

# CHANGES IN THE SPATIAL DISTRIBUTION OF TREE SPECIES IN A TERRA FIRME RAIN FOREST IN BRAZILIAN AMAZONIA AFTER LOGGING<sup>1</sup>

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**ABSTRACT:** The objective of this paper was to determine changes in the spatial distribution of tree species in a logged compared to an unlogged forest of the Tapajós National Forest in the municipality of Belterra, State of Pará, Brazil, over an eight-year period. The distribution pattern was determined for trees  $\geq 5$  cm dbh and, also, for trees  $\geq 30$  cm dbh. The relationship (a quadrature method) discussed by McGinnis was selected to be used in this study. Forty-seven percent of species with trees  $\geq 5$  cm dbh showed clumped distribution in the studied forests. *Geissospermum sericeum* Benth & Hook., *Minuartia guianensis* Aubl., *Pouteria bilocularis* (H. Winkler) Bachni, *Protium guacayanum* Cuatrec, *Sclerobium chrysophyllum* Poepp. et Endl. and the Sapotaceae family (9 species) occurred in clumps of small trees (5 cm  $\leq$  dbh < 30 cm) and big trees (dbh  $\geq 30$  cm) in both the logged and undisturbed forest. Trees in all sizes of these species certainly have aggregation characteristics in different light conditions during the whole growth-cycle. Only *Sclerobium chrysophyllum* out of fourteen species that occurred aggregated in all forest conditions was light demanding. The shade-tolerant *Lecythis lurida* (Miers) Mori and *Manilkara huberi* (Ducke) Standl. showed also aggregated distribution for small and big trees in the unlogged forest. An aggregated distribution is not always directly correlated to abundance, considering that most of the clumped species had less than seven trees per hectare.

**INDEX TERMS:** Spatial Distribution Pattern; Tree Species Aggregation; Tapajós National Forest; Amazonian Forest.

## MUDANÇAS NA DISTRIBUIÇÃO ESPACIAL DE ESPÉCIES ARBÓREAS EM UMA FLORESTA DE TERRA FIRME NA AMAZÔNIA BRASILEIRA, DEPOIS DA EXPLORAÇÃO FLORESTAL

**RESUMO:** Este trabalho avalia as mudanças na distribuição espacial de espécies arbóreas em um período de oito anos em uma área explorada, comparada a uma não-explorada, na Floresta Nacional de Tapajós, município de Belterra (PA), Brasil. O padrão de distribuição espacial foi analisado para todas as árvores com DAP  $\geq 5$  cm e, separadamente, para árvores com DAP  $\geq 30$  cm. Foi usado o método do quadrado de McGinnies. Quarenta e sete por cento das espécies, considerando árvores de DAP  $\geq 5$  cm, mostraram distribuição agrupada na floresta estudada. *Geissospermum sericeum*

<sup>1</sup> Aprovado para publicação em 16.10.2002

This paper is part of the results of the "Forest Structure Project" (08.2000.024), Embrapa Amazônia Oriental, supported by CNPq.

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Benth. & Hook., *Minuartia guianensis* Aubl., *Pouteria bilocularis* (H. Winkler) Bachni, *Protium guacayanum* Cuatrec., *Sclerolobium chrysophyllum* Poepp. et Endl. e o grupo Sapotaceae (9 species) tiveram seus indivíduos pequenos ( $5 \text{ cm} \leq \text{DAP} < 30 \text{ cm}$ ) e grandes ( $\text{DAP} \geq 30 \text{ cm}$ ) ocorrendo em grupos, tanto na floresta explorada como na não-explorada. Estas espécies, certamente, têm características de agregação em diferentes condições de luz, em todas as classes de tamanho, durante todo o ciclo da vida. Das 14 espécies que ocorreram agrupadas em todas as condições da floresta, somente *Sclerolobium chrysophyllum* é intolerante à sombra. As espécies *Lecythis lurida* (Miers) Mori e *Manilkara huberi* (Ducke) Standl., tolerantes à sombra, também mostraram distribuição agrupada tanto com árvores menores como com maiores, mas somente na floresta não-explorada. Uma distribuição agrupada não está sempre diretamente correlacionada com a abundância, considerando que a maioria das espécies que ocorreram em grupo tinham menos de sete árvores por hectare.

**TERMO PARA INDEXAÇÃO:** Padrão de Distribuição Espacial, Agregação de Espécies Arbóreas, Floresta Nacional de Tapajós, Floresta Amazônica.

## 1 INTRODUCTION

Spatial distribution pattern is the arrangement formed by the occurrence of individuals in space. In a forest, the spatial pattern of tree species is the arrangement by which individuals of the species population are distributed over the area (Brunig, 1986). The analysis of distribution pattern is one empirical approach to explain how so many tree species are apparently able to live together in the same habitat (NEWBERY; RENSHAW, BRUNIG, 1986). In tropical rain forest the study of spatial and size class distributions of tree species is essential for understanding the impacts of logging and silvicultural treatments (JONKERS, 1987). Extensive reviews on numerical methods used in ecology to describe the spatial distribution of trees have been made by Payandeh (1970), Dance (1973), Villanueva Agustin (1981), Greig-Smith (1983), Cardoso (1986) and Busing (1991), amongst many others.

According to Greig-Smith (1983), there are two 'categories of departure' from randomness: contagious in which individuals tend to be clumped, and regular in which individuals tend to be uniformly distributed. He added that the methods of analysis to be used in an investigation depend on its objective, considering the nature of data, the layout of stands, the type of analysis. Payandeh (1970) said that it is difficult to describe the spatial distribution of plants in precise and meaningful terms. He commented that the most commonly used methods to describe distribution of tree species are those termed methods of quadrats and methods of distance. He compared the results of five measures applied to five forest types. The measures were computed by a quadrat method, a nearest neighbour method, a point-to-plant distance method, Hopkins's (1954) coefficient of aggregation, and Holgate's (1965) ratio. He obtained best performance by the quadrat method, though the results

may have been affected by the quadrat size. The next best results were obtained by point-to-plant distance measure, which the author considered the best method because it is easy to use and it is not affected by plot size.

Distribution pattern in Malaysian rain forest was studied by Poore (1968) in 26 ha at the Jenka Forest Reserve, considering trees  $\geq 29.1$  cm dbh, by Greig-Smith (1979) in a dipterocarp forest in West Sarawak for trees  $\geq 19.4$  cm dbh, and by Newbery, Renshaw e Brunig, (1986) in 19.2 ha in a Sarawak kerangas forest for trees  $\geq 9.7$  cm dbh. These studies showed that even in apparently uniform and species-rich rain forest some, at least, of the commoner species show patchiness.

Dance (1973) studied the spatial distribution of 15 species in a Peruvian tropical rain forest using five methods of quadrats. He observed that those used by McGinnies (1934) and by Payandeh (1970) are the simplest and they produce applicable and reliable results. Also in a Peruvian rain forest Villanueva Agustin (1981) applied one graphical method and four mathematical indices of aggregation. The first one was a map of spatial distribution of trees in each species, based on measurements of the location of each plant. Two of the numerical indices considered the ratio of the observed density to expected density (McGINNIES, 1934; FRACKER; BRISCHEL, 1944), while the other two indices considered the ratio of the variance to the mean (HAZEN, 1966; PAYANDEH,

1970). He compared the numerical indices to the graphic and obtained 'similar results'.

This paper deals with changes in the spatial distribution of tree species over an eight-year period in a logged area, compared to an unlogged forest. It is assumed that the population studied is spatially heterogeneous, with the species showing different distribution patterns. The knowledge of the spatial distribution pattern of each species will allow decisions to be made on the silvicultural system to be employed in the forest. For example, the cutting of a certain species must take into account its distribution pattern. If it occurs in clumps, only part of its individuals of commercial size should be cut, while the others should be left to maintain its natural distribution, as well as to minimise damage, caused by the logging operations, to remaining trees, animals and soil. On the other hand, species that occur regularly distributed should be exploited taking care to maintain a similar distribution after logging. Such procedures may allow species to keep their original ecological behaviour or, at least, a similar one, and to ensure their role in the forest community.

## 2 MATERIAL AND METHODS

### 2.1 THE STUDY AREA

The study area lies in the Tapajós National Forest near kilometre 114 of the Santarém-Cuibá Road (BR 163) in the municipality of Belterra, State of Pará, Brazil. The Tapajós National Forest area is about 600,000 ha at an altitude of c. 175

above the sea level. Its latitude is 2° 40' - 4° 10' S and longitude is 54° 45' - 55° 30' W. The climate is classified by Köppen as Am, which is tropical with one dry season of 2-3 months and an annual rainfall of over 2000 mm. Mean annual air temperature is c. 25°C, range 18.4-32.6 °C; a mean relative humidity of 86% (76-93%); a mean annual rainfall of 2110 mm with high rainfall from March to May, and low rainfall from August to November (CARVALHO, 1982).

The topography is mostly level or slightly rolling. Soil is allic to moderate yellow latosol with heavy clay texture (60-94% of clay), with inclusion of concretionary yellow latosol, derived from clay stone (FUPEF, 1986). Following the general pattern for the soils of terra firme Amazonian forests it is low in nutrients. Dubois (1976) classified the forest type as zonal primary high terra firme forest without babaçu palm (*Orbignya barbosiana* Burret).

This area was selected because it represents the majority of the terra firme dense forests in the region. It is also sufficiently remote from any private settlement to be disturbed by the cutting of trees for building materials or fuel. Apparently the only disturbances in the area were due to hunting of animals for food, collecting edible fruits, tapping of some *Hevea brasiliensis* (HBK) Muell. Arg. trees, and barking trees of medicinal species such as *Aniba canelilla* (Kunth.) Mez, *Tabebuia serratifolia* (Vahl) Nicholson and *Stryphnodendron adstringens* Mart. Those activities probably did not cause any serious

damage or alter the structure and composition of the forest significantly.

## 2.2 METHODS

Most studies of spatial distribution pattern deal with trees greater than 20 cm dbh only, which gives enough information for preparation of logging plans. In the present study the distribution pattern was analysed for all trees  $\geq 5$  cm dbh and, separately, for trees  $\geq 30$  cm dbh. The first analysis aimed to give complete information about the whole population, considering that some species only occur as small individuals in the forest. It also shows whether a certain species has the same pattern as an adult as well as a youngster. The study area was 108 ha, with 36 plots of 0.25 ha, summing to 9.00 ha sample area. Two different intensities of logging (T1 = logging of trees  $\geq 45$  cm dbh, T2 = logging  $\geq 55$  cm dbh) and an unlogged area were studied. Measurements were made on four occasions in the two main treatments and on three occasions in the control area. Three hundred 10 m x 10 m quadrats were used in each treatment and in the control area.

The relationship discussed by McGinnies (1934) was selected to be used in this study because it suited the collection of data and the layout of the experiment. It is one of the simpler quadrats methods (GREIG-SMITH, 1983). It has been employed to study the spatial distribution pattern of tropical rain forest species (DANCE, 1973; VILLANUEVA AGUSTIN, 1981, CARVALHO, 1982,

1983; NASCIMENTO, 2000), and, compared to other quadrats methods and to a visual tree location map, it gave similar results (see VILLANUEVA AGUSTIN, 1981). The method assumes that the plants occur in clumps. It is calculated from the equation:  $DA=D/d$ , where DA is the degree of aggregation, D is the observed density, d is the density expected from a frequency ( $d=-\ln(1-F/100)$ ), and F is the percentage of plots where a certain species occurs. The degree of aggregation is greater than one for contagious distribution and less than one for regular distribution (GREIG-SMITH, 1983).

Those species that were difficult to identify in the forest were considered in groups. These groups are: *Inga* spp., Lauraceae, *Miconia* spp., *Protium* spp., *Saccoglottis* spp., Sapotaceae, *Sloanea* spp. and *Talisia* spp. For calculation purposes each group was counted as one species. In the discussion here, the word species includes species-groups.

Causes of aggregation, such as species geographical distribution (ASHTON, 1977; WHITMORE, 1984), topographic and edaphic factors (ASHTON, 1964; AUSTIN; ASHTON; GREIG-SMITH, 1972; BRUNIG, 1974; BEN-SHAHAR, 1991), morphological, sociological and local environmental factors (KERSHAW; LOONEY, 1985) or local stochastic events (NEWBERY; RENSHAW; BRUNIG, 1986), seed dispersal, and many others factors discussed in Greig-Smith (1979) and Whitmore (1984), are not dealt with in this

study. The terms aggregation, cluster and clump, in the discussion here, have the same meaning, which refers to individuals of a certain species growing close together in groups.

### 3 RESULTS AND DISCUSSION

Species with individuals occurring in clumps are shown in Table 1 (annex), considering trees  $\geq 5$  cm dbh and, separately, trees  $\geq 30$  cm dbh. A species was considered aggregated if the value of DA (degree of aggregation) was greater than 1.0 in at least one forest condition (logged or unlogged) and in one size class (dbh  $\geq 5$  cm or dbh  $\geq 30$  cm).

Forty-seven percent of species (104) showed their plants  $\geq 5$  cm dbh occurring in clusters. But considering dbh  $\geq 30$  cm only 5% (12) of species showed aggregation of trees. The percent of clumped species, covering trees  $\geq 5$  cm dbh was the same as those found for the 60 most abundant species in Kerangas forest, Sarawak, by Newbery, Renshaw and Brunig, (1986).

*Geissospermum sericeum*, *Minuartia guianensis*, *Pouteria bilocularis*, *Protium guacayanum*, *Sclerolobium chrysophyllum* and the group Sapotaceae were found to be aggregated for the populations of trees  $\geq 5$  cm dbh and those of trees  $\geq 30$  cm dbh in both logged and unlogged forests. It can be said with certainty that the plants of these species really have the characteristic of occurring in clumps. As these clumped species, except *Sclerolobium chrysophyllum*, are shade-tolerant and

probably grew up together, this fact could be 'a direct demonstration of the operation of the forest growth-cycle', as suggested by Whitmore (1988).

*Lecythis lurida* and *Manilkara huberi* occurred in clumps only in the unlogged forest, both for the populations of trees  $\geq 5$  cm dbh and of trees  $\geq 30$  cm dbh. *Rinorea guianensis* Aubl. was clumped in the unlogged area in both size classes, but in the logged area it occurred in clusters just for trees  $\geq 5$  cm dbh. On the other hand, *Couratari oblongifolia* Ducke et Knuth had its plants  $\geq 5$  cm dbh and those  $\geq 30$  cm dbh occurring clumped in the logged forest, but in the unlogged area only trees  $\geq 5$  cm dbh were found aggregated.

In general pioneer species occurred in clumps in the logged area for trees  $\geq 5$  cm dbh (e.g. *Aegiphila* sp., *Cecropia obtusa* Trecul, *Jacaranda copaia* (Aubl.) D. Don, *Jacaratia spinosa* (Aubl.) DC. etc.). *Cecropia sciadophylla* Mart. and *Sclerolobium chrysophyllum* were the only light-demanding species which showed aggregation for trees  $\geq 30$  cm dbh in the logged forest. The other light-demanding species started to die before reaching that diameter, and some of them, like *Ambelania grandiflora* Huber and *Vismia japurensis* Reichardt never succeeded in reaching it. The majority of the light-demanding species were not aggregated in the unlogged forest.

Forty-seven per cent of those 104 species, which showed characteristics of aggregation, occurred at low densities of

between 1 and 7 trees ha<sup>-1</sup> (3 to 21 sampled trees). Examples are *Bertholletia excelsa* HBK, *Brosimum guianensis* (Aubl.) Huber, *Lecythis lurida*, *Manilkara huberi* and *Tachigali myrmecophila* (Ducke) Ducke. Thirty-eight per cent were abundant with more than 7 trees ha<sup>-1</sup> such as *Bixa arborea* Huber, *Carapa guianensis* Aubl., *Couratari oblongifolia*, *Minuartia guianensis* and *Sclerolobium chrysophyllum*. Fifteen percent were rare species in that area, with an average of less than 1 tree ha<sup>-1</sup> including *Aniba* sp., *Caraipa grandiflora* Mart., *Castilloa ulei* Warb., *Mouriria plaschaerti* Pulle and *Protium guacayanum*. As stated by Fedorov (1966), some abundant tree species as well as some rare species characteristically form small patches or populations in tropical rain forests. In Kerangas forest, Sarawak, all clumped species were less abundant than the species with a non-clumped pattern, but having relatively more individuals in the smaller sizes, 10 cm - 20 cm, and fewer trees in the upper-storey (BRUNIG, 1986).

Some very abundant species, like *Iryanthera juruensis*, which was among the 40 most abundant, *Chimarris turbinata*, *Maquira calophylla* and *Diospyrus tetandra* showed regular distributions. There are some species, such as *Dinizia excelsa* Ducke which appeared to occur in clumps, from visual observations in neighbouring areas in the same forest, but they showed regular distributions, probably because of their very low abundance in the sample plots (*D. excelsa* showed only 2 trees in the 9 ha

sample area). Also *Maquira sclerophylla*, that had an aggregated distribution in the study of Silva and Lopes (1982) in the same forest, 47 km distant, showed regular distributions in the present study. On the other hand, *Virola melinonii* (Ben.) A.C. Smith, that had a regular distribution in the study of Silva and Lopes (1982), occurred in clumps in the present study for trees  $\geq 5$  cm dbh, both in the logged and unlogged areas. All the other eight species studied by them, which occurred in clumps, also showed aggregated distribution in the present study. Silva and Lopes (1982) used the non-randomness plant-to-plant distances index of aggregation (PIELOU, 1959) to study spatial distribution pattern of plants  $\geq 15$  cm dbh. Nascimento (2000) used the Payandeh index (PAYANDEH, 1970) to study 49 species in a 400 ha area also at the Tapajós National Forest and found 18 species with trees occurring aggregated. From these, only six species occurred in clumps in the present study.

Some species showed aggregation in one treatment and regular distribution in others. For instance, *Aegiphila* sp. was clumped only in the heavier logged area, *Laetia procera* (Poepp. & Endl.) Eichl. only in the lighter logged forest, *Bertholletia excelsa* only in the unlogged forest (control area), *Manilkara paraensis* Standl. just in the Treatment 2 plots before logging, but not in the control area. Other species such as *Aniba* sp., *Perebea guianensis* Aubl., *Pithecelobium racemosum* Ducke, *Pithecelobium* sp., etc. showed aggregation

for trees  $\geq 5$  cm dbh, but not for trees  $\geq 30$  cm dbh. Those species did not exhibit any individual with dbh  $\geq 30$  cm, even though they are canopy species. So it cannot be concluded with certainty that they lack the characteristic of aggregation for big trees. Other species such as *Ambelania grandiflora*, *Claviija lancifolia* Desf., *Mabea caudata* P. et H., *Rinorea flavescens* Kuntze, etc. did not occur in clumps with dbh  $\geq 30$  cm, because they belong to the forest understorey, never reaching that diameter.

Most species (55), in which plants occurred in clumps, demonstrated that characteristic in all conditions (one, five and seven years after logging, or in the unlogged forest). One of these species was *Carapa guianensis*, which showed a similarly clumped distribution for trees  $> 15.9$  cm dbh in Henriques and Sousa's (1989) study, which used 80 4m x 4m quadrats. However, where 8m x 8m or 16m x 16m quadrats were used in that study, the individuals of this species were found to be randomly, but never evenly distributed. This agrees with Payandeh's (1970) conclusion that the results may be affected by the quadrat size. Also Nascimento (2000) found different results for different quadrat sizes. As already mentioned, the quadrat method was used in the present study because it suited data collection and the layout of the experiment, which according to Greig-Smith (1983), is a valid justification. However, it cannot be concluded that the quadrat size (10 m x 10 m) used in the

present study is the most suitable to analyse distribution patterns of trees in the Amazonian forests. Different quadrat sizes, as well as other indices and methods for calculation of distribution patterns, should be tested in the forest community under study.

Fifteen species (trees  $\geq 5$  cm dbh) showed their individuals aggregated only in the unlogged forest. Eight species showed aggregation in the unlogged forest and from the fifth year after logging to the end of the period. *Apeiba burchellii* Sprague and *Theobroma speciosum* Will. ex Spreng showed a clustered pattern in the unlogged forest and seven years after logging, when solar radiation started to reduce. *Virola melinonii* showed aggregation in the unlogged forest and one year after logging, so in two very different radiation conditions. Plants of seven species occurred in clumps only in the seventh year after logging; nine species in the fifth and seventh years; and four species over the whole period after logging. *Schefflera morototoni* (Aubl.) Maguire and *Saccoglottis* spp. had their plants clumped only in the fifth year after logging, and *Lindackeria paraensis* Kuhlmann only in the first year after logging. Therefore, it is likely that the spatial distribution pattern of some species depends on intensity of solar radiation on the area, amongst other factors. Also, as stated by Brunig (1986), it indicates the dynamic state of the forest with respect to succession and to gap dynamics.

Logging plans must take into account the spatial distribution of tree species. In

order to maintain the forest structure after logging similar to that before, the clumped commercial trees might be cut with the intention of keeping the remaining trees with the same distribution pattern. The same might be considered in silvicultural treatments after logging in relation to non-commercial species. For instance, *Geissospermum sericeum*, a shade-tolerant species, occurred in clumps in both logged and unlogged areas, with small trees or big trees. This species is not commercial nor does it have any prospect of becoming so in the future, except as fuelwood, if it possesses that quality, because its small trees are badly formed and adults are completely hollow, being composed largely of bark. As this species is among the 40 most abundant, it should not have all its trees cut in treatments, because big gaps would be produced, giving a chance for pioneer species to grow, mainly some invaders like those of the genus *Cecropia*. This also should be observed during silvicultural treatments for other clumped shade-tolerant non-commercial species that, even though not having big trees, are highly abundant in smaller sizes, such as *Guarea kunthiana* A.Juss., *Lacunaria jermanii* Ducke, *Rinorea flavescens*, *Sagotia racemosa* Baill. and many others.

Further, if it is not intended to keep the same forest structure, if the purpose is to improve the commercial value of the forest, the non-commercial species occurring in clumps should be eliminated gradually by refinement (poisoning, girdling or cutting), but not all trees in a clump at



once. Considering the association existing between some species, sometimes a clump of trees of a non-commercial species provides conditions for trees of commercial species to grow up. This is subject to further study.

#### 4 CONCLUSION

Forty-seven percent of species, considering trees  $\geq 5$  cm dbh, showed clumped distribution in the study forest. *Geissospermum sericeum*, *Miconia guianensis*, *Pouteria bilocularis*, *Protium guacayanum*, *Sclerolobium chrysophyllum* and the group Sapotaceae (9 species) occurred in clumps for small trees ( $5 \text{ cm} \leq \text{dbh} < 30 \text{ cm}$ ) and big trees ( $\text{dbh} \geq 30 \text{ cm}$ ) in both the logged area and in the undisturbed forest. These species certainly have aggregation characteristics in different light conditions, in all size of trees, during the whole growth-cycle. Of the fourteen species that occurred aggregated in all forest conditions, only *Sclerolobium chrysophyllum* is light-demanding. The shade-tolerant *Lecythis lurida* and *Manilkara huberi* also showed aggregated distribution for small and big trees, but only in the unlogged forest.

Pioneer species occurred in clumps in the logged area, mainly from the fifth year after logging, and chiefly with small trees. Fewer reach 30 cm dbh, and among those, which attain that diameter, only *Cecropia sciadophylla* and *Sclerolobium chrysophyllum* showed aggregated spatial distribution.

An aggregated distribution is not always directly correlated to abundance, considering that most of the clumped species had less than seven trees per hectare (27 sampled trees). Also 15% of them had less than one individual per hectare. It seems that for some species the distribution pattern depends mainly on intensity of light on the area, among other factors. In fact, an eight-year period is not long enough to draw firm conclusions about the spatial distribution pattern of several species after logging, particularly for those that are shade-tolerant. Some species, which showed aggregated distributions after logging, could have a regular distribution in a longer period, due to the influence of canopy closure. But the results obtained from the unlogged forest give valuable information about the distribution pattern in the undisturbed areas, and this information could be taken into account in making plans of logging in the virgin forest.

#### LITERATURE CITED

ASHTON, P. S. A contribution of rain forest research to evolutionary theory. *Ann. Missouri Botanical Garden*, v. 64, p.649-705, 1977.

\_\_\_\_\_. *Ecological studies in the mixed dipterocarp forests of Brunei State*. Oxford: Oxford Forestry Institute, 1964.(Oxford Forestry, Mem, 25)

AUSTIN, M. P.; ASTHON, P. S.; GREIG-SMITH, P. The application of quantitative methods to vegetation survey III. A reexamination of rain forest data from Brunei. *Journal of Ecology*, v. 60, p. 305-324, 1972.

- BEN-SHAHAR, R. Successional patterns of woody plants in catchment areas in a semi-arid region. *Vegetatio*, v. 93, p. 19-27, 1991
- BRUNIG, E. F. *Ecological studies in the kerangas forests of Sarawak and Brunei*. Kuching: Borneo Literature Bureau. Govt. Printer, 1974.
- . Pattern and structure along gradients in natural forests in Borneo and in Amazonia: their significance for the interpretation of the stand dynamics and functioning. In: INTERNATIONAL WORKSHOP ON TROPICAL RAINFOREST REGENERATION AND MANAGEMENT. Guri Dam: MAB – Unesco/IUBS, 1986.
- BUSING, R. T. A spatial model of forest dynamics. *Vegetatio*, v. 92, p.167-179, 1991.
- CARDOSO, C. A. B. *The quantification of aggregation intensities in mapped point patterns*. 1986. Thesis (Ph.D) - University of Oxford, Oxford, 1986.
- CARVALHO, J. O. P. de. *Abundância, frequência e grau de agregação de pau-rosa (Aniba duckei Kostermans) na Floresta Nacional do Tapajós*. Belém: EMBRAPA-CPATU, 1983. (Boletim de Pesquisa, 53)
- . *Análise estrutural da regeneração natural em floresta tropical densa na região do Tapajós no Estado do Pará*. 1982. 129p. Dissertação (Mestrado em Ciências Florestais) - Universidade Federal do Paraná, Curitiba, 1982.
- DANCE, J. *Analisis de dispersion de 15 especies forestales de los bosques de Requena, Peru*. 1973. Tesis (Ingeniero Forestal) - Universidad Nacional Agraria, Lima, 1973.
- DUBOIS, J. L. C. *Preliminary forest management guidelines for the National Forest of Tapajós*. Belém: IBDF-PRODEPEF, 1976. 42p.
- FEDOROV, AN. A. The structure of the tropical rain forest and speciation in the humid tropics. *Journal of Ecology*, v. 54, p.1-11, 1966.
- FRACKER, S.; BRISCHEL, H. Measuring the local distribution of Ribes. *Ecology*, v. 25, p. 283-303, 1944.
- FUNDAÇÃO DE PESQUISAS FLORESTAIS DO PARANÁ. *Relações entre solos e a vegetação natural em área da Floresta Nacional de Tapajós*. Curitiba, 1986.
- GREIG-SMITH, P. Pattern in vegetation. *Journal of Ecology*, v. 67, p. 755-779, 1979.
- . *Quantitative plant ecology*. Oxford: Blackwell, 1983.
- HAZEN, W. E. Analysis of spatial pattern in epiphytes. *Ecology*, v. 47, p. 634-635, 1966.
- HENRIQUES, R. P. B; SOUSA, E. C. E. G. de. Population structure, dispersion and microhabitat regeneration of *Carapa guianensis* in Northeastern Brazil. *Biotropica*, v. 21, p. 204-209, 1989.
- HOLGATE, P. Some new tests of randomness. *Journal of Ecology*, v. 53, p.261-266, 1965.
- HOPKINS, B. A new method of determining the type of plant individuals. *Annals of Botany*, v. 18, p. 213-227, 1954.
- JONKERS, W. B. J. *Vegetation structure, logging damage and silviculture in a tropical rain forest in Surinam*. Wageningen: Agricultural University, 1987.
- KERSHAW, K. A.; LOONEY, J. H. H. *Quantitative and dynamic plant ecology*. 3rd ed. London: Edward Arnold, 1985.
- McGINNIES, W. G. The relation between frequency index and abundance as applied to plant populations in a semiarid region. *Ecology*, v. 15, p.263-282, 1934.
- NASCIMENTO, N. A. do. *Distribuição espacial de 49 espécies arbóreas em uma área de 400 hectares na Floresta Nacional de Tapajós, município de Belterra, Pará*. 2000. 42p. Dissertação (Mestrado em Ciências Florestais) – Faculdade de Ciências Agrárias do Pará, Belém, 2000.

NEWBERY, D. McC.; RENSHAW, E.; BRUNIG, E. F. Spatial pattern of trees in Kerangas forest, Sarawak. *Vegetatio*, v. 65, p. 77-89, 1986.

PAYANDEH, B. Comparison of method for assessing spatial distribution of trees. *Forest Science*, v. 16, p. 312-317, 1970.

PIELOU, E. C. The use of point-to-plant distances in the study of the pattern of plant populations. *Journal of Ecology*, v.47, p. 607-613, 1959.

POORE, M. E. D. Studies in Malaysian rain forest. I. The forest on triassic sediments in Jenka Forest Reserve. *Journal of Ecology*, v. 56, p.43-196, 1968.

SILVA, J. N. M.; LOPES, J. do C. A. *Distribuição espacial de árvores na Floresta Nacional do Tapajós*. Belém: EMBRAPA-CPATU, 1982. (Circular Técnica, 26).

VILLANUEVA AGUSTIN, G. *Avaliação estrutural e quantitativa de uma floresta úmida em Iquitos - Peru*. 1981. Dissertação (Mestrado em Ciências Florestais) - Universidade Federal do Paraná, Curitiba, 1981.

WHITMORE, T. C. The influence of tree population dynamics on forest species composition. In: DAVY, A. J.; HUTCHINGS, M. J.; WATKINSON, A.R. (Eds.). *Plant population ecology*. Oxford: Blackwell, 1988. p. 271-291.

———. *Tropical rain forests of the Far East*. 2 nd ed. Oxford: Clarendon Press, 1984.

# ANNEX

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Table 1 – Species with individuals occurring in clumps, according to McGinnies (1934) index of aggregation, in a 180 ha area (9 ha sample) at the Tapajós National Forest in Brazilian Amazonia. Analyses were done for trees  $\geq 5$  cm dbh and, separately, for trees  $\geq 30$  cm dbh in the unlogged (U) and in the logged (L) forest.

(follows in the next page)

BOTANICAL NAME	LOCAL NAME	dbh $\geq$ 5cm	dbh $\geq$ 30cm		
<i>Eugenia lambertiana</i> D.C.	Goiabinha	U	L		
<i>Ficus anthelminthica</i> Mart.	Caxinguba		L		
<i>Geissospermum sericeum</i> Benth.&Hook.	Quinarana	U	L	U	L
<i>Guarea kunthiana</i> A. Juss.	Andirobarana	U	L		
<i>Guarea</i> sp.	Jataúba	U	L		
<i>Guatteria poeppigiana</i> Mart.	Envira-preta	U	L		
<i>Hymenaea courbaril</i> L.	Jatobá	U			
<i>Inga</i> (10) spp.	Ingá	U	L		
<i>Jacaranda copaia</i> (Aubl.) D.Don	Parapará		L		
<i>Jacaratia spinosa</i> (Aubl.) DC.	Mamuí		L		
<i>Lacistema aggregatum</i> (Berg) Rusby	Matacalado	U	L		
<i>Lacunaria jermani</i> Ducke	Papo-de-mutum	U	L		
<i>Laetia procera</i> (Poepp. & Endl.) Eichl.	Pau-jacaré		L		
<i>Lauraceae</i> (9) spp.	Louro	U	L		
<i>Lecythis lurida</i> (Miers) Mori	Jarana	U		U	
<i>Licania incana</i> Aubl.	Caraipé	U	L		
<i>Lindackeria paraensis</i> Kuhlm.	Farinha-seca		L		
<i>Mabea caudata</i> P. et H.	Taquari		L		
<i>Manilkara huberi</i> (Ducke) Standl.	Maçaranduba	U		U	
<i>Manilkara paraensis</i> Standl.	Maparajuba	U			
<i>Maytenus pruinosa</i> Reiss.	Xixuá	U	L		
<i>Mezilaurus lindaviana</i> Schw. Et Mez	Itaúba-abacate	U	L		
<i>Micropholis velunosa</i> Pierre	Rosadinho	U	L		
<i>Miquartia guianensis</i> Aubl.	Acariquara	U	L	U	L
<i>Mouriria plasschaerti</i> Pulle	Muiráuba	U			
<i>Myrcia bracteata</i> D.C.	Murta	U	L		
<i>Myrcia paevaberto</i> Berg	Goiabarana	U	L		
<i>Neea floribunda</i> P. & E.	João-mole	U	L		
<i>Ocotea baturitenses</i> Vattimo	Louro-preto	U	L		
<i>Ocotea canaliculata</i> Mez	Louro-branco	U			

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(follows in the next page)

BOTANICAL NAME	LOCAL NAME	dbh $\geq$	
		5cm	30cm
<i>Ormosia</i> sp.	Tento	U	L
<i>Ouratea aquatica</i> Engl.	Pau-de-cobra		L
<i>Parkia gigantocarpa</i> Ducke	Faveira-barriguda	U	L
<i>Parkia multijuga</i> Benth	Faveira-arara-tucupi	U	
<i>Paypayrola grandiflora</i> Tul.	Paparola	U	L
<i>Perebea guianensis</i> Aubl.	Muiratinga	U	L
<i>Piptadenia suaveolens</i> Miq.	Faveira-folha-fina		L
<i>Pithecelobium racemosum</i> Ducke	Angelim-rajado	U	L
<i>Pithecelobium</i> sp.	Faveira		L
<i>Porouma longipendula</i> Ducke	Embaubarana	U	L
<i>Pouteria bilocularis</i> (H. Winkler) Bachni	Abiu-casca-grossa	U	L U L
<i>Protium guacayanum</i> Cuatrec.	Breu-manga	U	L U L
<i>Protium puncticulatum</i> Macbr.	Breu-manga	U	
<i>Protium</i> (8) spp.	Breu	U	L
<i>Quararibea guianensis</i> Aubl.	Inajarana	U	L
<i>Randia armata</i> (SW.) DC	Limorana	U	L
<i>Rinorea flavescens</i> Kuntze	Canela-de-jacamim	U	L
<i>Rinorea guianensis</i> Aubl.	Acariquarana	U	L U
<i>Ryania</i> sp.	Caneleira	U	L
<i>Saccoglottis</i> (2) spp.	Abiu		L
<i>Sagotia racemosa</i> Baill.	Arataciú	U	L
<i>Sahagunia racimifera</i> Huber	Janitá	U	L
<i>Sapotaceae</i> (9) spp.	Abiu	U	L UL
<i>Schefflera morototoni</i> (Aubl.) Maguire	Morototó		L
<i>Sclerolobium chrysophyllum</i> Poepp. et Endl.	<i>Taxi-vermelho</i>	U	L UL
<i>Sclerolobium guianensis</i> Benth.	<i>Taxi-branco</i>		L
<i>Siparuna dicipiens</i> A.DC.	Capitiú		L
<i>Sloanea</i> (3) spp.	Urucurana	U	L
<i>Sterculia pilosa</i> Ducke	Axixá	U	L

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BOTANICAL NAME	LOCAL NAME	(conclusion)	
		dbh $\geq$ 5cm	dbh $\geq$ 30cm
<i>Stryphnodedron adstringens</i> Mart.	Barbatimão	U	
<i>Swartzia barchyrachis</i> Harms	Paraputaca	U	L
<i>Swartzia stipulifera</i> Harms	Gombeira	U	
<i>Tachigali myrmecophila</i> (Ducke) Ducke	Taxi-preto-f.-graúda	U	L
<i>Tachigali</i> sp.	Taxi-preto-f.-miúda	U	L
<i>Talisia</i> (3) spp.	Pitomba	U	L
<i>Tapirira guianensis</i> Aubl.	Tatapiririca	U	L
<i>Theobroma speciosum</i> Willd. ex Spreng.	Cacau-da-mata	U	L
<i>Trattinickia rhoifolia</i> Willd.	Breu-sucuruba		L
<i>Trichilia micrantha</i> Bth.	Triquilha	U	L
<i>Virola cuspidata</i> Warb.	Ucuúba-vermelha		L
<i>Virola melinonii</i> (Ben.) A.C. Smith	Ucuúba-terra-firme	U	L
<i>Vismia guianensis</i> Choisy	Lacre-branco	U	L
<i>Vismia japurensis</i> Reichardt	Lacre-vermelho		L
<i>Xylopia aromatica</i> (Lam.) Mart.	Envira-folha-fina		L