E-2.3 Studies on Plant and Animal Interaction in Disturbed and Non-Disturbed Forests

Contact Person Toshinori Okuda
Global Environment Division
National Institute for Environmental Studies, Environment Agency
16-2 Onogawa, Tsukuba 305-0053 Japan
Tel: +81-298-50-2426 Fax: +81-298-50-2483
E-mail: okuda@nies.go.jp

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Key words: Canopy Dynamics, Regeneration, Plant-Animal Interaction, Herbivore

Abstract

In order to clarify the plant and animal interaction in disturbed and non-disturbed patches in a forest, canopy structure and gap formation process and their effects on the seedling establishment, plant defense mechanism against herbivore and animal behavior were studied in the Pasoh Forest Reserve. Canopy structure were found to be dependent on the soil and topography, whereas the distribution and size of the canopy gaps were found not to be greatly changed between the two census in 1995 and 1997. Mortality and growth of juvenile trees were much influenced by the presence of canopy gaps. In addition, density of insect herbivore and their damage on seedling growth were higher under gaps than closed canopy, whereas the predators on these insects were more abundant in gaps than in the closed canopy. Rodents, one of major seed predator, were inactivated by the gap formation, primarily due to that they try to avoid such open sites where they are easily attacked by their predator. These results suggested that the Pasoh F. R. appears to be in a equilibrium condition in terms of gap formation rate, but the regeneration after gap formation were strictly regulated by the interaction among the tree seedlings, herbivores and predators. If one component of such interaction does not function well, the regeneration process of the forest will be disordered.

Key words: Tropical rain forest, Plant-Animal Interaction, Plant Defense Mechanism, Canopy Structure and Gap dynamics, Gene flow of Canopy forming Trees, small mammals.

1. Introduction

It has long been demonstrated that herbivory has significant effects on the plant fitness[1, 2, 3] and has a potential to change the vegetation structure, composition and succession pattern by altering the competitive interaction among the species [4, 5, 6, 7, 8, 9, 10]. Previously published paper suggested that leaf area removal by herbivory ranges from 5 to 44 % in temperate forests [11, 12, 13] and from 1 to 23 % in tropical forests [14, 15] though in terms of net primary production, such losses are small, perhaps less than 10% [16, 17, 18]

Plant resistance to leaf removal by herbivore and their regeneration performance are dependent on the light environment of forest floor [19, 20]. Thus, canopy openings (gaps) caused by tree fall events are very important for the regeneration of tropical rain forest species [21, 22]. It is well known that the seedlings growing in shade of understory, survive with minimized energy cost with low photosynthesis and low respiration. Seedling establishment is the most vulnerable stage during the life history of plants [23]. In such a condition, leaf removal by herbivore may be critical for the subsequent growth of the seedlings and influence their regrowth ability. It is therefore expected that herbivores give fatal damage on these seedlings in tropical rain forest[24,25].

Herbivore density and their frequency of visit to plants are also dependent on the light environments of forest floor, primarily due to difference in the quantity of fresh foliage which are available to the insect herbivore. In these respects, effects of herbivore on plants need to be studied in relation to the heterogeneity in micro-environments associated to the gap formation.

In the present study, we focused a question how gap formation alter herbivore behavior and subsequently affects plant and animal interaction. In order to answer the question, we investigated gap formation and close rate, seedling survivorship and their chemical and morphological defense in relation to the light environment of understory. We also studied the activity of small mammals and insect herbivores in relation to the canopy openings.

2. Research Objectives

1) To examine the gap formation and close rates and their role in determining forest structure and dynamics in the lowland dipterocarp forest
2) To know the effects of seedling generation in relation to the gap formation and forest structure
3) To understand the effects of gap formation on the plant and animal interaction
4) To understand the role of pollinator in maintaining the genetic diversity of canopy forming species

3. Research Methods

1) Canopy dynamics and structure in lowland dipterocarp forest

Origin and fate of individual gaps in Pasoh 50 ha were analyzed with aerial pictures taken above the forest. Interested area is the eastern 38 ha of the core area of which aerial pictures were available both for May 1995 and February 1997. Areas whose canopy height was below 15 m were regarded as canopy gas and all the individual gaps larger than the minimum recognizable size ($6.3m^2$=1 cell) were followed.

2) Seed dispersal and seedling survivorship after mast fruiting in lowland dipterocarp forest.

Seed survival and seedling growth of four dipterocarp species (*Shorea macroptera, S. pauciflora, S. parvifolia* and *Dipterocarpus cornutus*) were studied in the canopy gap and under the closed canopy in Pasoh Forest Reserve. One parent tree was selected for each dipterocarp species. Each tree was standing at the edge of gaps and was isolated from reproductive-sized conspecific adults. Seven quadrates of 2 x 2 m were established both in the gap and under the closed canopy sites of the four species. Recruitment and survival of fallen mature seeds were monitored in each quadrat every week during the dispersal period (6 weeks). Established seedlings after germination were tagged in order to monitor the growth at monthly intervals from September 1996.

3) Variation of plant defense to herbivore under the different micro-environments in the forest

The relationships between leaf damage caused by insects and pathogens and three leaf traits (leaf toughness, total phenol content, and nitrogen content) of five dipterocarp species were examined in Pasoh Forest Reserve in peninsular Malaysia. The measurements were made on all leaves of 9-month-old dipterocarp seedlings that emerged at mast fruiting in September 1996.

4) Effects of light environments on the herbivore activity

To clarify the population dynamics and community structure of insects on the seedling, all the insects (except ants) were monthly sampled on a transplanted seedling during May 95 to June 96 in a research area. Seedlings of eight species including six dipterocarp (*Neobalanocarpus heimii, Shorea acuminata, S. leprosula, S. macrophylla, S. macroptera, S. maxima*) and non-dipterocarp species (*Santiria tomentosa, Sapium baccatum*) were used for the experiments. When the insects were collected, we recorded date and seedling number, checking all the seedling in the area 3 minutes per a seedling. Feeding type of insects are divided into tree categories (herbivore, predator and unknown) through a direct field observation and used these to the analysis. Totally 143 insects were collected.

5) Response of small mammal activity to gap formation

The experiment was carried out in the Pasoh Forest Reserve, Negeri Sembilan, Malaysia. Two plots (20 m x 20 m) were made in a primary forest and were divided into 1 m x 1 m grid. One was in the area of closed canopy (hereafter the 'closed plot') and another was around a gap with large tree falls (hereafter the 'gap plot'). The distance between the plots was *ca.* 100 m. The gap was formed about two years before our experiment.

Our experiment consisted of the four consecutive steps as follows; 1) measuring the light conditions, 2) observation of frugivory in the center of each plot using an automatic camera system, 3) observation of fruit disappearance in each plot before clearing the lower vegetation in the gap, and 4) observation of fruit disappearance in each plot after the clearing.

6) Gene flow of canopy forming species in the lowland forest

The inner bark of reproductive *Neobalanocarpus heimii* (King) Ashton (*Balanocarpus heimii* King) (Dipterocarpaceae) and the seedling of selected four reproductive trees were collected in 12ha study plot. Total DNA was extracted from inner bark and seedlings with CTAB method.

For genotyping, each genotype of examined trees and seedlings were determined by three microsatellite loci (shc01, shc07 and shc09) using GeneScan Ⅱ (PE Applied Biosystems) system.

4. Results and Discussion

1) Canopy dynamics and structure in lowland dipterocarp forest

509 gaps existed as of 1995 and the number of gaps decreased to 463 in 1995. Distribution patterns of gap size were J-shaped with extreme aggregation in small size in both years. Fate of the gaps was remarkably different depending on their size. Most of small gaps with the area under $63m^2$ disappeared within two years (73%), however, the percentage of disappeared gaps decreased to 31% in the gaps over $63m^2$ and under $188m^2$. No gaps with size over $188m^2$ vanished during this period. On the other hand, the ratio of the gaps which got divided into two or more gaps increased in the size class $63m^2$. In the size class 63-$188m^2$, 9.5% of the gaps divided and the ratio increased to 43% and to 75% in the size classes of 188-$438m^2$ and 438-$934m^2$, respectively. All the gaps with size over $934m^2$ divided. These results show that small gaps, which were probably made by fallen branches or small fallen trees, can recover to forest canopy in a short period of time, however, it takes longer time for larger gaps over $188m^2$ to retrieve completely. Since many of large gaps were observed to divide into (probably smaller) greater number of gaps, they seem to shrink from the periphery.

Origin of the gaps observed in 1997 was also analyzed by tracking their status in 1995. Nearly half of the gaps, 210 (45%), were found to have newly occurred during the two years. 27 of them (5.8%) were created by the fusion of two or more gaps and 266 of them have been existing since the first measurement. Size distribution of the gaps was distinctive in each origin. The newly occurred gaps mostly found to be the smallest size ($6.3m^2$) with a few exceptions of large ones, the maximum was $188m^2$. Integrated gaps were also mostly small ones, but generally larger than newly occurred ones, with the median of $300m^2$ and the maximum of $1556m^2$. Existing gaps showed J-shaped distribution in size with the median of $44m^2$ and the maximum of $713m^2$. Difference of area in each gap was also analyzed. Newly occurred gaps gained the area as their nature, however, the total increased area was as much as $3963m^2$. In integrated or existing gaps, some of them increased the areas, but both the numbers of those gaps and the total increased area were limited. Most of them reduced the area and some of them decreased more than $1000m^2$ in only two years.

These results showed that the occurrence of large gaps are rather rare events, and most of the changes of gaps were attributed to large number of very small gaps which occur and close quite frequently. It was also suggested that the contribution of enlargement of existing gaps were compatible with that of the newly occurred gaps regarding the changes in gap area.

2) Seed dispersal and seedling survivorship after mast fruiting in lowland dipterocarp forest

For all selected species (*Shorea macroptera, S. pauciflora, S. parvifolia and Dipterocarpus cornutus*), high mortality of seeds and seedlings were observed within a few months after seed dispersal. Survival was higher for S. macroptera in the gap, and higher for S. pauciflora and D. cornutus under the closed canopy. Survival of S. parvifolia was not different between the tow canopy conditions. Growth patterns depended on the light level on the forest floor for each species. No tendencies toward distance-dependent mortality was found for any of the four species. Seedling survival, establishment and growth for these dipterocarp species were considered to dependent on habitat heterogeneity.

3) Variation of plant defense to herbivore under the different micro-environments in the forest

Table 1. Comparisons of the number of leaves, mean leaf damage levels and percentages of percentage of damaged leaves in five dipterocarp species. Means ± standard deviations are shown.

Species	*N*	No. leaves per seedling	Mean of leaf damage levels	Percentage of damaged leaves		
				Lightly	Moderately	Heavily
D. cornutus	26	3.7 ± 1.2[a]	19.3 ± 13.5	26.8	32.0	12.4
D. sublamellatus	49	3.6 ± 1.2[a]	10.6 ± 10.6	31.4	22.9	5.1
S. leprosula	57	3.6 ± 1.3[a]	14.6 ± 13.6	31.7	27.3	10.2
S. multiflora	49	2.0 ± 0.6[b]	11.5 ± 13.0	30.0	26.0	5.0
S. pauciflora	22	3.6 ± 1.4[a]	15.4 ± 14.3	33.8	22.5	13.8

Means of leaf damage levels were significantly different among the species. Percentages of heavily damaged leaves (damaged leaf area > 50%) varied from 5.0% in *Shorea multiflora* to 13.8% in *S. pauciflora* (Table 1), Mean leaf damage levels were not correlated with the three leaf traits across species, but percentages of heavily damaged leaves showed significant negative correlation with total phenol content. This result suggests that phenolics may not necessarily reduce the average amount of leaf damage, but may limit heavy leaf feeding by herbivores. This may explain why many studies failed to find a significant correlation between phenolic concentration and plant resistance to herbivores.

The quantity of light is variable among physical environmental factors. Spatial and temporal distribution of light patches is largely associated with the structure of a forest canopy [26].

Secondly, we examined the effects of light environment on herbivory and leaf traits of four *Shorea* regenerating in different light condition sites within Pasoh Forest Reserve, in Peninsular Malaysia. Seedlings of each species were transplanted within plastic pots at sun (gap) and understory (shade) sites. Survivorship of *Shorea maxwelliana* defoliated under a low light condition was lower than those of other treatments and light conditions. Effects of light and defoliation on the rates of insect herbivory were significantly different among species. In all species, increased light availability enhanced relative growth rates of plant height in height and leaf production, and leaf toughness. Rates of insect herbivory were not significantly different between the gap and understory sites while the leaves in the gap site showed higher levels of total phenol than in the understory. The amount of leaf area loss by insects per individual in the gap site was more than those in the understory site in spite of the seedlings in the gap site had higher total phenol contents in leaves. This may imply that the abundance of insect herbivores was higher in the gap site than in the understory site [27].

4) Effects of light environments on the herbivore activity

There was a notable trend that number of herbivores peaked in August 95 and decreased toward March 96 and the number of predators increased from November 95 to January 96. Number of herbivores colonized on an open area tended to be larger than that colonized on a closed one and the same pattern was observed in a case of predators, although the significance was only marginal (Fisher's Exact test for number of herbivores and predators, $p < 0.1043$).

Table 1 shows the difference between the total number of planted seedlings and the performance of the herbivorous insects in an open and a closed area. It is distinctively clear that significant(χ2-test for no. of insects, d.f.=7, χ^2=141.055, $p < 0.0001$) more herbivores colonized to the seedlings of *S. macrophylla* and those of *Sapium sp.*, while less herbivores did to those of *S. macroptera*, *S. maxima*, *S. pervifolia*, *Neobalanocarpus heimii*, *Sanitria tomentosa* and *S. acuminata.*

It is also quite notable that unclipped seedlings were significantly (χ^2–test for no. of insects, d.f. = 2, χ^2=127.191, $p < 0.0001$) more favored by herbivores than clipped ones.

Table 2. The difference between the total number of planted seedlings and the performance of the herbivorous insects in the whole research area.

	Plant species							
	MH	MP	MX	SP	RP	CH	ST	AC
No. of seedlings planted	178	150	144	88	174	112	117	176
No. of Insect	68	6	12	22	5	5	5	2

χ2-test for no. of insects, d.f.=7, χ2=141.055, $p<0.0001$

*MH: *S. macrophylla*, MP: *S. macroptera*, MX: *S. maxima*, SP: *Sapium sp.*, RP: *S. pervifolia*, CH: *Neobalanocarpus heimii*, ST: *Sanitria tomentosa* and AC: *S. acuminata.*

This study shows that number of insects were quite a few compared with the study of temperate regions, suggesting that plant chemical defense have much evolved especially in a tropical forest. This study also clarified that more herbivores and predators colonized on an open area than a closed one, indicating that better growth rate of the host plant is much attractive to herbivores and consequently many predators colonized to an open area. Conversely less herbivores colonized to a closed area,

5) Response of small mammal activity to gap formation

The lower activity of diurnal species, mainly squirrels, in the gap plot may result from the avoidance of open area where predation pressure by raptores is considered to be higher. The clearance of lower vegetation in gap reduced the foraging activity of small mammals in the gap drastically. This suggests that the foraging activity of small mammals is much more reduced in the newly formed gaps without dense vegetation. Thus higher survival rates of seeds and early seedlings are expected in new gaps. Crown gap is one of the most important places where forest trees accomplish their regeneration. Our results suggests that gap formation influences forest regeneration via foraging activity of frugivory on the forest floor.

The light condition in the closed plot (range 0.23 - 1.60%, mean 0.72 ± 0.25 SD) was lower than that of the gap plot (range 0.32 - 11.0%, mean 2.65 ± 2.61 SD). The small mammal species observed by the automatic camera system were *Tupaia glis, Macaca nemestrina, Sundasciurus lowi, Callosciurus notatus, Callosriucus nigrovittaus, Lariscus insignis,* and *Rhinosriucus laticaudatus* for diurnal species, and *Leopoldamys sabanus, Maxomy*s spp., and *Echinosorex gymnurus* for nocturnal species. *Sundasciurus lowi* and *Callosciurus notatus* were common in the both plots. *Tupaia glis* was found only in the gap plot, while *Callosriucus nigrovittaus* was found only in the closed plot. The species composition of small mammals in the two plots in number of photos was different; diurnal species consisted of 90% of total photos in the closed plot, while 40% in the gap plot. Higher fruit disappearance rate was observed in the closed plot than in gap lot. The disappearance rate increased after the vegetation clearing treatment in the gap plot.

6) Gene flow of canopy forming species in the lowland forest

We detected three, nine and eleven alleles from 17 trees in locus shc01, shc07 and shc09 respectively. The observed heterozygosity for shc01, shc07 and shc09 was 0.8, 0867 and 0.6 respectively and average heterozygosity was 0.756. The paternity exclusion probability over three loci was 0.92. After genotyping, the pollen parent of each seedlings was estimated. About 20% of seedlings have unknown pollen parent (these pollen came from out of the 12ha study plot). The long distance pollen flow was observed in *N. heimii* . This nature may depend on the performance of pollinator. The pollinator of *N. heimii* is bee that have wide foraging area.

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