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Analysis of growth form types and floristic composition
due to past disturbance and plantation management
in the SHIFT experimental area¹

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Resumo:

Análise dos tipos das formas de crescimento e da composição florística, devido ao distúrbio anterior e o manejo do plantio na área experimental do projeto SHIFT

Em Terra Firme próximo a Manaus, Amazonas, está sendo executado um experimento com sistemas de policultivo de plantas úteis, estabelecido em um plantio de seringueira abandonado. São testadas diferentes combinações de plantas úteis em 90 parcelas e 5 blocos. Isso leva inevitavelmente a um manejo diferente da vegetação espontânea, possibilitando estudar seu impacto sobre as plantas úteis. Se por um lado, a vegetação espontânea pode competir com as culturas (luz, nutrientes, espaços etc.) e nesse caso, devem ser eliminadas, por outro lado pode, ser importante para armazenar nutrientes. Se esses processos opostos podem ser otimizados em favor das culturas, através do controle apropriado da vegetação silvestre, é uma questão que deve ser examinada. Quatro meses após a limpeza e seis meses após o plantio das culturas no campo, foram efetuadas análises da vegetação com o objetivo de descrever as estruturas das formas de crescimento e a composição florística. Os resultados mostram modelos de vegetação que dependem principalmente do uso anterior dos locais, mas há diferenças que podem ter sido causadas pelo manejo recente das parcelas. Muitas das mais de 300 espécies presentes na área experimental mostram uma reação específica ao distúrbio. O termo "distúrbio" é usado de acordo com Grime (1979). A vegetação sob estudo está ajustada ao conceito das estratégias de Grime. Uma classificação das espécies comuns, devido a teoria CSR, é portanto, possível e pode ser útil para a compreensão dos modelos de vegetação.

¹ Work presented as a poster on the symposium "Tropical Useful Plants: Biology - Ecology - Economy" held in Hamburg, Germany, September 22 - 24, 1993.

Zusammenfassung:

Analyse von Wuchsformtypen und der floristischen Zusammensetzung unter dem Einfluß der Störung des Wildpflanzenwuchses durch das Plantagen-Management auf der SHIFT-Versuchsfläche

Auf einem Terra Firme-Standort bei Manaus wird in einem 19 ha großen Feldversuch eine aufgelassene Kautschukplantage durch eine Mischkultur-Plantage rekultiviert. Dabei werden in 90 Parzellen und 5 Blöcken (Wiederholungen) verschiedene Nutzpflanzen-Kombinationen erprobt. Dieses führt zwangsläufig zu einem unterschiedlichen Management der spontanen Vegetation und der Möglichkeit, deren Wirkung auf die Nutzpflanzen zu untersuchen. Einerseits ist die Wildvegetation eine Konkurrenz, andererseits ein wichtiger Nährstoffspeicher für die Nutzpflanzen. Ob diese beiden entgegengesetzten Forderungen zugunsten des Wachstums der Nutzpflanzen optimiert werden können, ist ein längerfristiges Ziel der Untersuchungen. Vier Monate nach Flächenrodung und sechs Monate nach den Pflanzungsarbeiten wurden Vegetationsuntersuchungen durchgeführt, die die Wuchsformen-Struktur und die floristische Zusammensetzung zum Ziel hatten. Die Ergebnisse zeigen Vegetationsmuster, welche vorwiegend durch Unterschiede in der Vornutzung geprägt sind, jedoch lassen sich bereits Unterschiede durch das aktuelle Management der Parzellen erkennen. Viele der über 300 Pflanzenarten, die auf der Untersuchungsfläche vorkommen, zeigen eine charakteristische Reaktion auf Störung ("disturbance" im Sinne Grime's 1979). Die untersuchte Vegetation scheint innerhalb des Gültigkeitsbereiches von Grime's Strategiekonzept zu liegen. Eine Klassifizierung häufig vorkommender Pflanzenarten nach der CSR-Theorie wird für möglich und sinnvoll angesehen.

1 Basic ideas, assumptions and problems

On a *terra firme*² site near Manaus, Amazonas, an experiment in recultivating a fallow rubber plantation by establishing mixed plantations of selected useful plants is carried out. Different crop combinations and types of management (plantation systems) are to be tested in order to find a way for sustainable use of these unfertile sites (for a general overview on the design of the experiment see Lieberei et al. 1993 and Lieberei et al.). The spontaneous vegetation in the different plantation systems evolve in a different way, due to plot management.

² terra firme: firm or solid land, in contrary to inundated land of the river Amazon.

The field trial on a total area of 19 ha comprising 5 blocks with 18 plots each has been laid out on the crest of a hill. The area is elongated and undulating. When the land was cleared, only the above-ground parts of the spontaneous vegetation were destroyed. The roots and rhizomes remained in the soil, so that the previous vegetation pattern survived in latent form. The soil is yellow latosol throughout. There are differences in the soil characteristics, which appear to be mainly due to the different historical uses of the sites (see *Tavares, Preisinger & Martins*). These are not the ideal conditions for a field trial. Consequently, in order to analyse the plantation systems, plots and blocks and the overall system, it is necessary to have as much information as possible about the initial conditions and to analyse existing ecological gradients, site differences and their spatial patterns. Recording and subsequent comparative analysis of these different types of vegetation are therefore of special interest for at least three reasons:

1. to improve the understanding of the mechanisms of competition³ for light, space and nutrients between the useful plants and wild plants: On the one hand, the spontaneous vegetation can constitute competition for the crops, in which case it must be suppressed. On the other hand, the spontaneous vegetation can be an important store for nutrients, which become available to the crops after dieback and mineralization of the biomass. Whether these opposed processes can be optimized in favour of the crops by appropriate control of the wild vegetation, is a question that is to be examined.
2. to develop an adequate evaluation strategy of the block experiment (see also *Tavares, Preisinger & Martins*): This requires carrying out a gradient analysis, respectively examining the species composition of different stands, to detect underlying environmental gradients by correlating the vegetation patterns with known environmental factors.
3. To accumulate knowledge of the response of frequently occurring species to different kinds of disturbance (the term "disturbance" is used here in accordance with Grime 1979). This knowledge, is necessary to solve the problems indicated in (1).

A methodology for a vegetation survey on a *floristic* basis, which can represent an area of 19 ha on the basis of a quantitative data set (e.g. cover values of the species) and which can be carried out with one or two workers in a reasonable time is not possible

³ The problem is considered here to solve applied problems, but it is a fundamental but controversial problem in vegetation science which is still discussed and has not yet been solved satisfactorily (see e.g. Ellenberg 1953, Grime 1979, Austin 1980, Tilman 1988, Austin & Smith 1989)

to achieve (cf. Greig-Smith 1983, p 299 ff). Moreover, after clearing the area in October 1992 there was a need to do this work as soon as possible because the secondary vegetation regenerates rapidly during the wet season. Therefore the vegetation analysis was carried out in two steps:

1. Estimating the cover values of *growth form types* present in the plots. This survey results in a *quantitative data set* on a *structural basis*.
2. Collecting *presence/absence data* of the *floristic composition* of the plots under consideration.

Whether the two different data sets can be combined, giving improved insights into vegetation composition, is a question which will be considered elsewhere (Preisinger, Siqueira & Coelho, in preparation).

The present knowledge of the ecological behaviour of common primary and secondary forest species of Amazonian terra firme sites is poor, and ecological knowledge of single species is distributed over a wide range of publications which makes evaluation of this information difficult. Summarizing descriptions of common species of the flora are often unprecise and mostly related to floristical traits (e.g. Prance 1975, da Silva et al. 1977, Wessels Boer et al. 1976), or are on the level of genera (Gentry 1993). Therefore basic knowledge of autecology even of common species can still be accumulated by simple techniques and methodologies (observation, estimation, counting, comparison).

2 Methods

2.1 Analysis of growth form types (quantitative data set)

Life form and growth form types have proved to be a valuable tool to indicate environmental conditions of vegetation stands in the temperate zones of the world (Raunkiaer 1937, Ellenberg 1979 inter alia). Dansereau (1951) suggests a system of growth form types and their graphical presentation ("Dansereau-Diagrams") which include tropical vegetation types. Especially in situations of disturbance gradients there is no doubt that a significant change in growth form composition takes place (see Preisinger 1991 for an example of riverbank vegetation).

The approach presented here is based on the assumption that the composition of the growth forms present on a site and hence the growth form distribution in the test area is a key indicator of past use and of associated site differences. It is therefore convenient to use the growth-form structure of the spontaneous vegetation for a gradient analysis. Four months after clearing - and after the area had been surveyed and divided into plots - growth form types of the spontaneous vegetation of all 90 plots of the trial were assessed quantitatively, i.e. on the basis of their respective area coverage. To meet practical requirements, the following seven growth form types were distinguished:

1. Trees
2. Shrubs
3. Lianas and herbs, spreading with runners
4. upright growing herbs
5. Stolon grasses
6. Rhizome or tussock grasses
7. Ferns, spreading by rhizomes (*Pteridium aquilinum* predominant).

The plot size (48 x 32 m²) is taken as the reference area, because this will inevitably also be the most important unit of area in subsequent analyses. The vegetation matrix obtained consists of the seven identified growth forms of the 90 plots with the cover rates for the species of a given growth form.

There is a clear demand for a more sophisticated classification of growth form types for the plant species of the study area, but this must meet the practical requirements of the studies. Therefore an advanced classification system (cf. Box 1981) is not applicable. Above all, the trees must be divided into several sub-types, which could be related to the role of the species in forest succession.

2.2 Analysis of the flora (presence/absence-data set)

The floristic composition of a vegetation stand can be an indicator of the site history, especially for historical use or past disturbance, if there is sufficient autecological information available for the species under consideration. Harper (1982) doubts that ecological variation can be described adequately by taxonomic characters, because taxonomic groupings are based on stable, conservative traits and "it may be just the taxonomically useless characters that are mainly responsible for determining the precise ecologies of organisms". However, different comparative approaches in classification of the most common species of flora according to their ecological response to site factors (Ellenberg 1979, inter alia) or to eco-morphological traits which are favourable

for the plants under certain environments (Grime 1979, Grime, Hodgson & Hunt 1988) were successfully applied to solve practical problems in agriculture, nature conservancy and landscape ecology. Even on higher taxonomical levels there might be superior ecological traits and behaviours (e.g. all *Amaranthaceae* and *Chenopodiaceae* are disturbance tolerant or ruderal herbs).

An initial floristic study was carried out before the secondary forest in the test area was cleared in October 1992. One year later, after the installation of the mixed plantation, a more detailed floristic study was completed. The flora of 71 of the 90 plots of the experiment were surveyed separately. The monoculture systems were left unattended in the floristic analysis, except for two plots used for comparison. From each plot under consideration a sample of each plant species found was collected and prepared, identified and stored for future comparisons.

3 Results

3.1 Spatial distribution of growth form types

The vegetation pattern in the experimental area four months after clearance represents a moment in vegetation development. The growth form structure of the different plots is composed by those organisms which were able to build up a biomass after clearance by regenerating from

1. subterranean roots and shoots,
2. overground shoots which were not destroyed by the fire,
3. surviving seeds which were present before clearance,
4. anemochorous and zoochorous seeds which reached the area after clearance.

As known so far, a majority of the species belong to groups (1) and (4).

The spatial distributions of the growth form types with the highest cover values (trees, stolon grasses, creeping herbs/lianas, tussock/rhizome grasses) are shown below (Figs. 1-4). The experimental area is represented schematically. The smallest spatial unit considered is the 48 x 32 m² plot. Neighbouring vegetation types likely to influence growth form structure, respectively composition of species in the experimental area (by invasion of single species with the aid of seeds, roots, rhizomes or runners) are marked by an ellipse. From Figs. 1-4 the following trends can be seen:

Trees (Fig. 1)

The significance of this growth form diminishes from block a to block e. The main reason may be the longer lasting and more intensive use of the sites belonging to blocks d and e.

Stolon grasses (Fig. 2)

Sites with a high percentage of trees which regenerate poorly or not at all from stool shoots (mainly primary forest species?) are left with bare soil after clearing and burning, and are colonized first by stolon grasses (R-strategists), which are present everywhere by a seed potential.

Creeping herbs and lianas (Fig. 3)

The sowing of *Pueraria phaseoloides* as a cover crop in the former rubber plantation on the present experimental area and in the remaining rubber plantation explains much of the pattern of this growth form, but there are other plant species belonging to this group which are dominant in some places.

Tussock and rhizome grasses (Fig. 4)

These growth forms occur together with bracken (*Pteridium aquilinum*) in block e. The latter is found only here. The dominance of growth forms which propagate vegetatively by means of creeping underground shoots is favoured by frequent hoeing.

The potentiality to find ecological explanations which explain the growth form pattern observed will rise if there was more information about historical use than is available at present.

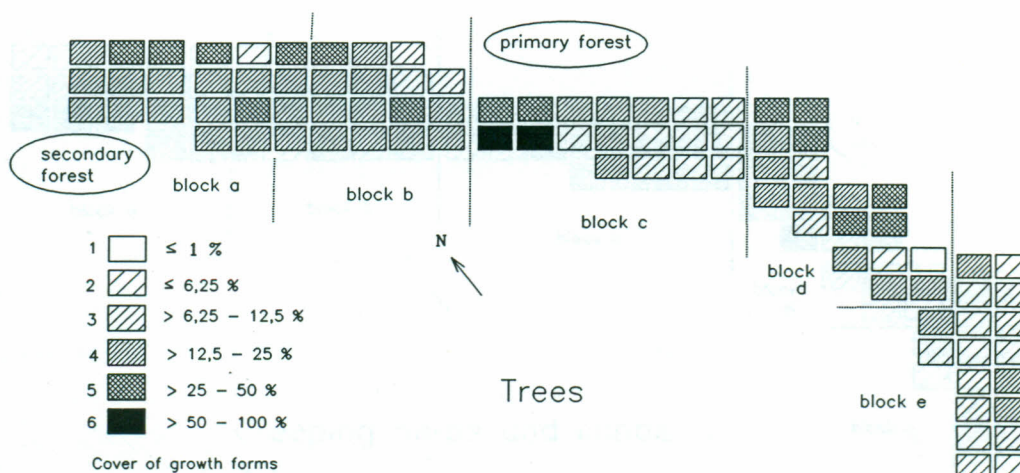


Fig. 1:

Spatial distribution of the growth forms in the experimental area: trees

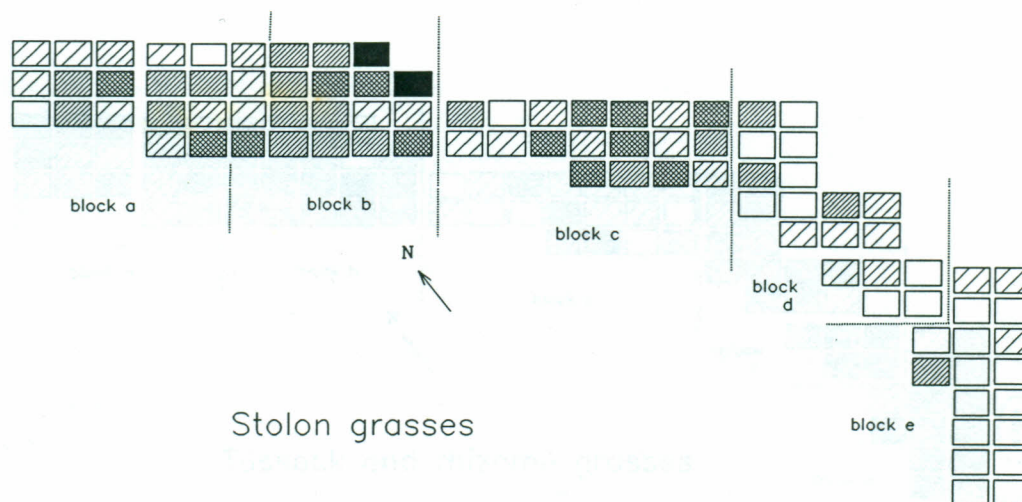


Fig. 2:

Spatial distribution of the growth forms in the experimental area: stolon grasses
(legend to cover of growth forms see Fig. 1)

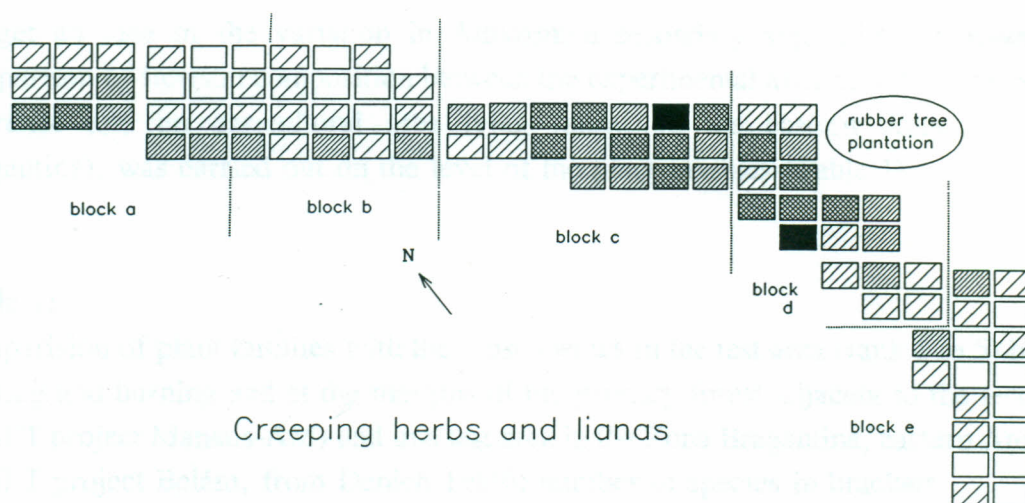


Fig. 3:

Spatial distribution of the growth forms in the experimental area: creeping herbs and lianas (legend to cover of growth forms see Fig. 1)

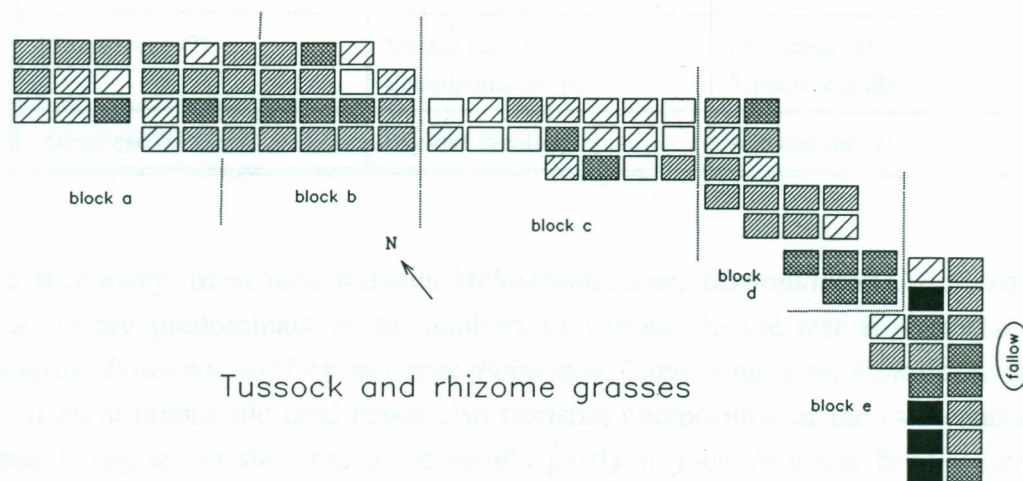


Fig. 4:

Spatial distribution of the growth forms in the experimental area: tussock and rhizome grasses (legend to cover of growth forms see Fig. 1)

3.1 Floristic composition

To get an idea of the variation in Amazonian secondary vegetation (*capoeira*), a comparison of floristic composition between the experimental area near Manaus before clearance and an agricultural area lying fallow in the eastern Amazon (Zona Bragantina), was carried out on the level of the plant families (Table 1).

Table 1:

Comparison of plant families with the most species in the test area (rank 1 to 5) before slashing and burning and at the margins of the primary forest adjacent to the test area (SHIFT project Manaus-AM) and in a test area in the Zona Bragantina, eastern Amazon (SHIFT project Belém, from Denich 1989); number of species in brackets

	Manaus, Amazonas		Igarapé-Açu, Pará
	experimental area	margin of prim. forest	(Denich 1989)
1	Melastomataceae (15)	Moraceae (7)	Myrtaceae (13)
2	Bignoniaceae (10) Moraceae (10) Rubiaceae (10)	Chrysobalanaceae (6)	Mimosaceae (12) Fabaceae (12)
3	Apocynaceae (9) Fabaceae (9)	Melastomataceae (5)	Caesalpiniaceae (10)
4	Mimosaceae (7)	Sapotaceae (4) Caesalpiniaceae (4)	Rubiaceae (8) Sapindaceae (8)
5	Arecaceae (6)	(various families)	Annonaceae (7)

In the secondary forest near Manaus *Melastomataceae*, *Bignoniaceae*, *Moraceae* and *Rubiaceae* are predominant as to numbers of species, in the test area of the Zona Bragantina *Myrtaceae* and *Leguminosae* (*Fabaceae*, *Caesalpiniaceae*, *Mimosaceae*). The very different taxonomic (and hence also floristic) composition of the two Amazonian secondary vegetation sites has to be sought partly in their different history (shifting cultivation for about 90 years in Igarapé-Açu, primary forest slashed and burned ten years ago in Manaus). The impact of other environmental factors as different geographic location and differences in soil types is difficult to estimate at present.

A comparison of the 27 plant families with the most species in the spontaneous vegetation in the experimental area, before and one year after the installation of the mixed culture plantation (Fig. 5), reveals a sharp increase of the portion of species of

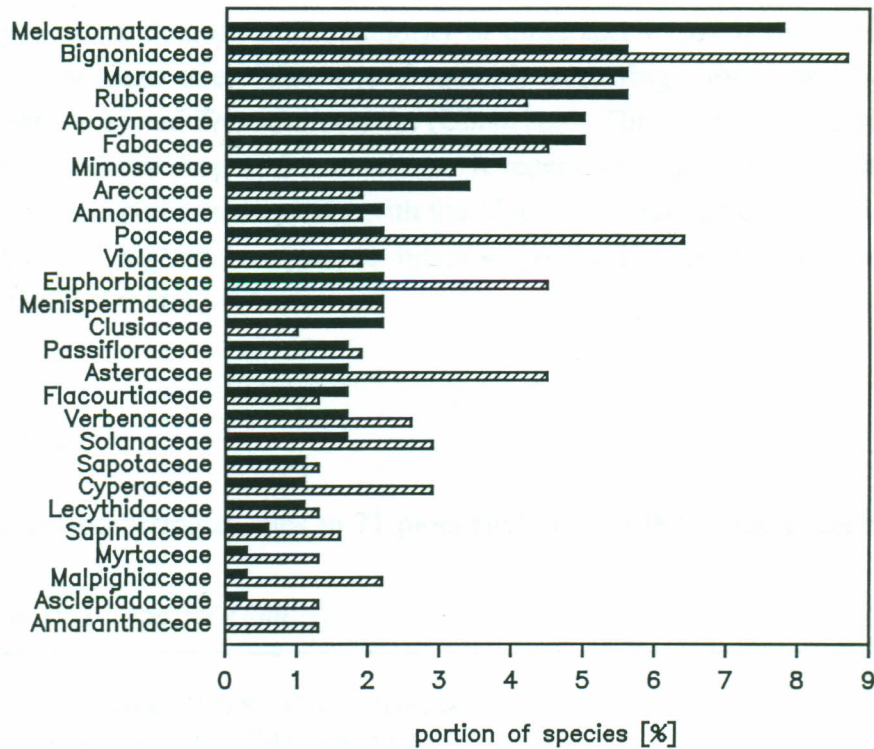


Fig. 5:

Plant families with the most species on the test area before clearance (solid bars), displayed in descending order, compared to those one year after clearance, respectively nine months after planting (hatched bars)

only herbaceous families (*Poaceae*, *Cyperaceae*, *Amaranthaceae*) and herbaceous representatives of other families (*Asteraceae*, *Solanaceae*, *Euphorbiaceae*, *Asclepiadaceae*). These species are "invaders" or "ruderals" in a wide sense or, expressed in terms of CSR-theory (Grime 1979), behave as ruderals (R), competitive ruderals (CR) and CSR-strategists, some as stress tolerant competitors (SC)⁴. However, the most spectacular change in taxonomic composition took place in *Melastomataceae*. The majority of the representatives of the plant family with the most species present on the area before clearance did not regenerate. The only genus of *Melastomataceae* found frequently on the area after slashing and burning is *Clidemia*, above all *Clidemia hirta* (L.) D. Don., a shrub which regenerates quickly by seeds and vegetatively from roots and shoots. In *Bignoniaceae* there are many lianas, shrubs and small trees which obviously regenerate or evolve, so the latter family is that one with the most species after clearance.

⁴ The classification involves specific types of growth form, behaviour of growth and regeneration. For details see Grime (1979), for a review Preisinger (1991).

Table 2 lists the 30 species (of 312), which occur most frequently in the experimental area one year after clearance. The majority of these species are herbs, grasses, shrubs and only a few small trees. The most frequently occurring shrubs are *Clidemia hirta* (*Melastomataceae*) and *Trema micrantha* (*Ulmaceae*). The liana *Pueraria phaseoloides* was sown as a cover crop in former times. It regenerated quickly after clearance and is now one of the herbaceous plants with the highest biomass production. The tree that accumulated the highest overground biomass production after clearance is *Vismia guianensis* (*Clusiaceae*).

Table 2:

Most frequent occurring species in 71 plots analysed (of 90) in the experimental area

frequency [%] / species (family)

92	<i>Homolepis aturensis</i> (H.B.K.) Chase (<i>Poaceae</i>)
72	<i>Croton miguelensis</i> Ferg. (<i>Euphorbiaceae</i>)
69	<i>Pueraria phaseoloides</i> (Rosed.) Benth. (<i>Fabaceae</i>)
69	<i>Clidemia hirta</i> (L.) D. Don. (<i>Melastomataceae</i>)
68	<i>Borreria verticillata</i> (L.) G.F.W. Mey. (<i>Rubiaceae</i>)
62	<i>Trema micrantha</i> (L.) Blume (<i>Ulmaceae</i>)
62	<i>Panicum laxum</i> Sw. (<i>Poaceae</i>)
61	<i>Davilla latifolia</i> Casar (<i>Dilleniaceae</i>)
61	<i>Rolandra fruticosa</i> (L.) Kuntze (<i>Asteraceae</i>)
59	<i>Machaerium hoehnearum</i> Ducke (<i>Fabaceae</i>)
59	<i>Irlbachia alata</i> (Aublet) Maas (<i>Gentianaceae</i>)
54	<i>Cecropia</i> spp. (<i>Moraceae</i>)
52	<i>Solanum rugosum</i> Dun. (<i>Solanaceae</i>)
49	<i>Emilia sonchifolia</i> D.C. (<i>Asteraceae</i>)
48	<i>Vismia cayenensis</i> (Jacq.) Pers. (<i>Clusiaceae</i> = <i>Guttiferae</i>)
47	<i>Borreria latifolia</i> (Aubl.) K. Schum (<i>Rubiaceae</i>)
47	<i>Passiflora coccinea</i> Aubl. (<i>Passifloraceae</i>)
45	<i>Lantana camara</i> L. (<i>Verbenaceae</i>)
45	<i>Piper</i> spp. (<i>Piperaceae</i>)
44	<i>Vismia guianensis</i> Choisy (<i>Clusiaceae</i> = <i>Guttiferae</i>)
44	<i>Arrabidaea</i> spp. (<i>Bignoniaceae</i>)
44	<i>Pogonophora schomburgkiana</i> Miers. (<i>Euphorbiaceae</i>)
44	<i>Paspalum maritimum</i> Trin. (<i>Poaceae</i>)
44	<i>Scleria pterota</i> Presl. (<i>Cyperaceae</i>)
42	<i>Passiflora auriculata</i> H.B.K. (<i>Passifloraceae</i>)
37	<i>Cecropia leucocoma</i> Mig. (<i>Moraceae</i>)
37	<i>Caryophylla</i> sp. (<i>Caryophyllaceae</i>)
37	<i>Memora</i> spp. (<i>Bignoniaceae</i>)
37	<i>Chimarrhis</i> spp. (<i>Rubiaceae</i>)
35	<i>Panicum rudgei</i> R. & S. (<i>Poaceae</i>)

The floristic analysis of 71 out of 90 plots revealed 312 species. Fig. 6 (top) displays the total numbers of species found in blocks a-e, showing a maximum in block e and a minimum in block b. To find out differences in the richness of species between the plots of five blocks, a one way analysis of variance was carried out (Kruskal-Wallis one way ANOVA on ranks). According to the test there are no statistically significant differences in the median values among the groups. Nevertheless, the bar chart and the box plot (Fig. 6) indicate a clear tendency of increasing maximum species numbers in the plots from block a to e (in particular see 90th and 95th percentiles of box plot). This increase can be explained by local migration of "opportunistic" (R-, CR- and CSR-) species which grow in patches, advancing from block e

to block a, leaving the secondary forest species growing between. To find out differences in species richness between the different plantation systems, the same statistical test was carried out as mentioned above, comparing systems 1, 2, 3, 4, two monoculture plots (system 9, citrus) and the fallow plots. The Kruskal-Wallis-Test reveals a significant difference between system 1 and the fallow plots only. The results (Fig. 7) can be interpreted as *a tendency of increasing species richness with a decreasing extent of disturbance*⁵. System 1, showing the lowest species numbers, is the most "intensive", system 4 the most "extensive" agricultural system. The highest species numbers occur in the fallow plots, where after slashing and burning no further disturbance took place. The species numbers of the monoculture systems, which are

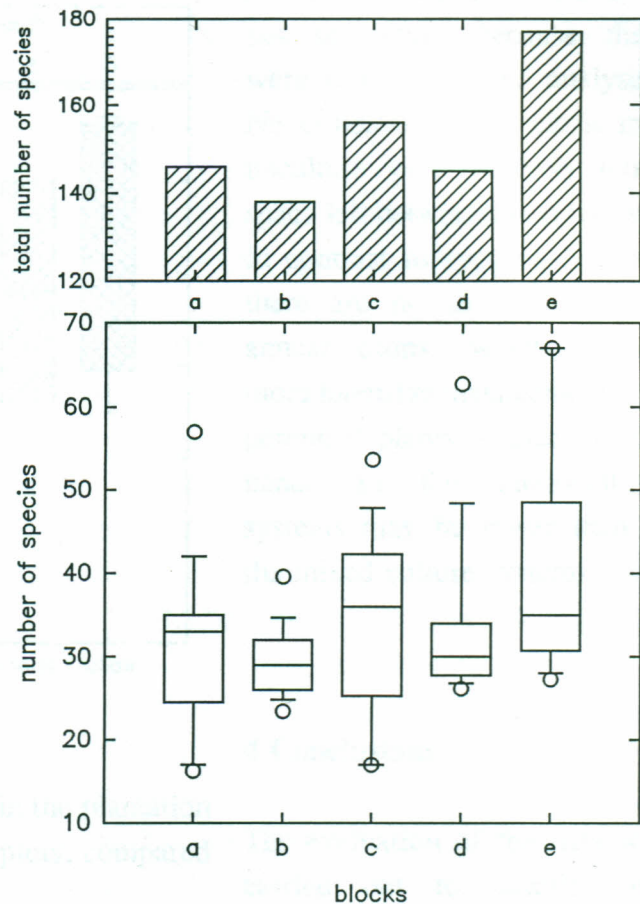


Fig. 6:

Total numbers (top) and median numbers of species (bottom, box plot) present in blocks a-e, the latter representing also 25/75th, 10/90th and 5/95th percentiles

⁵ A causality between richness of species and fertilization, respectively inoculation of mycorrhizal fungi spores, could be excluded by a test before.

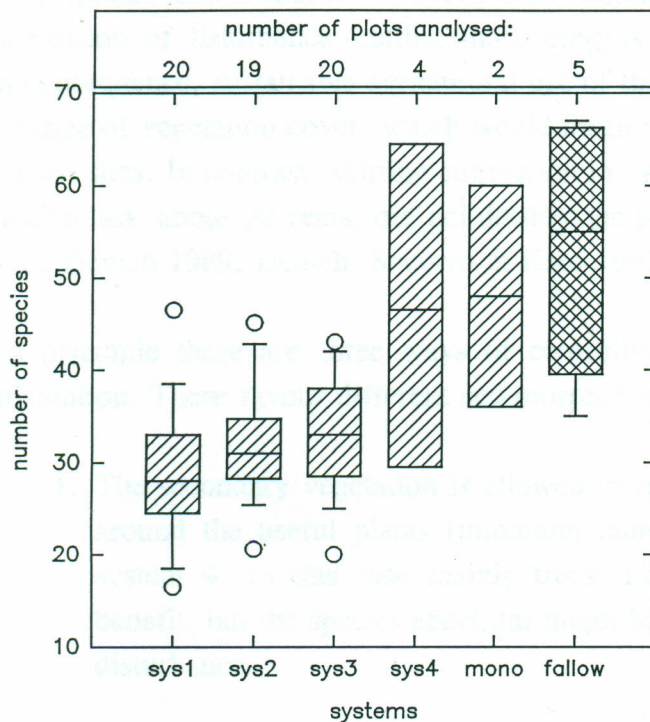


Fig. 7:

Median numbers of species present in the plantation systems 1, 2, 3, 4 and monoculture plots, compared to the fallow plots

similar to those in system 4, do not say much because there were only two plots analysed. Nevertheless, in the citrus monoculture plot there is much space left between the rows, and in contrast to systems 2 and 3 there are no short living and annual crops, which require more intensive management than perennial plants. Hence, disturbance in the monocultural systems may be lower than in the mixed culture systems.

4 Conclusions

The evaluation of the data was carried out to describe the spatial differences of selected traits of vegetation structure and floristic composition. The analysis detected a complex spatial environmental gradient, which needs a more detailed, multi-variate analysis (Preisinger, Siqueira & Coelho, *in preparation*).

The evaluation of the data was carried out to describe the spatial differences of selected

traits of vegetation structure and floristic composition. The analysis detected a complex spatial environmental gradient, which needs a more detailed, multi-variate analysis (Preisinger, Siqueira & Coelho, *in preparation*). The gradient is directed from block a to block e. The plots of block e show distinct characteristics different from the others (in particular the presence of bracken, *Pteridium aquilinum*). Trees dominate in blocks a, b and in some plots of c and rhizome/tussock grasses and ferns dominate in block e. The number of species found rises from block a to block e, due to an increasing number of herbaceous plant species, which spread by rhizomes, runners or seeds and invade the agricultural area from the south-eastern side. This pattern indicates differences in intensity and duration of past agricultural use. Agricultural experiments in the south-eastern part of the area (blocks e, d and partly c) started in 1982, the north western parts (blocks a, b and partly c) in 1985 (cf. Tavares, Preisinger & Martins).

A comparison of species richness between the different plantation systems indicates a tendency of decreasing species numbers with increasing intensity of present use, or disturbance respectively. In particular there is a decrease in woody species. Absence

of a species means absence of overground biomass, indicating that the period between the events of disturbance (cutting and hoeing) is not long enough for regeneration. As a consequence, sustainable agricultural use of the area would lead to a non reversible change of vegetation cover, which would mean a loss of biodiversity of forest species in the sites. In contrast, shifting cultivation in the eastern Amazon (Zona Bragantina), which lasts about 90 years, did not destroy the potentiality of secondary forest species (see Denich 1989; Denich, Socorro & Kato 1993, Baar & Conceição 1993).

In principle there are three ways of controlling growth of wild vegetation in the plantation. These favour different eco-morphological plant types or strategy types:

1. The secondary vegetation is allowed to regenerate, but is occasionally cleared around the useful plants (minimum management), as practised in plantation system 4. In this case mainly trees, i.e. long living growth forms, would benefit, but the species spectrum might be compressed owing to the occasional disturbance.
2. The cultivation area is kept free of taller growth forms, i.e. the regeneration of secondary forest species is frequently disturbed by cutting and hoeing, as practised in systems 1, 2 and 3 and in the monoculture blocks. This benefits, in particular, long lived grasses (strategy types "Competitive Ruderals" CR and "Stress tolerant Competitors" SC).
3. Lianas of the CR strategy type are sown, which was done for the first time in the former rubber plantation in the test area (*Pueraria phaseoloides*). This leads to species-poor sites, dominated by the Competitive Ruderal plant species.

The response of a species to disturbance can roughly be indicated from its spatial pattern of distribution, if there is knowledge available of past disturbance events on the sites under study. The observation, that the species which invade an area after severe disturbance have much in common with species growing on similar sites in the temperate regions of the world, indicates that the mechanisms responsible for vegetation patterns are similar as well. Therefore, CSR-theory can be applied to this vegetation. In contrast, the mechanisms responsible for the pattern of primary and secondary forests are different from those occurring in temperate regions. Therefore successional processes in secondary forest can only be described in part by the CSR model. This is even more true of succession mechanisms in primary forest, which in part fall outside the scope of the theory.

5 References

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