Exogenous Influences on the Growth Dynamics of High Quality Timber Species from the Amazon

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Summary

In this study the light, water, and nutrient demand of the important high quality timber species of the Amazon *Swietenia macrophylla* King, *Carapa guianensis* Aubl., and *Cedrela odorata* were studied. In addition the light, water, and nutrient supply of the trees were investigated in monoculture and enrichment plantations in comparison to natural site conditions. From these data the relationship of exogenous input and the biomass production of the trees was quantified. The investigations on the light, water, and nutrient demand of *Swietenia*, *Carapa*, and *Cedrela* showed that *Swietenia* and *Cedrela* have a high light demand for biomass production, although the quantum efficiency of the phostosynthesis is low. A low capacity for water uptake of these species was found in dry soils. In addition a high demand of K for biomass production was found, which only can be satisfied in more fertile soils. In comparison a lower light and nutrient demand for biomass production was found for *Carapa.* Water and nutrient uptake of *Carapa* was still possible in drier and poorer soils, respectively. The comparison of the light, water, and nutrient supply of natural sites and 2 plantation systems of *Swietenia, Carapa*, and *Cedrela* showed that natural growth of *Swietenia* and *Cedrela* was predominately found on open sites with fertile soils and a distinct change of a wet and a dry period during the year. In contrast natural growth of *Carapa* was also found in the understorey of wet and dry sites of lower fertility. Light intensities in the 2 plantation systems considered in this study differed significantly. The water and nutrient supply of the enrichment plantation was more stabilized compared to the monoculture. Studying the biomass production of *Swietenia, Carapa,* and *Cedrela* grown in plantations and on natural sites it turned out that to a high portion the biomass production of these species is correlated with the light, the water, and the nutrient supply of the site. Comparing the 3 species it became obvious that *Carapa* has a better capacity for the adaptation to different site conditions.

From these results it can be concluded that profound information on the light, water, and nutrient demand and on the site conditions, considering appropriate management practices, offers the chance for sustainable wood production of *Swietenia*, *Carapa*, and *Cedrela* in plantations, but it turned out that *Carapa* is better adapted to different and less favorable site conditions compared to *Swietenia* and *Cedrela.*

Keywords

Swietenia macrophylla King, *Carapa guianensis* Aubl., *Cedrela odorata* L., Light-, Water-, Nutrient-supply, Plantations, Natural sites

1 Introduction

In the Central Amazon the demand for wood is exclusively satisfied from primary forests (comp. LOUREIRO et al. 1979, RIZZINI 1990, FEARNSIDE and FERRAZ 1995). These logging activities lead to a strong reduction of high quality species in the primary forests and in many cases to a degradation of the exploited areas (LAMPRECHT 1986, BRÜNIG 1996). As to counteract this tendency during the last years in the Central Amazon special attention was given to the cultivation of native tree species for high quality timber production in plantations (LAMPRECHT 1986, WHITMORE 1995, BRÜNIG 1996, BAUCH et al. 1999). Due to the anthropogeneous impact site conditions in plantations are different from those in primary forests (BREDA et al. 1995, OREN et al. 1995), which might influence the growth of the planted trees significantly. Besides a nutrient imbalance in the soil of many plantations (HÖLSCHER et al. 1997, DÜNISCH and SCHWARZ 2000), with regard to sustainable wood production significant alterations in the water budget and the light conditions of plantations compared to primary forests are of main importance (GRANIER et al. 1987, LOTT et al. 1996, SCHROTH et al. 1999). The physiological activities, and with that the growth of the trees, is strongly influenced by the light, water, and nutrient supply (KOZLOWSKI et al. 1991, DÜNISCH and BAUCH 1994, LÖSCH 1996).

In this comparative study *Swietenia macrophylla* King, *Carapa guianensis* Aubl., and *Cedrela odorata* L. were selected due to the high economic value of these high quality timber species. The light, water, and nutrient demand of these species was studied in terms of gas exchange, water, and nutrient flux measurements. The light, water, and nutrient supply of the species was studied in monoculture and enrichment plantations in comparison to natural sites. The biomass production of the trees was studied and the results were compared with the biomass production calculated from the light, water and nutrient demand of the species and the light, water, and nutrient supply of the study sites as to develop appropriate management tools for the cultivation of these species in plantations.

2 Material and Methods

2.1 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 categorization, the soil is a poor xanthic Ferralsol (FAO, 1990 with a low cation exchange capacity (ZECH et al. 1998; DÜNISCH et al. 2000, SCHROTH et al. 2000). 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 two years 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).

The experiments were carried out in monoculture and enrichment plantations installed in January 1992 (study of 3 to 8-year-old plants and in January 1998 (study of 1 and 2-year-old plants).

For the installation of the monoculture plantations the secondary vegetation was clear cut without burning in 1991 and 1997, respectively (comp. DÜNISCH et al. 2000). After 5 months of site preparation 100 plants (4 to 6 months old) of each species were planted with a spacing of 3 x 3 m in 4 (1992) and 3 (1998) experimental plots of 25 plants each (representing a plant density of 1100 plants per hectare). The spontaneous vegetation of the plantation was dominated by the cover crops *Pueraria phaseoloides* (Rosed.) Benth and *Homolepis aturensis* (H.B.K.).

For the enrichment plantations lines of 30 m x 2.5 m of the same secondary vegetation were clear cut in 1991 and 1997, respectively (comp. DÜNISCH et al. 2000). Between these lines 5 m of the fallow vegetation remained untouched. In each line 10 plants (4 to 6 months old) were planted with a spacing of 3 m (representing a plant density 444 trees per hectare). The spontaneous vegetation of the cleared lines was cut by field workers twice a year.

Corresponsding studies were carried out on natural sites of *Swietenia macrophylla* King and *Cedrela odorata* L. in the north of Mato Grosso (close to the city of Aripuana) and on natural sites of *Carapa guianensis* Aubl. in the states of Amazonas (close to the cities of Manaus and Itacoatiara) and Parà (close to the city of Santarem).

2.2 Quantification of the light, water, nutrient demand for biomass production

The light demand of the trees was studied by means of light saturation curves of the photosynthesis of 5 to 8-year-old trees obtained from light measurements and gas exchange measurments (mini cuvette system WALZ) carried out on 5 trees of each species (250 measurements each).

After calibration of the measuring system (DÜNISCH et al. 1999, EILERS 2000), The water uptake of trees with diameters more than 2.5 cm was calculated from xylem sapflow measurements carried out according to GRANIER (1985). Two sensors per tree were installed at approximately 0.5 m and 2.5 m height in 4 trees of each species. As to calculate the water uptake transpiration of the trees from the xylem sapflow measurements the sapwood area of the selected trees was quantified from increment cores and subsequent labeling of the conducting vessel elements by color tracers (1% methylenblue, comp. ERBREICH 1997). The xylem sapflow measurements were carried out with an accuracy of ±12-36 % (comp. EILERS 2000).

The N, P, S, K, Ca, and Mg demand of the species was calculated from the nutrient content of different plant tissues (9 to 40 fractions per tree) and the biomass of the trees, which was annually quantified (DÜNISCH and SCHWARZ 2000). N analyses were carried out by means of a C/N analyzer (Heraeus), whereas the P, S, K, Ca, and Mg content was quantified by means of ICP-OES analyses carried out according to BERNEICKE et al. (1987).

2.3 Quantification of the light, water, nutrient supply of the study sites

The light supply of plantation and natural grown trees was studied by means of PAR sensors installed on the surface and in the crown of the trees (8 sensors per tree). Comparative measurements were carried out in the open field.

The water fluxes within the plantations were calculated for one-month-intervals (DÜNISCH 2000). The study was carried out in 1 to 8 year-old plantations and on natural sites. The precipitation, the throughfall, and the stemflow were quantified in one-month-intervals (sample collection was carried out weekly). The interception in the crown of the plantations was calculated from the difference of precipitation, throughfall, and stemflow. After calibration of the measuring system (DÜNISCH et al. 1999, EILERS 2000) the transpiration of trees with diameters more than 2.5 cm was calculated from xylem sapflow measurements carried out according to GRANIER (1985). According to a methodical approach of BREDEMEIER (1987) the water runthrough in the soil was quantified from water flux measurements. The water flux in the soil was quantified by weekly tensiometer measurements. 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 75-90 cm (RICHARDS 1949). The tensiometers were installed at 5 cm, 15 cm, 35 cm, 65 cm, and 125 cm depths. and at a distance of 1 and 2 m from the trunk. The water content of the soil with suction force values lower than –800 hPa was determined by means of an Aquaterr Soil Moisture Meter.

The evaporation from the soil was calculated as the difference of the water content of the soil, the water input into the soil, the water runthrough in the soil, and the transpiration of the vegetation. Due to a maximum declination of the study site less than 3° water surface runoff also was not considered in this study.

As to calculate the nutrient supply of the study sites nutrient fluxes were quantified according to DÜNISCH et al. (2000). In addition the nutrient stocks of the soil were quantified by the element analyses of annually collected soil samples and the density of the soil fractions quantified gravimetrically.

2.4 Quantification of the biomass production of the trees

As to study the relationship of exogenous input and the biomass production of the trees the biomass of the trees was annually quantified in the field (4 trees per species harvested, 13 to 93 trees measured dendrometrically (height, stem diameters, height of the crown, projection area of the crown)). These data were compared with the biomass production calculated by multiple regression analyses (polynomial functions) from the data on the light, water, and nutrient demand of the species and the light, water, and nutrient supply of the study sites.

3 Results

3.1 Light, water, and nutrient demand of *Swietenia macrophylla, Carapa guianensis* and *Cedrela odorata*

Based on 6 years of measurements the light demand for biomass production of the species was calculated. It turned out that *Swietenia* and *Cedrela* has a higher light demand for biomass production compared to *Carapa.* Studying the relationship of photoactive radiation and the net photosynthesis per leaf area and time it became obvious that the higher light demand of *Swietenia* and *Cedrela* is predominately due to the lower photosynthesis capacity of these species compared to *Carapa.* The maximum rate of photosynthesis at light saturation of *Carapa* is approximately 3 times higher than the maximum photosynthetic capacity of *Swietenia* and also significantly higher than corresponding data of *Cedrela.* In addition under shading the net photosynthesis of *Carapa* is higher than the net photosynthesis of *Swietenia* and *Cedrela.* At an photoactive radiation of 50 uE per m^2s the net photosynthesis of *Carapa* is 3.7 µmol/m^2s compared to 2.4 of *Cedrela* and 1.3 of *Swietenia.* Interpreting the results it has to be mentioned that the differences in wood production of the species are not equivalent the differences found in primary production due to the higher photosynthesis use efficiency and major portion of wood production of *Swietenia* and *Cedrela* compared to *Carapa* (comp. DÜNISCH and SCHWARZ 2000).

The water demand for biomass production of *Swietenia, Carapa*, and *Cedrela* was studied by means of xylem water flux measurements carried out at 5 trees of each species in 1998 and 1999. No significant difference was found between the water uptake per kg biomass production of *Swietenia* and *Carapa,* whereas *Cedrela* showed a higher demand of water for biomass production.

Due to significant differences of the water availability during the year, at different sites, and in different plantation systems the relationship of the water content of the soil and the water uptake of the trees is of importance for the water supply of the trees. Based on more than 3000 data collected on the experimental sites in 1998 and 1999 the relationship of the suction force of the soil and the water uptake in ml per cm^2 sapwood and s of *Swietenia, Carapa*, and *Cedrela* was calculated. Comparing the relationship obtained for *Swietenia, Carapa*, and *Cedrela* it turned out that the relationship obtained for *Swietenia* followed a similar pattern compared to *Cedrela* whereas the pattern obtained for *Carapa* was different. This is especially caused by structural and physiological differences of the roots between *Swietenia* and *Cedrela* on the one hand and *Carapa* on the other hand (NOLDT 2000). Maximum water uptake of *Swietenia* and *Cedrela* was found in wet soils with low soil water potentials. In contrast maximum water uptake of *Carapa* was found in soils with a soil water potential of approximately 250 hPa. The specific water uptake of *Carapa* exceeds the water uptake of *Swietenia* and *Cedrela* in soils with a suction force higher than 70 and 100 hPa, respectively indicating a better adaptation of this species to drier site conditions.

Plant growth on terra firme sites is often limited by the low nutrient supply of the soil. Beside a low content of phosphorus often an extremely low content of K is found in terra firme soils of the central Amazon. Therefore the K demand of *Swietenia, Carapa,* and *Cedrela* for biomass production was studied in more detail.

Comparing the mean K content per kg dry mass of *Swietenia*, *Carapa*, and *Cedrela,* it became obvious that the K demand for biomass production of *Swietenia* and *Cedrela* is significantly higher than the K demand of *Carapa,* which is only 4940 mg K/kg dry mass compared to 6967 mg/kg and 8604 mg/kg, respectively.

As to study whether *Swietenia* and *Cedrela,* which showed a high demand of K for biomass production, also show a high absorption capacity for K, the relationship of the K content of the soil and the K uptake per kg dry mass and year was investigated. Consequently to the high K demand of *Cedrela* in more fertile soils the K uptake of this species exceeds the K uptake of *Swietenia* and *Carapa.* Although *Swietenia* has a higher K demand for biomass production than Carapa, even in fertile soils the K uptake of *Swietenia* is lower than the K uptake of *Carapa,* which is predominately caused by anatomical and physiological differences in the root zone of these species. In soils with extremely low K contents, the K uptake of *Carapa* was significantly higher than the K uptake of *Swietenia* and *Cedrela* indicating a good adaptation of this species to poorer sites.

3.2 Light, water, and nutrient supply in plantations and on natural sites of *Swietenia macrophylla, Carapa guianensis* and *Cedrela odorata*

The light, water, and nutrient supply was studied in the monoculture and in the enrichment plantations at the experimental site of the EMBRAPA in Manaus in comparison to natural site conditions.

During the initial phase of the monoculture maximum light intensities are available for plant growth. After 8 years of growth 80% of the maximum light intensities are available in the *Swietenia* and *Cedrela* plots, whereas the light intensity of the *Carapa* plots was strongly reduced, which indicates that thinning is an urgent need. At the start of the enrichment plantation only 40% of the maximum light is available for the planted trees. With increasing age more light is available for the planted trees and after 8 years *Carapa* already reached the upper crown layer of the plantation. Natural growth of *Swietenia* and *Cedrela* was found at open sites with high light intensities. In contrast to that juvenile plants of *Carapa* were often found in the understorey of primary forests. Light intensities measured on these sites varied between 35 and 55% of the maximum light intensity.

Studying the water supply of plantations and natural sites it became obvious that the water supply of plantations can differ significantly from natural site conditions. The central Amazon is characterized by a season with high precipitation from December until June and a season of lower precipitation from July until November. Due to this reduced precipitation an increase of the water potential of the soil was found on all sites. With regard to the growth dynamics of planted trees short-term periods of higher soil water potentials, which were found in the monoculture also during the rainy season are of special interest. For most of the tree species on terra firme sites the rainy season is the main growth season. Therefore these short term changes of the soil water content during this period observed in the monoculture plots might have a strong impact on the growth and wood formation of the planted trees. In contrast to the monoculture the water budget of the enrichment plantation was more balanced. Short-term periods of reduced precipitation during the rainy season did not have a significant influence on the mean monthly soil water potential of the soil indicating a better water availability during that period. No significant difference was found between the maximum soil water potential of the monoculture and the enrichment plantation during the dry season. On natural sites of *Swietenia* and *Cedrela* low and well balanced soil water potentials were found during the wet season from December until June, whereas *Carapa* was often found on sites with a high ground water level with water logged soils from May until June and lower suction force values from July to November compared to native sites of *Swietenia* and *Cedrela.*

The nutrient balance of all macronutrients of the monoculture, the enrichment plantation, and natural sites was calculated from nutrient input and output data collected

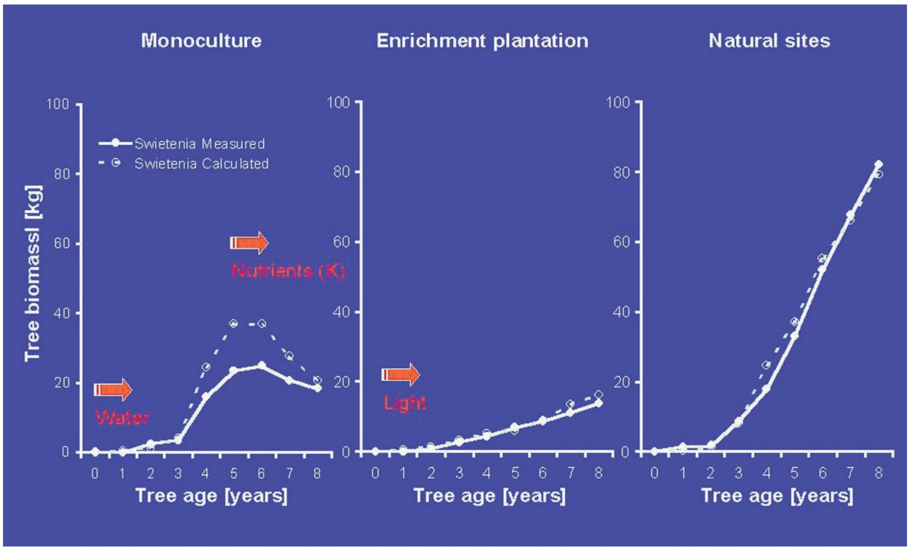

Fig. 1: Biomass (kg) of 1 to 8-year-old *Swietenia macrophylla* grown in monoculture and enrichment plantations and on natural sites. Measured data in the field and calculated data.

from 1995 until 1999 (DÜNISCH et al. 2000). Based on these measurements the K stocks of the soil (kg/ha) up to 60 cm depths of the monoculture, the enrichment plantation and of natural sites were quantified. A strong decrease of the K stocks of the soil was found in the 1 to 8 year-old monoculture plots. Beside the uptake of K by the vegetation this decrease was predominately caused by high leaching of K out of the soil and low litter decomposition during the initial phase of the monoculture plantation. After approximately 5 years the K stocks of the soil of the monoculture were stabilized at a level of 30 to 63% of the K stocks found before planting indicating a strong need for appropriate tools for the improvement of the nutrient supply of plantations especially during the initial phase of growth. In contrast to that the K input into the soil and the K output out of the soil of the enrichment this plantation system on the nutrient supply of disturbed sites. According to the findings in the enrichment plantation a balanced nutrient input and output was found on natural sites of *Swietenia*, *Carapa*, and *Cedrela*. Natural growth of *Swietenia* and *Cedrela* was only found in more fertile soils compared to the soil conditions in the monoculture and in the enrichment plantation considered in this study. In contrast to that the K content of the soil of natural growth of *Carapa* varied in the range of the K content of the soil of the 2 plantation systems

3.3 Biomass production of *Swietenia macrophylla, Carapa guianensis,* and *Cedrela odorata*

The biomass of the trees was annually quantified in the field. These data were compared with the biomass production calculated by multiple regression analyses from the data on the light, water, and nutrient demand of the species and the light, water, and nutrient supply of the study sites presented before.

In general the calculated biomass of *Swietenia* is in good agree with the measured biomass in the field indicating a high significance of the light, water, and nutrient supply for tree growth of *Swietenia* (Fig. 1). The lower biomass production of *Swietenia* measured in the monoculture compared to calculated values from light, water, and nutrient data is predominately due to severe insect attacks of *Hypsiphylla grandella* after 3 years of growth. The biomass production of *Swietenia* grown in the monculture as well as in the enrichment plantation was significantly lower compared to natural sites. At the initial phase tree growth of *Swietenia* grown in the monoculture was limited by the shortterm periods of reduced water supply during the growing season and the decreasing K supply of the soil with increasing age of the plantation. The reduced biomass production of *Swietenia* grown in the enrichment plantation compared to natural sites was predominately caused by the insufficient light supply in this plantation. In contrast to the biomass production of *Swietenia* obtained in the 2 plantations on natural sites the biomass production of this species was close to the maximum biomass production calculated from light, water, and nutrient saturation data. This indicates a low adaptation of *Swietenia* to unfavorable site conditions and might explain, why this species is not native in the Manaus region.

Also in the case of *Carapa* more than 90% of the biomass production of the trees is explained by the light, water, and

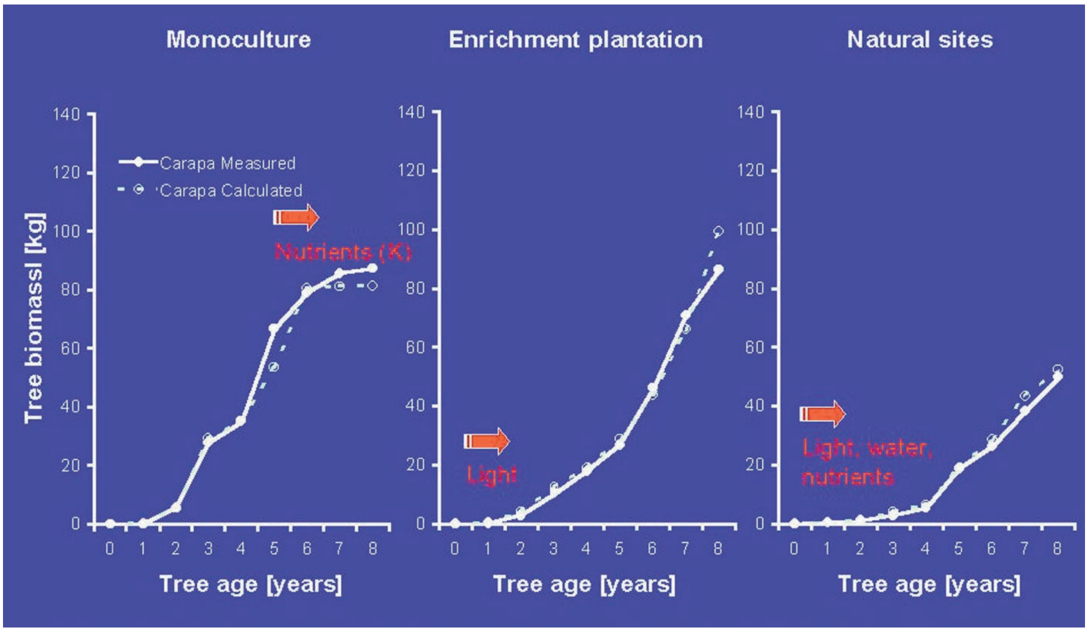

Fig. 2: Biomass (kg) of 1 to 8-year-old *Carapa guianensis* grown in monoculture and enrichment plantations and on natural sites. Measured data in the field and calculated data.

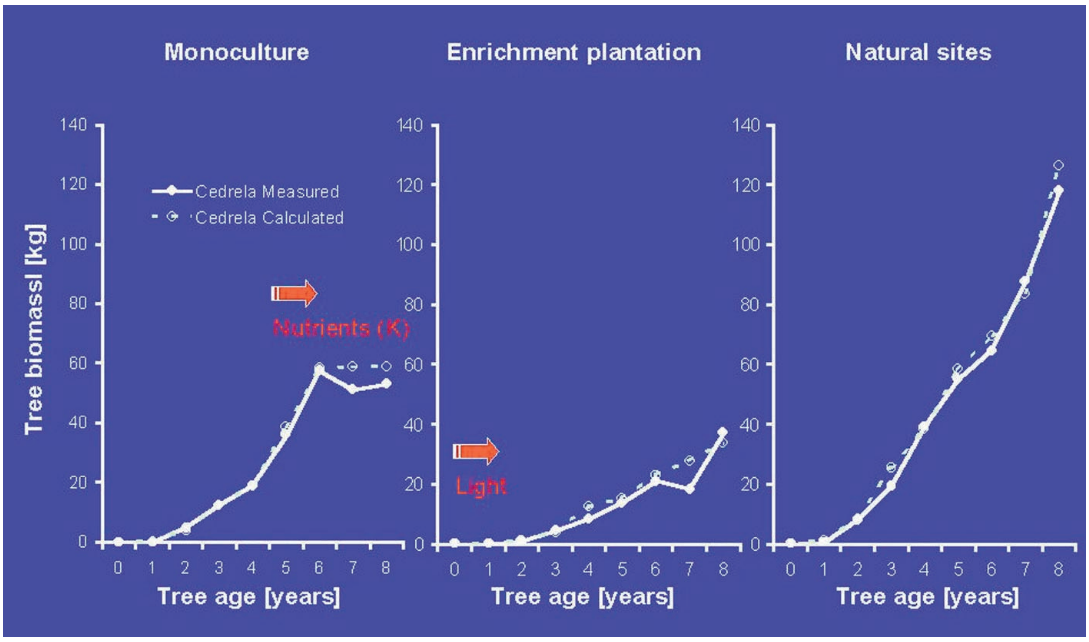

Fig. 3: Biomass (kg) of 1 to 8-year-old *Cedrela odorata* grown in monoculture and enrichment plantations and on natural sites. Measured data in the field and calculated data.

nutrient supply of the study sites (Fig. 2). Although after 3 years of growth *Carapa* was also attacked by *Hypsiphylla grandella* in the monocultue no significant difference between the measured and the calculated biomass of the trees was found. This indicates a better compensation capacity of *Carapa* against attacks of *Hypsiphylla grandella* compared to *Swietenia*. With increasing tree age growth of *Carapa* is also limited by the reduced K stocks of the soil in the monoculture. In addition after 6 years of growth the reduced light availability in this plantation had a significant impact on the biomass production of *Carapa*. In the initial phase of growth also the biomass production of *Carapa* grown in the enrichment plantation was significantly limited by the availability of light. Due to the better shade tolerance of this species compared to *Swietenia* and the more balanced nutrient supply of this plantation compared to the monoculture after 8 years the biomass production of *Carapa* is in the same order as the biomass production of the monoculture. The biomass production of natural growth of *Carapa* was reduced compared to plantation growth. Studying the light, water, and nutrient supply of natural sites it became obvious that on these sites the tree growth often was limited by a reduced light, water, and nutrient supply. This indicates that *Carapa* is also adapted to non-optimum site conditions. Corresponding to the biomass production of *Swietenia* after 6 years of growth in the monoculture the biomass production of *Cedrela* was limited by the reduced K supply of the soil, whereas in the enrichment plantation the reduced availability of light had a strong impact on the biomass of *Cedrela* as well. According to results obtained for *Swietenia* biomass production of *Cedrela* on natural sites was close to the maximum biomass production calculated from light, water, and nutrient saturation points indicating also a low adaptation capacity of this species to unfavourable site conditions and a similar natural habitat of these 2 species. Nevertheless, it has to be mentioned that under comparable site conditions the biomass production of *Cedrela* is 40 to 60% higher than the biomass production of *Swietenia.*

4 Discussion and conclusions

This study shows that the light, water, and nutrient demand of different tree species of the same region can differ significantly (KOZLOWSKI et al. 1991). It became obvious that *Carapa* is better adapted to unfavorable site conditions compared to Swietenia and Cedrela, which explains that *Carapa* is also often found on unfavourable sites whereas the natural distribution of *Swietenia* and *Cedrela* is restricted to sites, which offer growth conditions close to the physiological optimum of these species (LARCHER 1984). With regard to the cultivation of these species these results show that a cultivation of *Swietenia* and *Cedrela* is only promising in plantations, when the sites are carefully selected and appropriate management of the plantation is carried out. In contrast the cultivation of *Carapa* can be recommended also on poorer sites, although a slight decrease of biomass production has to be taken into consideration (LAMPRECHT 1986).

In accordance with other field studies carried out in tropical regions this study showed that the site conditions in plantations differ significantly from natural site conditions in primary forests (JORDAN and KLINE 1977, GRANIER et al. 1987, LEOPOLDO et al. 1995, BECKER 1996, SCHROTH et al. 1999). Therefore besides knowledge about the site demands of selected tree species (comp. LARCHER 1984, KOZLOWSKI et al. 1991) information on the site conditions are necessary to manage sustainable timber production in plantations (STURM et al. 1998). In many studies the significance of the plantation management for the regulation of the site conditions are emphasized (BREDA et al. 1993, BREDA et al. 1995, BRÜNIG 1996, LÜTTSCHWAGER et al. 1999). This comparative study on the site conditions of plantations and natural sites indicated that light and water conditions can be optimized by silvicultural practices (comp. ZECH et al. 1998), whereas for a sustainable nutrient supply of the soil in the long run appropriate fertilization is indispensable.

With regard to applied management tools for high quality timber production in complex plantation systems, it can be concluded that data on the light, water, and nutrient demand and corresponding data on the site conditions offer the chance to select suitable tree species for selected sites or to modify sites for the selected tree species for planting (e.g. by means of geographical information systems).

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