treatment carried out in the enrichment plantation a biomass stock of approximately 80 t/ha of secondary vegetation remained in the area before planting (Fig. 7). During the 7 years of experiments the biomass stock of the enrichment plantation was higher compared to the monoculture (at an age of 59 months differences were not significant at  $p < 0.05$ ). In contrast to the monoculture more than 90 % of the biomass of the enrichment plantation were located in the biomass of the untouched fallow vegetation during the first 4 years, but after 5 years a significant increase of the biomass was found, which was mainly caused by a strong biomass production of the *Carapa* trees (Fig. 7, Fig. 8a/b). After 7 years approximately 23 t/ha of the biomass of the enrichment plantation were located in the *Carapa* trees, whereas the biomass of the fallow vegetation was slightly reduced. After 7 years the curves of biomass production still indicated sustainable biomass production in the enrichment plantation, whereas the growth stagnated in the monoculture (Fig. 7).

## **Growth dynamics of the *Carapa* trees in the monoculture and the enrichment plantation**

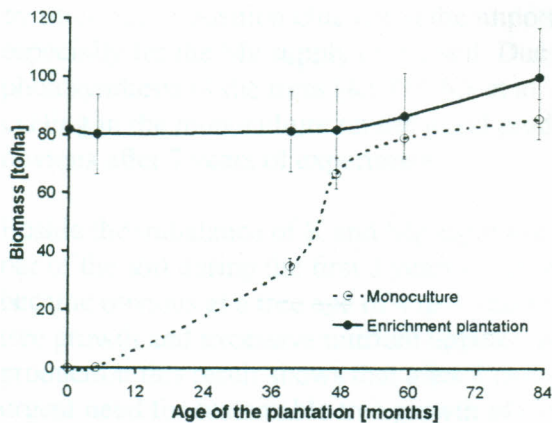
After 7 years of growth a survival rate of the planted *Carapa* trees of 83 % and 80 % was found in the monoculture and in enrichment plantation, respectively (Table 2). In addition, no significant differences in height increment of the trees were found in the two plantations, whereas the breast height diameter and the crown diameter of the trees grown in the enrichment plantation were significantly reduced compared to the monoculture plantation (Table 2). Also the tree biomass of the *Carapa* trees grown in the monoculture was higher compared to the trees grown in the enrichment plantation. The stem biomass of the trees grown in the enrichment plantation was higher compared to the trees in the monoculture (Table 2). This showed that the favour of height increment of the planted trees in the enrichment plantation compared to the monoculture caused a better growth form of the trees and with that major wood production. With regard to timber production the enrichment plantation already reached the same productivity per hectare after 7 years as the monoculture system (comp. Fig. 1a/b, Table 2).

**Table 2:** Survival rate [%], tree height [m], breast height diameter [cm], crown diameter [m], tree biomass [kg], and stem biomass [kg] of 7 years old *Carapa guianensis* grown in the monoculture and in the enrichment plantation (mean values and standard deviation).

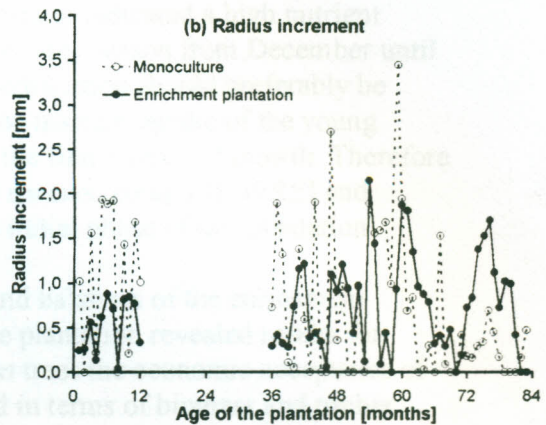
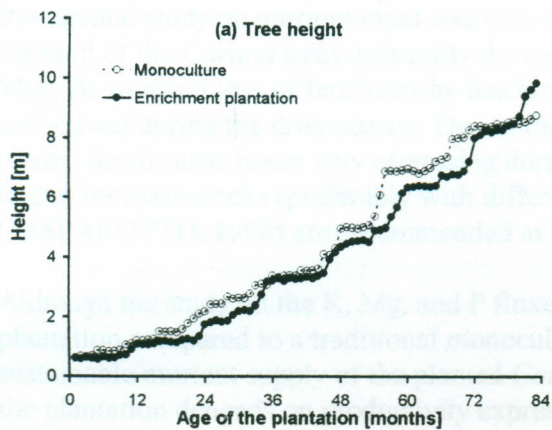
Dendrometric parameter	Monoculture	Enrichment plantation
Survival rate [%]	83	80
Tree height [m]	8.97±1.62	9.30±3.17
** Breast height diameter [cm]	13.10±2.49	9.82±3.15
* Crown diameter [m]	4.02±1.32	2.85±1.24
*** Tree biomass [kg]	81±13	58±7
*** Stem biomass [kg]	18±2	24±1

Intraannual investigations on the course of the height increment showed no distinct periodicity in height increment during the first 3 years of growth (Fig. 8a). Later maximum values of height increment were found in January and February. Biomass production as well as height increment were increasing less in the monoculture after 6 years, whereas still after 7 years an exponential height increment of *Carapa* grown in the enrichment plantation was found (Fig. 8b).

The lower breast height diameter of the trees grown in the enrichment plantation compared to the monoculture was caused by the reduced radius increment of the trees during the first 4 years of growth (Fig. 8b, Table 2). After the 5<sup>th</sup> year the annual radius increment of the trees grown in the enrichment plantation exceeded the annual radius increment of the trees grown in the monoculture. During the first 5 years of growth maximum values of monthly radius increment were found during the rainy season, but extremely high precipitation caused a growth stagnation. After the 5<sup>th</sup> year the seasonal variation in radius increment became more regular with high increment from January until July and low increment or even cambial dormancy during the dry period (Fig. 8b). Due to a stronger oscillation of environmental impact during the first 6 years of the experiment the seasonal variation of the monthly radius increment of *Carapa* was higher in the monoculture compared to the enrichment plantation (comp. Fig. 2a-c, Fig. 3a-c, Fig. 5a-c, Fig. 6a-c, Fig. 8b).



**Fig. 7:** Biomass of the vegetation [t/ha] of the monoculture and the enrichment plantation during the 84 months of experiments (December 1991 until November 1998).



**Fig. 8a/b:** (a) Tree height and (b) monthly radius increment of *Carapa guianensis* grown in the monoculture and the enrichment plantation during the 84 months of experiments (December 1991 until November 1998).

## Discussion and conclusions

In agreement to many field studies carried out on "terra firme" sites of the Central Amazon, our study indicated low K, Mg, and P stocks of the soil of the experimental area (STARK, 1970; SANCHEZ, 1976; ZECH et al., 1998). With regard to the installation of sustainable plantations for wood production in this region the stabilisation of the K, Mg, and P stocks of the soil is of main importance (KLINGE, 1976; JORDAN, 1982; SANCHEZ et al., 1982; SZOTT and PALM, 1996). Our comparative study on the K, Mg, and P balances of a monoculture and an enrichment plantation of the important timber tree species *Carapa guianensis* Aubl. showed that the nutrient output is higher than the nutrient input of the soil of a traditional monoculture after 7 years of plantation growth, whereas the fallow vegetation of the enrichment plantation favours the stabilisation of the nutrient stocks. Especially the strong reduction of the K and Mg leaching out of the soil of the enrichment plantation and the better external nutrient cycling due to litterfall and litter decomposition compared to the monoculture emphasises the ecological function of the secondary vegetation for the recuperation of cleared primary forests in this area (UHL et al. 1981). A comparison of the nutrient input into the soil by wet and dry deposition and

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by litter decomposition elucidated the importance of the secondary vegetation especially for the Mg supply of the soil. Due to the importance of Mg for the photosynthesis of the trees (KÜPPERS et al. 1985) a strong impact of the reduced Mg cycling in the monoculture on the wood production of the *Carapa* trees is already obvious after 7 years of experiments.

Beside the imbalance of K and Mg input and output caused by high element leaching out of the soil during the first 3 years of growth a strong deficit of the K, Mg and P became obvious at a tree age of 4 to 6 years in the monoculture (phase of exponential tree growth and excessive nutrient uptake). In comparison to the course of biomass production this result shows that after 5 to 6 years fertilisation with K, Mg, and P is an urgent need for sustainable tree growth of *Carapa* in the monoculture plantation. The intraannual study on nutrient input and nutrient output indicated a high nutrient demand of the *Carapa* trees especially during the rainy season from December until May. As to avoid loss of fertilisers by leaching fertilisation should preferably be carried out during the drier season. Due to the low nutrient uptake of the young plants, fertilisation is not very promising during the first 3 years of growth. Therefore higher biomass stocks (preferably with different species; comp. LIEBEREI and GASPAROTTO, 1998) are recommended at the initial phase of this plantation.

Although the study on the K, Mg, and P fluxes and balances of the enrichment plantation compared to a traditional monoculture plantation revealed results for sustainable nutrient supply of the planted *Carapa* trees the economic acceptance of the plantation depends on productivity expressed in terms of biomass and timber production and wood quality (ZOBEL and BUIJTENEN 1989; BAUCH and DÜNISCH, in press). For enrichment plantations the competition (light, water, mineral elements) with the secondary vegetation often is a serious problem for the cultivation of trees for wood production in enrichment plantations (LAMPRECHT, 1986). This study carried out with *Carapa* indicated a sustainable biomass production of *Carapa* in the enrichment plantation after 7 years of growth, whereas tree growth stagnated in the monoculture. The biomass of trees grown in the enrichment plantation was slightly reduced compared to the biomass of trees grown in the monoculture. Nevertheless due to the strong apical dominance during the first years and a subsequent increase in cambial growth of the stem of *Carapa* grown in the enrichment plantation a higher wood production was found compared to the trees grown in the monoculture. This indicates a good adaptation of *Carapa* to the site conditions and the competition in the enrichment plantation due to its wide ecological amplitude (PENNINGTON et al, 1981). In addition a better wood quality of *Carapa* grown in the enrichment plantation compared to *Carapa* grown in the monoculture could be expected due to the apical dominance and the more homogeneous growth dynamics in wood formation of the trees grown in the enrichment plantation (DÜNISCH et al., 1999 b; BAUCH and DÜNISCH, in press). Although the number of planted *Carapa* trees was low per hectare in the enrichment plantation, already after 7 years the enrichment plantation reaches 61 % of the productivity (annual wood production per hectare) of the monoculture.

From these results it was concluded that enrichment plantations are an appropriate tool for the stabilisation of the nutrient stocks of the poor soils of "terra firme" sites of the Central Amazon. Due to the strong competitiveness and the ecological adaptation



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of *Carapa guianensis* Aubl. the cultivation of this species in enrichment plantations is also promising from an economic point of view. For the application of the results obtained from the present experiment and an optimisation of the enrichment plantation a calculation of profits and costs is recommended.

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### 2.2.3. Cambial growth dynamics of *Swietenia macrophylla* King, *Carapa guianensis* Aubl., and *Cedrela odorata* L.

#### Introduction

In the Central Amazon the demand for wood for the local market and for export is exclusively satisfied from primary forests, which leads to strong exploitation especially of high quality species such as mahogany (comp. Loureiro et al. 1979, Dahms 1989, Mayhew and Newton 1998). In addition, logging in primary forests is often associated with serious negative affects on the ecosystem and a degradation of the area (Lamprecht 1986, Brunig 1996). As to counteract this tendency during the last years special attend is given to the cultivation of native tree species for high quality timber production in plantations (Lamprecht 1986, Whitmore 1995, Brunig 1996, Bauch et al. 1999). Particularly on the “terra firme” of the Amazon basin complex mixed plantations are promising for sustainable production (Sanchez 1976, Lieberei and Gasparotto 1998, Dunisch et al. in press). For the optimisation of plantations knowledge on the relationship of exogenous input and growth characteristics of the planted trees are a basic demand. Until today the knowledge about the growth dynamics and the influence of exogenous impact on the wood formation of most of the native timber tree species of the Amazon is still restricted (Jacoby 1989, Baas et al. 1995).

Investigations on the periodicity of cambial growth and the formation of increment zones of tropical trees revealed different pattern of structural variation in wood formation (Coster 1927,1928, Mariaux 1969, Worbes 1988, 1999, Detienne 1989). Dendroecological studies showed that on the one hand the structural variation in wood formation of tropical trees could by annual and correlated with exogenous input such as water supply and inundation (Worbes 1988, Pumijumnong et al. 1995). On the other hand wood formation of tropical trees often was not annual and not correlated with exogenous input (Jacoby 1989, Breitspecher and Bethel 1990, Limba ?).

With regard to exogenous input the seasonal variation of the water supply is of main importance in the Central Amazon (Dunisch et al. 1999 a). Due to the significance of the water supply for the turgor of differentiating xylem cells (Larson 1969, Dunisch et al. 1994), the biosynthesis of carbohydrates (Langenfeld-Heyser 1987), and the

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transport of substances (Kramer 1985, Kozłowski et al. 1991) the course of wood formation might be strongly correlated with the water supply.

The growth of *Meliaceae* is often limited by the attack of the insect *Hypsipylla grandella*, which causes severe damage of the primary meristems and the pith of the trees (Whitmore 1976, Newton et al. 1993). According to the concept for the compartmentalization of wounds proposed by Shigo (1984) wounding of the primary meristem caused by *Hypsipylla grandella* might influence wood formation at the cambium as well.

In addition field studies carried out with African mahagonys indicated high growth stresses in the xylem of some species of the *Meliaceae*, which influenced the microscopical structure of the wood (Kuebler 1987).

In order to characterize the relationship of exogenous input and the cambial growth dynamics of *Swietenia macrophylla* King, *Carapa guianensis* Aubl. and *Cedrela odorata* L. (*Meliaceae*), in this study the pattern of growth increments expressed in terms of increment labelling and the synchronisation of increment curves were investigated and the intraannual growth dynamics in wood formation were dated. Special regard was given to the influence of the water supply, insect attack (*Hypsipylla grandella*) and wounding, and growth stresses on the dynamics in wood formation and the formation of increment zones.

## Material and Methods

### Study sites and tree selection

For this study in total 61 trees of *Swietenia macrophylla* King, 94 trees of *Carapa guianensis* Aubl. and 89 trees of *Cedrela odorata* L. grown in plantations with defined age and grown in primary forests were selected (Table 1). Sample collection was carried out in the region of Manaus, Amazônia (03°08' S, 59°52' W), the region of Santarém, Pará (02°52' S, 54°45' W), and the region of Aripuanã, Mato Grosso (10°09' S, 59°26' W).

*Manaus region:* Sample collection of 8 years old plantation grown *Swietenia*, *Carapa*, and *Cedrela* as well as of 3 primary forest grown *Carapa* trees was carried out on the research station of the EMBRAPA Amazônia Ocidental, 24 km out of the city of Manaus. The area is located at approximately 50 m above sea level with an annual precipitation of about 2,500 mm (Min. 110 mm (August) / Max. 295 mm (February) per month), a mean air temperature of 26.4° C, and a mean humidity of the air of 87 %. According to categorisation, the soil is a poor xanthic Ferralsol (FAO, 1990) with a low cation exchange capacity. This study site is used for interdisciplinary research projects within the Brazilian-German cooperation program "SHIFT" since 1992 (comp. BAUCH et al., 1999). In addition two 17 years old *Carapa* trees of a plantation of the National Research Institute of Amazonas (INPA) located 45 km north of Manaus with corresponding climatic and soil conditions were selected (comp. Bauch and Dunisch in press).

*Santarem region:* Sample collection of eight 57 years old plantation grown *Swietenia*, *Carapa*, and *Cedrela* was carried out on the research station of the EMBRAPA Amazônia Oriental in Belterra, 35 km south of the city of Santarem. In addition sample collection of 3 primary forest grown *Carapa* trees was carried out at the "Floresta Nacional de Tapajós" located approximately 55 km south of Santarem. Climatic and soil conditions correspond to the Manaus region, but soil analyses (Dunisch unpublished) showed a higher K and Mg content of the soil in the Santarem region compared to the Manaus region (Schroth et al. in press).

*Aripuanã region:* Near the city of Aripuanã xylem samples were collected from two 23 years old plantation grown *Swietenia* trees planted by small farmers. In addition eight primary forest grown *Swietenia* and *Cedrela* trees grown in the "Reserva Rio Branco" 50 km west of the city were selected (comp. Loureiro and Lisboa 1979). The experimental area is located approximately 190 m above sea level with an annual precipitation of approximately 3000 mm (wettest months February/March, driest months September/October) and a mean temperature of 24.9° C. Soil analyses (Dunisch unpublished) showed a higher soil fertility of this site compared to the Manaus and the Santarem sites (comp. Lisboa et al. 1976).

**Table 1:** Number and age [years; n.d. not determined] of plantation and primary forest (PF) grown *Swietenia*, *Carapa*, and *Cedrela* selected for the study of pattern of growth increments (structure/width of increment zones, synchronisation of increment curves), the study of intraannual cambial growth dynamics (by means of dendrometer measurements, the pinning method, and cambium samples), as well as the relationship of the water supply, insect attacks and growth stresses and the growth dynamics of the trees.

Species	Swietenia				Carapa				Cedrela		
	8	23	57	PF (n.d.)	8	17	57	PF (n.d.)	8	57	PF (n.d.)
Structure/width of increment zones	43	2	8	8	78	2	8	6	73	8	8
Synchronisation	43	2	8	8	78	2	8	6	73	8	8
Dendrometer (1996-1999)	33				33				33		
Pinning method (1995-1999)	7				7				7		
Cambium samples (1997-1999)	10				10				4		
Water supply	37				44				6		
Insect attack/wounding	3				3				3		
Growth stresses	3	2	2	2	3		3	3	3	3	2

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### Microscopical characteristics and width of increment zones

The microscopical characteristics and the width of increment zones of all trees were analysed on discs or xylem samples collected with an increment borer in the four cardinal directions (Table 1). Sample collection was carried out at a tree height of 1 m. In addition stem discs were sampled every 50 cm stem upwards from three 8 years old plantation grown *Swietenia*, *Carapa*, and *Cedrela* trees. From two primary forest grown *Swietenia*, *Carapa*, and *Cedrela* trees stem discs were also analysed at 4 m and 10 m height.

The structure and width of increment zones were studied by light microscopy. The increment curves were cross-dated within and between trees according to Fritts (1976) and Schweingruber (1988) using percentage of parallel run and correlation analyses as statistical tools (comp. Aniol 1983).

### Dating of intraannual growth dynamics

The intraannual growth dynamics of the cambium were dated by means of dendrometer measurements, the "pinning method", and cambium samples (Table 1).

*Dendrometer measurements:* The radius increment of 32 4 to 8 years old plantation grown *Swietenia*, *Carapa*, and *Cedrela* trees was quantified by dendrometer measurements (4 points of measurements per tree, accuracy 0.1 mm) carried out at 1.3 m height according to VOGEL (1994). The measurements were carried out in weekly intervals from 1996 until 1999. In addition high sensitivity strain gauges (accuracy 0.01 mm) were installed at 1 tree of each species at 0.5 m height and data were sampled automatically in 10 minutes intervals in 1999.

*"Pinning method":* The periods of cell formation of 7 trees of each species were dated in monthly intervals by repeated wounding of the cambium (3 to 8 years old trees). The cambium was wounded with a scalpel according to Kuroda and Shimaji (1984). Fixation of the samples was carried out with ethanol (70%) and the monthly radius increment was studied by light microscopy in all three anatomical directions according to Dunisch et al. (1999 b). Accurate increment measurements were only possible by means of the "pinning method" for monthly increments higher than 0.3 mm.

*Cambium samples:* Mini-increment cores ( $\varnothing$  1.4 mm) of phloem, cambium, and xylem tissue were extracted from 10 8 years old plantation grown and 2 primary forest grown *Swietenia*, *Carapa*, and *Cedrela* trees (comp. Baucker et al. 1998, Sack 1998). The samples were fixed with 70 % alcohol or a FEA solution and embedded in polyethylene glycol. Cross sections (5  $\mu$ m thickness) were prepared by a LKB Historange 2218-020 microtome. The slides were stained by safranin and astrablue and studied by light microscopy with polarized light.

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## Mapping of insect attacks (*Hypsipyla grandella*) and microscopical study of the wound reaction

The attack of the *Swietenia*, *Carapa*, and *Cedrela* trees grown in the plantation of EMBRAPA Ocidental near Manaus was monitored in weekly intervals by field workers. As to study the influence of the attack 3 attacked trees of each species were felled in 1998. The wound reaction was studied from the attacked buds of the trees stem downwards by light microscopy in all three anatomical directions.

### Determination of growth stresses

The growth stresses of plantation and primary forest grown trees expressed in terms of deformation of extracted wood samples (comp. Kuebler 1987) were studied in the longitudinal and the tangential direction. Xylem samples of the outer xylem of the trees were collected in different tree heights with an increment borer ( $\varnothing$  5 mm) and were shock frozen with liquid nitrogen in the field. The deformation of the frozen samples was analysed with an accuracy of  $\pm 27\%$  with a light microscope according to Dunisch et al. (1995).

### Water supply of the soil

The water supply of the soil was studied by means of precipitation measurements and the study of the suction force of the soil. Data on the precipitation of the Manaus, the Santarem, and the Aripuanã region were available from meteorological stations of EMBRAPA Ocidental in Manaus, EMBRAPA Oriental in Belem, and the INPA in Manaus. Weekly tensiometer measurements (T3, UMS Munchen) were carried out in the plantations and the primary forest of the Manaus site in 10 cm, 20 cm, 60 cm, and 120 cm depth from 1995 until 1999 (comp. Dunisch et al. in press).

## Results

### Pattern of growth increments in the xylem of *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata*

Distinct growth increments were found in the xylem of *Swietenia*, *Carapa*, and *Cedrela*, but microscopical investigations showed different types and distribution of increment labelling within and between species (Table 2).

In the xylem of the 61 trees of *Swietenia macrophylla* 3 types of increment zones were observed (Table 2). The discs exhibited continuously developed vessel bands (with and without paratracheal-confluent parenchyma cells, Fig. 2a), parenchyma bands (Fig. 2b), and bands of resin channels (Fig. 2c). Labelling of increment zones by vessel bands was more common in the juvenile wood than in the adult wood, whereas increment labelling of trees older than 8 years was dominated by parenchyma bands (Table 2). Continuous bands of resin channels were rarely found and more common in the juvenile than in the adult wood, but further bands of resin channels



restricted to short dimensions around the disc were found in the juvenile and the adult wood as well.

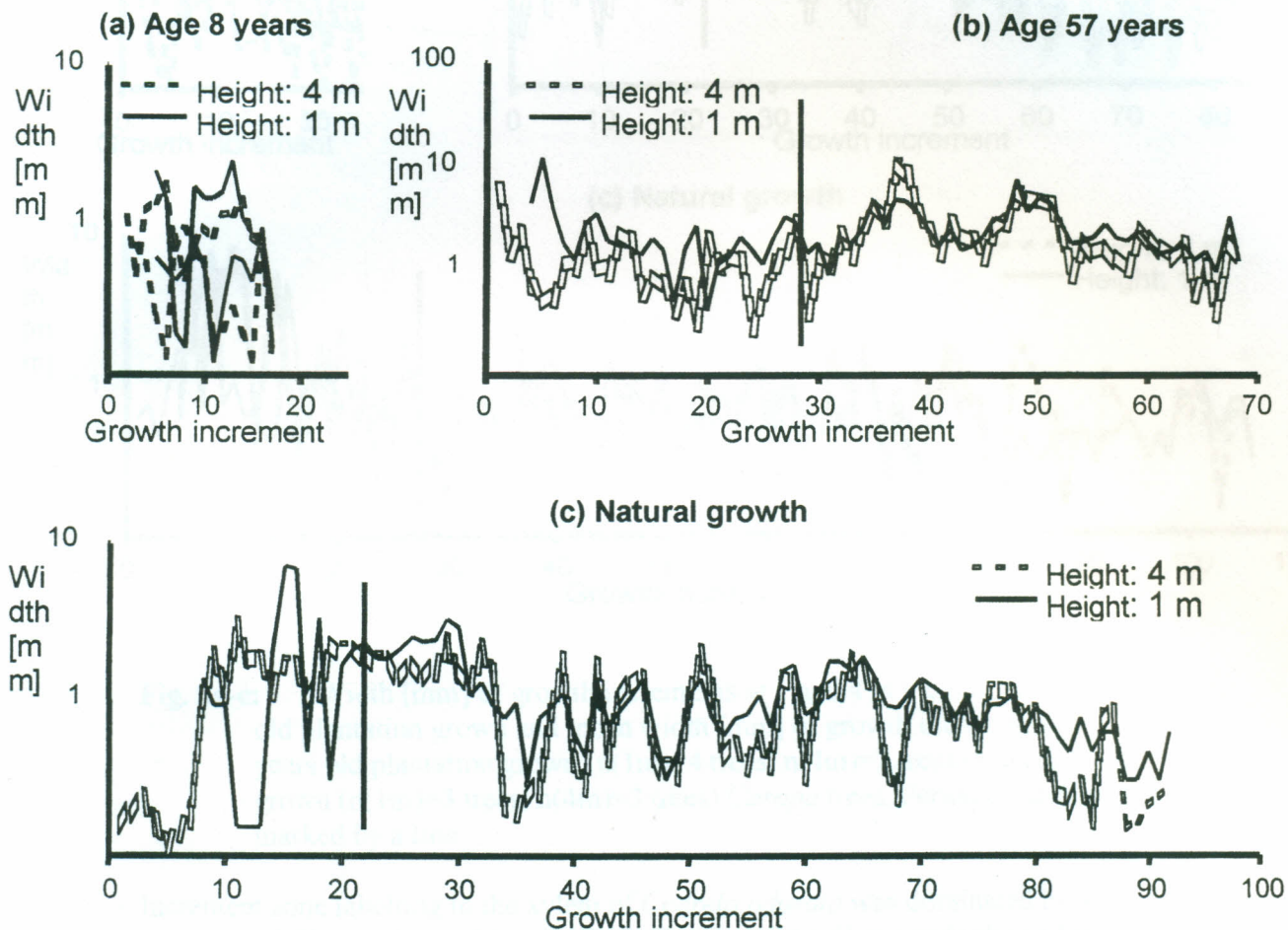
**Table 2:** Number of increment zones in the xylem of the stem (height 1 m) of the 8, 17, 23, and 57 years old plantation grown and two primary forest (age n.d. not determined) grown *Swietenia*, *Carapa*, and *Cedrela* trees.

Species	Type of increment labelling	Age 8 years	Age 17 years	Age 23 years	Age 57 years	Primary forest (n.d.)
Swietenia	Vessel band	6-9	-	4-7	5-7	7-11
	Parenchyma band	4-9	-	19-26	56-64	69-81
	Fibre band	-	-	-	-	-
	Band of resin channels	2-3	-	4-5	0-2	0-2
	<b>Total</b>	13-21	-	31-34	65-69	82-88 (19-20 cm)
Carapa	Vessel band	10-14	7-11	-	9-16	11-20
	Parenchyma band	4-7	12-15	-	65-73	84-90
	Fibre band	-	-	-	-	-
	Band of resin channels	1-3	0-3	-	3-7	5-9
	<b>Total</b>	19-24	26-29	-	82-89	99-113 (13-14 cm)
Cedrela	Vessel band	8-10	-	-	57-59	122-123
	Parenchyma band	0-2	-	-	-	-
	Fibre band	8-10	-	-	57-59	122-123
	Band of resin channels	0-2	-	-	-	0-2
	<b>Total</b>	8-12	-	-	57-59	122-124 (23-27 cm)

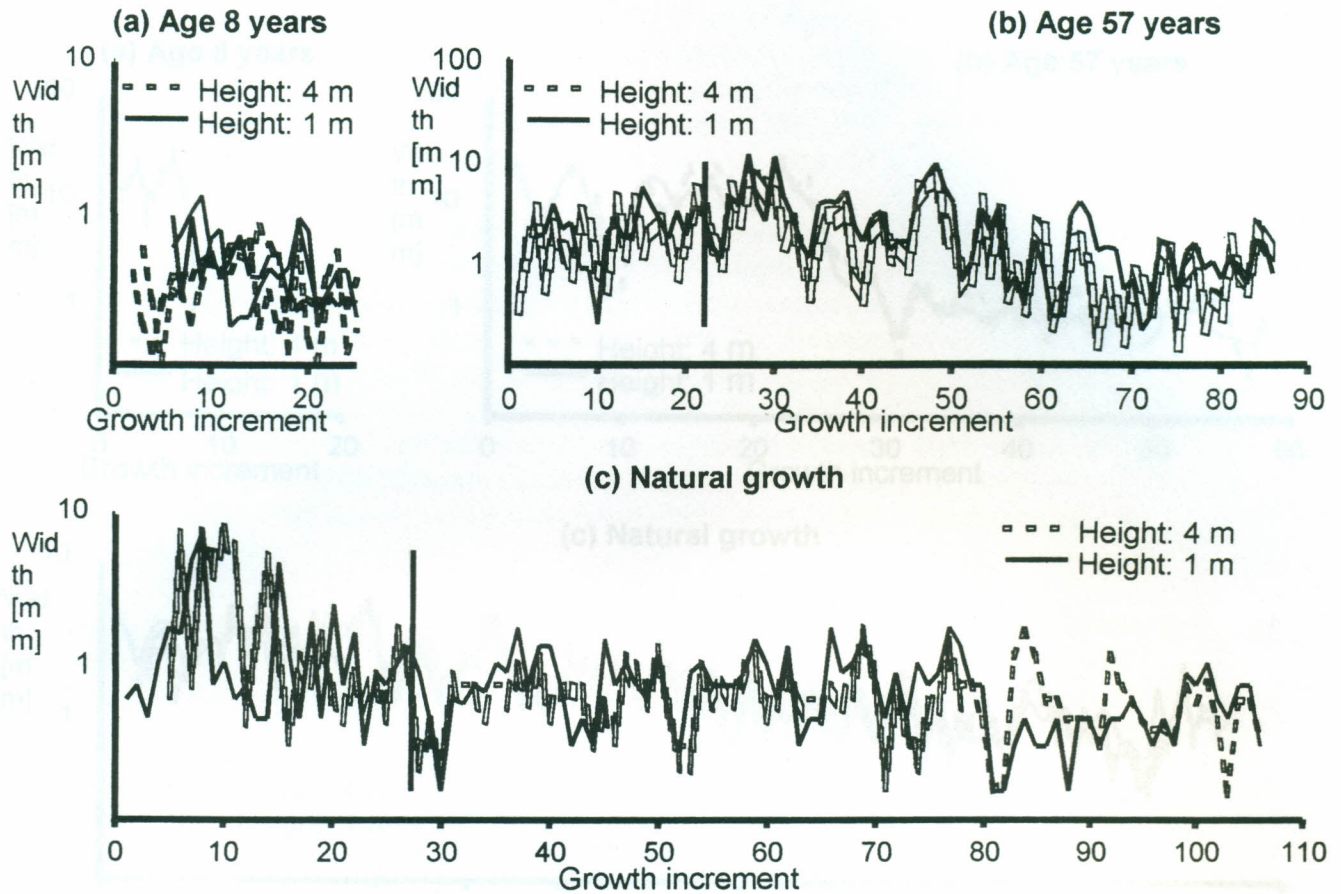
The number of increment zones in the xylem of the plantation grown trees exceeded the tree age in years, but the increase of the number of increment zones in the xylem of 23 and 57 years old trees compared to 8 years old trees indicated an annual formation of increment zones in the adult wood of *Swietenia* (Table 1). The synchronisation of the increment curves obtained from stem discs of different tree heights and different trees gave further evidence for annual cambial growth characteristics of adult wood of *Swietenia*. A parallel run of the width of growth increments of 5 out of 8 57 years old plantation grown and 6 out of 8 primary forest grown trees was found after 28 and 22 growth increments from the pith respectively (Fig. 1 a-c).

Vessel bands, parenchyma bands, and bands of resin channels, with similar structural characteristics and distribution from pith to cambium as observed in the xylem of *Swietenia* were found in the xylem of *Carapa guianensis*. The number of increment zones of 8 and 57 years old trees exceeded the number of increment zones observed in the xylem of *Swietenia* with the same age (Table. 2, Fig. 2 a/b). Synchronisation of the increment curves of *Carapa* showed parallel run of the increment curves of 4 (1 m height) / 2 (4 m height) out of 8 57 years old trees and 3 out of 3 primary forest grown

trees (study site: Manaus) after 22 and 27 increment zones from pith, respectively (Fig. 2 a-c). Although parallel run of the increment curves of *Carapa* was found in the adult wood, the number of 65 synchronous increment zones in the xylem of the 57 years old trees showed that the formation of increment zones of *Carapa* was not annual on this forest site (Fig. 2 b).

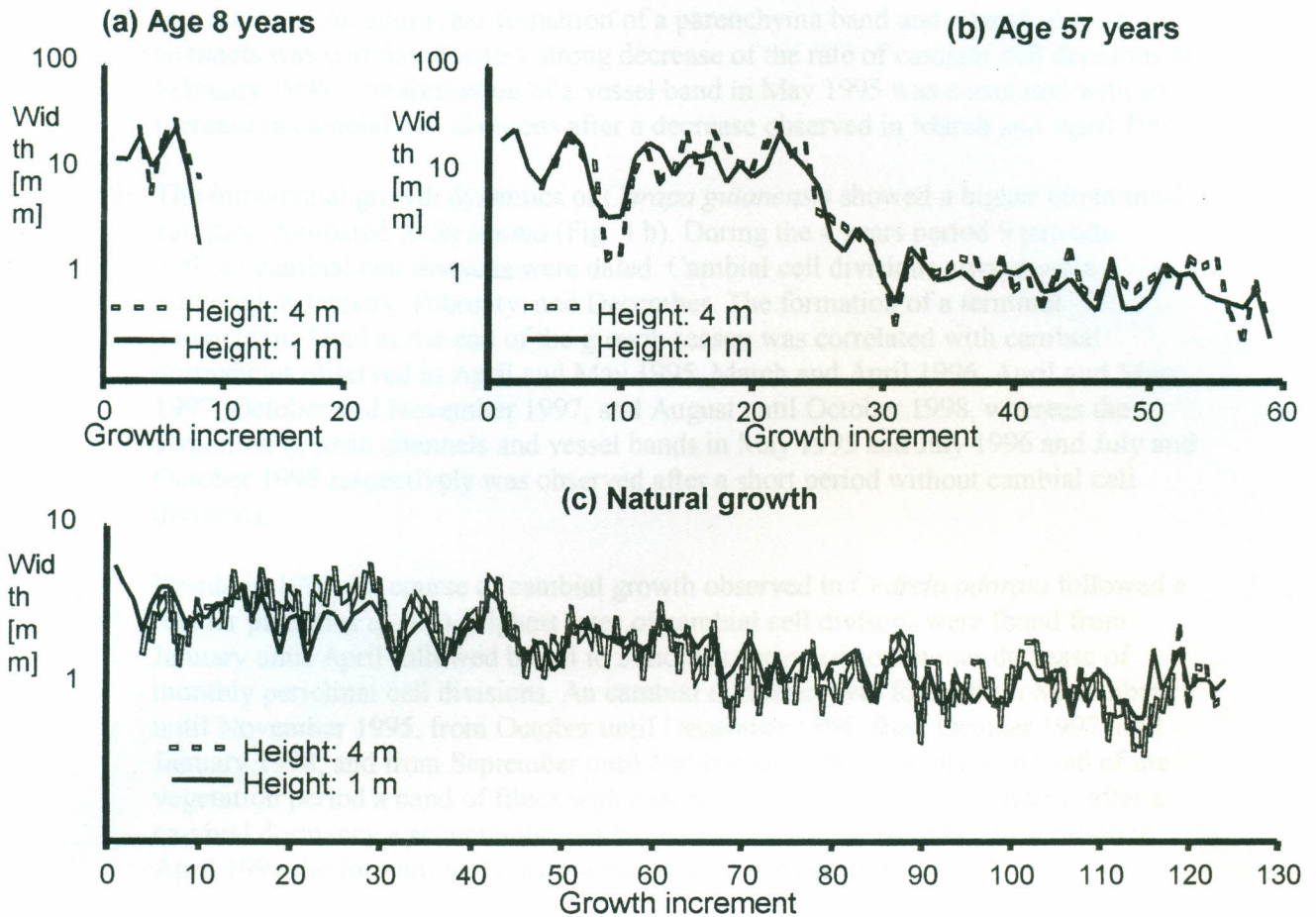


**Fig. 1 a-c:** Width [mm] of increment zones at 1 and 4 m height of 2 (a) 8 years old plantation grown and mean width [mm] of increment zones of (b) 57 years old plantation grown ( $n(1m)=5$  trees;  $n(4m)=5$  trees) and (c) natural grown ( $n(1m)=6$  trees;  $n(4m)=6$  trees) *Swietenia* trees. Period of parallel run is marked by a line.



**Fig. 2a-c:** Width [mm] of growth increments at 1 and 4 m height of 2 (a) 8 years old plantation grown and mean width [mm] of growth increments of (b) 57 years old plantation grown ( $n(1m)=4$  trees;  $n(4m)=2$  trees) and (c) natural grown ( $n(1m)=3$  trees;  $n(4m)=3$  trees) *Carapa* trees. Period of parallel run is marked by a line.

Increment zone labelling in the xylem of *Cedrela odorata* was dominated by a sequence of fibre and vessel bands (Table 2). The of the fibre bands showed reduced cell lumina and often were septated (?). In addition 1 to 2 parenchyma bands and bands of resin channels were found in the juvenile wood of 8 years old trees. The course of the width of the increment zones already showed parallel run in the juvenile xylem of plantation and primary forest grown *Cedrela* trees (Fig. 3 a-c). A comparison of the number of increment zones with the tree age of the plantation grown trees showed that the formation of increment zones as a rule followed an annual pattern (Fig. 3 a/b).



**Fig. 3a-c:** Mean width [mm] of growth increments at 1 and 4 m height of (a) 8 years ( $n(1m)=45$  trees;  $n(4m)=57$  trees), (b) 57 years old plantation grown ( $n(1m)=8$  trees;  $n(4m)=5$  trees), and (c) natural grown ( $n(1m)=6$  trees;  $n(4m)=7$  trees) *Cedrela* trees.

### Intraannual growth dynamics and structural variation in wood formation of *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata*

For the study of the relationship of exogenous input and the pattern of growth increments in the xylem of *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata* wood formation of 3 to 7 years old plantation grown trees of the Manaus site was dated intraannually (Fig. 4 a-c).

Studying the growth dynamics of *Swietenia macrophylla* at least one cambial dormancy became obvious within one year (Fig. 4 a). Cambial dormancies preferably were found in September, October, and November, whereas a maximum rate of cambial cell divisions was observed in January, February, and March. As a rule before

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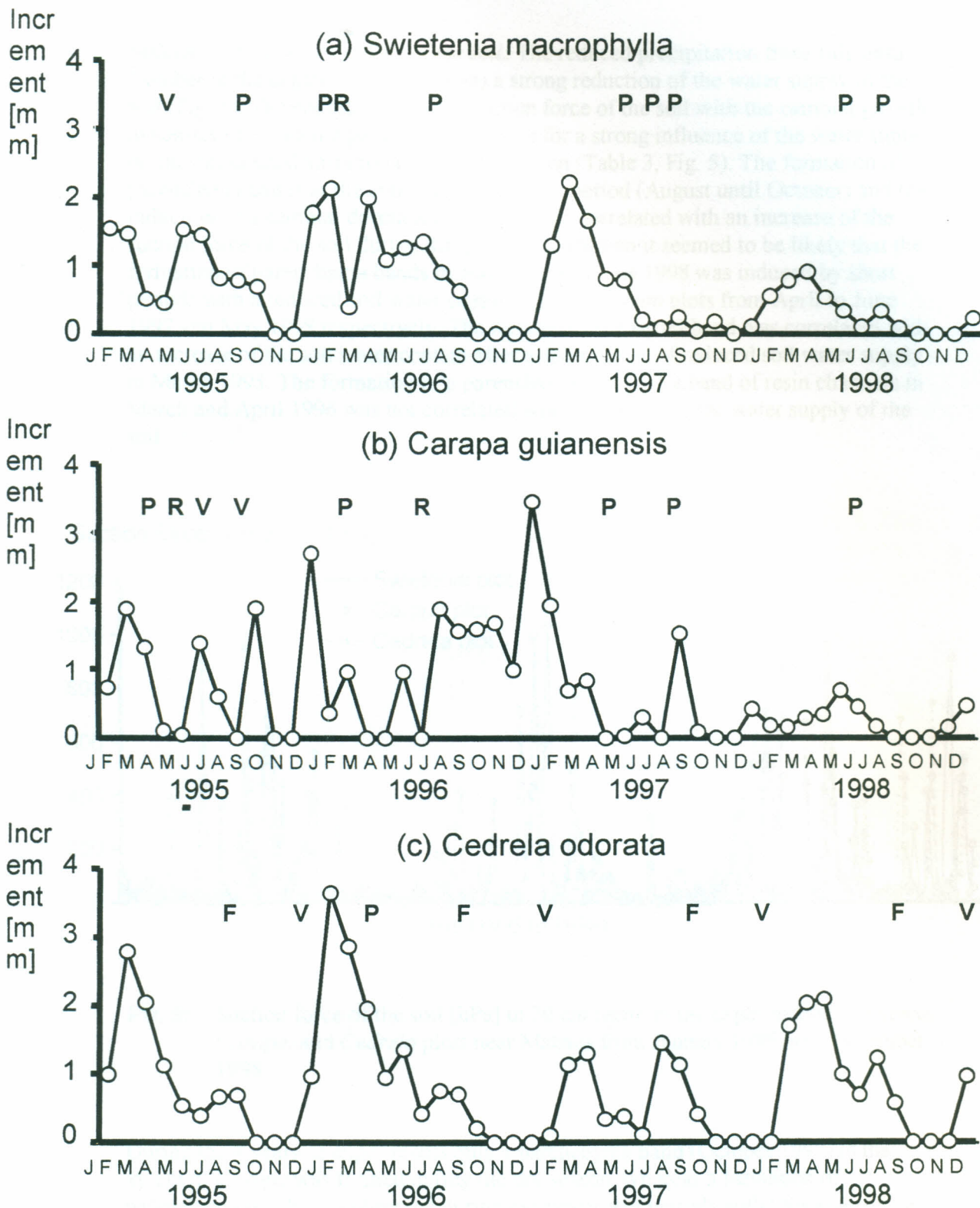
a cambial dormancy the formation of 1 (1995, 1996) to 3 (1997) parenchyma bands was induced. An additional formation of a parenchyma band and a band of resin channels was correlated with a strong decrease of the rate of cambial cell divisions in February 1996. The formation of a vessel band in May 1995 was correlated with an increase in cambial cell divisions after a decrease observed in March and April 1995.

The intraannual growth dynamics of *Carapa guianensis* showed a higher intraannual variation compared to *Swietenia* (Fig. 4 b). During the 4 years period 9 periods without cambial cell divisions were dated. Cambial cell divisions always were observed in January, February, and December. The formation of a terminal parenchyma band at the end of the growth season was correlated with cambial dormancies observed in April and May 1995, March and April 1996, April and May 1997, October and November 1997, and August until October 1998, whereas the formation of resin channels and vessel bands in May 1995 and July 1996 and July and October 1995 respectively was observed after a short period without cambial cell divisions.

Beside in 1997 the course of cambial growth observed in *Cedrela odorata* followed a regular pattern (Fig. 4 c). Highest rates of cambial cell divisions were found from January until April followed by a 4 to 5 months period of continuous decrease of monthly periclinal cell divisions. A cambial dormancy was found from September until November 1995, from October until December 1996, from October 1997 until January 1998, and from September until November 1998. As a rule at the end of the vegetation period a band of fibres with reduced lumina was formed, whereas after a cambial dormancy an accumulation of large sized vessels were found. In addition in April 1996 the formation of a parenchyma band was detected.

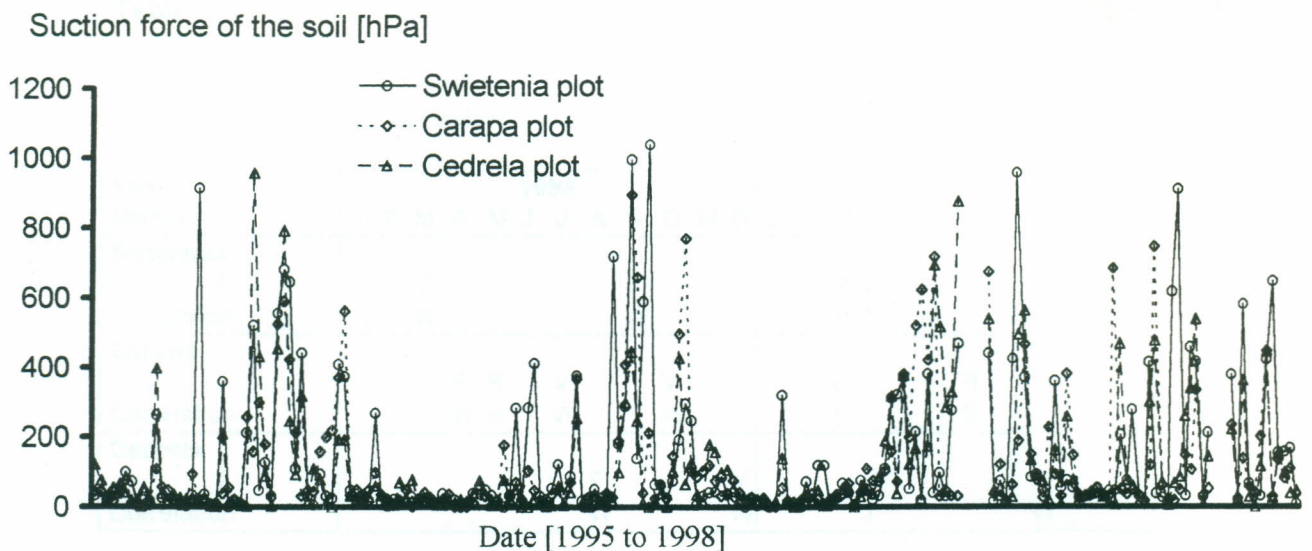
Concerning the influence of exogenous factors on the cambial growth dynamics and the formation of increment zones in the xylem of *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata* the results on the intraannual growth dynamics and structural variation were compared with the water supply of the soil, the attack of *Hypsipyla grandella*, and growth stresses also monitored during the 4 years period of experiments.

Fig. 4. Intraannual growth dynamics of *Carapa guianensis* (b) and *Cedrela odorata* (c) during the 4 years period of experiments. The x-axis represents the month of the year, and the y-axis represents the cambial cell divisions per month. The x-axis is labeled with the years 1995, 1996, 1997, and 1998. The y-axis is labeled with 'Cambial cell divisions per month' and has a scale from 0 to 10. The graph shows two lines: a solid line for *Carapa guianensis* and a dashed line for *Cedrela odorata*. Both lines show a similar pattern of high growth rates in the first half of the year and low growth rates in the second half, with a period of dormancy in the late summer/early autumn months.



**Fig. 4 a-c:** Monthly radius increment [mm] at 1.3 m height of a 3 to 7 years old plantation grown (a) *Swietenia*, (b) *Carapa*, and (c) *Cedrela* tree. The formation of vessel bands is marked by "V", of parenchyma bands by "P", of fibre bands by "F", and of bands of resin channels by "R".

*Influence of the water supply of the soil:* The reduced precipitation from July until October in the central Amazon causes a strong reduction of the water supply in the soil (Fig. 5). The comparison of the suction force of the soil with the cambial growth dynamics of *Swietenia* gave some evidence for a strong influence of the water supply on the intraannual variation in wood formation (Table 3, Fig. 5). The formation of parenchyma bands at the end of the vegetation period (August until October) and the induction of a cambial dormancy were strongly correlated with an increase of the suction force of the soil during this period. In addition it seemed to be likely that the formation of parenchyma bands in July 1997 and June 1998 was induced by short periods with a reduced soil water supply in the *Swietenia* plots from April to June 1997 and May 1998 respectively. The formation of a vessel band was correlated with an increase of the soil water content after a short period of reduced soil water supply in March 1995. The formation of a parenchyma band and a band of resin channels in March and April 1996 was not correlated with a decrease of the water supply of the soil.



**Fig. 5:** Suction force of the soil [hPa] in 20 cm depth in the experimental *Swietenia*, *Carapa*, and *Cedrela* plots near Manaus from January 1995 until December 1998.

During the 4 years of experiments only 1 parenchyma band (October 1997) in the xylem of *Carapa* was formed during the dry season, whereas a formation of parenchyma bands was observed during extremely wet periods with “Staunsaesse” in April 1995, March 1997, and April 1998 (Table 3, Fig. 5).

During the dry season in October 1997 as well as during the wet seasons in April 1995, March 1997, and April 1998 the formation of the parenchyma bands was followed by a cambial dormancy (Fig. 4 b). The formation of vessel bands in July 1995 and October 1995 were correlated with a reduced soil water supply, but due to

the fast change from dormancy to active cambial phase in 1995 no clear relationship between the formation of vessel bands and cambial dormancies was detected. No correlation was found between the water supply of the soil and the formation of a parenchyma band in March 1996 as well as the formation of bands of resin channels in May 1995 and July 1996.

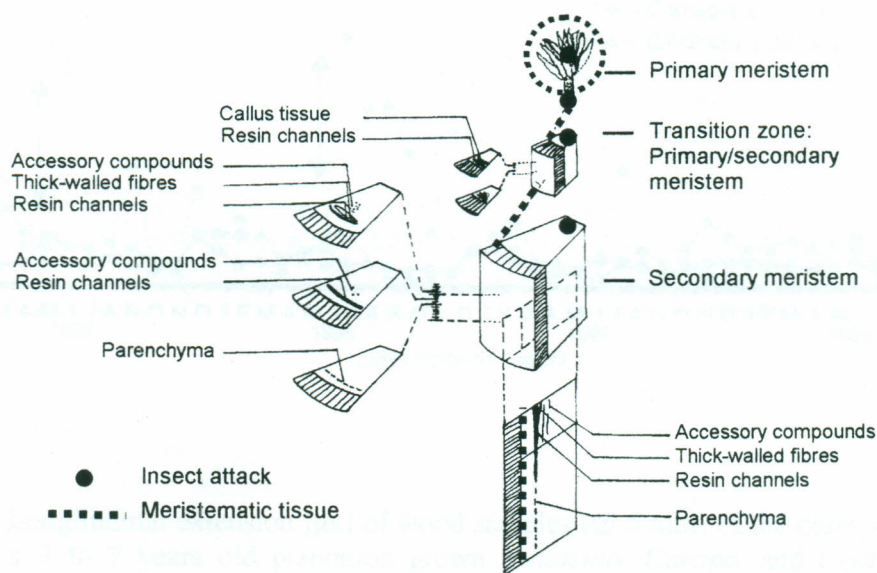
The comparison of the water supply of the soil and the cambial growth dynamics of *Cedrela* showed that as a rule active and dormancy phases of the cambium are determined by the change from the wet to the dry season (Fig. 4 c, Fig. 5, Table 3). This annual structural variation is not influenced by short drier periods during the wet season from January until July and short wetter periods during the dry season from August until December (Fig. 5). The formation of terminal fibre bands was correlated with the beginning of the dry season, whereas the vessel bands indicated the initial phase of cambial growth during the wet season. The formation of a parenchyma band in April 1996 was not correlated with the water supply of the soil (Table 3).

**Table 3:** Relationship between the induction (I) of vessel (V), parenchyma (P), fibre (F), resin channel (R) bands and the water supply of the soil (W), the attack of the insect *Hypsipyla grandella* (I), and longitudinal growth stresses (S) of a 3 to 7 years old *Swietenia*, *Carapa*, and *Cedrela* tree.

Year Month	1995												1996											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
<b>Swietenia</b>																								
I	V									P			P R			P								
Correlation	W									W			I I			W								
<b>Carapa</b>																								
I				P R		V		V			P			R										
Correlation				W S		W		W			I			S										
<b>Cedrela</b>																								
I							F			V			P			F								
Correlation							W			W			I			W								
Year Month	1997												1998											
	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
<b>Swietenia</b>																								
I							P			P P			P P											
Correlation							W			W W			W W											
<b>Carapa</b>																								
I	P									P			P											
Correlation	W									W			W											
<b>Cedrela</b>																								
I	V									F			V			F V								
Correlation	W									W			W			W W								



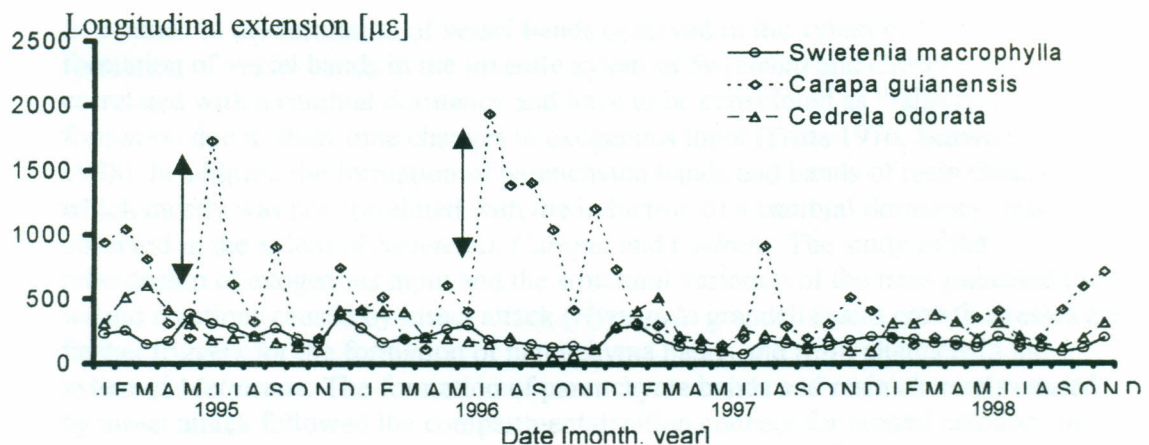
*Influence of insect attack (Hypsipyla grandella) and wounding:* The experimental trees of the EMBRAPA plantation near Manaus were attacked by the shoot borer *Hypsipyla grandella* in February 1996 causing strong damage of the primary meristem of the buds (Fig. 5 a). At this time tree height varied between 4 m and 6 m, with stem heights between 2 m and 4 m approximately. Studying the wound reactions along the tree axis it turned out that the wound reactions of the cambium of *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata* induced by the attack of *Hypsipyla grandella* followed a similar pattern (Fig. 5 b). Related to the degree of wounding wound reactions caused by insect attack were still observed in the xylem of *Swietenia* 0.5 m to 3 m, in the xylem of *Carapa* 0.1 m to 1.5 m, and in the xylem of *Cedrela* 0.5 m to 2 m distant from the injury. Due to the continuum from primary (buds) to secondary meristematic tissue (cambium) wound reactions were induced continuously over the cross section of the stem. Due to the damage of the primary meristem of the buds, in the transition zone from primary to secondary tissue (10 cm to 110 cm distant from the bud) parenchymatic callus tissue followed by traumatic resin channels was formed (Fig. 5 b, Fig. 6). In the more distant secondary xylem as a first wound reaction, the lumina of differentiated vessels were filled with accessory compounds (Fig. 5 b, Fig. 6). In addition a reduced cell enlargement and an increase of secondary wall formation of differentiating fibres became obvious (Fig. 5 b, Fig. 6). The formation of parenchymatic cells with lysigenous resin channels was observed up to 50 cm below the transition zone from primary to secondary tissue (Fig. 6), whereas the formation of parenchymatic cells of the cambium continued up to 3 m in *Swietenia*, up to 1.5 m in *Carapa*, and up to 2 m in *Cedrela* distant from the injury of the primary meristem (Fig. 5, Fig. 6). As a consequence, related to the place of sample collection no structural variation, bands of traumatic resin channels, or parenchyma bands induced by insect attack were found on the sampled stem discs of *Swietenia*, *Carapa*, and *Cedrela*.



**Fig. 6:** Scheme of the wound reaction of the cambium of *Swietenia*, *Carapa*, and *Cedrela* after the attack of *Hypsipyla grandella*.

Due to the study of the structural variation in the xylem along the tree axis of the experimental trees presented in Fig. 4 a-c it turned out that the formation of a parenchyma band in March 1996 and a band of resin channels in April 1996 in the xylem of *Swietenia* as well as the formation of a parenchyma band in March 1996 and April 1996 in the xylem of *Carapa* and *Cedrela* respectively was induced by insect attack (Table 3).

*Influence of growth stresses:* The study on growth stresses in the longitudinal direction of the xylem of *Swietenia macrophylla*, *Carapa guianensis*, and *Cedrela odorata* showed low growth stresses in the xylem of *Swietenia* and *Cedrela*, whereas a fast change from low to high growth stress values was observed in the xylem of *Carapa* (Fig. 7). A comparison of the intraannual course of growth stress generation (Fig. 7) with the rate of cambial cell divisions (Fig. 4 b) showed that maximum growth stresses were induced in periods in transition from low to fast growth. The fast change from low to high longitudinal growth stresses induces shear stress, which reaches 30 % to 50 % of the shear strength of the wood of *Carapa* (Wagenfuhr and Scheiber 1996). The maximum difference of growth stresses from one month to another from May to June 1995 and from June to July 1996 in the outer xylem of *Carapa* (Fig. 7) was correlated with the formation of a band of resin channels during this period (Table 3). Accompanying the bands of resin channels along the tree axis, it turned out that the resin channels are not continuous within the tree and the formation follows the course of growth stresses along the stem axis. This gave some evidence for the induction of local resin channel formation due to mechanical stress generated by the cambial growth dynamics of *Carapa*.



**Fig. 7:** Longitudinal extension [ $\mu\epsilon$ ] of wood samples ( $\varnothing$  5 mm) of the outer xylem of a 3 to 7 years old plantation grown *Swietenia*, *Carapa*, and *Cedrela* tree (January 1995 until December 1998). Sample collection was carried out at 1.3 m height.

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## Discussion

In the past investigations on the cambial growth dynamics of tropical trees were carried out with special regard to a better understanding of the trigger for the structural variation in the xylem of tropical trees (Coster 1927, 1928, Detienne and Mariaux 1977, Jacoby 1989). In addition due to the exploitation of high quality species in primary forests during the last decades information on the significance of extrinsic and intrinsic factors for the cambial activity is an urgent demand for a successful cultivation of tropical trees for wood production in plantations (comp. Brunig 1996, Bauch et al. 1999). The microscopical studies and dated increment labelling of plantation and natural grown trees of the important species for wood production *Swietenia macrophylla* King, *Carapa guianensis* Aubl., and *Cedrela odorata* L. showed a strong relationship between the cambial activity expressed in terms of periclinal cell divisions and the formation of increment zones. As a rule before a cambial dormancy terminal parenchyma bands were formed in *Swietenia* and *Carapa*, whereas the end of cambial growth of *Cedrela* was labelled by the formation of "septated" (?) fibres with reduced lumina. Parenchyma cells and living fibres (septated fibres) are considered as important tissue for the storage of reserve carbohydrates (Zimmmermann 1983, Holl 1985, Langenfeld-Heyser 1987, Kozlowski et al. 1991) and transport of nutrients (Dunisch et al. 1998, Kuhn et al. 1997), which is of main importance for a fast reactivation of cambial cell divisions after a cambial dormancy (Larson 1995). The high rate of periclinal cell divisions and the preferred formation of large sized vessels observed after a cambial dormancy gave further evidence for this function of terminal parenchyma bands in *Swietenia* and *Carapa* and the preferred formation of septated fibres in *Cedrela* at the end of the vegetation period.

In contrast to the formation of vessel bands observed in the xylem of *Cedrela*, the formation of vessel bands in the juvenile xylem of *Swietenia* and *Carapa* was not correlated with a cambial dormancy and have to be considered as "false ring" formation due to short time changes in exogenous input (Fritts 1976, Schweingruber 1988). In addition the formation of parenchyma bands and bands of resin channels, which mostly was not correlated with the induction of a cambial dormancy, was observed in the xylem of *Swietenia*, *Carapa*, and *Cedrela*. The study of the relationship of exogenous input and the structural variation of the trees indicated that wound reactions caused by insect attack (*Hypsipyla grandella*) and growth stresses are further triggers for the formation of parenchyma bands and resin channels in the xylem of *Meliaceae*. The formation of parenchyma bands and resin channels caused by insect attack followed the compartmentalization concept for wound reactions in the xylem of hardwoods proposed by Shigo (1984, comp. also Schmitt and Liese 1993). As a specific aspect for the induction of continuous cambial wound reactions over the stem cross section, the wounding of the primary meristem by *Hypsipyla grandella* is of main importance. Due to the continuum from primary and secondary meristematic tissue, wounding of the primary meristems of the trees caused the induction of continuously developed wound reactions over the stem cross section and the local formation of parenchyma bands and resin channels along the stem axis. The induction of anticlinal cell divisions and the formation of traumatic resin channels due to high growth stresses was already reported from investigations carried out with African mahagonys (*Entandophragma* sp. and *Khaya* sp.). A comparison of the

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growth stresses of *Swietenia*, *Carapa* and *Cedrela* showed that growth stress generation is mainly determined by the genetic predisposition of the trees, but a strong variation of cambial growth during the growing season favours the generation of high growth stresses (Kuebler 1987). Consequently to that the formation of traumatic resin channels due to longitudinal growth stresses in the xylem of *Carapa* was favoured during the juvenile phase of open plantations with unstable growth conditions (Dunisch et al. 1999 a, Dunisch et al. in press).

The synchronisation of increment curves showed that the juvenile phase of *Swietenia* and *Carapa* is not suitable for dendroecological studies due to the high sensitivity of wood formation to exogenous input (e.g. water supply, insect attacks, and mechanical stress) and a high rate of "false ring" formation during the juvenile phase (comp. Cook 1985). The course of structural variation of *Cedrela* follows a more regular pattern indicating a stronger endogenous regulation of cambial activity already during the juvenile phase of growth (Wareing 1981).

The adult phase in wood formation of *Swietenia*, *Carapa*, and *Cedrela* is strongly correlated with the water supply. As a rule the annual growth dynamics of *Cedrela* and *Swietenia* follows the course of the soil water supply, with a cambial dormancy during the dry period. In contrast to *Cedrela* short periods of reduced soil water supply induced a cambial dormancy and the formation of vessel and parenchyma bands in the xylem of *Swietenia* indicating a higher sensitivity to a reduced water supply of this species. Extremely wet and extremely dry periods induced a cambial dormancy and the formation of terminal parenchyma bands in the xylem of *Carapa*. Consequently on "terra firme" sites investigated in this study, the formation of increment zones of *Carapa* was not annual during the adult phase as well. The fast reactivation of cambial growth after a cambial dormancy proves the wide ecological amplitude of this species. On the other hand the induction of cambial dormancies and terminal parenchyma bands during dry and wet periods indicated that the natural habitat of *Carapa* on wet sites without inundation and without extremely dry periods offers the best growth conditions for this species (Pennington et al. 1981, Ribeiro et al. 1999).

From this study it was concluded that due to distinct annual increment labelling during the adult phase *Swietenia macrophylla* and *Cedrela odorata* are promising species for dendroecological studies on "terra firme" sites of the Amazon basin. Although increment curves of adult *Carapa guianensis* showed parallel run the suitability of this species for dendrochronological studies based on increment curves depends on the annual course of the water supply on the study site. With regard to the ecological adaptation to wet and dry conditions this study indicated a good adaptation of *Carapa* to changes of exogenous input, whereas *Swietenia* reacts more sensitive to environmental impact. The more endogenous growth dynamics of *Cedrela* indicate a good adaptation of this species to wet sites with one distinct dry period during the year.

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### **3. Cooperation and scientific exchange**

Cooperation with SHIFT-project ENV 23:

Autecological investigations of *Miconia* sp. and *Bellucia* sp. are carried out in cooperation with the SHIFT-project ENV 23 (Dr. H. Preisinger) as to study the relationship between secondary tree species and the planted trees in the plantation systems (comp. chapter 5, Preisinger et al. 1999)

Cooperation with the SHIFT-projects ENV 23 and ENV 45:

Investigations on the water supply of plantation grown trees are carried out in cooperation with the SHIFT-project ENV 23 and ENV 45 (Dr. G. Schroth, Prof. Dr. W. Zech, comp. chapter 5, Dünisch et al. 1999a).

Cooperation with SHIFT-project ENV 52:



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Studies on the heartwood formation and durability of the wood from plantation and natural grown trees are carried out in cooperation with SHIFT project ENV 52. In this study the fauna of decomposed wood samples is identified in the scientific group of ENV 52.

Investigations on the litter decomposition in the plantation system II are carried out by the SHIFT-project ENV 52 (Prof. Dr. Beck, Dr. C. Martius, Dr. Höfer). Data on the water and mineral element supply in this plantation system are studied within the project ENV 42 and will be evaluated in cooperation with project ENV 52.

Cooperation with the University of Paraná, Curitiba:

Chemical soil analyses and studies on the mineral nutrition of plantation grown *Ceiba pentandra* and *Virola surinamensis* are carried out in cooperation with Prof. Dr. B. Reissmann and Mr. E. Neves, University of Paraná (comp. chapter 5, Neves et al. 1999). The PhD.-thesis of Mr. E. Neves is in its content integrated in ENV 42. It is attended by Prof. Dr. J. Bauch and Dr. O. Dünisch (ENV 42). The thesis was finished in 1999 and Dr. O. Dünisch was part of the commission.

Cooperation with the Institute of Wood Chemistry, Federal Research Center for Forestry and Forest Products, Hamburg:

Studies on the seasonal variation of the content of reserve carbohydrates of plantation grown trees are carried out in cooperation with Dr. J. Puls, Institute of Wood chemistry, Federal Research Center for Forestry and Forest Products, Hamburg (comp. 2.3.).

Cooperation with the Institute of Wood Technology, Federal Research Center for Forestry and Forest Products, Hamburg:

Technological investigations on the mechanical wood properties of plantation grown trees (*Hymenaea*) are carried out in cooperation with Dr. Schwab and Dr. K. Kruse, Institute of Wood Technology, Federal Research Center for Forestry and Forest Products, Hamburg (comp. 2.1.).

Cooperation with the Institute of Forestry, Federal Research Center for Forestry and Forest Products, Hamburg:

Studies on the photosynthesis of *Swietenia macrophylla* and *Carapa guianensis* are carried out under controlled conditions in cooperation with Dr. Kriebitzsch, Institute of Forestry, Federal Research Center for Forestry and Forest Products, Hamburg.

Research stay of Thorsten Eilers at the EMBRAPA Amazonia Ocidental in Manaus from April 1999 until October 1999.

#### **4. Comparison of the investigations with the actual plan of the project**

After some technical problems in 1998 related to the import of equipment in Brasil and time consuming seed collection and germination of plants for the provenance study, in 1999 the investigations of the project were carried out according to the actual plan of the project.

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The study on the water supply of the trees could be intensified in 1999 and these studies will continue also when the SHIFT project will have finished in 2001 (PhD thesis of Ronaldo Morais INPA/EMBRAPA/University of Hamburg).

In 1999 the provenance study was extended to 5 species, whereas only 3 to 4 species were included in the actual plan of the project.

Assessing wood quality of the plantation grown trees, the case studies (comp. Bauch et al. 1999) were extended to heartwood formation and the durability of the wood of *Swietenia*, *Carapa*, *Cedrela*, *Dipteryx*, and *Hymenaea*.

## **5. Relevant project publications and supplementary individual contributions**

In 1999 the main results of the first phase of the project were published in the series „Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg“, 193 (135 p.), 1999). As supplement to this annual report the summary of the PhD thesis of Edinelson Neves, of the master thesis of Mr. D. Harm and the report of the research stay of Thortsten Eilers are added:

### **Relevant project publications**

- (1) Development of tree height and diameter of eight selected tree species under plantation conditions.  
C.P. de Azevedo, L. Gasparotto, R. de Lima, E. Neves, and O. Dünisch
- (2) Water supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in three plantation systems.  
O. Dünisch, G. Schroth, R. de Morais, and M. Erbreich
- (3) Supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. with K, Ca, and Mg in three different plantation systems.  
O. Dünisch, J. Bauch, and Th. Schwarz
- (4) Biomass production and mineral element content of *Swietenia macrophylla* King in the juvenile phase.  
P. Schmidt, R. Lieberei, J. Bauch, and L. Gasparotto
- (5) Nutritional status of *Ceiba pentandra* (L.) Gaertn. and *Virola surinamensis* (Rol.) Warb. under plantation conditions.  
E.J.M. Neves, C.B. Reissmann, C.A. Ferreira, A.F.J. Bellote, and O. Dünisch
- (6) Growth dynamics in wood formation of plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl.  
O. Dünisch, M. Sack, M. Müller, and J. Bauch

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- (7) Comparative study on wood characteristics of *Carapa guianensis* Aubl. from two plantations and a natural site in Central Amazonia.  
J. Bauch, O. Dünisch, F. Schuster, L. Gasparotto, and C.P. de Azevedo
- (8) Structure of primary roots of *Swietenia macrophylla* King under controlled conditions.  
G. Noldt, J. Bauch, U. Schmitt, and V.G. Balodis
- (9) Comparative studies on morpho-physiological traits of six Amazonian species of *Bellucia* and *Miconia* (*Melastomataceae*) and implications for their ecological behaviour.  
H. Preisinger, O. Dünisch, R.R. de Moraes, K. Richter, and R. de C. Araújo

#### Supplementary individual contributions

- (1) Edinelson Neves:  
Biomassa e acumulo de nutrientes nos diferentes compartimentos de *Ceiba pentandra* Gaertn. e *Virola surinamensis* (Rol.) Warb plantadas na Amazonia Ocidental Brasileira. PhD. Thesis Universidade Federal de Parana, Curitiba, 189 p.

Attended by B. Reissmann, J. Bauch, and O. Dünisch (ENV 42-2).

- (2) Dietrich Harm:  
Biomasse- und Bioelementverteilung in Monokulturpflanzungen dreier ausgewählter tropischer Wirtschaftsbaumarten in Zentralamazonien.  
Diplomarbeit Fachbereich Biologie, Universität Hamburg, 94 p.

Attended by J. Bauch and O. Dünisch (ENV 42-2).

- (3) Thorsten Eilers: Report on the research stay at the EMBRAPA, Amazonia Ocidental

(Univ.-Prof. Dr. J. Bauch)



(Dr. O. Dünisch)

Appendix

CURITIBA  
1989

EDINELSON JOSÉ MACIEL NEVES

RESUMO

Abstract text, partially legible and faded. It appears to describe the study area and objectives.

**BIOMASSA E ACÚMULO DE NUTRIENTES NOS DIFERENTES  
COMPARTIMENTOS DE *Ceiba pentandra* (L.) GAERTN E  
*Virola surinamensis* (ROL.) WARB PLANTADAS NA  
AMAZÔNIA OCIDENTAL BRASILEIRA**

Tese apresentada como requisito parcial à obtenção do grau de Doutor em Ciências Florestais, área de concentração em Silvicultura, Curso de Pós-Graduação em Engenharia Florestal, Universidade Federal do Paraná.

Orientador: Prof. Dr. Carlos Bruno Reissmann

CURITIBA  
1999

**ABSTRACT**

Silvicultural and nutritional aspects of planted *Ceiba pentandra* (L.) Gaertn and *Virola surinamensis* (Rol.) Warb were studied at ages 43 and 55 months on 225 m<sup>2</sup> plots established on Yellow Oxisols in the Brazilian Western Amazônia. For each species and both ages, four trees were selected. Studies related to silvicultural aspects were developed by measuring total height, diameter at breast height (DBH) and total volume determination. Soil samples were collected in each plot at the following depths: 0-10, 10-30 and 30-60 cm. On the other hand, those studies related to nutritional aspects were done after trees were felled and separated into biomass components. For the study of the root system, just one tree for each species was sampled at age 43 months. Among all ages evaluated, litter deposition was additionally quantified. Chemical composition of different biomass components, soil and litter was also evaluated. The silvicultural performance, for the two species was considered to be satisfactory. However, *C. pentandra* and *V. surinamensis* showed different nutritional characteristics. The highest litter deposition (made up mostly by leaves), for *C. pentandra*, has occurred in July, whereas for *V. surinamensis* the same phenomenon was verified in september. Except Ca and Zn, highest element contents were detected in the litterfall of the dry season. Overall, the highest nutrient concentrations was found in the soil under *C. pentandra*. This species proved to be more efficient in the utilization of nutrients than *V. surinamensis*.

# MASSE- UND BIOELEMENTVERTEILUNG IN MONOKULTURANPFLANZUNGEN

## DREIER AUSGEWÄHLTER TROPISCHER WIRTSCHAFTSBAUMARTEN IN

### ZENTRALAMAZONIEN

Diplomarbeit

zur Erlangung des akademischen Grades

DIPLOM – HOLZWIRT

An der Universität Hamburg

Fachbereich Biologie

vorgelegt von

**Dietrich R. Harm**

aus Tremsbüttel

Hamburg, Mai 1999

Schwerpunkt des deutsch – brasilianischen Forschungsprogramms SHIFT (**Studies on Human Impact on Forests and Floodplains in the Tropics**) ist die Erforschung von Grundlagen für die nachhaltige Bewirtschaftung agroforstwirtschaftlich orientierter Anpflanzungen in Zentralamazonien. Hierfür werden verschiedene, zum größten Teil in Amazonien beheimatete, land - und forstwirtschaftlich interessante Nutzpflanzen verwendet, die in verschiedenen Pflanzsystemen auf ihr Wuchs – und Ertragsverhalten hin untersucht werden. Das Ziel ist die Wiederinwertsetzung von Flächen, die durch falsche Nutzungsmethoden bereits degradiert wurden. Dadurch soll der Nutzungsdruck auf bisher verschont gebliebene Primärwaldflächen vermindert werden und die Erzeugung von land – und forstwirtschaftlichen Erzeugnissen zur Versorgung der Region um Manaus auf eine neue Grundlage gestellt werden.

Im Rahmen des SHIFT – Projektes Nr. ENV 42 werden auf einer im Jahre 1992 als Monokultur - Blockversuch angelegten Versuchsfläche einheimische Wirtschaftsbaumarten im Hinblick auf eine Verwendung in Plantagenpflanzungen untersucht.

In der vorliegenden Arbeit soll der Versuch unternommen werden, nach etwas mehr als sechs Jahren eine Zwischenbilanz in Bezug auf die Wuchsleistung und eventuelle Perspektiven der Baumarten *Carapa guianensis*, Aubl., *Dipteryx odorata* (Aubl.) Willd. und *Hymenea courbaril* L. zu erarbeiten.

Hierfür wurden sämtliche Individuen der drei untersuchten Arten auf der Versuchsfläche einer **dendrometrischen Vermessung** unterzogen. Anschließend wurde, nach einer Einteilung der Kollektive in fünf Größenklassen, jeweils vier Bäume einer Art, die als Serie mit zunehmender Größenklasse ausgewählt worden waren, geerntet. Das Erntegut wurde fraktioniert und die **Bestimmung der oberirdischen Biomasse** durchgeführt.

Weiterhin wurde von diesem Erntegut Mahlgut erzeugt und einer **Elementerfassung nach der ICP – OES – Methode** unterzogen. Von den beiden Arten *Hymenea courbaril* und *Carapa guianensis* wurden zusätzlich gemischte Blattproben jedes Individuums der Kollektive entnommen. Dies geschah auch mit

Bodenproben von sechs Blöcken der Versuchsfläche, von denen drei mit *H. courbaril* und drei mit *C. guianensis* bepflanzt sind.

Über die Wuchseigenschaften der drei untersuchten Arten lassen sich folgende Aussagen treffen: (1) *H. courbaril* ist bezüglich aller vermessener Parameter deutlich als größte der drei Arten einzustufen. (2) *C. guianensis* und *D. odorata* unterscheiden sich am deutlichsten im Hinblick auf den Stammumfang in Brusthöhe. Bezüglich der anderen Wuchsparameter schneidet *D. odorata* als Art eher etwas besser ab, als *C. guianensis*. (3) Insgesamt streuen die Werte der gemessenen Parameter bei *H. courbaril* und *D. odorata* deutlich stärker und vor allem deutlich stärker nach oben, als dies bei *C. guianensis* der Fall ist. Für *C. guianensis* besteht eine deutliche Tendenz der Meßwerte, nach unten zu streuen. Insgesamt entsteht für *C. guianensis* ein Eindruck von Stagnation in der Wuchsentwicklung, mit relativ niedrigen, aber massig wirkenden Bäumen.

Auf die Frage, inwieweit sich die einzelnen Pflanzblöcke einer Art vom Wuchs her unterscheiden, ergibt sich für *C. guianensis* und für *H. courbaril* jeweils ein sehr einheitliches Wuchsbild über alle vier Blöcke hinweg. Für *D. odorata* ließ sich ein deutlicher Größenunterschied herausarbeiten.

Bei einer oberflächlichen Betrachtung der oberirdischen Biomasse nimmt *C. guianensis* tendentiell den höchsten Rang der drei Baumarten ein. Auf den zweiten Blick entsteht aber ein viel differenzierteres Bild. Es treten folgende Befunde auf. (1) *C. guianensis* besitzt die größte Blattmasse der drei untersuchten Arten. (2) Bei *C. guianensis* und *D. odorata* nimmt der Anteil des Stammholzes an der Gesamtbiomasse und an der gesamten Holzmasse von Größenklasse zu Größenklasse deutlich ab. (3) Bei *H. courbaril* und *D. odorata* ist der Anteil kleiner Äste mit einem Durchmesser < 2 Zentimeter deutlich höher, als bei *C. guianensis*. (4) *H. courbaril* besitzt in allen Größenklassen den höchsten Stammholzanteil an der Gesamtmasse. (5) In der höchsten Größenklasse liegt *H. courbaril* in Bezug auf die Holzmasse mit ca. 86 Kg deutlich vor *C. guianensis* mit 67 Kg und *D. odorata* mit ca. 63 Kg. Bei einem Vergleich der Wuchsparameter der gefälltten Bäume ergibt sich ein ähnliches Bild: *H. courbaril* schneidet ziemlich hoch oder am höchsten ab. *D. odorata* und *C. guianensis* sind sich bei Betrachtung der Gesamtbiomasse nicht besonders, bei der Betrachtung der Holzmasse aber ziemlich ähnlich. Dies liegt an der deutlich höheren



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(0,55 – 0,6 g/cm<sup>3</sup>).

Ferner wurden die Gehalte der Elemente Calcium, Kalium, Magnesium, Natrium, Schwefel, Phosphor, Eisen und Aluminium in den gefällteten Bäumen bestimmt. Die Nährelemente Ca, K, Mg, Na, S, und P hatten ihre stärksten Konzentrationen in den Blättern und/ oder der Rinde der Bäume, während die Metalle Al und Fe als toxisch wirkende Elemente ihre höchsten Konzentrationen in den Feinwurzeln und in der Rinde der Grobwurzeln hatten.

*C. guianensis* neigt dazu, die mit Abstand höchsten Konzentrationen an Nährelementen in seinen Organen anzusammeln. Global betrachtet sind die Nährelementkonzentrationen bei *H. courbaril* am geringsten. Es zeichnet sich also ab, daß *H. courbaril* mit einer vergleichsweise geringen Menge an Nährelementen relativ viel Biomasse erzeugen kann. Bei der Betrachtung der durchschnittlichen Konzentrationen der Nährelemente in den Blättern von *H. courbaril* und *C. guianensis* zeigen sich nur geringe Unterschiede in den Konzentrationen dieser Elemente zwischen den beiden Arten. *H. courbaril* besitzt zudem eine geringere Blattmasse als *C. guianensis*.

Die Elementerfassung im Boden der Versuchsfläche läßt drei wichtige Aussagen zu: (1) Der Gehalt an Nährelementen im Boden ist in den drei jeweils untersuchten Blöcken der Arten *C. guianensis* und *H. courbaril* ähnlich. (2) Der Gehalt an Nährelementen ist in der oberen Bodenschicht (0 – 15 cm) im Schnitt deutlich höher, als in 30 – 45 Zentimeter Tiefe. Dies gilt besonders für das Element Phosphor, dessen Gehalt in 30 – 45 Zentimetern Tiefe beinahe 0 ist. Nur für Schwefel, das Nährelement mit den höchsten Konzentrationen im Boden, ist diese Tendenz uneinheitlich. (3) Der Gehalt der Elemente Eisen und Aluminium ist sehr hoch und nimmt in der Tiefe deutlich zu. Dies führt zu einer Verminderung der Speicherkapazität des Bodens für Nährelement – Kationen und macht eine Düngung der Pflanzen schwierig, da die durch Düngung eingebrachten Nährelemente bei mangelnder Bindungsfähigkeit des Bodens relativ rasch ausgewaschen werden.

Aus den vorliegenden Untersuchungen wird gefolgert, daß *H. courbaril* unter den speziellen Bedingungen der Untersuchungsfläche die besten Zuwachsergebnisse aufweist. *D. odorata* scheint sich, auch wenn sie derzeit noch etwas kleiner ist, als *C.*

*guianensis*, recht gut zu entwickeln und den Standortbedingungen angepasst zu sein. *C. guianensis* hingegen macht den Eindruck, als ob eine Stagnation im Wachstum eingetreten ist. Auch der relativ hohe Nährstoffbedarf zusammen mit dem auftretenden Schädlingsbefall läßt die Art für einen plantagenmäßigen Anbau auf der Untersuchungsfläche vergleichbaren Standorten nur eingeschränkt geeignet erscheinen.