Water supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in three plantation systems

O. Dünisch,[1] G. Schroth,[2, 3] R. de Morais,[4] and M. Erbreich[5]

1 Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg
2 Institute of Applied Botany, Hamburg University, Hamburg
3 Institute of Soil Science and Soil Geography, University of Bayreuth, Bayreuth
4 EMBRAPA Amazônia Ocidental, Manaus, AM, Brazil
5 Institute of Wood Biology, Hamburg University, Hamburg

Summary

The following investigations were initiated by the increasing demand for the development of sustainable landuse systems in the Central Amazon, including high quality timber production. Mixed plantations are able to reduce the strong exploitation of high quality timber trees in primary forests in this region. In order to develop sustainable plantation systems, knowledge on the site demands of the tree species is necessary. Especially the seasonal variation of the water supply of the Central Amazon influences tree growth and wood formation in plantation systems. Therefore, the water supply of the important commercial timber trees *Swietenia macrophylla* King and *Carapa guianensis* Aubl. (*Meliaceae*) was studied in three different plantation systems (monoculture system, mixed culture system, enrichment system established in 1992/ 1993) near Manaus, Brazil.

Seven trees each of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. were selected to study the xylem water conducting system expressed in terms of the morphology and anatomy of the leaves, the stem and the roots of 6-year-old plantation-grown trees. Furthermore, the permeability of the stem xylem was studied. The relationship between the soil water tension, studied by tensiometer measurements, and the water uptake and the water release of plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl. was investigated by xylem runthrough measurements carried out by the Granier method. The water balance of the plantations was quantified by evaporation, transpiration/ xylem flux measurements, as well as by the calculation of the water flux in the soil (Cl-method).

The morphological and anatomical investigations revealed a strong seasonal variation of the fine root biomass and the leaf area of *Swietenia* trees, with a strong reduction during the drier season from July until November. In contrast to that, only slight differences were found for the root biomass and the leaf area of *Carapa* trees. Consequently to this, the relationship of water uptake and water release of the two species showed significant differences in relationship to the soil water content. Even in short-time periods with a reduced soil water supply, a water deficiency was detected for *Swietenia,* whereas the water reservoirs of *Carapa* could be completely refilled during the night, even during dry periods. The spontaneous vegetation of the plantation systems, and with that the plantation management, had a strong influence on the water supply of the plantation-grown trees. In 6-year-old monoculture systems, evaporation and water percolation through the solum were of main importance for the water balance of the plantations, whereas in the mixed plantation system and the enrichment system 40 to 70% of the water output were due to transpiration.

From these investigations, it was concluded that *Carapa* is more adapted to overcome water stress during drier periods compared to *Swietenia.* The water-supply of the enrichment system is more stabilized compared to the monoculture and the mixed culture system, which indicates that a well-planned management for sustainable timber production in plantations is necessary. The reduced water uptake of *Swietenia* in the enrichment system III, in spite of the improved soil water supply, indicates a higher sensitivity of *Swietenia* to competition compared to *Carapa* in this system, especially during drier periods.

Resumo

Reserva de água de *Swietenia macrophylla* King e *Carapa guianensis* Aubl. em três sistemas de plantio

Os trabalhos foram desenvolvidos devido a demanda crescente voltadas ao desenvolvimento de sistemas sustentáveis de uso da terra na Amazônia Central, incluindo a produção de madeira de alta qualidade. Para esta região, os plantios mistos podem reduzir a intensa exploração de espécies produtoras de madeira de alta qualidade na floresta nativa. Para desenvolver os sistemas de plantios sustentáveis é necessário conhecer as demandas locais de espécies arbóreas. A variação sazonal do suprimento de água na Amazônia Central influencia, especialmente, no crescimento das árvores e na formação da madeira nos sistemas de plantio. Portanto, estudou-se o estoque de água das espécies arbóreas importantes comercialmente, *Swietenia macrophylla* King (mogno) e *Carapa guianensis* Aubl. (andiroba) (Meliaceae), em três diferentes sistemas de plantio (monocultivo, cultivo misto e floresta enriquecida no período de 1992 a 1993), próximo a Manaus, Amazonas.

Sete árvores de mogno e sete de andiroba foram selecionadas para estudar o sistema de condução de água no xilema expresso em função da morfologia e anatomia das folhas, do caule e das raízes de árvores cultivadas com seis anos de idade. Além disso, estudou-se também a permeabilidade do xilema do caule. A relação da força de sucção do solo, estudada pelas medições com tensiômetro, a absorção e a liberação de água do mogno e andiroba na área de plantio foram analisados pelas medições do fluxo de seiva no xilema através do método Granier. O balanço de água do plantio foi quantificado pela evaporação, medições da relação entre a transpiração e o fluxo no xilema, bem como pelo cálculo do fluxo de água no solo (método Cl).

As investigações morfológicas e anatômicas revelaram uma forte variação sazonal da biomassa das raízes finas e da área foliar do mogno, com uma forte redução durante o período mais seco, de julho até novembro. Por outro lado, apenas pequenas diferenças foram encontradas na biomassa da raiz e na área foliar da andiroba. Consequentemente, a relação da absorção e liberação de água pelas duas espécies, mostrou diferenças significativas em relação ao teor de água no solo. Mesmo em períodos curtos, com uma reduzida disponibilidade de água no solo, foi detectada uma deficiência de água para o mogno, enquanto que as reservas de água da andiroba foram completamente repostas durante à noite, mesmo nos períodos secos. A vegetação espontânea dos sistemas de plantio, com o sistema de manejo adotado, exerce uma forte influência sobre a disponibilidade de água das árvores cultivadas. Nos monocultivos com seis anos de idade, a evaporação e o fluxo de água no solo foram de grande importância para o balanço de água, enquanto que no plantio misto e no sistema de enriquecimento, 40 a 70% da água liberada foi causada pela transpiração.

A partir desses dados, conclui-se que a andiroba é mais adaptada aos períodos mais secos, se comparada ao mogno. A disponibilidade de água no sistema de enriquecimento é mais estável comparado com a monocultivo e o plantio misto, indicando a necessidade de um sistema de manejo bem planejado para a produção sustentável de madeira. A reduzida absorção de água pelo mogno no sistema de enriquecimento, apesar da melhor disponibilidade de água no solo, indica uma alta ou maior sensitividade do mogno para competir comparada à andiroba neste sistema, especialmente durante os períodos mais secos.

Introduction

In urban areas of the Central Amazon, an increasing demand for agricultural products and wood is obvious (BENCHIMOL, 1996). The main reason is the distinct trend of population growth in cities. Traditional systems for land use and monocultures around the cities cannot guarantee a sustainable production and cannot sufficiently supply the population with food and wood (HANNAN and BETALHA, 1995; FEARNSIDE, 1993). The consequence is the increasing demand for new land, which leads to extensions into the tropical forests (SANCHEZ et al., 1982; FERNANDES et al., 1997; FEARNSIDE, 1995).

Particularly the increasing demand for wood is exclusively satisfied from primary forests, which frequently leads to exploitation of high quality species, such as *Swietenia macrophylla* King and *Carapa guianensis* Aubl. (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 special high quality timber for Amazonia may even lead to the import of wood to some extent (BENCHIMOL, 1996).

The EMBRAPA Amazônia Ocidental in Manaus develops sustainable land use systems to counteract this tendency, accompanied since 1992 with a Brazilian-German cooperation (SHIFT). One of the main aspects is the recultivation of degraded areas. The main aim are polycultures with agroforestry tendencies. This means that agriculturally oriented systems should, to some extent, include native tree species for high valuable wood production (WHITMORE, 1995).

The knowledge about the site demands of commercial timber tree species of the Central Amazon is still restricted. Besides a restricted nutrient supply of many soils of the Central Amazon, the Manaus region is characterized by a strong seasonal variation of the soil water supply with high precipitation from December until May and reduced precipitation from June until November. The physiology, and with it the growth of the trees, is strongly influenced by the water supply, due to the significance of water for the turgor of the cells (KLEINIG and SITTE, 1992; DÜNISCH et al., 1994), the biosynthesis of carbohydrates and accessory compounds (HÖLL, 1985; SANTES, 1988; LANGENFELD-HEYSER, 1987) and the transport of substances (KRAMER, 1985; VIGOUROUX et al., 1989; KOZLOWSKI et al., 1991). Therefore, investigations on the water supply of plantation-grown trees are necessary to draw conclusions for the management of mixed plantations with regard to an optimum in productivity and sustainability.

The main objective of this study was to investigate the water supply of plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in three different plantation systems near Manaus, Brazil. The investigations were carried out with special regard to the water demand in wet and dry periods of these high quality timber tree species and its significance for the water supply of the plantation systems.

Experimental

Plantation systems and experimental trees

The experimental plots are located close to the EMBRAPA Amazônia Ocidental, 25 km north of the city of Manaus, 3°8' S, 59°52'W. The area is located 50 m above sea level with an annual precipitation of about 2,500 mm (average of 1962 – 1997). The soil is a poor yellow latosol with a reduced cation exchange capacity (comp. Dünisch et al., 1999 a) and a high water capacity. The investigations on the water supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. were carried out in three different plantation systems which are used for interdisciplinary research projects within the Brazilian-German cooperation program "SHIFT" (comp. Fig. 1):

System I (established in January 1992):

- Former monoculture of *Hevea brasiliensis* (H. B. K.) Muell.Arg., clear cut in 1991
- Monoculture systems of 20 selected tree species with 4 repeats and 25 plants per plot
- Spacing 3 x 3 m
- Fertilization 1992: 150 g superphosphate per tree
- Spontaneous vegetation is dominated by cover crops *Pueraria phaseoloides* (Rosed.) Benth and *Homolepis aturensis* (H. B. K.) Chase and cutting by field workers.
- Biomass of the system (December 1996): *Swietenia* 27 to/ ha, *Carapa* 46 to/ ha

System II (established in January 1993):

- Former monoculture of *Hevea brasiliensis* (H. B. K.) Muell. Arg. Former, burnt in 1992
- Mixed culture system of *Swietenia, Carapa, Schizolobium amazonicum* and *Hevea brasiliensis*, 5 repeats
- Spacing *Swietenia, Carapa*: 4 x 5 m, *Schizolobium, Hevea*: 3 x 5 m
- Fertilization 500 g $CaCO_3$, 155 g SFT, 100 g KCl, fertilization after 2 months: 65 g NH_4 , after 11 months: 50 g NH_4, 100 g SFT, 50 g KCl, 50 g $MgSO_4$, 20 g FTEBR8 (mixture Zn, B, Cu, Fe, Mn, Mo)
- Spontaneous vegetation is not suppressed (*Vismia guianensis* and *Vismia japonensis*).
- Biomass of the system (December 1996): *Swietenia, Carapa* 47-55 to/ ha

System III (established in January 1992):

- Former monoculture of *Hevea brasiliensis* (H.B.K.) Muell. Arg.
  Enrichment of a 25-year-old secondary vegetation with 10 species (line enrichment).
  10 plants per species, 4 repeats
- Spacing 3 x 6 m
- Fertilization 1992: 150 g superphosphate per tree
- Spontaneous vegetation was not cut or suppressed for 25 years; dense vegetation with 76 genera out of 39 families.
- Biomass of the system (December 1996): *Swietenia, Carapa* 105-120 to/ ha

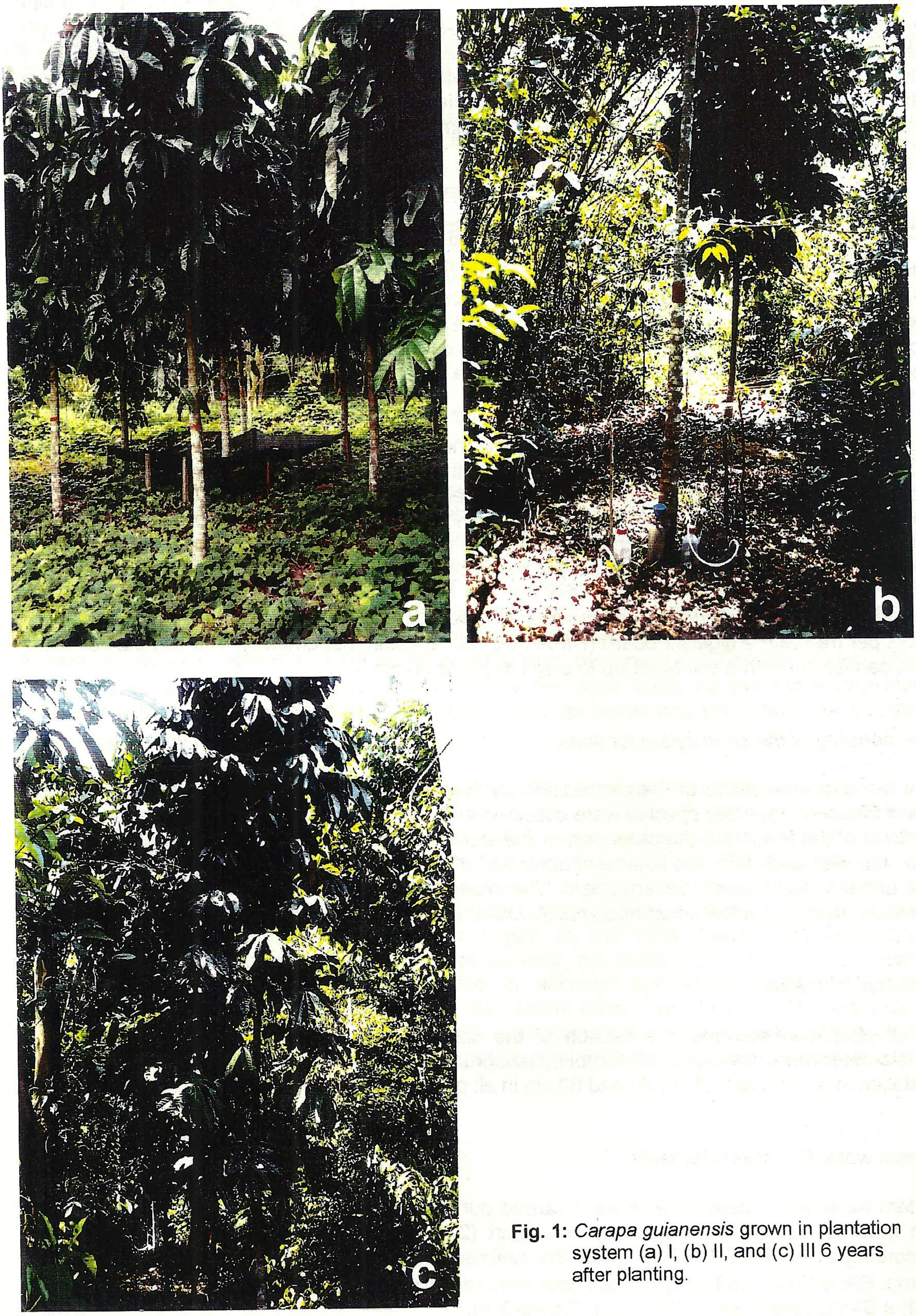

Fig. 1: *Carapa guianensis* grown in plantation system (a) I, (b) II, and (c) III 6 years after planting.

The investigations were carried out in 1996 and 1997. For the study of the morphological and anatomical characteristics of the trees, four *Swietenia* and four *Carapa* trees of plantation system I, and two *Swietenia* and two *Carapa* trees each of plantation system II and III were selected. Xylem flux measurements were carried out for three trees per species in each plantation system. For the quantification of the xylem water flux of the secondary vegetation of plantation system III, the ten most important species were selected (27% of the biomass of the secondary vegetation of plantation system III, comp. PREISINGER et al., 1994; PREISINGER et al., 1999).

Morphological and anatomical characteristics of leaves, stem xylem, and roots

The leaf area was quantified for 50 leaves per tree with a leaf-area integrator (Optical Area Meter, LI-COR, USA). In order to study the stomata, the epidermis, and the cuticula of the leaves, leaf samples were fixed in ethanol (70%). Maceration was carried out with Jeffrey´s solution (comp. GERLACH, 1977). As a means to calculate the number of stomata per mm^2 and the mean thickness of the epidermis and cuticula, 50 measurements per leaf were carried out under the microscope.

Cross sections were prepared with a microtome with the purpose of studying the vessel diameter and the vessel area percentage of the stem xylem. In order to study the length of the vessels, xylem samples were macerated with Jeffrey´s solution. Histometrical measurements were carried out for 150 vessels of the inner and the outer part of the xylem with a digitiser board (HIPAD PLUS, Houston Instruments). The number of pits (n>3000) and the diameter of the pits (n=150) were quantified directly in the microscope.

The length and diameter of fine roots were quantified during the wet and the dry season for 500 roots per tree with a digitiser board (HIPAD PLUS, Houston Instruments). The sample collection was carried out with a soil borer up to a soil depth of 80 cm.

Permeability of the stem xylem for water

For the characterization of the permeability of the stem xylem of *Swietenia* and *Carapa,* stem discs of seven trees per species were collected and shock frozen. Xylem samples with a length of 3 cm of the inner and the outer part of the stem were prepared with a drill (diameter 15 mm, four samples each from the inner and outer part of the disc). The dowel preparation was carried out under water to avoid air embolism. The water flux measurements were carried out with a pressure of 60 cm water column (comp. BAUCH, 1964).

Soil water tension

In all plantation systems, the tension of the soil water was monitored since July 1995 by tensiometer measurements (UP GmbH, Osnabrück) in one-week-intervals. Tensiometers were installed in a soil depth of 10, 20 and 60 cm in all plots with a distance of 1 m from the trunk.

Xylem water flux measurements

Xylem water flux measurements were carried out at breast height (1.3 m) in the outer (0 - 2.5 cm from the cambium) and in the inner part (2.5 - 5 cm from the cambium) of the stem, according to GRANIER (1985). After the calibration of the system (heating system 120 mA; comp. ERBREICH, 1997); xylem flux data were monitored every 30 s with an accuracy of ±10% with a SKYE data logger (UP GmbH, Osnabrück).

The relationship between the xylem water flux, measured by Granier sensors, the water uptake, and the water release of the trees was analyzed. A water reservoir, which was connected with the stem xylem by a needle, was installed (same diameter of the needle and the Granier sensors; comp. ZIMMERMANN, 1983, KRAMER, 1985). The water uptake out of the reservoir was quantified in one-hour-intervals.

Quantification of the water balance of the plantation systems

The evaporation of the crown of the plantation systems was quantified from the precipitation, the throughfall, and the stemflow, which was monitored in one-week-intervals. Soil evaporation was calculated as the difference between water input, transpiration, and water penetration.

The transpiration of the vegetation was calculated from xylem sap flow measurements carried out according to GRANIER (1985). The transpiration of the cover crops *Pueraria phaseoloides* and *Homolepis aturensis* (plantation system I) was quantified by container cultures installed in the field, which were weighed in one-day-intervals.

The water percolation in the soil was quantified by tensiometer measurements and the Cl-method (suction caps in a soil depth of 10, 20 and 60 cm) according to BREDEMEIER (1987).

Results

Xylem water conductance of 6-year-old Swietenia macrophylla and Carapa guianensis

The studies on the morphology and anatomy of the leaves of *Swietenia* and *Carapa* showed that the leaf area and the total leaf area per tree of *Swietenia* is strongly reduced compared to *Carapa*, whereas a higher number of stomata/ mm² was found in *Swietenia* compared to *Carapa* (Table 1). Furthermore, a strong seasonal variation of the leaf area of *Swietenia* was found, with low leaf biomass during the dry season (August until October) and a pronounced increase of leaf production at the beginning of the wet season in December. The leaf area of *Carapa* was only slightly reduced during the dry season compared to the wet season (Table 1). Consequently to this, the lifecycle of *Swietenia* leaves varied between 11 and 18 months, whereas an average lifecycle of 23 to 30 months was monitored for *Carapa* leaves. This indicates a strong regulation of the transpiration of *Swietenia* trees *via* the transpiring leaf surface area throughout the year. The thickness of the epidermis and the cuticula of *Carapa* leaves was slightly reduced compared to *Swietenia*.

Tracer experiments (methylene blue 1%) showed that the vessel system of the stem xylem is of main importance for the water transport within the stem of *Swietenia* and *Carapa,* and that fibres are of less importance (comp. ERBREICH, 1997). Wood-anatomical studies on the vessel system of the stem revealed slight differences between *Swietenia* and *Carapa* (Table 1). A higher vessel length and a reduced number of pits/ 0.01 mm² were found in the xylem of *Swietenia* compared to the xylem of *Carapa*. This indicates that wood-anatomical characteristics are not always parallel with regard to the xylem water flux efficiency. Consequently to that, no significant differences between the water permeability of the stem xylem of *Swietenia* and *Carapa* were found (Fig. 2), although high vessel length and a high number of pits strengthen the efficiency of the xylem water conductance. No significant differences in the permeability of the stem xylem were found between the inner and the outer part of the stem (Fig. 2), which indicates that at a tree age of six years, a strong senescence of the sapwood is not very likely, yet.

Table 1: Morphological and anatomical characteristics of the leaves, the xylem of the stem, and the fine roots of 6-year-old plantation-grown *Swietenia macrophylla* and *Carapa guianensis*.

Morphological and anatomical Characteristics	***Swietenia macrophylla*** **(25% - 50% - 75% Percentile)**	***Carapa guianensis*** **(25% - 50% - 75% Percentile)**
Leaves		
Leaf area [cm^2]	111 – 137 – 178	317 – 421 – 578
No. of stomata/ mm^2	563 – 738 – 811	384 – 518 – 549
Thickness of epidermis [µm]	12.7 – 14.0 – 16.9	8.9 – 10.5 – 12.9
Thickness of cuticula [µm]	14.9 – 19.5 – 20.7	16.3 – 17.0 – 19.4
Leaf area/ tree [m^2]		
Wet season	8.4 – 11.1 – 22.9	48.5 – 70.7 – 198.1
Dry season	5.2 – 6.3 – 10.8	44.7 – 61.6 – 158.2
Stem xylem		
Vessel area [%]	7.5 – 10.1 – 11.9	10.7 – 11.1 – 12.0
Vessel length [mm]	0.43 – 0.52 – 0.54	0.29 – 0.32 – 0.33
Vessel diameter [µm]	69 – 72 – 105	88 – 90 – 95
No of pits/ 0.01 mm^2	231 – 273 – 287	411 – 424 – 438
Pits diameter [µm]	2.9 – 3.7 – 4.7	2.4 – 3.6 – 4.8
Fine roots		
Length [mm]		
Wet season	17.6 – 22.3 – 27.8	8.1 – 10.3 – 11.2
Dry season	7.1 – 9.4 – 11.8	4.9 – 8.7 – 10.2
Diameter [mm]		
Wet season	0.46 – 0.54 – 0.71	0.30 – 0.39 – 0.46
Dry season	0.23 – 0.31 – 0.38	0.33 – 0.42 – 0.44
Fine root biomass/ tree [g]		
Wet season	36 – 65 – 92	148 – 265 – 371
Dry season	27 – 41 – 71	118 – 199 – 341

During the dry season, the length, the diameter, and the fine root biomass of *Swietenia* were strongly reduced in comparison to the wet season, as already shown for the leaf biomass. (Table 1). In the same period, only a small reduction of the length of the fine roots and the fine root biomass of *Carapa* was found compared to the wet season. Throughout the wet period, the length and the diameter of *Swietenia* fine roots were significantly higher compared to *Carapa* fine roots. This indicates a highly efficient water uptake and water transport of the fine root system of *Swietenia* trees during the wet period (comp. NOLDT et al., 1999). Nevertheless, the total fine root biomass of *Carapa* trees was four to five times higher than the fine root biomass of *Swietenia* trees, which reveals a high capacity for water uptake of *Carapa*, especially even in drier periods.

The strong seasonal variation of the leaf and root biomass of *Swietenia* compared to *Carapa* already indicates a strong influence of soil water supply on the water uptake of *Swietenia* trees. This was confirmed by the study of the relationship between the soil water supply and the water uptake and the water release of *Swietenia* and *Carapa* (comp. Fig. 3a-f). In periods of high soil water contents, high water uptake was registered for *Swietenia* (Fig. 3a). The high surplus of water uptake in this period is correlated with strong leaf, root, and cambial growth (comp. DÜNISCH et al. 1998, 1999b), and there is some evidence that the surplus is explained by the high demand for water of new tissue. Nevertheless, even in periods of high soil water contents during daytime, the water release is higher than the water uptake, and the water reservoirs of the tree are refilled especially during the night (lower water saturation deficit of the air, comp. DÜNISCH et al. 1999b).

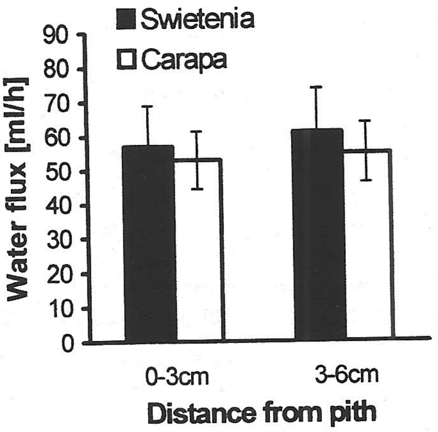

Fig. 2: Permeability [ml/ h] of the stem xylem (sample diameter 15 mm) for water of 6-year-old *Swietenia macrophylla* and *Carapa guianensis* 0 – 3 cm and 3 - 6 cm from the pith (stem radii 5.4 - 6.4 cm).

Under good soil water supply conditions, the course of water uptake of *Carapa* follows the course of water release (Fig. 3b), but only a small surplus of water uptake compared to water release was found. Even in periods with a slight reduction of the soil water content (suction force of the soil 200 - 400 hPa), the water release of *Swietenia* exceeded the water uptake of the tree significantly (Fig. 3 c), and a strong plant water deficiency occurred. In contrast to that, under the prevalent soil-water-conditions, the daily water balance of *Carapa* showed only a small surplus of water release compared to water uptake.

During the dry season, characterized by a strong reduction of the soil water content (Fig. 3e), the water uptake of *Swietenia* was strongly reduced and hardly detectable. The release of water was also strongly reduced due to the strong reduction of the leaf biomass and the reduced growth during this period. In this period also, the water release of *Carapa* exceeded the water uptake significantly, but high water uptake of *Carapa* was even found during the dry season (Fig.3f). In the same period, water reservoirs of *Carapa* were also preferably refilled during nighttime.

These findings indicate a high sensitivity of the water uptake of *Swietenia* to changing soil-water-conditions. In contrast to that, the water uptake and the water release of *Carapa* trees is better balanced throughout the whole year, and changing soil-water-conditions are of less importance for the water balance of *Carapa* trees.

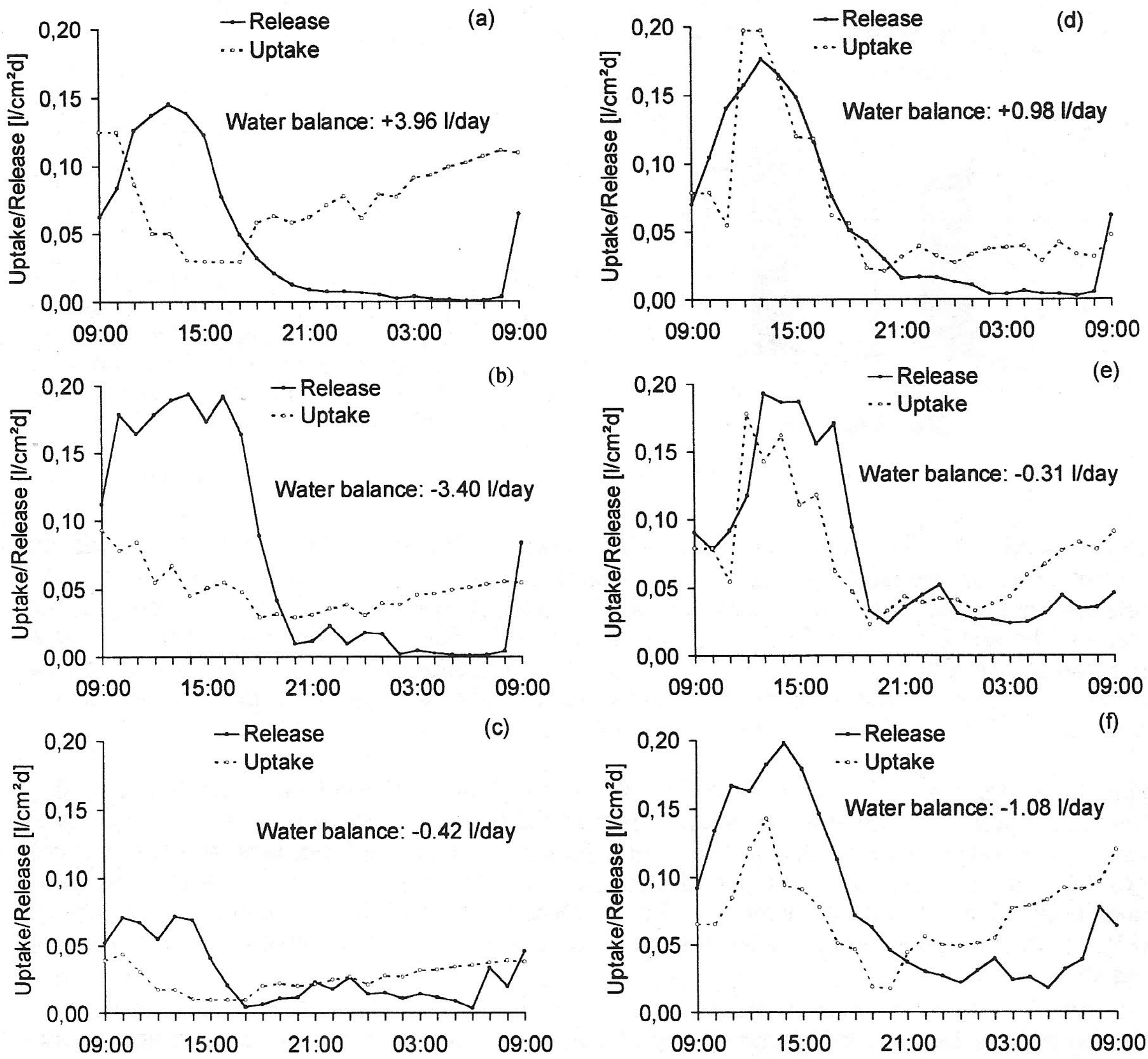

Fig. 3a-f: Diurnal variation of the water uptake and water release [l/ cm²d] of 6-year-old *Swietenia macrophylla* and *Carapa guianensis* at (a/ d) March 28, 1997 (suction force of the soil < 100 hPa), (b/ e) June 21, 1997 (suction force of the soil 200-400 hPa) and (c/ f) October 9, 1997 (suction force of the soil >700 hPa).

With regard to tensiometer measurements carried out in the field, a reduction in water supply on the plantations has to be taken into account from June until November, caused by the significant reduction of the precipitation during this period (Fig. 4a/ b). Nevertheless, short-time periods with a reduced soil water supply were observed even during the wet season from December until May. Although the monthly precipitation of this period varies between 120 and 470 mm, short-time periods with a reduced soil water supply with values up to a critical level of 300 hPa were detected, particularly in the upper soil layer of *Swietenia* monocultures. This is caused by the high water uptake of *Swietenia* trees during this period compared to *Carapa* (Fig. 4a/ b). During the dry season, lower soil water contents were registered in *Carapa* plantations compared to *Swietenia* plantations (Fig. 3a/ b) due to the higher water uptake of *Carapa* compared to *Swietenia* during this period.

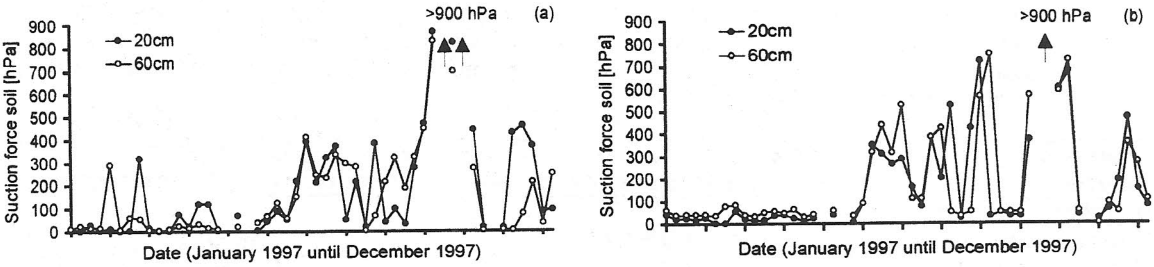

Fig. 4a/ b: Soil water tension [hPa] of (a) a 6-year-old plantation of *Swietenia macrophylla* and (b) *Carapa guianensis* (plantation system I) from January 1997 to December 1997.

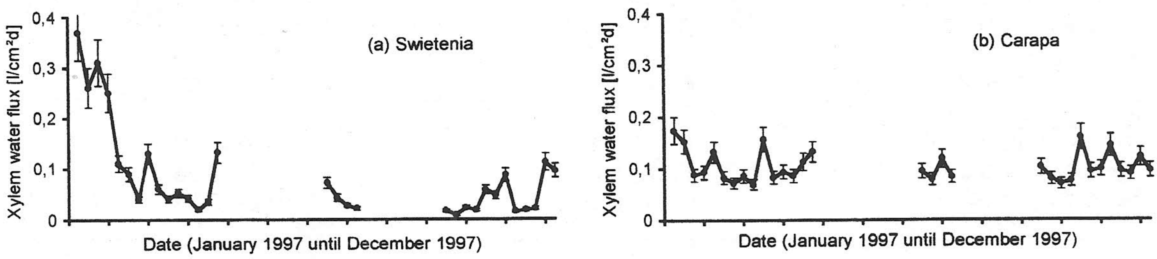

Fig. 5a/ b: Xylem water flux [l/ cm²d] of (a) 6-year-old *Swietenia macrophylla* and (b) *Carapa guianensis* (plantation system I) from January 1997 to December 1997.

Water supply of the three plantation systems

The water budget of the plantation systems is mainly influenced by the relationship between the water uptake of the planted trees and the spontaneous vegetation of the plantation systems (Table 2). The dominant cover crops of the plantation system I (monoculture) *Pueraria phaseoloides* and *Homolepis aturensis* showed a very high demand for water during the wet season, exceeding the specific water demand of the planted trees by a factor of four (*Swietenia*) to nine (*Carapa*). During the dry season, the water uptake of the cover crops was strongly reduced. This indicates a strong competition for water uptake between the planted trees and the spontaneous vegetation, especially during short-time periods with a reduced water supply from December until June (rainy season, comp. Fig. 4a/ b). During the dry season from July until November, especially *Carapa* is more competitive compared to the cover crops with regard to water uptake, which is confirmed by the reduced biomass production of the cover crops in *Carapa* plantations compared to *Swietenia* plantations (December 1996: *Swietenia* plantation 47 kg/ 100 m², *Carapa* plantation 3 kg/ 100 m²).

As already shown for the leaf biomass, the length, the diameter, and the fine root biomass of *Swietenia* were strongly reduced during the dry season compared to the wet season (Table 1), whereas only a small reduction of the length of the fine roots and the fine root biomass of *Carapa* was found during the dry season compared to the wet season. During the wet period, the length, and the diameter of *Swietenia* fine roots were significantly higher compared to *Carapa* fine roots, which indicates a high efficiency for water uptake and water transport of the fine root system of *Swietenia* trees during the wet period (comp. NOLDT et al., 1999). Nevertheless; the total fine root biomass of *Carapa* trees was four to five times higher than the fine root biomass of *Swietenia* trees, which reveals a high capacity for water uptake of *Carapa*, especially even in drier periods.

The water uptake per kg dry mass of *Vismia spp.*, the dominant spontaneous vegetation of the plantation system II (mixed culture system) varied to the same extent as the specific water demand of the planted trees throughout the year (Table 2). The water uptake of *Vismia spp.* was also significantly reduced during the dry season compared to the wet season, which is favourable to the competitiveness of *Swietenia* trees in this plantation system (comp. AZEVEDO et al., 1999). This is also confirmed by the higher water uptake of *Swietenia* in plantation system II compared to system I and III (Table 2).

Table 2: Water uptake per kg dry mass and day [l/ kgd] of 6-year-old plantation-grown *Swietenia macrophylla* and *Carapa guianensis* and the spontaneous vegetation of plantation system I (*Pueraria phaseoloides, Homolepis aturensis*), II (*Vismia spp.*) and III (30-year-old mixed secondary vegetation) during the wet period (December 1996 until June 1997) and the dry period (July 1997 until November 1997).

Plantation system/ Species	Water uptake [l/ kgd] Wet season (December to June)	Water uptake [l/ kgd] Dry season (July to November)
Plantation system I		
Swietenia macrophylla	0.48±0.05	0.16±0.05
Carapa guianensis	0.21±0.03	0.15±0.03
Pueraria phaseoloides	2.26±0.38	0.07±0.04
Homolepis aturensis	2.31±0.42	0.11±0.03
Plantation system II		
Swietenia macrophylla	0.73±0.08	0.18±0.05
Carapa guianensis	0.24±0.06	0.22±0.04
Vismia guianensis	0.48±0.09	0.23±0.06
Vismia japonensis	0.44±0.07	0.25±0.08
Plantation system III		
Swietenia macrophylla	0.51±0.05	0.09±0.03
Carapa guianensis	0.37±0.06	0.33±0.05
Secondary vegetation (10 species)	0.53±0.06	0.47±0.05

The specific water uptake of the secondary vegetation of the plantation system III (enrichment of a secondary forest) exceeds the water uptake of the planted trees, especially during the dry period (Table 2). This indicates that most of the species of the secondary vegetation are more adapted to drier site conditions than the planted trees, especially *Swietenia* trees (comp. PREISINGER et al., 1999). This indicates a strong competition of the secondary vegetation for the water uptake of the planted *Swietenia* trees, especially during the dry season, which is confirmed by the reduced growth and a high mortality of *Swietenia* in this plantation system (comp. AZEVEDO et al., 1999; DÜNISCH et al., 1999b).

In order to quantify differences in water supply between the wet period from December until June and the drier period from July until November water runthroughs for the three plantation systems (I - III) were studied.

In *Swietenia* monocultures soil evaporation, in *Carapa* monocultures evaporation from the crown is of main importance for the water output of the plantation (Fig. 6a). Furthermore, in *Swietenia* monocultures a high amount of water runthrough in the soil was quantified, which indicates a high leaching of mineral elements in this system (comp. DÜNISCH et al., 1999a). The high amount of water runthrough in the *Swietenia* monoculture compared to *Carapa* is mainly caused by the reduced transpiration of *Swietenia* trees compared to *Carapa* especially in June, July, and November.

In contrast to that, 45 to 60 % and 40 to 70 % of the water output of the plantation system II and III respectively, are caused by transpiration, whereas soil evaporation and runthrough are strongly reduced (Fig. 6b/ c). A comparison of the transpiration of the monocultures (System I, Fig. 6a) and the enrichment system (System III, Fig. 6 c) during the drier season from July until November indicates that the trees and shrubs of the secondary vegetation are more adapted to drier periods compared to the planted timber trees, which is indicated by high transpiration rates in system III even from July until November. This is confirmed by further studies on the plant-water relationships of the secondary vegetation on "terra firme" sites in the Manaus region (comp. PREISINGER et al., 1999).

These results showed that with regard to water supply, system III is more stabilized compared to system I and II. The reduced water uptake of *Swietenia* in system III in spite of the improved soil water supply indicates a higher sensitivity of *Swietenia* to competition compared to *Carapa* in this system, especially during drier periods.

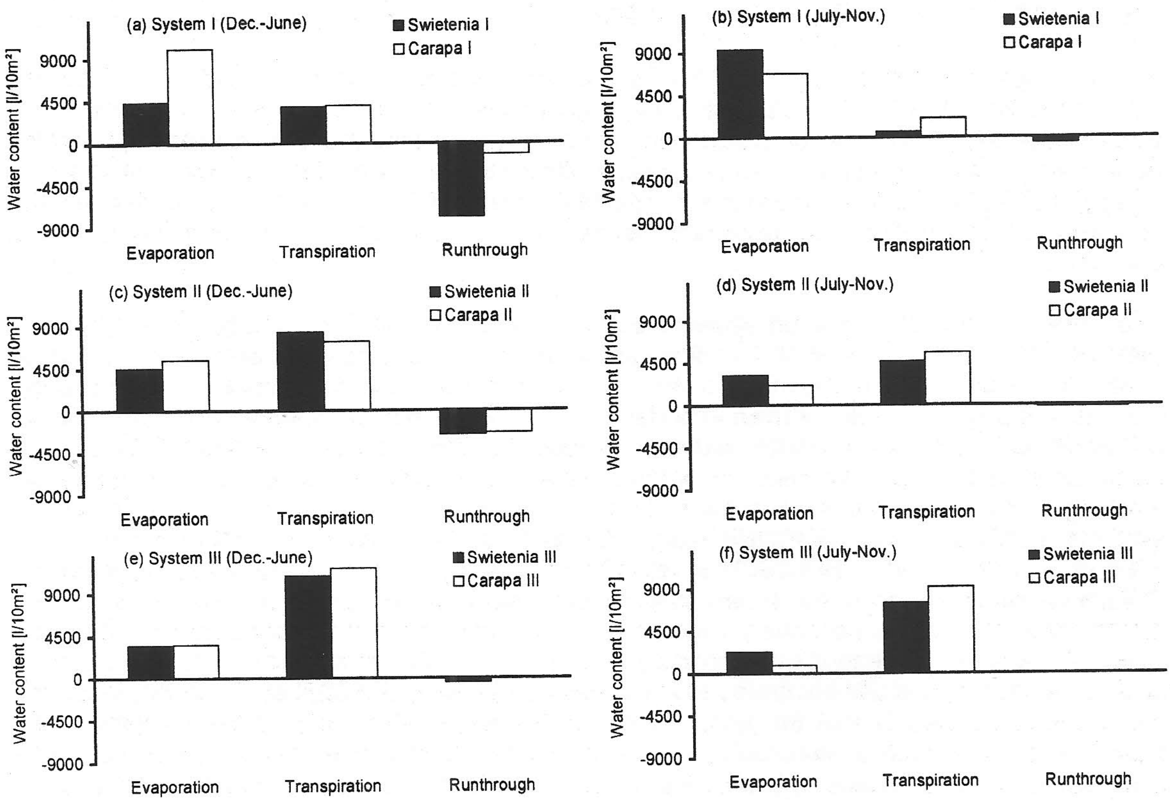

Fig. 6a-c: Evaporation (soil, crown), transpiration and soil water percolation in the soil [l/ 10 m²] of the plantation systems I (a/ b), II (c/ d), III (e/ f) during the wet period (December 1996 until June 1997) and the dry period (July 1997 until November 1997).

Discussion

The growth of trees is strongly influenced by the water supply due to the significance of water for the turgor of the cells (KLEINIG and SITTE, 1992; LARSON, 1995; DÜNISCH et al., 1994), the biosynthesis of carbohydrates and accessory compounds (HÖLL, 1985; SAUTER, 1988; LANGENFELD-HEYSER, 1987) and the transport of substances (VIGOUROUX et al., 1989; KOZLOWSKI et al., 1991). Dendroecological investigations revealed a strong influence of the soil water supply on the growth dynamics of trees, even under the humid conditions of tropical regions (COSTER, 1927; VETTER and BOTOSSO, 1989; WORBES, 1988; PUMJUMNONG et al., 1995; DÜNISCH et al., 1999).

Water uptake and water transport of the plants are mainly influenced by the morphological and anatomical characteristics of the tree species (ZIMMERMANN, 1983; KRAMER, 1985; TYREE and SPERRY, 1988). Differences observed for the water uptake and water transport of 6-year-old plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl. were mainly caused by seasonal alterations of the leaf and root system of the trees (comp. NOLDT et al., 1999), whereas only small differences in wood anatomical characteristics were found between these two species. This indicates that morphological and anatomical characteristics of different plant tissue are not always parallel with regard to the water use efficiency of the tree (comp. LÜTTGE, 1995; SIDIYASA and BAAS, 1998; PREISINGER, 1999).

A strong seasonal variation of the water uptake of *Swietenia* was found which was correlated with a significant reduction of the transpiring leaf surface and a reduction of the root biomass (comp. COSTER, 1927). In contrast to that, water uptake and water release of *Carapa* was balanced, even during dry periods, which indicates a reduced sensitivity of *Carapa* to a reduced soil water supply compared to *Swietenia.* These observations are confirmed by studies on the growth dynamics of *Swietenia* and *Carapa,* which indicated no significant influence of dry periods of the growth dynamics of *Carapa* (comp. BREITSPECHER and BETHEL, 1990), whereas a cambial dormancy was found in various studies for *Swietenia* during dry periods (comp. COSTER, 1927; DÜNISCH et al., 1999b).

The influence of wet and dry periods on the growth dynamics of *Swietenia* and *Carapa* has a strong influence on the sustainability of *Swietenia* and *Carapa* plantations due to the short-time water stress, which might occur in younger plantations also during the rainy season (DÜNISCH et al., 1998), especially in monoculture systems with a low vegetation density. High evaporation and soil water percolation were observed, which indicates water stress conditions for the growth of *Swietenia,* in periods with low precipitation, whereas *Carapa* is more adapted to drier conditions.

The water balance of plantation systems could be stabilized by the plantation management (selected species, horizontal and vertical structure of the plantations; comp. LAMPRECHT, 1986; LYR et al., 1992). In the mixed culture system and the enrichment system investigated in this study, transpiration was of main importance for the water output, whereas evaporation and soil water percolation were strongly reduced compared to the monoculture system. Besides the stabilization of the water balance, a reduced water runthrough of the soil also reduced the leaching of mineral elements out of the soil and stabilizes the mineral nutrition of the plantation systems (JORDAN, 1982; SANCHEZ et al., 1982; VIGOUROUX, et al., 1989; LILIENFEIN et al., 1998; ZECH et al., 1998; DÜNISCH et al., 1999a). Nevertheless, a reduced water uptake of Swietenia was found in the enrichment system compared to the monoculture system due to the strong competition of the secondary vegetation of this plantation system for the water uptake of *Swietenia.* Most of the important secondary tree species of the enrichment system are better adapted to drier conditions compared to *Swietenia* (comp. PREISINGER et al., 1999). This, on the one hand, indicates that the water supply of *Swietenia* is not automatically improved in plantation systems with a more balanced water supply. On the other hand, *Carapa* is more competitive for water uptake in this plantation system, which indicates sustainable tree growth of *Carapa* even in dense plantation systems.

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