

E-2.3 Diversity of Interactions between Plants and Animals

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Abstract To identify fine-scale functional differences among dipterocarp species in a tropical primary forest, seedling growth and survival in a forest gap were compared between *Shorea leprosula* and *Neobalanocarpus heimii*. In the gap, *Shorea* showed more enhanced growth and higher leaf turnover. Under the closed canopy, the survival rate was lower in *Shorea*. Regeneration of *Shorea* will be successful where gap formation is relatively frequent, while *Neobalanocarpus* may regenerate at places with infrequent gap formation. Three analyses of species diversity in a lowland dipterocarp forest were conducted to determine the nature of forest community dynamics with the data set obtained in a 50 ha plot in Pasoh Forest Reserve. Of the selected species for the analyses (444 species in total), 48 showed positive correlation with the distance from a conspecific adult. 35 species out of all those selected had their saplings clumped, while the adults were regularly or randomly distributed. As a group, the recruitment of saplings of species in the emergent or canopy layers increased significantly in proportion with mortality. This trend was not so apparent in the lower layers.

Key Words Phenology, Plant-animal interaction, Regeneration, Seedling establishment, Spatial distribution, Tropical rain forest

1. Fine-scale partitioning of regeneration niches for seedlings of two dipterocarp species in Pasoh Forest Reserve

For canopy tree species gap regeneration is a major process for maintaining plant populations (Brokaw, 1985; Denslow, 1987; Gomez-Pompa et al., 1991; Whitmore, 1978, 1986). A gap is a hole created within a forest canopy when single or multiple canopy tree(s) fall down. In a self-sustaining natural forest, where there are sufficient seed producing trees, a gap is repaired by regenerating young trees.

It has been well established that there is clear partitioning of regeneration niches between pioneer and late successional (climax) tree species (Denslow, 1980; Swaine & Whitmore, 1988; Whitmore, 1989). Pioneer species require high levels of light created by large gaps or forest clearing to germinate and grow to maturity, whereas in contrast, late successional species can germinate and survive under the shade of forest canopies. The biodiversity of tropical forests is partially maintained by niche partitioning between the pioneer and late successional species. However, pioneer species account for only a small part of the flora in a primary forest (Kochummen et al., 1990). Therefore, to understand the biodiversity of tropical rain forests, it is essential to know how ecologically similar species late successional species regenerate and coexist in a forest (Brown & Whitmore, 1992; Canham, 1989).

Seeds of late successional species germinate and survive for various periods under a closed canopy, and the seedlings and saplings experience repeated processes of suppression and release of growth, according to temporal changes in light conditions, before they reach the canopy layer (Canham, 1985). Therefore, an important question is whether different plant species categorised in the same group as late successional canopy tree species show partitioning of their regeneration niches. This is also important for a practical use such as enrichment planting using seedlings of timber trees in a logged-over forest.

The objective of this study is to compare responses of suppressed seedlings of two dipterocarp species to different light environments associated with a natural gap in a primary lowland forest in Malaysia.

1.1 The site

The study area is Pasoh Forest Reserve. The forest reserve covers an area of about 2,400 ha, with a core of 650 ha of primary lowland dipterocarp forest (Kochummen et al, 1990). In the 50 ha plot in Pasoh, 30 dipterocarp species are recorded (Manokaran & LaFrankie, 1990; Manokaran et al, 1992).

1.2 Transplant experiment

Based on preliminary observations and literature survey, two dipterocarp species: *Shorea leprosula* and *Neobalanocarpus heimii* were chosen. These species are the two most abundant dipterocarp species within the 50-ha plot at Pasoh. For both species, the total number of individuals with diameters exceeding 1 cm in the 50 ha plot is about 3000. These individual trees are distributed homogeneously and coexisting with each other. The seeds of the two species germinate immediately after dropping to the ground (Ng, 1980) and the seedlings survive and grow at various rates, depending mainly on the available light conditions.

To compare the responses of seedlings of the two species to different light conditions, a transplant experiment was conducted. In November 1992, three canopy trees fell and created a gap in the Plot 1 (2-ha permanent plot) in Pasoh. In December 1992, newly established seedlings were transplanted from the forest floor beneath mother trees to three different sites: the centre of the gap, the edge of the gap and the understory near the gap.

Survival, growth, leaf turnover of seedlings were monitored at a monthly interval until January 1995. A half of the seedlings were harvested to determine the dry weight of stems, branches and leaves. The leaf area was determined twice (one and two years after transplanting).

1.3 Light environment of the sites

Daily changes in photon flux density on a fine day at the three sites are illustrated in Fig. 1. At the gap centre, direct sunlight of more than 1000 $\mu\text{mol}/\text{m}^2/\text{s}$ illuminated the plants continuously for more than 1 h around midday. In contrast, the frequency and intensity of direct sunlight were much lower at the other two sites.

1.4 Survivorship and growth of seedlings

The number of surviving *Shorea leprosula* seedlings in the understory decreased from 25 to 18 during the first 6 months, and then after formation of the new gap, no mortality was observed. At the centre and at edge of the gap there was no seedling mortality during the experimental period. For *Neobalanocarpus heimii*, only 2 of 25 individuals died at the edge and in the understory. All seedlings survived at the gap centre.

These results indicate that under the deep shade of the canopy where the relative photon flux density is less than 1%, the seedling population of *Shorea leprosula* will not be maintained, whereas seedlings of *Neobalanocarpus heimii* can survive despite showing no significant growth. This also shows that light intensity equivalent to 2% relative photon flux will be enough for the survival of seedlings of both species. Such a light intensity could be obtained even in the understory of the forest canopy.

In both species, significant height growth was observed only at the gap centre, where the relative photon flux density was 7% for the first 8 months and 13% thereafter. Seedlings of *Shorea leprosula* however, show more rapid growth than *Neobalanocarpus heimii*. It appears that if favorable light conditions are maintained, seedlings of *Shorea leprosula* would dominate over those of *Neobalanocarpus heimii*, and would ultimately succeed in regenerating at this site.

The real situation is, however, more complicated. Favorable light conditions do not necessarily prevail forever, as expansion of the lateral branches of surrounding trees in the canopy and sub-canopy may decrease the level of light available to the seedlings. Therefore, another important factor for successful regeneration of canopy tree species is the degree of shade tolerance of seedlings after they have been exposed to favorable light conditions (Canham, 1985).

1.5 The architecture of seedlings

The architecture of seedlings or dry matter allocation to photosynthetic and non-photosynthetic organs is a useful measure of shade tolerance (Canham, 1988; Givnish, 1986; Kohyama, 1987; Kohyama & Hotta, 1990). At the gap centre, the ratio of the dry weight of leaves to stems and branches for *Shorea leprosula* was 0.96, while that for *Neobalanocarpus heimii* was 1.6. This means that *Shorea leprosula* allocated more dry matter to supporting organs such as stem and branches, than *Neobalanocarpus heimii*.

As is commonly observed (Loach, 1970), the allocation of dry matter to leaves relative to stems and branches was increased under lower light conditions. In the understory, the ratio for *Neobalanocarpus heimii* was 2.2 in contrast to 1.6 for *Shorea leprosula*. The higher ratio for *Neobalanocarpus heimii* is in accordance with its higher survival rate compared with *Shorea leprosula* under deep shade, because *Neobalanocarpus heimii* has a smaller amount of non-photosynthetic organs relative to photosynthetic leaves.

1.6 The allometry of seedlings

At the time one year after transplanting at the gap centre, *Shorea leprosula* had lower allocation of dry matter to leaves relative to supporting organs (stem + branches). However, the ratio may change during the course of seedling growth. The dynamic allocation pattern can be examined by plotting the weight of leaves to the weight of stem and branches for individuals with different sizes in a logarithmic scale.

The allometric relationships between leaves and stem + branches are analyzed for the two species. The data were obtained from two samplings: one and two years after transplanting, respectively. The slopes of the regression lines of the allometric relationships were not significantly different between the two species. The absolute values were 0.76 for *Shorea leprosula* and 0.77 for *Neobalanocarpus heimii*.

The slope indicates the ratio of the relative growth rate of leaves to that of stem and branches. Therefore, the value less than 1 means the allocation of dry matter to stem and branches (i.e. supporting organs) increases with plant growth in both species. The regression line of *Neobalanocarpus heimii* was always located at higher position than that of *Shorea leprosula*. In other words, the y- intercept of the regression line for *Shorea leprosula* was lower than *Neobalanocarpus heimii*. This result indicates the seedlings of *Shorea leprosula* had higher allocation of dry matter to stem and branches relative to leaves from the beginning of the experiment, when the seedlings were about at one-year old.

The allometric relationships between plant height and the dry weight of supporting organs (stem and branches) of the seedlings were analyzed for the two species grown at the gap centre. It was obvious that when the amounts of supporting organs were the same, plants of *Shorea leprosula* were taller than *Neobalanocarpus heimii*. However, the slope of the regression line for *Neobalanocarpus* was greater than that for *Shorea leprosula*, which means the height growth of *Neobalanocarpus heimii* will catch up with the height growth of *Shorea leprosula* in future. This situation can be expected, because at last both species must reach the canopy layer at adult stage.

Shorea leprosula showed higher efficiency for height growth in terms of architecture in an early stage of seedling growth after gap formation, but the efficiency will not be maintained. In contrast, *Neobalanocarpus heimii* showed relatively low efficiency for height growth in the beginning, but the efficiency gradually increased with plant growth. Therefore, it is not necessarily true that *Shorea leprosula* seedlings will show higher growth than *Neobalanocarpus heimii* and always succeeded in regenerating the gap, where the plants can enjoy the favourable light conditions.

1.7 Partitioning of regeneration niche

Based on the results of our field experiment, it can be concluded that there is fine-scale partitioning of regeneration niches between the two dipterocarp species we examined. After seed fall and germination, both species form a seedling bank under the shade of the canopy, but seedlings of *Neobalanocarpus heimii* can survive in shady conditions, e.g. at less than 1% relative photon flux density, whereas *Shorea leprosula* requires at least 2% relative photon flux for maintaining its seedling bank.

When the light conditions improve with gap formation, seedlings of *Shorea leprosula* will respond more quickly than those of *Neobalanocarpus heimii* and grow faster while the favorable light conditions continue. However, the probability of survival of these fast-growing seedlings

will be low when the light conditions deteriorate. In contrast, *Neobalanocarpus heimii* will be able to survive these suppressive conditions.

The process of gap regeneration is not a simple story, but rather a series of repeated processes of suppression and release of seedling growth depending on temporal variations in light conditions (Canham, 1985). In summary, it can be said that *Shorea leprosula* seedlings show an optimistic response to the variable light conditions, whereas *Neobalanocarpus heimii* show a strategic response (see also Kohyama & Hotta, 1990).

The results of our experiment have shown that under favorable light conditions, seedlings of *Shorea leprosula* can grow faster than those of *Neobalanocarpus heimii*. However, this does not necessarily mean that *Shorea leprosula* requires larger gaps for regeneration than *Neobalanocarpus heimii*, because the light conditions within a gap at the seedling level are considerably heterogeneous.

In other series of light measurements in gaps with different sizes, the within-gap horizontal variations of daily photon flux measured at a height of 50 cm above ground were analysed. If we compare the average and maximum daily photon flux, more favorable conditions are expected in a larger gap than in the understory. However, it should be noted that the minimum level is similar, irrespective of gap size. This means that even in a large gap, some seedlings may experience unfavorable light conditions which are equivalent to that of understory. Therefore, it is more realistic to say that seedlings of *Shorea leprosula* require more frequent improvement of light conditions for their regeneration than those of *Neobalanocarpus heimii*.

2. Juvenile recruitment and mortality of trees and shrubs in a lowland tropical rain forest- implications for regeneration and maintenance of species diversity

Tropical forests vary in species richness from site to site, and within plant communities. Such heterogeneity may be explained in terms of the prevalence of non-equilibrium condition in which the non-equilibrium status represents mid-successional stages of community development. According to the non-equilibrium hypothesis, species composition and abundance of each species in a stand are determined by historical and bio-geographical events that occurred randomly, such as the availability of a seed source when canopy gaps are formed. Some species therefore, are fated to be absent from a site while others become established. In contrast, the equilibrium hypothesis postulates that species coexist as an assemblage because each species can maintain a niche. For example, a given plant species is prevented from becoming the dominant species by host-specific predation (seed predators, herbivores and pathogens) which eliminate many individuals in the population due to density- and frequency-dependent mortality. As a result, minority species or juveniles (seeds or seedlings) are allowed to maintain a niche.

Understanding the equilibrium or non-equilibrium nature of community dynamics has practical implications for conservation biologists and forest managers. If the forest is in equilibrium, the abundance of each species is expected to be constant and succession of species assemblages are relatively predictable. However, if it is in a non-equilibrium state, many species may face the risk of extermination and such a loss may be detrimental if the forest area is not supplied by external seed sources. Using data obtained from the 50 ha plot of Pasoh Forest Reserve, Peninsular Malaysia, we have analyzed the juvenile and mature tree distribution pattern and the fate of juvenile trees of major species components of the forest, in order to predict the extent to which equilibrium and non-equilibrium forces contribute to the community dynamics.

2.1 Study area and method

The 50 ha plot was established and enumerated by the Forest Research Institute Malaysia (FRIM) in 1985 with supplementary funding from National Science Foundation (USA), Conservation, Food and Health Foundation, Inc. (USA); United Nations, through the Man and the Biosphere program, UNESCO-MAB grants and also UNESCO-ROSTSEA, and the continuing support of the Smithsonian Tropical Research Institute (USA), Barro Colorado Island, Panama. All woody plants of 1 cm DBH or larger were measured, identified and mapped to the nearest 10 cm. The total number of trees was 335,240, consisting of 814 species.

The initial tree census (started in 1985) data obtained in the 50 ha permanent plot were used to analyze the spatial distribution of saplings (>1, <2 cm in diameter) around the conspecific

adults. The minimum size of an adult tree was designated 30 cm for an emergent tree, 20 cm for a canopy tree, 10 cm for an understory woody plant, and 5 cm for a treelet or shrub. We counted the number of saplings within a 20 m radius of each adult tree which were located at least 40 m away from other conspecific adults.

To express the spatial pattern of saplings and adults for each species, the index of $I\delta$ was obtained for saplings and adults by subdividing the plots into rectangle-grids with each side of $1/2^6$ scale (7.8 x 15.6 m). i.e.

$$I\delta = \sum_{i=1}^q n_i (n_i - 1) / (N(N-1)) \times q$$

where q is the number of sub-quadrats divided by the rectangle-grid, n_i is the number of trees in each sub-quadrat and N is the total number of trees in the plot (50 ha). The same procedure was repeated by increasing the size of each sub-plot, namely, $1/2^6 \times 1/2^5$, $1/2^5 \times 1/2^5$, $1/2^5 \times 1/2^4$ $1/2^1 \times 1/2^0$. The index shows 1.0 for a random distribution, less than 1.0 for regular distribution, and greater than 1.0 for a clumped distribution (Morishita 1959). Significant differences of $I\delta$ from 1.0 was determined by the F-test. Values of $I\delta$ for adults, saplings, and all trees (adults, saplings and remainder which are smaller than adults but bigger than saplings) were plotted at each sub-plot size. Since we wanted to clarify the difference in local distribution pattern between adults and juveniles, values of $I\delta$ should be compared at the smallest scales. The distributional pattern of a species is regarded as clumped if the $I\delta$ value is significantly higher than 1.0 at more than three scaling levels within the first five sub-plot dimensions (from $1/2^6 \times 1/2^6$ to $1/2^4 \times 1/2^4$).

We classified the species into four categories: type 1, saplings are clumped but adults are random to regular in distribution; type 2, both saplings and adults are clumped; type 3, saplings are random to regular but adults are clumped; type 4, both saplings and adults are random to regular.

2.2 Result and discussion

2.2.1 Juvenile density in relation to the distance from conspecific adults

444 species (with more than 100 individuals) out of 814 recorded in the plot, were chosen for the analyses. Of these selected species, sapling density of 48 species showed a positive linear relationship with the distance from the conspecific adult. In some cases, the polynomial regression curve peaked, at a mid-section of the total distance from the conspecific adult ($P < 0.05$). Of the 48 species, 7 species were from the emergent layer (18.4% of the total number of species (38) in this layer), 17 species occurred in the canopy layer (10.5%), 16 species were understory trees (10.1%), and 8 species were treelets and shrubs (9.4%). Among the families, Dipterocarpaceae had the highest number of species with the distribution of saplings showing a positive relationship with distance from conspecific adults.

In contrast, 43 species showed a negative relationship with distance from conspecific adults and in most cases the sapling density decreased exponentially with distance. In comparison with species showing a positive relationship, only 1 species of this group was from the emergent layer (3.1% of all emergent species), 7 species were from the canopy layer (4.2%), 19 species were in the understory (11.9%) and 16 species were from the treelet and shrub layer (18.8%).

We also examined whether sapling mortality is dependent on the distance from the adults, but found no clear relationship for these species. This suggests that the density of individuals of these species was lowered before they reached sapling size (greater than or equal to 1 cm in DBH)

Seedlings of some species examined in Pasoh forest previously, showed a lower survival rate in close vicinity to mother trees, and peak density of juveniles shifted to the outer annulus with time (e.g. *Pentaspadon motleyi* and *Xerospermum noronhianum*). Therefore, in some of species, the lower density of saplings in the annulus close to the adult may be the result of an intensive attack by host-specific predators or parasites. However, whether 10% of species showing low density of saplings close to adults, are enough to contribute towards the maintenance of higher diversity, remains to be proven in further studies.

2.2.2 New recruitment and mortality of saplings.

For this analysis, data of recensus (started in 1990) were used, together with the primary census data. For each species, the total number of newly recruited saplings which were recorded in the re-census and the number of saplings which died between the two censuses were obtained.

There is significant relationship ($P \leq 0.001$) between the recruitment rate of new saplings and the mortality of individual species within each group of the emergent and canopy layers. The relationship was not so pronounced, however, in the understory, treelet and shrub layers ($P > 0.01$). When the species in all layers are examined, the relationship was significant ($P < 0.01$). These results indicate that in the emergent and canopy layers, the species which produce larger numbers of saplings, such as *Shorea leprosula* and *S. bracteolata*, tend to suffer high sapling mortality, while species with low recruitment numbers juveniles show high survivorship, (e.g. *Cynometra malaccensis*).

The indistinct relationship between sapling mortality and recruitment in the lower stories (understory, treelet and shrub layers) indicated that there was a large recruitment of saplings of some species in these stories and a low sapling mortality, while the reverse is true for some species.

It appears that equilibrium conditions may be present in the emergent or canopy layers, but are insufficient to explain the species abundance in every part of the forest strata. Lower stories of the forest may not be as stabilized as the upper layers in terms of the species composition, and they are probably in a non-equilibrium state. Such a conclusion needs to be taken into consideration when felling timber on constructing logging roads.

2.2.3 Spatial distribution pattern of saplings and adults

The total number of species where the distributions of saplings were clumped and adults showed a random or regular distribution (type 1) was 35 (7.9% of the total number of species in this layer). Within this group, 7 species were emergent (18.4 % of the total number of species in the emergent layer), 9 species were from the canopy layer (5.3% of the total number of species), 13 species were from the understory (8.2%) and 6 were shrub layer species (7.1%). As in the case of sapling density in relation to distance from conspecific adults, the proportion of the number of the species placed in type 1 was highest in the emergent layer. The largest number of species categorized as type 1 were members of Leguminosae, Euphorbiaceae and Guttiferae.

The largest number of the selected species (183 species, 41.2% of the total) fell into type 2, with both adults and saplings showing clumped distribution. Twelve species were from the emergent layer (31.6% of total number of species in the emergent layer), 46 were from in the canopy layer (28.4% of the total number of species), 79 species were in the understory (49.7% of the total number of species) and 46 species were from the shrub layer (54.1% of the total number of species). The number of species in this group was higher in the lower story of the vegetation (understory, treelet and shrub layers) than the upper layer of the vegetation (emergent and canopy layer). The difference in the distribution patterns of type 1 and 2 was represented by the differences in $I\delta$ for saplings and adult trees of *Koompassia malaccensis* (type 1) and *Shorea parvifolia* (type 2). No species fell into type 3, where saplings are random or regular in distribution, but adults show contagious distribution, or type 4, where both saplings and adults show random or regular distributions. Approximately half of the selected species (226 in total) could not be classified into a group because of the low density of the adults or saplings in the small quadrats sizes ranging from 1/212 to 1/28, which were not sufficient for adequate statistical analyses. Of the species classified into type 1, 6 species, namely *Shorea leprosula*, *Shorea ovalis*, *Mesua ferrea*, *Paropsia vareciformis*, *Mesua cornerii* and *Popowia pisocarpa*, were those whose sapling densities showed a positive relationship as a function of the distance from adult trees.

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