

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

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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 características 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, características biométricas das plantas e características morfológicas e anatômicas das folhas e da madeira. Adicionalmente, analisou-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 características 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
Herba- ceous	WH <u>W</u> inding <u>H</u> erbs = vines SC <u>S</u> pread <u>C</u> limbers*	GS <u>G</u> raminoid herbs, spreading by <u>S</u> tolons (<i>Poaceae</i>) GR <u>G</u> raminoid herbs, spreading by <u>R</u> hizomes (<i>Poaceae</i>) GT <u>G</u> raminoid herbs, forming <u>T</u> ussocks (<i>Poaceae</i> , <i>Cyperaceae</i>) BF <u>B</u> road-leaved <u>F</u> orbs (<i>Musaceae</i> inter alia) UH <u>U</u> pright or prostrate growing <u>H</u> erbs with medium or small leaves* HR <u>H</u> erbs, spreading by <u>R</u> hizomes (<i>Polypodiaceae</i>)
Woody	WT <u>W</u> inding or <u>T</u> wining plants = woody lianas (<i>Bignoniaceae</i> inter alia) SC <u>S</u> pread <u>C</u> limbers	SH <u>S</u> Hrubs** ST <u>S</u> parsely ramified, short-lived <u>T</u> reelets which regenerate mainly from seeds, forming broad or medium, simple, lobed or compound leaves (<i>Melastomataceae</i> , <i>Cecropiaceae</i>) RT <u>R</u> osette <u>T</u> rees, forming a single terminal crown of broad, compound leaves (<i>Arecaceae</i>) <i>Branched out trees, medium or small leaves:</i> LT <u>L</u> ow <u>T</u> rees, height <12 m, often regenerating from subterranean roots and shoots MT <u>M</u> edium <u>T</u> rees, height 12-20 m TT <u>T</u> all <u>T</u> rees (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. pyriformis* 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.

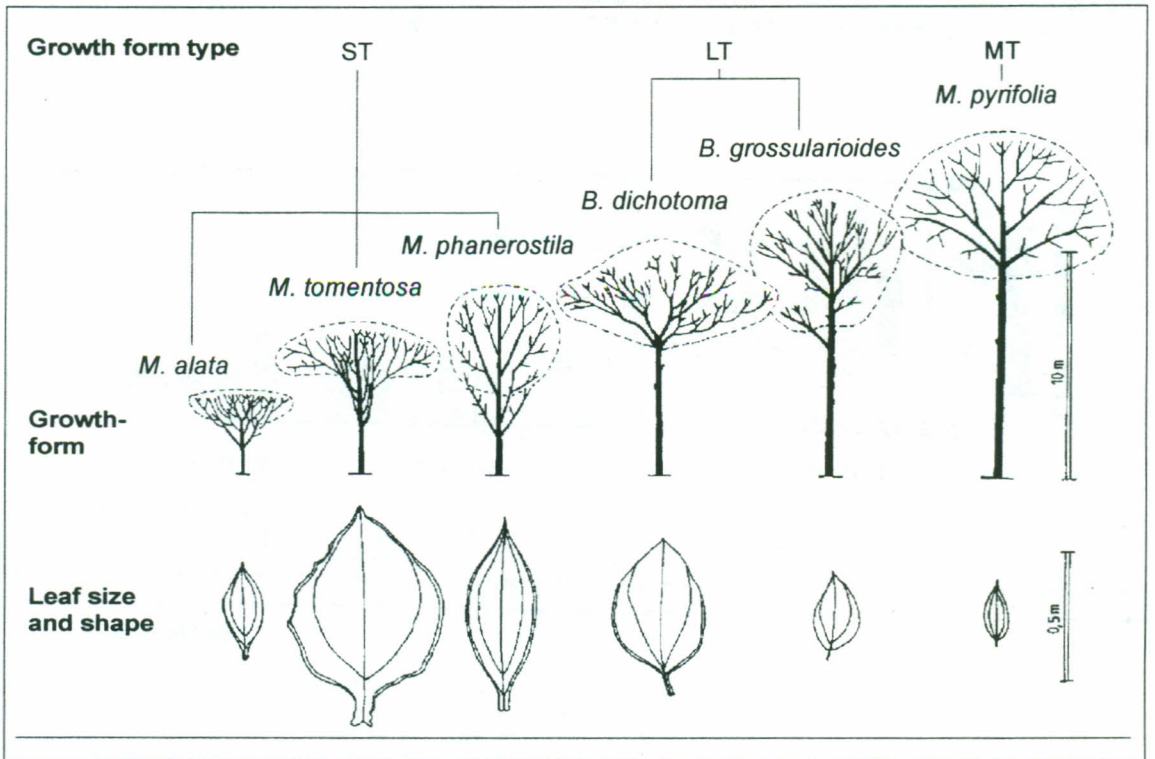


Fig. 1: Classification of *M. alata*, *Miconia tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia* with regard to growth form types of the growth form system (see Table 1), schemes of growth forms of the species and size and shape of leaves

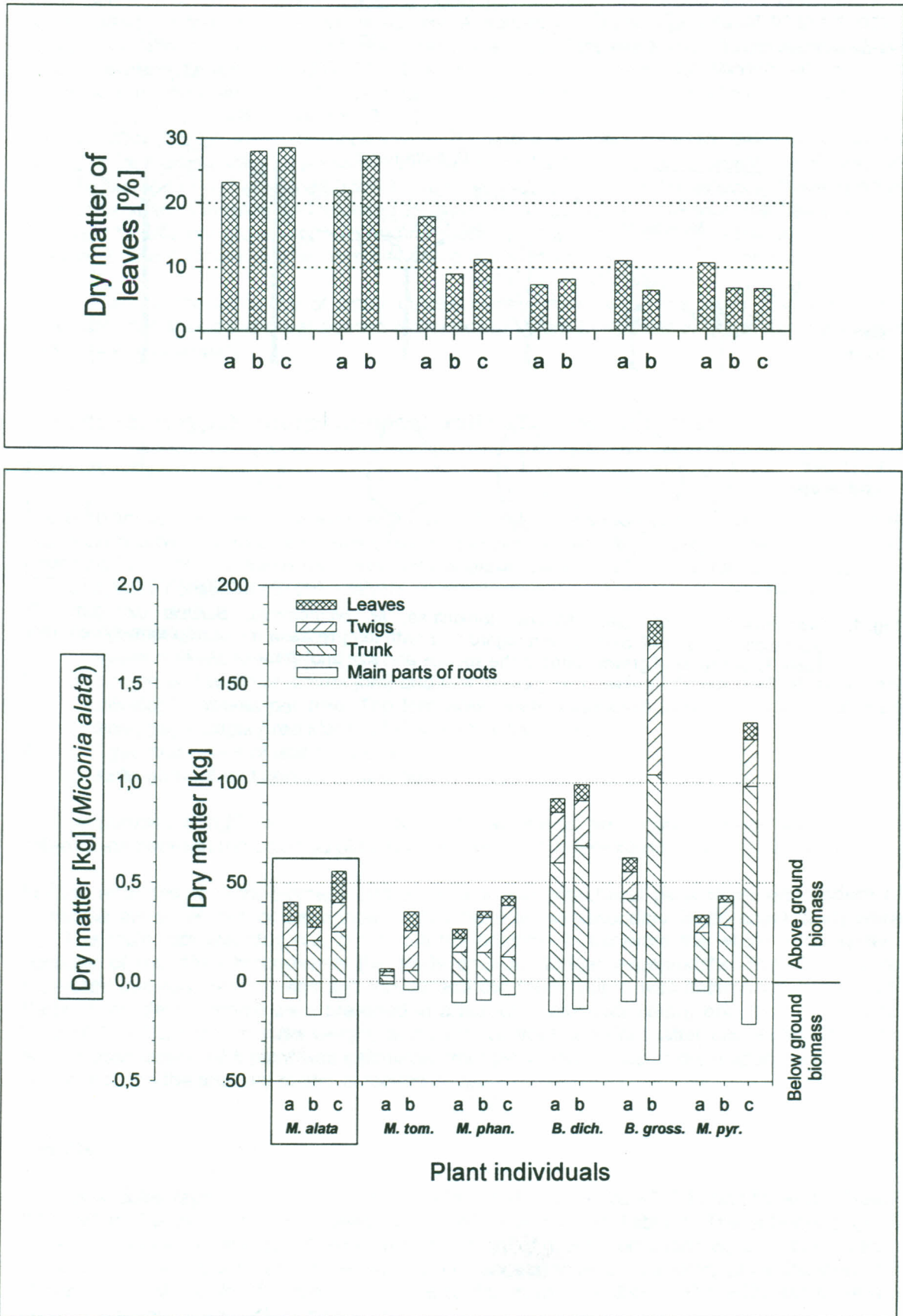


Fig. 2: Plant biomass total, overground and underground biomass and biomass of roots, trunk, twigs and leaves of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia* (plant individuals a, b, c)

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 [m ²]	Number of leaves
<i>M. alata</i>	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
<i>M. tomentosa</i>	a	7,59	8,0	13,0	14,0	163
	b	39,31	7,0	26,4	38,6	519
<i>M. phanerostila</i>	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
<i>B. dichotoma</i>	a	106,89	13,2	15,9	24,3	649
	b	112,60	12,7	15,3	42,4	1127
<i>B. grossularioides</i>	a	72,23	12,0	11,8	37,7	2711
	b	221,10	14,3	62,0	57,2	4286
<i>M. pyrifolia</i>	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).

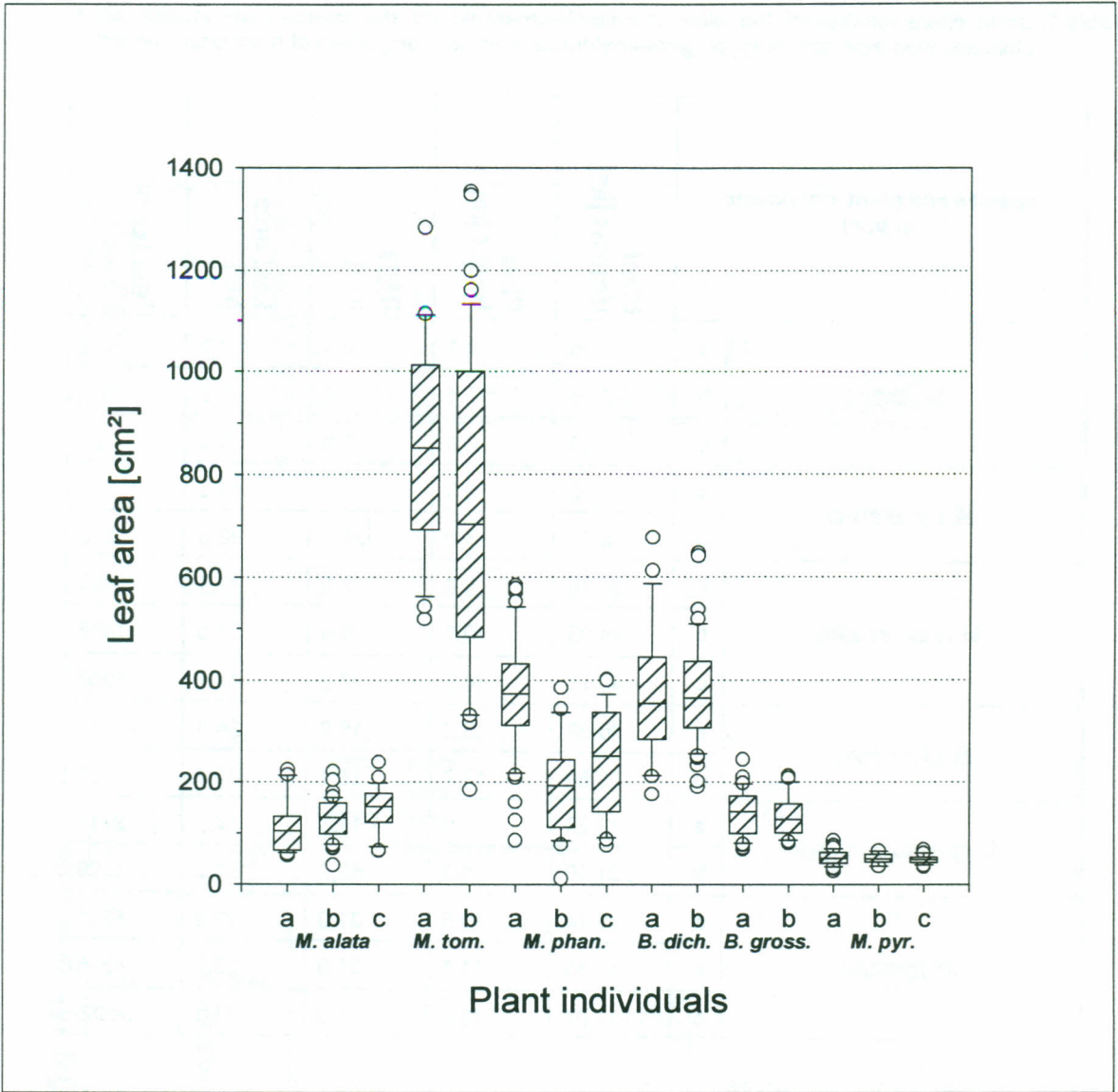


Fig. 3: Median, 75th, 90th percentiles and outliers of leaf areas of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia*, measured from 50 leaves per plant (plant individuals a, b, c)

Table 3: Characteristics of leaf surface

Species	Hairs	Mean no. of Stomata per mm ²
<i>M. alata</i>	Leaves with dense cover of white, soft-velvety hairs (stellate and glandular hairs), turning glabrous adaxially (only short glandular hairs)	80
<i>M. tomentosa</i>	Young leaves with dense brown, velvety hairs, older leaves turning glabrous adaxially; all nerves remaining densely covered with stellate hairs	142
<i>M. phanerostila</i>	Similar to <i>M. tomentosa</i> , but less hairy, stellate hairs reddish, also thicker and longer than in <i>M. tomentosa</i>	150
<i>B. dichotoma</i>	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
<i>B. grossularioides</i>	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
<i>M. pyrifolia</i>	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 amoniomolybdenate 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).

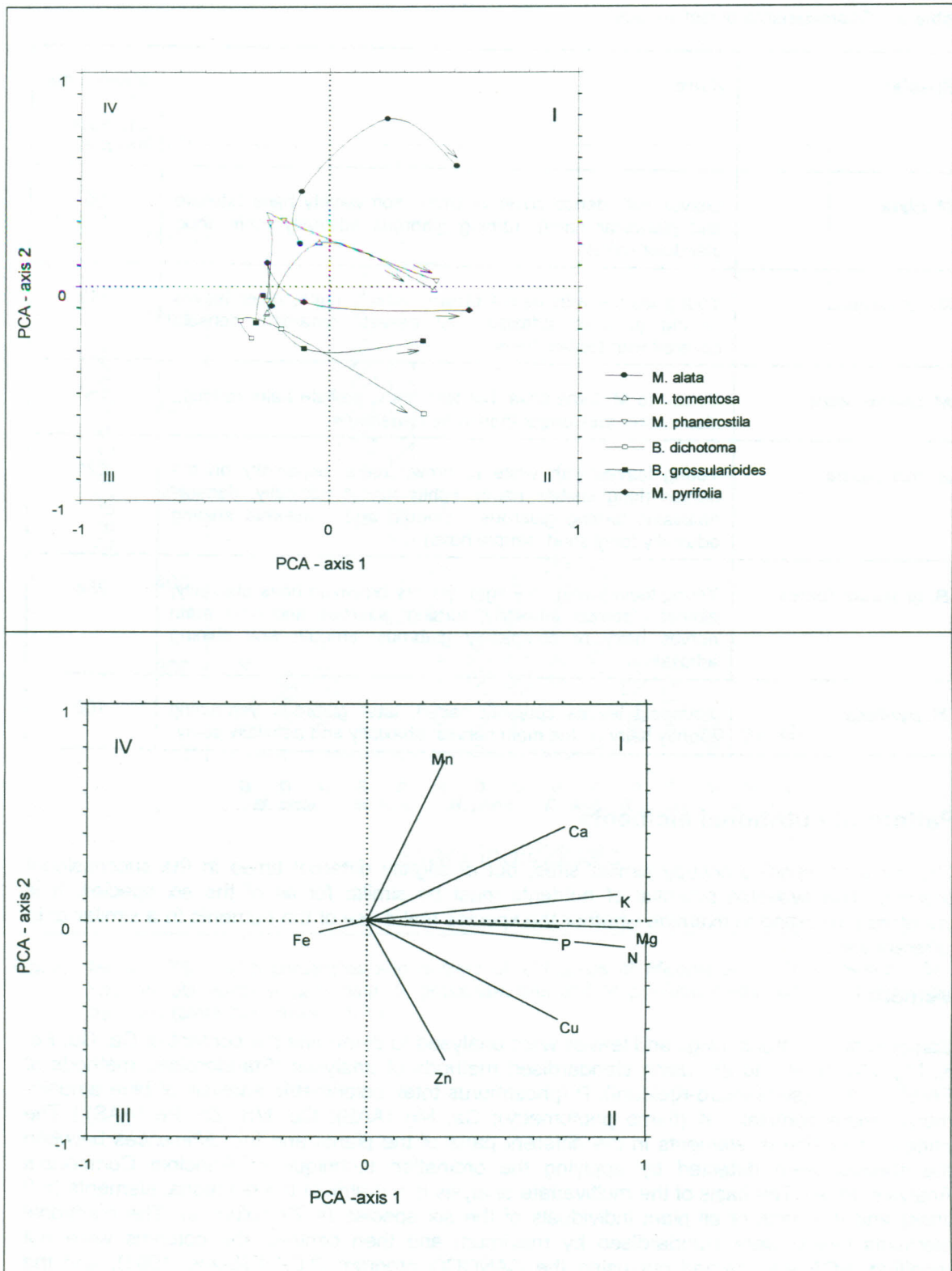


Fig. 4: Principal Component Analysis (PCA) of nutritional elements (Ca, Cu, Fe, Mg, Mn, K, N, P) of roots, trunk, twigs and leaves of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia* (centroids for the plant individuals a, b, c). Correlation 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. pyriformis*, *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 μ 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 $\pm 10\%$ (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 mm^2], arrangement of the longitudinal parenchyma) of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia*

Wood anatomical traits	<i>M. alata</i>	<i>M. tomentosa</i>	<i>M. phanerostila</i>	<i>B. dichotoma</i>	<i>B. grossularioides</i>	<i>M. pyrifolia</i>
Vessel diameter [μm]	37 \pm 10	59 \pm 10	79 \pm 20	133 \pm 14	92 \pm 12	69 \pm 10
Vessel area [%]	21,1 \pm 3,7	18,3 \pm 2,3	12,6 \pm 1,1	13,2 \pm 2,9	11,9 \pm 1,8	17,2 \pm 2,9
Vessel length [μm]	268 \pm 63	338 \pm 71	397 \pm 78	537 \pm 87	391 \pm 58	348 \pm 75
No. of pits per 0.01 mm^2	270 \pm 16	169 \pm 12	127 \pm 9	291 \pm 11	239 \pm 14	145 \pm 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. grossularioides* was found.

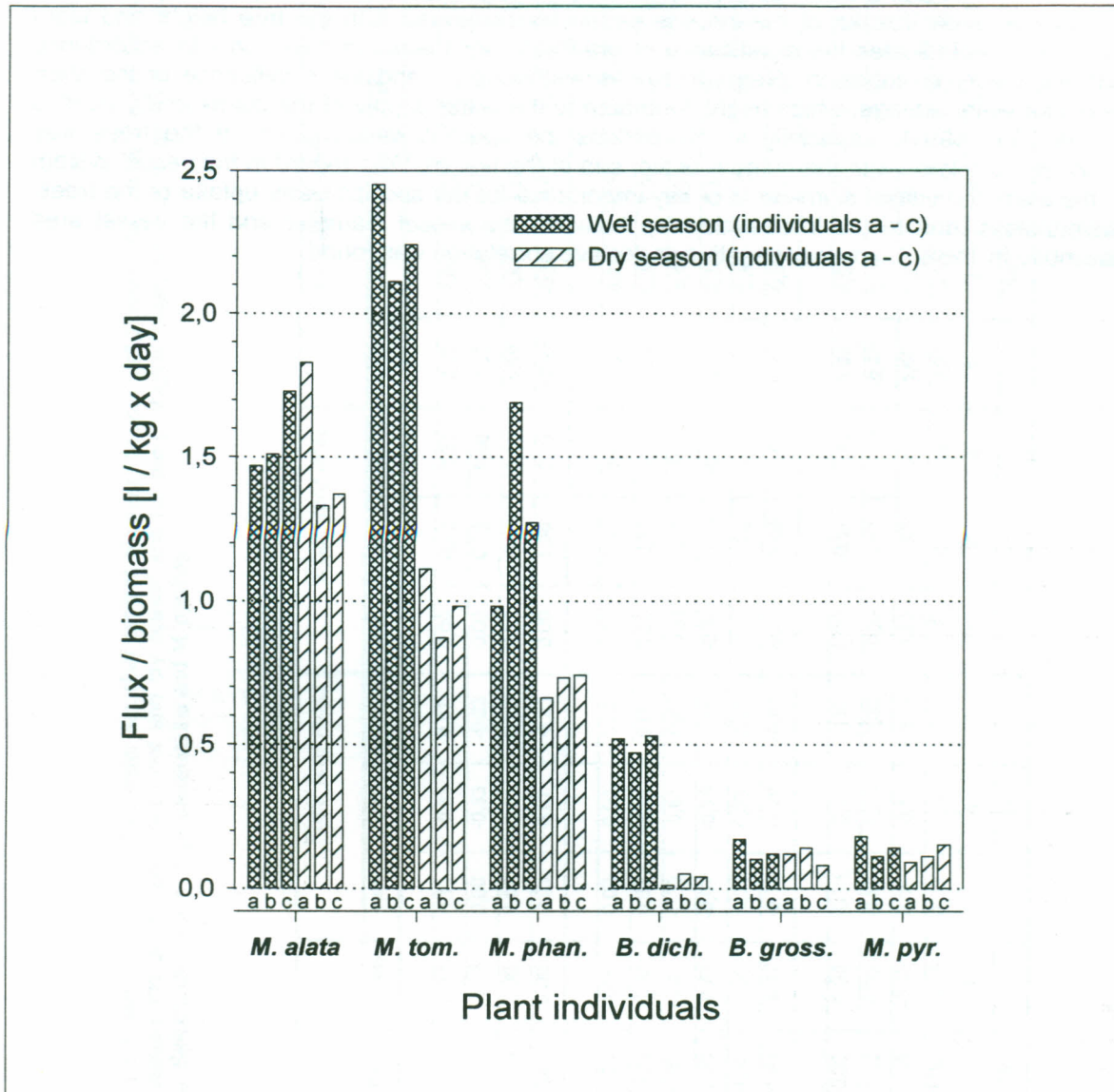


Fig. 5: Daily xylem water flux per tree biomass [l/kgd] of *Miconia alata*, *M. tomentosa*, *M. phanerostila*, *Bellucia dichotoma*, *B. grossularioides* and *M. pyrifolia* (plant individuals a, b, c) during the wet season (April 7 until April 17, 1998) and the dry season (November 10 until November 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 >66%
	wet	Dry	wet/dry	wet	dry	wet/dry	wet	dry	wet/dry	wet	Dry	wet/dry	wet	dry	wet/dry	
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	0,00	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 \pm 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).

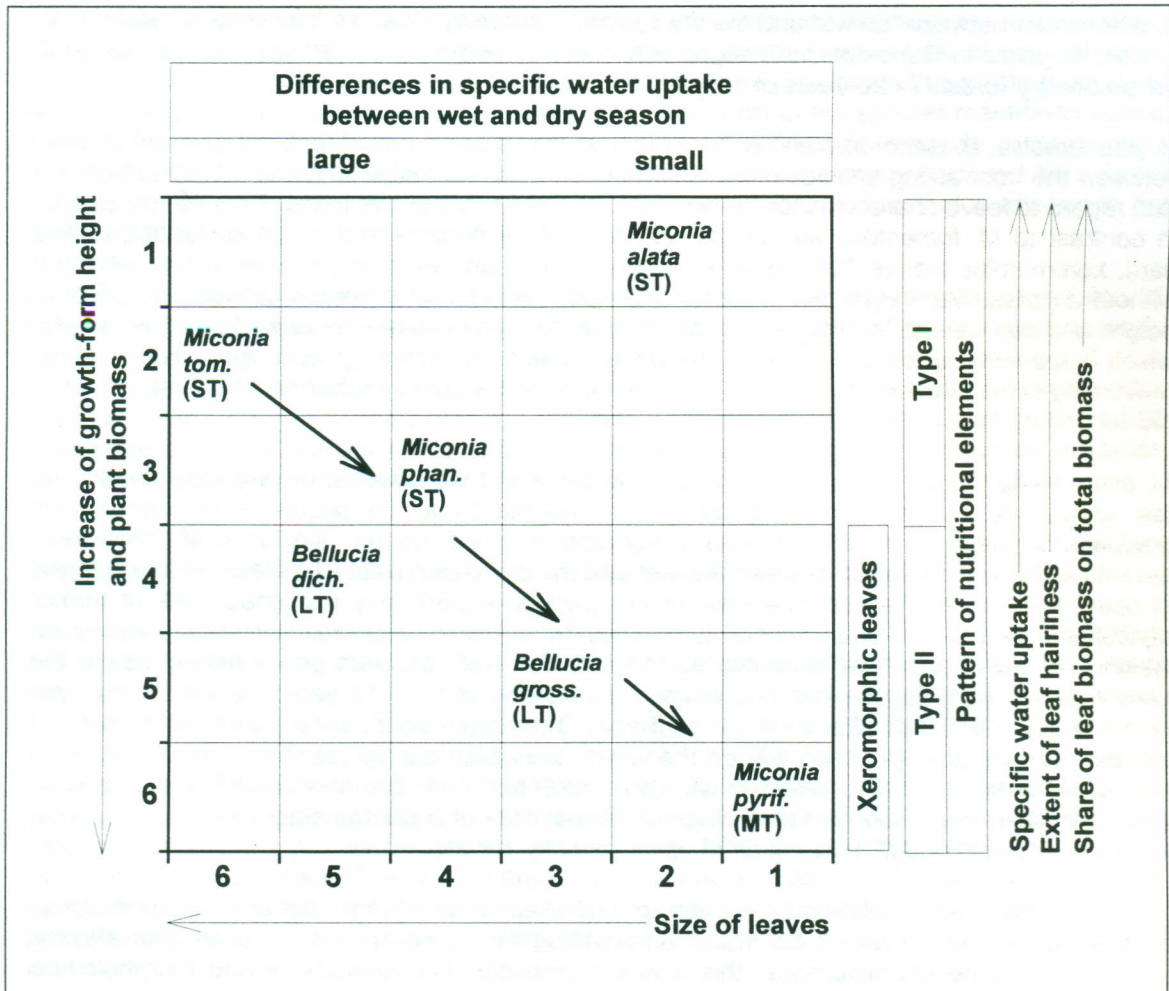


Fig. 6: Graphic summary of the results: Ranking of the six species with regard to the heights of growth form and size of leaves, displayed in a two-dimensional scheme, and correlation with other plant characteristics; diagonal arrows indicate the direction of progressive secondary succession

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 and 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 leaf 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 ecophysiologicaly 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), *Aparisthium 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.

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3. Appendix

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

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