Spatial Distribution Pattern of Representative Tree Species in a Foothill Rain Forest in West Sumatra

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ABSTRACT Spatial distribution was analysed for all plot trees and representative tree species in two duplicate 1-ha plots established in a foothill rain forest 16 km west from Padang, West Sumatra, Indonesia. All tree trunks ≥ 8 cm dbh were distributed randomly in both plots. Spatial correlation between dead trees and recruited trees during the 8-year period was locally negative while broadly positive, suggesting that the random spatial pattern is dynamically maintained by mechanisms of density-dependent regulation.

All of five abundant canopy/subcanopy non-pioneer species, i.e. *Hopea dryobalanoides*, *Gonystylus forbesii*, *Cleistanthus glandulosus*, *Mastixia trichotoma*, and *Grewia florida*, and typical pioneer *Macaranga* spp., including *M. gigantea*, *M. hypoleuca*, *M. pruinosa* and *M. triloba*, showed a clumped distribution, particularly for smaller size classes. Two subcanopy non-pioneer species, *Mastixia* and *Grewia* showed a shift from a regularly decreasing density with height in one plot with larger gap area to bimodal height distribution in the other plot with smaller gap area. They also showed a similar tendency in spatial pattern such that the negative spatial correlation was observed between seedlings (< 1 m high) and poles (1-10 m high) and between poles and tall trees (≥ 10 m high) in the plot with larger gap area but that was found between seedlings and tall trees in the plot with smaller gap area. Such pattern was also observed for gap-demanding *Macaranga* spp., and they were concluded to be less tolerant than *Hopea*, *Gonystylus* and *Cleistanthus*, in which no height distribution difference nor spatial pattern difference was observed between two plots. These more tolerant species showed a positive correlation between tall trees and seedlings, but no correlation between tall trees and poles. These results reflect the dynamic alternation of tree species within a limited area of forest.

Key Words: *Cleistanthus glandulosus* / *Gonystylus forbesii* / *Grewia florida* / *Hopea dryobalanoides* / Indonesia / *Macaranga* spp. / *Mastixia trichotoma* / spatial pattern / tropical rain forest

Recent studies on tree communities in tropical forests have paid attention to the dynamic pattern of spatial dispersion of trees. In particular, there has been considerable controversy regarding so-called Janzen-Connell hypothesis that tropical tree species diversity is promoted by a negative spatial correlation between adults and offsprings due to local density dependence (Augsburger, 1983a, b; Clark & Clark, 1984 for a positive view; Hubbell, 1980; Hubbell, Condit & Foster, 1990 for a negative view; Connell, Tracey & Webb, 1984; Augspurger, 1984 for an intermediate view). Further detailed observation of spatial patterns of co-occurring tree species is necessary, particularly in species-rich Malesian rain forests. To examine the population-level consequences of spatial regulation, the observation should cover the whole population including every seedling in research plots.

This report follows the previous papers on spatial distribution pattern of an emergent tree *Swintonia schwenkii* (T. & B.) T. & B. (Suzuki & Kohyama, 1991) and of a canopy tree *Calophyllum* cf. *soulattri* Burm. (Mukhtar *et al.*, 1992), dealing with the same forest plots. It analyses (1) the spatial pattern of all trees collective of species with its dynamics, and (2) the

* for correspondence.

spatial pattern of the whole population of representative tree species (other than the above two) in the two 1-ha permanent rain forest plots in West Sumatra. We conclude that the density-dependent regulation can occur at the guild level, i.e., collective of species, and that species-specific patterns should be analysed in the context of a pattern drawn for a whole guild.

METHODS

We investigated the spatial distribution pattern of representative species in duplicate 1-ha permanent plots, namely the Pinang Pinang Plot and the Gajabuih Plot, established in a foothill rain forest (alt. 590-635 m) in the Ulu Gadut area, the basin of Sungei (River) Gadut Gadang, 18 km east from Padang, West Sumatra; for detailed description of the sites see Kohyama *et al.* (1986), Suzuki & Kohyama (1991) and Mukhtar *et al.* (1992). The portion of an attached belt of the Gajabuih Plot was omitted from the seedling-sapling census as in earlier studies on spatial patterns.

The 8-year dynamics of all plot trees ≥ 8 cm dbh was recorded in early September 1981 and mid August 1989 for the Pinang Pinang Plot and in late December 1980 and late August 1989 for the Gajabuih Plot.

In September 1989, we carried out a census of all individuals, including seedlings and saplings < 8 cm dbh (= trunk diameter at 1.3 m above the ground level) for selected representative tree species in the forest: *Hopea dryobalanoides* Miq. (Dipterocarpaceae), *Gonystylus forbesii* Gilg (Thymelaeaceae), *Cleistanthus glandulosus* Jabl. (Euphorbiaceae), *Mastixia trichotoma* Bl. (Cornaceae), *Grewia florida* Miq. (Tiliaceae), *Macaranga* spp. (Euphorbiaceae), including *M. gigantea* (Rochb. f. et Zoll.) M. A., *M. hypoleuca* (Miq.) M. A., *M. pruinosa* (Miq.) M. A. and *M. triloba* (Bl.) M. A. Voucher specimens of these species in the plots were deposited in the Herbarium Bogoriense (BO), the Herbarium of the Department of Biology, Andalas University and the Herbarium of the Faculty of Science, Kagoshima University (KAGS).

The census for seedlings and saplings was carried out by tagging numbered tapes, measuring of top height and dbh (when taller than 1.3 m), and mapping the position of the stem base. We also measured height and dbh of all trees of these species ≥ 8 cm dbh. We recorded coordinates of all individuals from dispersion maps of two plots using a digitizer, and devised a program to draw maps of any species and/or categories using a microcomputer. The dispersion maps of each species are shown in Appendices 1-6.

The spatial pattern of individuals was analysed by subdividing plots into square-grids with sides of 20, 10, 5 and 2.5 m. The arrangement of 20×20 and 10×10 -m grids within two plots is shown in an earlier paper (Suzuki & Kohyama, 1991); each of 10×10 -m grids was further divided into four 5×5 -m grids and sixteen 2.5×2.5 -m grids. Twenty and eighteen units of 20×20 -m grids were set in the Pinang Pinang and the Gajabuih Plot respectively, and marginal portion was excluded from the analysis.

We applied the statistic indices of spatial distribution and correlation of Iwao (1977). The m^*/m index (the mean-crowding divided by mean density) of spatial distribution of a given population is 1 for a random distribution, > 1 for a clumped distribution, and < 1 for a regular distribution. This index expresses the spatial pattern independent of the number of sampled grids, and is almost identical to the I_δ index of Morisita (1958). Independently, we tested the

significance of the observed distribution from the Poisson model of random distribution using F tests (Morisita 1958), which is a function of the number of sampled grids. For the correlation of spatial distribution between two populations, we calculated the ω index of Iwao (1977). The ω index is zero for mutually independent distribution, positive value up to +1 for a positive correlation, and negative to -1 for a negative correlation.

General description of species

Hopea dryobalanoides

Species of the genus *Hopea* including *H. dryobalanoides* rarely grow to emergent layer of Malesian rain forests. The maximum dbh and height of *H. dryobalanoides* in two plots were 61.5 cm and 39.5 m in 1989, respectively. This species is distributed locally frequently in Sumatra, Malay Peninsula and Borneo (Ashton, 1982). It was a common canopy-layer species around the Ulu Gadut research area. We observed mast seeding in 1989 for trees 30–40 m tall. This species produces dry fruits with five calyx-origin-wings, and seed dispersal is anemochorous. We observed that almost all fruit were dispersed around mother trees. Another *Hopea* species (not determined) was also in the plots but was rare. We could distinguish these species; while the present census of small seedlings of *H. dryobalanoides* may contain some individuals of this other species.

Gonystylus forbesii

About 20 species of the genus *Gonystylus* are reported from Malesian tropical rain forests, almost all from mature stands (Airy Shaw, 1953). *Gonystylus forbesii* and *G. macrophyllus* (Miq.) Airy Shaw in our research area, but the latter was rare. *G. forbesii* is distributed in Sumatra and Kalimantan. We recorded 26 individuals of *G. forbesii* above 8 cm dbh in the two 1-ha plots. The largest individual in the plots in 1989 was 27.5 cm in dbh and 20.5 m tall, but we also recorded an individual of 43.7 cm dbh and 27 m tall in the Pinang Pinang Atas Plot (transect of 10 × 370 m), located about 300-m distant from the Pinang Pinang Plot. Including largest trees, all individuals of this species occurred exclusively under the canopy layer. Flowering was observed under canopies. The fruit is capsules, exposing rather large seed (3-cm long) with dehiscence. The seeds have arils and are probably dispersed by birds and mammals.

Cleistanthus glandulosus

About 150 species of *Cleistanthus* are known in the paleotropics, but require taxonomic revision. In the Malay Peninsula, Whitmore (1972) described no species as very common and most as rare. We recorded two species of this genus from the Ulu Gadut area. *C. glandulosus* was distributed commonly, while the other *C. sumatranus* (Miq.) M.A. occurred only in riparian habitats. Among 47 individuals above 8 cm dbh, only two individuals were taller than 20 m in top height (22.4 m with 29.1 cm dbh and 20.5 m with 29.2 cm dbh). Mortality over 10 years was low; only one tree died. This species is most abundant under the canopy layer. We observed fruiting only once in a stand-edge tree. The fruit is capsules, and seeds with red arils are probably dispersed by birds.

Mastixia trichotoma

The genus *Mastixia* is characterized by an opposite leaf orientation. Thirteen species are reported from south-east Asia and southern India, Sri Lanka, and north-east India; they often require moist habitat and never become emergent trees (Mathew, 1977). In the Ulu Gadut

Fig. 1. Spatial distribution of surviving (O) dead (●) and recruited trees (X) ≥ 8 cm dbh for 8 years in two plots.

area, *M. trichotoma* occurs relatively dry site along ridge, perhaps due to the extremely moist climate of the area. This species is widely distributed over Malesia, and Mathew (1977) subdivided it into five varieties. We think the population in Ulu Gadut is *M. trichotoma* var. *clarkeana* (King) Danser, but so far we lack flowering material. A dense population of *M. trichotoma* with trees of various size can be observed in the Pinang Pinang Plot, with a maximum height of 25.1 m in 1989. The fruits are subglobose drupes growing to 2-3 cm (Mathew, 1977), supposed to be dispersed by birds and mammals. We observed no flowering over the 10 years but there were many saplings in the study area, so dispersal seems to be efficient and the probability of establishment success is high.

Grewia florida

The genus *Grewia* and the division between the genera *Grewia* and *Microcos* is in need of taxonomic reexamination. In the Ulu Gadut research area, we found two species of *Grewia*;

mostly *G. florida*, which is distributed in Sumatra and Malay Peninsula (Ridley, 1922), and only one tree of another undetermined species in the Pinang Pinang Atas Plot. *G. florida* is distributed as an under canopy species in mature rain forests, but can be part of a canopy layer in secondary stands. This species has an intermediate tendency between climax and pioneer. The maximum height observed in our plots was 25.9 m. Fruiting was observed for 10-m tall individuals at stand edges. Fresh drupes contained many hard small seeds adapted to animal dispersion.

***Macaranga* spp.**

We recorded 10-year changes in the dbh of 63 trees of the genus *Macaranga* in the two 1-ha plots, i.e. *M. gigantea* (3 trees), *M. hypoleuca* (14), *M. pruinosa* (6) and *M. triloba* (40). Our record of *M. triloba* may contain *M. indistincta* Whitmore. It is easy to distinguish these four species at an adult stage, but quite difficult at the small seedling stage. Therefore in this paper, these populations are put together. There exists, however, clear differences among these species in ecological habit. *M. hypoleuca* and *M. pruinosa* have rather small leaf blade, leathery and deeply trilobed, and form densely foliated crowns. *M. gigantea* has large leaves and dense crowns. These three species are typical light demanders and no recruitment was observed under closed canopies. They occurred at canopy top (78% of them were taller than 20 m). Both mortality and recruitment rates were exceptionally high. In contrast, *M. triloba* (and relatives) has relatively thin leaves and their crowns have a rather low foliage density. Trees taller than 20 m were only 7.5% of the whole population ≥ 8 cm. The *M. triloba* group is presumed to be slightly more shade tolerant than the other species. Species of *Macaranga* produce capsules. They are known to have seed dormancy; the germination is induced by direct light (Longman & Jenik, 1987).

RESULTS

Spatial pattern for all trees irrespective of species

All plot trees ≥ 8 cm dbh throughout the census period showed a random distribution in both plots. There were no clear differences between larger (≥ 20 cm dbh) and smaller (8-20 cm dbh) trees, nor between the two plots (Table 1). Two size classes distributed mutually independently (Table 2).

The spatial pattern of surviving, dead and recruited trees over 8 years is shown in Fig. 1.

Table 1. Number of individuals and m^*/m index of spatial distribution (Iwao, 1977) in four grid classes in alive, dead and recruited trees (≥ 8 cm dbh) for 1980(1)-1989 period; and those for small trees 8-20 cm dbh and large trees ≥ 20 cm dbh in 1989.

Categories	Pinang Pinang Plot					Gajabuih Plot				
	# Indiv.	2.5×2.5m	5×5m	10×10m	20×20m	# Indiv.	2.5×2.5m	5×5m	10×10m	20×20m
living for 8 years	482	1.19	1.16	1.08	1.02	348	1.26	1.04	1.05	1.03
dead during 8 years	42	10.16	2.90	1.72	1.32	109	0.97	0.82	1.08	1.15
recruited during 8 years	157	1.04	1.22	1.19	1.23	141	1.04	0.99	1.14	1.23
dbh < 20 cm in 1989	439	0.97	1.08	1.03	1.02	359	1.11	0.99	1.10	1.09
dbh ≥ 20 cm in 1989	200	1.15	1.09	1.18	1.04	130	1.23	0.92	0.95	0.92

Significant clumped distribution from the Poisson distribution at 1% level are expressed by bold-face.

Table 2. ω index (Iwao, 1977) of spatial correlation in four grid classes between alive, dead and recruited trees (≥ 8 cm dbh), for 1980 (1)-1989 period; and that between small tree < 20 cm dbh and large tree ≥ 20 cm dbh in 1989.

Categories	Pinang Pinang Plot				Gajabuih Plot			
	2.5×2.5 m	5×5 m	10×10 m	20×20 m	2.5×2.5 m	5×5 m	10×10 m	20×20 m
alive vs. dead	-0.30	-0.12	-0.01	-0.01	-0.21	-0.19	-0.01	+0.09
alive vs. recruited	+0.00	-0.07	-0.09	-0.07	+0.01	-0.03	+0.07	+0.17
dead vs. recruited	-0.61	+0.02	-0.09	+0.17	-0.33	+0.06	+0.18	+0.23
small vs. large	+0.06	+0.07	-0.01	-0.03	+0.03	+0.04	+0.00	+0.03

Positive index $\geq +0.10$ is shown by bold-face; negative index ≤ -0.10 by bold-face underline.

The 8-year dynamics of tree populations revealed that dead trees was distributed in clumped manner in the Pinang Pinang Plot, while not in the Gajabuih Plot (Table 1). It reflects the scattered distribution of gaps in the Pinang Pinang Plot (Kohyama *et al.*, 1989; Suzuki & Kohyama, 1991). Recruitment of trees was also clumped in a large unit of 20×20 -m (Table 1). Dead trees were negatively correlated with living trees in smaller units of 2.5×2.5 and 5×5 m in the two plots, but no spatial correlation was detected between recruited trees and living trees (Table 2). In both plots dead trees were negatively correlated with recruited trees at the small scale of 2.5×2.5 -m units, but were positively correlated at the larger scale of 20×20 -m units (Table 2).

Spatial pattern for each species

Each species examined showed clumped distributions of its smaller size classes (Table 3). The populations of large trees of each species showed regular distribution in terms of m^2/m (Table 3), but these populations were not significantly different from a random distribution due to small samples.

Various patterns of spatial correlation were found between size classes within species. *Mastixia* and *Grewia* both showed the same in the difference between the two plots (Table 4). In the degenerated Gajabuih Plot which had a larger and extending gap area, negative correlation was found between poles (1-10 m) and tall trees (≥ 10 m) and between seedlings (< 1 m) and poles, and positive correlation existed between seedlings and tall trees. In the Pinang Pinang Plot, the opposite pattern was the case for these two species. *Macaranga* spp. also showed a difference in spatial correlation between two plots. By contrast, *Hopea*, *Gonystylus* and *Cleistanthus* showed a similar pattern of spatial correlation between size classes in both plots. These three species had a positive correlation between tall trees and seedlings, but no positive correlation between poles and tall trees.

The above species characteristics in spatial correlation pattern in both plots concurred with those in size structure. Figure 2 shows the height distribution of the species examined and the emergent-dominant *Swintonia schwenkii* (cf. Suzuki & Kohyama, 1991). *Mastixia* and *Grewia* had a regularly decreasing height distribution in Gajabuih Plot, and a bimodal distribution with a group of higher trees in Pinang Pinang Plot. Such difference in height distribution between two plots was more clearly observed in light-demanding *Macaranga*. The height distribution of *Hopea*, *Gonystylus* and *Cleistanthus* was similar between two plots, and the regularly decreasing distribution. Overall results suggest that the degenerated Gajabuih Plot with large gap area represents a younger stage than the Pinang Pinang Plot

Table 3. Number of individuals and m^*/m index (Iwao, 1977) of spatial distribution in three mesh sizes, for each species in three top-height classes.

Species	Height class	Pinang Pinang Plot				Gajabuih Plot			
		# Indiv.	5×5m	10×10m	20×20m	# Indiv.	5×5m	10×10m	20×20m
<i>Hopea dryobalanoides</i>	< 1 m	117	18.47	10.75	8.79	72	24.22	12.58	5.54
	1-10 m	112	3.57	2.97	2.21	60	7.36	4.24	3.01
	≥ 10 m	11	0.00	0.00	1.98	6	0.00	0.00	1.00
<i>Gonystylus forbesii</i>	< 1 m	57	3.15	2.41	1.88	39	3.79	2.18	1.47
	1-10 m	119	2.35	1.89	1.61	84	1.31	1.39	1.06
	≥ 10 m	8	0.00	0.00	0.00	12	0.00	0.00	0.50
<i>Cleistanthus granulatus</i>	< 1 m	340	2.39	1.79	1.60	82	4.80	2.83	1.94
	1-10 m	425	2.16	1.69	1.51	235	2.24	1.77	1.27
	≥ 10 m	22	0.00	1.32	0.83	9	0.00	0.00	0.89
<i>Mastixia trichotoma</i>	< 1 m	222	3.97	3.30	2.18	65	3.68	2.42	1.41
	1-10 m	46	3.03	2.04	1.74	24	0.00	0.50	0.69
	≥ 10 m	22	5.29	2.31	2.07	2	0.00	0.00	0.00
<i>Grewia florida</i>	< 1 m	97	3.26	1.96	1.23	51	1.99	1.72	1.17
	1-10 m	55	0.85	1.38	1.31	34	2.49	0.75	1.09
	≥ 10 m	23	1.21	1.51	1.29	4	0.00	0.00	2.25
<i>Macaranga</i> spp.	< 1 m	126	26.65	18.80	7.13	57	3.01	1.77	1.72
	1-10 m	12	8.89	2.22	1.39	47	4.17	2.48	1.79
	≥ 10 m	24	2.22	2.78	2.29	13	13.63	3.41	1.07

Significant clumped distribution from poisson distribution at 1% level are shown by bold-face.

Table 4. ω index (Iwao, 1977) of spatial correlation in three mesh sizes between three height classes, for each species.

Species	Height classes compared	Pinang Pinang Plot			Gajabuih Plot		
		5×5m	10×10m	20×20m	5×5m	10×10m	20×20m
<i>Hopea dryobalanoides</i>	< 1 m vs. 1-10 m	+0.04	-0.03	+0.01	+0.28	+0.39	+0.55
	1-10 m vs. ≥ 10 m	+0.04	+0.02	+0.09	+0.06	+0.11	+0.11
	< 1 m vs. ≥ 10 m	+0.31	+0.41	+0.54	+0.20	+0.23	+0.78
<i>Gonystylus forbesii</i>	< 1 m vs. 1-10 m	+0.33	+0.62	+0.82	+0.21	+0.12	+0.16
	1-10 m vs. ≥ 10 m	<u>-0.33</u>	+0.09	+0.18	+0.02	<u>-0.21</u>	+0.06
	< 1 m vs. ≥ 10 m	+0.10	+0.08	+0.52	+0.02	+0.14	+0.20
<i>Cleistanthus granulatus</i>	< 1 m vs. 1-10 m	+0.48	+0.64	+0.77	+0.31	+0.60	+0.57
	1-10 m vs. ≥ 10 m	<u>-0.21</u>	<u>-0.20</u>	-0.05	+0.01	+0.18	+0.08
	< 1 m vs. ≥ 10 m	+0.05	+0.13	+0.25	+0.19	+0.32	+0.52
<i>Mastixia trichotoma</i>	< 1 m vs. 1-10 m	+0.24	+0.40	+0.67	<u>-0.82</u>	+0.01	+0.11
	1-10 m vs. ≥ 10 m	-0.05	+0.09	+0.03	<u>-1.00</u>	+0.05	<u>-0.25</u>
	< 1 m vs. ≥ 10 m	-0.08	+0.03	-0.08	+0.04	+0.12	+0.18
<i>Grewia florida</i>	< 1 m vs. 1-10 m	+0.11	+0.18	+0.31	<u>-0.17</u>	<u>-0.29</u>	+0.03
	1-10 m vs. ≥ 10 m	+0.11	+0.12	+0.07	<u>-1.00</u>	<u>-1.00</u>	<u>-0.34</u>
	< 1 m vs. ≥ 10 m	<u>-0.14</u>	<u>-0.14</u>	-0.09	+0.21	+0.28	+0.19
<i>Macaranga</i> spp.	< 1 m vs. 1-10 m	+0.21	+0.42	+0.37	+0.18	+0.23	+0.73
	1-10 m vs. ≥ 10 m	+0.01	<u>-0.17</u>	-0.03	<u>-0.53</u>	<u>-0.29</u>	+0.11
	< 1 m vs. ≥ 10 m	<u>-0.15</u>	<u>-0.23</u>	+0.20	+0.01	+0.06	<u>-0.15</u>

Positive index ≥ +0.10 is shown by bold-face; negative index ≤ -0.10 by bold-face underline.

Fig. 2. Top height distribution of trees for species examined in two plots.

covered mostly by mature closed canopies; *Mastixia*, *Grewia*, and *Macaranga* change their local population structure in size and spatial distribution with stand development, while more tolerant *Hopea*, *Gonystylus* and *Cleistanthus* keep their population stably independent of the developmental stage of stands.

DISCUSSION

Regulation of spatial pattern occurs in terms of a whole guild of tree populations, as the fundamental requirements are the same between co-occurring trees irrespective of species. Apparent random dispersion of all trees is caused by local density-dependent regulation, as the process of death and recruitment shows non-random local pattern and spatial correlation. Local crowding at a small spatial scale (resulting in the negative correlation between dead and recruited stems) and the existence of sites with faster tree replacement, such as gaps, at a larger spatial scale (resulting in the positive correlation between them) simultaneously regulate the stand-level random spacing of trees. The regeneration behaviour of each species is controlled by such a whole tree-level constraint. Species-specific pattern should be therefore analysed in the context of the overall guild of forest trees; results of spatial pattern analysis without information about overall tree distribution (cf. Sterner, Ribic & Schatz, 1986) are difficult to evaluate.

Each species with its own traits takes part in the stand-level regulation of spatial pattern, resulting into species-specific pattern of aggregation and intraspecific negative spatial correlation between size classes. A simple view of topographic segregation among species does not explain the observed pattern, because none of the species we examined showed a clumped pattern with stable positive auto-correlation between size classes.

Mastixia and *Grewia* are recognized to be more sensitive to gap dynamics than *Hopea*, *Gonystylus* or *Cleistanthus*. Their size structure is different in a degenerated plot with larger gap area than in a well-closed plot with smaller gap area, and the pattern of spatial correlation between size classes changes with the stage of forest plots. They are similar to *Calophyllum* cf. *soulattri* which has a unimodal distribution of poles, without tall trees nor seedlings, in the Gajabuih Plot and a bimodal distribution with a few canopy trees and dense seedlings in the Pinang Pinang Plot (Mukhtar *et al.*, 1992). We found that the emergent dominant *Swintonia schwenkii* showed a clear negative correlation between adult trees and seedlings (Suzuki & Kohyama, 1991). Again in *Swintonia* population, the bimodality in size distribution was more obvious in the Pinang Pinang Plot (Fig. 1). In the Gajabuih Plot, pole class (1-10 m tall) of *Swintonia* was dominant among the whole local population. Therefore, we can conclude that there is a syndrome of species traits that (1) the adult-offspring negative correlation is locally distinguishable in closed stands, (2) the size distribution tends to show a bimodality there, and (3) rather patchy and spontaneous regeneration occurs in relation to the stand development in shifting gap mosaic. Species with this syndrome we found in our research plots will be less shade-tolerant than species with the counter syndrome, i.e. (1') there is no obvious negative correlation between adults and offsprings, (2') the size distribution is stably inverse-J shaped, and (3') the regeneration success tends to be independent of gap dynamics. We could not find any clear relationship between the above population-level syndromes and allometric traits of the branching architecture of saplings (Kohyama & Hotta, 1990). It is worth mentioning, further, that the types of seed dispersal are not related to the above regeneration syndromes. Processes after seedling establishment are more important in generating the species pattern of local populations.

The present results suggest that the phenomenon of adult *versus* offspring segregation employed by the Janzen-Connell hypothesis is rather commonly observed for a particular

guild of trees in the research site. Further, the coincidence between spatial correlation and height class distribution suggests that the apparent negative correlation among size classes of a given species can be understood in relation to gap dynamics. The negative correlation among size classes is possibly related to the regeneration limitation and the resulting heterogenous structure of local populations. The contribution of the observed negative correlation to the maintenance of species diversity is yet open question until we will relate it to stand-level dynamics and evaluate it with reasonable whole-population simulators.

Within the category of non-pioneer tree species (Swaine & Whitmore, 1988), there exists a gradient of species traits in terms of shade tolerance throughout their life histories. For instance, we cannot say any of *Swintonia*, *Calophyllum*, *Mastixia* and *Grewia*, exhibiting the gap mosaic-sensitive syndrome, is a pioneer like *Macaranga* spp., because they establish and maintain a dense seedling bank under the closed canopy. The effects of gap dynamics should differ among species and should be evident in a species' spatial pattern and spatial auto-correlation at different stages of stand development. To understand species-specific patterns of spatial dynamics, it is necessary to carry out comparative studies between many co-occurring tree species.

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甲山隆司, 鈴木英治, 堀田満 西スマトラ州の熱帯山麓雨林における主要樹種の空間分布パターン

西スマトラ州のパダン市16 km西方に位置する二つの1 ha継続調査プロットで、全林木集団と主要樹種個体群の空間分布を解析した。胸高直径8 cm以上の全林木は両プロットで機会分布をしていた。8年間の調査期間中に枯死した個体と新規加入した個体は小区画単位(2.5 m メッシュ)では背反的に出現したが、大区画(20 m メッシュ)では同所的に現われる傾向を示した。これは、機会分布が、非機会的な密度依存制御のもとに、動的に維持されていることを示唆する。

林冠および亜林冠性の非パイオニア種5種, *Hopea dryobalanoides*, *Gonystylus forbesii*, *Cleistanthus glandulosus*, *Mastixia trichotoma*, および *Grewia florida* と、典型的なパイオニア種である *Macaranga* 属 (*M. gigantea*, *M. hypoleuca*, *M. pruinosa* と *M. triloba*) は、いずれも集中分布をしており、特に実生では集中性が顕著だった。亜林冠性の2種 *Mastixia* と *Grewia* は、ギャップの面積比の高いプロットでは逆J字型の安定的なサイズ分布を示していたが、ギャップ比の低いプロットでは成木と後継集団からなるふた山分布をしていた。これら2種は、空間分布でも似た傾向を示した。すなわち、ギャップ比の高いプロットでは実生(高さ< 1 m)と幼木(1-

10 m)の間, および幼木と高木 (≥ 10 m)の間に負の分布相関があり, 実生と高木の間には正の分布相関があったが, ギャップ比の低いプロットでは, これらの相関関係が入れ替わって, 実生と高木の間に負の分布相関が認められた。同様の傾向はギャップ依存性の *Macaranga* 属にも認められたので, これら2種は, 両プロット間で明瞭な変化傾向を示さなかった *Hopea*, *Gonystylus* および *Cleistanthus* よりも耐陰性に劣るものと考えた。より耐陰性が高いと思われたグループでは, 実生と高木の間に正の分布相関が認められたが, 高木と幼木の間に明瞭な相関関係はなかった。以上の結果は, 林内の限られた空間のなかで動的な種の交代が常に行われていることを示唆するものである。