ISSN 0368-8798

Mitteilungen

der

Bundesforschungsanstalt für Forst- und Holzwirtschaft

HAMBURG

Nr. 193 Februar 1999

INVESTIGATIONS ON TREE SPECIES SUITABLE FOR THE RECULTIVATION OF DEGRADED LAND AREAS IN CENTRAL AMAZONIA

BRAZILIAN-GERMAN COOPERATION WITHIN THE PROJECT „STUDIES ON HUMAN IMPACTS ON FORESTS AND FLOODPLAINS IN THE TROPICS" (SHIFT) SUPPORTED BY THE MINISTRY OF EDUCATION, SCIENCE, RESEARCH, AND TECHNOLOGY, BONN, FRG (0339638) AND THE CONSELHO NACIONAL DE DESENVOLVIMENTO CIENTIFICO E TECNOLOGICO (CNPq), BRASILIA, BRAZIL (ENV 42) AND INSTITUTO BRASILEIRO DO MEIO AMBIENTE E RECURSOS NATURAIS RENOVÁVEIS (IBAMA)

Edited by J. Bauch, O. Dünisch and L. Gasparotto

1999
Kommissionsverlag
Buchhandlung Max Wiedebusch
Dammtorstraße 20, 20354 Hamburg

ISSN 0368-8798

Mitteilungen

der

Bundesforschungsanstalt für Forst- und Holzwirtschaft
Hamburg

Nr. 193 Februar 1999

INVESTIGATIONS ON TREE SPECIES SUITABLE FOR THE RECULTIVATION OF DEGRADED LAND AREAS IN CENTRAL AMAZONIA

BRAZILIAN-GERMAN COOPERATION WITHIN THE PROJECT „STUDIES ON HUMAN IMPACTS ON FORESTS AND FLOODPLAINS IN THE TROPICS" (SHIFT) SUPPORTED BY THE MINISTRY OF EDUCATION, SCIENCE, RESEARCH, AND TECHNOLOGY, BONN, FRG (0339638) AND THE CONSELHO NACIONAL DE DESENVOLVIMENTO CIENTIFICO E TECNOLOGICO (CNPq), BRASILIA, BRAZIL (ENV 42) AND INSTITUTO BRASILEIRO DO MEIO AMBIENTE E RECURSOS NATURAIS RENOVÁVEIS (IBAMA)

Edited by J. Bauch, O. Dünisch and L. Gasparotto

1999
Kommissionsverlag
Buchhandlung Max Wiedebusch
Dammtorstraße 20, 20309 Hamburg

Preface

The multifunctional role of forest ecosystems is widely acknowledged. Nonetheless, degradation and conversion into other land uses continues at increasing rates, worsening the social, environmental and economic problems on a large scale in many regions of the world. In spite of existing practical experiences and scientific knowledge, the implementation of conservation measures directed towards sustainable management is not efficient for counteracting these destructions. Forest policies, rules and regulations are either not enforced or simply overruled by other immediate interests or needs.

For long times, it has been clearly understood that the strengthening of research and development is urgently required to increase the understanding of the complex structures of forest ecosystems, their interactions and dynamics. Likewise, the dialogue between politics and research has to be improved considerably. However, in both respects the interdisciplinary approach is of fundamental importance to any significant progress.

An important example of such an approach is the programme on "Studies on Human Impact on Forests and Floodplains in the Tropics (SHIFT)", supported by the German Federal Ministry of Education, Science, Research and Technology. This programme was initiated by German and Brazilian scientists and politicians in 1989 with the main goals:

- to broaden the knowledge on the structure and the function of tropical ecosystems in order to develop land use concepts for the sustainable use and protection of endangered areas
- to diminish already existing environmental problems
- to provide management concepts for the recuperation of abandoned areas
- to understand and define the problems regarding the interaction of human needs and the maintenance of the integrity of natural systems.

A range of valuable results have been produced so far, and the programme is well-established within the Brazilian research network. Thus, SHIFT offers an outstanding opportunity also for the international research cooperation of the Federal Research Centre of Forestry and Forest Products (BFH) and for the University of Hamburg. Both organizations cooperate closely, based on a contract established by the creation of the Institutes of World Forestry, Wood Biology, and Wood Technology. These University institutions and the BFH, since its foundation in 1950, have contributed to the development of interdisciplinary concepts with special emphasis on sustainable use of tropical ecosystems as e. g. in the Central Amazon region.

In this context, preliminary investigations were carried out from 1992 to 1995, together with the Institute of Applied Botany, Hamburg University, and the EMBRAPA Amazonia Ocidental, Manaus. In 1995, an additional project was started and dedicated to the "Selection of tree species for high quality timber production, which are suitable for polycultural plantation systems". As another example, this interdisciplinary approach for determining growth dynamics in relationship to exogenous impact, wood structure and wood properties turned out to be a promising perspective for the ecological and economic strategy in the SHIFT-programme. Thus, the scope of this programme gradually widened as to address the needs for increased collaborative research work.

J. Heuveldop

Content

Untersuchung geeigneter Baumarten für die Wiederbegründung degradierter Flächen Zentralamazoniens

Zusammenfassung

Die vorliegende brasilianisch-deutsche Forschungskooperation für Untersuchungen des Wachstums und der Holzbildung der heimischen Baumarten in Zentralamazonien ist Teil des SHIFT-Projekts (Studies on Human Impact on Forests and Floodplains in the Tropics). Dessen Ziel ist es, nachhaltige Bewirtschaftungsmethoden für diese Region zu entwickeln. Besonders bei der Rekultivierung degradierter Flächen können einige langlebige Baumarten, die qualitativ hochwertiges Holz liefern, zur Stabilisierung von Mischkulturplantagen beitragen. Jedoch ist bisher bei den meisten der Baumarten, die in Manaus angepflanzt werden, sehr wenig über ihr Wachstum und ihren Nährelementbedarf bei der Produktion qualitativ hochwertigen Holzes bekannt.

Deshalb wurde dieses Forschungsprojekt darauf konzentriert, den Einfluß des Standortes dieser degradierten Flächen auf das Baumwachstum und die Holzbildung von acht ausgesuchten heimischen Baumarten (*Swietenia macrophylla* King, *Carapa guianensis* (Aubl.), *Cedrela odorata* L., *Dipteryx odorata* (Aubl.) Willd., *Hymenaea courbaril* L., *Ceiba pentandra* (L.) Gaertn., *Virola surinamensis* (Rol.) Warb., *Tabebuia heptaphylla* (Vell.) Toledo) zu erforschen. Zu diesem Zweck wurden die Versuche in drei verschiedenen Plantagensystemen durchgeführt (Monokultur, Mischkultur und Anreicherungskultur eines 25-jährigen Sekundärwaldes). Die Versuche begannen 1992/ 1993 am Centro de Pesquisa Agroflorestal da Amazônia Ocidental (EMBRAPA Amazônia Ocidental) – Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) in Manaus. Aufgrund der spezifischen Standortbedingungen degradierter Flächen, wurde bei den Versuchen besonderes Augenmerk auf die Wasserversorgung und den Mineralelementgehalt der Bäume sowie ihre Auswirkungen auf die Wachstumsdynamik und die Entwicklung der jährlichen Holzproduktion gelegt.

Aus diesem Grund wurden in allen drei Systemen meteorologische Daten gesammelt und der Elementeintrag, die Elementauswaschung, die Wasserversorgung und der Wasseraustrag der Systeme kontinuierlich seit Juni 1995 registriert. Das Wasserleitsystem der Bäume wurde mit Hilfe morphologischer und anatomischer Parameter sowie mit Messungen des Wasserflusses untersucht. In der gleichen Zeit wurde der Bedarf der verschiedenen Pflanzengewebe und Meristeme an wichtigen Mineralelementen zellulär und subzellulär analysiert. Die Biomasse-Produktion der Bäume wurde jährlich quantifiziert. Die Wachstumsdynamik über das Jahr hinweg wurde charakterisiert durch „lifecycle"-Analysen der Blätter und Wurzeln sowie durch Datierungen der kambialen Wachstumsdynamik mit Hilfe der pin-marker Technik. Zusätzlich wurden Versuche unternommen, um aus den Eigenschaften des juvenilen Holzes die Eigenschaften des entstehenden „adult wood" vorhersagen zu können.

In den vorliegenden Untersuchungen liegt der Schwerpunkt auf der Familie der *Meliaceen*. Es stellte sich heraus, daß *Swietenia* trockenheitsanfälliger ist als *Carapa*. Selbst in nur kurzzeitig geringerer Wasserversorgung reagierte *Swietenia* bereits mit Wassermangel im Baum. In der Mischplantage und in der Anreicherungskultur setzte sich *Carapa* bei der Wasseraufnahme stärker durch als *Swietenia*. Was die Elementversorgung betrifft, war bei beiden Baumarten ein internes K-Recycling und ein externes Mg- und Ca-Recycling feststellbar. Verglichen mit den beiden anderen Systemen war die Anreicherungskultur in der K-, Mg- und Ca-Versorgung am stabilsten.

Der hohe Gehalt an K, Ca und P in den Pflanzen zeigt, daß ein nachhaltiges Baumwachstum für qualitativ hochwertige Holzproduktion auf lange Sicht nur durch genau definierte Düngergaben gewährleistet werden kann. Die niedrige Basensättigung und der sehr niedrige Nährelementanteil der Bodenlösung, der nur kurzzeitig durch Brandrodung erhöht werden kann, zeigen ebenfalls den geringen Nährstoffgehalt des Bodens an. Neben den drei *Meliaceae*-Arten konnte auch für *Ceiba* und *Virola* ein unterschiedlicher Nährelementbedarf und Toleranzgrad für Schwermetalle nachgewiesen werden. Einen weiteren negativen Einfluß auf das Wachstum von

Meliaceae-Arten hat der Befall von *Hypsipyla grandella,* der die Stammform beeinträchtigt und damit gleichzeitig auch die spätere Qualität des Holzes für die Furnierherstellung mindert.

Während der Projektdauer zeigte sich, daß die Zuwachszonen im Holz von *Swietenia* und Carapa keine jährliche Entwicklung anzeigen: *Carapa* stellte bei Dürre das Holzwachstum nicht ein, während *Swietenia* das Holzwachstum, besonders gegen Ende der Trockenheitsperiode, meßbar unterbrach. *Carapa* ist also offensichtlich an trockene Standortbedingungen besser angepaßt als *Swietenia* und zeigte zudem das Jahr über ein auffallend nachhaltiges Wachstum.

Die Ausgangsdaten über Struktur und Funktion von *Swietenia*- und *Carapa*-Feinwurzeln sowohl während der Regenperioden als auch während der Trockenzeiten ließen vermuten, daß *Carapa* an Dürrezeiten besser angepaßt sein könnte. Neben den acht ausgewählten Baumarten für eine qualitativ hochwertige Holzproduktion wurden auch sechs Arten aus dem Sekundärwaldsystem der Familie *Melastomataceae* im Zusammenhang mit ihrer Wasser- und Nährstoffversorgung untersucht. Damit sollte u. a. Einblick in die Wettbewerbsmechanismen zwischen den Pflanzen des im Sekundärwald angelegten Anreicherungssystems gewonnen werden. Es zeigte sich, daß Pflanzen spezielle Strategien nutzen, um wettbewerbsfähig zu sein.

Von einer synthetischen Bewertung der Ergebnisse lassen sich praktische Hinweise zur Auswahl von Baumarten für die Produktion qualitativ hochwertigen Holzes in Mischkulturplantagen auf degradierten Flächen ableiten. Dabei können auch Informationen im Hinblick auf ökologische und ökonomische Aspekte gegeben werden.

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

Summary

The present Brazilian-German research cooperation on growth and wood formation of native tree species of Central Amazonia is part of the SHIFT-project (Studies on Human Impact on Forests and Floodplains in the Tropics) for the development of sustainable landuse systems in this region. Especially for the recultivation of degraded land areas, a small portion of long-life trees for high-quality timber production might contribute to the stabilization of mixed culture plantation systems. For most of the tree species used for timber production in the Manaus region, only few information on growth and site demands for high-quality timber production are available.

Therefore, in this project the influence of site conditions of degraded land areas on growth and wood formation of eight selected native tree species (*Swietenia macrophylla* King, *Carapa guianensis* (Aubl.), *Cedrela odorata* L., *Dipteryx odorata* (Aubl.) Willd., *Hymenaea courbaril* L., *Ceiba pentandra* (L.) Gaertn., *Virola surinamensis* (Rol.) Warb., *Tabebuia heptaphylla* (Vell.) Toledo) were investigated. In order to study the influence of the management of degraded areas on growth and wood formation of the tree species, the investigations on the relationship of environmental input and tree growth were carried out in three different plantation systems (monoculture system, mixed culture system, enrichment of a 25-year-old secondary forest) established in 1992/ 1993 at the Centro de Pesquisa Agroflorestal da Amazônia Ocidental (EMBRAPA Amazônia Ocidental) – Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), Manaus. Due to the specific site conditions of degraded land areas, the investigations were carried out with special reference to water and mineral element supply of the trees and their impact on the growth dynamics and wood production throughout the year.

For this reason, in all experimental plots meteorological data, the element input, the element output, the water input, and the water output of the plant systems were registered continuously since June 1995. The water conducting system of the trees was investigated by morphological and anatomical investigations, as well as by sap-flow measurements. The demand of different plant tissues and meristems for mineral elements was studied by bulk and subcellular element analyses. The biomass production of the trees was quantified annually. The intraannual growth dynamics of the trees is characterized by lifecycle analyses of leaves and roots, as well as by the study of cambial growth dynamics dated by the pin-marker technique. In addition, studies on parameters suitable for the prediction of wood properties which might be expected in the future were carried out.

In this project, the main interest was focused on the family of *Meliaceae*. *Swietenia* turned out to be more sensitive to drought than *Carapa*. Even within short-time periods of reduced water supply, *Swietenia* already responded with water deficiency within the tree. Within the mixed plantation and the enrichment system, *Carapa* was more competitive than *Swietenia* with regard to water availability. Both species indicated an „internal recycling“ for K and an „external recyling“ for Mg and Ca, as concerns the mineral element supply. Compared to the two other systems, the enrichment system is more stable with regard to K-, Mg-, and Ca-supply.

The high contents of K, Ca, and P within the plant underline that in the long run, a sustainable growth of trees for high-quality wood production can only be guaranteed if well-defined fertilization is applied. The low base saturation and the very low nutrient content in the soil solution, which can be elevated by burning only for a short period, also indicate an insufficient nutrient supply. Besides, for the three species of *Meliaceae* and for *Ceiba* and *Virola,* the different demand for nutrients and also their tolerance in relation to heavy metals could be demonstrated. Another negative impact on the growth of the species of *Meliaceae* is the attack of *Hypsipyla grandella*, which affects the cylindrical trunk growth and consequently the quality of veneer production.

During the study, it turned out that the increment zones in the wood of *Swietenia* and *Carapa* are not annual. *Carapa* did not respond to drought with dormancy in wood formation, whereas *Swietenia* revealed distinct interruption of growth, particularly close to the end of the dry season.

Carapa was more adapted to dry conditions than *Swietenia* and was outstanding in its sustainable growth throughout the year.

Preliminary results of the structure and function of the fine roots in *Swietenia* and *Carapa* during the wet and the dry season suggest that *Carapa* might be better adapted to drought than *Swietenia*. In addition to the eight selected tree species for high-quality wood production, also six species from the secondary forest system of the family of *Melastomataceae* were studied in relation to water and nutrient supply in order to get some insight in possible relations of competition within the enrichment system in the secondary forest. It turned out that special strategies put the species to a more competitive position within the system.

From these investigations, some practical help for the selection of tree species for high-quality timber production in mixed culture plantation systems on degraded land areas with special regard to ecological and economic aspects can be derived.

Estudos de três espécies sustentáveis para o reflorestamento de áreas degradadas na Amazônia Central

Resumo

A cooperação de pesquisa atual entre o Brasil e a Alemanha quanto ao crescimento e à formação de madeira a partir de espécies arbóreas nativas da Amazônia Central faz parte do projeto SHIFT (Studies on Human Impact on Forests and Floodplains in the Tropics) para o desenvolvimento de sistemas sustentáveis de uso da terra nesta região. Especialmente, para o reflorestamento de áreas degradadas, um pequeno numero de espécies arbóreas que produzem madeira de alta qualidade pode contribuir para a estabilização dos sistemas de cultivo misto. Para a região de Manaus, existe pouca informação quanto ao crescimento e a demanda local para a produção de madeira de alta qualidade.

Conseqüentemente, neste projeto, estudou-se a influência das condições locais das áreas degradadas quanto ao crescimento e a formação de madeira a partir de oito espécies arbóreas nativas (*Swietenia macrophylla* King, *Carapa guianensis* Aubl., *Cedrela odorata* L., *Dipteryx odorata* (Aubl.) Willd, *Hymenaea courbaril* L., *Ceiba pentandra* L., *Virola surinamensis* (Rol.) Warb., *Tabebuia heptaphylla* (Vell) Tol.). A fim de estudar a influência do manejo de áreas degradas no crescimento e na formação de madeira a partir de espécies arbóreas, investigações com relação aos fatores ambientais e ao crescimento da árvore foram realizadas em três sistemas diferentes de plantio (monocultivo, cultivo misto e enriquecimento de capoeira com 25 anos de idade) estabelecidos em 1992 e 1993 no Centro de Pesquisa Agroflorestal da Amazônia Ocidental (EMBRAPA Amazônia Ocidental) – Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA), em Manaus. Devido às condições específicas do local das áreas degradadas, as investigações foram realizadas com referência especial para suprimento de água e elementos minerais para as árvores e seus impactos nas dinâmicas de crescimento e produção de madeira durante o ano.

Por essa razão, foram registrados continuamente desde junho de 1995, em todos os experimentos, os dados meteorológicos, input e output de elementos, input e output de água dos sistemas de plantio. O sistema de condução de água das árvores está sendo estudado através de estudos morfológicos e anatômicos, bem como pela medida de fluxo da seiva do tronco. A demanda de diferentes tecidos e meristemas da planta por elementos minerais são estudados por análises de parte da planta e análises dos elementos subcelulares. A biomassa das árvores foi quantificada anualmente. A dinâmica de crescimento intraanual das árvores é caracterizado pela análise do ciclo de vida das raízes e das folhas, bem como pelo estudo da dinâmica de crescimento do câmbio, datada pela técnica "pin-marker". Além disso, foram feitos estudos de parâmetros sustentáveis para a medição das propriedades da madeira que podem ser esperados no futuro.

Neste projeto, o maior interesse está concentrado na família Meliaceae. O mogno se mostrou mais sensível à seca do que a andiroba. Nos períodos curtos de baixo suprimento de água, o mogno reagiu com deficiência hídrica na árvore. Em plantios mistos ou sistemas de enriquecimento, a andiroba mostrou-se mais competitiva que o mogno, com relação a avaliação de água.

As altas concentrações de K, Ca e P na planta permitem dizer que futuramente, o crescimento sustentável das espécies produtoras de madeira de alta qualidade possa estar garantido se for feita uma fertilização bem definida. A baixa saturação de bases e o baixo teor de nutrientes na solução do solo, que pode ser elevado por meio de queimada apenas por um curto período, indica um estoque insuficiente de nutrientes. Outrossim, para as espécies arbóreas de Meliaceae, Ceiba e Virola, um estoque de diferentes nutrientes e também suas tolerâncias em relação aos metais pesados poderam ser demonstrados. Outro impacto negativo no crescimento das espécies de Meliaceae, consiste no ataque da *Hypsipyla grandella*, que afeta o crescimento cilíndrico do tronco e conseqüentemente, a produção de compensado de qualidade.

Ao longo do estudo, verificou-se que as zonas de incremento na madeira de mogno e de andiroba não são anuais. A andiroba não reagiu à seca com dormência na formação de madeira, enquanto que o mogno, revelou uma aparente interrupção no crescimento, particularmente, para o final da estação seca. A andiroba adaptou-se melhor às condições de seca do que o mogno, conforme verificado no crescimento ao longe do ano.

Resultados preliminares da estrutura e função das raízes do mogno e da andiroba durante a época de chuva e a época de seca, sugerem que a andiroba possa ser melhor adaptada à seca (falta de chuva) do que o mogno. Além do mais, as oito espécies arbóreas selecionadas para a produção de madeira de alta qualidade, e também seis espécies procedentes do enriquecimento de capoeira, da família das Melastomastaceae, foram estudadas com relação a questão da disponibilidade de água e do estoque de nutrientes, a fim de compreender as relações de competição no sistema de enriquecimento de capoeira. Mostrou-se com isso, que estratégias especiais colocam as espécies em posição mais competitiva no sistema.

A partir dessas investigações, alguns auxílios práticos na seleção de espécies arbóreas para a produção de madeira de alta qualidade em áreas degradadas do sistema de cultivo misto com ênfase aos aspectos ecológicos e econômicos podem ser deduzidos.

1. Introduction and concept of the interdisciplinary project

The Federal Ministry of Education, Science, Research, and Technology (BMBF), Bonn, initiated the programme on „Studies on Human Impact on Forests and Floodplains in the Tropics" (SHIFT) in 1989. This programme supports a bilateral research cooperation of Brazil (Conselho Nacional de Desenvolvimento Cientifico e Tecnologico, CNPq, Brasilia) and Germany (BMBF, Bonn). SHIFT mainly concentrates on the development of concepts for sustainable use and preservation of tropical ecosystems. High priority is given to the tropical rainforests in Central Amazonia. Already in 1992, R. Lieberei (Institute of Applied Botany, University of Hamburg) established a project for the „Recultivation of degraded areas into polyculture areas" together with L. Gasparotto (Centro de Pesquisa Agroflorestal da Amazonia, EMBRAPA Amazônia Ocidental) at the „terra firme" in Manaus (Fig. 1). The main aim was to understand the ecological impacts to productive plant systems and to establish mixed plantation systems under sustainable ecological conditions for economic success. In this respect, it was desirable to evaluate to which extent some species with high-quality timber production could be considered from the large „gene pool" of native forest trees.

Fig.1: The investigations of SHIFT are carried out in four regions: Manaus, Belem, Cuiaba, São Paulo of Brazil. High priority is dedicated to Central Amazônia in Manaus.

The experimental plantation, 19 ha in size, located near EMBRAPA Amazônia Ocidental, consists of different mixed cultures. In one of these cultures, species of the mahogany family were considered, as well, for their outstanding wood quality.

It can be predicted that an increasing demand for high-quality timber will occur in the Manaus region, and that it will be important to supply this region with sustainable mixed plantations in order to protect the primary forest against exploitation.

After a preliminary study in the years from 1992 to 1995 (SCHMIDT, 1996) carried out on biomass production and mineral element content of selected tree species of the mixed plantations, a cooperative investigation on tree species suitable for the recultivation of degraded land areas was intensified.

The concept of this study on the „terra firme“ and the main aims were planned in 1992 (SHIFT). At the same time, the mixed plantations started, containing eight economically important tree species planted in 1992, as well, which were of interest for the EMBRAPA Amazônia Ocidental, Manaus.

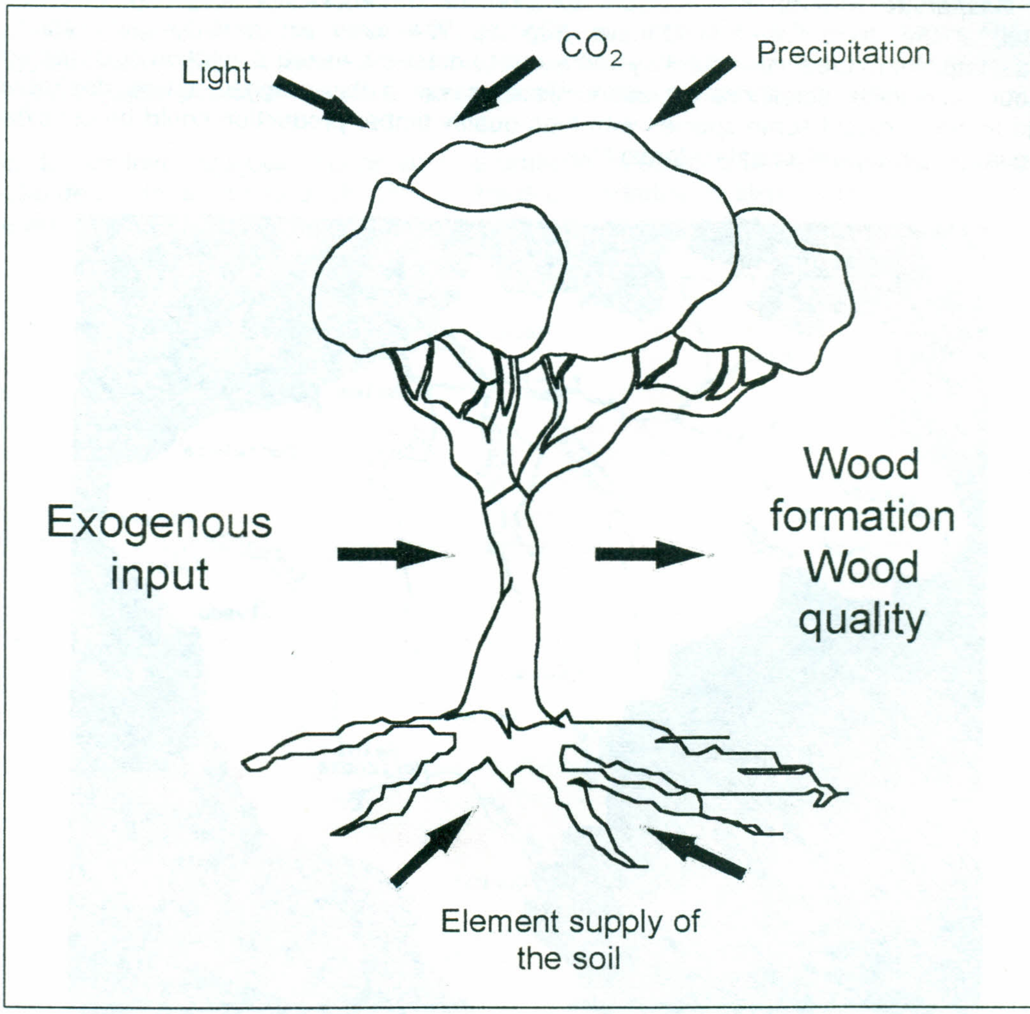


Fig.2: Relationship of exogenous input and wood formation

In addition to the experimental work on agrobiology, vegetation, mycorrhiza (ENV 23), on water and element fluxes and balances (ENV 45), on soil fauna and flora and litter degradation (ENV 52), our study was concentrated on the following (Fig.2):

- In order to understand the process of wood formation and quality of the wood under exogenous inputs such as CO_2, light, water, and element supply, three different growth systems (monoculture, mixed culture and enrichment culture in secondary forests) were selected, totalling eight tree species (*Swietenia macrophylla* King, *Carapa guianensis* Aubl., *Cedrela odorata* L., *Dipteryx odorata* (Aubl.) Willd., *Hymenaea courbaril* L., *Ceiba pentandra* (L.) Gaertn., *Virola surinamensis* (Rol.) Warb., and *Tabebuia heptaphylla* (Vell.)). For most of the tree species used for timber production in the Manaus region, only few informations on growth and site demands are available.

- The growth dynamics and the structural dynamics of wood in relationship to the environmental conditions are of particular importance to plantations and primary forests. These growth characteristics, which are controlled at the cambium, for example by carbohydrates and phytohormones, to a great extent determine the quantity and quality of the wood.

- In the interpretation of the growth of trees, the structure and function of the fine roots and their strategy to survive drought periods, as they occur in Manaus, have to be considered, as well.

- With regard to the advantage of an enrichment culture in a secondary forest, also attention was dedicated to a cooperation with the project ENV23, considering growth, nutrient supply and the characteristics of wood and leaves, particularly of *Melastomataceae* in comparison to the species in the enrichment culture.

In the individual experimental contributions, the main emphasis is laid on an insight into the behaviour of the individual tree, and the tree species respectively, in its environment.

The study of the interrelationship of the different species in a mixed system is the perspective of a subsequent field work.

2. Results

Development of tree height and diameter of eight selected tree species under plantation conditions in Central Amazonia

C. P. de Azevedo,[1] R. M. B. de Lima,[1] E. J. M. Neves,[2] L. Gasparotto[1], and O. Dünisch[3]

[1] EMBRAPA Amazônia Ocidental, Manaus, AM, Brazil
[2] EMBRAPA – Centro Nacional de Pesquisa Florestal – CNPF, Colombo, PR, Brazil
[3] Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg

Summary

In 1992/ 93, studies on the recultivation by forest trees on abandoned and/ or degraded areas were executed at the experimental field of the EMBRAPA Amazônia Ocidental, Manaus. The main aim was to study the growth behaviour, as concerns height and diameter, of twenty forest species in different plantation systems (monoculture, mixed culture, and enrichment culture). For the monoculture and the enrichment culture, a complete randomized plot design with four repetitions was used, and in the mixed culture, a complete randomized block design with five repetitions was selected.

Since January 1995, within the scientific Brazilian-German cooperation program SHIFT, the growth of eight of these twenty species (*Carapa guianensis* Aubl., *Cedrela odorata* L., *Ceiba pentandra* (L.) Gaertn., *Dipteryx odorata* (Aubl.) Willd., *Hymenaea courbaril* L., *Swietenia macrophylla* King, *Tabebuia heptaphylla* (Vell.) Tol., and *Virola surinamensis* (Rol.) Warb.), planted in the three different systems, was investigated. In this publication, the initial results of tree diameter and height, survival, and incidence of weed and diseases of the species during the first four and five years respectively, are presented. The parameters diameter at breast height (DBH), height and basal area differ considerably among the species and between the plantation systems, which suggests that they might be criteria for the selection of the species to be planted in each plantation system. In the monocultures, the best results of growth and survival of the species were registered in comparison to the enrichment cultures and the mixed culture. Among the species planted, *Carapa guianensis* revealed the highest increment. In the monoculture system, *Ceiba pentandra* also showed outstanding results. The *Meliaceae (S. macrophylla, C. guianensis,* and *C. odorata)* were entirely attacked by *Hypsipyla grandella (Lepidoptero)* to 100% of its trees, independently of the plantation system, causing high mortality among trees of *S. macrophylla*. *Lepidoptero* causes the „broca dos ponteiros", which means the destruction of the apex meristem that reduces growth. In addition, it induces the bad habitus of the trees which as a rule leads to commercial loss in value.

Resumo

Desenvolvimento em altura e diâmetro de árvores de oito espécies selecionadas sob condições de plantação na Amazônia Central

No campo experimental do EMBRAPA Amazônia Ocidental, Manaus, instalaram-se em 1992/ 93 ensaios (agro)florestais sobre áreas abandonadas e/ ou degradadas, com objetivo de conhecer o comportamento de vinte expécies florestais em diferentes sistemas de plantações (plena abertura, plantio misto e faixas de enriquecimento). Nos plantios à plena abertura e faixas de enriquecimiento, utilizou-se o delineamento inteiramente casualizado com quatro repetições e no sistema misto, o delineamento em blocos ao acaso com cinco repetições.

Desde Janeiro de 1995, no acordo de cooperação científica Brasil-Alemanha, programa "SHIFT" tem sido investigado o crescimento de oito destas vinte espécies (*Carapa guianensis* Aubl., *Cedrela odorata* L., *Ceiba pentandra* (L.) Gaertn., *Dipteryx odorata* (Aubl.) Willd., *Hymenaea courbaril* L., *Swietenia macrophylla* King, *Tabebuia heptaphylla* (Vell.) Tol., e *Virola* *surinamensis* (Rol.) Warb.), plantadas nos três diferentes sistemas de plantios. Apresentam-se os resultados iniciais do crescimento em diâmetro e altura, sobrevivência e incidência de pragas e doenças das espécies durante os primeiros quatro e cinco anos de idade, organizados por espécies e sistemas de plantação. Os parâmetros DAP, altura, área basal e respectivos incrementos médios, variaram muito entre as espécies e entre os sistemas de plantação, o qual sugere uma seleção muito criteriosa da espécie a ser plantada em cada sistema de plantação. Nos plantios a plena abertura, registraram-se os melhores resultados de crescimentos e sobrevivência das espécies em comparação com os obtidos nas faixas de enriquecimento e plantio misto. Entre as espécie plantadas a *C. guianensis* apresentou o melhor resultado nos três sistemas de plantio. Entretanto, no sistema de monocultivo, a *C. pentandra* mostrou os melhores resultados. As *Meliaceae (S. macrophylla, C. guianensis e C. odorata)* tiveram 100% das suas árvores atacadas por *Hypsipyla grandella (Lepidoptero)* independente do sistema de plantação causando alta mortalidade, principalmente, para as árvores de *S. macrophylla*. Este *lepidoptero* causa a broca dos ponteiros, ocasionando a destruição do meristema apical que retarda o crescimento e induz a má formação das árvores, as quais usualmente produzem bifurcações e/ ou ramificações excessivas e conseqüente desvalorização comercial da madeira.

Introduction

Within the latitudes 23,5° N and 23,5° S that include part of Central America, South America, Africa, Australia, India, and South East Asia, there are around 650 million hectares land used as growing areas and almost two billion hectares in different stages of degradation (VIDAKOVIC, 1986; according to JESUS, 1992).

The increasing demand for wood and agricultural areas and the population growth in the Amazon region in the last 20 years have caused a significant increase in destroyed forest areas in different degrees of degradation. In December 1996, a percentage of 13% of the original forest was reached, corresponding to 517,069 km².

At the forest in question, the great concentration of species can be recognized, as well as the quick loss of the vegetation diversity. The majority of these species were already described botanically, but little studied with regard to the silvicultural aspects. The lack of information about the nutritional necessities of each species leads to a void in knowledge about those species (MONTAGNINI, 1992).

On account of this development, silvicultural and agroforestry systems constitute the alternatives to incorporate these areas in a productive system, in a way to increase or sustain the land productivity without causing degradation (MONTAGNINI, 1992).

The use of agroforestry systems implies the selection of appropriate species. However, there is few biological information on potential forest species for use in these systems, especially in the Amazon region (MARQUES, 1990). The research in silviculture has contemplated comparative studies on tests of native and exotic species. The majority of them was exposed to sunny conditions, others to partial shadow in secondary vegetation (YARED et al., 1988; SAMPAIO et al., 1991; NEVES et al., 1993). The lack of knowledge on forest species that can be used under sunny conditions has made the use of nonproductive areas difficult. From the species investigated by CPATU (KANASHIRO and YARED, 1991) and INPA (JANSEN and ALENCAR, 1991), few are effectively used in forest culture.

So far, the recommendation of forest species for plantations in the Amazon region is based on the experience derived from only a few field experiments and from ecological areas to reforest in Brazil (GOLFARI et al., 1978). The recommendation of suitable species is limited especially by the conifers and eucalypts.

The inadequacy of silvicultural information about native species is normally mentioned as one of the causes for reforestation. ALENCAR et al. (1979) believe that to get adequate genetic material for plantation poses severe problems.

EMBRAPA Amazônia Ocidental began in 1991. It is a Forest Test Project to study the adaptability of different forest species commonly planted in the tropics, species with commercial values and lesser known native species.

In the present study, the results on height and diameter growth of eight species of high commercial value *(mogno, cedro, andiroba, cumaru, jatobá, sumaúma, ucúuba,* and *ipê)* are presented for three different culture systems in relation to survival and occurrence of weeds and diseases.

Characteristics of the planted species

Carapa guianensis Aubl. – _Meliaceae_ (Andiroba)

Andiroba is a fast-growing and tall tree, reaching 30 m in height, with a thick and bitter bark. It frequently forms associations. The species is of great commercial value because of its abundance and the oil content of the seeds and its wood quality. Andiroba occurs naturally in the Manaus region in the shallow Amazon and Solimões river, and in the upper Erepecuru river. It is frequent at the north coast of Para State, the shallow Tocantins river, until Maranhão State, Central America and the West Indies. In general, it is distributed from Belize and Honduras to Ecuador, Peru, Brazil and the Guineas, the West Indies, Cuba, Dominican Republic, Haiti, Guadeloupe, Dominique, San Vincent, and Trinidad.

According to LOUREIRO and SILVA (1968), the andiroba wood is moderately heavy (0.68 – 0,75 g/ cm^3). It is generally used for joinery products, inside construction, for plywood, furniture, canoes, squares, pencils etc.

Cedrela odorata L. – _Meliaceae (Cedro)_

Cedro is a fast-growing, large tree of 30 – 35 m height. The species prefers deep and damp soils. In the Amazon, it is found on the clay soil of the „terra firme" and also on sandy soil, being also frequent on the inundated banks of some rivers (LOUREIRO et al., 1979).

The common utilization is for plywood, squares, intern work, cigar box, carpentry, and soft raft. Similar to mogno, it has high commercial value and is widely used by wood industries of the region (LOUREIRO and SILVA, 1968). The seeds can be used, as well.

Ceiba pentandra (L.) Gaertn. – _Bombabaceae_ (Sumaúma)

Ceiba is a fast-growing tree. On the terra firme, the species is of a minor size compared to trees on the flood plain land, although it is bulky. During the juvenile phase, the branches and trunk develop thick conic thorns. Naturally, the species is found in Mexico, in the south of Central America to Colombia, Venezuela, and Ecuador. It also occurs on the east coast of Africa, on Andaman Island and a Malayan Peninsula. The tree species is introduced on the Bermudas and the Bahamas and cultivated in Florida and California. It prefers the flooded or swampy plains, and it also occurs on the upper „terra firme" with clay and fertile soil (LOUREIRO et al., 1979).

According to LOUREIRO and SILVA (1968), the wood is very light (0.30 to 0.37 g/ cm^3) and is used in the raft-shift construction, for boxes, toys, barrels of short life, plywood and the production of cellulose.

Dipteryx odorata (Albl.) Willd. – _Fabaceae_ (Cumaru)

Cumaru is a tall tree of 30 m height. The species is considered in the reforestation. It blossoms early, already at an age of four years, developing aromatic seeds, from which an essential oil, which is used in perfumery (cumarina) can be extracted.

The hard wood, as one of the best wood species, contains a high natural durability, and it does not develop cracks when exposed to the sun. It is used for agricultural implements, in naval construction, joinery, carpentry, for laminated articles, handle tools, fence rails, wagons, stakes, etc. (LOUREIRO et al., 1979).

***Hymenaea courbaril* L. – *Caesalpinaceae* (Jatobá)**

Jatobá is a tall tree that can reach a height from 10 to 25 m and a diameter of 1 m or more. It is especially characterized by its resin called „jutaí-cica“ or „copal of America“, which is used industrially for varnish of inferior quality and for medical uses. The species is distributed geographically from Mexico, across Central America, occurring widely at the Hiléia, reaching down to São Paulo. It also is found in the Guineas, Surinam, Venezuela, Colombia, the West Indies and Bolivia. It inhabits the terra firme land; frequently occurring in clay soil and at some upper plains. However, it is rare in fields and „capoeiras“, where the tree exhibits minor portions.

In general, the wood is used in hydraulic works, wagons, pillars, cask barrels, all kinds of construction, furniture, laminates, props, timber work, instruments, piano construction, and stakes (LOUREIRO et al., 1979).

***Swietenia macrophylla* King – Meliaceae (Mogno)**

This species exhibits trees of 30 – 50 m height and 50 – 200 cm in diameter. It has a very large distribution in Colombia, Venezuela, Peru, and Brazil. In Brazil, its distribution reaches to the superior basin of Juruá and Purus, passes the basin of median Madeira, north of Mato Grosso and south of Pará (basin of upper Tapajós and upper Xingu) and extends to the northeast until the Tocantins and the Balsas river. It often occurs on solid land, sometimes in swampy areas, but frequently at "ribanceiras" and slopes well-drained that receive heavy precipitation (LOUREIRO et al., 1979).

Mogno shows a moderate natural durability against fungal and insect attacks. It is used as veneer for luxury furniture, civil constructions, inside decorations, scientific instruments of high precision, aviation industry, musical instruments, etc.

***Tabebuia heptaphylla* (Vell.) Tol. - *Bignoniaceae* (Ipê)**

It is found from the south of Bahia to Guanabara. *Tabebuia* is also common at the Atlantic forest of Rio de Janeiro and Guanabara, north of the Serra do Mar. The wood is difficult to saw, and it is used for heavy construction and outdoor structures, civil and naval, ship keels, bridges, sticks etc.

***Virola surinamensis* (Rol.) Warb. – *Myristicaceae* (Ucúuba)**

The tree species reaches a medium size with a height of 30 – 35 m and a diameter of 60 – 90 cm. The geographical distribution encloses Pará State, the east part of Amazonas State including the shallow Negro river, Roraima, the northeast of Brazil (from Maranhão to Pernambuco, possibly farther), Guinea, Venezuela, Trinidad, and some small West Indies. It also occurs in Peru, next to Iquitos.

Material and methods

At the experimental field of EMBRAPA Amazônia Ocidental (Manaus-AM), agroforestry test plots were installed in 1992 and 1993 on abandoned and/ or degraded areas, with the objective to know the behaviour of twenty forest tree species in different systems of plantation (monoculture, mixed culture and enrichment culture).

In January 1995, a scientific cooperation of Brazil and Germany, within the „SHIFT"-programme initiated an investigation of the growth of eight timber species of great commercial value. The species *Carapa guianensis* Aubl., *Cedrela odorata* L., *Ceiba pentandra* (L.) Gaertn., *Dipteryx odorata* (Aubl.) Willd., *Hymenaea courbaril* L. var *courbaril*, *Swietenia macrophylla* King, *Tabebuia heptaphylla* (Vell.) Tol., and *Virola surinamensis* (Rol.) Warb.) were selected from three different culture systems: **System 1** – *Monoculture, S. macrophylla, C. guianensis, C. odorata, D. odorata, H. courbaril, C. pentandra, V. surinamensis, T. heptaphylla,* **System 2** – Mixed agroforestry system, *S. macrophylla, C. guianensis,* and **System 3** – Enrichment in 25-year-old „capoeira" lines, *S. macrophylla, C. guianensis, C. odorata, D. odorata, H. courbaril.*

The tests in plenty sun or in enrichment cultures at the „capoeira" were installed in January 1992, located at km 24 of the highway that connects Manaus and Itacoatiara, Amazonas State. The geographic coordinates are 3°8' latitude south, 59°52' longitude west and 50 m above sea level.

The local climate is classified as Afi, by Köppen's system. Based on the observations made in the period from 1984 to 1993, the annual average of precipitation approximately is 2.656 mm. The annual average temperature is 25.7°C. The relief is flat and the soil is classified as a yellow latosol with a clay texture. The soil chemical characteristics at the initial stage of the plantation are shown in table 1.

Table 1: Soil chemical characteristics in the different experimental areas.

Test	Depth (cm)	PH (H_2O)	N (%)	P	K	Ca	Mg	Al
				Ppm		Meq		
Plenty sun	(0 – 20)	4.3	0.17	1.0	20.0	0.26	0.11	1.70
Enrichment lines	(0 – 20)	4.4	0.17	1.0	30.0	0.39	0.21	1.80

For the tests realized in plenty sun, the experimental area previously was covered with primary equatorial forest, followed by a plantation of *Hevea brasiliensis* (rubber tree) and *Pueraria phaseoloides* as soil cover. In 1989, the rubber trees, then 20 years old, were felled, leaving only the *Pueraria* in the area. The tree species were planted in plots of 225 m² with 25 plants, spaced in 3.0 m x 3.0 m, complete randomized plots design, with four repetitions, being evaluated by the nine individuals in the centre.

The enrichment line test was installed in "capoeira" with approximately 25-year-old trees. At this plantation, a variety of species was registered, composed of 76 genera and 39 families. The species were planted in linear plots with 10 plants/ species, spaced at 3.5 m among the plants and 7.0 m between lines, in a completely randomized plot design, with four repetitions, being evaluated in its totality. The culture lines were opened at the east-west direction, with a width of 3.0 m.

In the two tests, fertilization was applied at the time of planting, equivalent to approximately 10 grams of phosphorus per plant.

In the mixed culture, it was used a complete randomized blocks design, with five repetitions. It includes 12 trees of *Hevea brasiliensis* spaced at 8.0 x 20.0 m, four of *Schizolobium amazonicum,* spaced at 12.0 m x 20.0 m, four of *S. macrophylla,* and four of *C. guianensis* spaced of 7.0 m x 20.0 m. The secondary vegetation settled between the lines of the culture (*Vismia guianensis* and *Vismia japonensis*). The fertilization plan is described in table 2.

The determination of survival percentages (SUR), height (H), diameter at breast height (DBH) and the attacks of weeds and disease were carried out in one-year-intervals. For the measurement of tree height, the Haga hipsometer was used, and the twig was graded of 5.0 m with the precision in centimetres. A diametric tape with precision in millimetres was used to measure diameters.

Table 2: Fertilization plan in grams/ plant (g/ pl) for the forest species

Product	Fertilization (g/ pl)					
	GRAVE – FEV/ 93		COVER – MAR/ 93		COVER – DEZ/ 93	
	100%[1]	30%[2]	100%	30%	100%	30%
Lime	500	150	----	----	----	----
Urea[1]	----	----	65	20	50	15
SFT	155	47	----	----	100	30
KCL	100	30	----	----	50	15
$MgSO_4$	----	----	----	----	50	15
FTE BR8	----	----	----	----	20	6

[1] 100% fertilization recommended in literature
[2] 30% fertilization recommended in literature

The seeds of the native species were collected in Manaus-AM and Santarém-PA. The seeds of *Tabebuia heptaphylla* were from São Paulo. The seeds were put in polyethylene bags at the nursery of the EMBRAPA. After a period of 4 – 6 months, they were planted in the field. Further site characteristics with regard to the water and element supply of the trees are described by DÜNISCH et al. (1999a) and DÜNISCH et al. (1999 c).

The characteristics described are according to BAUCH and DÜNISCH (1996). In all culture systems, the water availability is higher at the superior surface of the soil (0 – 20 cm). The field capacity in the systems 2 and 3 is larger in all the soil depths, compared to system 1, which indicates serious water problems to planted species in the system 1 during the dry period.

Results and discussion

Several abiotic and biotic factors influenced the behaviour and the growth of the selected forest species. In particular, climate, soil, fertilization, competition, weeds and diseases are of importance at the experimental areas.

Hypsipyla grandella frequently attacks the species of *Meliaceae,* which has a negative influence on the growth and survival rates of these species. It can be concluded from Fig. 1 that in particular *Swietenia macrophylla* was heavily attacked, which was expressed by a percentage of survival in system 1 of 50%, of 45% in system 2, and of only 20% in system 3 after five years. Moreover, also the growth rate of *Swietenia* in system 3 is very much restricted. Although *Carapa* also suffers from *Hypsipyla* attacks, the rate of survival in all three systems is higher than 85%. Similar values were obtained for *Cedrela.* The other species correspond to *Cedrela* in their rate of survival.

In general, the average increments in height, DBH and basal area, were significantly larger in system 1, compared to system 2 and 3 (Table 3). This can be explained to a great extent with some site characteristics already described, such as low competition among the species, higher element concentrations in the trees, and the soil cover (*Pueraria* and *Homolepis*) that had positive influence on the K supply in system 1.

The average values in height, obtained for all species (Table 3), shows the general tendency of intensified growth with the conditions of monoculture. Also the average values of DBH in monoculture conditions was superior, when compared to systems 2 and 3. The wood volume at the three systems (Figure 2) showed great differences among the plantation systems, due to the survival index and the differences of spaces used.

The results of the average stem volume (Fig. 2) for *Ceiba* in system 1 with $0.27 m^3$ after five years of growth is most striking. Considering the low wood density of this species, the stem biomass production per tree reaches the maximum value of all species tested. Calculating the value of the stem biomass, as well, leads to favourable results for the growth of the other species under the conditions of system 1. After five years, *Carapa* exhibits $0.064 m^3$, *Cedro* $0.100 m^3$, *Dipteryx* $0.024 m^3$ (a very heavy and durable species), *Hymenaea* $0.098 m^3$, *Swietenia* $0.053 m^3$, *Tabebuia* $0.040 m^3$ and *Virola* $0.043 m^3$. The growth of *Carapa* and

Swietenia under mixed culture conditions (system 2) is only about half, compared to system 1, and the enrichment system does only allow reduced growth rates for all five species examined. The results, described by BAUCH and DÜNISCH (1996) and DÜNISCH et al. (1999b) on the growth dynamics for the period from April 1995 to March 1997, showed large increments for *Ceiba* and *Hymenaea*. There is no cambial cell division of *C. odorata* and *T. pentaphylla* during the dry season, indicating a strong influence of water supply on the cambial activity of these species. The rates of cellular division of *H. courbaril* and *C. pentandra* were reduced during the dry period (August/ September and September/ October, respectively). *D. odorata* showed little seasonal variation in the rate of cellular division. *S. macrophylla, C. pentandra,* and *V. surinamensis* showed a high rate of cellular division during the period from May to June 1995.

The same authors, comparing the dynamics of growth among the plantation systems, concluded that the tree growth is also strongly influenced by genetic factors. A typical growth pattern was detected for *C. odorata, D. odorata* and *H. courbaril* in monoculture conditions and enrichment cultures. It was also observed a high biomass production of *C. guianensis* at the plantation systems 2 and 3. This indicates less susceptibility to competition, when compared to the other species.

C. guianensis turned out to be more competitive than other species. *Carapa,* occurring abundantly at the plain forest of Amazonas and Pará, and on the terra firme, is a species of great commercial interest due to the wide range in use of its wood in construction and carpentry. This species occupies a leadership position among the exported wood of Amazonian-like, the most important medical plants of the region (LOUREIRO et al., 1979).

Table 3: Height, average increment (DBH) and basal area (BA) per tree at an age of four years under the conditions of three plantation systems. In addition, average growth (height, increment, basal area) per year is listed.
SYS: System 1 (monoculture), system 2 (mixed culture), system 3 (enrichment culture).

AGE (years)	SPECIES	SYS	SPACING (m)	HEIGHT (m)	DBH (cm)	BA (dm^2)	HEIGHT (m/ year)	DBH (cm/ year)	BA (dm^2/ year)
4.0	*Carapa*	1	3.0 x 3.0	4.97	9.8	0.7745	1.24	2.5	0.1936
4.0	*Cedro*	1	3.0 x 3.0	6.43	10.9	0.9199	1.61	2.7	0.2300
4.0	*Dipteryx*	1	3.0 x 3.0	6.02	4.7	0.2092	1.51	1.2	0.0523
4.0	*Hymenaea*	1	3.0 x 3.0	7.36	8.2	0.5805	1.84	2.1	0.1451
4.0	*Swietenia*	1	3.0 x 3.0	5.29	8.4	0.5868	0.99	2.1	0.1467
4.0	*Ceiba*	1	3.0 x 3.0	8.59	17.2	2.3579	2.15	4.3	0.5895
4.0	*Tabebuia*	1	3.0 x 3.0	4.19	6.6	0.5207	1.05	1.6	0.1302
4.0	*Virola*	1	3.0 x 3.0	4.54	6.5	0.3239	1.14	1.6	0.0810
4.0	*Carapa*	2	7.0 x 20.0	5.46	8.3	0.5611	1.37	2.1	0.1403
4.0	*Swietenia*	2	7.0 x 20.0	5.84	7.4	0.4311	0.88	1.8	0.1078
4.0	*Carapa*	3	3.5 x 7.0	4.36	4.9	0.2024	1.09	1.2	0.0506
4.0	*Cedro*	3	3.5 x 7.0	3.67	4.0	0.1244	0.92	1.0	0.0311
4.0	*Dipteryx*	3	3.5 x 7.0	3.23	2.0	0.0374	0.81	0.5	0.0093
4.0	*Hymenaea*	3	3.5 x 7.0	2.67	1.8	0.0283	0.67	0.5	0.0071
4.0	*Swietenia*	3	3.5 x 7.0	2.83	2.7	0.1074	0.71	0.7	0.0268

At the Ducke Reserve of INPA, in an experiment with lateral shadow of approximately 20% with four-year-old plants, *Swietenia* presented survival rates of 54% with 2.08 m height and 1.4 cm diameter (DBH) in the spacement of 5.0 m x 2.5 m (LOUREIRO et al., 1979).

This species is frequently attacked by a larva of a moth *(Hypsipyla grandella),* in the nursery phase and under field condition. The larva generally attacks the apical shoot, causing the loss of apical domination. As a result, there is a formation of many secondary shoots besides a delay in the height growth, which can cause the death of the plant.

In the Amazon, the species *Swietenia* has been tested with some success, in plantations with agricultural system management and with other forest species. At these conditions, the attack is minimized, not causing serious damage to the plant development (BRIENZA, jr., 1983; SOUZA, 1996).

The attack of *H. grandella* was first observed, in system 1. Although, due to the proximity of the experimental plots, the caterpillar *(H. grandella)* quickly manifested itself in the shadow environment. Presently, 100% of the plants of *Swietenia* are attacked, regardless of the vegetation system and the species protection. The stem in the majority of the trees is badly formed and consequently of reduced commercial value.

Although *Swietenia* is a potential species for the culture in humid tropical regions, it cannot be recommended to be planted under the selected conditions. This species has to be planted under partial shadow conditions or selected for polycultural systems with other forest species. Fast-growing tree species can be offered as a protection against the attack of *H. grandella*.

Swietenia is the most promising for its growth in diameter and height, it is moderately resistant to the "broca dos ponteiros" attack and for a good rate of survival in the systems 1, 2, and 3, respectively. Besides, the species can be planted in association with other forest species and under agricultural conditions. At the Ducke Reserve, Manaus, it develops well at plenty sun (100% of light), presenting a survival of 98% at an age of nine years with 6.24 m height, and 7.3 cm DBH (LOUREIRO et al., 1979).

In partial shadow, it was observed an average growth in diameter, always inferior to the condition of monoculture (Table 3). According to VOLPATO et al. (1972) and LOUREIRO et al. (1979), it is commonly observed that in partial shadow Carapa plants lose in diameter to win in height. Up to the present, such facts could not be verified. In monoculture, the annual diameter increment can reach 1.91 cm/ year with seven-year-old plants (YARED et al., 1988; VOLPATO et al., 1972). ALENCAR and ARAÚJO (1980), also indicated higher growth-rates in partial shadow related to the height.

The figures on the growth of *Cedro* in distinct situations indicate a great variety. The differences in height and diameter growth were significant among the vegetation systems 1 and 3 (Table 3). At the age of five years, the annual increment oscillated between 1.48 m/ year to 0.97 m/ year and in diameter 2.5 cm/ year to 0.9 cm/ year.

The species *H. courbaril, V. surinamensis,* and *C. pentandra* are promising by the performance presented in the monoculture. *H. courbaril* showed excellent survival rates: 100% in the culture in open area and around 80% in partial shadow. However, the height and diameter growth in partial shadow is inferior compared to the culture in open area (Table 3), showing the non-adaptability of the species to this kind of site. In open area, *V. surinamensis* showed an excellent survival (90%), fast growth and good shape. The growth in height and diameter was good (Table 3). *C. pentandra* presented an excellent growth, and a necessity for planting it in wider space already became obvious.

Other species that potentially can be used in reforestation and that have presented an acceptable growth and a good shape are *T. pentaphylla* and *D. odorata*.

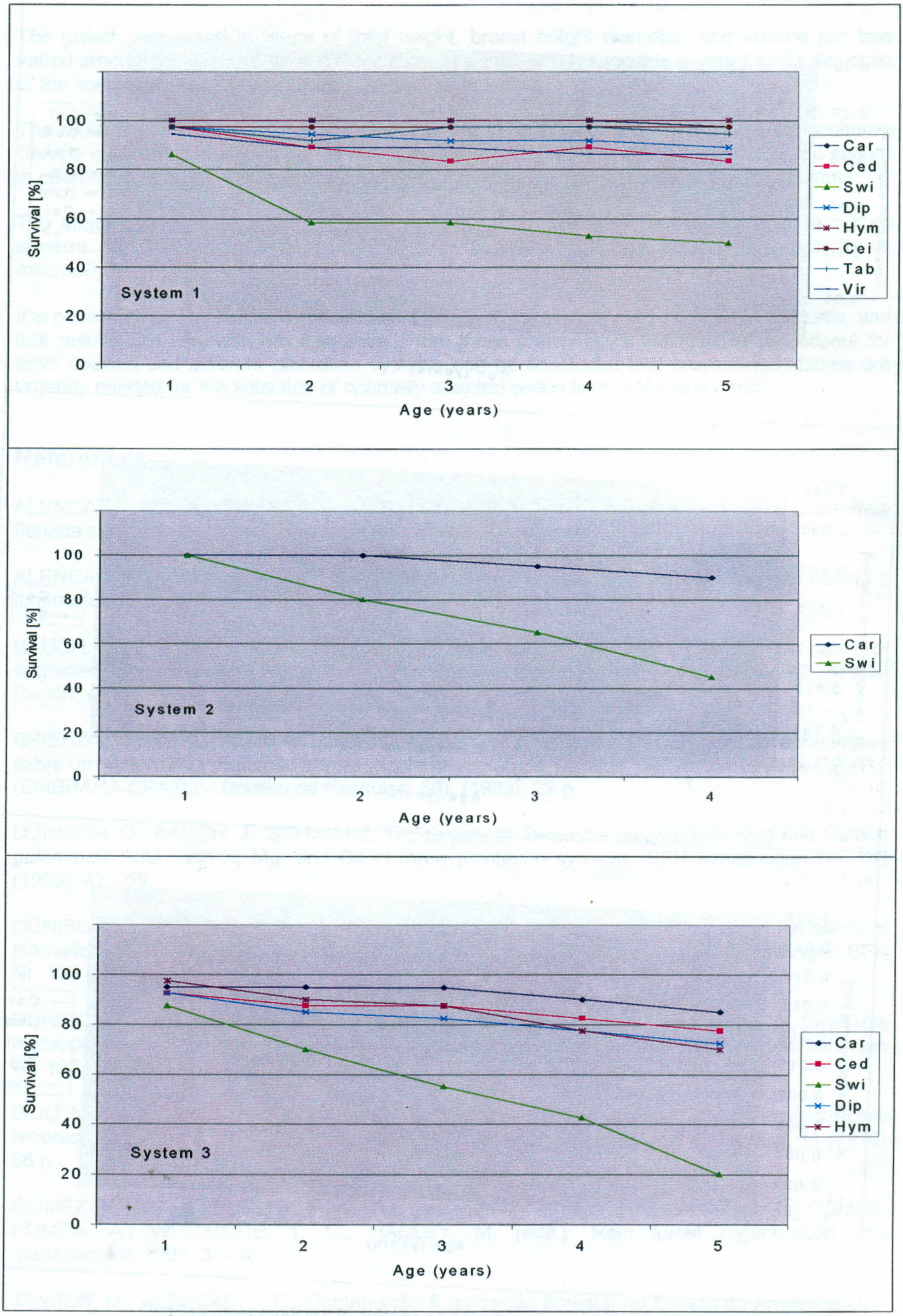


Fig. 1: Percentage of survival [%] of the planted tree species of the three systems. System 1 (monoculture), system 2 (mixed culture), system 3 (enrichment culture). Car = *Carapa*, Ced = *Cedrela*, Cei = *Ceiba*, Dip = *Dipteryx*, Hym = *Hymenaea*, Swi = *Swietenia*, Tab = *Tabebuia*, Vir = *Virola*

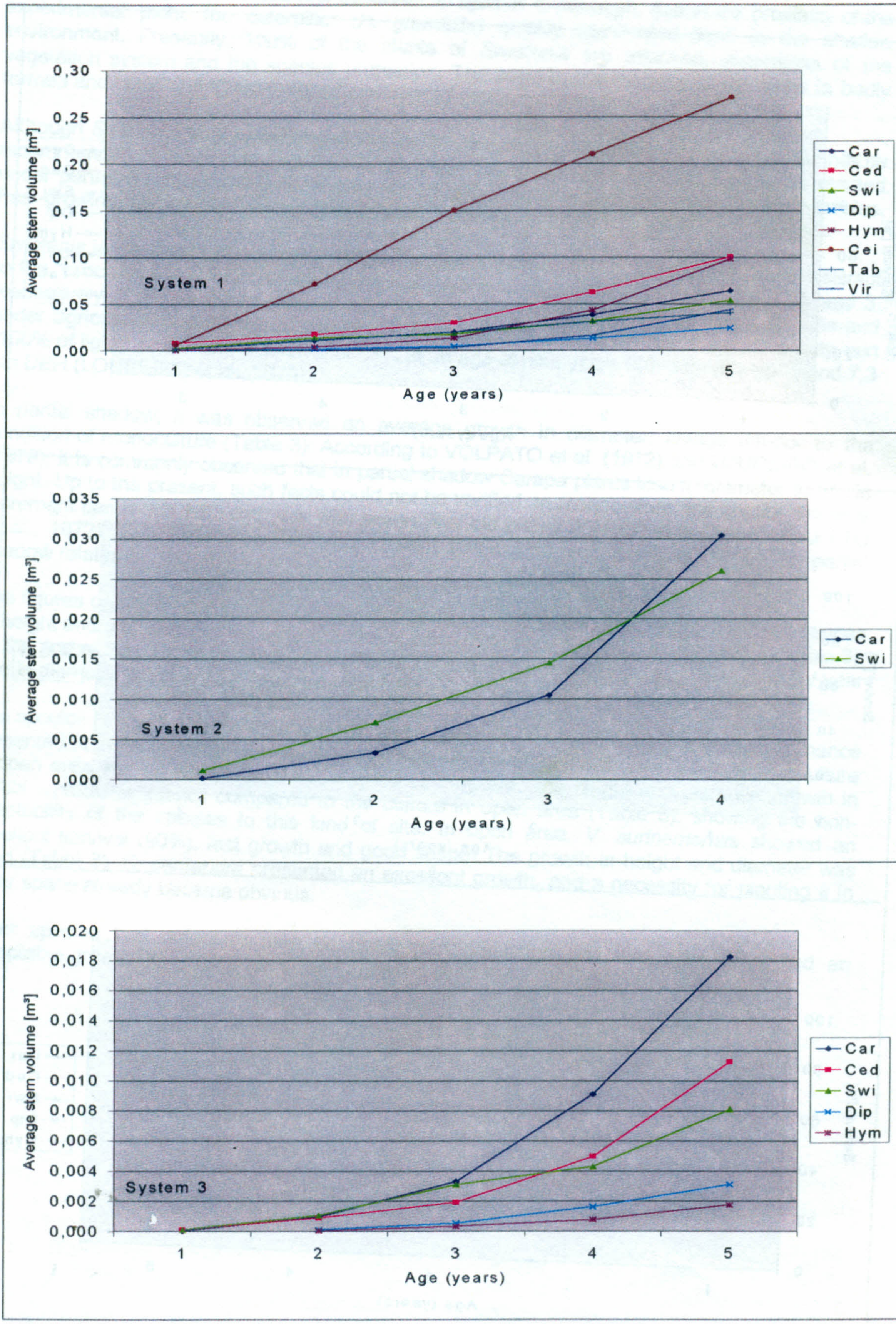


Fig. 2: Average volume of the stem [m³] per tree species of the three plant systems System 1 (monoculture), system 2 (mixed culture), system 3 (enrichment culture) Car = *Carapa*, Ced = *Cedrela*, Cei = *Ceiba*, Dip = *Dipteryx*, Hym = *Hymenaea*, Swi = *Swietenia*, Tab = *Tabebuia*, Vir = *Virola*

Conclusion

The growth expressed in terms of total height, breast height diameter, and volume per tree varied among species and among the culture systems, which suggests a very careful selection of the species to be planted in a specific plantation system.

The most promising culture system, according to growth results, is system 1 (monoculture). *Carapa guianensis,* due to its ecological adaptation, is the most adaptable species to the culture in open area and on partial shadow, and is suitable as a component of agroforestry systems.

The attack of *Hypsipyla grandella*, on the *Meliaceae* species, was noted in all of the culture systems. It negatively influenced the growth in height and caused mortality, especially for *S. macrophylla*.

It is necessary to emphasize that the results presented are only based on one seed source, and that results can vary with other sources. From these preliminary investigations carried out for eight species und different plantation systems can be concluded that provenance studies are urgently needed for the selection of optimally adapted seeds for the Manaus region.

References

ALENCAR, J. C.; MAGALHÃES, L. M. S; LOUREIRO, A. A.: Considerações sobre problemas florestais da amazônia brasileira. Acta Amazônica, Suplemento, 9 (1979) 147 – 153.

ALENCAR, J. C.; ARAÙJO, V. C.: Comportamento de espécies florestais amazônicas quanto a luminosidade. Acta Amazônica, 10 (1980) 435 – 444.

BAUCH, J.; DÜNISCH; O.: Investigation on tree species suitable for the recultivation of degraded land areas in Central Amazonia. SHIFT project BMBF/ CNPq – ENV 42, Annual Report, (1996) 69 p.

BRIENZA, jr., S.; KITAMURA, P. C.; DUBOIS, J.: Considerações biológicas e econômicas sobre um sistema de produção silvo-agrícola na região do Tapajós. Belém, EMBRAPA-CPATU, (EMBRAPA-CPATU – Boletim de Pesquisa, 50), (1983), 22 p.

DÜNISCH, O.; BAUCH, J.; SCHWARZ, Th.: Supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. with K, Mg, and Ca in three plantation systems. BFH Mitteilungen Nr. 193 (1999), 47 - 59.

DÜNISCH, O.; BAUCH, J.; SACK, M.; MÜLLER, M.: Growth dynamics in wood formation of plantation-*grown Swietenia macrophylla* King and *Carapa guianensis* Aubl., Mitteilungen BFH Nr. 193 (1999) 79 - 96.

DÜNISCH, O.; SCHROTH, G.; MORAIS, R. de; ERBREICH, M.: Water supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in three plantation systems, BFH-Mitteilungen Nr. 193 (1999) 29 - 45.

GOLFARI, L.; CASER, R. L.; MAURO, V. G.: Zoneamento ecológico esquemático para reflorestamento no Brasil. (2ª aproximação). Belo Horizonte: CPFRC, Série Técnica, 11 (1978) 66 p.

GÓMEZ-POMPA, A ; BURLEY, F. W.: The management of natural tropical forests. In: GÓMEZ-POMPA, A.; WHITMORE, T. C.; HADLEY, M. (eds.): Rain forest regeneration and management, 1991, 3 – 18.

JANSEN, M.; ALENCAR, J. C.: Contribuição ã reposição florestal no Estado do Amazonas. In: VAL, A. L.; FIGLIUOLO, R.; FELDBERG, E. (eds.): Bases científicas para estratégias e desenvolvimento da Amazônia: fatos e perspectivas. Manaus (1991) 187 – 195.

JESUS, P. M.: Recuperação de áreas degradadas. In: Anais – 2° Congresso Nacional Sobre Essências Nativas, v. 2, (1992) 407 – 412.

KANASHIRO, M.; YARED, J. A. G.: Experiências com plantios florestais na bacia Amazônica. In: SEITZ, R. A.; REISSMANN, C. B.; CARNEIRO, J. G. de A.; MALINOVSKI, J. R.; SOARES, R. W. (eds.): O desafio das florestas neotropicais. Curitiba, (1991), 117 – 137.

LOUREIRO, A. A.; SILVA, M. F.: Catálogo das madeiras da Amazônia, SUDAM, Belám, 2 (1968) 411.

LOUREIRO, A. A.; SILVA M. F.; ALENCAR, J. C.: Essências madeiras da Amazônia, Manaus, INPA/ Suframa, 1 (1979) 245.

MARQUES, L. C. T.: Comportamento de paricá, tatajuba e eucalipto em plantio consorciado com milho e capim-marandu, em Paragominas, Pará. Master Thesis, Viçosa, 1990, 92 p.

MONTAGNINI, F.: Sistemas agroflorestales: principios y aplicaciones en los tropicos. San José, Organización Para Estudios Tropicales. 1992, 622.

NEVES, E. J. M.; SILVA, S. E. L.; MATOS, J. C. S.; CANTO, A. C.: Comportamento de espécies florestais a pleno sol e em linhas de enriquecimento em Manaus-AM. In: Congresso Florestal Panamericano 1, Curitiba, PR, Anais, Curitiba: SBS-SBEF, 2 (1993) 756.

SOUZA, S. G. A.; MATOS, J. C.; ARCOVERDE, M.; WANDELLI, E.; PERIN, R.; FERNANDES; E.: Comportamento do Mogno (*Swietenia macrophylla* King) em sistemas agroflorestais na Amazônia Ocidental. In: Forest 1996 – 4° Simpósio Internacional sobre ecosistemas florestais, volume de resumos (1996) 183 – 184.

VOLPATO, E.; SCHMIDT, P. B.; ARAÙJO, V. C.: *Carapa guianensis* Aubl. *(Andiroba).* Acta Amazônica, 3 (1972) 71 – 82.

YARED, J. A. G.; KANASHIRO, M.; CONCEIÇÃO, J. G. L.: Espécies florestais nativas e exóticas: comportamento silvicultural no planalto do Tapajós-PA. Belém: EMBRAPA-CPATU, (EMBRAPA.CPATU. Documentos, 49), 1988, 29.

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).

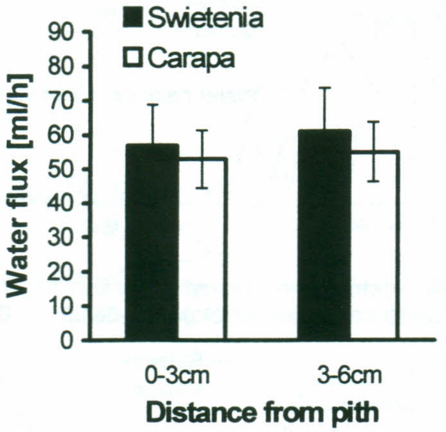


Fig. 2: Permeability [ml/ h] of the stem xylem (sample diameter 15 mm) for water of 6-year-old *Swietenia macrophylla* and *Carapa guianensis* 0 – 3 cm and 3 - 6 cm from the pith (stem radii 5.4 - 6.4 cm).

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.

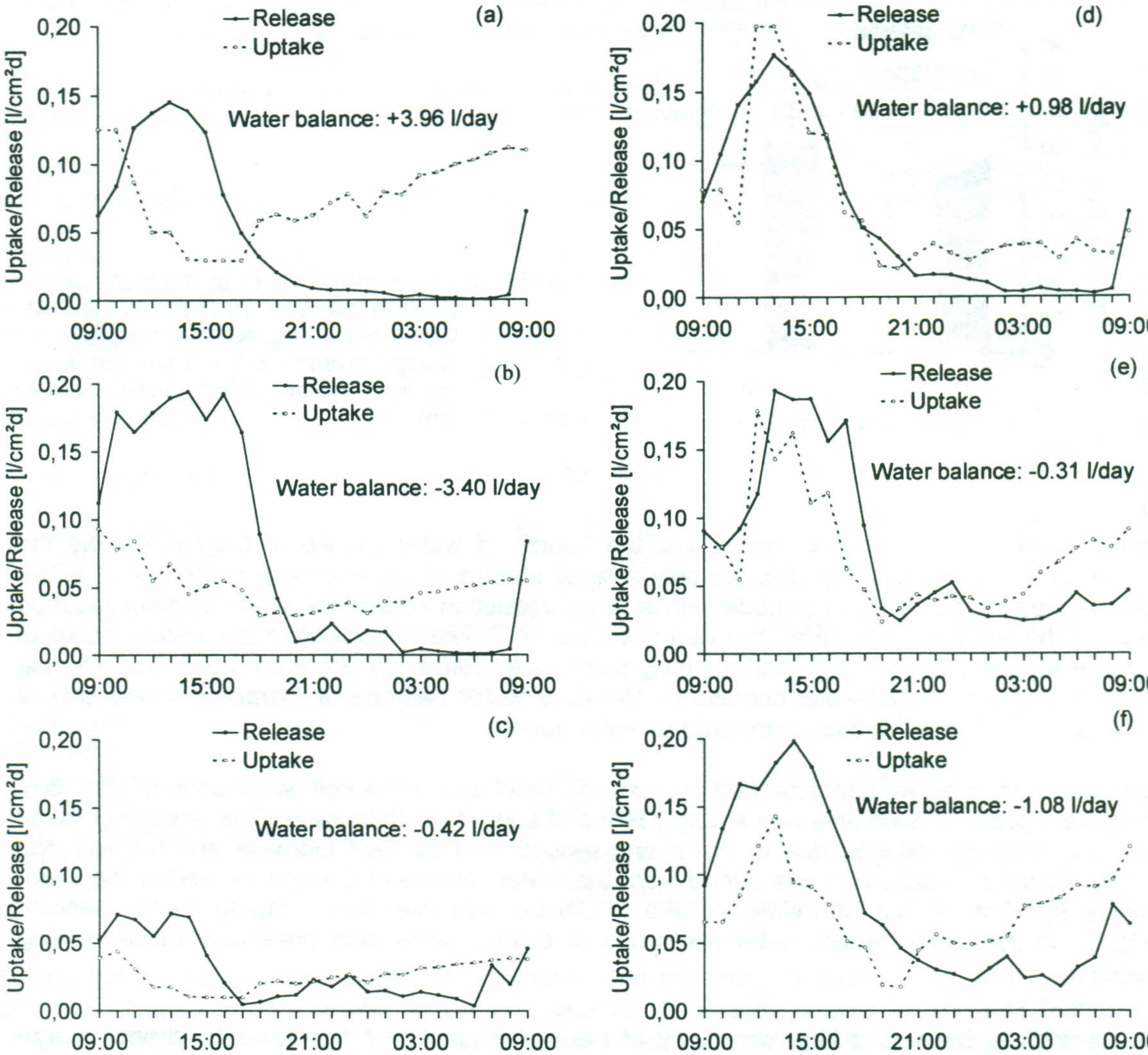


Fig. 3a-f: Diurnal variation of the water uptake and water release [l/ cm²d] of 6-year-old *Swietenia macrophylla* and *Carapa guianensis* at (a/ d) March 28, 1997 (suction force of the soil < 100 hPa), (b/ e) June 21, 1997 (suction force of the soil 200-400 hPa) and (c/ f) October 9, 1997 (suction force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

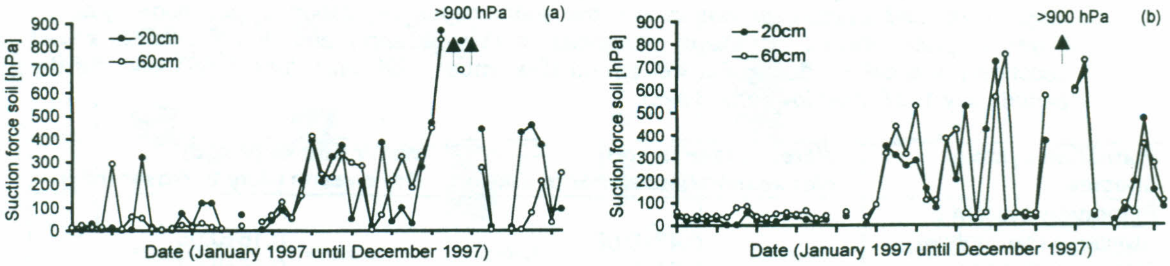


Fig. 4a/ b: Soil water tension [hPa] of (a) a 6-year-old plantation of *Swietenia macrophylla* and (b) *Carapa guianensis* (plantation system I) from January 1997 to December 1997.

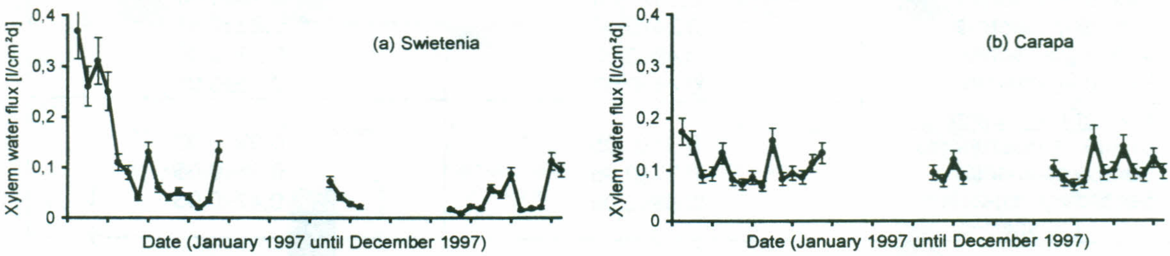


Fig. 5a/ b: Xylem water flux [l/ cm²d] of (a) 6-year-old *Swietenia macrophylla* and (b) *Carapa guianensis* (plantation system I) from January 1997 to December 1997.

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.

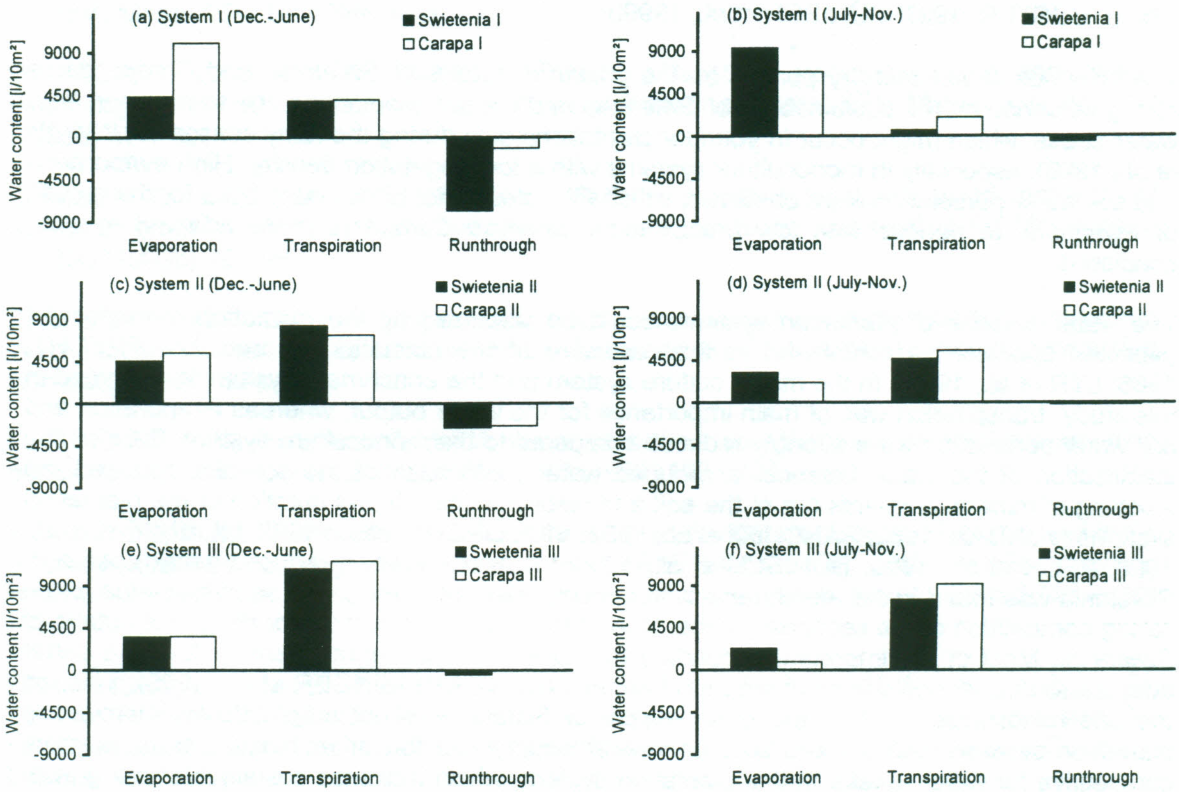


Fig. 6a-c: Evaporation (soil, crown), transpiration and soil water percolation in the soil [l/ 10 m²] of the plantation systems I (a/ b), II (c/ d), III (e/ f) during the wet period (December 1996 until June 1997) and the dry period (July 1997 until November 1997).

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.

References

AZEVEDO, C. P. de; LIMA, R. M. B. de; NEVES, E. J. M.; GASPAROTTO, L.; DÜNISCH, O.: Development of tree height and diameter of eight selected tree species und plantation conditions in Central Amazonia. BFH Mitteilungen Nr. 193 (1999) 17 - 28.

BAUCH, J.: Die axiale Durchlässigkeit von Kiefern-Splintholz für wässrige Lösungen. Planta, 61 (1964) 196 - 208.

BENCHIMOL, S.: Manual de introdução à Amazônia. Universidade do Amazonas. Manaus, 1996, 320 p.

BREDEMEIER, M.: Stoffbilanzen, interne Protonenproduktion und Gesamtsäurebelastung des Bodens in verschiedenen Waldökosystemen Norddeutschlands. Ber. Forschungszentrum Waldökosysteme der Universität Göttingen 33, 1987, 183 p.

BREITSPECHER, A.; BETHEL, J. S.: Stem growth periodicity of trees in a tropical wet forest of Costa Rica. Ecology, 71 (1990) 1156 - 1164.

COSTER, C.: Zur Anatomie und Physiologie der Zuwachszonen- und Jahrringbildung in den Tropen. I. Ann. Jard. Bot. Buitenzorg, 37 (1927) 49 -161.

DAHMS, K. G.: Das Holzportrait - echtes oder amerikanisches Mahagoni *(Swietenia macrophylla* King, Familie *Meliaceen*), Holz als Roh- und Werkstoff 47. 1989, 1 - 6.

DÜNISCH, O.; BAUCH, J.: Influence of water and mineral elements on wood formation of spruce (*Picea abies* [L.] Karst.) under controlled conditions. Holzforschung, 49 (1994) 9 - 15.

DÜNISCH, O.; BAUCH, J.; GASPAROTTO, L.; NEVES, E.; AZEVEDO, C. de; LIMA, R. de; MORAIS, R. de: Environment-tree growth relationships of plantation-grown tropical tree species as a basis for sustainable timber production in mixed culture systems in Central Amazonia. In:

LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 – 19, 1998, 13 p.

DÜNISCH, O.; BAUCH, J.; SCHWARZ, T.: Supply of *Swietenia macrophylla* King. and *Carapa guianensis* Aubl. with K, Ca, and Mg in three plantation systems. BFH Mitteilungen Nr. 193 (1999a) 47 – 59.

DÜNISCH, O.; SACK, M.; MÜLLER, M; BAUCH, J.: Growth dynamics in wood formation of plantation-grown *Swietenia macrophylla* King. and *Carapa guianensis* Aubl., BFH Mitteilungen Nr. 193 (1999b) 79 - 96

ERBREICH, M.: Untersuchungen zur Xylemwasserleitung ausgewählter tropischer Wirtschaftsbaumarten in Zentralamazonien. Diplomarbeit Fachbereich Biologie, Universität Hamburg, (1997) 83 p.

FEARNSIDE, P. M.: Forests or fields? A response to the theory that tropical forest conservation poses a threat to the poor. Land Use Policy, 10 (1993) 108 - 121.

FEARNSIDE, P. M.: Agroforestry in Brazil´s Amazonian development policy: The role and limits of a potential use for degraded lands. In: CLUSENER-GOOD, M. and SACHS, I. (eds.): Brazilian perspectives on sustainable development of the Amazon region. Oxford University Press, Oxford, 1995, 311 p.

FERNANDES, E. C. M.; BIOT, Y.; CASTILLA, C.; ACILINO, C. C.; MATOS, J. C.; GARCIA, S.; PERIN, R.; WANDERLI, E.: The impact of selective logging and forest conversion for subsistence agriculture and pastures on terrestrial nutrient dynamics in the Amazon. Ciencia e Cultura. 1997, 34 p.

GERLACH, D.: Botanische Mikrotechnik. Thieme Verlag, Stuttgart, 1977, 311 p.

GOTTWALD, H.: Handelshölzer. Ferdinand Holzmann Verlag, Hamburg, 1961, 249 p.

GRANIER, A.: Une nouvelle methode pour la mesure de flux de seve brute dans le tronc des arbres. Annales Des Sciences Forestieres, 42 (1985) 193 - 200.

HANNAN, S. A.; BETALHA, B. H. L.: Amazônia: Contradições no paraíso ecológico. Cultura Editores Associados, São Paulo, 1995, 265 p.

HÖLL, W.: Seasonal fluctuation of reserve materials in the trunkwood of spruce (Picea abies [L.] Karst.). J. Plant Physiology, 117 (1985) 355 - 362.

JORDAN, C. F.: The nutrient balance of an Amazonian rain forest. Ecology, 63 (1982) 647 - 654.

KLEINIG, H.; SITTE, P.: Zellbiologie. Gustav Fischer Verlag Jena, Stuttgart, 1992, 591 p.

KOZLOWSKI, T. T.; KRAMER, P. J.; PALLARDY, S. G.: The physiological ecology of woody plants. Academic Press San Diego, New York, 1991, 657 p.

KRAMER, P. J.: Water relations of plants. Academic Press Orlando, 1985, 489 p.

LAMPRECHT, H.: Waldbau in den Tropen: Die tropischen Waldökosysteme und ihre Baumarten - Möglichkeiten und Methoden zu ihrer nachhaltigen Nutzung. Paul Parey Verlag, Hamburg, Berlin, 1986, 319 p.

LANGENFELD-HEYSER, R.: Distribution of leaf assimilates in the stem of *Picea abies* L. Trees, 1 (1987) 102 - 109.

LARSON, P. R.: The vascular cambium. Springer Verlag, Berlin, 1995, 725 p.

LILIENFEIN, J.; WILCKE, W.; NEUFELDT, H.; AYARZA, M. A.; ZECH, W.: Land-use effects on organic carbon, nitrogen, and sulphur concentrations in macroaggregates of differently textured Brazilian oxisols. Z. Pflanzenernähr. Bodenk., 161 (1998) 165 - 171.

LIMA, R. M. B. de; NEVES, E. J. M.; GASPAROTTO, L.; DÜNISCH, O.: Development of tree height and diameter of eight selected tree speices under plantation conditions in Central Amazonia. BFH Mitteilungen Nr. 193 (1999) 17 – 28.

LÜTTGE, U.: Clusia: Ein Modellfall der ökophysiologischen Plastizität in einer tropischen Gattung. Rundgespräche der Kommission für Ökologie, 10 (1995) 173 - 186.

LYR, H.; FIEDLER, H. J.; TRANQUILINI, J.: Physiologie und Ökologie der Gehölze. Gustav Fischer Verlag Jena, Stuttgart, 1992, 620 p.

NOLDT, G.; BAUCH, J.; SCHMITT, K.; BALODIS, V. G.: Structure of primary roots of *Swietenia macrophylla* King *(Meliaceae)* under controlled conditions. BFH Mitteilungen Nr. 193 (1999) 107 - 112.

PEARCY, R. W.; SCHULZE, E. D.; ZIMMERMANN, R.: Measurement of transpiration and leaf conductance. In: PEARCY, R. W.; EHLERINGER, J.; MOOVEY, H. A.; RUNDEL, P. W. (eds.): Plant Physiological Ecology. Chapman and Hall, London, New York, 1989, 137 – 160.

PREISINGER, H.; COELHO, L. F.; SOCORRO, M.; SIGUIERA, G., LIEBEREI, R.: Analysis of growth form types and floristic composition of the spontaneous vegetation in an agricultural test area near Manaus, Amazonas, Brazil. Ang. Botanik, 68 (1994) p. 40 – 46.

PREISINGER, H.; DÜNISCH, O.; MORAIS, R. R. de; RICHTER, K.; ARAÚJO, R. da C.: Comparative studies on morpho-physiological traits of six Amazonian species of *Bellucia* and *Miconia (Melastomataceae)* and implications for their ecological behaviour. BFH Mitteilungen Nr. 193 (1999) 113 – 133.

PUMIJUMNONG, N.; ECKSTEIN, D.; SASS, U.: Tree ring resarch on *Tectona grandis* in Northern Thailand. IAWA Journal, 16 (1995) 385 - 392.

RIZZINI, C. T.: Àrvores e madeiras úteis do Brasil. Edgar Bleicher LTDA, São Paulo, Brazil (1990) 296 p.

SANCHEZ, P. A.; BANDY, D. E.; VILLACHICA, J. H.; NICHOLAIDES, J. J.: Amazon basin soils: Management for continuous crop production. Science, 216 (1982) 821 - 827.

SAUTER, J. J.: Seasonal changes of the efflux of sugars from parenchyma cells into the apoplast in poplar stems (*Populus x canadensis „robusta“*). Trees, 2 (1988) 242 - 249.

SIDIYASA, K., BAAS, P.: Ecological and systematic wood anatomy of Alstonia (Apocynaceae). IAWA Journal, 19 (1998) 207 - 229.

TYREE, M. T.; SPERRY, J. S.: Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. Plant Physiology, 88 (1988) 574 - 580

VETTER, R. E.; BOTOSSO, P. C.: Remarks on age and growth-rate determination of Amazonian trees. IAWA Journal, 10 (1989) 133 - 145.

VIGOUROUX, A.; BUSSI, C.; BERGER, J. F.: Importance of water consumption for calcium nutrition of trees. Ann. Sci. For., 46 (1989) 369 - 371.

WAGENFÜHR, R.; SCHEIBER, C.: Holzatlas. VEB Fachbuchverlag, Leipzig, 1985, 750 p.

WHITMORE, T. C.: Tropische Regenwälder. Spektrum Akad. Verlag, Heidelberg, 1995, 275 p.

WORBES, M.: Variety in structure of annual growth zones in *Tabebuia barabata* (E. Mey) *Sandw. Nignoniaceae*, a tropical tree species from Central Amazonian inundation forests. Dendrocronologia, 6 (1988) 7 - 89.

ZECH, W.; SCHROTH, G.; CRAVO, M. da S.; TEIXEIRA, W. G.; KAISER, K.; LEHMANN, J.: Water and nutrient fluxes as indicators for the sustainability of different land-use systems on the terra firme near Manaus. In: LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 – 19 (1998) 6 p.

ZIMMERMANN, M. H.: Xylem structure and the ascent of sap. In: TIMELL, T. E. (ed.), Springer Series in Wood Science, Vol. 1. Springer Verlag Berlin, Heidelberg, New York, Tokyo (1983) 143 p.

Acknowledgements

We thank the "Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie", Bonn, Germany and the CNPq/ IBAMA, Brasilia, Brazil for financial support within the German-Brazilian cooperation program SHIFT (Studies on Human Impacts on Forests and Floodplains in the Tropics). We also wish to thank L. Coelho and Dr. H. Preisinger for vegetation analyses. The assistance of V. Seabra and A. Souza is especially appreciated.

Supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. with K, Ca, and Mg in three different plantation systems

O. Dünisch,[1] J. Bauch,[2] and Th. Schwarz[1]

[1] Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg
[2] Institute of Wood Biology, Hamburg University, Hamburg

Summary

In the present study, the K, Ca, and Mg supply of the economically important timber tree species *Swietenia macrophylla* Aubl. and *Carapa guianensis* King were investigated in three plantation systems (monoculture, mixed culture, enrichment of a secondary forest) near Manaus, Central Amazon. In order to get insight into the element input in the 5-year-old plantation systems, the K, Ca, and Mg content of precipitation, throughfall, stemflow, and litter was quantified in one-week-intervals. The element demand of the trees was quantified by element analyses of different tree fractions. The element output of the plantations caused by leaching out of the soil was calculated by soil solution samples collected in one-week-intervals in soil depths of 10, 20 and 60 cm (Cl-method). The element uptake of the vegetation was calculated from biomass data and the element content of different tree fractions carried out in December 1996 and in December 1997. The K, Ca, and Mg stocks of the soil were quantified by means of soil samples (exchangeable K, Ca, Mg content; total K, Ca, Mg content) and the analyses of the soil solution.

The mean K, Ca, and Mg content of the precipitation was fairly low and varied between 0.07 and 0.7 mg/ l. A strong increase of the element content of the throughfall and the stemflow compared to the precipitation (2 to 16 times higher) was found, which was caused by leaching of mineral elements out of the crown and by dry deposition. A higher specific K demand was calculated for *Swietenia* (6788 µg/ g) compared to *Carapa* (5735 µg/ g), whereas a higher mean Ca and Mg content of the biomass of *Carapa* was found. Young leaves are a strong sink for K, whereas the Ca content of older leaves increased compared to younger leaves. This indicates that both species favour an "internal recycling" for K and an "external recycling" mechanism for Ca. The high Mg content of young leaves of *Carapa* already indicated a high photosynthetic activity of young leaves, whereas the Mg content of younger *Swietenia* leaves was reduced compared to older leaves. Litter decomposition experiments indicated an improved K, Ca, and Mg cycling in the enrichment system compared to 5-year-old monoculture and mixed culture plantations.

Quantified input and output data of the plantations showed that the enrichment system is more stabilized with regard to K, Ca, and Mg supply than the 5-year-old monoculture and mixed culture system. Nevertheless, the quantification of the element stocks of the plantations indicated high K (872/ 1057 g/ 10 m²), Ca (818/ 1502 g/ 10 m²), and Mg (623/ 1011 g/ 10 m²) stocks in the monoculture system and, therefore, at this state it could not be predicted in how far sustainable growth is also possible in the monoculture system, as well. Higher K, Ca, and Mg stocks were found in *Carapa* plantations compared to *Swietenia* plantations, which indicates that the stabilization of the K, Ca, and Mg stocks during the initial phase of plantations is favoured more by *Carapa* than by *Swietenia*.

Resumo

Abastecimento com K, Ca e Mg de *Swietenia macrophylla* King e *Carapa guianensis* Aubl. em três sistemas diferentes de plantação

No presente estudo, o suprimento de K, Ca e Mg para *Swietenia macrophylla* King e *Carapa guianensis* Aubl., árvores importantes na economia madeireira, foi investigado em três sistemas de plantio (monocultura, cultura mista e enriquecimento de floresta secundária) próximo a Manaus, Amazônia Central. No sentido de compreender o aporte de elementos em sistemas de plantio com 5 anos de idade, o teor de K, Ca e Mg foi quantificado em intervalos semanais na precipitação, precipitação através das copas, escorrimento ao longo dos troncos e no litter. As necessidades dos elementos pelas árvores foram quantificadas através da análise elementar nas diferentes frações da biomassa. A saída dos elementos dos plantios, causada por lixiviação do solo, foi calculada a partir de amostragens da solução do solo coletadas semanalmente nas profundidades de 10, 20 e 60 cm (Método-Cl). A absorção dos elementos pela vegetação foi calculada a partir de dados da biomassa. O teor de elementos de diferentes frações das árvores, foram determinados em dezembro de 1996 e dezembro de 1997. Os estoques de K, Ca e Mg do solo, foram quantificados através de análises em amostras de solo (teores trocáveis e totais de K, Ca e Mg) e em amostras da solução do solo.

Os teores médios de K, Ca e Mg da precipitação foram razoavelmente baixos e variaram entre 0.07 e 0.7 mg/ l. Foi encontrado um expressivo aumento no teor dos elementos na precipitação através da copa, e no escorrimento ao longo do tronco, quando comparado com a precipitação (2 a 16 vezes), tendo sido causado pela lixiviação dos elementos minerais da copa e pela deposição seca. Foi calculada uma maior, demanda específica de K para *Swietenia* (6788 µg/ g), comparado com *Carapa* (5735 µg/ g), enquanto foram encontradas médias mais altas para os teores de Ca e Mg na biomassa de Carapa. Folhas jovens representam uma forte demanda para K, enquanto o teor de Ca aumentou nas folhas velhas em comparação com folhas jovens. Isto indica que ambas as espécies favorecem uma "reciclagem interna" para K, e um mecanismo de "reciclagem externa" para Ca. O elevado teor de Mg de folhas jovens de *Carapa* indicou uma alta atividade fotossintética destas folhas jovens, enquanto o teor de Mg das folhas jovens de *Swietenia* foi reduzido em comparação com as folhas velhas. Experimentos de decomposição do litter indicaram uma maior eficiência na ciclagem de K, Ca e Mg no sistema de plantio enriquecido em relação aos plantios em sistema de monocultura, com 5 anos de idade, e plantios mistos.

Valores quantificados de dados de entrada e saída dos plantios, mostraram que o sistema de enriquecimento mostra-se mais estável com relação ao suprimento de K, Ca e Mg do que os sistemas de cultura mistos e de monocultura com 5 anos de idade. No entanto, a quantificação do estoque de elementos dos plantios indicou elevados estoques de K (872/ 1057 g/ 10 m^2), Ca (818/ 1502 g/ 10 m^2), e Mg (623/ 1011 g/ 10 m^2) no sistema de monoculturas e, por esta razão, neste estágio, não é possível prever até que ponto é possível assegurar sustentabilidade do crescimento no sistema de monocultura. Estoques mais elevados de K, Ca e Mg foram encontrados nos plantios de *Carapa* quando comparado aos de Swietenia, o que indica que a estabilização dos estoques de K, Ca e Mg durante a fase inicial dos plantios são mais favorecidos pela *Carapa* do que pela *Swietenia*.

Introduction

Mineral elements are involved in photosynthesis (KÜPPERS et al., 1985), tree growth, and wood formation (LARSON, 1967; LARSON, 1969, WARDROP, 1981; KOZLOWSKI et al., 1991; LARSON, 1995). Therefore, information on the mineral element demand of tree species and the nutrient stocks of forest sites are of main interest in the study of environment–tree growth relationships as a basis for sustainable timber production.

Especially in tropical rain forests of the Central Amazon, tree growth is limited by the restricted mineral element supply of the soils (DRECHSEL and ZECH, 1991; KLINGE, 1976; 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 reduction of the element stocks of the soil in this region (FEARNSIDE, 1995; FERNANDES et al., 1997). In order to counteract this tendency, investigations on the recultivation of degraded areas for fruit and high quality timber production are carried out in an interdisciplinary German-Brazilian research cooperation since 1992 (LIEBEREI et al., 1998). For the selection of suitable tree species for high quality timber production in mixed culture systems, information on the mineral element supply of commercial tree species in plantation systems is necessary.

With regard to tree growth and wood formation, the macronutrients K, Ca, and Mg are of main importance. K is involved in enzyme reactions and the turgor of the cells (BAUCH, 1993; MARSCHNER, 1995; DÜNISCH, 1998). Ca stabilizes cell membranes and is involved in cell wall formation, especially in the lignification of the cell wall (WARDROP, 1981; WESTERMARK, 1982). Mg is essential in the photosynthesis of the trees and, therefore, directly related to the biomass production of the plants (KÜPPERS et al., 1985).

Therefore, in this study, the K, Ca, and Mg supply of the high quality timber trees *Swietenia macrophylla* Aubl. and *Carapa guianensis* King (DAHMS, 1989; GOTTWALD, 1961; WAGENFÜHR and SCHEIBER, 1985) were investigated in three plantation systems of the Central Amazon. Emphasis was laid on the investigation of the K, Ca, and Mg demand of these important timber species and the element balance and the element stocks of the plantations. This was done to get some practical help with the sustainable high quality timber production of *Swietenia macrophylla* Aubl. and *Carapa guianensis* King on degraded areas of the Central Amazon.

Experimental

Plantation systems and experimental trees

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. According to categorization, the soil is a poor yellow latosol with a reduced cation exchange capacity (comp. ZECH et al. 1998, DÜNISCH et al., 1999a). The investigations on the K, Ca, and Mg 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. DÜNISCH et al., 1999a):

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 four 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, burned in 1992
- Mixed culture system of *Swietenia macrophylla, Carapa guianensis, 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

The investigations on the K, Ca, and Mg supply of plantation-grown *Swietenia* and *Carapa* were carried out in 1996. For the study of the element content of the precipitation, the throughfall and the stemflow, sample collection was carried out for three trees of each species. Element analyses of biomass fractions were carried out for two trees of each plantation system.

Element analysis

The element analyses (K, Ca, Mg) of biomass samples were carried out in December 1995 and December 1996 for 17 fractions per tree to get an inside in the nutrient status of 5-year-old plantation-grown *Swietenia* and *Carapa* trees. These data also served as a basis for the calculation of the net element uptake of the vegetation per year. After preparation according to RADEMACHER et al. (1992), the samples were analysed by optical emission spectroscopy with an inductively coupled plasma flame (ICP-OES, comp. BERNEIKE et al., 1985).

The element input into the plantations caused by litterfall and litter decomposition was calculated from the weekly litterfall (collectors 3x3 m) and a litter decomposition experiment carried out in 1996 (litterbags 40x40 cm, mesh width 1x1 mm, 4 repeats). The samples were also analysed by optical emission spectroscopy with an inductively coupled plasma flame (ICP-OES).

The element content of the soil solution was quantified in one-week-intervals in soil depths of 10, 20, and 60 cm. Suction caps (P80, UMS Umweltanalytische Meßsysteme, München) were installed in a distance of 1 and 2 m from the trunk. The total element content of the soil was determined after HF treatment of the soil in December 1995 and December 1996 as to quantify the element stocks of the soil. The exchangeable K, Ca, and Mg content of the soil was quantified after a percolation of the soil samples with NH_4Cl (1 N), according to KÖNIG and FORTMANN (1996).

The leaching of K, Ca, and Mg out of the soil was quantified by the chemical analyses of the soil solution in different soil depths. Corresponding data for the element input were obtained *via* precipitation and throughfall (Cl-method; comp. BREDEMEIER, 1987).

Results

K, Ca, Mg content of precipitation, throughfall, stemflow, and different plant fractions

Element analyses on the K, Ca, and Mg content of precipitation, throughfall, stemflow and different plant fractions served as a basis for the calculation of the element input into the plantations (comp. Table 1 and 3). Only a small amount of K, Ca and Mg enters the plantations via precipitation due to the low element content of the rain water in the Manaus region (Table 1). The K, Ca, and Mg content of the throughfall is two to seven times higher compared to the element content of the precipitation, which indicates a strong leaching of mineral elements from the leaves. Leaching of K is more pronounced for the leaves of *Swietenia* compared to *Carapa*, whereas significantly higher leaching of Mg was detected for *Carapa* (Table 1). This is explained by the high K-content of the leaves and the biomass of *Swietenia* compared to *Carapa,* and the higher Mg-content of the leaves and the tree biomass of *Carapa* compared to *Swietenia* (comp. Tables 2 and 3). The extremely high element content of the stemflow, which exceeds the element content of the precipitation by a factor of 4 to 16, could not exclusively be explained by leaching out of the phloem of the twigs and the stem and might be caused by dry deposition located in the crown, as well (Table 1).

Table 1: K-, Ca-, and Mg-content [mg/ l] of the precipitation, the throughfall, and the stemflow of 5-year-old plantation-grown *Swietenia macrophylla* and *Carapa guianensis*.

Sample	K [mg/ l]	Ca [mg/ l]	Mg [mg/ l]
Precipitation	0.71 ± 0.43	0.39 ± 0.28	0.07 ± 0.01
Throughfall			
Swietenia	1.48 ± 0.58	0.94 ± 0.38	0.14 ± 0.09
Carapa	1.31 ± 0.47	1.38 ± 0.75	0.49 ± 0.25
Stemflow			
Swietenia	11.11 ± 8.42	4.29 ± 2.64	0.76 ± 0.51
Carapa	5.50 ± 3.73	1.62 ± 0.73	0.65 ± 0.57

The element input in the plantation systems was compared to the specific K, Ca, and Mg demand of the planted tree species (Table 2). A very high demand for K and Ca was detected for *Swietenia* and *Carapa*, whereas the demand for Mg was in the same range as for timber tree species of temperate regions (comp. ZECH and POPP, 1983; ISERMANN, 1985; ZÖTTL, 1987; HÜTTL, 1991; RADEMACHER et al., 1992). Nevertheless, the Mg supply also might limit tree growth on these sites, due to the low Mg input in the plantations (comp. Table 1) and a restricted Mg supply of the soil (comp. Table 4 a-c). A higher demand for Ca and Mg was detected for *Carapa* compared to *Swietenia*, whereas the demand for K was reduced.

Table 2: Mean K, Ca, and Mg content per kg biomass [mg/ kg] of 5-year-old plantation-grown *Swietenia macrophylla* and *Carapa guianensis*.

Sample	K [mg/ kg]	Ca [mg/ kg]	Mg [mg/ kg]
Young leaves			
Swietenia	12813 ± 1508	14803 ± 5319	1264± 427
Carapa	7181 ± 948	13968 ± 3617	2882 ± 795
Old leaves			
Swietenia	6943 ± 1742	27755 ± 4719	1664 ± 918
Carapa	5319 ± 847	15306 ± 2992	2274 ± 518
Litterfall			
Swietenia	6092 ± 731	40282 ± 2764	1545 ± 410
Carapa	4656 ± 1078	17781 ± 5819	2141 ± 318

Within the plant, especially leaves are a strong sink for K, Ca, and Mg (Table 3, comp. also Table 2). Higher K- and Ca-contents were found in leaves of *Swietenia* compared to *Carapa*, whereas the Mg-content was reduced. The K-content of old leaves and litter of *Swietenia* and *Carapa* decreased compared to younger leaves, which indicates an "internal" recycling mechanism for K (comp. SCHMIDT et al., 1999). In contrast to that, a strong increase in the Ca-content of old leaves compared to young leaves was found, which indicates a translocation of Ca especially in older leaf tissue ("external recycling"). Highest Mg-contents were registered in young leaves of *Carapa*, whereas the Mg-content of older leaves was slightly reduced. In contrast to that, the Mg-content of older leaves of *Swietenia* increased compared to young leaves. This indicates a higher photosynthetic activity of young leaves of *Carapa* compared to *Swietenia*.

Table 3: K, Ca, and Mg content [mg/ kg] of young leaves, old leaves, and the litterfall of 5-year-old plantation-grown *Swietenia macrophylla* and *Carapa guianensis*.

Species	K [mg/ kg]	Ca [mg/ kg]	Mg [mg/ kg]
Swietenia	6493-6788-7065	6905-11099-12128	824-905-928
Carapa	5328-5735-5820	11759-12010-12063	1687-1753-1847

The element content of leaves and litter influences the nutrient cycles of plantation systems. Especially in tropical ecosystems, nutrient recycling *via* litterfall and litter decomposition is of main importance for sustainable plant nutrition (KLINGE, 1976; LAMPRECHT, 1986). Litter decomposition experiments showed that K decomposition is faster than the decomposition of Ca and Mg (Fig. 1a-f). After a period of 12 months in all three plantation systems, more than 90% of the K of the litterfall was decomposed and available for uptake by the vegetation (Fig. 1 a/ b). In contrast to that, only 25 to 88% of the Ca content of the litterfall (Fig. 1 c/ d) and 43 to 90% of the Mg content of the litterfall (Fig. 1 e/ f) were decomposed after a one-year-interval. In general, highest decomposition rates were detected in the plantation system III (enrichment system, except Mg decomposition), which indicates a more stabilized soil fauna in this plantation system (comp. BECK et al., 1998) compared to the plantation systems I (monoculture system) and II (mixed culture system). Comparative studies carried out in the primary forest showed that 100% of the K, Ca, and Mg content of the litter of *Swietenia* and *Carapa* are decomposed during a one-year-interval, which indicates that K, Ca, and Mg recycling via litterfall and litter decomposition is not completely balanced in the plantations. This was also the case for the 29-year-old secondary vegetation of plantation system III (comp. BECK et al., 1998). A comparison of the decomposition rates of *Swietenia* and *Carapa* litter showed that decomposition of K, Ca, and Mg from leaves of *Swietenia* is slightly faster compared to element decomposition of *Carapa* (Fig. 1a-f), which favours nutrient recycling in *Swietenia* plantations, but also raises the danger of nutrient loss (especially for K) caused by leaching of mineral elements out of the soil in these plantations (comp. Table 4 a-c).

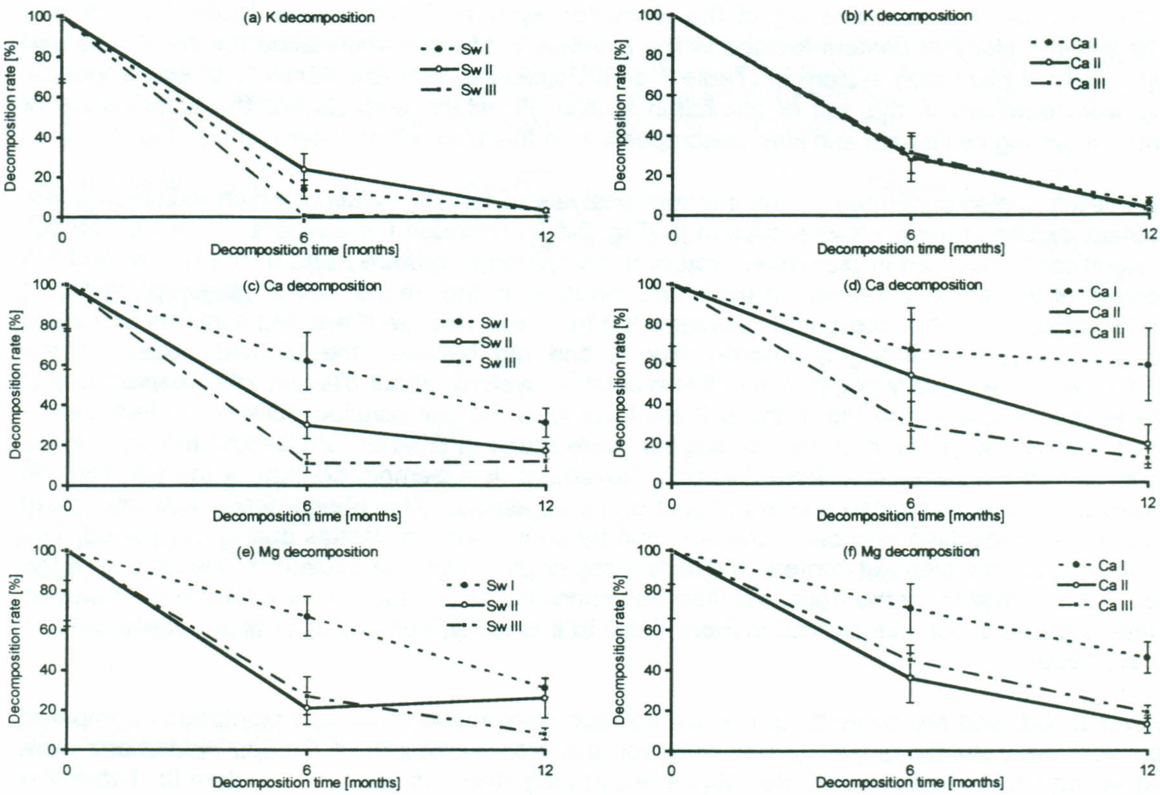


Fig. 1a-f: (a/ b) K, (c/ d) Ca, and (e/ f) Mg decomposition [%] of the litter of *Swietenia macrophylla* and *Carapa guianensis* after a period of 6 and 12 months in the plantation systems I, II, and III.

K, Ca, Mg balance and K, Ca, Mg stocks of three 5-year-old plantation systems

The K, Ca, and Mg supply of the trees was studied in terms of quantified input and output data and of the K, Ca, and Mg stocks within the plantation systems. From these investigations, it becomes obvious that in the 5-year-old monoculture system the K input and K output is not balanced (Table 4 a), which is mainly caused by high K and Mg leaching out of the soil and by high uptakes of Ca in *Swietenia* plantations. In *Carapa* monocultures, the imbalance of K, Ca, and Mg input and output is mainly caused by the high element uptake of this species. This indicates a better absorption capacity for mineral elements of *Carapa guianensis* compared to *Swietenia macrophylla*. In the 5-year-old mixed culture system (plantation system II), a slight K, Ca, and Mg deficit was detected which was mainly caused by the element leaching out of the soil (Table 4 b). The uptake of K, Ca, and Mg of the planted trees and the spontaneous vegetation is fairly low, caused by a low growth rate and a low biomass production in this plantation system (comp. PREISINGER et al., 1994; AZEVEDO et al., 1999). In the enrichment system (system III), the K output also exceeds the K input (Table 4 c), but a surplus of Ca input and a stabilized Mg balance was found (Table 4 c). This indicates that in all three plantation systems, the K input and K output are not stabilized. Without fertilization, a future impoverishment of the soil is to be expected. A strong reduction of the Ca and Mg stocks of the soil are very likely in plantation system I, as well (Table 4 a), whereas especially the enrichment system (system III) seems to be more stabilized, especially with regard to the Ca and the Mg supply (Table 4 c). As a consequence, a reduction of the K stock of the soil was observed in the plantation systems during the first years, especially in plantation system I (data not published here, comp. DÜNISCH et al., 1998). Although a strong imbalance of K, Ca, Mg input and output was detected in plantation system I, the total K, Ca, and Mg content of the plantation system was higher (comp., *Swietenia* plantation I, II, *Carapa* plantation I-III) or at least in the same range as in the plantation systems II and III (comp., *Swietenia* plantation I, II; Table 4 a-c). The lowest element stocks were found in the 5-year-old plantation system II, which indicates a low productivity of this plantation system. This shows that, due to the high element output of the soil in system I, at this stage, it could not be predicted how far sustainable growth is possible in the monoculture system.

High amounts of K, Ca, and Mg of the plantation systems I and II were located in the soil, whereas the element content located in the biomass is of main importance for the K, Ca, and Mg supply of plantation system III (Table 4 a-c). Especially, very low contents of exchangeable Mg were detected in the soil of plantation system III, which emphasizes the significance of nutrient cycling by litterfall and litter decomposition in this plantation system (comp. Fig. 1 a-f).

This result is also confirmed by the element analysis of the soil solution, which indicates a fast nutrient cycling in the plantation system III (Fig. 2 a-f). Although the element content of the soil is significantly reduced in plantation system III compared to system I and II, the K, Ca, and Mg content of the soil solution was in the same range as in the "fertile" soil of plantation system I and significantly higher compared to system II (Fig. 2 a-f). The low K and Mg contents of the soil solution indicate a strong competition for K and Mg between the planted trees and the spontaneous secondary vegetation in this plantation system (about 5% and 25% respectively of the exchangeable K and Mg of the soil are located in the soil solution). Distinct differences in the chemical composition of the soil solution were found in different soil depths throughout the year. During the dry season from July until November, the element content of the soil solution increased due to a reduced nutrient uptake of the vegetation. This phenomenon was intensified by a reduced leaching rate out of the soil, and by an increase in litterfall during this period. The differences of the element content in different soil depths might be caused by the texture of the soil, the root system of the trees, the litter decomposition in the top soil, and leaching. However, these issues are not investigated in more detail in this study (comp. ZECH et al., 1998; NOLDT et al., 1999).

Lower K, Ca, and Mg contents of the soil solution were found in *Carapa* plantations compared to *Swietenia* plantations (Fig. 2 a-f), although the element stocks of *Carapa* plantations were higher, compared to *Swietenia* plantations (except Mg stocks in plantation system III; Table 4 a-c). This indicates that the stabilization of the K, Ca, and Mg stocks of plantations is more favoured by *Carapa* than by *Swietenia*.

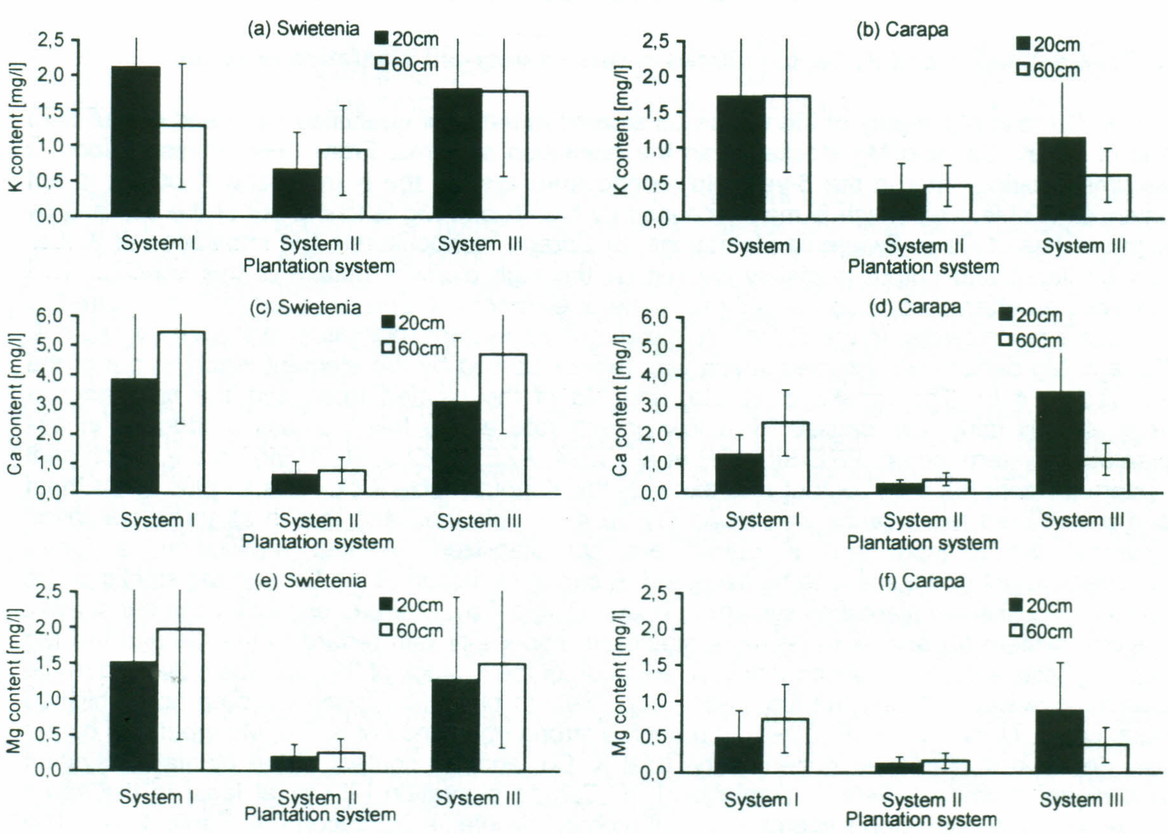


Fig. 2a-f: Mean (a/ b) K, (c/ d) Ca, and (e/ f) Mg content of the soil solution [mg/ l] of the year 1997 (n=43 - 50) of *Swietenia macrophylla* and *Carapa guianensis* in soil depths of 20 and 60 cm. Plantation systems I, II, and III.

Table 4a-c: K, Ca, and Mg input and output [g/ 10 m²] of 5-year-old plantations of *Swietenia macrophylla* and *Carapa guianensis*, K, Ca, and Mg content of the soil (soil depth 0 - 80 cm; NH_4Cl exchangeable element content/ total element content [g/ 10 m²]), and K, Ca, and Mg content of the vegetation [g/ 10 m²]. Plantation systems (a) I, (b) II, and (c) III.

Plantation system I	*Swietenia*			*Carapa*		
Sample	K [g/ 10 m²]	Ca [g/ 10 m²]	Mg [g/ 10 m²]	K [g/ 10 m²]	Ca [g/ 10 m²]	Mg [g/ 10 m²]
Input/ Output (1996)						
Input	108	126	38	30	113	40
Uptake planted trees	231	318	48	299	614	118
Uptake spontaneous vegetation	61	12	3	71	24	6
Leaching out of the soil	214	148	61	85	60	41
Input – Output	- 398	- 352	- 74	- 525	- 585	- 125
Element content of the soil (0 – 80 cm)	416/ 639	234/ 540	110/584	443/659	218/419	178/862
Element content of the vegetation	233	278	39	398	1083	149
Total element content	872	818	623	1057	1502	1011

Plantation system II	*Swietenia*			*Carapa*		
Sample	K [g/ 10 m²]	Ca [g/ 10 m²]	Mg [g/ 10 m²]	K [g/ 10 m²]	Ca [g/ 10 m²]	Mg [g/ 10 m²]
Input/ Output (1996)						
Input	42	15	2	43	17	3
Uptake planted trees	9	9	2	8	13	5
Uptake spontaneous vegetation	16	7	2	14	7	2
Leaching out of the soil	39	10	4	45	9	3
Input – Output	- 22	- 11	- 2	- 24	- 12	-7
Element content of the soil (0 – 80 cm)	434/478	65/333	26/40	432/483	67/345	25/40
Element content of the vegetation	131	113	48	195	178	63
Total element content	609	446	88	678	523	103

Plantation system III	*Swietenia*			*Carapa*		
Sample	K [g/ 10 m²]	Ca [g/ 10 m²]	Mg [g/ 10 m²]	K [g/ 10 m²]	Ca [g/ 10 m²]	Mg [g/ 10 m²]
Input/ Output (1996)						
Input	51	83	15	45	91	16
Uptake planted trees	10	17	4	51	26	16
Uptake spontaneous vegetation	19	15	6	- 18	- 21	- 5
Leaching out of the soil	81	11	3	44	3	1
Input – Output	- 59	40	2	- 32	83	4
Element content of the soil (0 – 80 cm)	297/355	43/124	22/400	297/357	41/118	23/318
Element content of the vegetation	475	707	273	526	812	308
Total element content	830	831	673	883	930	626

Discussion

The mineral element supply (e. g. K, Mg, P) is a growth limiting factor in many areas of the Central Amazon (KLINGE, 1976; SANCHEZ et al., 1982; LAMPRECHT, 1986; BRÜNIG, 1996) due to the low element content of the soil and low element input by wet and dry deposition. Therefore, the role of the vegetation for the element cycling in this area is emphasized in many field studies (JORDAN, 1982; WHITMORE, 1995; FERNANDES et al., 1997). As shown in this study, high amounts of K and Mg leached out of the crown of *Swietenia* and *Carapa*, but litterfall and litter decomposition were more important for the nutrient cycling of the trees. Litter decomposition was more stabilized in the enrichment system, which shows that the soil fauna and the microclimatic conditions (comp. DÜNISCH et al., 1999a) influence the nutrient cycling of plantations significantly. On the one hand, the high decomposition rate detected for K favours the nutrient cycling especially of *Swietenia* due to the high K demand of *Swietenia* trees. On the other hand, fast K decomposition raises the danger of fast K leaching out of the soil due to the high precipitation in this region. Especially in *Swietenia* monocultures, high percentages of K leaching out of the soil were found due to the seasonal growth dynamics of this species (comp. DÜNISCH et al., 1999b). In contrast to the demand for K, a high Mg demand was found for *Carapa* compared to *Swietenia,* which indicates a high photosynthetic activity of *Carapa* compared to *Swietenia* (KÜPPERS et al., 1985). This is also confirmed by the higher biomass production of *Carapa* compared to *Swietenia*. The translocation of K from older to younger leaves was more pronounced in *Swietenia*, whereas a corresponding translocation of Mg was more pronounced in *Carapa* ("internal recycling", comp. SCHMIDT et al., 1999). This indicates that tree growth of *Swietenia* is strongly limited by the K supply, whereas tree growth of *Carapa* seems to be more influenced by the Mg supply of the plantation systems (comp. ÅGREN, 1985; INGESTAD, 1987).

The comparison of the K, Ca, and Mg supply of three plantation systems (monoculture, mixed culture, enrichment of a secondary forest) of the same age showed that the element supply of the trees can be stabilized by management practices such as density of the plants and vertical structure of the plantation (comp. LAMPRECHT, 1986; BRÜNIG, 1996). During the initial phase of *Swietenia* plantations, high leaching rates out of the soil were found especially for the very mobile element K. In order to counteract this tendency, a higher plant density is proposed at the beginning of *Swietenia* plantations. An enrichment of a secondary vegetation with *Swietenia* does not seem to be very promising due to the strong competition of the secondary vegetation to the K uptake of *Swietenia* trees (comp. PREISINGER et al., 1994; AZEVEDO et al., 1999). Higher K, Ca, and Mg uptake was found for *Carapa* compared to *Swietenia*, which indicates that *Carapa* favours the stabilization of the K, Ca, and Mg stocks of younger plantations and reduces element loss due to element leaching out of the soil.

Although high amounts of K, Ca and Mg are stored in the biomass of the enrichment system (system III) and despite the reduction of element leaching out of the soil compared to the monoculture (system I) and mixed culture system (system II), at this stage it could not be predicted in how far sustainable growth is also possible in the monoculture systems due to the relatively high K, Ca, and Mg content of the soil. Therefore, time series analyses are necessary to compare the plantation systems in the long run with regard to sustainability (comp. ULRICH, 1981; DRECHSEL and ZECH, 1991).

These investigations pointed out that the K, Ca, and Mg supply of tree species with similar wood characteristics (comp. GOTTWALD, 1961; DÜNISCH et al., 1999b) can significantly differ. Consequently, the selection of suitable tree species for high quality timber production in plantation systems is of main importance for the sustainability of the K, Ca, and Mg supply of the plantations.

References

ÅGREN, G. I.: Theory for growth of plants derived from the nitrogen productivity concept. Physiol. Plant, 64 (1985) 17 - 28.

AZEVEDO, C. P. de; LIMA, R. M. B. de; NEVES, E. J. M.; GASPAROTTO, L.; DÜNISCH, O.: Development of tree height and diameter of eight selected tree species under plantation conditions in Central Amazonia. BFH Mitteilungen Nr. 193 (1999) 17 – 28.

BAUCH, J.: Mineralelementversorgung von Nadelbäumen und ihre Bedeutung für das Wachstum. Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Nr. 172 (1993) 75 - 84.

BECK, L.; GASPAROTTO, L.; FÖRSTER, B.; FRANKLIN, E.; GARCIA, M.; HARADA, A.; HÖFER, H.; LUIZÃO, F.; LUIZÃO, R.; MARTIUS, C.; MORAIS, J. W. de; OLIVEIRA, E.; RÖMBKE, J.: The role of soil fauna in litter decomposition in primary forests, secondary forests, and a polyculture plantation in Amazonia – methodical considerations. LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop Manaus, March 15 – 19 (1998) 11 p.

BERNEIKE, W.; SCHÖNBURG, M.; WEITKAMP, C.; MICHAELIS, W.; RADEMACHER, P.; BAUCH, J.: Optische Emissionsspektroskopie mit induktiv geheizter Argonplasmafackel: ein wichtiges Verfahren zur Bestimmung von Nähr- und Schadelementen in Fichten. In: Vorschritte in der atomspektrometrischen Analytik, VCH Verlagsgesellschaft Weinheim, 1985, 505 - 513.

BREDEMEIER, M.: Stoffbilanzen, interne Protonenproduction und Gesamtsäurebelastung des Bodens in verschiedenen Waldökosystemen Norddeutschlands. Ber. Forschungszentrum Waldökosysteme der Universität Göttingen 33, 1987, 183 p.

BRÜNIG, E. F.: Conservation and management of tropical rainforests. An integrated approach to sustainability. CAB International, Wallingford, 1996, 339.

DAHMS, K. G.: Das Holzportrait: echtes oder amerikanisches Mahagoni (*Swietenia macrophylla* King, Familie Meliaceen). Holz als Roh- und Werkstoff, 47 (1989) 1 – 6.

DRECHSEL, P., ZECH, W.: Foliar nutrient levels of broad-leaved tropical trees.: A tabular review. Plant and Soil, 131 (1991) 29 - 46.

DÜNISCH, O.; BAUCH, J.: Influence of water and mineral elements on wood formation of spruce (Picea abies [L.] Karst.) under controlled conditions. Holzforschung, 49 (1995) 9 - 15.

DÜNISCH, O.; BAUCH, J., GASPAROTTO, L.; NEVES, E.; AZEVEDO, C. de; LIMA, R. de; MORAIS, R. de: Environment-tree growth relationships of plantation-grown tropical tree species as a basis for sustainable timber production in mixed culture systems in Central Amazonia. LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop Manaus, March 15 – 19 (1998) 13 p.

DÜNISCH, O.; SCHROTH, G.; MORAIS, R. de; ERBREICH, M.: Water supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in three plantation systems. BFH Mitteilungen Nr. 193 (1999a) 29 – 45.

DÜNISCH, O.; BAUCH, J.; SACK, M.; MÜLLER, M.: Growth dynamics in wood formation of plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl., BFH Mitteilungen Nr. 193 (1999b) 79 - 96.

FEARNSIDE, P. M.: Agroforestry in Brazil's Amazonian development policy: The role and limits of a potential use for degraded lands. In: CLUSENER-GOOD, M.; SACHS, I. (eds.): Brazilian perspectives on sustainable development of the Amazonian region. Oxford University Press, Oxford, 1995, 311.

FERNANDES, E. C. M.; BIOT, Y.; CASTILLA, C.; ACILINO, C. C.; MATOS, J. C.; GARCIA, S.; PERIN, R.; WANDERLI, E.: The impact of selective logging and forest conversion for subsistence agriculture and pastures on terrestrial nutrient dynamics in the Amazon. Ciencia e Cultura, 1997, 34 p.

GOTTWALD, H.: Handelshölzer. Ferdinand Holzmann Verlag, Hamburg, 1961, 249 p.

HÜTTL, R. F.: Die Nährelementversorgung geschädigter Wälder in Europa und Nordamerika. Freiburger Bodenkundliche Abhandlungen, 28 (1991) 440.

INGESTAD, T.: New concepts on soil fertility and plant nutrition as illustrated by forest trees and stands. Geoderma, 40 (1987) 237 - 252.

ISERMANN, K.: Diagnose und Therapie der neuartigen Waldschäden aus der Sicht der Waldernährung. VDI Berichte, VDI Verlag, Düsseldorf, 560 (1985) 897 - 920.

JORDAN, C. F.: The nutrient balance of an Amazonian rain forest. Ecology, 63 (1982) 647 - 654.

KLINGE, H.: Bilanzierung von Hauptnährstoffen im Ökosystem tropischer Regenwald (Manaus). Bibliographica (Neotropische Ökosysteme), 7 (1976) 59 - 77.

KÖNIG, N.; FORTMANN, H.: Probenvorbereitungs-, Untersuchungs- und Elementbestimmungs-Methoden des Umweltanalytik-Labors der Niedersächsischen Forstlichen Versuchsanstalt und des Zentrallabors II des Forschungszentrums Waldökosysteme. Band 46 (1996) 26 p.

KOZLOWSKI, T. T., KRAMER, P. J., PALLARDY, S. G.: The physiological ecology of woody plants. Academic Press San Diego, New York, 1991, 657 p.

KÜPPERS, M., ZECH, W.; SCHULZE, E. D.; BECK, E.: CO_2-Assimilation, Transpiration und Wachstum von Pinus silvestris L. bei unterschiedlicher Magnesiumversorgung. Forstw. Cbl., 104 (1985) 23 - 36.

LAMPRECHT, H.: Waldbau in den Tropen. Verlag Paul Parey, Hamburg, Berlin, 1986, 318 p.

LARSON, P. R.: Assessing wood quality of fertilized coniferous trees. Forest fertilization symposium Gainsville, (1967) 275 - 280.

LARSON, P. R.: Wood formation and the concept of wood quality. New Haven, Yale University: School of Forestry, Bulletin No. 74, 1969.

LARSON, P. R.: The vascular cambium. Springer Verlag, Berlin, 1995, 725 p.

LIEBEREI, R.; GASPAROTTO, L.: Agroecological profile of plants used as production factors and as management components in tropical polyculture systems. LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop Manaus, March 15 – 19 (1998) 9 p.

MARSCHNER, H.: Mineral nutrition of higher plants. Academic Press London, New York, 1995, 889 p.

NOLDT, G.; BAUCH, J.; SCHMITT, U.; BALODIS, V. G.: Structure of primary roots of *Swietenia macrophylla* King under controlled conditions. BFH Mitteilungen Nr. 193 (1999) 107 - 112.

PREISINGER, H.; COELHO, L. F.; SOCORRO, M.; SIQUEIRA, G.; LIEBEREI, R.: Analysis of growth form type sand floristic composition of the spontaneous vegetation in an agricultural test area near Manaus, Brazil. Angewandte Botanik, 68 (1994) 40 – 46.

RADEMACHER, P.; BAUCH, J.; MICHAELIS, W.: Bilanzierung der Elementvorräte und Elementflüsse innerhalb der Bestandeskompartimente Krone, Stamm, Wurzel und Boden eines belasteten Fichtenbestandes am Standort „Postturm". In: Luftverunreinigungen und Waldschäden am Standort „Postturm", Forstamt Farchau/ Ratzeburg. (Hrsg. W. MICHAELIS, J. BAUCH), GKSS 92/ E/ 100, (1992) 187 - 211.

SCHMIDT, P.; LIEBEREI, R.; BAUCH, J.; GASPAROTTO, L.: Biomass production and mineral element content of *Swietenia macrophylla* King in the juvenile phase under plantation conditions in Central Amazonia. BFH Mitteilungen Nr. 193 (1999) 61 - 70.

ULRICH, B.: Destabilisierung von Waldökosystemen durch Akkumulation von Luftverunreinigungen. Der Forst- und Holzwirt, 36 (1981) 525 - 532.

WAGENFÜHR, R.; SCHEIBER, C.: Holzatlas. VEB Fachbuchverlag, Leipzig, 1985, 334 p.

WARDROP, A. B.: Lignification and xylogenesis. In: Xylem cell development (ed. BARNETT, J.R.) Castle House Publ. Ltd., London, (1981) 115 - 152.

WESTERMARK, U.: Calcium promoted phenolic coupling by superoxide radical - a possible lignification reaction in wood. Wood Sci. Technol., 16 (1982) 71 - 78.

WHITMORE, T. C.: Tropische Regenwälder. Spektrum Akad. Verlag, Heidelberg, 1995, 275 p.

ZECH, W.; POPP, E.: Mg-Mangel, einer der Gründe für das Fichten und Tannensterben in NO-Bayern. Forstw. Cbl., 102 (1983) 50 - 55.

ZECH, W.; SCHROTH, G.; CRAVO, M. da S.; TEIXEIRA, W. G.; KAISER, K.; LEHMANN, J.: Water and nutrient fluxes as indicators for the sustainability of different land-use systems on the terra firme near Manaus – a project review. LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop Manaus, March 15 - 19 (1998) 6 p.

ZÖTTL, H. W.: Nährelementversorgung mitteleuropäischer Wirtschaftswälder. In: Möglichkeiten und Grenzen der Sanierung immissionsgeschädigter Waldökosysteme (Hrsg. GLATZEL, G.) FIW Wien, (1987) 54 - 64.

Acknowledgements

We thank the "Bundesministerium für Bildung, Wissenschaft, Forschung, und Technologie", the DLR, Bonn, Germany and the CNPq/ IBAMA, Brasilia, Brazil for financial support within the German-Brazilian cooperation program SHIFT (Studies on Human Impacts on Forests and Floodplains in the Tropics). We also wish to thank L. Coelho and Dr. H. Preisinger for the vegetation analyses. The assistance of V. Seabra and A. Souza is especially appreciated.

Biomass production and mineral element content of *Swietenia macrophylla* King in the juvenile phase under plantation conditions in Central Amazonia

P. Schmidt,[1] R. Lieberei,[1] J. Bauch,[2] and L. Gasparotto[3]

[1] Institute of Applied Botany, Hamburg University
[2] Institute of Wood Biology, Hamburg University
[3] EMBRAPA Amazônia Ocidental, Manaus, AM, Brazil

Summary

The experimental study was carried out in order to evaluate in which way a sustainable growth of mixed plantation systems under the prevailing site conditions is possible. For this reason, the biomass production and the mineral element supply of six 2½-year-old plants of the high-quality wood species *Swietenia macrophylla* King including roots were determined. Up to twelve fractions (leaves, wood, bark, etc.) were separated and the element content (Ca, Mg, K, P, S, Fe, Al) of the different tissues was determined by Optical Emission Spectrometry (ICP-OES). The fractions allowed a high differentiation of the element content and can reveal physiological sinks within the plants. Parallel to this, the availability of nutrient elements in the soil was analyzed. As potassium is continuously transported from old to young leaves, this mineral element is „internally recycled". However, Ca accumulates in the old leaves and will, therefore, follow an „external recycling". The elements Al and Fe can be blocked in the cortex of the fine roots. The high demand for Ca, K, and P in the plant underlines that in the long run, a specific fertilization will be an urgent need, in order to guarantee a sustainable growth for high-quality timber trees. The low alkaline saturation of the soil and the low concentration of nutrient elements in the soil, which can only be improved immediately after burning for some months, reflect this insufficient nutrient supply.

Resumo

Produção de biomassa e o teor de elementos minerais de *Swietenia macrophylla* King na fase juvenil sob condições de plantio da Amazônia Central

Este estudo foi feito com o objetivo de avaliar de que maneira é possivel obter um crescimento sustentável de sistemas de plantio mistos sob determinadas condições locais. Para tal fim, foram determinados a produção de biomassa e o teor de elementos minerais de seis plantas de Mogno (*Swietenia macrophylla* King), espécie produtora de madeira nobre, com 2 anos e meio de idade. Paralelamente analisou-se a disponibilidade de nutrientes no solo. As plantas foram repartidas em até 12 frações (folhas, madeira, casca, raízes, etc.) e o teor dos elementos minerais Ca, Mg, K, P, S, Fe e Al foi determinado através de um Espectrômetro de Emissão Ótica (ICP-OES). As diversas frações mostraram uma grande diversidade com respeito ao teor de elementos minerais, o que implica a formação de determinados "depósitos fisiológicos" em locais determinados na planta.

Como Potássio (K) é transportado contínuamente das folhas velhas para as folhas novas, pode-se dizer que este elemento parece sujeito a uma "reciclagem interna". Por outro lado, Cálcio (Ca) tende a acumular-se nas folhas velhas, indicando uma "reciclagem externa". Os elementos Alumínio (Al) e Ferro (Fe) encontraram-se retidos localmente no córtex das raízes finas.

A alta demanda por Ca, K e P nas plantas mostra que, a largo prazo, uma fertilização específica torna-se imprescindível para garantir um crescimento sustentável de árvores produtoras de madeira nobre sob um regime de plantio. A baixa saturação alcalina e as reduzidas concentrações de elementos minerais no solo, que aumentam apenas por alguns meses após a queima, refletem esta insuficiência geral de elementos minerais no solo.

Introduction

Agroforestry systems with different native plant species seem to be a solution for a sustainable agriculture in the Amazon region – a region with extreme site conditions, where a high percentage of primary forest still is slashed and burned. Large areas are lost due to inexperienced non-site adapted agriculture. Furthermore, the knowledge about most of the native plants from the Amazon region, which potentially can be used for sustainable agroforestry systems, is still very low.

The aim of this study was to gain fundamental data on *Swietenia macrophylla* King, a highly valuable timber species, which may allow an evaluation, in which way a sustainable growth of this species in a suggested plant system is possible under the prevailing site conditions. In this respect, the biomass production and the mineral element supply of 2½-year-old plants of *Swietenia macrophylla* were determined. The plants were separated into different tissue fractions to allow a distinct differentiation in element content and to reveal physiological sinks within the plants.

The soils in the Amazon region are known to be very acid and poor in nutrients, a very important aspect for agroforestry systems containing tree species which already implicates a long-term use. For this reason, parallel to the biomass and element content studies of the plants, the effect of slash and burn, a common form of land clearing in this region, on the availability of nutrient elements in the soil was analysed.

Material and Methods

Swietenia macrophylla King, a mahogany species, which belongs to the *Meliaceae*, was chosen, because of its high economic value on the Brazilian wood market and particularly in export markets (Fig. 1). Depending on the prevailing site conditions, adult trees can reach a height between 24 and 50 metres and diameters from 0.5 to 2.5 metres (DAHMS, 1993). Because of its excellent manufacturing qualities and very good resistance against different weather conditions, the wood of *S. macrophylla* is considered to be among the best on the world market, and it can be used in a wide range.

The extraction of whole plants out of the experimental field (comp. DÜNISCH et al., 1999) would have caused extreme disturbances in the single systems. Therefore, it was inevitable to establish a reference area where plants, roots included, could be taken out for total biomass and element content determination. For a good comparison, this reference area bordered directly to the experimental field. Together with the experimental area, it was slashed and burned and, like four other species, *Swietenia macrophylla* was planted in rows and treated like the *Swietenia* plants in the experimental plots.

At an age of approximately 2½ years, six of these 28 plants grown from collected seeds from primary stands were sampled after measuring height and diameter of all of them. The total biomass of each plant including the roots was determined gravimetrically. Up to 12 fractions (young leaves, old leaves, wood, bark, roots etc.) were separated and prepared in association of a methodology from RADEMACHER (1986). The kiln-dry plant material was powdered in a mill (Retsch Zentrifugalmühle 82219) and with a microwave (MLS 1200), 500 mg of each sample was brought into solution with HNO_3. The element content (Ca, Mg, K, P, S, Fe, Al) in these solutions of the different plant tissues was determined by Optical Emission Spectrometry (ICP-OES). N was analyzed by Micro-Kjeldal. For the evaluation in which way a sustainable growth of this species in a suggested plant system under the prevailing site conditions is possible, some tissues of a 15-year-old *S. macrophylla* plant were analyzed equally.

Parallel to this, the availability of nutrient elements in the soil was analyzed before slash-and-burn, directly after burning and six months after. Therefore, soil samples in a depth down to 15 cm were taken, and the element content (Ca, Mg, K, P, S, Fe, and Al) in the water-soil solutions was determined by Optical Emission Spectrometry (ICP-OES).

Fig. 1: a) 2½-year-old plant with a height of ca. 2 metres and a diameter of approximately 4 – 8 cm.
b) Ca. 15-year-old *Swietenia* plant with good annual increment.
c) Fruit with fertile seeds for later natural regeneration.
d) Wood of an adult plant with high quality for veneer production.

Results

Biomass production

At an age of 2½ years, the six plants had reached a height between 1.31 and 2.75 metres and diameters between 2.9 and 6 cm (Table 1), which does not differ much from the averages of 2 metres respectively 4 cm of all 28 measured *Swietenia* plants.

The total biomass (dry weight) amounted to the average 1.75 kg with a range between 0.91 kg and 3.24 kg. This high variation between the six plants examined may be due to the fact that all of the trees were to a higher or lesser degree infected with *Hypsipyla grandella*, which causes great damage to the biomass production. Nevertheless, the results showed that with an average of nearly 64%, most of the biomass in these young plants was already fixed in the stem, while almost 21% was taken from the roots and only 15% was covered by the leaves.

Table 1: Tree height, diameter 20 cm above ground, and biomass dry weight of different plant fractions of 2½-year-old *Swietenia macrophylla* plants

Tree-number	Height [m]	Diameter in 20 cm height [cm]	Biomass dry weight						
			Roots [kg]	Roots [%]	Leaves [kg]	Leaves [%]	Stem [kg]	Stem [%]	Total plant [kg]
2	2.75	6.0	0.69	21.3	0.32	10.0	2.23	68.7	3.2
6	1.31	3.5	0.20	20.8	0.15	15.4	0.61	63.8	1.0
11	1.70	3.6	0.21	22.5	0.07	8.0	0.64	69.5	0.9
18	2.40	5.7	0.65	22.4	0.14	4.9	2.11	72.7	2.9
22	2.02	3.5	0.18	15.4	0.45	39.3	0.52	45.3	1.2
26	1.78	2.9	0.32	23.7	0.21	15.5	0.83	60.8	1.4
$\bar{x}$ n = 6	1.99 ± 0.52	4.20 ± 1.31	-----	21.02 ± 2.93	-----	15.52 ± 12.37	-----	63.47 ± 9.86	1.77 ± 1.01

Element analyses

The results of the total element content determination demonstrated high values of all elements and a high range of each element between the six *Swietenia* plants. While iron only showed small variations of approximately 29% of the average, phosphorus displays variations of the average of around 57%, potassium around 62%, sulphur and aluminium around 67%, magnesium over 85% and calcium 87%. But as regards the single elements in each plant, it can be clearly demonstrated that the tendencies of element accumulation in the different plant tissues are the same in all six plants.

In all 2½-year-old *Swietenia* plants, calcium for example had the highest rate in each total biomass dry weight with values between 0.48% and 1.22%. For the six trees, 53% up to 90% of the total calcium content was found in the leaf tissues of each plant.

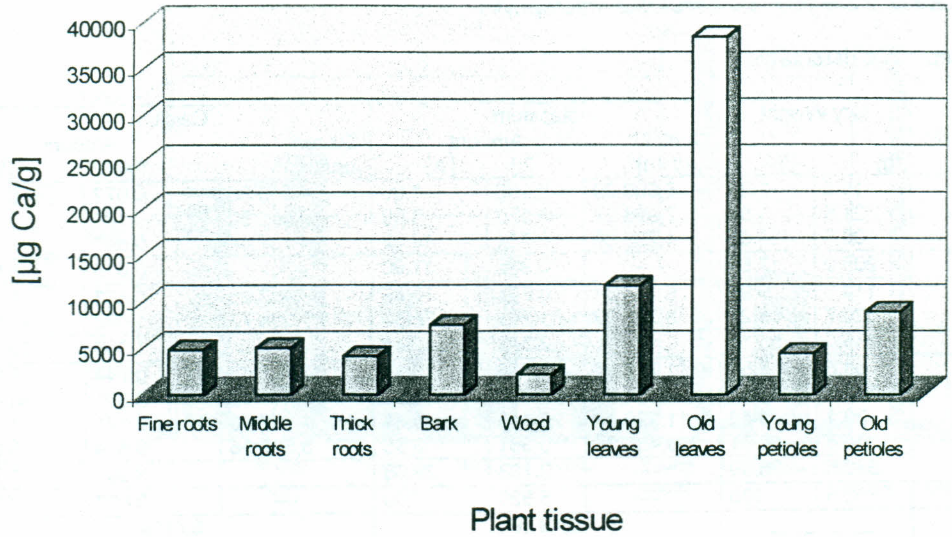


Fig. 2: Absolute calcium content in different plant tissues of an approx. 2½-year-old plant of *Swietenia macrophylla*

The relationship between biomass, element content per gram dry weight, and total element content, demonstrated in Table 2 with the data of one plant as an example, showed that physiological sinks within the plant essentially determine the growth of the plant. This can be demonstrated in particular by the Ca-content per gram dry weight of the old leaves (Fig. 2). The old leaves contain a biomass of only 12.5% of the total plant, but accumulate 56% of the total Ca-content of the plant (compare also Table 2).

Another example of the dependency of the plant growth from physiological sinks within the plant can be demonstrated by the results of potassium contents in the *Swietenia* plants. Potassium, after calcium, was found out to be the element with the highest values in the dry plant biomass with percentages between 0.3% and 0.57%. The total element contents of the different plant tissues (Table 2) demonstrate that with values between 5,000 ppm and 30,000 ppm, the highest potassium contents are found in the young leaf tissues (young leaves, young petioles). Compared with the absolute element contents of the other plant fractions, it can be shown that this species revealed a very intensive internal exchange for K from the old to the young leaves (Fig. 3).

Table 2: Quantitative determination of the biomass and element content of potassium, calcium, magnesium, phosphorus, sulphur, iron, and aluminium per g dry weight and average element content of a 2½-year-old *Swietenia macrophylla*

n. det. = not detectable

Plant fraction	Dry Weight		Potassium			Calcium		
			Content	Amount		Content	Amount	
	[g]	[%]	[µg/ kg]	[g]	[%]	[µg/ kg]	[g]	[%]
Fine roots	15.0	1.30	6,990.00	0.105	1.90	4,780.00	0.072	0.73
Middle sized roots	21.5	1.87	7,923.27	0.170	3.08	5,055.60	0.109	1.11
Thick roots	108.5	14.65	4,238.60	0.714	12.92	4,137.44	0.697	7.11
Σ Roots	205.0	17.82	—	0.989	17.90	—	0.878	8.95
Bark	114.3	9.93	5,256.34	0.601	10.87	7,462.58	0.853	8.70
Wood	520.7	45.26	3,352.32	1.746	31.57	2,084.72	1.086	11.07
Σ Stem	635.0	55.19		2.346	42.44	—	1.938	19.77
Young leaves	63.6	5.53	11,716.57	0.745	13.48	11,701.65	0.744	7.59
Old leaves	143.2	12.45	4,564.08	0.654	11.82	38,411.18	5.501	56.09
Young petioles	39.1	3.40	11,330.34	0.443	8.01	4,377.40	0.171	1.74
Old petioles	64.6	5.61	5,437.35	0.351	6.35	8,892.38	0.574	5.86
Σ Leaves	310.5	26.99	—	2.193	39.66	—	6.991	71.28
Σ Total plant	1,150.5	100	—	5.529	100	—	9.807	100
Average element content of the plant	———		0,48 %			0.85%		

Plant fraction	Magnesium			Phosphorus			Sulphur		
	Content	Amount		Content	Amount		Content	Amount	
	[µg/ kg]	[g]	[%]	[µg/ kg]	[g]	[%]	[µg/ kg]	[g]	[%]
Fine roots	935.00	0.014	1.09	498.00	0.007	0.85	881.00	0.01	1.43
Middle sized roots	914.47	0.020	1.53	453.52	0.010	1.11	698.86	0.015	1.62
Thick roots	374.29	0.063	4.91	221.54	0.037	4.24	347.99	0.059	6.34
Σ Roots	—	0.097	7.53	—	0.055	6.19	—	0.087	9.39
Bark	1,565.72	0.179	13.93	967.90	0.111	12.55	775.74	0.089	9.58
Wood	409.61	0.213	16.60	742.75	0.387	43.89	339.42	0.177	19.10
Σ Stem	—	0.392	30.53	—	0.497	56.45	—	0.265	28.68
Young leaves	1,840.69	0.117	9.11	1,327.89	0.084	9.58	2,124.94	0.135	14.60
Old leaves	2,919.14	0.418	32.54	1,028.52	0.147	16.72	2,631.78	0.377	40.72
Young petioles	1,229.54	0.048	3.74	1,688.21	0.066	7.49	494.72	0.019	2.09
Old petioles	3,292.40	0.213	16.55	487.70	0.032	3.58	647.94	0.042	4.52
Σ Leaves	—	0.796	61.94	—	0.329	37.36	—	0.57324	61.94
Σ Total plant	—	1.285	100	—	0.9	100	—	0.9	100
Average element content of the plant	0.11%			0.08%			0.08%		

Plant fraction	Iron			Aluminium		
	Content	Amount		Content	Amount	
	[µg/ kg]	[g]	[%]	[µg/ kg]	[g]	[%]
Fine roots	522.00	0.008	16.52	3,880.00	0.058	31.77
Middle sized roots	385.54	0.008	17.48	2,549.04	0.055	29.92
Thick roots	50.28	0.008	17.87	294.38	0.050	27.08
Σ Roots	—	0.025	51.87	—	0.163	88.76
Bark	38.33	0.004	9.24	n. det.	n. det.	n. det.
Wood	6.09	0.003	6.69	n. det.	n. det.	n. det.
Σ Stem	—	0.008	15.93	—	0.000	0.00
Young leaves	56.00	0.004	7.51	47.25	0.003	1.64
Old leaves	63.61	0.009	19.21	76.51	0.011	5.98
Young petioles	26.67	0.001	2.20	63.63	0.002	1.36
Old petioles	24.05	0.002	3.28	63.99	0.004	2.26
Σ Leaves	—	0.015	32.20	—	0.02058	11.24
Σ Total plant	—	0.05	100	—	0.2	100
Average element content of the plant	0.004%			0.02%		

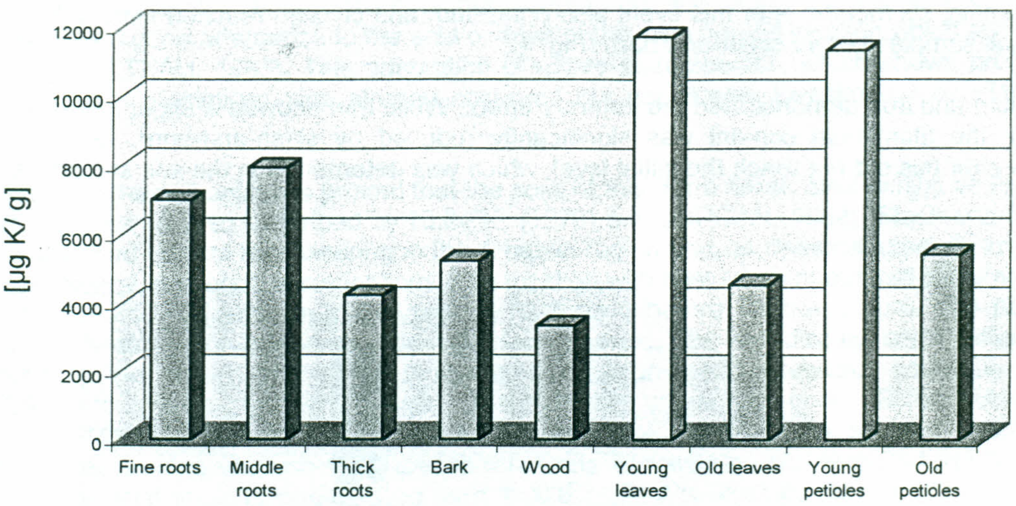


Fig. 3: Absolute potassium content in different plant tissues of a 2½-year-old plant of *Swietenia macrophylla*

Table 2 reveals for Ca, as well as for Mg, the highest element contents in old leaves. In total, 61.94% of Mg is located in the leaves. Also for P and S, the trend to maximum concentrations in old leaves is obvious.

Referring to the absolute aluminium and iron contents in the different plant fractions, it can be demonstrated that *Swietenia macrophylla* shows protection barriers in the roots against these toxic elements. (Table 2) While the fine roots accumulated up to 3,880 ppm aluminium, this value was reduced to contents between 240 ppm – 488 ppm in the thick roots and to values under 100 ppm in the leaves. Similar results were found for iron with absolute contents ten times lower than the ones of aluminium.

The element data of the individual tree demonstrated in Table 2 show 0.48% K, 0.85% Ca, 0.11% Mg, 0.08% P, 0.08% S, 0.004% Fe, and 0.02% Al related to the dry weight of the plants. These figures particularly indicate a high mineral element demand.

The absolute element contents of the tissues analyzed from a 15-year-old *Swietenia* tree showed some changes compared to the 2½-year-old plants. They demonstrate a significant increase of potassium, calcium, and magnesium in the roots during plant growth. The extremely high values of calcium which were found in the old leaves of the 2½-year-old plants could not be observed in the tissues of the older plants. But even in this case, also the 15-year-old plant showed significant differences between the calcium content of old and young leaves.

Soil analyses

The analyses of the soil samples demonstrated a very low alkaline saturation of these soils of maximally 5 – 13% before slash-and-burn. After slash-and-burn, the values raised up to 26 and 53%, but six months later, they were already reduced again to figures between 5 and 26%.

As demonstrated in Fig. 4, slash-and-burn of the area caused a significant change in the different element contents of the soil samples. The distinctly higher values of calcium, potassium, magnesium, and sulphur, and to a lesser degree manganese and sodium, directly after burning lead to the conclusion that these elements were released by burning the plant material. Especially the soil contents of potassium and calcium demonstrate this effect very distinctly. While the absolute values for potassium before slash-and-burn lay between 2.06 and 4.61 ppm, and the ones for calcium around an average of 1.53 ppm, they increased after burning to a range from 5.81 to 31.05 ppm and an average of 14.68 ppm respectively. But like magnesium and sulphur that raised about 50%, manganese about 10% and sodium about 15% after burning, six months after this event also potassium and calcium reached almost the values of the soil samples before slash-and-burn (Fig. 4).

Aluminium and iron demonstrated the contrary effect. While iron showed a slight decrease after burning, the aluminium content was significantly reduced by slash-and-burn, and even six months after this did not reach the initial level, which was determined in the soil samples before burning.

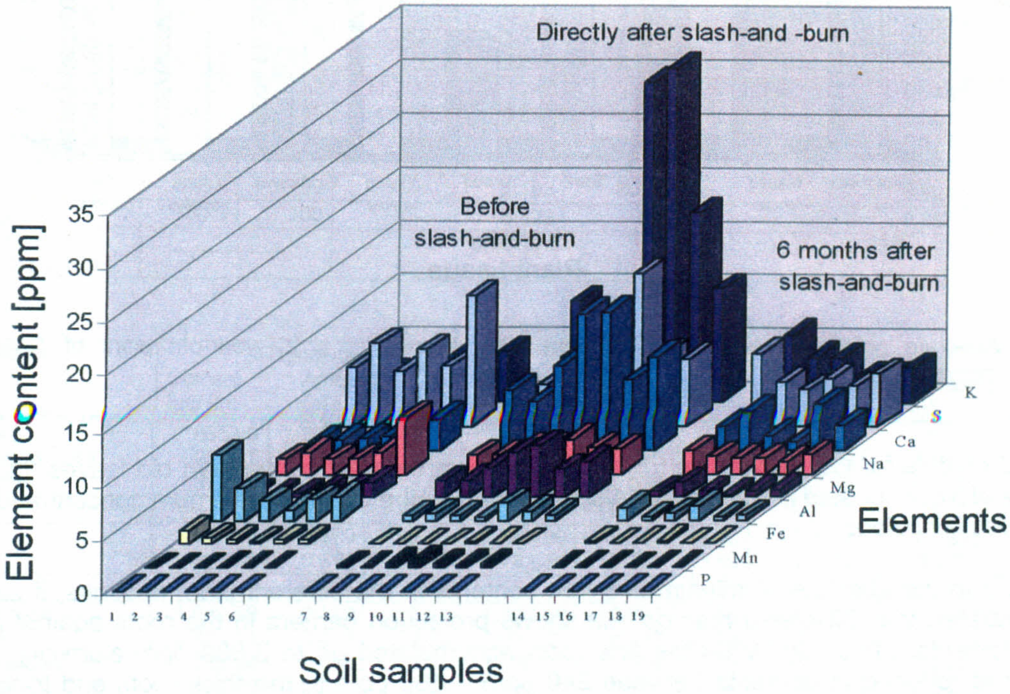


Fig. 4: Element content of 19 different soil samples before slash-and-burn, directly after burning, and six months after slash-and-burn. Numbers on the abscissa indicate samples. Soil solution evaluated in a depth of 0 to 30 cm.

Discussion

The biomass determination demonstrated that tropical wood species can reach a higher biomass production in the same time than species from areas with a moderate climate. The results of the element analyses in the different *Swietenia* plants showed that those plants have a high need of nutrient supply, especially for calcium, potassium and phosphorus.

While KLINGE (1976) demonstrated a low calcium value in the leaf compartment during his investigations in a rainforest near Manaus, the results of this investigation in contrast showed extremely high concentrations of calcium in the leaves. It is known that calcium, because of its low mobility, cannot be mobilized any more after deposit, and that it usually is accumulated in the old leaf compartments (AMBERGER, 1983; MARSCHNER, 1986). But the measured values between 53 and 90% of the whole calcium content referring to the dry weight of one 2½-year-old *Swietenia* plant are extremely high. The accumulation of calcium in the old leaves with an average of approximately 49% shows a very effective recycling system in which Ca can be reused after litter fall. This allows the plant a reduction of her dependency of the extremely low rates of Ca available to the plants in the soil of the Amazon region that is poor of limes (KLINGE, 1976; SALATI and VOSE, 1984).

The plant toxic element aluminium can lead to a high inhibition of the root development as shown by investigations of GOBOLD et al. (1988) with spruce seedlings (*Picea abies*). In contrast to this plant species, which is not adapted to acid soils, *Swietenia macrophylla* demonstrates a good adaptation to the acid oxisoils of the investigated location which are rich in aluminium (FITTKAU, 1983). This adaptation of native plant species, which shows protection barriers against aluminium, was already observed but not closely investigated by FURLANI (1989).

The results of the soil analyses proved that the soils of this "terra firme" area exhibit an extreme lack of nutrients, as also described by KLINGE (1976) and JORDAN (1982). Slash-and-burn is a generally used form of land clearing in the Amazon region and, as demonstrated, this method sets free mineral elements. Investigations on a location with pasture point out that the amount of nutrients liberated depends on the vegetation form used before slash-and-burn. The pasture, poor of high stocks of biomass-producing plant species, did not display equal effects as observed in this work. Only small increases of calcium and potassium could be found (McKERROW, 1992). In accordance to the data presented here, BRINKMAN and NASCIMENTO (1973) made similar observations on the decrease of iron and aluminium contents after burning. As also described in this work, BRINKMAN and NASCIMENTO (1973) demonstrated that there is only a short-term fertilizer effect caused by slash-and-burn due to leaching of the released nutrients.

In order to get information about the possibility whether these acid soils poor of nutrients are useful for long-term plantations, the relation of the mineral element content in the soil and the mineral element need of the plants had to be established. Therefore, the mineral element need of 10-year-old plants was calculated, assuming a linearly growing biomass production as wood species usually do (BRÜNIG, 1971). For a 10-year-old non-fertilized plant with a dry weight of about 58 kg and a percentage of the leaf compartments of about 10, stem about 60 and roots about 30%, the following element demand can be calculated: 27.5 g K, 49 g Ca, 6.6 g Mg, 4.5 g P, and 4.5 g S. With a plant distance of 6 x 7 metres, 240 *Swietenia* plants can be used per hectare monoculture. On such an area, 6.6 kg K, 11.76 kg Ca, 1.58 kg Mg, 1.08 kg P, and 1.08 kg S would be fixed in the plant material. Comparing this data with the element stock of the soils in the Amazon region, it can be demonstrated that long-term agroforestry with wood species without fertilization will not be possible.

Conclusions

The results of the biomass determination demonstrated that tropical plants like *Swietenia macrophylla* are able to reach a high biomass production in a very short time. In agreement to this, the element analyses showed a high mineral element demand of the plant species. Besides, *Swietenia macrophylla* have internal and external recycling systems at their disposal. The species revealed a very intensive internal exchange for K from the old to the young leaves (internal recycling), whereas Ca extremely accumulates in the old leaves to be reused after litter fall (external recycling). In addition to this, the plants showed protection barriers against aluminium.

The soil analyses indicated poor nutrient supply conditions. The fertilizer effect caused by slash-and-burn was only short-termed.

The relation of the mineral element content in the soil and the mineral element need of the plant points out that specific fertilization for each plant species is necessary. Gradually disintegrating fertilizer (mulching) and mixed cultures from annual and perennial species with priority to the native species are the only possibility of sustainable agriculture in the Amazon region.

References

AMBERGER, A.: Pflanzenernährung. Ökologische und physiologische Grundlagen. Dynamik und Stoffwechsel der Nährelemente. 2. verbesserte Auflage, Eugen Ulmer Verlag, Stuttgart, 1983, 250 p.

BRINKMAN, W. L. F.; NASCIMENTO, J. C.: The effect of slash-and-burn agriculture on plant nutrients in the tertiary region of Central Amazonia. Turrialba, 23 (1973) 284 – 290.

BRÜNIG, E. F.: Forstliche Produktionslehre. Europäische Hochschulschriften, Herbert Lang Bern, Peter Lang Frankfurt/ M., 1971, 318 p.

DAHMS, K.-G.: Mahagoni, Neue Importholzkunde Teil IV, Lateinamerika. Holz-Zentralblatt, Stuttgart, 95/ 96 (1993) 1508.

DÜNISCH, O.; SCHROTH, G.; MORAIS, R. de, ERBREICH, M.: Water supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in three plantation systems. BFH Mitteilungen Nr. 193 (1999) 29 - 45.

FITTKAU, E. J.: Grundlagen der Ökologie Amazoniens. Versuch einer Zusammenschau. SPIXIANA, Supplement, München, 9 (1983) 201 – 218.

FURLANI, P. R.: Efeitos fisiológicos do alumínio em plantas. In: II Simpósio avançado de solos e nutrição de plantas. Fundação Cargill, Campinas. SP, 1989, 73 – 90.

GODBOLD, D. L.; FRITZ, E.; HÜTTERMAN, A.: Aluminium toxicity and forest decline. Proc.-Natl. Acad. Sci. USA 85 (1988) 3888 – 92.

JORDAN, C. F.: The nutrient balance of an Amazonian rain forest. Ecology, 63 (1982) 647 – 654.

KLINGE, H: Nährstoffe, Wasser und Durchwurzelung von Podsolen und Latosolen unter tropischem Regenwald bei Manaus/ Amazonien. Bibliographica (Neotropische Ökosysteme. Festzeitschrift zu Ehren von H. SIOLI), 7 (1976) 45 – 58.

MARSCHNER, H.: Mineral nutrition in higher plants, Academic Press, London, 2nd edition, 1995, 889 p.

McKERROW, A. J.: Nutrient stocks in abandoned pastures of the Central Amazon basin prior to and following cutting and burning. M.Sc.-Thesis, Raleigh, USA, 1992, 112 p.

RADEMACHER, P.: Morphologische und physiologische Eigenschaften von Fichten (*Picea abies* (L.) Karst.), Tannen (*Abies alba* Mill.), Kiefern (*Pinus sylvestris* L.) und Buchen (*Fagus sylvatica* L.) gesunder und erkrankter Waldstandorte. Diss. Fachbereich Biologie der Univ. Hamburg GKSS 86/ E/ 10, 1986, 274 p.

SALATI, E.; VOSE, P. B.: Amazon Basin: A system in equilibrium, Science, 225 (1984) 129 – 138.

SCHMIDT, P.: Biomasseproduktion und Mineralelementversorgung ausgewählter tropischer Nutzpflanzen im Amazonasgebiet Brasiliens. Doctoral thesis, Department of Biology, Hamburg University, 1996, 304 p.

Acknowledgements

The investigation was part of a project of EMBRAPA Amazônia Ocidental, Manaus, and Hamburg University titled "Recultivation of degraded and abandoned monocultures in stable mixed cultures with special reference to soil biological factors". It was supported by the BMBF-Bonn and the CNPq-Brasilia from 1992 to 1996, and is embedded in the bilateral program "**S**tudies on **H**uman **I**mpact on **F**orests and Floodplains in the **T**ropics" (SHIFT). We are also grateful to Prof. W. Zech and co-worker for their cooperation in the soil analyses and Dr. H. Preisinger, coordinator in Brazil, for his manifold support in Manaus.

Nutritional status of *Ceiba pentandra* (L.) GAERTN. and *Virola surinamensis* (Rol.) WARB. growing on poor soils in the Brazilian Amazon Region

E. J. M. Neves[1], *C. B. Reissmann*[1], *C. A. Ferreira*[2], *A. F. J. Bellote*[2], *O. Dünisch*[3]

[1] Federal University of Paraná, Curitiba, Brazil
[2] EMBRAPA – Florestas, Curitiba, Brazil
[3] Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg, Germany

Summary

Many species in the Amazon region grow on very infertile soils. This paper focuses on the nutritional status of two important species of this region, namely *Ceiba pentandra* (L.) GAERTN. and *Virola surinamensis* (Rol.) WARB. with 55 months of age. Considering the low fertility of the soil in the study area on the "terra firme", as already stated in earlier studies, nutrient cycling seems to be the main factor in sustaining this system. Moreover, there are specific differences between the two species studied. N, P, K, Ca, and Mn concentrations can be considered the most discriminating elements. Both species also behave differently in relation to Al and to nutritional relations like K/ Ca and Fe/ Mn. In *Ceiba,* as a consequence of very low Mn levels, the ratio Fe/ Mn is > 1, whereas for *Virola,* the ratio Fe/ Mn is < 1.

Resumo

Status de nutrição de *Ceiba pentandra* (L.) GAERTN. e *Virola surinamensis* (Rol.) WARB. crescidos en solos pobres na região Amazônia do Brasil

Na região Amazônica muitas espécies crescem em solos de baixa fertilidade natural. Este trabalho aborda, aos 55 meses de idade, o estado nutricional de duas importantes espécies desta região denominadas de *Ceiba pentandra* (L.) GAERTN. e *Virola surinamensis* (ROL.) WARB. Considerando a baixa fertilidade do solo da área em estudo, a ciclagem de nutrientes parece ser o fator mais importante na sustentabilidade do sistema. Além disso, existem diferenças específicas entre as espécies estudadas. As concentrações de N, P, K, Ca e Mn podem ser consideradas como sendo as mais diferenciadas entre os elementos. As duas espécies também apresentam comportamento diferenciado em relação ao Al e do mesmo modo para as relações K/ Ca e Fe/ Mn. Em *Ceiba*, como consequência do baixo nível de Mn nas folhas, a relação Fe/ Mn é >1, enquanto que para *Virola*, esta é <1.

Introduction

The foliar analysis is a very useful and reliable procedure to determine the nutritional status of plants, as well as their nutrient requirements. Frequently, the results are based on the nutrient content of the leaves on a dry weight basis. Many factors can affect the results, as species, physiological age of the leaves, sampling position in the crown, season, type of the soil, and age of the plant (BATAGLIA and DECHEN, 1986; MARSCHNER, 1995). In this respect, an accurate interpretation of the results needs take into account the growth pattern of the plant, the nutrient availability in the soil, how the elements behave and/ or remobilize internally, and also their interactions. Particularly in relation to the latter, MARSCHNER (1995) emphasizes the influence of specific and non-specific interactions that may affect critical contents, as observed between N and P. In relation to the internal remobilization, N, P, and K are considered highly mobile, Cu, Zn, Mn, Fe, and S present variable mobility, while Ca is considered immobile (MENGEL and KIRKBY, 1982). The pattern of visual symptoms manifestation when deficiency occurs, gives a rough idea of the behavior of the element. Symptoms in older leaves are an indication of element remobilization, while symptoms in young or new leaves indicate that there is no remobilization of the required element (REIS and BARROS, 1990).

Information about the nutritional requirements of forest trees, especially on those native from the Amazon region, are incipient. The specialized literature on this matter finds some support in the studies developed by KLINGE (1985), in which macro-nutrients in the foliage of the "terra firme" and the "várzea" forest are compared. KLINGE et al. (1983) and FURCH et al. (1983), studied the chemical composition of the "várzea" forest, all of their studies conducted near Manaus. GRIMM and FASSBENDER (1981) developed nutritional surveys in the occidental Andean region of Venezuela, and GOLLEY et al. (1980a; 1980b) investigated the Amazon forest in the Brazilian and Venezuelan territory.

The present study is part of an ongoing Ph.D. dissertation of the first author at the Federal University of Paraná, supported by the cooperation agreement between the EMBRAPA Amazônia Ocidental, Manaus, the University of Hamburg, Germany, and the National Agency for Scientific and Technological Development (CNPq).

The main purpose of the project is to characterize the nutritional status of *Ceiba pentandra* (L.) GAERTN. and *Virola surinamensis* (Rol.) WARB., as well as the distribution of the nutrients and of Al in the different compartments of the trees. In this paper, only data from the leaves are presented.

Material and methods

In this paper, *Ceiba pentandra* and *Virola surinamensis* with 55 months of age, planted at a space of 3 m x 3 m in experimental plots with 25 trees each, in a randomized block design, are discussed. The study area is located in the EMBRAPA Amazônia Ocidental, Research Station ("Amazonia Ocidental" Center), at the 24^{th} km of the AM-010 road, Manaus, Amazonas, with 03^{o} 00' 00" and 03^{o} 08'00" South; 59^{o} 52' 40" and 52^{o} 58' 00" West. The altitude comprises 50 m above sea level. The climate is the Afi type, according to Köppen's classification system. The mean annual precipitation recorded in the period of 1992-1996 presented an average of 2,720 mm. The maximum and minimum temperature values in the above mentioned period, achieved 34.1 ^{o}C and 20.3 ^{o}C respectively.

The soil in the study area had been classified earlier by RODRIGUES et al. (1972) as "Latossolo Amarelo distrófico textura muito argilosa", being a typical Oxisol. Some of the chemical characteristics are presented in the tables 1 and 2, representing samples from the uppermost horizon, collected at a depth of 0 - 10 cm, where most of the fine roots are concentrated. The following analyses were performed: pH in a 1 : 2.5 soil:$CaCl_2$ proportion; P and K extracted with a 0.05N HCl+ 0.025N H_2SO_4; Ca, Mg and Al extracted with KCl 1N (BLOISE et al., 1979). The potential acidity was determined with the SMP-solution (RAIJ and QUAGIO, 1983); Fe, Mn, Cu, and Zn were extracted with the same solution as employed for P and K-extraction (EMBRAPA, 1997).

Four trees of *Ceiba pentandra* and *Virola surinamensis* were cut and separated into the different compartments for the tissue analysis. In this issue, only results from the leaves are presented and discussed. *Virola* foliage exhibited different morphological characteristics according to the age of the leaves, allowing to separate them in three categories of leaves (new, mature, and old). On the contrary, no clear evidence could be noticed in *Ceiba* in relation to leaf age, leading to the choice of only one type of leaf admitted to be mature ones. After sampling, the leaves were dried at 75 ^{o}C, until they reached constant weight, and were ground in a Herzog mill, model HSM. The elements P, K, Ca, Mg, S, Al, Fe, Mn, Cu, and Zn were determined by ICP-OES after being submitted to the wet oxidation digestion procedure (SARRUGE and HAAG, 1974). N was determined using the micro-kjeldahl procedure.

Results and discussion

The data presented in Tables 1 and 2, show chemical composition of *Ceiba pentandra* and *Virola surinamensis* plantations.

For *Virola,* different leaf ages were possible to be identified and analyzed separately, as explained in the prior section. According to literature and in a broad sense of view, most of the results are similar to the range of data presented in earlier studies (STARK, 1970a; GOLLEY et al., 1980a; SCHMIDT, 1996). But in relation to the data of KLINGE et al. (1983), only N and P in *Ceiba* can be considered as being in good supply. For N, this may be considered as normal, since it is the most abundant element in lowland tropical forests (MEDINA, 1981)[1] apud KLINGE et al., (1983). Considerations about the contribution of the phyllosphere to the N-fixation (BENTLEY and CARPENTER, 1984) should also be taken into account in the present ecosystem, due to the quantitative importance of this phenomenon. This also agrees with the observations of JORDAN et al. (1982).

Table 1: Concentration of macro-nutrients (g · kg^{-1} dry weight) in leaves of *Ceiba pentandra* and *Virola surinamensis* with 55 months of age.

Tissue	Species	N	P	K	Ca	Mg	S
Leaf	*Ceiba*	28.3± 4.5*	2.0± 1.7*	11.0± 4.0*	10.1± 3.5*	3.0± 1.9*	1.9± 1.0*
New leaf	*Virola*	16.7± 3.5*	1.5± 1.0*	9.0± 3.5*	4.4± 2.9*	1.8± 1.5*	1.4± 0.9*
Mature leaf	*Virola*	15.4± 2.9*	0.9± 0.8*	4.9± 3.1*	8.7± 3.0*	2.1± 2.4*	1.4± 0.7*
Old Leaf	*Virola*	15.1± 2.7*	0.8± 0.7*	3.8± 3.1*	10.3± 7.8*	2.03± 2.0*	1.3± 0.6*

*= Standard deviation

At a specific level, it is clear that the two species behave differently. N, P, K, Ca, and Mn are the most remarkable discriminating elements. Due to the respective opposite behavior of K and Ca, the different leaf ages in *Virola* offer a good example of remobilization/ accumulation. In this respect, the K/ Ca ratio assumes values of 2.1 : 1 in young; 0.6 : 1 in mature, and 0.4 : 1 in old leaves. In *Ceiba,* with the recognition of only one leaf-age category, this ratio is approximately 1. Depending on species, ratios of 0.2 : 1 up to 11.0 : 1 are indicated for adult leaves (KLINGE et al., 1983). The observation and monitoring of this ratio is of uppermost importance considering the role that K plays in the water economy regime of the plant. Recent studies of DÜNISCH et al. (1998) identified strong imbalances in the K-supply for different plant communities in the present study area.

Table 2: Concentration of micro-nutrients and Al (mg · kg^{-1}) in leaves of *Ceiba pentandra* and *Virola surinamensis* with 55 months of age

Tissue	Species	Fe	Mn	Cu	Zn	Al
Leaf	*Ceiba*	59.21± 8.5*	13.69± 3.4*	17.41± 6.5*	20.33± 4.6*	0.09± 0.5*
New leaf	*Virola*	58.16± 13.0*	317.51± 24.6*	12.22± 4.0*	20.49± 11.5*	0.06± 0.8*
Mature leaf	*Virola*	57.71± 13.7*	241.27± 20.5*	10.43± 3.9*	22.56± 8.3*	0.03± 0.5*
Old leaf	*Virola*	47.16± 7.1*	183.22± 19.6*	10.32± 4.4*	19.53± 3.9*	0.02± 0.2*

*= Standard deviation

The Fe/ Mn ratio also represents a special feature where *Ceiba* and *Virola* differ considerably. The two species split into plants with a Fe/ Mn quotient higher (*Ceiba*) and lower (*Virola*) than 1. It has been frequently observed that in forest trees, moreover in conifers, and also in native broad-leaved trees, a Fe/ Mn ratio minor than 1 prevails at a rate of at least 65% (BRITEZ, 1994; GOLLEY et al., 1980a; BRITEZ et al., 1997, REISSMANN et al., 1994). On the contrary, in agriculturally cultivated plants a ratio between 1.5 and 2.5 is desired for healthy plants (KABATA and PENDIAS, 1985). In *Ceiba*, the Mn concentration is very low. It is even lower than the concentrations of Cu and Zn. Both are more likely to be expected according to the general pattern of regional foliage data. According to PAGEL et al. (1982), Mn is absorbed in

MEDINA, E.: Nitrogen content, leaf structure and photosynthesis in higher plants: a report to the UNEP study group on photosynthesis and bioproductivity, London. 1981.

much higher quantities than Cu. Furthermore, it is well-known that plants can absorb highly different quantities of Mn (MENGEL, 1984), being that the environmental conditions are favorable in terms of pH and redox, (PAGEL et al., 1982; GAMBREL, 1996) and organic compounds (SHESTAKOV et al., 1991). Rhizosphere and N-ionic forms play an important role too, as a consequence of root-induced pH-changes (MARSCHNER et al., 1986). Derived from the assumption that the soil provides a reasonable amount of Mn for *Ceiba,* see table 4, it seems that an inherent effect is responsible for the Mn uptake. This phenomenon might be related to rhizosphere phenomena. The Mn-concentration in *Ceiba* fine roots is twice as high as that of *Virola,* according to unpublished results from ongoing studies by NEVES (1998) This does not represent an isolated case. Very low Mn-concentrations have been detected earlier in a small number of botanical families (STARK, 1970a). In some tropical trees, concentrations around 20 mg · kg^{-1} are considered to be in the range of deficiency (DRECHSEL and ZECH, 1991). The effect on variations needs confirmation.

The systematic decrease in Al-concentration with the age of *Virola* leaves, see table 2, offers another interesting question. Even considering the disputed assumption that Al stimulates the growth of native plants adapted to acid soils (WATANABE et al., 1997), there is no concrete reason to assume an Al-remobilization. Despite of this phenomenon, it has been a more common observation that Al accumulates in older leaves (REISSMANN et al., 1976; RADOMSKI et al., 1992; BIONDI, 1995; WATANABE et al., 1997) the tendency of an inhibited Al-movement to older leaves in some species, accomplished with or without a leaching effect, is a hypothesis to be verified.

Table 3: Chemical characterization of the soil of *Ceiba pentandra* and *Virola surinamensis* experimental plots: exchangeable elements and organic matter (OM)

Species	Soil depth (cm)	PH ($CaCl_2$)	P (mg/ dm^3)	K	Ca	Ca + Mg	Al	H + Al	OM (%)
				Cmol$_c$/ dm^3					
Ceiba	0 - 10	3.8	5	0.07	0.28	0.76	1.5	7.5	35.5
Virola	0 - 10	4.1	5	0.10	0.86	1.88	0.9	5.7	32.3

Table 4: Chemical characterization of the soil (0 – 10 cm) of *Ceiba pentandra* and *Virola surinamensis* experimental plots: micro-nutrients

Species	Soil depth (cm)	Fe	Mn	Cu	Zn
		Mg · kg^{-1}			
Ceiba	0 - 10	228	44	2	1
Virola	0 - 10	213	10	11	2

In Table 3, the exchangeable macro-nutrients of the leaves are presented. The low fertility level is in agreement with the findings of BAUCH and DÜNISCH (1996), who observed that, with exception of Ca, all the other elements were extremely low in the soil solution. The condition of an apparently satisfactory nutritional status of the trees can only be explained on the basis of an efficient nutrient cycling mechanism (SCHMIDT, 1996). For the micro-nutrients, a relative heterogeneity between the two sampling areas has been observed, as can be seen in Table 4. According to CAMARGO (1988), Cu and Zn in *Ceiba* and Mn in *Virola* can be considered to be in short supply. The studies developed by STARK (1970b), show results based on total digestion of the micro-nutrients in the Amazonian soils. However, the discrepancy between the methodologies makes any comparison with the present data unreliable. Furthermore, the lack of calibration analysis for forest soils, especially for micro-nutrients, does not allow a more consistent discussion and should be understood as a complementary information about the ecosystem to be fulfilled in future studies.

The considerations discussed above, based on foliar data, are by far not conclusive. However, there is conspicuous evidence for important interactions among nutrients in this ecosystem. Considering the capacity of these two species to recultivate degraded sites, these results represent one more step towards elucidative investigations.

References

BATAGLIA, O. C.; DECHEN, A. R.: Critérios alternativos para diagnose foliar. In: Simpósio avançado de química e fertilidade do solo. (Piracicaba, 1986) Anais. Campinas: Fundação Cargil, 1986, pp. 115 - 136.

BAUCH, J.; DÜNISCH, O.: Untersuchung forstlich geeigneter Baumarten für die Wiederbegründung degradierter Flächen im Amazonasgebiet Brasiliens. Hamburg: Universität Hamburg. Jahresbericht, 1996, 96 p. (SHIFT PROJECT BMBF 0339638/ CNPq ENV - 42).

BENTLEY, B. L.; CARPENTER, L. E.: Direct transfer of newly-fixed nitrogen from free-living epiphyllous microorganisms to their host plant, Oecologia, 63 (1984) pp. 52 – 56.

BIONDI, D.: Caracterização do estado nutricional de *Acer negundo* L. e *Tabebuia chrysotricha* (Mart. Ex. DC) Standl utilizadas na arborização urbana de Curitiba-PR, Curitiba: Universidade Federal do Paraná (1995) 146 p. (Doctoral thesis).

BLOISE, R.M. ; MOREIRA, G.N.C. ; DYNIA, J.F. Métodos de análises de solos e calcários. Boletim Técnico. EMBRAPA/ SNLCS, Rio de Janeiro (1979) 55, pp. 1-32.

BRITEZ, R. M. de: Ciclagem de nutrientes minerais em duas florestas da Planície Litorânea da Ilha do Mel, Paranaguá, PR. Curitiba: Universidade Federal do Paraná (1994) 240 p. (Master thesis).

BRITEZ, R. M. de; REISSMANN, C. B.; SILVA, S. M.; ATHAYDE, S. F.; LIMA, R. X.; QUADROS, R. M. B.: Chemical characterization of two forests on the coastal plains of the Ilha do Mel, Paraná, Brazil. In: Plant Nutrition for Sustainable Food Production and Environment. Japan : Kluwer Academic Publishers (1997) pp. 461 - 462.

CAMARGO, O. A. de: Micronutrientes no solo. In: EMBRAPA/ IAPAR/ SBS. Enxofre e micronutrientes na agricultura brasileira. Reunião Brasileira de Fertilidade do Solo. London (1988) 317 p.

DRECHSEL, P.; ZECH, W.: Foliar nutrient levels of broad-leaved tropical trees: a tabular review. Plant and Soil. 131, 1991, pp. 29 - 46.

DÜNISCH, O.; BAUCH, J.; GASPAROTTO, L.; NEVES, E.; AZEVEDO, C. de; LIMA, R. de; MORAIS, R. de: Environment-tree growth relationships of plantation grown tropical tree species as a basis for sustainable timber production in mixed culture systems in Central Amazonia. In: LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 – 19 (1998) 13 p.

EMBRAPA: Manual de Métodos de Análise do Solo. Centro Nacional de Pesquisa de Solos. Rio de Janeiro. 1997, 212 p.

FURCH, K.; JUNK, W. J.; DIETERICH, J.; KOCHERT, N.: Seasonal variation in the major cation (Na, K, Mg, and Ca) content of the water of Lago Camaleão, an Amazonian floodplain-lake near Manaus, Brazil. Amazoniana, 8 (1983) pp. 75 - 89.

GAMBREL, R. P.: Manganese. In: J. M. BARTELS and J. M. BIGHAM. Methods of Soil Analysis. [S. l] : Madison (1996). pp. 665 - 682. SSSA Book Series 5.

GOLLEY, F. B.; YANTKO, J.; RICHARDSON, T.; KLINGE, H.: Biogeochemistry of Tropical Forests: The frequency distribution and mean concentration of selected elements in a forest near Manaus, Brazil. Tropical Ecology. 21, 1 (1980a) pp. 59 – 70.

GOLLEY, F. B.; YANTKO, J.; JORDAN, C.: Biogeochemistry of Tropical Forests: The frequency distribution and mean concentration of selected elements near San Carlos de Rio Negro - Venezuela. Tropical Ecology, 21 (1980b) pp. 71 – 80.

GRIMM, U.; FASSBENDER, H. W.: Ciclos bioquímicos en un ecosistema forestal de los Andes Occidentales de Venezuela: Inventario de las reservas orgánicas y minerales (N, P, K, Ca, Mg, Mn, Fe, Al, Na). Turrialba, 31 (1981) pp. 27 - 36.

JORDAN, C.; CASKEY, W.; ESCALANTE, G.; HERRERA, R.; MONTAGNINI, F.; TODD, R.; UHL, C. *The nitrogen cycle in a "Terra Firme" rainforest on oxisol in the Amazon territory of* Venezuela. Plant and Soil, 67 (1982) pp. 325-332.

KABATA, A. P. ; PENDIAS, H.: Trace Elements in Soils and Plants. Boca Raton: CRC, 1985, 315 p.

KLINGE, H.: A contribution to the knowledge of the biogeochemistry of Amazon Inundation Forests. In: Workshop on Biogeochemistry of Tropical Rain Forests: Problems for Research. Piracicaba, USP/ CENA (1985) pp. 17 - 27.

KLINGE, H.; FURCH, K.; HARMS, E.; REVILLA, J.: Foliar nutrient levels of native tree species from Central Amazonia: Inundation Forests. Amazoniana. 8 (1983) pp. 19 - 45.

MARSCHNER, H.: Mineral nutrition of higher plants. 2.ed. London: Academic Press, 1995, 889 p.

MARSCHNER, H.; RÖMHELD, V.; HORST, W. J.; MARTIN, P.: Root-induced changes in the rhizosphere: importance for the mineral nutrition of plants. Z. Pflanzenernähr. Bodenk., 149 (1986) pp. 441 - 456.

MENGEL, K.: Ernährung und Stoffwechsel der Pflanze. Stuttgart: Gustav Fischer Verlag. 1984, 431 p.

MENGEL, K.; KIRKBY, E. A.: Principles of plant nutrition. International Potash Institute, Bern. 1982, 655 p.

NEVES, E. J. M.: Biomassa e acúmulo de nutrientes nos diferentes compartimentos de *Ceiba pentandra* e *Virola surinamensis* plantadas na Amazônia Ocidental brasileira. Diss. Univ. da Paraná, Curitiba (1999) in print.

PAGEL, H.; ENZMANN, J.; MUTSCHER, H.: Pflanzennährstoffe in tropischen Böden - Ihre Bestimmung und Bewertung. Berlin : VEB Deutscher Landwirtschaftsverlag, 1982. 272 p.

RADOMSKI, M. I.; SUGAMOSTO, M. L.; GIAROLA, N. F. B.; CAMPIOLO, S.: Avaliação dos teores de macro e micronutrientes em folhas jovens e velhas de erva-mate nativa. Revista do Instituto Florestal, 4 (1992) pp. 453 - 456.

RAIJ, B. van ; QUAGGIO, J. A. Métodos de análise de solo para fins de fertilidade. Boletim Técnico do Instituto Agronômico. Campinas, 81 (1983), pp.1-31.

REIS, M. G. F.; BARROS, N. F.: Ciclagem de nutrientes em plantios de eucalipto. In: BARROS, N. F.; NOVAIS, R. F.: Relação solo-eucalipto. Viçosa: Ed. Folha de Viçosa (1990), pp. 265 - 302.

REISSMANN, C. B.; HILDEBRAND, E. E.; BLUM, W. E. H.; BURGER, L. M.: Metodologia da amostragem e análise das acículas de *Araucária angustifolia* Bert. O. Ktze. 1. Influência da idade das acículas. Revista Floresta, 7 (1976) pp. 5 - 12.

REISSMANN, C. B.; RADOMSKI, M. I.; QUADROS, R. M. B.: Relação entre os teores totais e a fração hidrossolúvel dos elementos K, Ca, Mg, Fe, Mn, Cu, Zn e Al em folhas de erva-mate (*Ilex paraguariensis* St. Hil.). Arq. Biol. Tecnol., 37 (1994) pp. 959 - 971.

RODRIGUES, T. E.; REIS, R. S. dos; MORIKAWA, I. K.; FALESI, I. C.; SILVA, B. N. R. da: Levantamento detalhado dos solos do IPEAAOC. Manaus: IPEAAOc, 1972, 63 p. (IPEAOOc. Boletim Técnico, 1).

SARRUGE, J.R.; HAAG, H. P.: Análise química em plantas. Piracicaba: ESALQ/ USP. 1974, 56 p.

SCHMIDT, P.: Biomasseproduktion und Mineralelementversorgung ausgewählter tropischer Nutzpflanzen im Amazonasgebiet Brasiliens. Hamburg: Universität Hamburg (1996) 304 p. (PhD-thesis)

SHESTAKOV, Y. I.; KAURICHEV, I. S.; KARPUKHIM, A. I.; RACHINSKI, V. V.: Composition stability and availability for plants of water-soluble organic compounds of manganese. Pochvovedeniye. 10 (1991) pp. 38 - 50.

STARK, N.: The nutrient content of plants and soils from Brazil and Surinam. Biotropica. 2 (1970a) pp. 51 - 60.

STARK, N.: Nutrient cycling: 1. Nutrient distribution in some Amazonian soils. Tropical Ecology. 12 (1970b) pp. 24 - 50.

WATANABE, T.; MITSURO, O.; TADANO, T.: Response of plants adapted in low pH-soils to aluminium. In: Plant Nutrition for Sustainable Food Production and Environment. Japan: Kluwer Academic Publishers (1997) pp. 459 - 460.

Growth dynamics in wood formation of plantation-*grown* *Swietenia macrophylla* King and *Carapa guianensis* Aubl.

O. Dünisch,[1] J. Bauch,[2] M. Sack,[2] and M. Müller[2]

[1] Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg.

[2] Institute of Wood Biology, Hamburg University, Hamburg.

Summary

In the present study, the growth dynamics in wood formation of four to six-year-old plantation-grown *Swietenia macrophylla* King and *Carapa guianensis* Aubl. was investigated. As to study the influence of the plantation management on the cambial growth dynamics of the trees, the investigations were carried out in three different plantation systems ((I) monoculture system, (II) mixed culture system, (III) enrichment system). The anatomical structure of the cambial zone of nine *Swietenia* and six *Carapa* trees was investigated by means of light microscopy of small samples collected throughout the year with a borer (diameter 1.4 and 1.9 mm, respectively). Special attention was given to the formation of increment zones and the state of the cambium (period of cell division/ cambial dormancy). In addition, the growth dynamics in wood formation of ten *Swietenia* and ten *Carapa* trees was dated by the „pinning method" from April 1995 until March 1997 in monthly intervals. Due to anatomical characteristics of the wound reactions studied by light microscopy, accurate measurements were carried out for increment measurements >0.3 mm.

The wood anatomical studies indicated that the formation of increment zones of *Swietenia* and *Carapa* are not annual and not correlated between individual trees. In the xylem of *Swietenia* and *Carapa,* two types of increment zones were found. In the inner part of the stem, a formation of vessel bands was observed, whereas in the outer part of the stem a distinct formation of parenchyma bands was found. From the study on the growth dynamics of the trees, it became obvious that the formation of parenchyma bands in the xylem of *Swietenia* in August/ September is correlated with the initiation of a cambial dormancy during the dry season. In contrast to that, no significant relationship was found between the rate of periclinal cell divisions of *Carapa* and the seasonal variation of the soil water supply. Furthermore, a reduced increment of *Swietenia* in the plantation systems II and III compared to system I was found, due to a low rate of periclinal cell divisions and a reduced period of cambial activity. Only slight differences in growth increment were found for *Carapa* grown in system I, II, and III.

From these findings, it was concluded that *Carapa guianensis* Aubl. is more adapted to sustainable growth throughout the year and under various site conditions compared to *Swietenia macrophylla* King.

Resumo

Dinâmicas de crescimento na formação da madeira de *Swietenia macrophylla* King e *Carapa guianensis* Aubl. em áreas de plantio

Estudaram-se as dinâmicas de crescimento na formação da madeira de *Swietenia macrophylla* King (mogno) e *Carapa guianensis* Aubl. (andiroba) em árvores com quatro a seis anos de idade. As pesquisas envolvendo a influência do sistema de manejo sobre as dinâmicas de crescimento do câmbio das árvores foram desenvolvidas em três diferentes sistemas de plantio (I - monocultivo, II - cultivo misto e III – enriquecimento de capoeira). A estrutura anatômica da zona cambial de nove árvores de mogno e seis de andiroba foi estudada com auxílio de um microscópio de luz, utilizando pequenas amostras de madeira coletadas, durante o ano todo, com um trado (1,4 e 1,9 mm de diâmetro, respectivamente). Foi dada atenção especial para a formação das zonas de incremento e o estado do câmbio (período de divisão celular/ dormência cambial). As dinâmicas de crescimento na formação da madeira de 10 árvores de mogno e 10 de andiroba foram datadas com auxílio do método de ferida do câmbio, no período de abril de 1995 a março de 1997, em intervalos mensais. Devido as características

anatômicas das reações aos ferimentos estudadas a microscópio de luz, medições precisas foram executadas para incrementos > 0,3 mm.

Os estudos anatômicos da madeira indicaram que a formação das zonas de incremento de mogno e andiroba não são anuais e nem correlacionadas entre árvores individuais. No xilema do mogno e da andiroba encontraram-se dois tipos de zonas de incremento. Na parte interna do caule observou-se a formação de uma faixa de vasos no limite da zona, enquanto que na parte mais externa observou-se uma formação de uma faixa de células parenquimáticas. A partir dos estudos sobre as dinâmicas de crescimento das árvores tornou-se óbvio que a formação das faixas de células parenquimáticas no xilema do mogno, no período de agosto a setembro, está correlacionado com o início da dormência cambial durante a estação seca. Entretanto, não foi encontrada relação significativa entre a taxa de divisões celulares periclinais da andiroba e a variação sazonal da disponibilidade de água no solo. Adicionalmente, encontrou-se um reduzido incremento do mogno nos sistemas de plantio II e III comparado com o sistema I, devido a uma baixa taxa de divisão celular periclinal e um período reduzido de atividade cambial. Apenas pequenas diferenças de incremento foram encontradas para andiroba cultivadas nos sistemas I, II e III.

A partir destes resultados, conclui-se que a andiroba é mais adaptada para o crescimento sustentável durante o ano todo e sob várias condições locais, comparadas ao mogno.

Introduction

The growth dynamics in wood formation of trees are determined by genetic factors (MÖLLEKEN et al., 1997) as well as by exogenous factors such as light (KOZLOWSKI et al., 1991), temperature (SCHWEINGRUBER, 1983), precipitation (FRITTS, 1976) and the mineral element supply of the soil (DÜNISCH et al., 1994). Dendroecological investigations carried out in temperate regions revealed the significance of these exogenous factors for cambial cell divisions and cell differentiation (VYSOTSKAYA and VAGANOV, 1989; v. WILPERT, 1990; SASS et al., 1993; DÜNISCH and BAUCH, 1994b) of various tree species. These findings elucidated the growth limiting factors and the site demands of the trees, which are important for the forest management with regard to an optimum in productivity and sustainability.

The knowledge on the growth dynamics and the site demands of important commercial timber trees of the tropics is still restricted. Due to methodical difficulties dating cambial cell divisions of tropical trees, which do not form distinct increment zones (MARIAUX, 1969; JACOBY, 1989; VETTER and BOTOSSO, 1989; SASS et al., 1995), only few investigations were carried out in the past to study the relationship between the site conditions and the cambial growth dynamics of the trees (COSTER, 1927, 1928, MARIAUX, 1969; WORBES, 1988, 1989; DÉTIENNE, 1989; PUMIJUMNONG et al., 1995). Nevertheless, due to the strong exploitation of high-quality trees of primary forests of the tropics, information on the site demands in relation to the intraannual growth dynamics of tropical timber trees is an urgent demand as to substitute exploitation out of primary forests by high-quality timber production in sustainable plantation systems (FEARNSIDE, 1993; HANNAN and BETALHA, 1995).

Already some decades ago, dendrometer measurements were carried out (MARIAUX, 1969) to characterize the intraannual growth dynamics of tropical trees. In recent studies, the "pinning method" (comp. MARIAUX, 1969; DÈTIENNE and MARIAUX, 1977; YOSHIMURA et al., 1981; KURODA and SHIMAJI, 1984; NOBUCHI et al., 1993) was used as to study the influence of the intraannual variation of the precipitation on the growth dynamics of tropical trees (comp. WORBES, 1989). Due to the restricted accuracy of the pinning method, a cambial dormancy of the trees could only be proven definitely by microscopic investigations of the cambial tissue (FUJITA and HARADA, 1979; GÖTTSCHE-KÜHN, 1988).

In order to investigate the environment-tree growth relationship, which is the basis for the selection of suitable tree species for high-quality timber production in plantations, the intraannual growth dynamics of the important timber trees of the Central Amazon *Swietenia macrophylla* King and *Carapa guianensis* Aubl. were studied. Dating of cambial cell divisions was carried out by the "pinning method". Light microscopic studies on the structure of the cambium were carried out throughout the year. Special attention was given to an optimum in accuracy of the pinning method and the relationship between the soil water supply and the cambial growth dynamics of the trees.

Experimental

Plantation systems and experimental trees

The experimental plots are located at the EMBRAPA Amazônia Ocidental, 25 km out of the city of Manaus, 3°8' S, 59°52'W. The area is located ca. 50 m above sea level with an annual precipitation of about 2500 mm (mean of the years 1962 until 1997). The soil is a poor yellow latosol with a reduced cation exchange capacity (comp. ZECH et al., 1998; DÜNISCH et al., 1999a). The investigations on the growth dynamics in wood formation of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. were carried out in three different plantation systems, which were used for interdisciplinary research projects within the Brazilian-German cooperation program "SHIFT" (comp. DÜNISCH et al., 1999a):

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, burned 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 month: 65 g NH_4 , after 11 month: 50 g NH_4, 100 g SFT, 50 g KCl, 50 g $MgSO_4$, 20 g FTEBR8 (mixture Zn, B, Cu, Fe, Mn, Mo)
- Spontanous 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 years 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

The investigations on growth dynamics in wood formation of plantation-grown *Swietenia* and *Carapa* were carried out from 1995 until 1997. For the study of the anatomical structure of the cambial zone of the trees, nine *Swietenia* trees (five of plantation system I, one of plantation system II, thee of plantation system III) and six *Carapa* trees (four of plantation system I, one of plantation system II, one of plantation system III) were selected. The growth dynamics in wood formation of ten *Swietenia* trees (four of plantation system I, three of plantation system II, three of plantation system III) and ten *Carapa* trees (four of plantation system I, three of plantation system II, three of plantation system III) was dated by the „pinning method" from April 1995 until March 1997 in monthly intervals. For the same trees, as well as for a *Swietenia* tree and a *Carapa* tree grown in plantation system I selected for anatomical studies on the structure of the cambial zone, the structure and width of increment zones was investigated.

Wood anatomical study on the characteristics of the stem xylem

The width of increment zones was measured at four radii and up to four height levels by means of an Eklund machine with an accuracy of 0.01 mm. The anatomical structure of the increment zones was investigated by light microscopy after the preparation of cross sections (section thickness ca. 20 µm) with a microtome (staining: safranine/ astrablue).

Light microscopy of the cambial zone

Sample collection of phloem, cambial zone, and xylem tissue was carried out in 1997 by a small borer (Fig. 1a/ b, comp. BÄUCKER et al., 1998; SACK, 1998). The fixation of the samples was done with a FEA solution (comp. GERLACH, 1977) and embedded in polyethylene glycol

(1500). Cross sections were prepared by a rotation (Jung) and a LKB Historange 2218-020 microtome.

In order to study the ontogenetic development of the cells, the slides were stained with safranine and astrablue and studied by light microscopy with polarized light (Fig. 2a/ b). By means of polarization microscopy, cells of the primary wall phase (cambium, differentiation zone of the xylem and phloem) could be separated from cells of the phase of secondary wall formation.

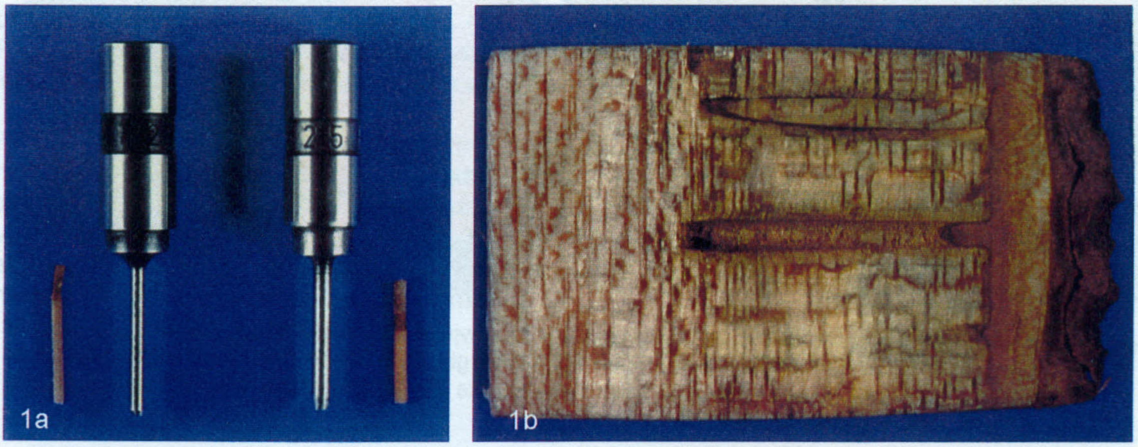


Fig. 1a/b: Methodical approach for the collection of cambium samples by small borers. (a) Diameter of the samples: 1.4 mm (left) and 1.9 mm (right). (b) Wounding 40 days after the injury (*Carapa guianensis*).

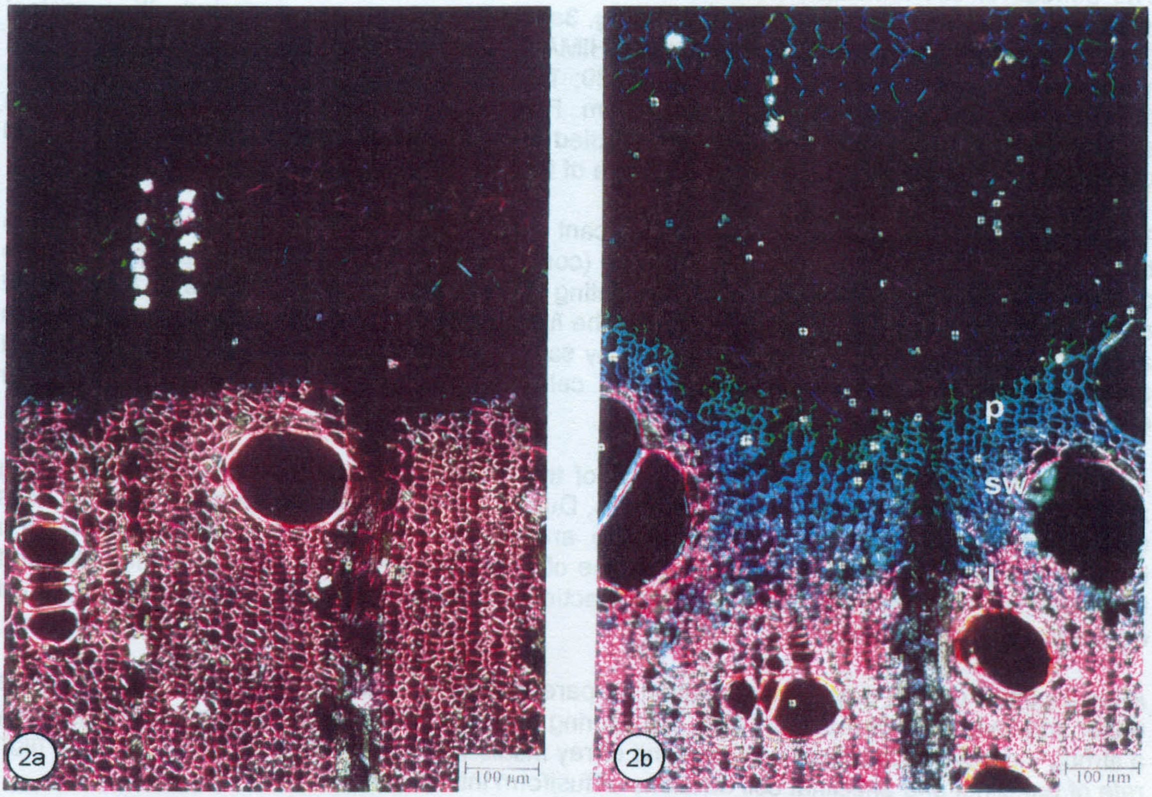


Fig. 2a/b: Cambial zone of *Carapa guianensis* investigated by polarization microscopy. (a) Cambial dormancy. (b) Active cambium. P=primary wall phase, SW=secondary wall formation, L=lignification.

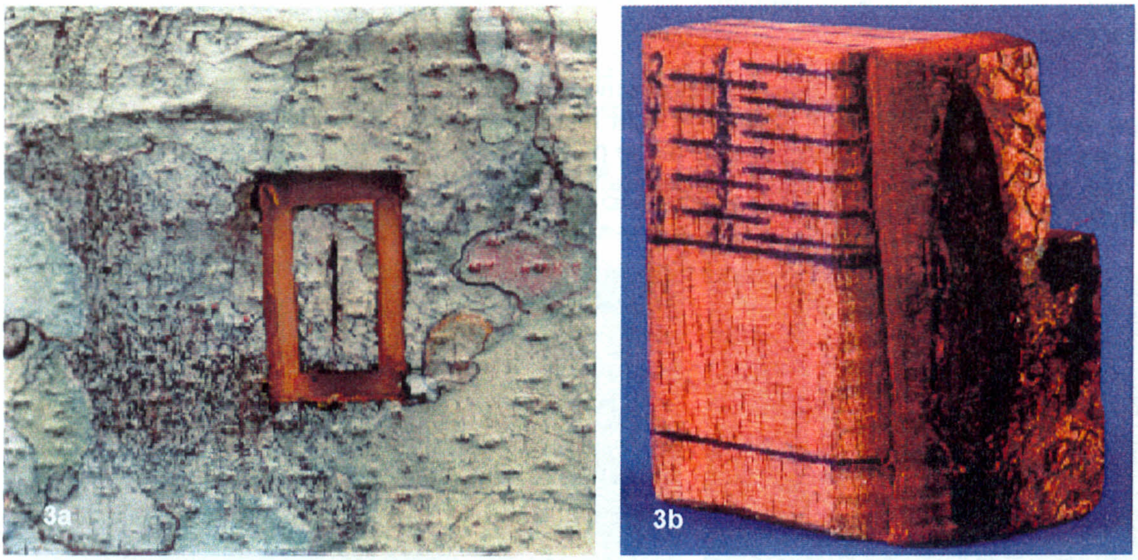


Fig. 3a/b: Methodical approach for the dating of cambial cell divisions by the pinning method. (a) Sample preparation of wounded tissue; wounding 20 mm length. (b) Preparation of microtome slides of different parts of the wounded tissue as to investigate the wound reaction at different positions of the wound (*Carapa guianensis*).

Dating of cambial cell divisions by the "pinning-method"

The periods of cell formation were dated intraannually by repeated wounding in one-month-intervals from April 1995 until March 1997 (Fig. 3a). The cambium was wounded with a scalpel (20 mm) according to KURODA and SHIMAJI (1984; comp. also MARIAUX, 1969; YOSHIMURA et al., 1981; SHIOKURA, 1989; NOBUCHI et al., 1993). The wounds were inflicted on stem upwards at distance of 5 cm. Fixation of the samples was carried out with ethanol (70%). The wound reaction was studied by light microscopy in all three anatomical directions at different distances from the centre of the wound (Fig. 3b).

The wood anatomical studies indicated significant differences in the wound reactions, related to time and the position within the wounded zone (comp. 5a-d), which is of main importance for the accuracy of the „pinning-method" for the dating of cambial cell divisions. As a first wound reaction, after a period of 6 hours to 10 days the lumina of differentiated vessels were filled with accessory compounds (Fig. 4a/ b). Staining by safranine/ astrablue indicated that two different substances were exudated by parenchyma cells into the vessels as to avoid further air embolism (comp. SHIGO, 1984).

After a period of 3 to 15 days, an alteration of the ontogenetic development of differentiating xylem cells already became obvious (Fig. 4 c). Due to the injury cell enlargement of these cells was reduced during the primary wall phase and an increase of secondary wall formation became obvious. Consequently to that no zone of cells with a reduced radial cell diameter and thickened cell walls was found as a wound reaction due to injuries carried out during a cambial dormancy (comp. Fig.10a/ b, Fig. 10a/ b).

After a period of four days, the formation of parenchymatic callus tissue was observed in the upper and lower part of the injury (Fig. 4d). During the initial phase of callus formation especially a strong increase of anticlinal cell divisions of ray intials was observed, whereas later on, a high rate of periclinal and anticlinal cell divisions of fusiform initials was found as well.

The formation of traumatic resin channels was observed (Fig. 4a-b) within the differentiating parenchymatic callus tissue of *Carapa* 11 days after the date of wounding, for *Swietenia* after 21 days respectively. A secretion of accessory compounds from parenchymatic callus cells into the intercellular space was observed with *Swietenia* (Fig. 4b), whereas no formation of epithelic cells was found. This indicates a lysigenic formation of the traumatic resin channels (Fig. 4a). Bands of resin channels were always found in the upper and lower part of the injury (not in the centre) of *Swietenia* and *Carapa*. Therefore, traumatic resin channels are suitable anatomical characteristics for the dating of cambial cell divisions by means of the „pinning method" of *Swietenia macrophylla* and *Carapa guianensis*. For this reason, in this study the formation of resin channels was used as a characteristic for monthly increment measurements. Callus formation of *Carapa* was terminated after a period of three weeks, whereas callus formation of *Swietenia* was observed during a 4-week-period.

In general, no significant differences were found between the wound reactions of *Swietenia* and the wound reactions of *Carapa*. Nevertheless, a strong relationship was found between the rate of cambial cell divisions and the intensity and velocity of the wound reactions (comp. Fig. 9 a/ b, Fig. 10 a/ b), which have to be taken into account for the application of the „pinning method" for increment measurements of *Swietenia* and *Carapa* trees.

From these anatomical studies, according to „Gauß´s law" a total error percentage for increment measurements by means of the „pinning method" was calcuated (Fig. 6). For the accuracy of this method, the position of the investigated wound reaction, the time of wounding, and the variation of cambial activity within the stem are of main importance. These findings showed that accurate increment measurements are only possible by means of the „pinning method" for monthly increments higher than 0.3 mm (Fig. 6).

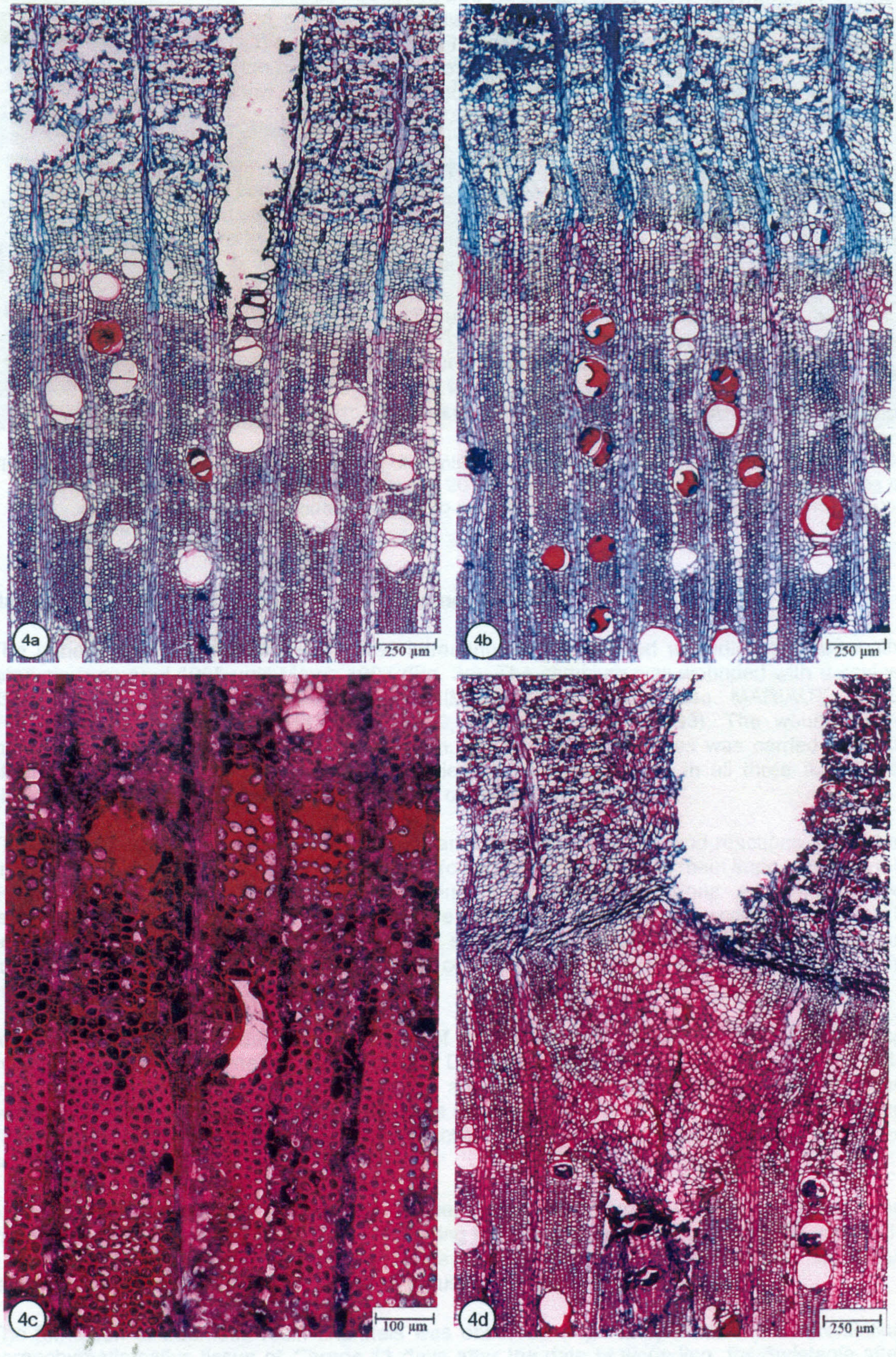


Fig. 4a-d: Wound reactions of 6-year-old *Carapa guianensis*. (a) Accessory compounds within the lumina of vessels, 6 hours after the injury. (b) Accessory compounds within the lumina of vessels, 14 days after the injury. (c) Fibres with thickened secondary cell walls and reduced lumina, 14 days after the injury. (d) Parenchymatic callus tissue, 14 days after the injury.

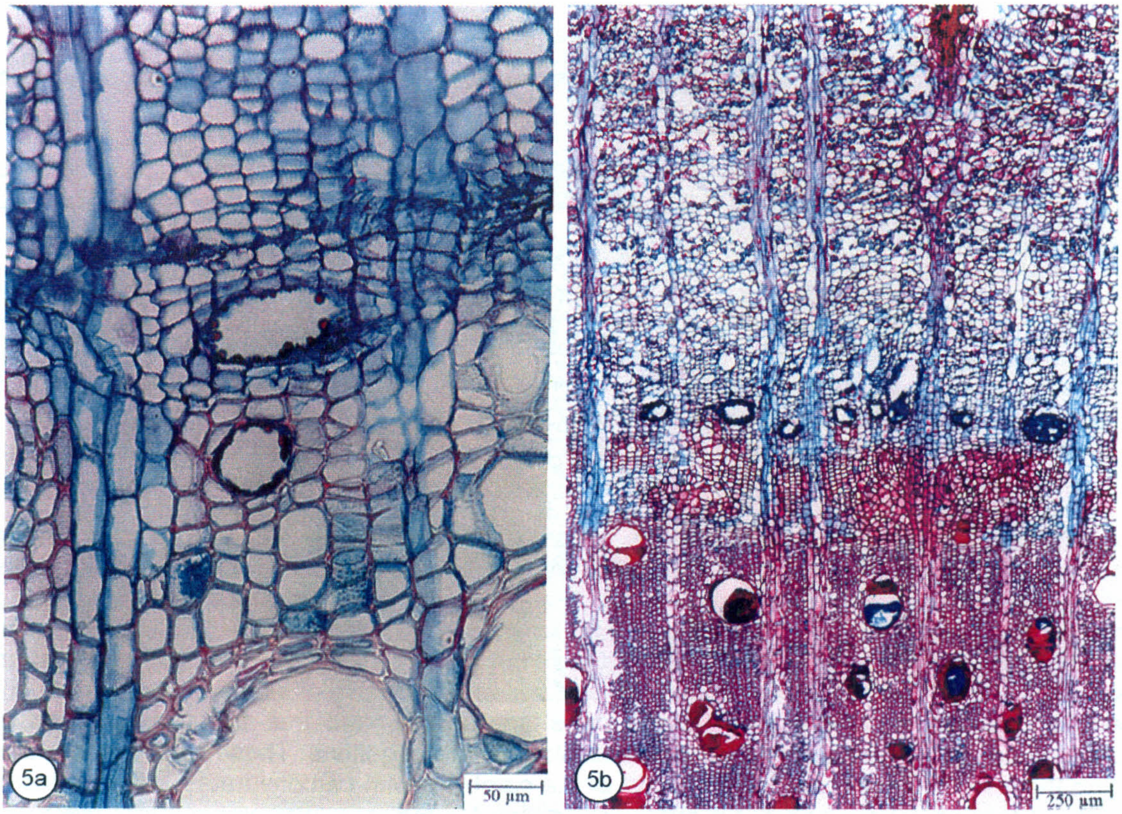


Fig. 5a/b: Formation of traumatic resin channels. (a) Lysigen separation of parenchyma cells and secretion of accessory compounds of parenchyma cells into the intercellular space. (b) Band of resin channels (*Carapa guianensis*).

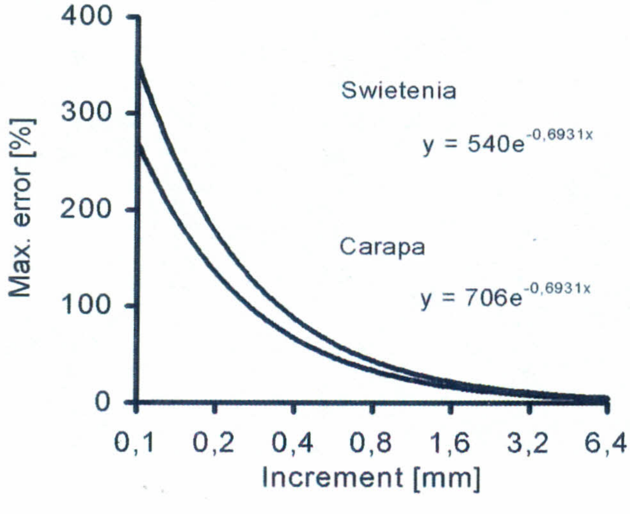


Fig. 6: Gauß error (position of the investigated wound reaction x time of wounding x variation within the stem) of increment measurements based on the pinning method.

Results

Anatomical characteristics of the xylem of plantation-grown *Swietenia macrophylla* and *Carapa guianensis*

The study on the anatomical characteristics of the juvenile xylem of *Swietenia* and *Carapa* were carried out with special regard to the formation of increment zones and their relationship to exogenous factors.

In contrast to adult wood, two types of increment zones were observed in the juvenile xylem of *Swietenia* and *Carapa* trees (Fig. 7a-b). In the inner part of the stem, vessel bands (accompagned/ not accompagned with paratracheal-confluent parenchyma cells) were found, whereas in the outer part of the stem parenchyma bands were observed, which are existent both in the adult wood of *Swietenia* and *Carapa* (Fig. 8a-b; comp. COSTER, 1927; GOTTWALD, 1961; WAGENFÜHR and SCHREIBER, 1974; BREITSPECHER and BETHEL, 1990; BAUCH et al., 1999).

Some of the „increment zones" observed in the stem discs of *Swietenia* and more than 80% of the „increment zones" of the outer stem of *Carapa* were not closed all over the stem cross section. After cross-dating of the width of increment zones of stem discs of different trees and different tree heights, no correlation was found between the width curves of the increment zones measured at four stem radii. This and the high number of increment zones of the stem discs of 4- to 6-year-old trees (up to 15 increment zones) indicated that at least not all increment zones of juvenile *Swietenia* and *Carapa* trees are annual, and that the width curves of increment zones are not suitable for dendroecological investigations. These results show that during the juvenile phase the „local supply" of the cambium with carbohydrates, water, mineral elements, and phytohormones is of more importance for the structural dynamics of the trees (comp. ALONI, 1989). Furthermore, from these findings it was concluded that the structural dynamics in wood formation of *Swietenia* and *Carapa* are not only correlated with exogenous factors.

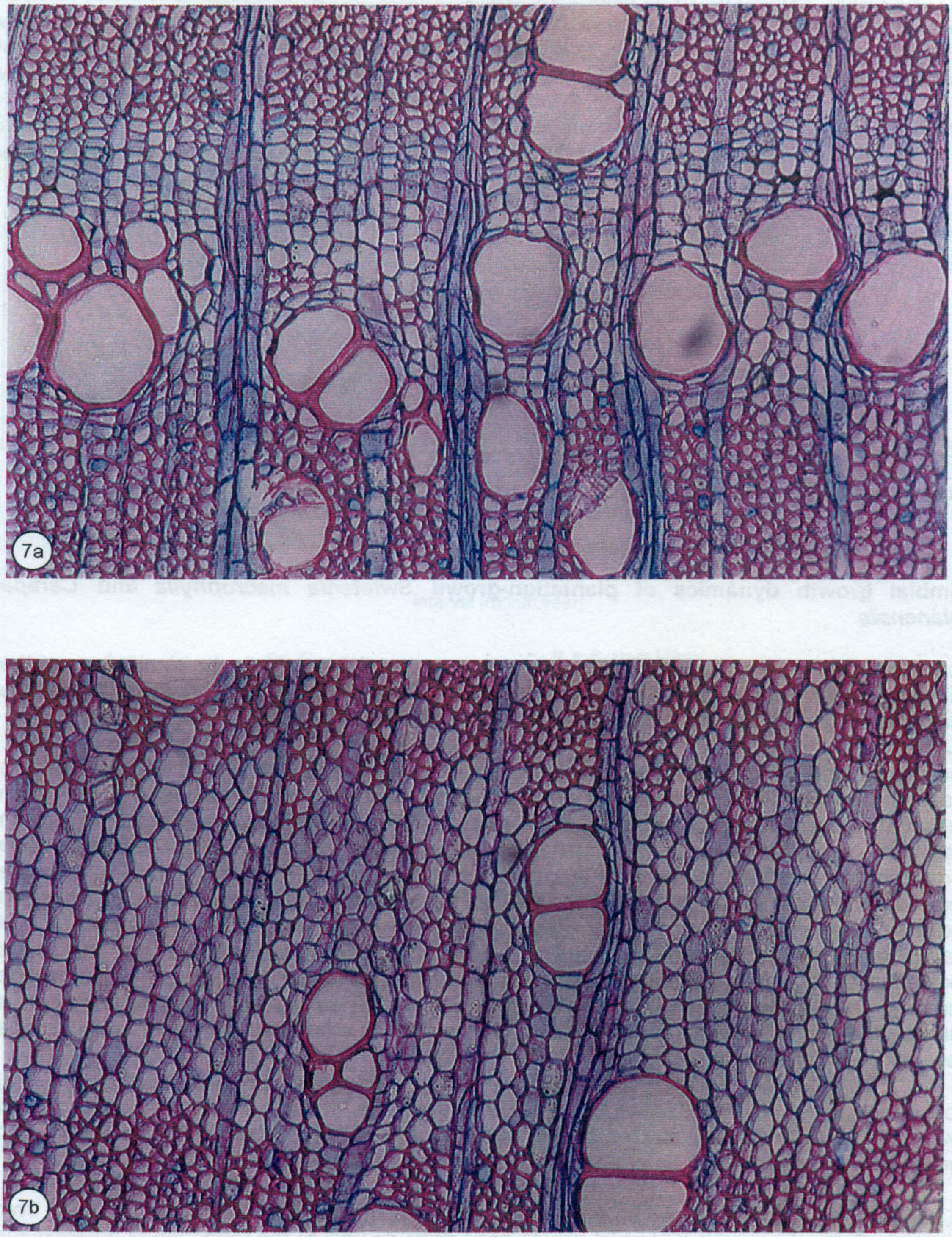


Fig. 7a/b: Increment zones of *Swietenia macrophylla* formed by (a) vessel bands and (b) parenchyma bands

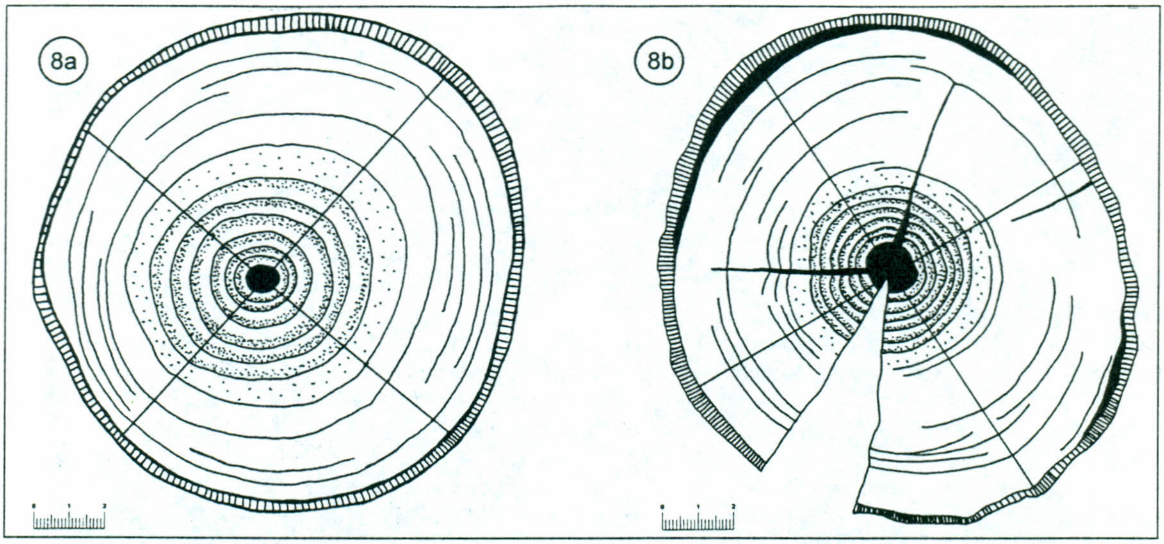


Fig. 8a/b: Distribution of increment zones within a stem disc of (a) *Swietenia macrophylla* and (b) *Carapa guianensis*. Dotted line=vessel bands, line=parenchyma bands

Cambial growth dynamics of plantation-grown *Swietenia macrophylla* and *Carapa guianensis*

Concerning the study of the significance of exogenous factors, especially the significance of the soil water supply, for the cambial growth dynamics of the trees the monthly increment of the trees was compared with the water supply within the plantation systems.

The quantification of the water supply in the plantation systems I, II, and III showed that the seasonal variation of the precipitation causes a strong reduction of the soil water supply from August until December (comp. DÜNISCH et al., 1999a). The intraannual cambial growth dynamics of *Swietenia*, expressed in terms of monthly increment (Fig. 9a) showed a corresponding decrease of the rate of cambial cell divisions, which was correlated with the decrease of the soil water content. Wood anatomical studies of the cambial zone of *Swietenia* showed that already after a couple of days with a reduced soil water content (suction force of the soil >700 hPa) a cambial dormancy was initiated (comp. Fig. 10a-b). At the end of the vegetation period (August/September), in all *Swietenia* trees the formation of at least one parenchyma band was observed (Fig. 9a, comp. Fig. 8 c). This indicated that the formation of parenchyma bands in the xylem of *Swietenia* is initiated by a reduced soil water supply of the trees.

Corresponding to the significance of the water supply for the cambial growth dynamics of *Swietenia,* wood anatomical studies of differentiating xylem showed that cell differentiation and lignification of vessels are to be preferred to fibres and parenchyma cells.

In contrast to that, no correlation was found between the reduced soil water content from August to December and the cambial growth periodicity, as well as the formation of parenchyma bands of plantation-grown *Carapa* (Fig. 9b). Nevertheless, from the increment curves and wood anatomical studies it became obvious that a cambial dormancy occurs in *Carapa* trees, as well. For the study of the relationship between exogenous factors and the cambial growth dynamics of *Carapa,* further investigations on the carbohydrate, water, element and phytohormone supply of the cambium are necessary. Nevertheless, these findings already showed that wood formation of *Carapa* is less influenced by drier periods than the wood formation of *Swietenia*.

Furthermore, a reduced xylem production of *Swietenia* grown in the plantation systems II and III compared to system I is of main interest (Fig. 9a), which is not explained by differences in the soil water supply between the plantation systems (comp. DÜNISCH et al., 1999a). The reduced xylem formation of *Swietenia* grown in the plantation system II and III, compared to the plantation system I, is caused by a reduced rate of periclinal cell divisions during the growing season and a reduced period of cambial cell divisions (Fig. 9a, Fig. 10a-b). The period of cambial cell divisions of *Swietenia* grown in system I lasts from December until October, whereas cambial cell divisions of *Swietenia* grown in system III only were observed from January until September. The reduced xylem production of *Swietenia* in system III is correlated with a surplus of cambial cell divisions compared to xylem differentiation per time unit (number of cambial cells: number of not completely differentiated xylem cells: *Swietenia* system I: 3.3, *Swietenia* system III: 6.2). This indicates an insufficient supply of differentiating xylem cells with carbohydrates and/ or water and/ or mineral elements in plantation system III.

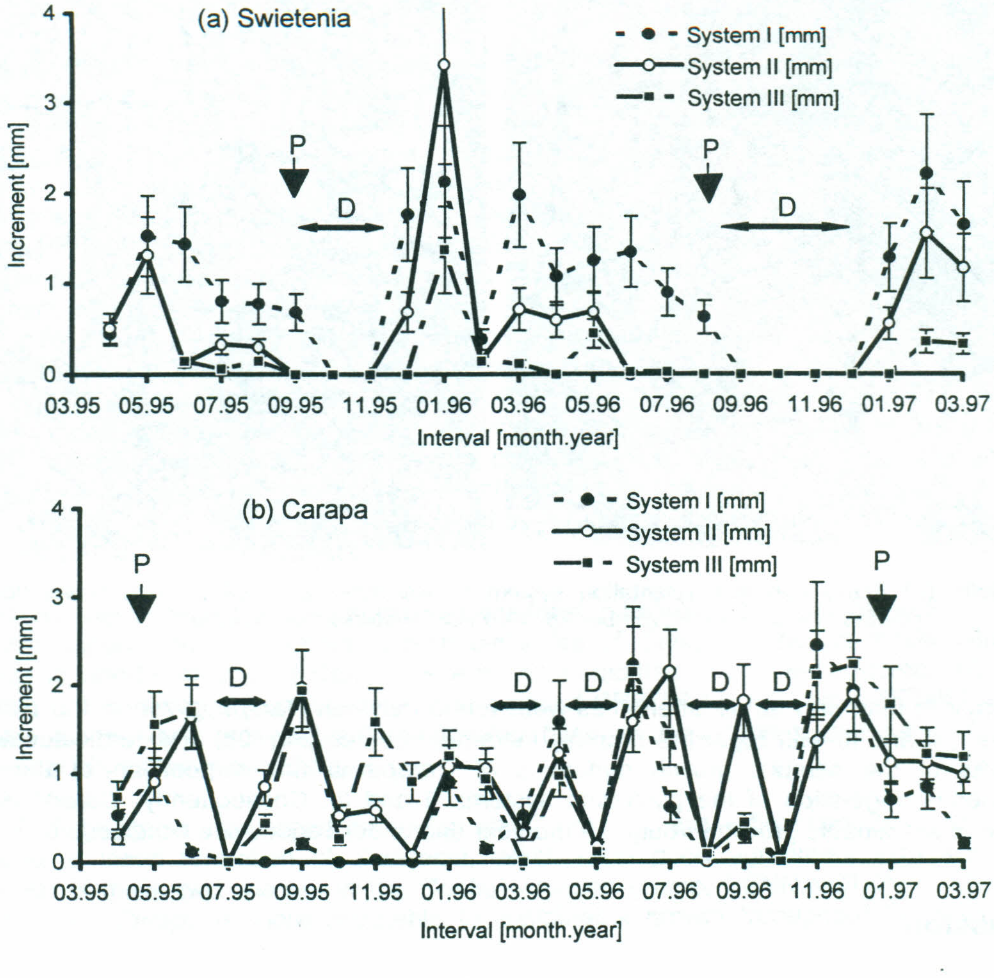


Fig. 9a/b: Monthly increment [mm] of (a) *Swietenia macrophylla* and (b) *Carapa guianensis* grown in plantation system I, II, and III. April 1995 until March 1997. Formation of parenchyma bands is marked by (P), cambial dormancy is marked by (D).

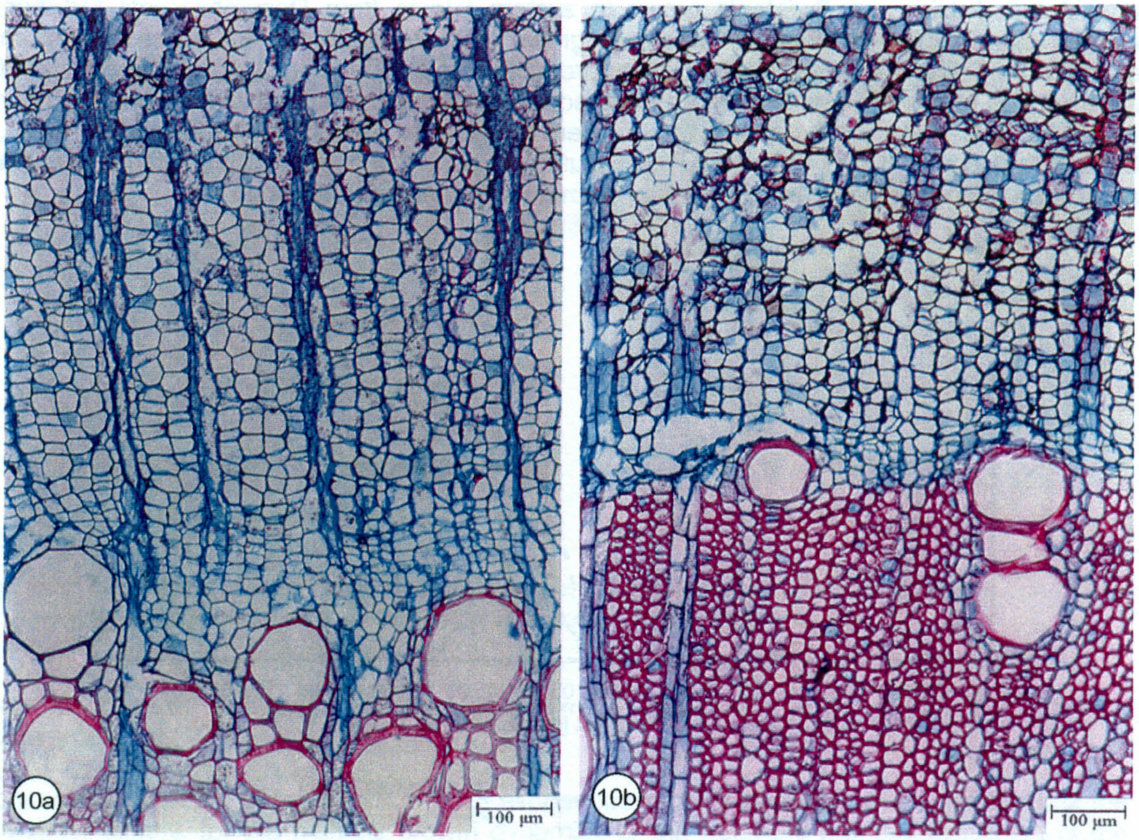


Fig. 10a/b: (a) Active cambium (plantation system I, November 27, 1997). (b) Cambial dormancy (plantation system III, November 28, 1997) of *Swietenia macrophylla*.

In contrast to that, only small differences were found between *Carapa* grown in the plantation systems I, II and III with regard to monthly increment curves (Fig. 9b). This indicates a lower sensitivity of the cambial growth dynamics of *Carapa* to the competition of the dense spontaneous vegetation of the plantation systems II and III. Consequently, *Carapa* is more adapted to sustainable growth throughout the year and under various site conditions.

Discussion

Recent investigations on the growth dynamics of tropical tree species were carried out with special regard to the significance of extrinsic and intrinsic factors for the cambial activity of the trees (comp. COSTER, 1927, 1928; ECKSTEIN et al., 1981; WORBES, 1988; DÉTIENNE, 1989). These studies also emphasized the methodical difficulties related to growth rate determination and the characterization of the cambial activity of the trees. In this study, the „pinning method“ (comp. MARIAUX, 1969; KURODA and SHIMAJI, 1984; SHIOKURA, 1989; SACK, 1998) was used for dating the cambial activity of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. The obligatory formation of traumatic resin channels after wounding according to the compartimentalization concept proposed by SHIGO (1984) offered the chance for reproducible increment measurements. From these findings, it was also concluded that the formation of resin channels in these two species is initiated by exogenous factors and is not determined by genetic factors (comp. GOTTWALD, 1961; WAGENFÜHR and SCHREIBER, 1974). Nevertheless, a high error percentage was calculated for the growth rate determination of *Swietenia* and *Carapa* by means of this method, especially in periods with low increment. Due to this error percentage, an accurate determination of a cambial dormancy and of variations in the structural dynamics of the trees (e. g. formation of vessel and parenchyma bands) was not possible.

Therefore, sample collections and microscopical investigations on the structure of the cambial zone are an urgent need for the study of the cambial growth dynamics of *Swietenia* and *Carapa* trees. The sample collection with small borers (comp. BÄUCKER et al. 1998; SACK, 1998) offers the chance for repeated sample collections at different positions of the tree without strong „callus effects" (comp. SHIGO, 1984; SCHMITT and LIESE, 1993). Nevertheless, sample collection of cambial tissue as well as the dating of cambial activity by means of the „pinning method" allow only „spot measurements". The investigations of SACK (1998) showed that strong differences of the cambial activity of *Swietenia* and *Carapa* occur even at the same stem height, which might by explained by local alterations of the phytohormone, carbohydrate, water and element supply of the tree (comp. LARSON, 1969; WODZICKI, 1973; WAREING, 1981; FUJITA and HARADA, 1979). Therefore, in further investigations in addition to these studies on the growth dynamics in wood formation of *Swietenia* and *Carapa*, dendrometer measurements should be carried out (comp. FRITTS, 1976; VOGEL 1994).

Most of the dendrecological investigations on the relationship between climatic factors and the cambial growth dynamics of tropical trees were carried out with a strong emphasis on the influence of the soil water supply (comp. DÉTIENNE and MARIAUX, 1977; WORBES, 1989; PUMIJUMNONG et al., 1995). A strong impact of the water supply on the increment of *Swietenia* was found. The formation of parenchyma bands and a cambial dormancy of *Swietenia* was correlated with a reduced water supply of the trees (comp. COSTER, 1927; DÜNISCH, 1999a). Nevertheless, the formation of increment zones was not annual and increment zones characterized by vessel bands (inner part of the stem) and parenchyma bands (outer part of the stem) were found as well. Due to the ecological significance of vessel formation for the water supply of the trees, the formation of vessel bands as well might indicate a reduced water supply of *Swietenia* even in periods with high monthly precipitation (DÜNISCH et al., 1999a; comp. ZIMMERMANN, 1983; KRAMER, 1985; SASS, 1993). The reduced increment of *Swietenia* in dense plantation systems (system II and III) due to a low rate of periclinal cell divisions and a reduced period of cambial activity indicates a strong competition in the growth of *Swietenia* trees in these plantation systems (comp. GÖTTSCHE-KÜHN, 1988; DÜNISCH et al., 1994), which might be caused by a reduced element supply (DÜNISCH et al., 1999b), as well as by light deficiency.

In the study, there was not found a significant relationship between the seasonal variation of the soil water supply and the cambial growth dynamics of *Carapa*, although similar structural dynamics in wood formation of *Carapa* were found, compared to *Swietenia* (comp. BAUCH et al., 1999). These findings correspond with findings of BREITSPECHER and BETHEL (1990), who also did not find a significant relationship between precipitation and cambial growth dynamics of plantation-grown *Carapa*.

These findings show that wood formation of *Carapa* is less influenced by drier periods compared to wood formation of *Swietenia*, which is in good agreement with the natural distribution of these two species in the Central Amazon (comp. PENNINGTON et al., 1981). Consequently, *Carapa* is more adaptable to sustainable growth throughout the year in the Manaus region.

References

ALONI, R.: Control of xylogenesis within the whole tree. Ann. Sci. For., 46 (1989) 267 – 272.

BÄUCKER, E.; BUES, C.T., VOGEL, M.: 1998, Radial growth dynamics of spruce (*Picea abies*) measure by micro-cores. IAWA Journal, 19 (1998) 301 - 309.

BREITSPECHER, A.; BETHEL, J. S.: Stem-growth periodicity of trees in a tropical wet forest of Costa Rica. Ecology, 71 (1990) 1156 – 1164.

COSTER, C.: Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen I. Ann. Jard. Buitenzorg, 37 (1927) 49 – 161.

COSTER, C.: Zur Anatomie und Physiologie der Zuwachszonen und Jahresringbildung in den Tropen II. Ann. Jard. Buitenzorg, 38 (1928) 1 – 114.

DÉTIENNE, P.: Appearance and periodicity of growth rings in some tropical woods. IAWA Journal, 10 (1989) 123 – 132.

DÉTIENNE, P.; MARIAUX; A.: Nature et périodicité des cernes dans les bois roughes de Méliacées africaines. Revue Bois et Forêts des Tropiques, 175 (1977) 52 – 61.

DÜNISCH, O.; SCHROTH, G.; MORAIS, R. de; ERBREICH, M.: Water supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. in three plantation systems. BFH Mitteilungen Nr. 193 (1999) 29 – 45.

DÜNISCH, O.; BAUCH, J.; SCHWARZ, Th.: Supply of *Swietenia macrophylla* King *and Carapa guianensis* Aubl. with K, Ca, and Mg in three different plantation systems. BFH Mitteilungen Nr. 193 (1999) 47 – 59.

DÜNISCH, O.; BAUCH, J.: Influence of mineral elements on wood formation of spruce (*Picea abies* L. Karst.). Holzforschung, 48 (1994) 5 - 14.

DÜNISCH, O.; BAUCH, J.; GASPAROTTO, L.; NEVES, E.; AZEVEDO, C.; LIMA, R. de; MORAIS, R. de: Environment-tree growth relationships of plantation-grown tropical tree species as a basis for sustainable timber production in mixed culture systems in Central Amazonia. In: LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 – 19 (1998) 13 p. (in print).

ECKSTEIN, D.; OGDEN, J.; JACOBY, G. C.; ASH, J.: Age and growth rate determination in tropical trees: The application of dendrochronological methods. In: Age and growth rate of tropical trees: new directions for research, BORMANN; F. H.; BERLYN, G., Yale University, New Haven. 1981, 83 – 106.

FEARNSIDE, P. M.: Forests or fields? A response to the theory that tropical forest conservation poses a threat to the poor. Land Use Policy, 10 (1993) 108 – 121.

FRITTS, H. C.: Tree rings and climate. Acad. Press, London, New York, San Francisco. 1976, 567 p.

FUJITA, M.; HARADA, H.: Autoradiographic investigations on cell wall development. Mokuzai Gakkaishi, 24 (1979) 89 – 94.

GERLACH, D.: Botanische Mikrotechnik. Georg Thieme Verlag, Stuttgart, 1977, 311 p.

GÖTTSCHE-KÜHN, H.: Bildung und Eigenschaften des Holzes von Fichten (*Picea abies* L. Karst.) aus Waldschadensgebieten. Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, 157 (1988) 171 p.

GOTTWALD, H.: Handelshölzer. Ferdinand Holzmann Verlag, Hamburg, 1961, 249 p.

HANNAN, S. A.; BETALHA, B. H. L.: Amazônia: Contradições no paraíso ecológico. Cultura Editores Associados, São Paulo, 1995, 265 p.

JACOBY, G. C.: Overview of tree-ring analysis in tropical regions IAWA Journal Vol. 10 (1989) 99 – 108.

KOZLOWSKI, T. T., KRAMER, P. J., PALLARDY, S. G.: The physiological ecology of woody plants. Academic Press San Diego, New York, 1991, 657 p.

KRAMER, P. J.: Water relations of plants. Academic Press Orlando, 1985, 489 p.

KURODA, K.; SHIMAJI, K.: The pinning method for marking xylem growth in hardwood species. Forest Science, 30 (1984) 548 – 554.

KURODA, K.; SHIMAJI, K.: Wound effects on xylem cell differentiation in a conifer. IAWA Journal, 5 (1984) 295 - 305.

LARSON, P. R.: Wood formation and the concept of wood quality. New Haven, Yale University: School of Forestry, Bulletin No. 74, 1969.

MARIAUX, A.: La periodicité de formation de cernes dans le bois de limba. Bois et Forêts des Tropiques, 128 (1969) 39 – 45.

MÖLLEKEN, H.; ECKSTEIN, D.; VENNE, H.; SCHOLZ, F.: Growth of young Norway spruce (*Picea abies* L. Karst.) clones as controlled by genotype and environment. Dendrochronologia, 12 (1997) 23 – 32.

NOBUCHI, T.; FUJISAWA, T.; SAIKI, H.: An application of the pinning method to the marking of the differentiating zone and to the estimation of the time course of annual ring formation in Sugi (*Cryptomeria japonica*). Mokuzai Gakkaishi, 30 (1993) 716 – 723.

PENNINGTON, T. D.; STYLES, B. T.; TAYLOR, D. A. H.: Flora Neotropica. Monograph, New York, 28 (1981) 421 S.

PUMIJUMNONG, N.; ECKSTEIN, D.; SASS, U.: Tree-ring research on *Tectona grandis* in Northern Thailand. IAWA Journal, 16 (1995) 385 – 392.

SACK, M.: Charakterisierung der Holzbildung und des Zuwachses von *Swietenia macrophylla* King und *Carapa guianensis* Aubl. aus der Familie der *Meliaceae* unter Plantagenbedingungen in Zentralamazonien. Master thesis, Hamburg University (1998) 93 p.

SASS, U.: Die Gefäße der Buche als ökologische Variable. Bildanalytische Erfassung, dendroklimatologische Prüfung, ökologische Bewertung. PhD.-thesis Hamburg University (1993), 172 p.

SASS, U.; KILLMANN, W.; ECKSTEIN, D.: Wood formation in two species of Dipterocarpaceae in peninsular Malaysia. IAWA Journal, 16 (1995) 371 – 384.

SCHMITT, U.; LIESE, W.: Response of xylem parenchyma by suberization in some hardwoods after mechanical injury. Trees, 8 (1993) 23 – 30.

SCHWEINGRUBER, F. H.: Der Jahrring. Paul Haupt Verlag, Bern, Stuttgart, 1983, 234 p.

SHIGO, A. L.: Compartmentalization: conceptual framework for understanding how trees grow and defend themselves. Phytopathology, 22 (1984) 189 – 214.

SHIOKURA, T.: A method to measure radial increment in tropical trees. IAWA Journal, 10 (1989) 147 – 154.

VETTER, R. E.; BOTOSSO; P. C.: Remarks on age and growth rate determination of Amazonian trees. IAWA Journal, 10 (1989) 133 – 145.

VOGEL, M.: Automatische Radialzuwachsfeinmessung in einem Fichtenaltbestand und Möglichkeiten der Interpretation kurzfristiger Schwankungen der Zuwachswerte. Allg. Forst- und Jagdztg., 165 (1994) 34-40.

VYSOTSKAYA, L.G., VAGANOV, E.A.: Components of the variability of radial cell size in tree rings of conifers. IAWA Bulletin, 10 (1989) 417-427.

WAGENFÜHR, R.; SCHREIBER, C: Holzatlas. VEB Fachbuchverlag, Leipzig, 1974, 334 p.

WAREING, P. F.: Plant growth substances. Academic Press London, New York, 1981, 682 p.

WILPERT v., K.: Die Jahrringstruktur der Fichten in Abhängigkeit vom Bodenwasserhaushalt auf Pseudogley und Parabraunerde. Freiburger Bodenkundliche Abhandlungen, 24 (1990) 184 p.

WODZICKI, T. J: Auxin stimulation of cambial activity in *Pinus silvestris* L. II. Dependence upon basipetal transport. Physiol. Plant, 29 (1973) 288 – 292.

WORBES, M.: Variety in structure of annual growth zones in *Tabebuia barata* (E. Mey) Sandw., Bignoniaceae, a tropical tree species from Central Amazonian inundation forests. Dendrochronologia, 6 (1988) 71 – 89.

WORBES, M.: Growth rings, increment and age of trees in inundation forests, savannas and a mountain forest in the Neotropics. IAWA Journal, 10 (1989) 109 – 122.

WORBES, M.; JUNK, W. J.: Dating tropical trees by means of ^{14}C from bomb tests. Ecology, 70 (1989) 503 – 507.

YOSHIMURA, K.; HAYASHI, S.; ITOH, T.; SHIMAJI, K.: Studies on the improvement of the pinning method for marking xylem growth I. Minute examination of pin marks in *taeda* pine and other species. Wood Research, 67 (1981) 1 – 16.

ZECH, W.; SCHROTH, G.; CRAVO; M. da S.; TEIXEIRA, W. G.; KAISER, K.; LEHMANN, J.: Water and nutrient fluxes as indicators for the sustainability of different land-use systems on the terra firme near Manaus – a project overview. LIEBEREI, R.; BIANCHI; H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 – 19 (1998) 6 p.

ZIMMERMANN, M. H.: Xylem structure and the ascent of sap. In: TIMELL, T. E. (ed.), Springer Series in Wood Science, Vol. 1. Springer Verlag Berlin, Heidelberg, New York, Tokyo (1983) 143 p.

Acknowledgements

We are grateful to the "Bundesministerium für Forschung, Bildung, Wissenschaft und Technologie", Bonn, Germany and the CNPq/ IBAMA, Brasilia, Brazil for financial support within the German-Brazilian cooperation program SHIFT (Studies on Human Impacts on Forests and Floodplains in the Tropics). We thank the Deutsche Luft- und Raumfahrt (DLR), Bonn for additional support. We also wish to thank Dr. Vincente for help during the sample preparation in the laboratory of the EMBRAPA Amazônia Ocidental. The assistance of V. Seabra and A. Souza is especially appreciated.

Comparative study on wood characteristics of *Carapa guianensis* Aubl. from two plantations and a natural site in Central Amazonia

J. Bauch,[1] O. Dünisch,[2] F. Schuster,[1] L. Gasparotto,[3] and C. P. de Azevedo[3]

[1] Institute of Wood Biology, Hamburg University, Hamburg
[2] Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg
[3] EMBRAPA Amazônia Ocidental, Manaus, AM, Brazil

Summary

The study has shown that, especially for the recultivation of degraded land areas, a small portion of long-lived trees for high quality timber production might contribute to the stabilization of mixed culture plantation systems. Nevertheless, the environmental influences on high-quality timber production of many tree species are not known in detail.

The present study with *Carapa guianensis* Aubl. was directed to find out the parameters prevalent already in young trees which determine their growth. These parameters could be useful to predict the wood characteristics and the quality of the adult trees, when they will be sufficiently mature for utilization.

The study related to two monocultures at an age of 4 (eight trees) and 17 (two trees) years respectively and to a primary forest (two trees). The growth dynamics of the eight 4-year-old trees selected revealed 11 to 15 increment zones which could not be correlated with the labelling of increment zones by vessel enrichment. The study proved that, already in the 5th year, parenchyma bands indicate the pattern of adult wood. The very early formation of adult wood is traceable in the pattern of the percentual composition of vessels, fibres, and parenchyma (ray and strand parenchyma). Furthermore, the fibre length already reaches its plateau of 1.45 – 1.59 mm at the early growth stage of about four years. It could be shown, as well, that the fibre lengths of plantation-grown trees correspond to those of primary forest trees. Average density also could be demonstrated to correspond with about 0.63 g/ cm^3. Therefore, it can be expected from the growth increment that under plantation conditions, 30- to 40-year-old trees can be harvested. According to the study, *Carapa guianensis* can be recommended for plantations in order to produce timber of high quality.

The findings of the present study on wood formation and wood characteristics of native tree species of the Central Amazon, therefore, can contribute to the development of sustainable landuse systems in this region.

Resumo

Estudo comparativo das caraterísticas da madeira de *Carapa guianensis* Aubl. procedente de duas áreas de plantío na floresta nativa da Amazônia Central

Os estudos têm mostrado que, especialmente, para o recultivo de áreas degradadas, uma pequena quantidade de árvores que produzem madeira de alta qualidade pode contribuir para a estabilização dos sistemas de cultivo misto. Contudo, não são conhecidos detalhadamente as influências do meio ambiente sobre a produção de madeira de alta qualidade de muitas espécies arbóreas.

A pesquisa com *Carapa guianensis* Aubl. objetivou definir os parâmetros existentes, predominantes nas plantas jovens e que determinam o seu crescimento. Estes parâmetros serão úteis para predizer as características e a qualidade da madeira das árvores adultas, quando atingirem a idade de corte.

Os trabalhos foram desenvolvidos em duas áreas de monocultivo, sendo uma, com oito árvores de quatro anos de idade e a outra, com duas árvores de 17 anos de idade, e em floresta nativa, com duas árvores. As dinâmicas de crescimento das árvores com quatro anos de idade revelaram 11 a 15 zonas de incremento, as quais não puderam ser correlacionadas com a marcação das zonas de incremento pelo enriquecimento dos vasos. O estudo provou que no quinto ano, parênquima em faixas indicam o padrão da madeira adulta. A formação muito precoce da madeira adulta está traçada no padrão de composição percentual dos vasos, fibras e parênquima (parênquima radial e longitudinal). Além disso, o comprimento da fibra atinge seu ápice de 1,45 a 1,59 mm no estágio inicial de crescimento aos quatro anos de idade. Verificou-se que o comprimento das fibras das árvores cultivadas é semelhante ao das árvores da floresta nativa. A densidade média foi de 0,63 g/ cm^3. Conclui-se que a *Carapa guianensis* pode ser recomendada para plantio a fim de produzir madeira de alta qualidade, com a expectativa das árvores atingirem a idade de corte entre 30 a 40 anos.

Os resultados dos estudos sobre a formação e as características da madeira de espécies nativas da Amazônia Central podem contribuir para o desenvolvimento de sistemas sustentáveis de uso da terra nesta região.

Introduction

The capital of the Federal State Amazonia, Manaus, at present experiences a high increase in population rates. This in turn leads to an increased pressure of the rapidly growing city on the surrounding tropical primary forest. The population has to be supplied with agricultural products. Additionally, there is a great demand of wood for various utilization aspects.

For this reasons, in Central Amazonia, particularly on the „terra firme", there are projects to establish mixed plantations on sites, where degradation of former forest areas occurred. In this respect, for sustainably managed, mixed plantations, tree species with high-quality timber production should be considered, as well. However, many tree species (such as *Tectona grandis*, *Shorea* spp. or *Pinus strobus*) grown under plantation management produce timber with less wood characteristics and, therefore, produce less valuable wood than under primary forest conditions (comp. BHAT et al., 1989; BOSMAN et al., 1994).

With the plantations on the „terra firme" in the Manaus region, species of the family of *Meliaceae* are favoured for their high-quality wood production. In particular, there will be a considerable demand for *Swietenia macrophylla* King., *Carapa guianensis* Aubl. and *Cedrela odorata* Roxb. for construction wood, furniture production, and veneer quality wood in the future. So far, there have not been biological, chemical, and technological studies on the wood characteristics of these species under plantation conditions on the „terra firme".

In the following study, we try to compare the wood characteristics of plantation trees of *Carapa guianensis* Aubl. in the Manaus region with those of trees from old growth primary forests. It will be attempted to demonstrate the possibilities and limits of predicting the adult wood phase at harvest for wood utilization already from characteristics of the juvenile phase. Moreover, the extent of the sustainable growth of the plantation trees will be calculated from the growth pattern to show the perspectives and limits of this method and to indicate which plantation management should be favoured.

Site and tree selection

In association with the experimental area of 19 ha of the SHIFT-project ENV 23, established in 1992, where *Carapa guianensis* Aubl. was considered for timber production, as well, the Research Centre EMBRAPA Amazônia Ocidental in Manaus planted this species in January 1992 in plots of 25 trees each, with four repeats for the study of wood characteristics and growth behaviour.

At the beginning of this study, it could not be expected that already juvenile plants at an age of only four years would allow predictions of the wood quality to be expected later on, when harvesting is calculated.

Therefore, a comparable *Carapa*-plantation of the INPA (Instituto Nacional de Pesquisa da Amazônia) at an age of 17 years might support this study. Finally, trees from a neighbouring primary forest served as a reference to the wood quality obtainable under the prevalent climatic and soil conditions.

In December 1995, eight trees in total of four plots were harvested from the 4-year-old plantation, and two very similar trees were comparatively selected from the 17-year-old plantation. Finally, two adult trees of the primary forest served as a reference. Naturally, the age of the latter could not be determined, but it certainly amounts to more than 50 years (Table 1).

Table 1: Trees of the species *Carapa guianensis* Aubl., selected from two plantations and a primary forest

Tree No.	Location	Age (years)	Diameter (centimetres)	Height (metres)
1	Plantation EMBRAPA	4	10.7	7.0
2	Plantation EMBRAPA	4	8.8	5.4
3	Plantation EMBRAPA	4	9.2	4.6
4	Plantation EMBRAPA	4	9.4	5.5
5	Plantation EMBRAPA	4	9.4	5.3
6	Plantation EMBRAPA	4	10.8	6.2
7	Plantation EMBRAPA	4	9.1	5.8
8	Plantation EMBRAPA	4	9.8	5.8
9	Plantation EEST (INPA)	17	24.5	16.7
10	Plantation EEST (INPA)	17	19.0	18.2
11	Primary forest	n. d.	26.5	27.8
12	Primary forest	n. d.	37.5	32.0

Experimental

The investigations on the wood characteristics relate to the 12 selected trees: The discs were taken in December 1995 from the freshly cut trees in a height of 1.30 m. For comparison, discs were harvested from the treetop, as well.

Macroscopically determined structural patterns on discs

Photos (1:1) from the polished discs served for the determination of bark, sapwood, heartwood, and pith portion by means of a digital board (HIPAD Plus; company: Houston Instruments). The growth increments were measured by an Eklund machine in all directions.

Microscopical observations

Along the radius in all cardinal directions of the discs, blocks were used continuously from cambium to pith for the determination of the composition (%) of the cell species (vessels, fibres, strand and ray parenchyma). These data were obtained by means of an integration ocular lens and a counting instrument (Leucodiff; company: Boskamp). By this procedure, the structural dynamics from cambium to pith can be illustrated.

The variation of the individual vessel area was measured, as well, on cross sections from 10 – 20 µm thin slides, in order to understand exogenous influences on vessel size during the annual growth.

Other important parameters of wood quality evaluation are the fibre length, the wall thickness, and the cell lumen. The fibre length, the wall thickness, and the cell lumen from cambium to pith were determined after maceration (Jeffrey solution) of small blocks continuously cut out along the radius of the discs. The dimensions of the isolated fibres were additionally determined by using the digital board.

Wood density

Carapa guianensis is, among other uses, commercially important as a wood species suitable for construction purposes. Therefore, wood density is a key parameter in the evaluation of quality. For this purpose, gradients from cambium across the pith to cambium were taken from all discs and subsequently determined gravimetrically (density r_0).

Results

Pattern of growth increments

Carapa guianensis belongs to the tree species in Amazonia which develop distinct growth increments. The parameters responsible for these growth patterns are not yet known. Therefore, it was important from the beginning onwards to determine the growth patterns macroscopically and microscopically for all of the twelve selected trees, as the dynamics of growth to a great extent determines the wood characteristics of the adult tree. The discs of the eight selected trees of the 4-year-old plantation with a diameter of up to 10.8 cm and 7.0 metres height exhibited 11 to 15 growth increments in regular distribution. The selected disc for illustration (Fig. 1) reveals 14 continuously developed zones with two to four additional indications of zones restricted to short dimensions around the disc. It turned out that a synchronization of the growth increments between the eight trees was not possible. It became obvious that individual growth behaviour dominated.

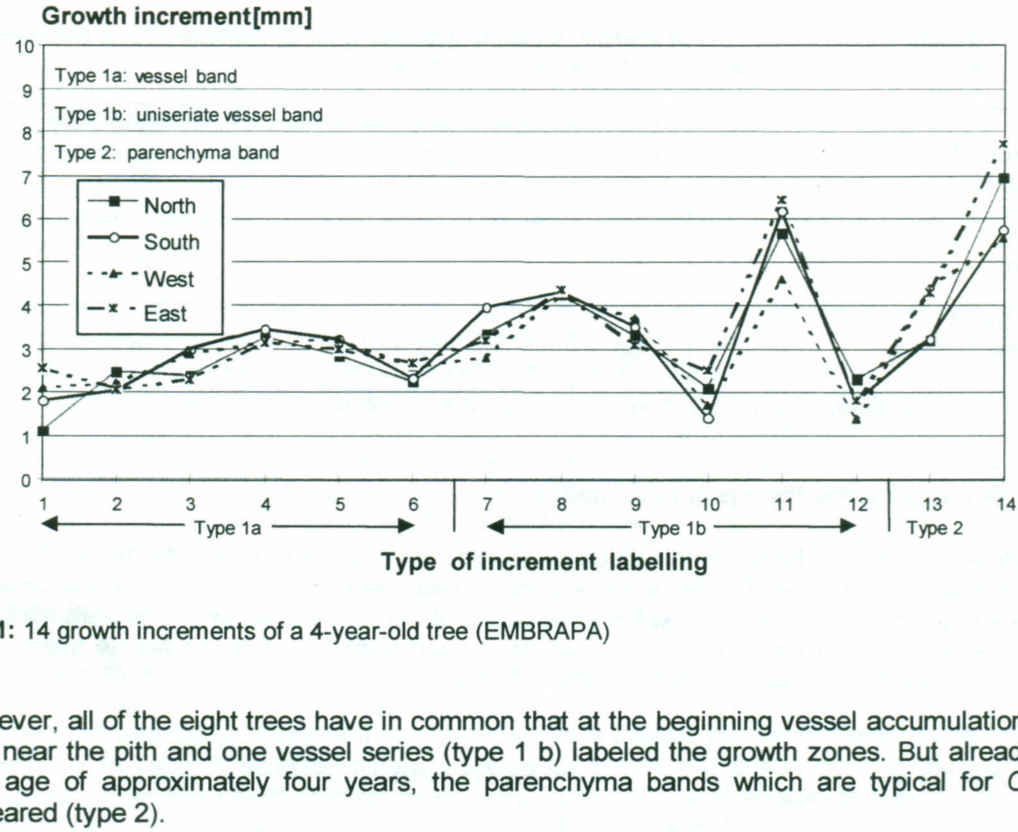


Fig. 1: 14 growth increments of a 4-year-old tree (EMBRAPA)

However, all of the eight trees have in common that at the beginning vessel accumulation (type 1 a) near the pith and one vessel series (type 1 b) labeled the growth zones. But already at a tree age of approximately four years, the parenchyma bands which are typical for *Carapa* appeared (type 2).

In addition, the growth patterns of the trees of the 17-year-old plantation and those of the primary forest coincide with that of the 4-year-old plantation. These corresponding growth patterns of the three different sites indicate that *Carapa* trees change from juvenile phase to adult phase after a tree age of only about four years already. This early change to adult wood structure is of dominant importance for the quality of wood produced under plantation conditions. Moreover, the 17-year-old plantation tree with 24.5 cm diameter and 16.7 metres height already exhibits a high portion of durable heartwood. Corresponding to that tree, the tree from primary forest (37.5 cm diameter, 32 metres height) exhibited a heartwood portion of approximately 50% already. But it is conspicuous that at an age of about four years, their growth rate was only half of the growth of trees grown on the plantation. In addition to the comparison of growth patterns under plantation and primary forest conditions, the composition of the wood from the cell species is of importance for the evaluation of wood characteristics.

Percentual composition of vessels, fibres, and parenchyma

The percentual composition of vessels, fibres, longitudinal and ray parenchyma was determined in all of the twelve selected trees. The average values were printed for the gradient pith to cambium in 20 mm steps, beginning from pith.

It is obvious that the juvenile phase of *Carapa* at all three sites indicates a high ray parenchyma (24%) and a low vessel portion (9%), as illustrated by the EMBRAPA-plantation in Table 2. In an advanced adult phase such as in trees of the primary forest, the vessel portion remarkably increased, whereas the percentages for ray parenchyma decreased.

In Table 2, the total average of the gradient pith to cambium was determined for the two plantations and the primary forest. It is significant that the percentage of the formation of fibre iss almost constant with 59 to 63% throughout the lifetime of the individual trees. The values indicated in the literature coincide with this pattern of cell composition. It can be concluded from cell composition that wood from plantations corresponds in quality to that of primary forest trees.

Table 2: Percentual composition [%] of vessels, fibres, longitudinal and ray parenchyma in the wood of the twelve selected trees of two plantations and a primary forest

Site	Vessels	Fibres	Longitudinal parenchyma	Ray parenchyma
Plantation EMBRAPA (eight trees)	9	<u>59</u>	8	24
Plantation EEST (two trees)	14	<u>63</u>	7	16
Primary forest (two trees)	17	<u>60</u>	9	14

*Percentages in literature: vessels 16%, fibres 60%, longitudinal parenchyma 7 %, ray parenchyma 17%.

Pattern of fibre lengths from pith to cambium

The high percentage of fibres in the wood of *Carapa* to a great extent determines the high quality of this wood species. But for a more detailed interpretation of the wood characteristics, the fibre length, the lumen, and the wall thickness are of importance, as well. The determination of the fibre length occurred continuously from pith to cambium for all of the twelve trees. One example of each of the three sites is indicated in Fig. 2.

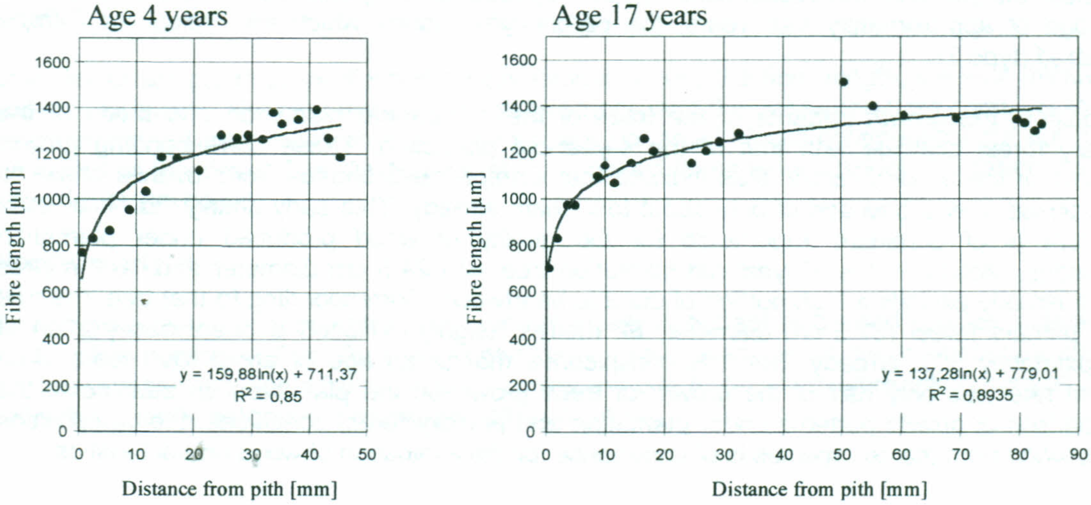


Fig. 2a/b: Fibre length from pith to cambium exemplified for the two plantations

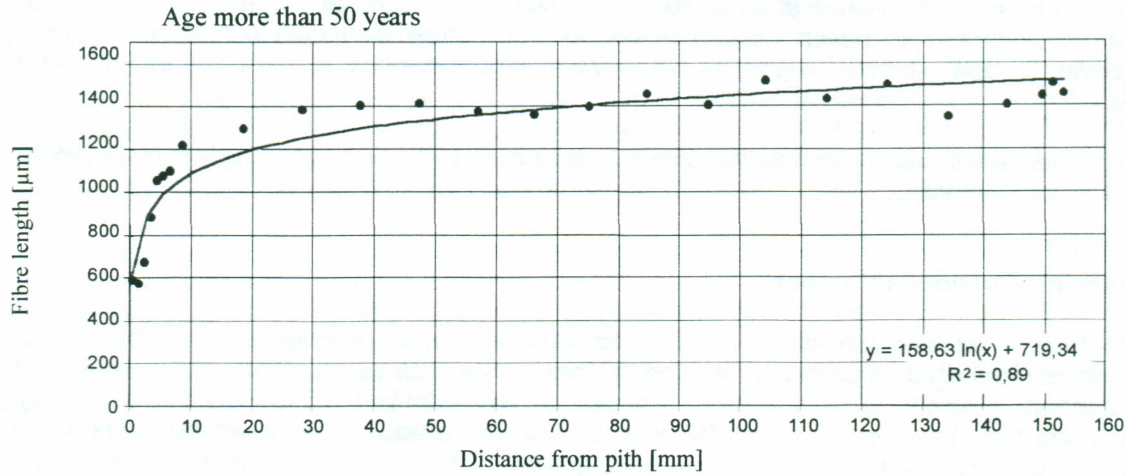


Fig. 2c: Fibre length from pith to cambium for a tree of the primary forest

On the parameter fibre length, the rapid development from juvenile to adult wood can be confirmed, as well. Already after four years growth (which is similar to about 40 mm tree radius), the fibre length of the two plantations tends to a plateau. Due to a lower increment per year of the two primary forest trees, the curve for fibre length indicating the increasing tree diameter is even steeper.

By means of a regression equation, fibre lengths of up to 1.45 to 1.59 mm could be measured for tree dimensions of about 30 cm diameter. From this calculation, it can be concluded that the fibre lengths in plantation-grown wood and of primary forest trees correspond.

Moreover, also wall and lumen dimensions exhibit corresponding values from 3.1 to 4.0 µm wall thickness and 11.0 to 14.3 µm lumen diameter at 40 mm from the pith. These data lead to the conclusion that also wood density is to be expected to be in a corresponding range, which determines the elastomechanical characteristics of the wood.

Wood density

With regard to estimate the elastomechanical characteristics of wood from plantation trees compared to that of trees from primary forests, the density (R_0: g/ cm^3, oven dry wood) is a key parameter for evaluation. Density measurements were carried out for all twelve trees from pith to cambium. In Table 3, selected data are shown for the zone 0 to 40 mm, beginning from pith for all trees, in addition to the thicker trees (EEST-plantation and primary forest) also the outer xylem zone (40 mm, neighbouring to the cambium) was included.

Table 3: Determination of the density [R_0: g/ cm^3] from pith to cambium for twelve selected trees of three sites

Site	Measure [n]	Density [g/ cm^3]	Variation coefficient [%]
Plantation EMBRAPA 0 – 40 mm	145	0.59	5.33
Plantation EEST 0 – 40 mm outer xylem	36 39	0.55 0.63	6.57 5.73
Primary forest 0 – 40 mm outer xylem	37 37	0.59 0.62	7.39 5.94

As a basic result, it can be emphasized that the juvenile wood density with 0.55 - 0.59 g/ cm^3 already is close to the values of adult wood with 0.62 and 0.63 g/ cm^3 respectively. This high density, comparable to beech wood, can be obtained under plantation conditions, as well. Moreover, *Carapa* is outstanding for its low variation in density within a single tree and between trees.

As a consequence, wood of plantation-grown *Carapa* is as suitable for construction purposes as wood of primary forests.

Trends in heartwood formation

In contrast to construction wood, wood for furniture and veneers mainly is classified by its decorative heartwood. In particular, accessory compounds such as flavonoids are the cause of the decorative colour. Monitoring the cross-section area [cm^2] of the discs at breast height (DBH) and their heartwood portion [%], it is striking that already 17-year-old plantation trees show 14 to 17% heartwood of good veneer quality (Table 4). The formation of heartwood increases disproportionally to the tree age. Therefore, a similar portion of heartwood, as in primary forest trees, with 64 and 78% can be predicted for plantation trees of the same age. The decorative character in combination with a high natural durability will guarantee a high economic value with an increasing tendency for *Carapa*.

Table 4: Comparison of the cross section area to its proportional content of heartwood

Site	Cross-section area (disc) [cm^2]	Portion of heartwood [%]
Plantation EMBRAPA	59 - 91	**0**
Plantation EEST	237 and 401	**14** and **17**
Primary forest	511 and 913	**64** and **78**

Discussion

For *Carapa guianensis*, the development from juvenile to adult wood was not yet described. Therefore, comparative histological and histometrical studies on wood from plantations and a primary forest of this species were necessary to predict the quality of adult wood from juvenile wood, as far as wood properties are considered. Whereas in a previous study, the growth dynamics throughout the year were of main interest (SACK, 1998; DÜNISCH et al., 1999), the present study is concentrated in the structural dynamics and the wood quality of the selected twelve trees.

After the cutting of tropical and subtropical plantation trees, in several cases it became obvious that the wood characteristics and the wood quality of these trees do not reach the same high level as the trees grown in the primary forest (BEN DISEN, 1978; ZOBEL, 1985; BRAZIER, 1985). This is due to the fact that fast-growing plantation trees with identical stem diameter develop a higher portion of juvenile wood compared to primary forest trees. This development is independent of tree age, which can vary significantly in the number of years (ZOBEL and BUIJTENEN, 1989).

The variability of the structural dynamics within a tree depends on the endogen triggered ageing of the cambium and on the exogen inputs in the meristem (PANSHIN and DE ZEEUW, 1980). Physiologically, it functions as a sink for water, carbohydrates, nutrient elements, and phytohormones. The structural dynamics from pith to cambium revealed a remarkably rapid development from juvenile to adult wood. There is strong evidence that in the juvenile phase, the scarcely visible increment zones are formed by vessel enrichment as short, tangentiallyoriented bands or by bands continuously developed around the 360° circumference. However, the 11 to 15 bands in a 4-year-old tree of *Carapa* do not reveal any clear relationship with dry and wet seasons. Moreover, already from about a tree-age of four years, the bands are determined by longitudinal parenchyma as is usual for adult wood (comp. VETTER, 1995). Compared with the development of adult wood in other tropical hardwoods (comp. MÜLLER, 1987; BOSMAN et al., 1994), *Carapa guianensis* reaches adult structural dynamics at a very early age. This result, which is a very positive one for the utilization of the wood, can be confirmed by several cell characteristics and by parameters determining wood quality.

The variability of the portion of the cell-species measured across from pith to cambium is relatively low, compared to other species. Even in juvenile wood, about 60% of the wood volume consist of fibres, similar to average adult wood. With increasing tree diameter, the portion of vessels increases to some extent. A corresponding decrease is obvious in the ray-parenchyma portion. This vessel increase is combined with an increasing vessel diameter in the juvenile phase, which could be already demonstrated by OBAYASHI and SHIOKURA (1989) for three fast-growing tropical tree species.

The fibre length, which is strongly genetically determined, represents a suitable parameter for predicting the development from juvenile to adult wood (ZOBEL and JETT, 1995). By means of regression analyses of the development of fibre length from pith to cambium, for *Carapa* a maximum plateau from 1.45 to 1.59 mm can be expected. The fibre-length is genetically determined. This genetical determination can be shown convincingly by the fact that, as to fibre-length, the fast-growing and slow-growing 4-year-old trees in the monoculture and the enrichment system respectively correspond as concerns age, but not as concerns diameter.

The results on the wood-anatomical characteristics of juvenile and adult wood of *Carapa guianensis* indicate that wood from a plantation and a primary forest corresponds in the structural composition. Additionally, the measurements of wood density, which determines the elastomechanical properties, measured across the tree diameter showed a high density already in the juvenile phase with about 0.55 to 0.59 $g \cdot cm^{-3}$ respectively in all twelve experimental trees with a low deviation of the mean values. The slight increase of density up to 0.62 and 0.63 $g \cdot cm^{-3}$ respectively can be explained with an increase of wall-thickness in the adult wood zones. PANSHIN and DE ZEEUW (1980) showed that most of the diffuse porous hardwood species follow this trend. But they could also identify two other types of density patterns across the stem, which were later on confirmed by BHAT et al. (1989). According to these studies, density can increase from pith outwards to the adult wood, as shown for *Carapa*. The density can increase until the cambium even in the adult wood (comp. WIEMANN and WILLIAMSON, 1988). Finally, KURODA et al. (1995) confirmed a third density pattern, where the density increased in younger trees and changed in older trees outwards to a slight decrease.

The relatively high and uniform density of *Carapa guianensis* combined with straight and large trunks on the one hand favours the utilization also for construction purposes. On the other hand, heartwood of *Carapa guianensis* is estimated for veneers, because of its natural durability and its decorative structure.

The 17-year-old plantation of *Carapa guianensis* shows that also under plantation growth conditions, heartwood formation already begins in young trees of this species and that the heartwood portion increases rapidly in volume and colour quality. Considering the distinctly different site factors, such as temperature, soil water supply, light intensity, element supply and insect calamities, in plantations and primary forests respectively, this finding is very promising for high-quality timber production under suitable plantation conditions.

In recent years, several methods of management for sustainable mixed plantations were favoured in tropical regions, in order to decrease the high exploitation pressure on primary forests. With respect to the „terra firme“ in the Central Amazon, preliminary results on the management of mixed plantations with fruit, crops, and to some extent high-quality timber production, *Carapa* is one of the favoured species for good harvests concerning quantity and quality. Considering the increasing future demand for high-quality wood in Brazil, high-quality timber production can be highly recommended.

References

BENDTSEN, B. A.: Properties of wood from improved and intensively managed trees. Forest Products Journal, 28, 10 (1978) 61 – 72.

BHAT, K. M.; BHAT, K. V.; DHAMODARANT, T. K.: Radial pattern of density variation in eleven tropical Indian hardwoods. Holzforschung, 43 (1989) 45 – 48.

BOSMAN, M. T. M.; KORT, I. de; GENDEREN, M. K. van; BAAS, P.: Radial variation in wood properties of naturally and plantation grown Light Red Meranti (*Shorea, Dipterocarpaceae*). IAWA Journal, 15, 2 (1994) 111-120.

BRAZIER, J. D.: Juvenile Wood. In: KUCERA, L. J.: Xylorama. Birkhäuser Verlag, Basel, Boston, Stuttgart (1985) 25 – 32.

DÜNISCH, O.; BAUCH, J.; SCHWARZ, Th.: Supply of *Swietenia macrophylla* King and *Carapa guianensis* Aubl. with K, Ca, and Mg in three different plantation systems. BFH Mitteilungen Nr. 193 (1999) 47 – 59.

DÜNISCH, O.; BAUCH, J.; SACK, M.; MÜLLER, M.: Growth dynamics in wood formation of plantation-grown *Swietenia macrophylla* King. and *Carapa guianensis* Aubl., BFH Mitteilungen Nr. 193 (1999) 79 – 96.

KURODA, N.; TUKAU, A.; IBRAHIM, A. W.: Intra-stem variations of basic density and green moisture content of eight species grown in Sarawak. Proc. Inter. Symp. Tree Anatomy & Wood Formation 1995, Wood Anatomy Research (1995) 12 – 19.

MÜLLER, F. B.: Untersuchungen zur Entwicklung der Holzeigenschaften während des juvenilen Wachstums bei tropischen Laubhölzern. Diss. TU Dresden,1987, 209 p.

OBAYASHI, H.; SHIOKURA, T.: Anatomical structure of fast-growing tropical tree species with differing growth rates. IAWA Bulletin, 10, 3 (1989) 342 – 343.

PANSHIN, A. J.; DE ZEEUW, C.: Textbook of Wood Technology. McGraw-Hill Book Company, New York, 1980, 722 p.

SACK, M.: Charakterisierung der Holzbildung und des Zuwachses von *Swietenia macrophylla* King und *Carapa guianensis* Aubl. aus der Familie der *Meliaceae* unter Plantagenbedingungen in Zentralamazonien. Dipl. Arbeit, Universität Hamburg (1998) 124 p.

VETTER, R. E.: Untersuchungen über Zuwachsrhythmen an tropischen Bäumen in Amazonien. Diss. Univ. Freiburg, 1995, 109 p.

WIEMANN, M. C.; WILLIAMSON, G. B.: Extreme radial changes in wood specific gravity in some tropical pioneers. Wood and Fiber Science, 20, 3 (1988) 344 – 349.

ZOBEL, B. J.: Juvenile wood in tropical forest plantations: its characteristics and effect on the final product. CAMCORE Bulletin on Tropical Forestry, 2 (1985) 1 – 19.

ZOBEL, B. J.; BUIJTENEN VAN, S. P.: Wood variation – its causes and control. Springer Verlag Berlin, Heidelberg, New York, 1989, 336 p.

ZOBEL, B. J.; JETT, J. B.: Genetics of wood production. Springer Verlag, Berlin, 1995, 337 p.

Structure of primary roots of *Swietenia macrophylla* King (*Meliaceae*) under controlled conditions

G. Noldt[1], J. Bauch[2], U.Schmitt,[1] and V. G. Balodis[3]

1 Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg and Institute of Wood Biology, Hamburg University, Germany
2 Institute of Wood Biology, Hamburg University, Hamburg
3 Department of Botany and Ecology, University of Latvia, Riga, LATVIA

Summary

For *Swietenia macrophylla* King grown under suitable conditions in the greenhouse, the anatomical structure of primary roots and their mycorrhization were examined using light and electron microscopy (TEM). The roots displayed structural diversity, namely a high portion of cortex tissue composed of two different cell types: These types are large-sized isodiametric cells and axially elongated small cells with differently developed cell contents. Both of them are regularly distributed. In the cortex of the fine roots, vesicular-arbuscular mycorrhizal fungi could be identified.

Resumo

Estrutura de raízes primarias de *Swietenia macrophylla* King (*Meliaceae*) sob condições controladas

Para *Swietenia macrophylla* King crescendo sob condições controladas na casa de vegetação, a estrutura anatômica de raizes finas e sua micorrização. Foi investigada usando-se microscópio luz e e microscópio eletrônico de transmissão. As raizes apresentam uma estrutura diversa característica, com uma alta porção de tecido cortical e dois tipos de células no parênquima cortical. Elas são de tamanhos grandes isodiamétricos e pequenas células regulares com um simplast diferente desenvolvido. Fungo micorrizios vesiculo Arbusculares (FMVA) podem ser identificados no cortes de raizes finas.

Introduction

Swietenia macrophylla King grows on the east coast of Central America, in South America, preferably in Brazil and the eastern part of Bolivia, less in Ecuador, Columbia, the eastern part of Peru, and in Venezuela (DAHMS, 1989). It is highly estimated as an important high-quality tropical timber, and it is exported worldwide. This species does not grow naturally in the region of Manaus, Brazil, but it is planted in mixed plantation systems on degraded areas, because of its high-quality wood properties. As the growth and the wood production of *Swietenia macrophylla* in the area of Manaus are influenced by stress factors such as intense drought periods and nutrient deficiency in the soil (BAUCH et al., 1996), the adaptability of the root system to these conditions is of eminent importance. Within the last three decades, several studies provided informatin on the root systems of tropical plant species (FÖRSTER, 1970; SCHROTH, 1989; WHITMORE, 1993; MEYER, 1995; SINGH, 1996). But as concerns *Swietenia macrophylla* King, there are scarcely any detailed descriptions of the anatomy of healthy and functioning fine roots available (SIEBER, 1985; SCHMIDT, 1996; BARBOSA and DAVIDE, 1997).

In general, the morphology, as well as the anatomy of a root system are genetically determined and differ between species, as well as between individuals. According to KOTTKE (1986), the determination of root changes caused by stress has to be preceded by the knowledge of the healthy status of the roots.

For these reasons, the present study aims at describing the anatomy of primary roots. The study was carried out under greenhouse conditions which were approached to natural conditions. This was done in order to distinguish anatomical changes caused by stress factors such as drought and nutritional deficiency from normal developments.

Material and methods

At the beginning of the study, one 20-month-old Swietenia macrophylla plant per pot was planted in mixed soil. The seeds and the soil were taken from the plantation field of the EMBRAPA, Manaus, Brazil, situated on the "terra firme" (comp. SCHMIDT, 1996). The pots were exposed to the controlled conditions of the tropical greenhouse of the Federal Research Centre for Forestry and Forest Products Hamburg (relative humidity 70 - 80%, temperature 26 - 28°, light conditions 250 µE/ m^2S PAR, 12 h day/ 12 h night). (Fig. 1)

Fig. 1: Growth of *Swietenia macrophylla* plants under controlled conditions

After six months, 3 – 5 mm long fine root segments were dissected out, fixated in neutrally buffered formaldehyde according to LILLIE (ROMEIS, 1968), dehydrated in an ascending alcohol series, and embedded in glycol-methacrylate (RUETZE and SCHMITT, 1986) in order to examine the root structure at the light microscope level. For the histochemical studies, cross-sections of fresh roots were prepared using the parafilm hand-sectioning technique of FROHLICH (1984). For all anatomical and histochemical tests, three sections were examined from each zone of every root. A total of ten plants were used. An Olympus BH-2 was used for light microscopy.

The root specimens for the TEM-studies were first fixated in a paraforme-glutaraldehyde mixture according to KARNOWSKY (1965) and postfixed in a 2% solution of OsO_4. In the following, they were washed with 0,1 M Cacodylatbuffer (pH 7,2) and embedded in SPURR's (1969) epoxy resin. After staining with uranylacetate and lead citrate, the ultrathin sections were examined with a Philips CM 12 TEM.

Light and electron microscopical findings

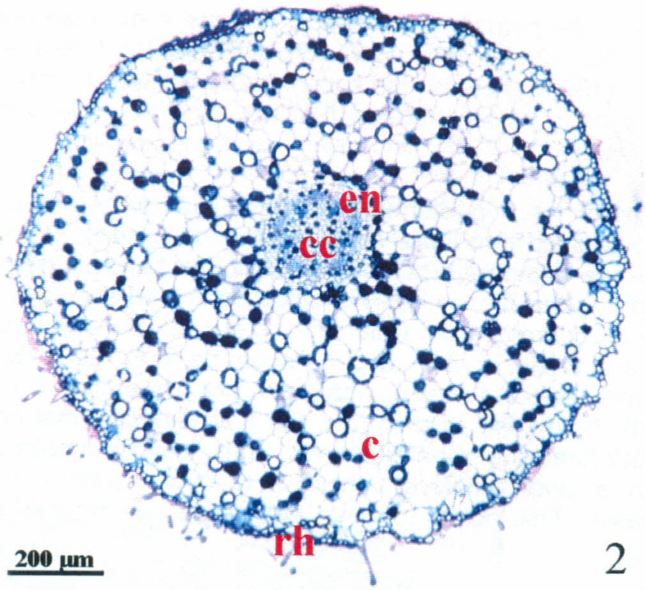
In numerous studies, the general anatomy of the primary roots of dicotyledons from temperate zones has been described (for example ESAU, 1960; FAHN, 1967; BRAUNE, 1971). However, apart from orientating studies by SCHMIDT (1996), there is little known about the root structure of tropical tree species of the *Meliaceae* or of closely related families such as *Rutaceae, Anacardiaceae, Burseraceae, Simaroubaceae.*

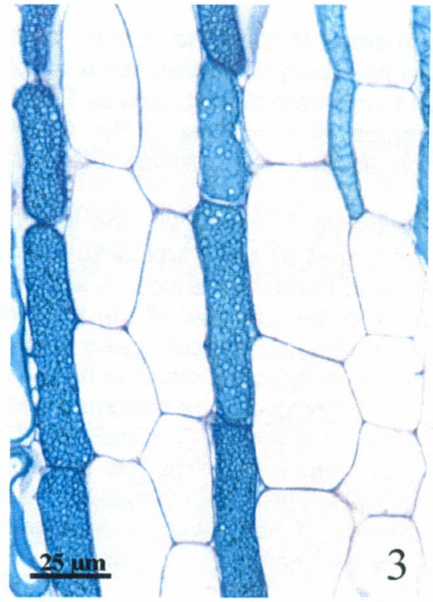
In *Swietenia macrophylla,* the primary roots have a diameter of 0.6 – 1.5 mm and are characterized by some typical structures that differ from those observed in primary roots of tree species in temperate zones. A striking feature is the high percentage of cortex parenchyma in relation to the diameter of the primary root, while there is only a small portion of the central cylinder. (Fig. 2) Two cell layers form the rhizodermis, from which the outer cells develop long, hose-like, thin-walled rhizome hairs with a diameter of 8 – 18 µm. According to KOZLOWSKI (1971), the diameters of rhizome hairs in most species of temperate zone are longer than 5 µm (e. g. fir 10 – 30 µm (THOMSON, 1989)). Below the rhizodermis, the first subepidermal cell layer, i. e. the exodermis, has assumed the functions of an epidermis. In the middle lamella of these cells, which surround the root in a layer, positive benzidine reactions confirm the occurrence of cell wall-bounded peroxidases. This points to a not yet initiated or incomplete lignification (Fig. 5).

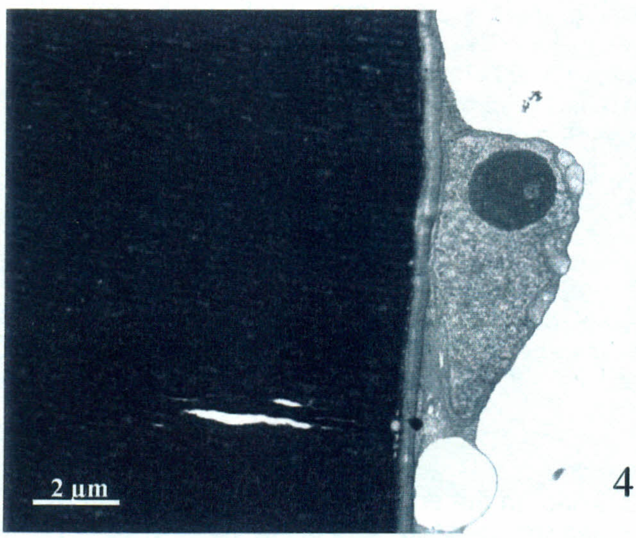
Observation of longitudinal secions of the cortex reveals that the cortex parenchyma consists of several layers formed by two cell types. Firstly, there are the large, isodiametric cells with a diameter of 39 – 53 µm, secondly, there are smaller cells with a diameter of 17 – 27 µm, both of them are of about the same length and regularly distributed (Fig. 3). Beside these differences in the cell dimensions, the cell contents are sharply contrasting as already observed by light microscopy. The larger cells display an empty lumen, whereas the smaller cells are filled with distinctly stained substances. Transmission electron microscopy revealed additional details of their fine structure. Both cell types contain a narrow, wall-attached cytoplasm. In the case of the larger, isodiametric cells, their large vacuole on the one hand appears to be free of any stainable substances. On the other hand, the smaller, axially elongated cells are characterized by the electron dense meaterial that probably represents phenolic compounds (Fig. 4). It can be assumed that the larger cells preferably are involved in the apoplastic water and mineral nutrient transport through the cortex to the central cylinder as suggested by ESAU (1977). The function of the smaller cells still has to be verified. (Fig. 3)

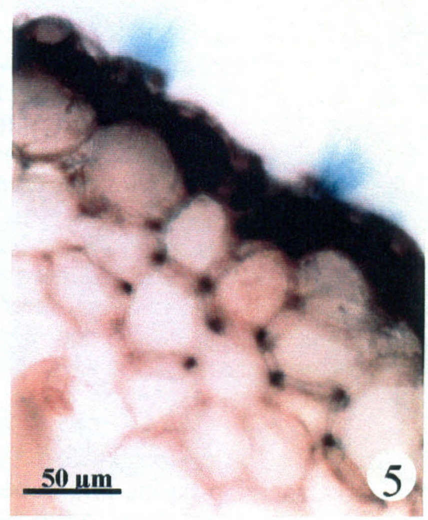
In general, several authors (PRIESTLEY and NORTH, 1922; ESAU, 1965; BONETT, 1968; CLARKSON, 1971) revealed that the innermost cortex layer of roots, the endodermis, develops suberized Casparian bands and suberin lamellae. In the endodermis, suberin lamellae usually develop in those cells close to the phloem, leaving passage cells along the protoxylem poles (McKENZIE and PETERSON, 1994). This structural feature could be confirmed also for the endodermis of *Swietenia macrophylla* that showed the presence of lignin in the walls of endodermal cells (Fig. 6) The Casparian bands and suberin lamellae function as a permeability barrier, blocking the apoplastic transport of substances (NAGAHASHI and THOMSON, 1974; PETERSON, 1993). The pericycle is composed of two to three layers. Vascular bundles are triarch to hexarch, consisting of xylem parenchyma and lignified vessels, as well as of phloem tissue more or less alternating with the xylem.

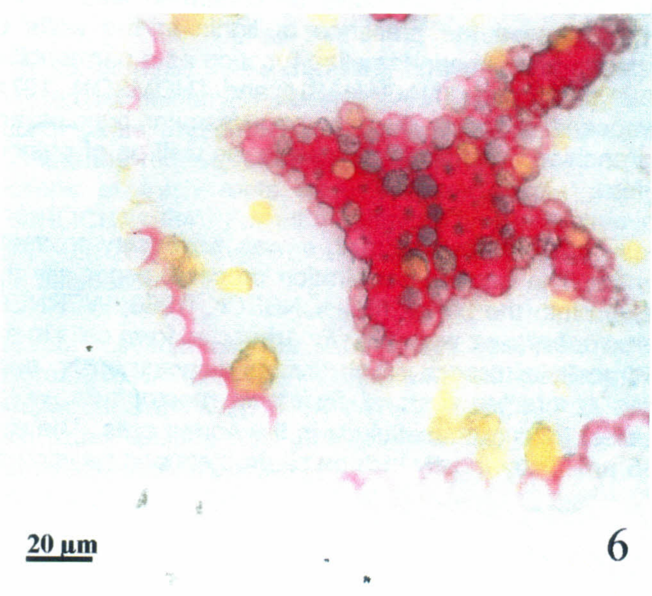
As the experimental soil originates from a natural site in Brazil, it was necessary to verify whether the fine roots develop a mycorrhiza. The general penetration process, especially the penetration of hyphae of the outer mycelium into the cortex (SCHÖNBECK, 1980; WERNER, 1987) could be confirmed for *Swietenia macrophylla,* as well (Fig. 7). Arbuscles form cells in the inner cortex by creation of one lateral intracellular branch which divides dichotomously, each ending in bush-like ramifications. Vesicles in infected roots of *Swietenia macrophylla*, which often avoid swellings of the hyphae (vesicles), occur intracellularly in the cortex cells. The size of the vesicles ranges between 20 and 35 µm. They mostly include oil droplets and function as storage organs (SCHÖNBECK, 1980).

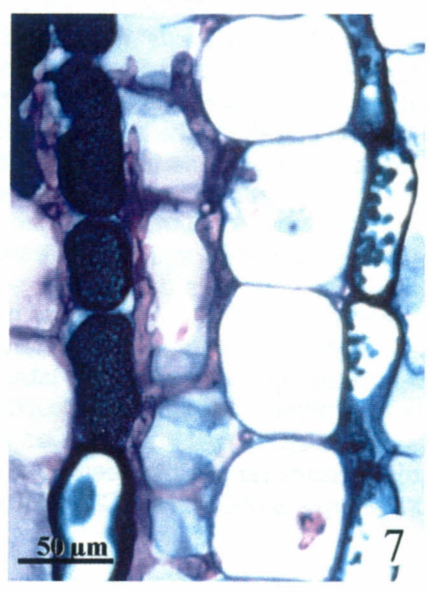

en
cc
c
rh
200 µm
2


25 µm
3


2 µm
4


50 µm
5


20 µm
6


50 µm
7

Conclusion

The anatomical characterization of the primary roots of *Swietenia macrophylla,* grown under controlled conditions in the greenhouse, reveals specific structures, which serve as an important prerequisite for the interpretation of the uptake of water and nutrients. In subsequent studies under field conditions, general conclusions can be drawn in combination with the greenhouse experiments of the present study. Particularly, exogenous influences on the structure of plantation-grown *Swietenia macrophylla* (drought, nutrient deficiency) can be identified. The results contribute to a better understanding on how primary roots adapt to the extreme stress by drought and nutrient deficiency on the "terra firme" in the region of Manaus.

References

BAUCH, J; DÜNISCH, O.; GASPAROTTO, L.; AZEVEDO, C.; LIMA, R. de; MORAIS, R. de: Untersuchung forstlich geeigneter Baumarten für die Wiederbegründung degradierter Flächen im Amazonasgebiet Brasiliens. SHIFT Projekt BMBF 0339638/ CNPq ENV 42, Jahresbericht 1996, 69 p.

BONETT, H. T. jr.: The root endodermis: fine structure and function. The Journ. of Cell Biol., 37 (1968) 199 - 205.

BRAUNE, W.; LEMAN, A.; TAUBERT, H.: Pflanzenanatomisches Praktikum. Gustav Fischer Verlag, Stuttgart, 1971, 331 p.

CLARKSON, D. T.; ROBARDS, A. W.; SANDERSON, J.: The tertiary endodermis in barley roots: fine structure in relation to radial transport of ions and water. Planta (Berl.), 96 (1971) 292 - 305.

DAHMS, K.-G.: Das Holzportrait echtes oder amerikanisches Mahagoni. Holz als Roh-und Werkstoff, 47 (1989) 1 - 6.

ESAU, K.: Plant anatomy. Wiley and Sons, New York, 1960, 376 p.

ESAU, K.: Anatomy of Seed Plants. 2nd ed.Wiley and Sons, New York. 1977, 550 p.

FAHN, A.: Plant anatomy. Pergamon Press, Oxford, 1967, 534 p.

FÖRSTER, M.: Einige Beobachtungen zur Ausbildung des Wurzelsystems tropischer Waldbäume. Allg. Forst-u. Jagdztg., 141 (1970) 185 - 188.

FROHLICH, W. M.: Freehand sectioning with parafilm. Stain Technol., 59 (1984) 61 - 62.

KARNOVSKY, M. J.: A formaldehyde-glutaraldehyde fixative of high osmolality for use in electron microscopy. J. Cell Biol., 27 (1965) 137A – 138A.

KOTTKE, I.; RAPPS, C. H., OBERWINKLER, F.: Zur Anatomie gesunder und "kranker" Feinwurzeln von Fichten: Meristem und Differenzierungen in Wurzelspitzen und Mykorrhizen. Eur. J. Forest Pathol., 16 (1986) 159 - 171.

Fig. 2: Transverse section 3 mm apart from the fine root tip, rh-rhizodermis, c-cortex, en-endodermis, cc-central cylinder, LM.

Fig. 3: Longitudinal section through the cortex showing the two cell types; Giemsa staining, LM.

Fig. 4: Cortex parenchyma cells with narrow, wall-attached cytoplasm. Axially elongated cells contain dark-stained accessory compounds, TEM.

Fig. 5: Peroxidase activity in the exodermis and in the outer cells of the cortex; peroxidase-benzidine reaction, LM.

Fig. 6: Transverse section of the central cylinder 28 mm apart from the fine root tip with lignified thickenings in the endodermis; phloroglucinol-HCl, LM.

Fig. 7: VA mycorrhiza in the cortex; Giemsa staining, LM.

KOZLOWSKI, T. T.: Growth and development of trees. Vol. II: Cambial growth, root growth and reproductive growth. New York and London, 1971, 234 p.

McKENZIE, B. E.; PETERSON, C. A.: Root browning in *Pinus banksiana* Lamb. and *Eucalptus pilularis* Sm. 1. Anatomy and permeability of the white and tannin zones. Bot. Acta, 108 (1995) 127 – 137.

MEYER, U.: Feinwurzelsysteme und Mykorrhizatypen als Anpassungsmechanismen in Zentralamazonischen Überschwemmungswäldern – Igapo und Várzea. Universität Hohenheim, Dissertation im Fachbereich Agrarwissenschaften, 1991, 229 p.

NAGAHASHI, G.; THOMSON, W. W.: The Casparian Strip as a Barrier to the Movement of Lanthanum in Corn Roots. Science, 183 (1974) 670 - 671.

PETERSON, C. A.: Location of the major barriers to water and ion movement in young roots of *Zea mays* L. Planta, 190 (1993) 127 - 136.

PRIESTLEY, J. H.; NORTH, E. E.: The structure of the endodermis in relation to its function. The New Phytol., 3 (1922) 8 - 139.

RÖMEIS, B.: Mikroskopische Technik. R. Oldenbourg Verl., 1968, 757 p.

RUETZE, M.; SCHMITT, U.: Glykol-Methacrylat (GMA) als Einbettungssystem für histologische Untersuchungen von Koniferen-Nadeln. Eur. J. Forest Pathol., 16 (1986) 321 - 324.

SCHMIDT, P.: Biomassenproduktion und Mineralelementversorgung ausgewählter tropischer Nutzpflanzen im Amazonasgebiet Brasiliens. Universität Hamburg, Dissertation im Fachbereich Biologie, 1996, 304 p.

SCHÖNBECK, F.: Endomycorrhiza. Ökologie, Funktion und phytopathologische Aspekte. Forum Mikrobiologie, 2 (1980) 90 - 96.

SCHROTH, G.: Wurzelkonkurrenz zwischen holzigen und krautigen Pflanzen im Agrarforstsystem von Kazaboua/ Zentral-Togo. Mitteilgn. Dtsch. Bodenkundl. Gesellsch., 59/ II (1989) 797 - 802 p.

SIEBER, M.: Anatomical structure of roots of two species of Khaya in Ghana. Xylorama Trends in wood research, (1985) 176 - 183.

SPURR, A. R.: A low-viscosity epoxy resin embedding medium for electron microscopy. J. Ultrastr. Res., 26 (1969) 31 – 43.

THOMSON, J.; MELVILLE, R. L.; PETERSON, R. L.: Interaction between the Ectomycorrhizal Fungus *Pisolithus tinctorius* and root hairs of *Picea Mariana (Pinaceae)*. Amer. J. Bot., 76/ 4 (1989) 632 – 636.

WERNER, D.: Pflanzliche und mikrobielle Symbiosen. Stuttgart, New York, Thieme, 1987, 241 p.

WHITMORE, T.C.: Tropische Regenwälder. Heidelberg, Berlin, New York, Spektrum Akad. Verl., 1993, 275 p.

Acknowledgements

With financial support by the "Soroptimist-Hilfsfonds", Mannheim (Germany) and the Deutsche Luft- und Raumfahrt (DLR), Bonn.

Comparative studies on morpho-physiological traits of six Amazonian species of *Bellucia* and *Miconia* (*Melastomataceae*) and implications for their ecological behaviour

H. Preisinger,[1] *O. Dünisch,*[2] *R. R. de Morais,*[3] *K. Richter,*[1] *and R. da C. Araújo*[3]

[1] Institute of Applied Botany, Hamburg University, Hamburg
[2] Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Hamburg
[3] EMBRAPA, Amazônia Ocidental, Manaus, AM, Brazil

Summary

Plants of six species from the *Melastomataceae* family (*Miconia* spp. and *Bellucia* spp.), taken from secondary forest stands of Terra Firme near Manaus, Amazonas, Brazil, were studied with regard to growth form, biometric traits of the plants, morphological and anatomical characteristics of leaves and wood. In addition, plant biomass and the content of mineral nutrients of different parts of the plants were analysed, and xylem flux measurements were carried out to determine the specific water uptake of the plants. The aim of the studies was to detect causal links between the parameters measured and the ecological behaviour of the species as observed in the field, in order to provide an autecological description of the species. The results show that the plant biomass of the species studied is negatively correlated with leaf sizes, with the percentage of leaf biomass related to total biomass and with the specific water uptake of the species examined. The species with large leaves show large differences in water uptake between the rainy and the dry season, whereas these differences are not found in the species with smaller leaves. The pattern of nutritional elements in roots, trunk, twigs and leaves in species of small plant biomass differs from those of large biomass. These sets of traits indicate different strategies for an economic use of resources in a changing environment during a progressive succession. The results obtained are discussed with regard to their general importance for the secondary vegetation and for successional processes in the study area, beyond the species studied.

Resumo

Estudos comparativos das caraterísticas morfo-fisiológicas de seis espécies amazônicas de *Bellucia* e *Miconia* (*Melastomataceae*) e suas implicações para o comportamento ecológico

Plantas de seis espécies da família *Melastomataceae* (*Miconia* spp. e *Bellucia* spp.), retirada de sítios de floresta secundária da Terra Firme próximo a Manaus, Amazonas, Brasil, foram estudadas considerando a forma de crescimento, caraterísticas biométricas das plantas e caraterísticas morfológicas e anatômicas das folhas e da madeira. Adicionalmente, analizou-se a biomassa das plantas, o teor de nutrientes minerais em diferentes partes das plantas e mediu-se o fluxo no xilema para se determinar o consumo específico de água na planta. O estudo tem como objetivo detectar relações causais entre os parâmetros medidos e o comportamento ecológico das espécies que foram observadas no campo, bem como, contribuir para uma descrição da auto-ecologia dessas espécies. Os resultados mostram que a biomassa das espécies testadas está correlacionada negativamente com o tamanho das folhas, com o percentual da biomassa das folhas em relação à biomassa total, e com o consumo específico de água. As espécies que têm folhas grandes apresentam grandes diferenças no consumo de água, na estação chuvosa e na seca, enquanto que as espécies que têm folhas pequenas não apresentam estas diferenças. As espécies de pequena biomassa revelam um padrão de conteúdo de elementos nutritivos na raiz, tronco, galhos e folhas diferente daquele encontrado nas plantas que apresentam grande biomassa. Esses conjuntos de caraterísticas parecem indicar diferentes estratégias para o uso econômico dos recursos disponíveis em ambientes que sofrem alterações durante a sucessão progressiva. Os resultados obtidos são discutidos tanto para as espécies estudadas, como para a vegetação secundária e os processos sucessionais nas áreas experimentais.

Introduction, conceptual basis and objectives

Secondary forests are vegetation formations which evolve after slashing, burning and/ or subsequent use and abandonment (cf. CORLETT, 1994). They are occupying more and more areas of primary rain forest sites throughout the humid tropics. In the Brazilian Amazon (Amazônia Legal), covering an area of 517.069 km², currently (1995/ 96) primary forest is being cleared at an annual rate of 0,51 % or 18.161 km² every year (INPE, 1998). A large percentage of these areas is not being used or is abandoned after some time and develops into different types of secondary forest. Studies on secondary forests are therefore of increasing scientific and practical interest. They cover species composition, potential use of certain species, succession and regeneration problems and regeneration potential (e.g. DENICH, 1989; DUBOIS, 1990; DENICH, 1991; PREISINGER, 1994; PAROTTA and KANASHIRO, 1995). For an understanding of the mechanisms responsible for these processes, a profound knowledge of the autecological behaviour of the species most frequently represented in the succession process is imperative. For tropical plant species, this knowledge is not available yet (cf. JANZEN, 1975). This is also true of common species of well known taxonomic groups such as *Melastomataceae*. This plant family plays an important role in the Terra Firme secondary forests of the Central Amazon, in terms of number of species, frequency of individuals and plant biomass. In a study area of 1 ha near Manaus, Amazonas, Brazil, consisting of various stages of secondary forest succession, 17 species of *Miconia* and two of *Bellucia* were found (PREISINGER, unpubl.). These species, taxonomically closely related, show a wide range of growth form types, morphological traits and ecological behaviour. In this study, a selection of six species of *Melastomataceae* which occur frequently in the study area is to be compared with regard to growth form, morphological and anatomical characteristics and to the functional role of these traits for the different types of ecological behaviour. The species represent a selection out of approximately 400, which were classified into 15 growth form types in a growth form system designed for Central Amazonian primary and secondary forest species (Table 1). The six species represent a section of the flora of up to 10 years old, mainly progressive stages of secondary succession in the study area.

In the approach presented here we proceed from the well-known fact that growth forms of vascular plants (in the sense of RAUNKIAER, 1937) represent a complex of characteristics closely linked to the ecological behaviour of the species and their site conditions (cf. also HALLE et al., 1978). Growth forms must therefore be the starting point for detailed autecological studies. The comparative study of the six species of *Miconia* and *Bellucia* is based on observations made in the study area, taking into account single morphological and anatomical traits which were likely to explain ecological behaviour, but leaving traits of regenerative reproduction and spreading unattended:

1. Biometric, morphological and anatomic characteristics of the plants, especially of the wood and the leaves,
2. plant biomass and rates of biomass between root, trunk, twigs and leaves,
3. pattern of nutritional elements in the different plant organs,
4. water use efficiency and anatomic traits of the vessel system.

Attempts to study autecological behaviour of common Amazonian plant species in a comparative and systematic form, and a subsequent classification into "functional types" (GRIME, 1985), have never been made. The reasons might be the *high species diversity* and gaps in the knowledge of certain Amazonian taxa, due to identification problems. Another difficulty, which has to be taken much more seriously, is the *high morphological diversity* and, therefore, a large diversity in the ecological behaviour of the species, compared to the vegetation of temperate zones (cf. JANZEN, 1975). Nevertheless, secondary forests are less diverse with regard to taxa and morphological elements than primary forests. We therefore suggest that an attempt to study some basic lines of ecological behaviour, or strategies in accordance with GRIME (1979), is worth trying. The approach assumes that the 15 growth form types (Table 1) represent "functional types" in a general form, but the classification of trees with regard to plant size is a preliminary one. Moreover, it is assumed that some morphological and anatomical traits can be identified which indicate a certain ecological behaviour of the species (morpho-physiological traits).

Table 1: Growth form system for the most commonly occurring growth form types of Central Amazonian Terra Firme (secondary) forests, developed for practical use (*in brackets*: plant families which typically represent species with that growth form type)

	Non self-supporting	**Self-supporting**
Herbaceous	**WH** Winding Herbs = vines **SC** Spread Climbers*	**GS** Graminoid herbs, spreading by Stolons (*Poaceae*) **GR** Graminoid herbs, spreading by Rhizomes (*Poaceae*) **GT** Graminoid herbs, forming Tussocks (*Poaceae, Cyperaceae*) **BF** Broad-leaved Forbs (*Musaceae* inter alia) **UH** Upright or prostrate growing Herbs with medium or small leaves* **HR** Herbs, spreading by Rhizomes (*Polypodiaceae*)
Woody	**WT** Winding or Twining plants = woody lianas (*Bignoniaceae* inter alia) **SC** Spread Climbers	**SH** SHrubs** **ST** Sparsely ramified, short-lived Treelets which regenerate mainly from seeds, forming broad or medium, simple, lobed or compound leaves (*Melastomataceae, Cecropiaceae*) **RT** Rosette Trees, forming a single terminal crown of broad, compound leaves (*Arecaceae*) *Branched out trees, medium or small leaves:* **LT** Low Trees, height <12 m, often regenerating from subterranean roots and shoots **MT** Medium Trees, height 12-20 m **TT** Tall Trees (height >20 m)
additional life form: **EPI** = Epiphytes		

* partly with woody stem at base

** "real shrubs" with a basitonic growth in accordance with RAUNKIAER (1937) evidently do not exist in the humid tropics. The SH-type is of a shrubby growth form with a mesotonic ramification (e.g. *Borreria verticillata* (L.) G. Mey., *Rubiaceae*)

Sites and the selection of plant species and individuals

In species-rich, humid-tropical rain forests, a large variety of successional pathways is possible. The type of succession and the plant species emerging at different stages of succession depend to a large extent on the initial conditions prevailing after a vegetation disturbance event. "Disturbance events" can be falling of a tree, cutting, slashing, burning, agricultural use and subsequent abandonment. The use history of a study area is therefore of major importance in understanding successional processes and hence, in understanding autecological behaviour of certain species. We therefore refer to the history of the stands of the plant individuals and species we analysed in this study.

The study area of 1 ha, where we collected the plants, is part of the experimental area of EMBRAPA Amazônia Ocidental, which is situated 29 km north of Manaus (2□ 52' 57" of southern latitude and 59□ 59' 57" of western longitude). The local primary forest growing on clay-rich latosolic soils was slashed and burned in 1984. One year later the EMBRAPA installed a rubber tree field trial. In March of 1985 Kudzu (*Pueraria phaseoloides* (Roxb.) Benth.) was sown as a cover crop. With the installation of the experiment, fertilization measures were carried out (supertriphosphate, potassium chloride, magnesium sulfate, Zn, Cu and Mn). The primary forest was cleared mechanically by pushing the burned plant material and parts of the upper soil layers to the margins of the area, which caused changes in topography and compacting of the upper soil layers. The experiment was cancelled soon after the second year, because of a severe attack of the fungus *Microcyclus ulei*. A secondary forest regenerated to the species composition and structural traits of which were analysed eight years after abandonment of the rubber tree experiment (PREISINGER et al., in preparation). When the *Miconia* and *Bellucia* plants were cut between June 1995 and June 1998, the forest had reached 15 m in height.

For this study, the following six species of *Melastomataceae* were selected: *Bellucia dichotoma* Cogn., *B. grossularioides* (L.) Triana, *Miconia alata* (Aubl.) DC., *M. phanerostila* Pilger, *M. pyrifolia* Naud. and *M. tomentosa* (Rich.) D. Don ex DC.. The reason for selecting these species were observations in the field indicating differences in ecological behaviour, the fact that they belonged to different growth form types and the frequency of the species in the field, the latter ensuring that a sufficient number of plant individuals were available for the analyses.

The studies on the efficiency of water uptake were carried out in the study area with three individuals per species and per season (rainy season from December to June and dry season from July to November).

Growth form types, morphological traits and plant biomass

Methods

The six plant species were classified with regard to their growth form types. The classification is based on a growth form system designed for the primary and secondary forests of the study area (see Table 1). The following morphological parameters, which can be easily measured and recorded, were considered in the analysis:

1. Total height of the plant [m];
2. Trunk diameter (BHD) [cm];
3. Length and width of leaves [cm] and leaf areas [cm²], taking into account up to 50 well developed leaves per tree. The leaf areas were measured using an optical leaf area analyser (Optical Area Meter, LI-Cor, Nebraska, USA);
4. Type and extent of leaf hairiness;
5. Arrangement and density of stomata.

The proportions (length:width) and shapes of the leaves are characteristics not suited to differentiate between the selected plant species and were therefore not taken into account.

For the analyses of plant biomass, morphological and anatomical parameters and pattern of nutritional elements, two or three individuals typical of the secondary forest under study were cut. The main root was dug out, but it was not possible to excavate the whole roots system because of the need to conserve the study area for further experiments. The plants were separated into root, trunk, twigs and leaves and the fresh weight was determined in the field. Parts of the plant material were pre-dried in a sun drier (secador solar), and dried in a drying oven at 103 □C until constant weight, and water content and dry matter calculated. The total area of assimilation of a plant was calculated from the mean values of dry matter, the leaf area of one leaf and the total dry matter of leaves.

Results

The six species represent a range from "Treelets" (ST), "Low Trees" (LT) and "Medium Trees" (MT) within the total range of growth form types presented in Table 1. The scheme (Fig. 1) shows the species arranged with an increasing height of growth form, forming a continuum from small, shrub-like plants to large trees and from mesopetal to acropetal forms of ramification. It is stated that *all* of the species are "trees" in accordance with RAUNKIAER (1937), but there are no shrubs among the species under study.

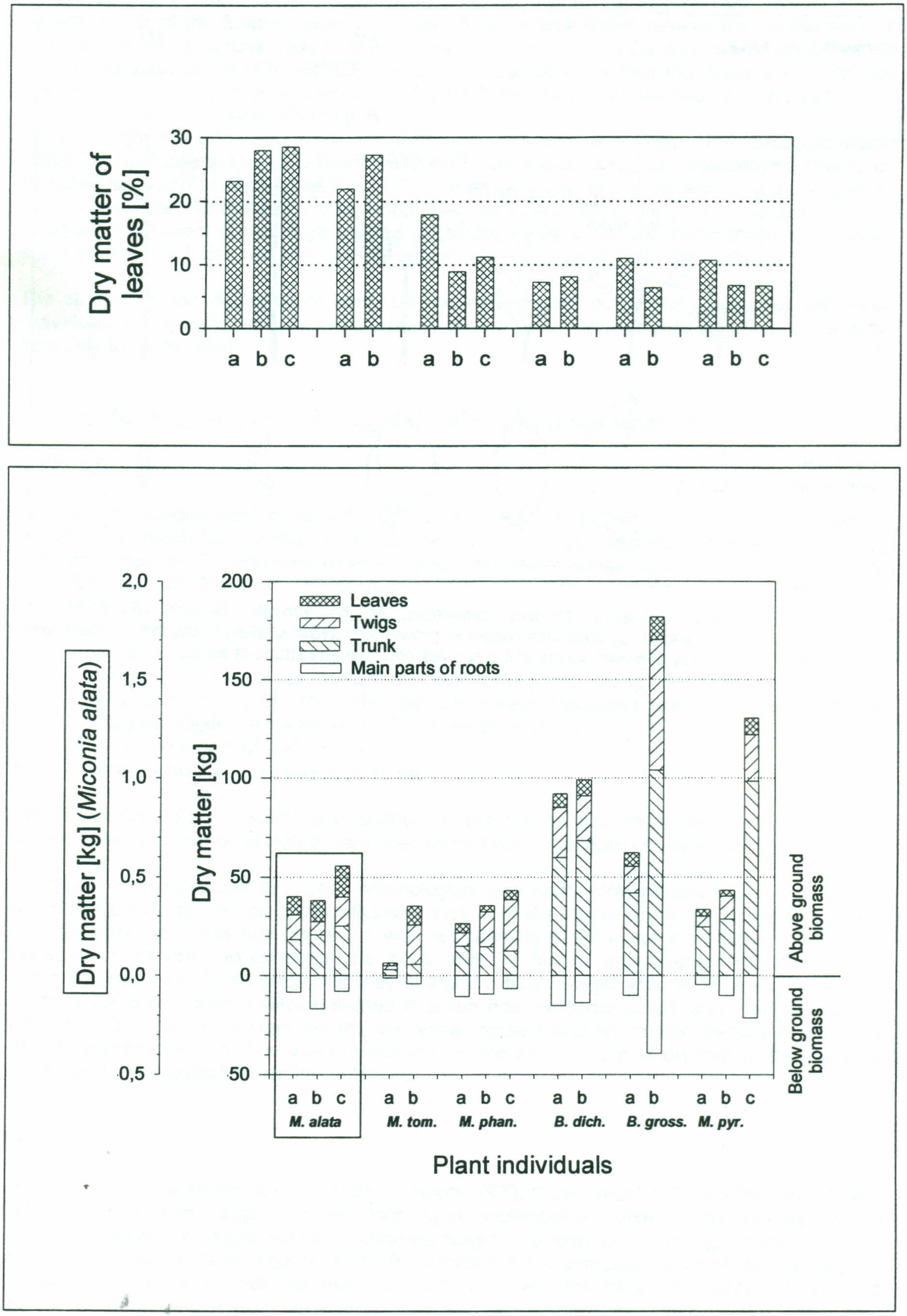


Fig. 2: Plant biomass total, overground and underground biomass and biomass of roots, trunk, twigs and leaves of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia* (plant individuals a, b, c)

Table 2: Basic characteristics of the plant individuals analysed for the comparative studies on plant biomass, biometric and morphological-anatomical traits and on pattern of nutritional elements

Species and plant individuals (a, b, c)		Plant biomass [kg]	Plant height [m]	BHD [cm]	Leaf area [m²]	Number of leaves
M. alata	a	0,48	2,1	5,5	1,5	129
	b	0,55	2,4	1,6	1,2	103
	c	0,63	3,0	6,8	1,0	81
M. tomentosa	a	7,59	8,0	13,0	14,0	163
	b	39,31	7,0	26,4	38,6	519
M. phanerostila	a	36,70	9,8	9,5	37,1	893
	b	44,93	10,0	26,0	27,5	1468
	c	49,71	10,3	27,0	47,1	1906
B. dichotoma	a	106,89	13,2	15,9	24,3	649
	b	112,60	12,7	15,3	42,4	1127
B. grossularioides	a	72,23	12,0	11,8	37,7	2711
	b	221,10	14,3	62,0	57,2	4286
M. pyrifolia	a	38,24	10,5	31,0	28,2	5533
	b	53,38	11,1	31,0	23,2	4546
	c	151,67	13,0	47,0	71,1	14655

Key parameters of the surveyed plant individuals are presented in Table 2, the species being ordered by increasing height of growth form as in Fig. 1. The individuals of the same species are ordered by increasing plant biomass. Table 2 shows that the small growth form types with few, but large leaves in part have a total assimilation area as large as the high growth form types with a large number of small leaves (e.g. *M. tomentosa* b / *M. pyrifolia* a). The plant biomass and the proportions of plant biomass in root, trunk, twigs and leaves of the surveyed plants are presented in Fig. 2: an increase in the height of the growth form and in plant biomass is coupled with a decline in leaf biomass as a proportion of total biomass (Fig. 2, above) and in the medium values of the leaf areas (Fig. 3). *M. alata* has the lowest biomass of all species (scale of dry matter for *M. alata* multiplied by 100 in Fig. 2). The leaves of all the species under study are hairy, at least on the abaxial side and along the main veins. Nevertheless, the extent of hairiness and the morphological types of hairs are different. The extent of hairiness roughly declines with an increase in height of growth form and in biomass (Table 3). In all the species analysed, the stomata are located on the abaxial side of the leaves only. The number of stomata per mm² is negatively correlated with the extent of hairiness of the leaves, with the only exception of *M. pyrifolia* (Table 3).

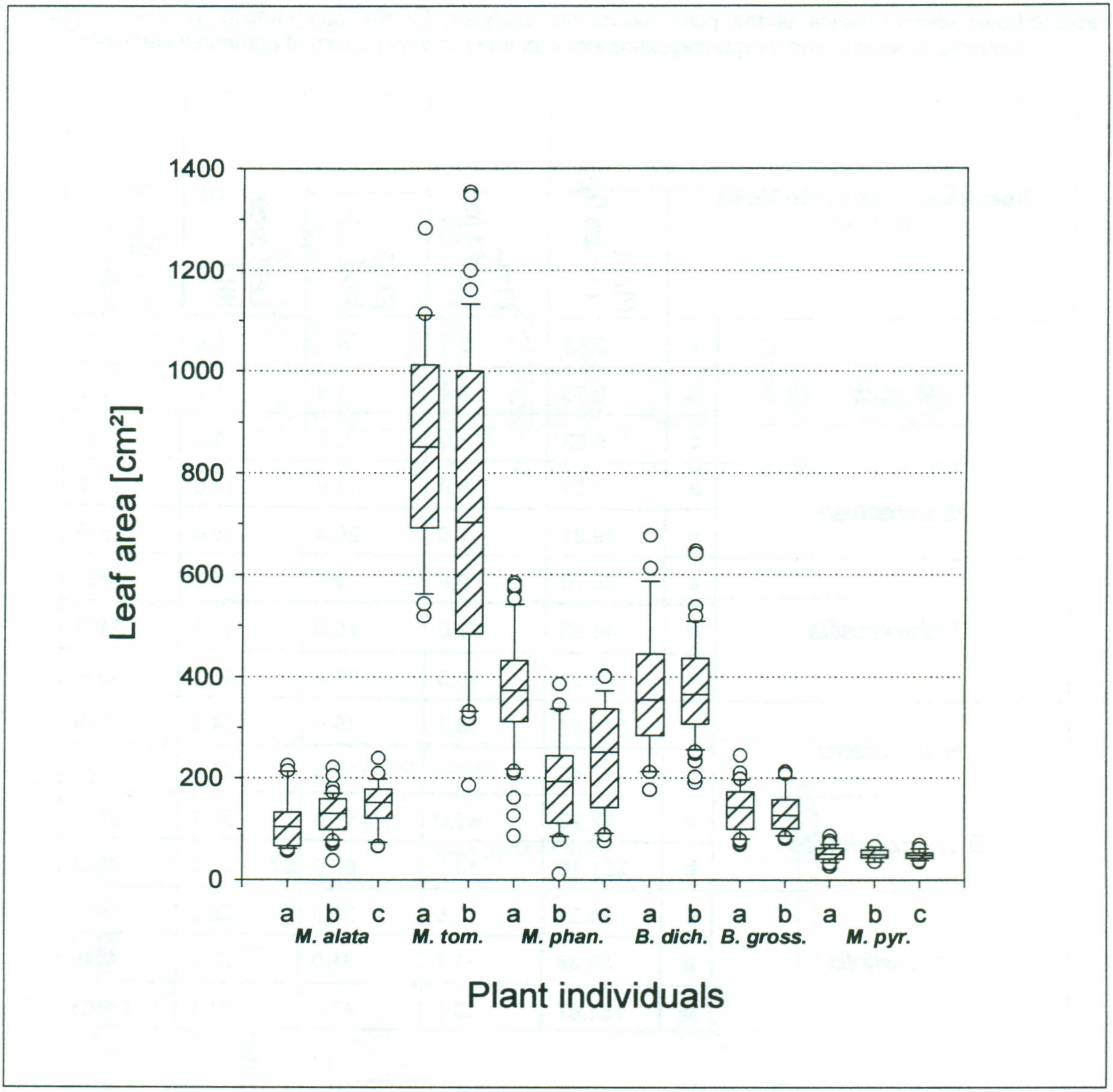


Fig. 3: Median, 75th, 90th percentiles and outliers of leaf areas of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia*, measured from 50 leaves per plant (plant individuals a, b, c)

Table 3: Characteristics of leaf surface

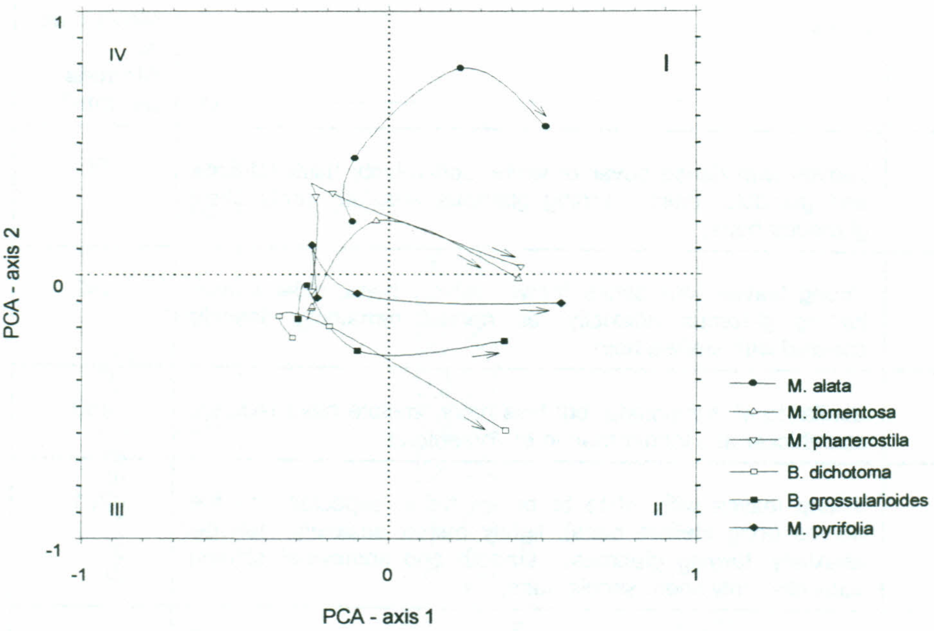
Species	Hairs	Mean no. of Stomata per mm²
M. alata	Leaves with dense cover of white, soft-velvety hairs (stellate and glandular hairs), turning glabrous adaxially (only short glandular hairs)	80
M. tomentosa	Young leaves with dense brown, velvety hairs, older leaves turning glabrous adaxially; all nerves remaining densely covered with stellate hairs	142
M. phanerostila	Similar to *M. tomentosa*, but less hairy, stellate hairs reddish, also thicker and longer than in *M. tomentosa*	150
B. dichotoma	Young leaves with white to brown hairs, especially on the nerves (long stellate hairs), lightly haired adaxially, densely abaxially; turning glabrous, smooth and somewhat shining adaxially (only short, simple hairs)	221
B. grossularioides	Young leaves with very light, velvety brownish hairs abaxially, almost glabrous adaxially; turning glabrous and only main nerves hairy or completely glabrous; smooth and shining adaxially	284
M. pyrifolia	Youngest leaves sparsely haired, later glabrous, remaining slightly hairy on the main nerves; abaxially and adaxially shiny	100

Pattern of nutritional elements

The six plant species occupy similar sites, but at slightly different times in the successional process. The available potential of nutrients must be similar for all of the six species. It is therefore interesting to examine whether the species make use of the nutrients in a similar or in different ways.

Methods

Samples of root, trunk, twigs and leaves were analysed to determine the content of Ca, Cu, Fe, K, Mg, Mn, N, P and Zn, using standardised methods of analyses (Standardised methods of EMBRAPA: N (semi-micro-Kjeldahl); P (phosphorus total: colorimetric analysis of blue amonio-molybdenate complex); K (flame photometry); Ca, Mg (AAS); Cu, Mn, Zn, Fe (AAS).) The pattern of nutritional elements in the different parts of the plants and the differences between the species were detected by applying the ordination technique of Principle Component Analysis (PCA). The basis of the multivariate analysis is a matrix of the nutritional elements (= 9 lines) and the parts of all plant individuals of the six species (= 72 columns). The nutritional elements (lines) were standardised by maximum and then centred, the columns were not modified. PCA was carried out using the CANOCO program (TER BRAAK, 1991), and the results were displayed graphically in a correlation biplot (CORSTEN and GABRIEL, 1976).



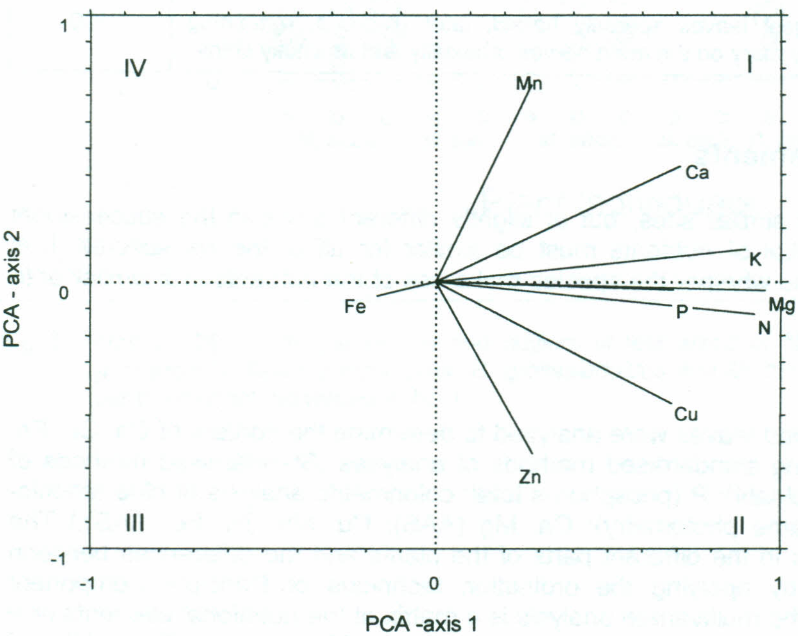


Fig. 4: Principal Component Analysis (PCA) of nutritional elements (Ca, Cu, Fe, Mg, Mn, K, N, P) of roots, trunk, twigs and leaves of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia* (centroids for the plant individuals a, b, c). Correlation biplot showing the pattern of nutritional elements changing from roots to leaves (top; see direction of arrows) and vectors of nutritional elements (bottom)

Fig. 4 (above) presents the centroids of root, trunk, twigs and leaves of the plant individuals for the species separately, displayed as locations in the ordination plane. For greater clarity, the centroids of the same species are connected by lines, and the directions of root > trunk > twigs

> leaves marked by arrows. Fig. 4 (below) indicates the directions and the extent of the increasing content of the nutritional elements, displayed as vectors (for details of interpretation of the correlation biplot see JONGMAN et al., 1987).

Results

In all the species studied, the concentration of the macro-nutrients Ca, Mg, K, N and P increases from roots to leaves, represented in the ordination model mainly by the first PCA axis, but the extent of enrichment differs according to the species. In contrast, there is a marked difference in the content of micro-nutrients Cu, Mn and Zn for the species investigated. For Zn and Mn, the variation is represented in the ordination model mainly by the second PCA axis. *M. alata* and, to a lesser extent, *M. phanerostila* and *M. tomentosa* tend to accumulate a great deal of Ca and Mn, whereas *M. pyrifolia*, *B. grossularioides* and *B. dichotoma* tend to accumulate more Cu and Zn. The content of Fe does not have a differentiating effect on the species, but shows a slight tendency in the model to decrease from roots to leaves.

From the results of Fig. 4 it can be concluded that the six species show clear differences with regard to nutrient uptake and accumulation. The ordination model is a graphic summary of the differences in nutrient pattern. (The range of the absolute concentrations of the nutritional elements measured is as follows (minimum - maximum concentrations): N: 2-31 g/ kg; P: 0,1-2,5 g/ kg; K: 0,5-18,0 g/ kg; Ca: 0,1-15,0 g/ kg; Mg: 0,1-5,5 g/ kg; Fe: 22-1800 mg/ kg; Zn: 2-49 mg/ kg; Mn: 5-150 mg/ kg; Cu: 2-27 mg/ kg.) This article does not attempt to provide an ecophysiological interpretation of the results because, although the physiological function of single nutritional elements in the plant is fairly well understood, too little is known about the *interaction* of these elements in the plant (see INGESTAD, 1987).

Efficiency of water uptake

The climate of the Central Amazon is humid-tropical all the year round, but there is a "rainy" and a "dry" season (type of climate in accordance with WALTER and LIETH, 1967: I(II)b). In Capoeira and secondary forest sites of Terra Firme, the plants sometimes suffer from water deficiencies during the dry season. The ability of the plants to tolerate the dry season, which normally lasts for some weeks of the year only, might therefore be a differentiating factor for the secondary forest species. It was therefore decided to study the six plant species of *Melastomataceae* to determine their efficiency of water uptake and their ability to regulate their water consumption according to the water availability in the soil and in the air.

Methods

Wood anatomical studies of the stem xylem of the species were carried out, focussing in particular on the significance of wood anatomical characteristics for the water uptake and the water transport of the trees. The water-conducting system of fresh xylem samples was therefore filtrated with methylene blue (1:100) to mark the water-conducting cells (cf. BAUCH, 1964; ERBREICH, 1997). For qualitative and quantitative wood anatomical investigations, thin sections (section thickness approx. 20 □m) of the xylem were prepared using a REICHERT microtome. At the cross-sections the vessel diameter and the vessel density of the inner and the outer part of the xylem were quantified in the light microscope (50 measurements each). The vessel length and the number of pits of the inner and the outer part of the stem were measured at the longitudinal sections (also 50 measurements each). The quantitative wood anatomical measurements were carried out with a calibrated ocular.

Xylem sap flow measurements were carried out for three trees of each species during the dry season from November 10 until November 24, 1997 and the wet season from April 7 until April 17, 1998, according to GRANIER (1985). For trees with stem diameters > 10 cm the measurements were carried out at two stem depths (0 - 2.5 cm and 2.5 - 5 cm). The measuring system was calibrated with an accuracy of ±10% (cf. ERBREICH, 1997). The measurements were carried out with a constant current of 120 mA. The data were stored as mean values at 5 minute intervals by a Skye data hog Logger (Skye Instruments Ltd., Llandrindod Wells).

In order to study the relationship between the xylem sap flow of the trees and their anatomical and morphological characteristics, correlation analyses for parallel run and regression analyses were carried out.

Results

Anatomical and morphological traits

The tracer experiments indicated that the vessel system is of key importance for the water transport in the xylem. Fibres and axial parenchyma cells are only involved in water transport by the osmoregulation of the xylem sap (cf. BRAUN, 1988a), which might be of special interest for the xylem water conductance of *M. tomentosa, M. phanerostila* and *B. dichotoma* due to the high percentage of paratracheal parenchyma cells of these species (Table 4).

Table 4: Wood anatomical characteristics (vessel diameter [µm], vessel area [%], vessel length [µm], number of vessel pits [number per 0.01 mm²], arrangement of the longitudinal parenchyma) of *Miconia alata, M. tomentosa, M. phanerostila, Bellucia dichotoma, B. grossularioides* and *M. pyrifolia*

Wood anatomical traits	*M. alata*	*M. tomentosa*	*M. phanerostila*	*B. dichotoma*	*B. grossularioides*	*M. pyrifolia*
Vessel diameter [µm]	37±10	59±10	79±20	133±14	92±12	69±10
Vessel area [%]	21,1±3,7	18,3±2,3	12,6±1,1	13,2±2,9	11,9±1,8	17,2±2,9
Vessel length [µm]	268±63	338±71	397±78	537±87	391±58	348±75
No. of pits per 0.01 mm²	270±16	169±12	127±9	291±11	239±14	145±7
Longitudinal parenchyma	solitary	in bands	in bands	in groups	in bands	in bands

Therefore the further anatomical investigations were carried out with special regard to the vessel system of the trees. The water conductance of the vessel system is limited by the vessel size, the vessel area and the pits. The highest vessel sizes expressed in terms of vessel diameter and vessel length were found in the xylem of *B. dichotoma, B. grossularioides* and *M. phanerostila*, whereas the vessel diameter and the vessel length of *M. alata* was fairly low (Table 4). The xylem water conductance of *M. tomentosa, M. alata* and *M. pyrifolia* is more effective compared to the other species because of a larger vessel area. A high number of pits was found at the vessel cell walls of *B. dichotoma* and *M. alata*, which might contribute to an improved water permeability of the vessel system of these species.

These data show that no synchronous behaviour between the investigated anatomical parameters was found with regard to the xylem water conductance of the trees (cf. Table 5). The large vessel size of *B. dichotoma, B. grossularioides* and *M. phanerostila* was correlated with a low vessel density, whereas *M. alata* has the smallest vessels but the highest vessel density. This indicates different strategies to maintain a sufficient water conductivity. According to ZIMMERMANN (1983) high vessel diameters favour an effective water transport, but also increase the danger of air embolism, especially in periods of drought. The risk of air embolism is reduced in small sized vessels, but the water conductance of these vessels is less effective (cf. TYREE and SPERRY, 1988).

Xylem water flux

The xylem sap flow measurements carried out during the dry and the wet season indicated that the water uptake of *M. tomentosa, M. phanerostila* and *B. dichotoma* is strongly reduced during the dry season compared to the wet season (Fig. 5). In contrast, no significant influence of the soil water supply on the water uptake of *M. pyrifolia, M. alata* and *B. grossularoides* was found.

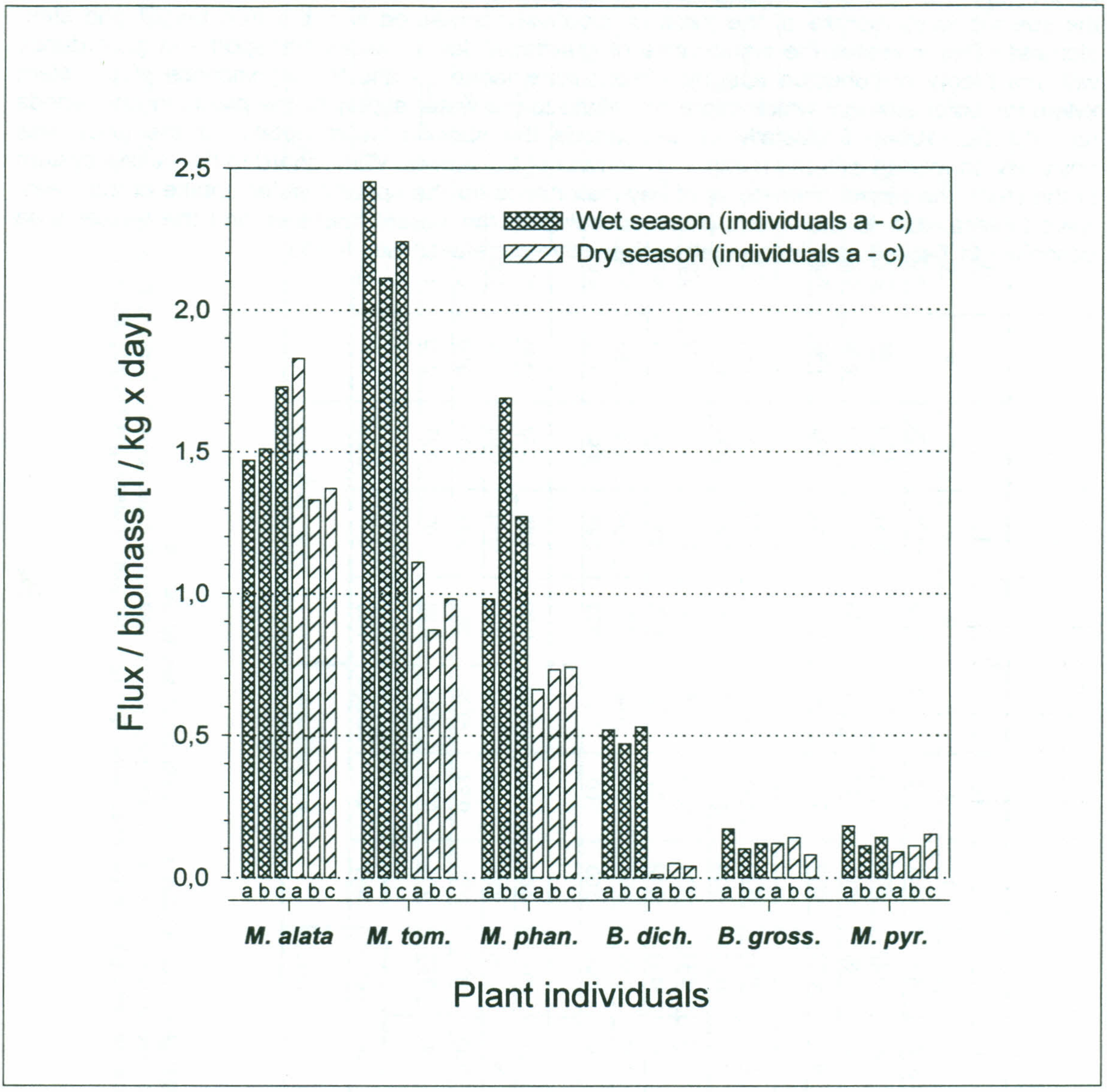


Fig. 5: Daily xylem water flux per tree biomass [l/ kgd] of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia* (plant individuals a, b, c) during the wet season (April 7 until April 17, 1998) and the dry season (November 10 until November 24, 1997)

High specific water uptake in relation to the tree biomass was found for *M. tomentosa, M. phanerostila* and *M. alata*, whereas the specific water demand of *M. pyrifolia, B. dichotoma* and *B. grossularioides* was fairly low (Fig. 5). This indicates that the specific water demand of the species is not significantly correlated with their seasonal patterns of water uptake during dry and wet periods. With regard to the adaptation to different soil water conditions it has to be pointed out that *M. alata* is able to satisfy the high specific demand for water in wet and dry seasons, whereas the water supply of the soil is of more importance for a sufficient water supply of *M. tomentosa* and *M. phanerostila* trees.

Relationship between anatomical and morphological characteristics and the xylem water flux

No close relationship between the specific water uptake of the trees during wet and dry periods and the leaf and stem anatomy and morphology as well as the tree biomass was found by regression analysis. Nevertheless, correlation analysis for parallel run between the specific xylem water flux and anatomical and morphological characteristics of the species showed that the specific water uptake of the trees is negatively correlated with the tree height and stem biomass. This indicates the significance of gravitation for the water transport - in accordance with the theory of cohesion (German "Kohäsionstheorie") - and the significance of the stem xylem for water storage, which might contribute to the water supply of the plants in dry periods (cf. VOGEL, 1994). Especially in dry periods the specific water uptake of the trees was positively correlated with the number of stomata of the leaves. With regard to the vessel system of the stem, the vessel diameter is of key importance for the specific water uptake of the trees. Nevertheless, due to the interrelationship between the vessel diameter and the vessel area described in Table 5, no clear negative or positive correlation was found.

Table 5: Coefficients for parallel run between the specific xylem water flux (flux per tree biomass, flux per leaf biomass, flux per leaf area, flux per vessel area, flux per root biomass) during the wet season, the dry season, mean wet and dry season and the morphological/ anatomical characteristics investigated for *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia*

+ = positively correlated
- = negatively correlated

Morphological/ anatomical characteristics	*Flux/ biomass*			*Flux/ leaf mass*			*Flux/ leaf area*			*Flux/ vessel area*			*Flux/ root mass*			Parallel run
	wet	Dry	wet/dry	wet	dry	wet/dry	wet	dry	wet/dry	wet	Dry	wet/dry	wet	dry	wet/dry	>66%
Leaf morphology																
Leaf area	0,33	-0,33	0,33	0,33	-0,33	0,67	0,00	0,00	0,33	0,33	1,00	0,33	0,00	0,00	0,33	2
Leaf area/tree	-0,33	-0,33	-0,33	0,00	-0,33	-0,33	0,00	0,33	0,00	0,00	0,00	0,00	0,00	0,00	-0,33	0
Leaf mass	0,00	-0,33	0,00	0,67	-0,33	0,33	0,33	-0,67	0,00	1,00	0,67	1,00	0,33	0,00	0,00	5
No. of stomata	-0,67	0,67	0,00	0,00	0,67	-0,33	0,00	1,00	0,33	-0,67	-0,33	-0,67	0,00	0,33	-0,33	6
Tree biomass																
Leaf biomass	0,67	0,00	0,67	0,00	0,00	0,33	0,33	0,33	0,67	0,00	0,67	0,00	0,33	0,33	0,67	5
Branch biomass	0,00	-0,33	0,00	0,33	-0,67	0,00	0,33	-0,33	-0,33	1,00	0,33	1,00	0,33	0,00	0,00	3
Stem biomass	-0,67	-0,67	-0,67	-0,33	-0,67	-0,67	-0,33	-0,67	-1,00	0,33	-0,67	0,33	-0,33	-0,33	-1,00	9
Root biomass	-0,67	-0,33	-0,67	-0,67	-0,33	-1,00	-0,33	-0,33	-0,33	0,33	0,33	0,33	-0,33	-0,67	-0,67	6
Diameter	0,00	0,33	0,00	-0,33	0,33	0,00	-0,33	0,33	0,33	-0,33	0,33	-0,33	-0,33	0,00	0,00	0
Height	-0,67	-1,00	-0,67	-0,33	-1,00	-0,67	-0,33	-1,00	-1,00	0,33	-0,33	0,33	-0,33	-0,67	-0,67	9
Vessel system																
Vessel diameter	-0,33	-0,33	-0,33	-0,33	-0,33	-0,67	0,00	-0,67	-0,67	1,00	0,33	1,00	-0,33	-0,67	-0,67	7
Vessel density	0,00	-0,33	0,00	-0,67	-0,33	-0,33	-0,33	-0,67	-0,33	-0,67	0,00	-0,33	-0,33	-0,33	0,00	3
Vessel lengt	-0,33	-0,33	-0,33	0,00	-0,33	-0,33	0,33	-0,67	-0,33	1,00	0,33	1,00	0,33	-0,33	-0,33	3
No. of pits	-0,33	0,00	-0,33	0,00	0,00	-0,33	0,00	-0,33	-0,33	0,00	-0,33	0,00	0,00	-0,33	-0,33	0
Parallel run	5	3	4	3	4	5	0	7	4	6	4	5	0	3	5	58
>66%		12			12			11			15			8		58

Implications of the results for the ecological behaviour of the species

Growth form types, morpho-physiological traits and behaviour of the species in the plant community

The six plant species of *Melastomataceae* have some ecological characteristics in common: On the one hand, they all can become established, and/or regenerate on heavily disturbed sites (cf. chapter 2). This characteristic is related to the generative mechanisms of regeneration and spreading with the help of small or medium-sized fruits and small seeds, which are propagated by birds (see e.g. ELLISON et al., 1993; RENNER, 1986/ 87 for *Bellucia*). On the other hand, the abilities of the studied species of *Miconia* and *Bellucia* to regenerate and spread vegetatively is poorly developed, compared to other secondary and even primary forest species (e.g. *Vismia* spp. (*Clusiaceae*); *Goupia glabra* Aubl. (*Celastraceae*)).

The results of the analysis show some of the differences in ecological behaviour and correlated morphological-anatomical traits of the six species examined. They form a sequence of growth forms, covering the growth form types ST, LT and MT within the growth form system (Table 1). Increasing growth form heights are correlated with ±decreasing leaf sizes. *M. alata* is the only species under study which does not fit in with the sequence: it represents the smallest growth form of all the species, but has small leaves. The ranking list of the six species with regard to growth form and leaf size is presented as a two-dimensional scheme (Fig. 6: see ordinal scales on left and lower side of diagram). Growth form and leaf size were matched with the plant characteristics surveyed, revealing the following, general links (Fig. 6: see right and upper side of diagram):

1. The proportion of leaf biomass and the specific water uptake decrease with an increase in growth form height and plant biomass. The degree of leaf hairiness and partly the stomata density decrease in the same direction. The leaves of the species of large growth forms show xeromorphic characteristics.

2. The species with large leaves show large differences in water uptake between the rainy and the dry season, while the species with small leaves do not show any difference at all. This relationship indicates that species with small leaves might withstand dry periods better than species with large leaves.

3. The species with a small growth form and the correlated characteristics summarized in Fig. 6 have a different pattern of nutritional elements in roots, trunk, twigs and leaves than those with large growth forms ("type 1" vs. "type 2": see Fig. 6).

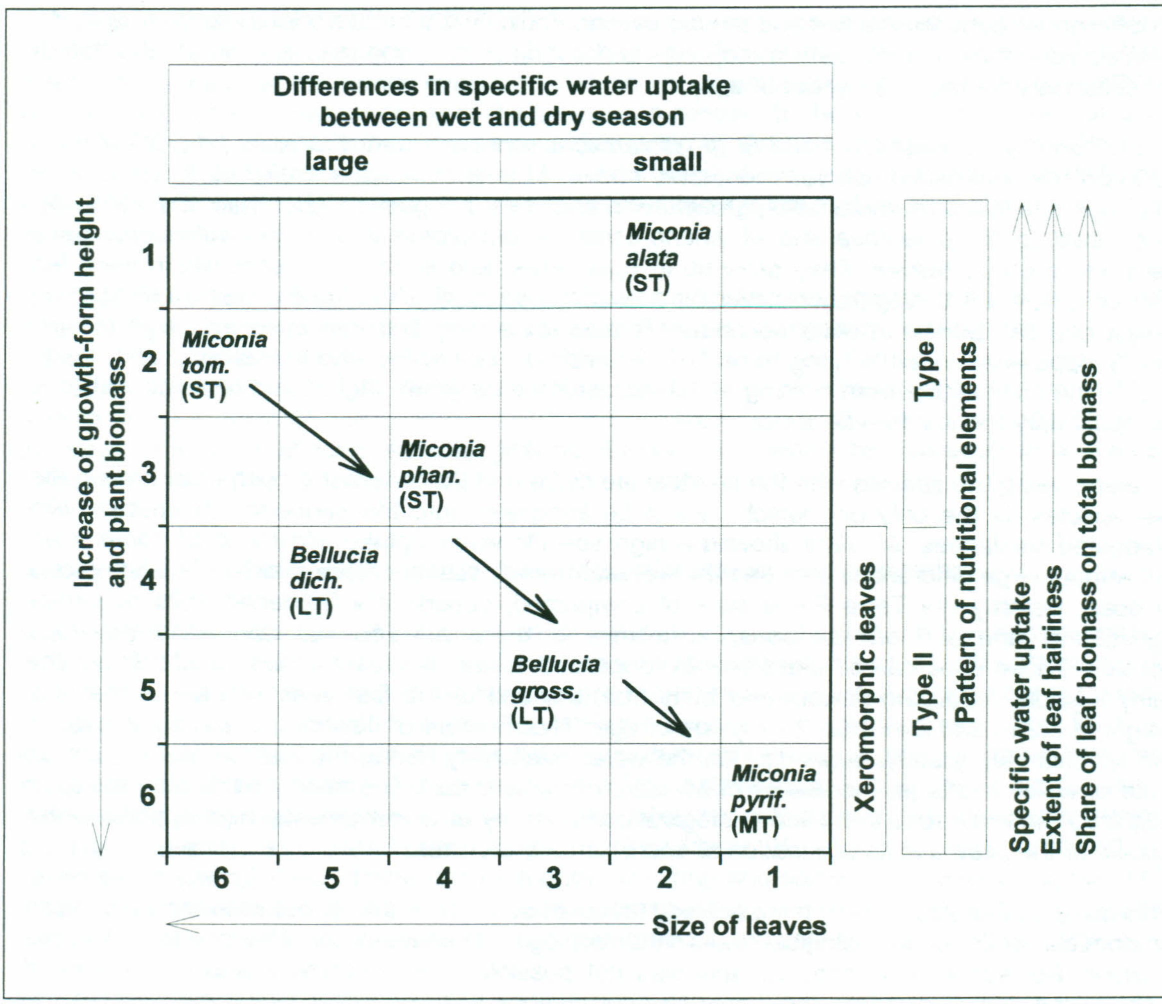


Fig. 6: Graphic summary of the results: Ranking of the six species with regard to the heights of growth form and size of leaves, displayed in a two-dimensional scheme, and correlation with other plant characteristics; diagonal arrows indicate the direction of progressive secondary succession

The knowledge available so far of *M. alata*, *M. tomentosa*, *M. phanerostila*, *B. dichotoma*, *B. grossularioides* and *M. pyrifolia*, drawn from observation, measurement in the field and analyses of biometric, morphological and anatomical traits, enables us to present a preliminary and partial description of their autecological behaviour.

M. tomentosa is a fast-growing species with a short life cycle, which invests little energy in building up a durable plant body. It develops few, but large and apparently efficient leaves, that are photosynthetically active for a short time only. The leaves are therefore soft and not well protected against phytophages, mechanical damage and drying out. *M. tomentosa* had the highest water consumption of all the species studied. *M. tomentosa* is indeed a tree in accordance with RAUNKIAER (1937), but because of its growth form und the proportions of trunk, twigs and leaves it is like a giant, perennial herb ("Treelet", ST of the growth form system). Because of the characteristics referred to, *M. tomentosa* is not tolerant to drought and deep shade. It therefore grows mainly on heavily disturbed primary or secondary forest sites which did not remain uncovered by vegetation for a lengthy period. These are e. g. natural gaps in primary forests, agricultural areas soon after slashing and burning, forest margins and roadsides. According to our own observations, plants of *M. tomentosa* can reach a height of 5 m and an age of approximately 10 years.

M. pyrifolia is a species which shows a contrasting ecological behaviour to *M. tomentosa*, within the scale of the comparison considered in this study. *M. pyrifolia* is a tree of up to 20 m of height (MT of the growth form system), with a comparatively small portion of leaf biomass in relation to total biomass. The adult leaves are small, slightly xeromorphic, nearly glabrous and shiny. The species showed the lowest specific water consumption of the species under consideration and no differences between the wet and the dry season, indicating a certain tolerance to drought. *M. pyrifolia* appears in Capoeiras with saplings and young plants, and reaches the adult stage in old secondary forests (> 20 years of age).

M. phanerostila, *B. dichotoma* and *B. grossularioides* represent a multifactorial gradient of traits between the contrasting species mentioned above. *M. phanerostila* is similar to *M. tomentosa* with regard to leave characteristics, growth form and sites, but grows higher than *M. tomentosa*. In contrast to *M. tomentosa* and *M. phanerostila*, *B. dichotoma* and *B. grossularioides* have hard, xeromorphic leaves. They grow up in open sites, and even in dry sites which were left without a (forest-like) vegetation cover for a lengthy period. *B. dichotoma* grows up to 15 m in height and can persist in older secondary forests for a long time, because the large leaves, which apparently need a long time to decompose, cover the ground around the trunk, preventing competitors from coming up. *B. grossularioides* grows higher and remains longer in old secondary forests than *B. dichotoma*.

M. alata, being the species with the shortest life cycle and the smallest growth form among the test species, is the only one which cannot be integrated into the sequence of species with graduated similarities. *M. alata* showed a high specific water uptake, similar to *M. tomentosa*, but without large differences between the wet and the dry season. Nevertheless, *M. alata* grows in open, partially dry Terra Firme sites of compacted, superficially hardened soils of former agricultural land and on roadsides, sometimes in mass development and as a dominant species. Those sites can be classified as "degraded areas". *M. alata* grows mainly during the rainy season, producing flowers and fruits from the end of the first year, reaches a maximal height of 3.5 m and dies after 2 - 4 years of age. The moment of flowering and the life span of the species vary greatly, depending on the water availability during the lifetime of the plant. In case of water shortage, the leaves of *M. alata* droop and curl. The short and flexible life span might be the main reason for the ecological compatibility of a permanently high specific water uptake of the plant and its occupation of open, partially dry sites.

This comparative approach in plant ecology revealed some causal links between morphological-anatomical and ecophysiological traits and ecological behaviour of *Bellucia* and *Miconia* species. For some characteristics, this was not possible. The anatomical and morphological traits of the vessel systems show only few correlations with the water use coefficient, so the relevant theory (BRAUN, 1988 b) cannot be confirmed here. There are apparently more plant characteristics involved in the mechanisms of water uptake than could be considered in this study. The ecological relevance of leaf hairiness, xeromorphic characteristics and stomata density and the combinations of these traits as realized in the six species cannot be estimated from the results of this study. On the one hand, the results confirm that it is possible to detect characteristics in secondary forest species which are easy to analyse and ecologically relevant, and which are suitable to indicate site conditions. On the other hand, the results also confirm that with the present knowledge of autecology of Amazonian secondary forest species, complete causal chains cannot be built up.

The roles of the species in successional processes

All of the species analysed can be called "pioneer species", in the broad sense of the term, indicating that the species appear in early successional stages. *Bellucia* species were even regarded as "tropical weeds" and "r-strategists" within the r-K-continuum (RENNER, 1986/ 87). A more sophisticated ecological classification of the plant types under consideration would be desirable. This depends to a large extent on the scale used. If short-lived herbaceous plants are included in a successional sequence, the species studied here have to be classified between "CR-" and "SC-strategists" within the CSR-system (GRIME, 1979), *M. alata* as an "SR"-strategist (There are problems in classifying species of tropical rain forests into the CSR system, because of the definitions for the plant types used by GRIME (1979), which relate to the temperate regions of the world. The problems cannot be discussed in detail here.))

The observations in the field and the comparative studies carried out lead to the conclusion that *M. tomentosa*, *M. phanerostila, B. dichotoma*, *B. grossularioides* and *M. pyrifolia* represent not only a sequence with graduated combinations of traits, but show *one* general direction of a *progressive* secondary succession in the study area (Fig. 6: diagonal arrows). The combination of characteristics, summarized in Fig. 6, can be seen as an expression of different strategies

("strategies" in accordance with GRIME, 1979) for an economic use of resources, which change during succession due to the changing site conditions. This is true as well of the pattern of nutritional elements in the plants, even though it did not prove possible in this article to interpret ecophysiologically the pattern found in the species. In contrast to the species mentioned above, *M. alata* must be classified into a *regressive* sequence of succession because of its morpho-physiological traits and the sites occupied. The final state of this sequence will not be a forest vegetation, but a shrubby vegetation form with a low biomass production, that is tolerant to dry periods during the year.

A sequence of characteristics similar to that described for the progressive succession of different plant types and species can be observed within the ontogenetic development of single plants in various species: they start as small plants with few large, often hairy leaves and grow up to ±large trees with many small, ±glabrous leaves (e.g. *M. phanerostila*, *Pouroma* spp. *(Cecropiaceae), Aparisthmium cordatum (Adr. Juss.)* Baill. (*Euphorbiaceae*)). This indicates that the strategies of the species are changing during ontogeny, which can be seen as a flexible response to changing site conditions.

General validity of the results for Central Amazonian secondary vegetation

The present study was carried out with a small number of species within one taxonomical group growing in one specific site. The results with regard to the links between morpho-physiological traits and ecological behaviour of the species are therefore à priori valid only for the sequence of species studied. General rules for Terra Firme secondary vegetation and their lines of succession cannot be unreservedly derived from the results, but it can be stated that the sequence of functional plant types summarized in Fig. 6 plays an important role in successional processes of secondary vegetation in Terra Firme sites. Nevertheless, there are species which behave differently, e.g.: *Vismia guianensis* (Aubl.) Choisy, *V. japurensis* Reichardt und *V. cayennensis* (Jacq.) Pers.. These are frequently occurring and sometimes dominant species of secondary forests in the Amazon, small-leaved, regenerating vegetatively by roots and shoots and by small seeds. They compete with *M. tomentosa* and *Cecropia* spp. in the same sites.

References

BAUCH, J.: Die axiale Durchlässigkeit des Kiefern-Splintholzes für wässrige Lösungen. Planta 61 (1964) 196 - 208.

BRAUN, H. J.: Dynamik des Wassersteigens bei Bäumen in verschiedenen Klimazonen. Holz-Zentralblatt 144 (1988a) 2226 - 2227.

BRAUN, H. J.: Bau und Leben der Bäume. Rombach Verlag Freiburg i. Breisgau, 1988b, 65 pp.

CORLETT, R. T. What is secondary forest? J. Tropical Ecology 10 (1994) 445 - 447.

CORSTEN, L. C. A.; GABRIEL, K. R.: Graphical exploration in comparing variance matrices. Biometrics 32 (1976) 851 - 863.

DENICH, M.: Untersuchungen zur Bedeutung junger Sekundärvegetation für die Nutzungssystemproduktivität im östlichen Amazonasgebiet, Brasilien. Göttinger Beitr. zur Land- u. Forstwirtschaft in den Tropen und Subtropen 46 (1989) 265 pp.

DENICH, M.: Die Sekundärvegetation nach flächenhafter Entwaldung - Ein Beispiel aus dem östlichen Amazonasgebiet Brasiliens. Göttinger Beitr. zur Land- u. Forstwirtsch. in den Tropen u. Subtropen 60 (1991) 31 - 46.

DUBOIS, J. C. L.: Secondary forests as a land-use resource in frontier zones of Amazonia. In: Anderson, A. B.: Alternatives to deforestation: steps toward sustainable use of the Amazon rain forest (International Conference Belém, Brazil, Jan. 27-30, 1988) Columbia Univ. Press, New York, 1990, 183 - 194.

ELLISON, A. M.; DENSLOW, J. S.; LOISELLE, B. A.; BRENÉS, D.: Seed and seedling ecology of neotropical *Melastomataceae*. Ecology 74 (1993) 1733 - 1749.

ERBREICH, M.: Untersuchungen zur Xylemwasserleitung ausgewählter tropischer Wirtschaftsbaumarten Zentralamazoniens. Diplomarbeit Fachbereich Biologie Universität Hamburg (1997) 83 pp.

GRANIER, A.: Une nouvelle methode pour la mesure de flux de seve brute dans le tronc des arbres. Annales des Sciences Forestieres 42 (1985) 193 - 200.

GRIME, J. P.: Plant strategies and vegetation processes. Wiley & Sons, Chichester, 1979, 222 pp.

GRIME, J. P.: Towards a functional description of vegetation. In: White, J. & Beeftink, J. (eds.): Handbook of vegetation science 3, The population structure of vegetation, Dr. W. Junk Publ., Dordrecht, 1985, 503 – 514.

HALLÉ, F.; OLDEMAN, R. A. A.; TOMLINSON, P. B.: Tropical trees and forests. An architechtural analysis. Springer: Berlin, Heidelberg, New York (1978).

INGESTAD, T. New concepts on soil fertility and plant nutrition as illustrated by forest trees and stands. Geoderma 40 (1987) 237 - 252.

INPE: Divulgação das estimativas do desflorestamento bruto na Amazônia Brasileira - 1995, 1996 e 1997. Instituto Nacional de Pesquisas Espaciais - INPE (1998).

JANZEN, D.: Plant ecology in the tropics. Edward Arnolds, London, 1975, 66 pp.

JONGMAN, R. H. G.; TER BRAAK, C. J. F.; VAN TONGEREN, O. F. R.: Data analysis in community and landscape ecology. Pudoc, Wageningen, 1987, 299 pp.

PAROTTA, A.; KANASHIRO, M.: Management and rehabilitation of degraded lands and secondary forests in Amazonia. USDA, Río Piedras, Puerto Rico, 1995, 246 pp.

PREISINGER, H.; COELHO, L. F.; SIQUEIRA, M. do S. G.; LIEBEREI, R.: Analysis of growth form types and floristic composition of the spontaneous vegetation in an agricultural test area near Manaus, Amazonas, Brazil. Angew. Botanik 68 1/ 2 (1994) 40 - 46.

PREISINGER, H.; SKATULLA, M.; MARTINS, G. C.; COELHO, L. F.: Comparative analysis of species composition and structure of differently pre-used Terra Firme sites in the Central Amazon (in preparation).

RAUNKIAER, C.: Plant life forms. Clarendon, Oxford, 1937, 104 pp.

RENNER, S. S.: Reproductive biology of *Bellucia* (*Melastomataceae*). Acta Amazonica 16/ 17 (1986/ 87) 197 - 208.

TER BRAAK, C. J. F.: CANOCO - a FORTRAN program for canonical community ordination by (partial) (detrended) correspondence analysis, principal components analysis and redundancy analysis (version 3.1.2). Agricultural Mathematics Group, Ministerie van Landbouw en Visserij, Groep Landbouwwiskunde, Wageningen, 1991, 95 pp.

TYREE, M. T.; SPERRY, J. S.: Do woody plants operate near the point of catastrophic xylem disfunction caused by dynamic water stress? Plant Physiology 88 (1988) 574 - 580.

VOGEL, M.: Automatische Radialzuwachsfeinmessung in einem Fichtenaltbestand und Moglichkeiten der Interpretation kurzfristiger Schwankungen der Zuwachswerte. Allg. Forst- und Jagdztg. 165 (1994) 34 - 40.

WALTER, H.; LIETH, H.: Klimadiagramm Weltatlas. VEB Gustav Fischer Verlag, Jena, 1967.

ZIMMERMANN, M. H.: Xylem structure and the ascent of sap. Springer Verlag, Berlin, Heidelberg, New York Tokio, 1983, 143 pp.

Acknowledgements

This study is based on partial results of a project financed by the German Federal Ministry of Science and Technology (project no. 0339457A and project no. 033 96 38) and by CNPq/ IBAMA of Brazil (project ENV 23 and 42), within the SHIFT-program (Studies on Human Impact on Forests and Floodplains in the Tropics). We are grateful to Rosemary McLaren, Brussels, Dr. João Ferraz and Madalena Otaviano Aguir, Manaus, for valuable comments on the manuscript. We would also like to thank Dr. L. Gasparotto, Manaus, for his interest in our work and for the cooperation.

3. Appendix

Participating Institutions:

- Centro de Pesquisa Agroflorestal da Amazônia Ocidental (EMBRAPA Amazônia Ocidental), Rodovia AM 010, km 24, 69011-970 Manaus/ Amazonia, Brazil.
- Department of Soil Science, University of Paraná, Rua de Bom Jesus 650, 80035-050 Curitiba/ Paraná, Brazil.
- Centro Nacional de Pesquisa de Florestas, EMBRAPA,/ CNPF, Estrada da Ribeira, Km 111, 83411-00 Colombo, PR, Brazil.
- Institute of Wood Biology, Hamburg University, Leuschnerstr. 91, D-21031 Hamburg, Germany.
- Institute of Wood Biology and Wood Preservation, Federal Research Centre of Forestry and Forest Products, Leuschnerstr. 91, D-21031 Hamburg, Germany.
- Institute of Applied Botany, Hamburg University, Marseiller Str. 7, D-20355 Hamburg, Germany.
- Institute of Soil Science and Soil Geography, University of Bayreuth, D-95440 Bayreuth.
- Department of Botany and Ecology, University of Latvia, Kronvalda bulv. 4, Riga LV-1586, Latvia.

Doctoral theses:

- SCHMIDT, P.: Biomasseproduktion und Mineralelementversorgung ausgewählter tropischer Nutzpflanzen im Amazonasgebiet Brasiliens. Diss. Univ. Hamburg, 1996, 304 p. (in cooperation with Prof. Dr. R. LIEBEREI, ENV 23)
- NEVES, E. J. M.: Biomassa e acúmulo de nutrientes nos diferentes compartimentos de *Ceiba pentandra* e *Virola surinamensis* plantadas na Amazônia Ocidental brasileira. Diss. Univ. da Paraná, Curitiba, 1999, in print.

Master Theses:

- SCHUSTER, F.: Qualitative und quantitative Untersuchungen von *Carapa guianensis* Aubl. im Hinblick auf eine Frühdiagnose für die Eigenschaften des Holzes von Plantagen in Amazonien. Dipl.-Arbeit Univ. Hamburg, 1996, 105 p.
- ERBREICH, M.: Untersuchungen zur Xylemwasserleitung ausgewählter tropischer Wirtschaftsbaumarten in Zentralamazonien. Dipl.- Arbeit. Univ. Hamburg, 1997, 89 p.
- SACK, M.: Charakterisierung der Holzbildung und des Zuwachses von *Swietenia macrophylla* King und *Carapa guianensis* Aubl. aus der Familie der Meliaceae unter Plantagenbedingungen in Zentralamazonien. Dipl.-Arbeit Univ. Hamburg, 1998, 124 p.
- WOHLER, K. C.: Holzstruktur und Holzwachstum *von Hymenaea courbaril* L. unter Plantagenbedingungen in Zentralamazonien. Dipl.-Arbeit Univ. Hamburg, 1998, 56 p.

Project Publications:

- SCHMIDT, P.; LIEBEREI, R.; BAUCH, J.; GASPAROTTO, L.: Balances of bioelements in useful tropical plants. Proc. of an Internat. Symposium, Santarem PA/ Brazil, in April 1993, eds.: PARROTTA, J. A.; KANASHIRO, M., 1995, p. 207 – 213 (in cooperation with ENV 23).

- BAUCH, J.; DÜNISCH, O.; GASPAROTTO, L.; NEVES, E. J. M.; LIMA, R. M. B. de; BUENO, M.: Investigations on tree species suitable for the recultivation of degraded areas in the Central Amazon, Proc. 2nd Workshop, 1995, Cuiaba, Mato Grosso/ Brazil. In: DENICH, M.; KANASHIRO, M. (eds.): Potential land-use and management of altered and abandoned areas in the Brazilian Amazon region. SHIFT, CNPq/ BMBF, 1998, 138 – 142.

- SCHMIDT, P.; LIEBEREI, R.; PREISINGER, H.; GASPAROTTO, L.; BAUCH, J.: Biomass production and mineral element content of selected useful tropical plants. Proc. 2nd Workshop, 1995, Cuiaba, Mato Grosso/ Brazil. In: DENICH, M.; KANASHIRO, M. (eds.): Potential land-use and management of altered and abandoned areas in the Brazilian Amazon region. SHIFT, CNPq/ BMBF, 1998, 136 - 138.

- DÜNISCH, O.; BAUCH, J.; GASPAROTTO, L.; NEVES, E. J. M.; AZEVEDO, C. de; LIMA, R. M. B. de; MORAIS, R. de: Environment-tree growth relationships of plantation-grown tropical tree species as a basis of sustainable timber production in mixed culture systems in Central Amazonia. LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 - 19, 1998, 13 p.

- AZEVEDO, C. de; FRANÇA, M. B.; NEVES, A. C. C. das; LEEUWEN, J. van: Wood characteristics of *Ceiba pentandra* (L.) Gaertn. cultivated at the terra firme and várzea ecosystems. LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 - 19, 1998, 13 p.

- NEVES, E; AZEVEDO, C. P. de; DÜNISCH, O.; BAUCH, J.: Biomass production and nutrition aspects of plantation trees in Amazonia. LIEBEREI, R.; BIANCHI, H.; VOSS, K. (eds.): Proceedings of the Third SHIFT-Workshop, Manaus, March 15 - 19, 1998, 6 p.

Participation in Congresses and Workshops (papers and posters):

I. Workshop, Santarem, Para, Brazil, April 10 – 14th, 1993:

- SCHMIDT, P.: Balances of bioelements in useful tropical plants. Proc. of an Internat. Symposium, Santarem PA/ Brazil, in April 1993 (paper, cooperation with ENV 23).

II. SHIFT-Workshop, Cuiaba, July 10 – 14, 1995, Univ. Fed. Mato Grosso, Brazil:

- BAUCH, J.; DÜNISCH, O.; GASPAROTTO, L.; NEVES, E. J. M.; LIMA, R. M. B. de; BUENO, M.: Investigations on tree species suitable for reforestation of degraded areas in the Amazon region (paper).

- SCHMIDT, P.; LIEBEREI, R.; PREISINGER, H.; GASPAROTTO, L.; BAUCH, J.: Biomass production and mineral element content of selected useful tropical plants (poster, cooperation with ENV 23).

Society for Tropical Ecology (GTÖ), Annual Conference, February 13 – 16, 1997, Leipzig, Germany

- SCHMIDT, P.; BAUCH, J.; LIEBEREI, R.; GASPAROTTO, L.: Biomasseproduktion und Mineralelementgehalt ausgewählter tropischer Nutzpflanzen (poster, in cooperation with ENV 23).

Symposium „Tropische Nutzpflanzen“, Sept. 25 – 27, 1997, Hamburg, Germany:

- BAUCH, J.; DÜNISCH, O.; NEVES, E.; SCHUSTER, F.: Comparative study of wood characteristics of *Carapa guianensis* Aubl. from two plantations and a natural site in Central Amazonia (paper).

- DÜNISCH, O.; BAUCH, J.; SCHWARZ, T.; GASPAROTTO, L.; NEVES, E.: Mineral element supply of plantation-grown tropical tree species in Central Amazonia (paper).

III.**SHIFT-Workshop, Manaus, March 15 – 19, 1998, Amazonia, Brazil:**

- AZEVEDO, C. de; DÜNISCH, O.; FRANÇA, M.; NEVES, E. J. M.; LEEUVEN, J. van: Wood characteristics of plantation-grown *Ceiba pentandra* from „terra firme“ and „várzea“ sites (paper).

- AZEVEDO, C. P. de; LIMA, R. M. B. de; NEVES, E. J. M.; GASPAROTTO, L.; Growth of Selected Tropical Tree Species in Three Different Plantation Systems near Manaus, Central Amazonia (poster).

- BAUCH, J.; DÜNISCH, O.; SCHUSTER, F.; GASPAROTTO, L.; NEVES, E. J. M.: Comparative Study of Wood Characteristics of *Carapa guianensis* Aubl. from Two Plantations and a Natural Site in Central Amazonia (poster).

- DÜNISCH, O.; BAUCH, J.; GASPAROTTO, L.; NEVES, E. J. M.; AZEVEDO, C. de; LIMA, R. M. B. de; MORAIS, R. de: Environment tree-growth relationships of plantation-grown tree species as a basis of sustainable timber production in mixed culture systems in Central Amazonia (paper).

- DÜNISCH, O.; BAUCH, J.; MÜLLER, M.; GREIS, O.: Comparative Study on the Significance of K for Wood Formation of *Swietenia macrophylla* and *Carapa guianensis* (poster).

- DÜNISCH, O.; BAUCH, J.; MÜLLER, M.; SCHWARZ, T.; POLACZEK, S.; GASPAROTTO, L.; NEVES, E. J. M.; AZEVEDO, C. P. de, LIMA, R. M. B. de; MORAIS, R. de: Investigations on tree species suitable for the Recultivation of Degraded Land Areas in Central Amazonia (poster).

- DÜNISCH, O.; ERBREICH, M.; GASPAROTTO, L.; SCHROTH, G.: Xylem Water Conductance of 5-year-old *Swietenia macrphylla, Carapa guianensis, Cedrela odorata, Dipteryx odorata,* and *Hymenaea courbaril* (poster, in cooperation with ENV 23).

- DÜNISCH, O.; SACK, M.; MÜLLER, M.; BAUCH, J.: Structural Dynamics in Wood Formation of Plantation-Grown *Swietenia macrophylla* and *Carapa guianensis* (poster).

- DÜNISCH, O., SCHROTH, G., ZECH, W.: Water Supply of *Swietenia macrophylla* and *Carapa guianensis* in Three Different Plantation Systems near Manaus, Central Amazonia (poster, in cooperation with ENV 23 and ENV 45).

- DÜNISCH, O.; SCHWARZ, T.; BAUCH, J.; NEVES, E. J. M.: K Supply of *Swietenia macrophylla* and *Carapa guianensis* in Three Different Plantation Systems near Manaus, Central Amazonia (poster).

- LIMA, R. M. B. de, OLIVEIRA, M. C. de; AZEVEDO, C. P. de; NEVES, E. J. M.; DÜNISCH, O.; BAUCH, J.; SCHROTH, G.; GASPAROTTO, L.: Influence of Pruning Intensity and Pruning Period on Growth and Wood Quality of Castanha do Brasil (*Bertholletia excelsa* H. B. K.) and *Virola* (*Virola surinamensis*) (poster).

- MORAIS, R. R. de; DÜNISCH, O.: Leaf Morphology and Leaf Anatomy of Selected Tropical Timber Trees of the Central Amazon (poster).

- MORAIS, R. de; PREISINGER, H.; DÜNISCH, O.: Wood Anatomical Studies on the Xylem Water Conductance of Four Secondary Forest Species (*Miconia* spp., Melastomataceae) of the Central Amazon (poster, in cooperation with ENV 23).

- MUROYA, K.; AZEVEDO, C. P. de: Study of the Asexual Propagation of Sumaúma (*Ceiba pentandra* (L.) GAERTN) and Castanha do Brasil (*Bertholletia excelsa* H. B. K.) (poster).

- NEVES, E. J. M.; GASPAROTTO, L.; REISSMANN, C. B.; FERREIRA, C. A.; BELLOTE, A. F. J.; DÜNISCH, O.: Phosphorus and Aluminium in Soil, Leaves, and Litter *of Ceiba pentandra* (L.) GAERTN. and *Virola surinamensis* (ROL.) WARB. (poster).

- NEVES, E. J. M., AZEVEDO, C. de; GASPAROTTO, L.; DÜNISCH, O.; BAUCH, J.: Biomass and aspects of mineral nutrition of trees in the Amazon region (paper).

- NOLDT, G.; BAUCH, J.; DÜNISCH, O.; BALODIS, V. G.: Structure of Primary Roots of *Swietenia macrophylla* King Under Controlled Conditions (poster).

- SCHMIDT, P.; LIEBEREI, R.; BAUCH, J.; GASPAROTTO, L.: Biomass production and mineral element content of *Swietenia macrophylla* King in the juvenile phase (poster, in cooperation with ENV 23).

Acknowledgements

We owe thanks to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) Brasilia, to the Instituto Brasileiro do Meio Ambiente e dos Recursos Renováveis (IBAMA), Brasilia, and to the director of EMBRAPA Amazônia Ocidental, Manaus, for their support. Especially we are indebted to the Bundesministerium für Bildung, Wissenschaft, Forschung und Technologie (BMBF), Bonn, to the Internationales Büro Deutsche Forschungs- und Versuchsanstalt für Luft- und Raumfahrt (DLR), Bonn, to the Projektträger BEO, Jülich, to the Büro für Internationale Beziehungen, Forschungszentrum GKSS, Geesthacht, for the financial support of this SHIFT-project (No. 033 96 38).

We also are grateful to the Coordinator SHIFT, Prof. Dr. R. Lieberei, for his scientific support and cooperation. We owe thanks to Prof. Dr. W. Zech, University of Bayreuth, for cooperation in soil investigations and to Prof. Dr. O. Greis, Technical University Hamburg-Harburg, for cooperation in cellular element analysis.

Furthermore, we express our deep gratitude to Johanna Bauch, Dr. Gerald Koch, Gerd Pfizenmayer, Beate Polaczek, and Christina Waitkus, Hamburg, and to Ricardo Rebello, Alberto Souza, and Valdez Seabra at EMBRAPA Amazônia Ocidental for their comprehensive assistance.

Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg

Nr. 1*	WECK, J.: Neue Unterlagen für eine Waldbrandbekämpfung. Teil I. Auswertung der Statistik, 1947	
Nr. 2*	SCHMIDT, H.: Beiträge zur Kenntnis der Darmsymbionten der holzfressenden Termiten, 1947	
Nr. 3*	GANSSEN, R.: Versuch einer Gliederung deutscher Waldböden, 1948	
Nr. 4	BUCHHOLZ, E.: Die Forst- und Holzwirtschaft der Sowjet-Union nach dem Kriege, 1948	0,60 DM
Nr. 5	GEIGER, R.: Neue Unterlagen für eine Waldbrandbekämpfung. Teil II. Die Witterungsbedingungen für Waldgroßbrände, 1948	0,80 DM
Nr. 6	BECKER, G.; SCHULZE, B.: Zur Prüfung der vorbeugenden Wirkung von Holzschutzmitteln gegen Insekten, 1948	1,00 DM
Nr. 7	BAVENDAMM, W.: Die pilzwidrige Wirkung der im Holzschutz benutzten Chemikalien, 1948	0,90 DM
Nr. 8	GANSSEN, R.: Bodenkundliche Beiträge zur Kalkdüngung im Forstbetrieb, 1949	0,70 DM
Nr. 9	DÖNHOFF, CH. VON: Beitrag zu einer Systematik der Naturschutzgebiete, 1949	2,90 DM
Nr. 10	WECK, J.: Untersuchung zur möglichen Obergrenze einer nachhaltigen Ertragsleistung der Waldgebiete Deutschlands, 1949	1,00 DM
Nr. 11	GROSSKOPF, W.: Bestimmung der charakteristischen Feinwurzel-Intensitäten in ungünstigen Waldbodenprofilen und ihre oekologische Auswertung, 1950	3,50 DM
Nr. 12*	BUCHHOLZ, E.: Der Kampf gegen die Dürre in der Sowjetunion, 1950	
Nr. 13	ARNSWALDT, H.J. VON: Wertkontrolle, 1950	0,50 DM
Nr. 14*	GANSSEN, R.: Mitteilungen über die Winderosion auf Böden Niedersachsens, 1950	
Nr. 15*	WILHELMI, TH.: Fluchtlinienmethoden bei Aufstellung forstlicher Hilfstafeln, 1950	
Nr. 16*	WILHELMI, TH.: Über die Konstruktion britisch-indischer forstlicher Tafeln. Wachstumsverlauf und Massenproduktion von gleichaltrigen Salbeständen gegenüber Fichte und Buche, 1950	
Nr. 17*	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 1, 1950	
Nr. 18	MELLINS, L.: Die Forst-und Holzwirtschaft der Baltischen Staaten, 1950	2,50 DM
Nr. 19	HESKE, F.: Besitz und Verpflichtung. Ein Beitrag der Waldwirtschaft zur sozialökonomischen Problematik unserer Zeit, 1950	10,00 DM
Nr. 20*	WILHELMI, TH.: Die Zuwachsleistung von Tectona grandis nach indischen und niederl.-indischen Ertragstafeln, 1950	
Nr. 21	KAMEKE, C. VON.: Grundlagen und Verfahren des Holztransportes im Oberharz, 1950	2,50 DM
Nr. 22	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 2, 1951	10,00 DM
Nr. 23*	REICHENSTEIN, E.; DAHMS, K.; LESCHNER, F.: Holzverbrauchsstudie für Westdeutschland, 1951	
Nr. 24	ECKERT, K. H.: Untersuchung über die Eignung und Anwendung statistischer Methoden als Hilfsmittel forstlicher Inventuren, 1951	9,00 DM
Nr. 25	WILHELMI, TH.: Wachstum und Massenproduktion gleichaltriger Reinbestände von Cedrus deodara, Pinus excelsa und Pinus longifolia verglichen mit den Wuchsleistungen von Pinus silvestris in Deutschland, 1951	1,90 DM
Nr. 26	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 3, 1951	16,00 DM
Nr. 27	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 4, 1952	12,00 DM
Nr. 28	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 5, 1952	15,00 DM
Nr. 29	RUNKEL, R.O.H.: Pulp from tropical woods. Historical development and results of a research work 1925-1952, 1952	12,50 DM
Nr. 30	MOHNSEN, K.: Die Grundlagen einer äquatorial-westafrikanischen Gesamtwaldlandnutzung, unter besonderer Berücksichtigung der Faserstoffgewinnung, 1953	8,00 DM
Nr. 31	HASE, W.: Waldeigentum und Forstaufsicht in Schleswig-Holstein, 1953	10,00 DM
Nr. 32	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 6, 1953	15,00 DM
Nr. 33*	BERGEMANN, J.: Grundlagen und Probleme der Mykorrhizaforschung in ihrer Bedeutung für die Forstwirtschaft, 1953	8,00 DM
Nr. 34	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 7, 1954	12,00 DM
Nr. 35	HASENKAMP, J. G.: Die Genauigkeit der systematischen Stichprobennahme bei forstlichen Vorratsinventuren, 1954	12,00 DM
Nr. 36	ANON.: Bibliographie des ausländischen forst- und holzwirtschaftlichen Schrifttums. Folge 8, 1954	18,00 DM
Nr. 37	BELLMANN, H.: Über den Einfluß der Tüpfelkapillaren und Micellarinterstizien auf die Mechanik von Imprägniervorgängen mit Lösungen, 1955	9,00 DM
Nr. 38	BUCH, M. W. VON; HAARDT, M.; FRIEDRICH, A.G.: Erfolgreiche Erstaufforstung bei schwierigen Standortverhältnissen im Privatrevier Bliestorf, 1956	7,00 DM
Nr. 39	KAMINSKY, G.: Arbeitsphysiologische Beobachtung bei der Arbeit mit Motorsägen. Arbeitsphysiologische Grundlagen des Leistungsgrades, 1956	4,50 DM

Die mit * aufgeführten Nummern sind vergriffen

Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg

Nr. 40*	SCHÜTT, P.: Züchtung mit Kiefern, Teil I. Individualunterschiede und Provenienzversuche, 1958	14,00 DM
Nr. 41	WILHELMI, TH.: Die Schnittholzsortierung in den Vereinigten Staaten (USA) mit vergleichendem Hinweis auf deutsche Sortierregeln, 1958	7,00 DM
Nr. 42	SCHÜTT, P.: Züchtung mit Kiefern, Teil II: Kreuzungen, Resistenzzüchtung und Zytologie, 1959	7,00 DM
Nr. 43	HALLER, K.E.: Untersuchungen über die zahlenmäßige Erfassung des Wertes stehender Waldbäume am Beispiel der Rotbuche, 1959	10,00 DM
Nr. 44	JENTZSCH, H.: Die Zünd- und Brenneigenschaften des Holzes und ihre Prüfung, 1959	9,00 DM
Nr. 45	MAACK, R.: Die Veränderung der Naturlandschaft und ihre Folgen in Nordparaná durch die Besiedlung, 1960	3,00 DM
Nr. 46	KAMINSKY, G.: Arbeitsphysiologische Grundlagen für die Gestaltung der Forstarbeit. Methodik und Stand der Forschung ein arbeitsphysiologischen Betrachtung der Holzgewinnung, 1960	18,00 DM
Nr. 47	KLINGE, H.: Ergebnisse bodenkundlicher Standortserkundungen in El Salvador, Zentralamerika, 1960	2,50 DM
Nr. 48	WEITLAND, J.: Jahrringchronologische Untersuchungen an Laubbaumarten Norddeutschlands, 1960	9,00 DM
Nr. 49	KUNZ, R.G.: Über die Verwertung von Holz aus sommerlichen Sturmschäden, 1961	10,00 DM
Nr. 50	WILHELMI, TH.: Die Riesenbambusen und ihre wirtschaftliche Kultur, 1961	5,00 DM
Nr. 51	WIEBECKE, C.; HESCH, R.: Inhalt, Systematik, Darstellung und Quellen der Statistiken über Forst- und Holzwirtschaft in der Bundesrepublik Deutschland, 1961	10,00 DM
Nr. 52	GUPTA, M.P.: Kritische Diskussion der Methoden zur Erkundung der Wirkung des Waldes auf den Wasserhaushalt und ihre Anwendbarkeit in Indien, 1961	18,00 DM
Nr. 53	WECK, J.: Koniferen in den Tropen und Hilfspflanzen für Holzplantagen in den Tropen, 1962	5,00 DM
Nr. 54	MEYER, F.H.: Die Buchen- und Fichtenmykorrhiza in verschiedenen Bodentypen, ihre Beeinflussung durch Mineraldünger sowie für die Mykorrhizabildung wichtige Faktoren, 1962	7,00 DM
Nr. 55	LÜNZMANN, K.: Der Widerstandsbeiwert beim Rücken von Rundholz und sein Zusammenhang mit der Bodenmechanik, 1964	8,00 DM
Nr. 56	HATTEMER, H.H.: Die Reaktion und der osmotische Wert des Nadelzellsafts von Kiefern (P. silvestris L.) verschiedener geographischer Herkunft im Zusammenhang mit deren Anfälligkeit gegen die Schütte (Lophodermium pinastri(Schrad.)Chev.), 1964	8,00 DM
Nr. 57	MAYDELL, H.-J. VON: Der Waldbesitz der Sowjetunion in der Statistik, 1964	5,00 DM
Nr. 58	DIETRICHS, H.H.: Chemisch-physiologische Untersuchungen über die Splint-Kern-Umwandlung der Rotbuche, 1964	10,00 DM
Nr. 59	BUCHHOLZ, G.; MAYDELL, H.-J. VON: Aufforstungen in den ariden Gebieten der Sowjetunion. Bericht über russische Erfahrungen seit 1841, 1965	15,00 DM
Nr. 60	RECK, S.: Die Variation und Kovariation einiger anatomischer Holzmerkmale und ihre Beziehung zur Raumdichte bei Fichtenholz, 1965	10,00 DM
Nr. 61*	HARTWIG, F.: Landschaftswandel und Wirtschaftswandel in der chilenischen Frontera, 1966	10,00 DM
Nr. 62	CHRISTOPH, N.: Untersuchungen über die thermische Stabilität nativer hochpolymerer Werkstoffe und ihre relevanten physikalischen Observablen. Beitrag zur Entwicklung neuer Prüfverfahren für die Thermostabilität von Holz, 1966	10,00 DM
Nr. 63	OLLMANN, H.: Preisstatistik in Forst- und Holzwirtschaft, 1966	12,00 DM
Nr. 64	GOTTWALD, H.; NOACK, D.: Anatomische und physikalisch-technologische Untersuchungen an Holzarten der Republik Sudan, 1966	10,00 DM
Nr. 65	BECKER, H.: Akustische Prüfverfahren zur Untersuchung von verleimtem und beschichtetem Holz, 1966	10,00 DM
Nr. 66*	LIESE, W.; HÖSTER, H.R.; RICHTER, J.: Buchenholz-Dokumentation, Teil I. Biologische Eigenschaften, Pathologie und Holzschutz, 1967	
Nr. 67	GOTTWALD, H.; KNIGGE, W.; NOACK, D.; SACHTLER, M.: Anatomische und physikalisch-technologische Untersuchungen an vier liberianischen Holzarten, 1968	6,00 DM
Nr. 68	BRUENIG, E.F.: Der Heidewald von Sarawak und Brunei. Band I u. II, 1968	27,50 DM
Nr. 69	MAYDELL, H.-J. VON; ERICHSEN, H.: Vorkommen und Nutzung wirtschaftlich wichtiger Palmen, 1968	12,00 DM
Nr. 70	WIEBECKE, C.; OLLMANN, H.; KELLER, B.: Die Entwicklung des Grubenholzmarktes in der Bundesrepublik Deutschland, 1968	6,00 DM
Nr. 71	WASNER, U.: Holz als Wirtschaftsfaktor in Nigeria, 1969	6,00 DM
Nr. 72	ALBIN, R.; OLLMANN, H.; MAYDELL, H.-J. VON: Stand und Entwicklungstendenz der Holzwirtschaft in Thailand, 1969	8,00 DM

Die mit * aufgeführten Nummern sind vergriffen

Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg

Nr. 73	ANON.: Hamburg-Reinbeker Forst-und Holztagung 1968. „Holzwirtschaftliches Symposium“ 4.- 6. Dezember, 1969	6,00 DM
Nr. 74	PANZER, K.F.: Tagungsbericht der Arbeitsgruppe „Probleme der Messungs-, Schätzungs- und Auswertungsmethodik tropischer Waldinventuren“, 1969	10,00 DM
Nr. 75	GROSS, H.: Bauordnung und Holzverwendung. Einfluß der Gesetze, DIN-Normen und behördliche Ermessensspielräume – Verbesserungsvorschläge, 1969	8,00 DM
Nr. 76	ZÖHRER, F.: Das Computerprogramm BETKLA zum Ausgleich von Stammzahl-Durchmesser-verteilung oder beliebigen anderen Häufigkeitsverteilungen, 1970	5,00 DM
Nr. 77	BAUCH, J.; ECKSTEIN, D.; LIESE, W.: Dendrochronologie in Norddeutschland an Objekten der Archäologie, Architektur und Kunstgeschichte, 1970	6,00 DM
Nr. 78	BERBERICH, K.; MAYDELL, H.-J. VON: Voraussetzungen und Entwicklungsmöglichkeiten der Holzwirtschaft in Guayana, Surinam und Französisch-Guayana, 1970	7,00 DM
Nr. 79	REICHHELM, W.: Möglichkeiten zur Beurteilung der kurzfristigen wirtschaftlichen Entwicklung in der Holzindustrie der Bundesrepublik Deutschland unter besonderer Berücksichtigung univariabler Modelle, 1971	10,00 DM
Nr. 80	BECKER, M.: Zur Methodik und Zuverlässigkeit langfristiger Holzbedarfsprognosen, 1971	7,00 DM
Nr. 81	FREAS, A.D.; LIESE, W.: Properties and Utilization of Tropical Woods, „Symposium of IUFRO Section 41“, 26.-27. Nov. 1970, 1971	6,00 DM
Nr. 82	ANON.: 2. Hamburg-Reinbeker Forst- und Holztagung 1970. „Holzwirtschaftliches Symposium 24. – 25. November 1970“. Zusammenstellung der Referate, 1971	14,00 DM
Nr. 83	NYLINDER, P.; LIESE, W.: Water Storage of Roundwood, „Symposium of IUFRO Section 41“, 23. November 1970, 1971	6,00 DM
Nr. 84	OLLMANN, H.: Der Holzverbrauch der Bundesrepublik Deutschland, Prognose der Entwicklung bis 1980, 1971	5,00 DM
Nr. 85*	GROSSER, D.: Beitrag zur Histologie und Klassifikation asiatischer Bambusarten, 1971	35,00 DM
Nr. 86	MAYDELL, H.-J. VON: Forstliche Nebennutzungen in den Atlasländern als Grundlage für die Regionalentwicklung, 1971	12,00 DM
Nr. 87	COX, F.: Dichtebestimmung und Strukturanalyse von Pflanzenpopulationen mit Hilfe von Abstandsmessungen, 1971	7,00 DM
Nr. 88	GÖTTSCHE, D.: Verteilung von Feinwurzeln und Mykorrhizen im Bodenprofil eines Buchen- und Fichtenbestandes im Solling, 1972	8,00 DM
Nr. 89	UNMÜSSIG, O.; WIEBECKE, C.: Börseneigenschaften, Struktur und Eigenart verschiedener "Holzbörsen", 1972	6,00 DM
Nr. 90	BARGHOORN, A.W.: Entwicklung und Stand der forst- und holzwirtschaftlichen akademischen Ausbildung und Forschung in Lateinamerika und Vorschläge zu deren künftiger Weiterentwicklung, 1972	15,00 DM
Nr. 91	HEIGENHAUSER, B.: Möglichkeiten des Einsatzes und Auswirkungen bei Anwendung der Netz-plantechnik in der Termin- und Einsatzmittelplanung für Fertigungsarten typischer Betriebsgrößen-klassen der Holzwirtschaft, 1972	12,00 DM
Nr. 92	FAIX, O.: Vergleichende Untersuchungen an Kunstligninen (DHP) verschiedener Zusammensetzung mit Hilfe isotopentechnischer und spektroskopischer Methoden sowie durch chemischen Abbau, 1973	10,00 DM
Nr. 93	ANON.: 3. Hamburg-Reinbeker Forst- und Holztagung 1973. „Holzwirtschaftliches Symposium 15. bis 16. Mai 1973“. Zusammenstellung der Referate, 1973	12,00 DM
Nr. 94*	MAYDELL, H.-J. VON: Forst- und Holzwirtschaft der Sowjetunion. Teil I: Die Baltischen Republiken Estland, Lettland, Litauen, 1973	12,00 DM
Nr. 95	LOETSCH, F.; ZOHRER, F.: Methodik der Voluminierung und Beurteilung der Holzqualität bei Waldinventuren, 1973	12,00 DM
Nr. 96	LEUKENS, U.; OLLMANN, H.; WIEBECKE, C.: Die wirtschaftliche Bedeutung der Standardisierung - insbesondere der DIN-Normung - für die Holzwirtschaft, 1974	14,00 DM
Nr. 97	SCHRÖDER, P.: Grundlagen, Entwicklung und Bedeutung der Waldwirtschaft in Tunesien und Algerien – zugleich ein Beitrag zur Systematik der Weltforstwirtschaft, 1974	20,00 DM
Nr. 98	WOBBE, G.: Die arbeitswissenschaftlichen Grundlagen der Zeitdatenermittlung und die Optimierung des innerbetrieblichen Transportes mit Hilfe anwendungsspezifischer Methoden des Operations Research im Industriebetrieb, 1974	16,00 DM
Nr. 99	PANZER, K.F.; ZÖHRER, F.: Beiträge zur Methodik der Waldinventur, 1974	16,00 DM
Nr. 100	WIEBECKE, C.: Beiträge zur Weltforstwirtschaft (1). World forestry miscellanea (1), 1974	14,00 DM
Nr. 101	HEUVELDOP, J.; GLITZ, D.: Brachland Entstehung - Entwicklung – standörtlich differenzierte Nutzungsmöglichkeiten, 1974	12,00 DM

Die mit * aufgeführten Nummern sind vergriffen

Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg

Nr. 102	GUNIA,E.: Die Waldrodung in der Osteuropäischen Tiefebene, 1974	17,00 DM
Nr. 103	KAMINSKY, G.; BORZUTZKI, R.; LEMBKE, E.: Die Schallausbreitung des Lärms von Motorsägen und seine Wirkungen auf das Gehör des Waldarbeiters, 1974	10,00 DM
Nr. 104	SINNER, M.: ß-1→4-Xylan-4-xylanohydrolasen (E.C.3.2.1.8.) und ihre Wirkung auf Laubholzxylane, 1975	10,00 DM
Nr. 105	MAYDELL, H.-J. VON: Forst- und Holzwirtschaft der Sowjetunion Teil 2: Weißrussische SSR, Ukrainische SSR, Moldauische SSR, 1975	17,00 DM
Nr. 106	SCHWEERS, W.; EZZAT, S.: Erfahrungsstudie über die Möglichkeiten einer umweltfreundlichen Herstellung von Sulfatzellstoff, 1975	8,00 DM
Nr. 107	STROHM, A.: Standortentscheidungen der Fertighausindustrie und Industrieansiedlung durch die öffentliche Hand, 1975	17,00 DM
Nr. 108	STEPHAN, B.R.; MILLAR, C.S.: Lophodermium an Kiefern - Referate des 5. Europäischen Kolloquiums für Forstpathologen 15. bis 17. April 1975 in Schmalenbeck, 1975	17,00 DM
Nr. 109*	BRUENIG, E.F.; ASHTON, P.S.,; BUCH, M. VON; BECKER, M.; HEUVELDOP, J.; KLINGE, H.; MAYDELL, H.-J. VON; PANZER, K.F.: Tropical Moist Forest (Tropischer Feuchtwald), 1975	15,00 DM
Nr. 110	WIEBECKE, C.: Beiträge zur Weltforstwirtschaft (II). (World forestry miscellanea (II), 1975	15,00 DM
Nr. 111	PANZER, K.F.: Quantifizierung von Stammfäule in hohlen Bäumen des Dipterocarpaceen-Mischwaldes von Sarawak (Borneo). Ein Beitrag zur Methodik der Fäulebohrung bei tropischen Waldinventuren, 1976	16,00 DM
Nr. 112	MAYDELL, H.-J.: Forstpolitische Maßnahmen zur Förderung von Investitionen in Entwicklungsländern, 1976. Beiträge der Arbeitsgruppe 4.06.2 zum XVI. IUFRO-Kongreß, 1976	15,00 DM
Nr. 113	NOACK, D.; BRÖKER, F.W.: Dokumentation der Untersuchungen und Prüfungen, die von der Bundesforschungsanstalt für Forst- und Holzwirtschaft an Tropenhölzern durchgeführt wurden, 1976	25,00 DM
Nr. 114	COMPART, J.P.: Simulation und Optimierung mehrschichtiger, anisotroper Platten auf einem Rechner, unter Berücksichtigung der Stabilitätsgrenze, 1977	17,00 DM
Nr. 115	HEUVELDOP, J.; INOUE, M.T.; WHITEMORE, T.C.: Tropical Moist Forest (II). Tropischer Feuchtwald (II), 1977	16,00 DM
Nr. 116	GLITZ, D.: Die ökologische Landschaftsgliederung mittels Bodenform und Vegetationsstruktur im Jungmoränenbereich der Oberalster, 1977	13,00 DM
Nr. 117	MAYDELL, H.-J. VON: Forstpolitische Maßnahmen zur Förderung von Investitionen in Entwicklungsländern (II) Tagungsbericht der IUFRO-Arbeitsgruppe 4.06.2, 1977	13,00 DM
Nr. 118	ANON.: 4. Hamburg-Reinbeker Forst- und Holztagung 1977. Forst- und holzwirtschaftliches Symposium aus Anlaß der Einweihung der Neubauten der Bundesforschungsanstalt für Forst- und Holzwirtschaft 10. und 11. Mai 1977 Zusammenstellung der Referate, 1977	21,00 DM
Nr. 119	WIEBECKE, C.: Beiträge zur Weltforstwirtschaft (III). World forestry miscellanea (III), 1978	12,00 DM
Nr. 120	MAYDELL, H.-J. VON : Forst- und Holzwirtschaft der Sowjetunion. Teil 3: Die transkaukasischen Republiken Armenien, Aserbeidschan, Grusinien, 1978	17,00 DM
Nr. 121	MOHRDIEK, O.: Ergebnisse des Schmalenbecker Klonprüfprogramms für Schwarz- und Balsampappeln, 1978	13,00 DM
Nr. 122	BECKER, M.: Die Entwicklung von Unternehmensverbänden der Sägeindustrie in Südwestdeutschland seit dem Jahr 1900, 1978	13,00 DM
Nr. 123	ALBIN, R.: Die Bedeutung technischer Kriterien für die Planung von Betrieben der mechanischen Holzindustrie in Entwicklungsländern, 1978	17,00 DM
Nr. 124	ANON.: Forests for People. Thirteen papers submitted to the Eighth World Forestry Congress (October 1978-Jakarta/Indonesia) by the Federal Research Centre for Forestry and Forest Products Hamburg-Reinbek, 1979	22,00 DM
Nr. 125	MELEHOV, I.S.: Waldtypologie - aus dem Russischen übersetzt von S. Cejchan, 1979	19,00 DM
Nr. 126	MOHRDIEK, O.: Zusammenstellung der Schmalenbecker Kreuzungen mit Schwarz- und Balsampappeln 1948-1967, 1979	9,00 DM
Nr. 127	SCHRADER, S. (Ed.): Proceedlngs of the International Symposium of IUFRO Subject Group 6.03 Information Systems and Terminology held at the Federal Research Centre for Forestry and Forest Products Hamburg, F.R.G. 15.-18. May 1979, 1979	24,00 DM
Nr. 128	RUETZE, M.; LIESE, W.: Biologie und Bedeutung der amerikanischen Eichenwelke, 1980	19,00 DM
Nr. 129	TINT, K.; SCHNEIDER, T.W.: Dynamic growth and yield Models for Burma Teak, 1980	16,00 DM
Nr. 130	ANON.: 5. Hamburg-Reinbeker Forst- und Holztagung 1980, Forst- und holzwirtschaftliches Symposium 5. und 7. Mai 1980, 1980	24,00 DM

Die mit * aufgeführten Nummern sind vergriffen

Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg

Nr. 131	BAUCH, J. (Ed.): Natural Variations of Wood Properties Proceedings of IUFRO Working Party S.5.01-02 held at the All-Division 5 Conference in Oxford, UK, April 8.-16. 1980, 1980	28,00 DM
Nr. 132	BRUENIG, E.F.; MAYDELL, H.-J. VON: Beiträge zur Weltforstwirtschaft (IV), World forestry miscellanea (IV), 1980	19,00 DM
Nr. 133	SCHMIDT, O.: Zum Verhalten von Bakterien gegenüber der verholzten Zellwand, 1981	23,00 DM
Nr. 134	SCHNEIDER, T.W.: Bestandespflege in Norddeutschland, Möglichkeiten zur rationellen und zielorientierten Baumzahlreduktion, 1981	28,00 DM
Nr. 135	SCHNEIDER, T.W.; KREYSA, J.: Dynamische Wachstums- und Ertragsmodelle für die Douglasie und die Kiefer, 1981	22,00 DM
Nr. 136	BECKER, M.: Holzhandelspolitik - Praktische Gestaltung und wissenschaftliche Analyse -, 1981	22,50 DM
Nr. 137	SEEHANN, G.; HAMANN, H.: Das Arboretum der Bundesforschungsanstalt für Forst- und Holzwirtschaft in Hamburg-Lohbrügge, 1983	12,00 DM
Nr. 138*	SCHRADER, S.; GREVE, U.; SCHÖNWALD, H.R: Saure Niederschläge und Waldschäden. Bibliographie (Acid Precipitation and Forest Damage Bibliography), bearbeitet, 1983	18,00 DM
Nr. 139	KURZ, W.R.: Biomasse eines amazonischen immergrünen Feuchtwaldes: Entwicklung von Biomasseregressionen, 1983	19,50 DM
Nr. 140	MAYDELL, H.-J. VON: Forst- und Holzwirtschaft der Sowjetunion. Teil 4: Kasachstan und die mittelasiatischen Sowjetrepubliken Usbekistan, Kirgisien, Tadshikistan, Turkmenien, 1983	36,00 DM
Nr. 141*	ECKSTEIN, D.; WROBEL, S.; ANIOL, R.W.: Dendrochronology and Archaeology in Europe, Proceedings of a Workshop of the European Science Foundation (ESF), held in Hamburg April 28.-30. 1982, 1982	33,00 DM
Nr. 142	FUCHS, R.: Unfallsituation im Kleinprivatwald, eine Analyse der Unfälle und Arbeitssicherheitsprobleme unter besonderer Berücksichtigung der Verhältnisse im niedersächsischen Kleinprivatwald, 1984	19,50 DM
Nr. 143	SCHOLZ, F.: Bericht über Wirkungen säurebildender und anderer Luftverunreinigungen auf Wälder, im Auftrage der United Nations Economic Commission for Europe, Environment and Human Settlements Division, Air Pollution Unit, Recherche und Redaktion: Martin Lorenz, 1984	18,00 DM
Nr. 144	OPITZ, M.G.: Sicherung nachhaltiger Nutzholzversorgung durch forstliche Plantagen in Ostafrika, Zustandsanalyse und Realisationsalternativen, dargestellt am Beispiel Kenia, August, 1984	29,00 DM
Nr. 145	SCHRADER S.; SCHÖNWALD, H.R.; GREVE, U.: "Immissionen und Waldschäden Bibliographie" "Air Pollution and Forest Damage Bibliography", August, 1984	29,00 DM
Nr. 146	ANON.: 6. Hamburger Forst- und Holztagung 1984, Forst- und holzwirtschaftliches Symposium 8. u. 9. Mai 1984 - Plenarvorträge, 1984	28,00 DM
Nr. 147	BLOCH, G.: Beiträge zur Analyse und Synthese eines Mensch-Maschine-Systems - dargestellt am Beispiel einer Motorsäge, Dezember, 1984	27,00 DM
Nr. 148	BRUENIG, E.F.; MAYDELL, H.-J. VON: Beiträge zur Weltforstwirtschaft (V) World Forestry Miscellanea (V), 1984	28,00 DM
Nr. 149	SCHRADER, S.; SCHÖNWALD, H.R.; DUJESIEFKEN, D.: "Immissionen und Waldschäden Bibliographie III 1984" "Air Pollution and Forest Damage Bibliography III 1984", 1984	26,00 DM
Nr. 150	MUHS, H.-J.: IUFRO Project Group P1 10-00 „Improvement and Silviculture of Beech Amelioration et Sylviculture du Hetere"; Verbesserung und Waldbau der Buche; First Symposium held at Großhansdorf from May 31. to June 4., 1984, 1984	25,00 DM
Nr. 151	ANON.: 19. Internationales Symposium „Mechanisierung in der Waldarbeit" vom 6. bis 11. Mai 1985 in Diemelstadt/Hessen – Vortragssammlung, 1985	28,00 DM
Nr. 152*	BRUENIG, E.F.: Terminologie für Forschung und Lehre in den Fachgebieten und Vorlesungen, 1986	20,00 DM
Nr. 153	SCHRADER, S.; SCHÖNWALD, H.R.; DUJESIEFKEN, D.: "Immissionen und Waldschäden Bibliographie IV" 1985 "Air Pollution and Forest Damage Bibliography IV", 1985	22,00 DM
Nr. 154	MUHS, H.-J.: IUFRO Joint meeting of WP S2. 04-OS and S2. 03-14 on „ Biochemical genetics and legislation of forest reproductive material"; Proceedings of the meeting held at Großhansdorf from June 25. to June 28., 1985, 1986	23,00 DM
Nr. 155	SCHNEIDER, T.W.; LORENZ, M.; POKER, J.: Abschätzung der ertraglichen Folgen der neuartigen Waldschäden im Bereich der Landesforstverwaltung Hamburg mit Hilfe dynamischer Wachstumsmodelle, 1987	18,50 DM
Nr. 156	LORENZ, M.: Assessment of changes in increment and standing volume in damaged forests, Juli, 1987	14,00 DM
Nr. 157	GÖTTSCHE- KÜHN, H.: Bildung und Eigenschaften des Holzes von Fichten (Picea Abies(L.) Karst.) aus Waldschadensgebieten, 1988	20,50 DM

Die mit * aufgeführten Nummern sind vergriffen

Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg

Nr. 158	SCHRADER, S.; SCHÖNWALD, H.R.; SUMSER, M.: "Immissionen und Waldschäden Bibliographie V -1986" "Air Pollution and Forest Damage Bibliography V: 1986", September, 1988	29,00 DM
Nr. 159	SCHNEIDER, T.W., POKER,J.: "Bewertung der ökologischen Folgen des Waldsterbens anhand eines Szenarios. Dargestellt am Beispiel der Hamburger Forsten." Oktober 1988, 1988	19,50 DM
Nr. 160	ANON.: 7. Hamburger Forst- und Holztagung1988, 31.05. und 01.06. 1988, „Forschung für die Forst- und Holzwirtschaft, Folgen von Waldschäden, Zukunft der Holzproduktion, neue Technologien", 1988	39,00 DM
Nr. 161	WÖLL, H.: Struktur und Wachstum von kommerziell genutzten Dipterocarpaceenmischwäldern und die Auswirkungen von waldbaulicher Behandlung auf deren Entwicklung, dargestellt am Beispiel von Dauerversuchsflächen auf den Philippinen, Oktober, 1989	29,00 DM
Nr. 162	SCHRADER, S.; SCHÖNWALD, H.R.: Immissionen und Waldschäden – Bibliographie VI - 1987, November, 1989	39,00 DM
Nr. 163	NOACK, D. (Red.): BML-Forschungsprogramm: Waldschäden durch Luftverunreinigungen 1986-1988, 1989	27,00 DM
Nr. 164	STEPHAN, B.R. (Red.): Erhaltung forstlicher Genressourcen Berichtsband einer Vortragstagung der Arbeitsgemeinschaft für Forstgenetik und Forstpflanzenzüchtung vom 14. bis 16. Juni 1988 in Großhansdorf, 1990	38,00 DM
Nr. 165	MAYDELL, H.-J. VON (Red.): Beitrag zum XIX. IUFRO-Weltkongress in Montreal 6. – 11. Juli 1990. Contributions to the XIX. IUFRO-World Congress in Montreal 6. to 11. July 1990; 1991	16,00 DM
Nr. 166	NIMZ, H. (Red.): II. Expertengespräch "Lignocellulosen" am 7. Nov. 1989, 1991	17,00 DM
Nr. 167	ANON.: Festkolloquium anläßlich der Verabschiedung von Professor Dr. Dr. h.c.mult. Walter Liese am 22. März 1991 in der Bundesforschungsanstalt für Forst- und Holzwirtschaft, August, 1991	19,00 DM
Nr. 168	ANON.: 1st European Workshop on Lignocellulosics and Pulp (EWLP) „Utilization and Analysics of Lignins" - Hamburg-Bergedorf, Federal Republic of Germany, Sept. 18.-20. 1991, 1991	43,50 DM
Nr. 169	MAYDELL, H.-J. VON; PANZER, K. F. (Red.).: Beiträge zur Weltforstwirtschaft (VI). World forstry miscellanea (VI), Nov. 1991, 1991	32,00 DM
Nr. 170	MAYDELL, H. J. VON (Red.): 60 Jahre Forschung im Dienste der Weltforstwirtschaft, 1992	27,00 DM
Nr. 171	FRÜHWALD, A.; PEEK, R.-D.; SCHULTE, M.: Nutzung von Kokospalmenholz am Beispiel von Nordsulawesi, Indonesien, 1992	55,00 DM
Nr. 172	ANON.: 8. Hamburger Forst- und Holztagung 1992, 22.-23. September 1992, „Europa im Umbruch. Auswirkungen für die Forst- und Holzwirtschaft". Aufgaben für die Forschung, 1993	43,00 DM
Nr. 173	ANON.: Agroforstwirtschaft/Agroforestry Lexikon und Glossar / Dictionary and Glossar Deutsch Englisch - English / German, 1993	26,00 DM
Nr. 174	POKER, J.: Struktur und Dynamik des Bestandsmosaiks tropischer Regenwälder - Entwicklung eines Modellansatzes zur Simulation natürlicher Mischbestände, Juni, 1993	35,00 DM
Nr. 175	LORENZ, M.: Zur Integration von Zuwachsanalysen in die Internationale Waldschadenserhebung, November, 1993	33,00 DM
Nr. 176	BRÖKER, F.-W. (Red.).: Kongressforum "Holz" im Rahmen der internationalen Grünen Woche in Berlin 1994, 1994	33,50 DM
Nr. 177	BICK, U.; CEJCHAN, S.; FILIPTSCHUK, A. N.; MAYDELL, H.-J. VON: Terminologie Forsteinrichtung/Waldinventur mit deutsch-russischem und russisch-deutschem Fachwörterbuch. 165 S., 1994	21,00 DM
Nr. 178	HEUVELDOP, J. (Ed).: Assessment of sustainable tropical forest management (A contribution to the development of concept and structure) Compiled by J. Heuveldop, 1994	34,50 DM
Nr. 179	MAYDELL, H.-J. VON; CEJCHAN, S.: Forst- und Holzwirtschaft der Gemeinschaft Unabhängiger Staaten - GUS (ehemals Sowjetunion). Teil 5: Die Russische Föderation, 1994	39,00 DM
Nr. 180	DAHM, S.: Bundeswaldinventur - Auswertungsmodelle und Vorschläge zur Effektivitätssteigerung. Federal Forest Inventory - Models for evaluation and proposal for increasing efficiency, 1995	33,00 DM
Nr. 181	HAMANN, H.; SEEHANN, G.; WOHLTORF, H.: Das Arboretum der Bundesforschungsanstalt für Forst- und Holzwirtschaft Hamburg Lohbrügge. The Arboretum of the Federal Research Centre for Forestry and Forest Products Hamburg-Lohbrügge, 1995	22,00 DM
Nr. 182	ANDERS, S. (Red.): Waldökosystemforschung Eberswalde - Struktur, Dynamik und Stabilität von Kiefern- und Buchenwaldökosystemen unter Normal- und und multiplen Streßbedingungen unterschiedlicher Ausprägung im nordostdeutschen Tiefland, 1996	36,00 DM
Nr. 183	POLLEY, H.; SASSE, V.; ENGLERT, H.: Entwicklung des potentiellen Rohholzaufkommens bis zum Jahre 2020 für das Gebiet der Bundesrepublik Deutschland, 1996	33,00 DM
Nr. 184	SCHWEINLE, J. : Analyse und Bewertung der forstlichen Produktion als Grundlage für weiterführende forst- und holzwirtschaftliche Produktlinien-Analysen, 1996	31,00 DM
Nr. 185	ANON.: 9. Hamburger Forst- und Holztagung in Eberswalde. „Wald im Wandel", 1996	66,00 DM

Die mit * aufgeführten Nummern sind vergriffen

Mitteilungen der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg

Nr. 186	HERTEL, H.: Biochemisch-genetische Untersuchungen bei Kiefer (*Pinus sylvestris*) - Anleitung zur Trennmethodik und Auswertung der Zymogramme, 1997	26,00 DM
Nr. 187	GARVES, K.; WEHLTE, S.; FAIX, O.; PULS; J.: Neue Zellstoffgewinnungsverfahren und Möglichkeiten der Nebenproduktverwertung, 1997	42,00 DM
Nr. 188	VOß, A.: Aufkommen und Zusammensetzung schutzmittelbehandelter Althölzer und ihre Entsorgung. 1998	46,00 DM
Nr. 189	SCHWAB, E. (Red.): Zukunft der Holzforschung und Holznormung. Fachtagung anläßlich der Verabschiedung von Professor Dr. Detlef Noack, 1998	41,00 DM
Nr. 190	ELLENBERG, H. (Red.): Vorträge und Poster der 8. Jahrestagung der Deutschen Gesellschaft für Tropenökologie, 1998	72,00 DM
Nr. 191	HEUVELDOP, J:; CEJCHAN, S.; FILIPTSCHUK, A.N.; SCHRÖDER, J.-M.; STRACHOW, V.W. (Red.): Aktuelle Probleme der Forstwirtschaft in der Russischen Föderation, 1998	42,00 DM
Nr. 192	KOCH, G.: Sekundäre Veränderungen im Holz dynamisch beanspruchter Fichten (*Picea abies* [L.] Karst.) aus immissionsbelasteten und windexponierten Hochlagenbeständen, 1999	