Indicator Value of Anthropogenic Vegetation in the Amazon

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1 Objectives, assumptions and concepts

The comparative vegetation-science approach to the project "Recultivation ..." (ENV 23/2) is a continuation and amplification of the studies carried out from 1992 to 1996 for the predecessor ENV 23/1 project. These first studies on the spontaneous vegetation at the EMBRAPA/SHIFT experimental site near Manaus-AM had shown that the species combination and structural traits (e.g. cover, stratification and composition of growth-forms) of vegetation stands are closely linked to the pre-use and present management of the sites (see PREISINGER et al. 1994), which suggests that disturbance (as defined in GRIME 1979) is one of the key factors in the variation of vegetation. It was therefore decided to focus the follow-up studies on the indicator value of common species and of vegetation types, mainly with regard to disturbance (i.e. slashing and burning, cutting, trampling, hoeing).

It is assumed that the behavior of vascular plants in the humid tropics can be explained in part with the help of CSR theory (GRIME 1974, 1979), a life history concept which has already proven its practical validity for anthropogenic vegetation of temperate regions (see e.g. PREISINGER 1991). The starting point for the autecological studies is the classification of species in a growth-form system (Tab. 1, see PREISINGER et al., 1998, 1999) and morphological traits that are thought likely to be closely linked to important ecological factors, such as types of pre-use or of management (= extent and frequency of disturbance events), which are key factors in the suitability of sites for agriculture. The conclusions are to be incorporated in an indicator value system of practical applicability. Such a system would be useful for assessing the potential of fallow land for agricultural recultivation. In this context, the vegetation subproject can be divided into five partial objectives, each of which must first be accomplished in order to proceed to the next stage:

1 Recording of important autecological traits of frequently occurring secondary forest species and comparison with corresponding traits of useful plants which were planted in the experimental site.
2 Attempts to devise a functional description of successional stages of vegetation, growing in the agricultural experimental plantation and in surrounding secondary and primary forests.
3 Development of an indicator value system of practical applicability, especially to indicate types of pre-use, i.e. suitability for agricultural use.
4 Analysis of the field experiment using multivariate analysis techniques and the indicator system.
5 Comparison of structural traits of the vegetation in the experimental site with selected agricultural sites of smallholders of the Manaus region.

The approach requires three main branches of activity: floristic, autecological and synecological (see Fig. 1): Recording of the flora is the basic precondition for the other approaches. Because very little is known of the ecological behavior of the vast majority of the approximately 1.100 species of vascular plants occurring in the experimental site, it is necessary to accumulate a basic knowledge of the autecology of selected secondary forest "sample species". The species to be studied in detail were selected by personal judgement, taking into account both the (assumed) importance of the species in the successional sequence and the species' frequency and biomass production. In a synecological approach, a sequence of vegetation types, ranging from extensively used primary forest sites to agricultural land, is compared with regard to floristic composition and structural traits (composition of growth-form types, propagation and regeneration types, inter alia; see Tab. 2 for an overview of the data sets).

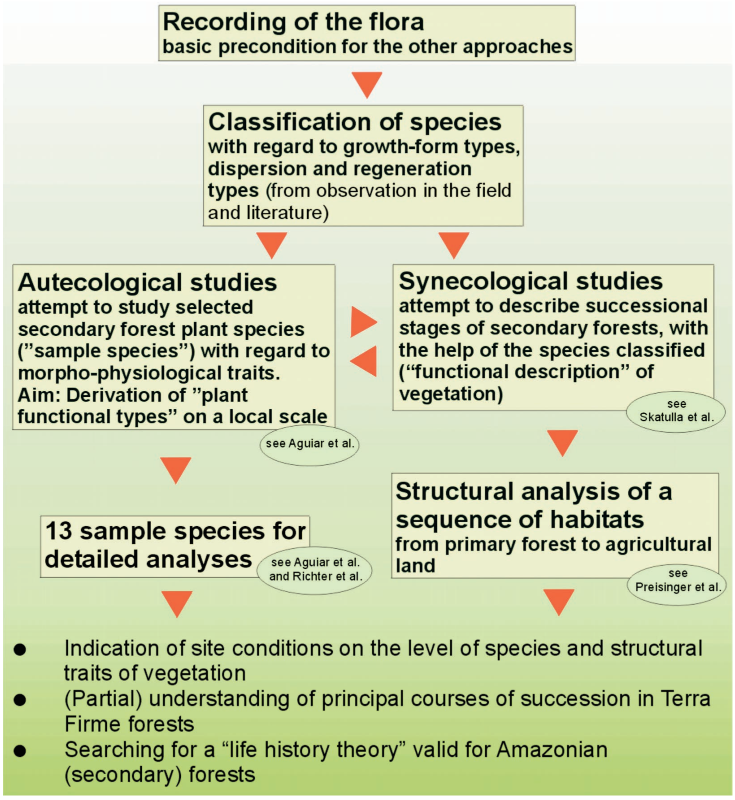


Fig. 1: Indicator value of anthropogenic vegetation in the Amazon - a comparative approach in vegetation science: Conceptual basis.

	non self-supporting	self-supporting
herbaceous	**WH** Winding Herbs = vines* **SC** Spread Climbers*	**GS** Graminoid herbs, spreading by Stolons (e.g. *Poaceae*) **GR** Graminoid herbs, spreading by Rhizomes (e.g. *Poaceae*) **GT** Graminoid herbs, forming Tussocks (e.g. *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* (e.g. *Bignoniaceae, Dilleniaceae*) **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 (e.g. *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 <12m, often regenerating from subterranean roots and shoots **MT** Medium sized Trees, height 12-20m **TT** Tall Trees (height >20m)
additional life form: **EPI** = Epiphytes		

* partly with woody stem at base

** "real shrubs" with a basitonic growth in accordance with Raunkiaer (1934) do evidently 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)

Tab. 1: Growth-form system (Preisinger et al. 1998, 1999).

1. Floristic data

- **Recording of all vascular plants** in the habitats mentioned below, preferably on the species level (approx. 1.100 species);
- **Classification** of the most frequently occurring species with regard to **growth form types** and **regenerative behaviour** (approx. 300 species classified).

2. Synecological data

- **Habitats recorded:** extensively used primary forest plots of 100 m^2 each (2.200 m^2 total), secondary forest plots of 100 m^2 each of 8 years of age and more (10.000 m^2 total) and plots of 1.600 m^2 used for the agricultural systems to be tested in the EMBRAPA/SHIFT experimental site (140.000 m^2 total); plots of 100 m^2 on farm land and fallow areas of smallholders near Manaus (total area of approx. 3.000 m^2);
- **Structural traits recorded:** stratification, distribution and dynamics of diameters of tree individuals (> 1 cm), total vegetation cover and cover of single growth form types [%] in the plots of the experimental site; biomass of all tree individuals (> 1 cm of diameter) in a 100 m^2 secondary forest plot;
- **Temporal sequences recorded:** 1. in all plots of the experimental sites: vegetation cover before planting of the useful plants (1993) and two and four years after, last survey planned in 1999; 2. in the secondary forest: all plots in 1994, 10 plots in 1996 and 1998 (planned);
- **Seed rain and dynamics of seedling populations** in primary forest, secondary forest and Capoeira plots.

3. Autecological data

- **Morphological and anatomical traits** of individuals of four species of *Miconia* and two of *Bellucia* (Melastomataceae), as well as biomass and content of mineral nutrients of the overground parts of plants;
- **Life history of leaf development** of individuals of 11 species of different plant families, including the six species of Melastomataceae mentioned;
- **Phenology** of frequently occurring species of flowering plants; characteristics of fruits and seeds.

Tab. 2: Overview of the data sets built up in the vegetation subproject.

2 Synecological studies

The vegetation types which were studied in the EMBRA-PA/SHIFT experimental site represent a combination of a spatial and a temporal sequence (cf. Tab. 2), and are the result of different types of pre-use (= different intensities and frequencies of disturbance). The vegetation was recorded in a quantitative form and its floristic and structural traits analyzed. Table 2 summarizes the floristic, taxonomic and structural traits of the vegetation types studied.

The number of species found in the 1.600 m^2 plots decreases drastically with the intensity and frequency of disturbance, from approximately 500 in the primary forest to 30 in the agricultural plots. The different vegetation types are characterized by a specific range of plant families, indicating that different taxonomic groups show a specific range of ecological behavior. Hence, some of the plant families present in a vegetation can be used as "key families" for the different types of habitat. The structural and functional traits presented in Tab. 3 are stratification, growth-form types and types of reproduction and/or regeneration. In Tab. 3, the different layers are named after the growth-form type of which they are mainly composed, and numbered from top to bottom.

The physiognomy of the Terra Firme primary forest studied is characterized by a canopy of tall trees up to 40 m of height and an understorey layer of palm trees *(Astrocaryum* spp., *Oenocarpus* spp., inter alia). Applying the Beard (1955) classification system, the forest has to be classified as "tropical rain forest", but showing a tendency towards an "evergreen seasonal forest". It is not possible to decide whether the forest type is similar to the "open forest with palms" of PIRES & PRANCE (1985), because of the concise description given there. KLINGE (1973) and PRANCE, *RODRIGUEZ & DA SILVA* (1976) do not propose any classification. In our first vegetation survey, carried out in 1994, the secondary forest had reached a height of 10 m. It was dominated by low trees, e.g. *Vismia guianensis* agg., and treelets, whereas *Miconia* (Melastomataceae) represented the largest number of species. These characteristics are special to the site studied and cannot be generalized for other secondary forests of the same age in the Central Amazon, because the course of succession greatly depends on the initial site conditions soon after the disturbance event, which might be different elsewhere. The spontaneous vegetation of the agricultural plots show a decline in the proportion of tree species, compared to primary and secondary forest, but the proportion of liana species remained ± constant (see Fig. 2). There are also differences in the number of species and structural traits between the different mixed cropping systems (see PREISINGER et al. 2000).

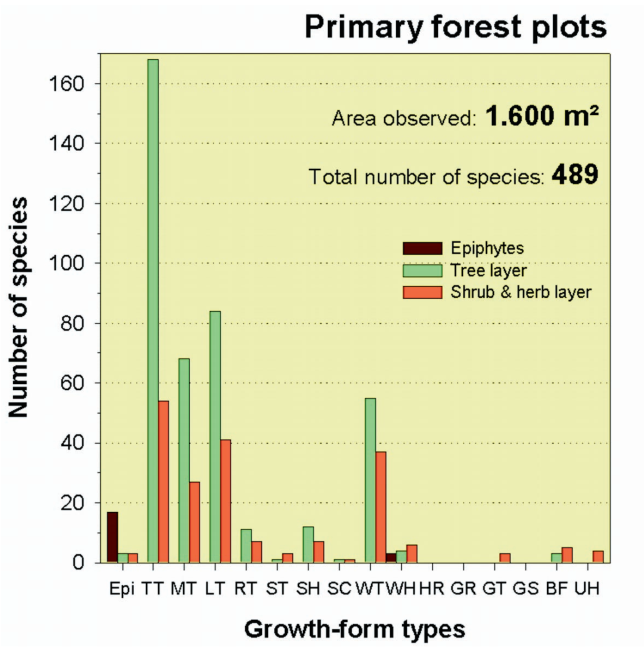
The reproduction of woody plant species by seeds plays an important role in the primary and secondary forest. In the primary forest, seed production is comparably low, the majority of the seeds are large and the dispersors are mainly larger animals. Seed production in the secondary forest is higher and the seeds are smaller than in the primary forest. In both the primary and the secondary forest, the site conditions are favourable to seed germination, but poor light conditions on the ground normally prevent the immediate growing of the seedlings. Seed production in the Capoeira and in the secondary forest is similar, but the majority of the seedlings in the Capoeira does not survive for more than one year (cf. SKATULLA et al. 2000). In the agricultural plots, the woody plants regenerate vegetatively by roots and shoots, but do not reach the reproduction phase.

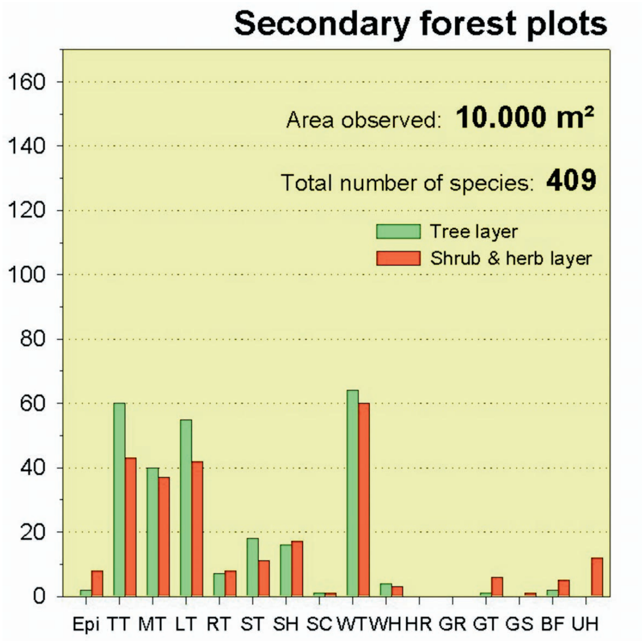
The ability to regenerate vegetatively after slashing and/or burning is one of the most important attributes governing the survival of the majority of woody plant species in a frequently disturbed environment. Lianas, grasses and herbs, but only few tree species can invade such open sites, spreading by stolons and rhizomes and reproducing by small seeds. In the experimental site, the habitats "primary forest", "secondary forest" and "Capoeira" are situated in close proximity to one another. Nevertheless, plant species do not often spread from one habitat to another and a spreading of primary forest species into the Capoeira was seldom observed, probably because the dispersors (e.g. large mammals and birds) avoid the open landscape (HOWE 1990).

Vegetation type	History of sites		Floristic and taxonomic traits		Some structural and functional characteristics of vegetation	
			n	Key families[1] *Dominant species*	Stratification and growth form types of spontaneous vegetation	Characteristics of reproduction and regeneration
(1) Primary forest	extensively used for timber extraction (mainly *Minquartia guianensis* Aubl. = Acuaricuara)		500	Sapotaceae Chrysobalanaceae Burseraceae Lecithidaceae *Astrocaryum spp.*	1. Epiphytes 2. Tall Trees 3. Medium and Low Trees; Lianas and Spread-climbers 4. Rosette Trees (palms) 5. Regenerating Trees 6. Herbs	Preferably reproduction by low quantities of large seeds; autochory, anemochory (large, winged seeds); zoochory (bats, large specialized frugivorous birds, large mammals)
(2) 8 year old secondary forest	Primary forest slashed and burned, rubber trees planted and abandoned 2 years after		200	Melastomataceae Moraceae Rubiaceae Bignoniaceae *Vismia guianensis agg.* *Miconia spp.* *Bellucia spp.*	(Epiphytes) 1. Medium and Low Trees; Lianas 2. Treelets 3. Regenerating Trees 4. Stolon Grasses and Herbs	Preferably reproduction by higher quantities of small seeds; autochory, anemochory, zoochory (unspecialised, frugivorous birds, bats, large mammals)
(3) 5 year old Capoeira	as in (2), but slashed and burned for a second time	sites left unattended	30-60	Bignoniaceae Rubiaceae *Vismia spp.*	1. Low (Medium and Tall) Trees 2. "Shrubs"[2] and Lianas 3. Stolon Grasses	Regeneration and subsequent spreading of woody plants by shoots and roots; reproduction by small seeds; anemochory, zoochory (unspecialised frugivorous birds and bats)
(4) Forestry system		timber trees planted in rows	30-60			
(5) Mixed cropping system		3 plantation systems	20-50	Poaceae Bignoniaceae Rubiaceae *Pueraria phaseoloides* (Roxb.) Benth., *Homolepis aturensis* (Kunth) Chase; locally dominace is reached by other species, e.g. *Clidemia hirta* (L.) D.Don)	1. Stolon and Tussock Grasses, herbaceous and woody Lianas, Herbs, regenerating Trees, "Shrubs"[2]	Regeneration of woody plants and grasses by stolons, rhizomes, roots and by tillering, reproduction of herbs and grasses by small seeds; anemochory, zoochory (unspecialised frugivorous birds and bats)
(6) Monoculture system		4 plantation systems	30-60			

1 Families which respresent the largest number of species in the vegetation types
2 "Real shrubs", marked by a basipetalic growth (see Raunkiaer 1934), obviously do not exist in the humid tropics. The growth form type "shrub" in the table is characterized by a mesopetalic growth and a low maximum height.

Tab. 3: Characteristics of a sequence of Terra Firme sites with different use histories in the Central Amazon (EMBRAPA/SHIFT experimental site near Manaus-AM); n = number of species of vascular plants found in an area of 1.600 m^2.





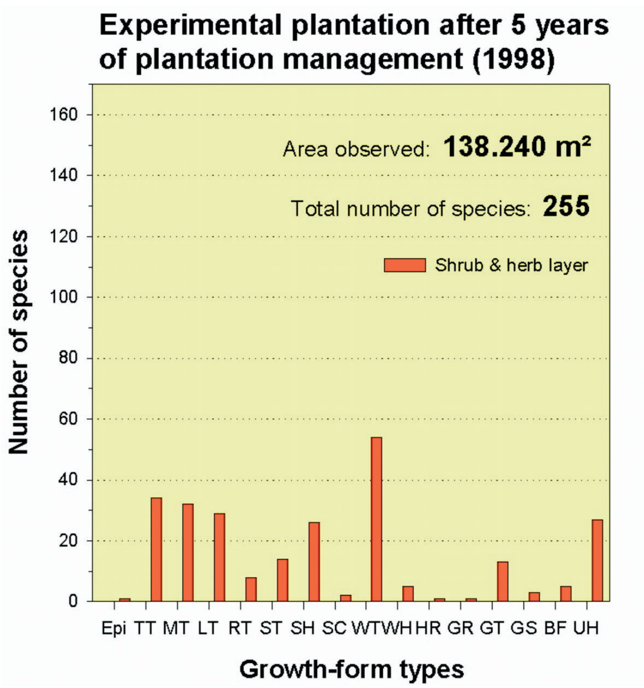


Fig. 2: Shift of growth-form composition in the spontaneous vegetation from forest to plantation (for abbreviations of growth-form types see Tab. 1).

3 Autecological studies

Prognoses on vegetation development after severe disturbance events like slashing and burning require a good knowledge of the autecological behavior of the plant species involved in the successional processes. This is not yet available for Amazonian plant species.

Thirteen common secondary forest tree species of Terra Firme sites near Manaus, Amazonas, Brazil, covering a wide range of growth-form types and of ecological behavior in the successional sequence, were selected for a comparative study designed to develop basic knowledge of their autecology. Growth-form, biometric traits and the morphological and anatomical characteristics of leaves and wood were compared. Plant biomass and the mineral nutrient content of different organs were analyzed in individual plants. In addition, the life history of individual twigs and leaves was recorded. In the approach we proceeded from the well-known fact that growth-forms of vascular plants represent a complex of characteristics closely linked to the ecological behavior of the species and their site conditions. The selected species ("sample species") form a sequence of morphological types, whereas the morphological traits are linked to a distinct ecological behavior in the pattern of spatial and temporal site conditions.

The analysis revealed at least three fundamentally different ecological types of secondary forest tree species and some of their functional traits. The sets of traits indicate different strategies for an efficient use of resources in a changing environment during a progressive succession. Type 1 is fast growing, short lived (± 10 years), invests little energy in trunk and twigs and appears early in succession. The hairy leaf surface might protect the leaves from drought in the open landscape. Type 2 are low and medium sized trees which invest much energy in large and durable leaves. The leaves are well protected against phytophages and mechanical damage. Type 3 invests much energy in a durable trunk and twigs, but little in the single leaf. The many, small leaves reduce the risk of loosing a considerable part of the canopy because of the destruction of single leaves.

The majority of recent studies on "plant functional types and disturbance dynamics" refers to a large geographic scale or the global scale (cf. BOX 1981, BOX 1996, DÍAZ & CABIDO 1997, MCINTYRE et al. 1999, inter alia). The present study identified functional traits and types on a local scale. The contrasting types identified in the example occur in the same sites, either at the same time or at different times in the successional sequence.

For additional aspects on the sample species and the results of the analysis see PREISINGER et. al. (1999), RICHTER (1999) and AGUIAR et al. (2000).

4 Valuation and summarization of the subproject and its results

The study is based on a vegetation survey of example sites of Terra Firme in the Central Amazon, which were altered by former or actual agricultural use. The interest was focussed mainly on the SHIFT experimental site, situated in the area of EMBRAPA Amazônia Ocidental in the north of Manaus, Amazonas. In the approach, flora and structural traits of the example sites were analyzed. In this context, structure is the organization in space of the plant individuals composing a vegetation stand, and the elements of vegetation structure are all the morphological elements composing the vegetation cover. The aim of the study was an indication of site conditions from the vascular plants present in a site. It was therefore necessary to be informed on their ecological behavior, which can be in part predicted from certain morphological traits of the plants. Hence, the identification of morphological traits which play a functional role for the plants were of major importance for the approach. Such characteristics are as well superior entities like growth-form, stratification and cover as morphological elements in the strict meaning of the word, like e.g. the surface structure of leaves. The analysis of such "morpho-physiological traits" is part of the autecological approach carried out in the project.

As a first step for a functional description of the Terra Firme vegetation altered by man in the Central Amazon, a growth-form system had been developed, and the species occurring in the experimental area were classified into the system. The system is adapted to the anthropogenic vegetation under study and kept as simple as possible. The classification of flora of a number of vegetation types revealed that the system in its present form is suited to differentiate between different stages of succession. More than that, the results show that it is possible to draw conclusions from the growth-form structure with regard to environmental conditions, e.g. like different durations and intensities of pre-use of a site. The first large data sets analyzed with the help of the growth-form system were eight sites of different use histories from the Central and Eastern Amazon (PREISINGER, BAAR & DENICH 1998). The evaluation of the data sets, applying Principal Component Analysis (PCA), resulted in an ordination model showing different directions for progressive and regressive successional processes. The corresponding vegetation types were characterized by specific growth-form spectra. However, the results showed also that the rough classification of the branched-out trees limited the potential of interpretation.

A comparative analysis of the growth-form spectra of the experimental plots in an extensively used primary forest, an eight year old secondary forest and in the experimental plantation, carried out separately for the tree layer and the shrub/herb layer, revealed in which way the forest vegetation responds to increasing intensities and frequencies of disturbance events (like trampling, cutting and hoeing, slashing and burning). The number of "Tall trees" declined drastically even after the first slashing and burning. Nevertheless, the detailed analysis of the secondary forest plots uncovered a high number of tree species still present in the shrub/herb layer, i.e. as saplings or young plants. A multivariate analysis of the secondary forest plots, also carried out separately for the two strata, showed two distinct floristic groups, representing tree and shrub/herb layer, and each of them forming a continuum of floristic composition. At long date it can therefore be expected that the secondary forest will develop progressively towards a mature forest similar to the primary forest, an undisturbed development provided. It is obvious that the growth-form type "Treelet" plays a key role in the succession of the forests in the experimental area. This type is defined here as a short-lived, woody plant with few ramifications and few, but large leaves, and which regenerates mainly from seeds. In the secondary forests of the experimental region, treelets are represented by numerous species of different families. In the experimental site, the abundance of many species of *Miconia* (Melastomataceae), which largely belong to that growth-form type, is striking. In the autecological approach, the studies were therefore initiated with 6 species of Melastomataceae (sample species), belonging to the growth-form types "Treelets", "Low trees" and "Medium sized trees".

The comparative studies in autecology of *Miconia tomentosa, M. phanerostila, Bellucia dichotoma, B. grossularioides* and *Miconia pyrifolia* revealed that the 6 species - all belonging to Melastomataceae - form a sequence with an increasing plant height and biomass, with specific morphological traits (of growth-forms, leaf size and structure, pattern of nutritional elements in the plant organs, inter alia) and with regard to the behaviour in succession (Preisinger et al. 1999). The comparative study on *Bellucia dichotoma* and *B. grossularioides,* being taxonomically and ecologically very similar, indicate which of the morphological differences leads to the slight differences in their ecological behavior (Richter 1999). The most important differentiating traits were identified as leaf size, mechanical structure and chemical substances (phenolic substances) of the leaves. The sequence of the sample species was extended to 13, the additional species belonging to other plant families than Melastomataceae. Anatomical characteristics of the leaves and the wood were studied and the results, being mainly results in fundamental research, were laid down in detailed reports (Morais 1998, Aguiar 2000). The functional plant types derived from the autecological studies relate to the successional stages found in the experimental sites. The results imply that a classification of frequently occurring plant species of the Amazonian flora would be possible. However, the number of species and morphological traits which could be surveyed within the present project was too limited to derive a functional classification of general validity. The autecological studies on the 13 sample species did therefore not lead to a fundamental amplification or change of the growth-form system, but to more precise definitions of the types. In this context, an attempt was made to define the growth-form types with reference to Grime's strategy types (see Table 4).
The spatial and temporal patterns of flora and structural traits of the spontaneous vegetation in the SHIFT experimental plantation had been surveyed for 8 years, using the growth-form system. The following questions had to be answered:

1 How did the spontaneous vegetation develop in the plots of the different plantation systems and under the regime of the plantation management?
2 Is it possible to indicate changes of site conditions from changes in structural traits of the spontaneous vegetation?
3 Which prognoses can be made, from the development of the spontaneous vegetation, for a sustainable agricultural use of the sites?

Re 1:
In the beginning of the experiment in 1993, the vegetation survey showed a spatial gradient with regard to flora and growth-form composition in the experimental site of elongated shape, ranging from experimental block A to E (Preisinger et al. 1994, Preisinger et al. 1997). The proportions of the growth-form types "Rhizomatous herbs", "Shrubs" and "Tussock grasses" increase from block A to block E, while the proportions of the regenerating "Trees" decrease. The cause of the gradient has to be interpreted as differences in the duration of pre-use between the experimental blocks. The spatial gradient could still be detected 5 years later in 1998, but the differences had in part been equalized under the regime of plantation management. A marked temporal gradient from 1993 to 1995, consisting of a shift in growth-form composition, showed increasing proportions of lianas and shrubs and decreasing proportions of regenerating trees, rhizomatous and tussock grasses. The total number of species decreased during the same period. In contrast, from 1995 to 2000 the proportions of rhizomatous and tussock grasses increased again, just as (dicotyledonous) herbs and shrubs. Moreover, the total vegetation cover decreased. The vegetation developed differently in the different plantation systems: In the monoculture plots, the number of species was higher than in the polyculture plots. Intensity and frequency of disturbance for the wild plants were higher in the polyculture than in the monoculture plots, propably because the cultivation measures in the polyculture systems were more intensive than in the monoculture systems. An effect of the fertilization measures on the spontaneous vegetation could not be detected. The multivariate analysis of flora, carried out in all the plots where Cupuaçu (*Theobroma grandiflorum*) had been planted (plantation systems 1, 2, 3 and 7), showed that the yield of Cupuaçu (= weight of fruits) is lower in blocks D and E than in the others. From the results of the analysis, presented graphically in an ordination model, plant species and growth-form types can be identified which indicate unproductive sites (e.g. bracken, *Pteridium aquilinum* and growth-forms "Tussock" and "Rhizomatous grasses") and productive sites (e.g. lianas as Kudzu, *Pueraria phaseoloides*). The results of this analysis are presented in detail in Preisinger et al. (2000).

Re 2:
The results presented above show that it is possible to indicate site conditions and their changes in space and time from structural characteristics of vegetation. In agricultural sites, the complex environmental factors "duration and

intensity of pre-use" and "actual plantation management" determine the floristic composition and structural traits of the spontaneous vegetation. These factors mean disturbance and/or stress to the plants (terms used in accordance with Grime 1979). They cannot be measured directly and are therefore only available from indirect deduction, i.e. the indicator value of vegetation. It can be assumed that agricultural use of tropical rain forest sites will lead to drier site conditions at long date. In particular the top soil can dry out and change its physical attributes during the rain-lacking season, because of the sparse vegetation cover which is regularly cut and hoed (cf. Teixeira 2001). Rhizomatous and tussock grasses, being indicators for sites used for long periods of time, can grow on temporarily dry sites with the help of deep root systems or rhizomes.

Re 3:

The yields obtained from the polyculture plots and the development of the spontaneous vegetation during the 8 years of observation show that there is no uncertainty on the potentiality for an agricultural use of the sites within that period of time. However, the spatial and temporal tendencies in vegetation development indicate that even the use by polyculture systems leads to drier sites at long date. For that reason there will be a temporal limit for the agricultural use on these sites. Observations showed patches in some of the plots of the experiment which were bare of vegetation (e.g. plot no. a9; see Photo Fig. 3). They can be interpreted as starting-points for a degradation of the sites and/or for soil erosion. The problem of the treatment of the spontaneous vegetation in Amazonian plantations is still

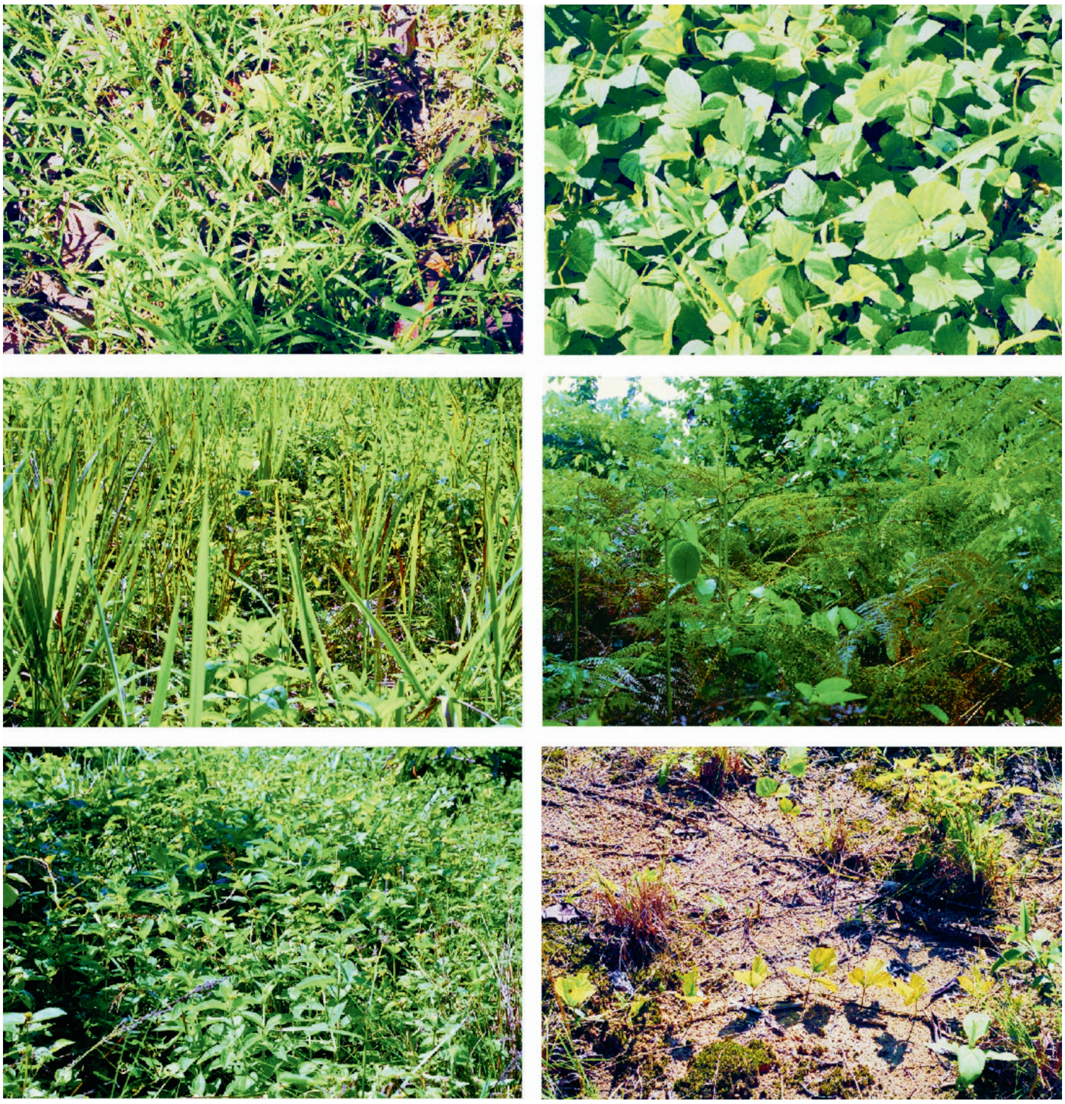


Fig. 3: Types of spontaneous vegetation in the experimental site:
Above / left: Stolon grasses (mainly Homolepis aturensis); above / right: Lianas (Kudzu - Pueraria phaseoloides); middle / left: rhizomatous grasses; middle / right: bracken (Pteridium aquilinum); below / left: shrubs (mainly Clidemia spp.); below / right: patch with bare soil.

unsolved: The farmer considers the spontaneous vegetation as a competitor for the useful plants (= weeds) and tries to control it mechanically. This leads at first to a sparse vegetation cover and later to degradation and at least to the abandonment of the sites. Sowing of a cover crop like Pueraria offers advantages. However, the smallholders mostly reject the introduction of Pueraria, because they cannot afford the additional labor necessary to keep the useful plants free of the tendrils of Pueraria (pers. commun. with farmers). More than that, the introduction of Pueraria leads to a drastic decrease of the species diversity of the spontaneous vegetation. This would prevent or delay a forest regeneration in case of the abandonment of the site. However, if the useful plants are not kept free from wild vegetation, they would be overgrown and eliminated by the wild plants.

The study of mechanisms responsible for the regeneration of the Amazonian forest vegetation (see SKATULLA 2000) followed a similar concept than the one presented above, i.e. a comparative analysis of flora and structural traits of example sites. This approach was directed to those morphological elements of the vegetation stand showing a relation to the generative and vegetative spreading of the plants (e.g. density of saplings, spatial-temporal patterns of flowering and fruiting, dispersal types).

Many of the results, experiences and observations accumulated during the project work were fed into a classification of more than 1.000 vascular plant species with regard to growth-form and dispersal types.

Growth-form types*	Morphological characteristics	Response to disturbance and/or stress	Range of strategy types	
1 **Trees** (LT, MT, TT)	Branched out trees with an acrotonic ramification, medium or small leaves	Sensitive against frequently occurring disturbances, but rare disturbance events can be survived, e.g. by sprouting from roots and stumps	(CR -) C - SC	Plants mostly native to rainforests
1 **Treelets** (ST)	Short-lived treelets with mesotonic, sparse ramifications, which regenerate mainly from seeds, forming a canopy consisting of few, but broad or medium, simple, lobed or compound leaves	Flexible response to disturbance events by growing new plants from seeds in suitable places (= forest gaps, disturbed areas); rapid growth rates	CR (- SR)	
2 **Shrubs** (SH)	Woody, at least at base, mostly fast growing, short to longer-lived plants with basitonic to mesotonic ramifications and medium to small leaves	Flexible response to frequently occurring disturbances, by rapid sprouting from the base of the stem, sometimes from roots	(CR -) SC	
3 **Lianas and spread-climbers** (WT, WH, SC)	Winding or twining plants, herbaceous or woody	Ecologically heterogenous plant group which mostly responds very flexible to disturbance (= mechanical damage) *and* stress (= shading, inter alia)	all strategy types except R	
4 **Rhizom. and tussock grasses** (GT, GR)	Graminoid herbs, forming tussocks or spreading by rhizomes	Tolerant against occasionally occurring destruction of overground biomass and periods of drought, but sensitive to shading; regenerating by tillering from the axils of leaves or from rhizomes and roots	SC - CSR	mostly invasive plants of cultivated areas
5 **Rhizom. herbs** (HR)	Long-lived, herbaceous plants with rhizomes (in the experimental site: bracken - *Pteridium aquilinum*)		SC	
6 **Stolon grasses** (GS)	Graminoid herbs, spreading by stolons	Flexible response to frequently occurring disturbances by sprouting and rooting from fragmented shoots	R - CSR	
7 **Herbs** (UH)	Short-lived, herbaceous, upright or prostrate growing herbs with medium or small leaves	Tolerant against frequently occcurring disturbances by producing seeds in an early ontogenetic stage	R	

* simplified version as used for the survey of growth-form types in the experimental plantation

Table 4: Generalisations of morphological characteristics and ecological behaviour of the growth-form types (see Table 1), with reference to strategies (strategy concept in accordance with Grime 1979).

5 References

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