SPATIAL DISTRIBUTION OF TREE SPECIES OF A *TERRA FIRME* RAIN FOREST IN BRAZILIAN AMAZONIA

João Olegário Pereira de Carvalho
José Natalino Macedo Silva
Eng. Ftal., PhD., Pesquisador EMBRAPA/CPATU
José do Carmo Alves Lopes
Eng. Ftal., M.Sc., Pesquisador EMBRAPA/CPATU

ABSTRACT

Changes in the spatial distribution of tree species of a *terra firme* dense forest in Brazilian Amazonia were recorded over an eight-year period. Two logging intensities were studied and compared with an undisturbed forest. Forty-eight permanent sample plots were established in the logged area and twelve in the undisturbed forest. Four measurements were done in the exploited forest: one year before logging, then one, five and seven years after logging. The undisturbed forest was measured three times over the study period. Forty-seven percent of species, considering trees $\geq$ 5 cm dbh, showed clumped distribution in the study forest. Pioneer species occurred in clumps in the logged area, mainly from the fifth year after logging, and chiefly with small trees. Most of them hardly ever reach 30 cm dbh. Aggregated distribution is not always directly correlated to abundance of species, considering that most of the clumped species had less than seven trees per hectare (27 sampled trees).

RESUMO

Foram registradas as mudanças na distribuição espacial de espécies em uma floresta densa de terra firme na Amazônia brasileira, num período de oito anos. Foram estudadas duas intensidades de exploração e comparadas à uma floresta não explorada (testemunha). Foram estabelecidas 48 parcelas permanentes na flroesta explorada e 12 na testemunha. A área explorada foi medida quatro vezes: um ano antes da exploração; um, cinco e sete anos depois da exploração. A floresta não explorada foi medida tres vezes durante o período estudado. Quarenta e sete por cento das espécies, considerando árvores com dap $\geq$ 5 cm, mostraram distribuição agrupada. Espécies pioneiras ocorreram em grupo na área explorada, principalmente a partir do quinto ano após a exploração, e especialmente com árvores pequenas. A maioria delas dificilmente atinge dap de 30 cm. A distribuição espacial não está sempre relacionada com a abundância das espécies, considerando que a maioria das espécies agrupadas tinham menos de sete árvores por hectare (27 árvores amostradas).

Key Words: aggregation, Brazilian Amazonia, distribution pattern, Tapajós Forest, tropical rain forest.

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 and 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 (1981), Greig-Smith (1983), Cardoso (1986) and Busing (1991), amongst many others.

This paper deals with changes in the spatial distribution of tree species over an eight-year period in a logged area, compared with 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.

THE STUDY AREA

The study area lies in the Tapajós National Forest near the km 114 of the Santarém-Cuibá Road, BR 163, municipality of Santarém, State of Pará, Brazil. The Tapajós National Forest covers approximately 600,000 ha. Its latitude is 2° 40' - 4° 10'S and Longitude is 54° 45' - 55° 30'W. Altitude is around 175 m above the sea level. The climate is classified by Köppen as Ami, which is a tropical climate with an annual dry season of 2-3 months and an annual rainfall over 2000 mm. Mean annual air temperature is about 25°C, ranging from 18.4 to 32.6°C; a mean relative humidity of 86% (76 - 93%); a mean annual rainfall of 2110 mm, with a high rainfall from March to May, and a low rainfall from August to November; and mean annual insolation of 2150 hours (Carvalho 1982).

The relief is mostly level or slightly rolling. The soil is Alic to Moderate Yellow Latosol with heavy clay texture (60 - 94% clay), with inclusion of Concretionary Yellow Latosol, derived from clay stone (Brasil-FUPEF 1986). Following the general pattern for the soils of *terra firme* Amazonian forests it is low in nutrients. The forest type was classified by Dubois (1976) as zonal primary high *terra firme* forest without *babaçu* palm (*Orbygnia barbosiana* Burret.).

MATERIAL AND METHODS

The research was initiated in the area in 1981 with a 100% pre-felling forest inventory of trees $\geq$ 45 cm dbh over a total area of 144 ha. This year climber cutting was undertaken and the permanent sample plots were established and measured at the first time within the 144 ha. In 1982 the area was logged. The subsequent measurements took place in 1983 - one year after logging, 1987 - five years after logging and in 1989 - seven years after logging. A 36 ha control with permanent plots was established in 1983. It was measured firstly this year, then in 1987 and 1989.

Two treatments and a control area were analyzed:

T1 - this treatment consisted of cutting trees $\geq$ 45 cm dbh from 38 commercial species.

T2 - cutting of trees $\geq$ 55 cm dbh from 38 commercial species.

T0 - the control area remained in its natural condition.

The statistical design was randomized blocks with four replications per block. Each treatment was replicated four times, with a 9 ha treatment plot per block. The procedures of Silva and Lopes (1984) were followed to stablih the sample plots. Three hundred 10 m x 10 m quadrats were used in each treatment and in the control area. All individuals ≥ 5 cm dbh were number tagged identified and measured. In total, each treatment was applied over 36 ha, and included 3 ha of measured sample plots.

Species were classified by wood quality groups and ecological classes. The wood quality groups were: commercial - species presently sold in the national or international market; potential - species likely to be sold in the near future mainly due to their wood characteristics; non-commercial - species not marketable and without potential characteristics, or species whose wood is not yet sufficiently known. This distribution was based on the characteristics and uses of wood, the timber market in Brazil and export, according to Brasil-IBDF (1980, 1981, 1988), Brasil-SUDAM (1981), Silva (1989) and Teixeira, Santana and Souza (1988). The species were classified as light-demanding and shade-tolerant species, based on the requirement of their seedlings for solar radiation observed casually in the field during the study period (Carvalho 1992), and according to special characteristics suggested by Swaine and Whitmore (1988) and Whitmore (1989, 1990).

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 1981, Carvalho 1982, 1983), and, compared to other quadrats methods and to a visual tree location map, it gave similar results (see Villanueva 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.

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.

RESULTS AND DISCUSSION

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 ≥ 5 cm or dbh ≥ 30 cm).

Forty-seven percent of species (104) showed their plants ≥ 5 cm dbh occurring in clusters. But considering dbh ≥ 30 cm only 5% (12) of species showed aggregation of trees. The percent of clumped species, covering trees ≥ 5 cm dbh, was the same as those found for the 60 most abundant species in kerangas forest, Sarawak, by Newbery *et al.* (1986).

Geissospermum sericeum Benth. & Hook., *Minquartia guianensis* Aubl., *Pouteria bilocularis* (H. Winkler) Baehni, *Protium guacayanum* Cruatec., *Sclerolobium chrysophyllum* Poepp. et Endl. and the group Sapotaceae occurred aggregated considering trees ≥ 5 cm dbh or trees ≥ 30 cm dbh in both logged and unlogged forests. These species certainly have aggregation characteristics in different light conditions, in all size of trees, during the whole growth-cycle. *Lecythis lurida* (Miers) Mori and *Manilkara huberi* (Ducke) Standl. occurred in clumps only in the unlogged forest, both for trees ≥ 5 cm dbh and trees ≥ 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 ≥ 5 cm dbh. On the other hand, *Couratari oblongifolia* Ducke et Knuth had its plants ≥ 5 cm dbh and those ≥ 30 cm dbh occurring clumped in the logged forest, but in the unlogged area only trees ≥ 5 cm dbh were found aggregated.

In general pioneer species occurred in clumps in the logged area for trees ≥ 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 ≥ 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* H. G. Reigh. never succeeded in reaching it. The majority of the light-demanding species were not aggregated in the unlogged forest.

Forty-seven per cent of these 104 species, which showed characteristics of aggregation, occurred at low densities, with between 1 and 7 trees ha^{-1} (3 to 21 sampled trees), e.g. *Bertholletia excelsa* H.B.K., *Brosimum guianensis* (Aubl.) Huber, *Lecythis lurida*, *Manilkara huberi*, *Tachigalia myrmecophila* Ducke, etc. Thirty-eight per cent were abundant with more than 7 trees ha^{-1}: *Bixa arborea* Huber, *Carapa guianensis* Aubl., *Couratari oblongifolia*, *Minquartia guianensis*, *Sclerolobium chrysophyllum*, etc. And 15% were rare species in that area, with an average of fewer than 1 tree ha^{-1}: *Aniba guianensis*, *Caraipa grandiflora* Mart., *Castiloa ulei* Warb., *Mouriria plaschaerti* Pulle and *Protium guacayanum* Cuatrec., amongst others. 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* Warb., *Chimarris turbinata* DC., *Maquira calophylla* and *Diospyrus tetandra* Hier., 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* (Ducke) A. C. Smith, 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*, that had a regular distribution in the study of Silva and Lopes, occurred in clumps in the present study for trees ≥ 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 ≥ 15 cm dbh.

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. et Endl.) Eichl. only in the lighter logged forest, *Bertholletia excelsa* only in the unlogged forest (control area), *Manilkara paraensis* Standl. just in the T2 plots before logging, but not in the control area. Other species such as *Aniba guianensis*, *Perebea guianensis* Aubl., *Pithecellobium racemosum* Ducke, *Pithecellobium* sp., etc, showed aggregation for trees ≥ 5 cm dbh, but not for trees ≥ 30 cm dbh. Those species did not exhibit any individual with dbh ≥ 30 cm, even thoûgh being 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*, *Clavija lancifolia* Desf., *Mabea caudata* P. et H., *Rinorea flavescens* Kuntze, etc, did not occur in clumps with dbh ≥ 30 cm, because they belong to the forest understorey, never reaching that diameter.

Fifteen species (trees ≥ 5 cm dbh) showed their individuals aggregated only in the unlogged forest; eight species in the unlogged forest and from the fifth year after logging to the end of the period. *Apeiba burchellii* Sprague and *Theobroma speciosum* Willd. 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. *Didymopanax morototoni* (Aubl.) Decne et Planch and *Saccoglottis* spp. had their plants clumped only in the fifth year after logging, and *Lindackeria paraensis* Kuhlm 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 in the area (Carvalho 1992), 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.

CONCLUSION

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.

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