



**UNIVERSITI PUTRA MALAYSIA**

**CROWN DYNAMICS OF SEVERAL TREE SPECIES  
IN A TROPICAL RAIN FOREST**

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**CROWN DYNAMICS OF SEVERAL TREE SPECIES  
IN A TROPICAL RAIN FOREST**

**By**

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**Thesis Submitted in Fulfillment of the Requirements for the  
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**January 1998**

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The study was conducted in Pasoh Forest Reserve, Negeri Sembilan. By considering trees as a metapopulation of modules, leaf phenology and crown dynamics were analyzed, specifically in relation to the complexity of their stratification that characterizes the tropical rain forests.

The results of leaf phenology study clearly demonstrated that the number of trees flushed was synchronized with the seasonality of rainfall. As a result, two flushing season existed in a year. However, flowering season was restricted to first heavy rainfall season from March to April. Shoot elongated intermittently in most species and only two species showed the continuous growth type. Leaf flushing and falling were synchronized in most of the species.



Crown dynamics were analyzed from the change in leaf number inside the crown. Most of small species (less than 15 m tall) expanded their crowns even though they were strongly suppressed. Because canopy around the tower systems was closed and light condition of understory was limited, only shade-tolerant species could regenerate. On the contrary, crown dynamics of middle-height species (from 15 m to 30 m tall) differed according to their light availability. Two canopy trees (larger than 30 m) maintained their crowns without increasing leaf number in the upper parts with high leaf turnover rate. The minimum leaf longevity was 7.9 months in one canopy tree. Smaller trees had the smaller leaf turnover ratio. This is consistent with the reported results of previous research.

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**DINAMIK SILARA BAGI BEBERAPA SPESIES POKOK  
DI DALAM HUTAN HUJAN TROPIKA**

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Kajian telah dijalankan di Hutan Simpan Pasoh, Negeri Sembilan. Dengan mengambilkira pokok sebagai suatu modul metapopulasi, fenologi daun serta dinamik silara dianalisis. Ini dijalankan khususnya terhadap hubungan dengan kekompleksan penstrataan yang mencirikan hutan hujan tropika. Hasil kajian fenologi daun jelas menunjukkan bahawa bilangan pokok memulakan “penunasan daun”/ pendaunan mempunyai hubungkait dengan musiman curahan hujan. Akibatnya terdapat dua musim pendaunan sepanjang tahun. Walau bagaimanapun, pemusiman bunga hanya terhad kepada curahan hujan yang tinggi daripada bulan Mac ke April. Sebahagian besar daripada spesies, pemanjangan pucuk berlaku secara bersenggatan/ “intermittent”, dan hanya dua spesies kajian yang menunjukkan pertumbuhannya berlaku secara berterusan. Penunasan dan pengguguran daun berlaku secara sinkronis bagi semua spesies.

Dinamik daun silara telah dianalisis berasaskan perubahan bilangan daun di dalam silara. Keseluruhan spesies yang rendah (ketinggian kurang dari 15 m) berkembang silaranya walaupun ianya tertekan. Oleh kerana sudur di persekitaran “sistem menara” tertutup dan suasana cahaya di lantai bumi hutan sangat terhad, maka hanya spesies yang “tahan-teduh” beregenerasi. Di sebaliknya, dinamik spesies silara sederhana tinggi (ketinggian daripada 15 hingga 30 m) berbeza mengikut kedapatan cahaya. Dua pokok bersudur (lebih daripada 30 m) mengawalatur silaranya tanpa penambahan jumlah daun pada bahagian atasnya dengan kadar tukaran daun yang tinggi. Terdapat kekekalan minimum daun selama 7.9 bulan pada suatu pokok. Pokok yang lebih kecil memperlihatkan nisbah tukaran daun yang lebih rendah. Keadaan ini adalah “konsisten” dengan apa yang telah dilaporkan di dalam kajian yang terdahulu.

## CHAPTER I

### INTRODUCTION

Tropical rain forests are the most species-rich forests in the world (Huston 1994). Most of the species characteristics in the tropical rain forests are still unknown and they have been expected to contain huge wealth for human being. In spite of this fact, most of them are rapidly diminishing now (Wilson 1992). To understand why and how so many species coexist in the tropical rain forests is important to preserve the tropical rain forests. The mechanisms to maintain species diversity in tropical rain forests are divided into two types, horizontal and vertical way in a small scale level (Richards 1952, Whitmore 1984). Whitmore(1984) pointed out the importance of the mechanism to maintain the diversity through gap dynamics, and termed it as forest growth cycle which is referred as the horizontal mechanism.

Many studies have treated horizontal heterogeneity by studying population dynamics and these population dynamics of trees in tropical rain forests have been studied by making small area plots (Ashton 1964, Manokaran and Swaine 1994, Whitmore 1989, Wong and Whitmore 1970). Since so many species coexist in a tropical rain forest and population densities of most species are low, it has been impossible to analyze the population dynamics of such species. Only recently, large-scale plots have been used as reported by Hubbell and Foster (1983), Manokaran et al. (1990) and Yamakura et al. (1995) to study the dynamics of rare species which



compose a large proportion of the species number that enables to understand how the diversity is maintained in a horizontal level. In addition to this, tropical rain forests have a vertical diversity maintenance mechanism through stratification. As the radiation energy is large in a tropical region, trees in tropical rain forests have tall and straight stems. It has been suggested that the complex stratification of tropical rain forests depends on this trait. Many species of various heights can coexist inside this complex structure (Ashton 1964, Richards 1983).

In the present study, observations on the crowns of trees at several heights were carried out directly by using a tree tower and canopy walk-way system in order to examine how the complex structure is maintained dynamically in a tropical rain forest.

### **Significance of the Study**

Hitherto, it has been difficult to study crown dynamics because there was no way to access the tall canopy of tropical rain forests. However, the crowns of tall trees could be studied directly by using a tree tower and canopy walk-way system in the present study. Since the tree species diversity in tropical rain forests depends on the stratification, it is important to study how the complex stratification is maintained in a tropical rain forest.

This study is only one example of the crown dynamics in a tropical rain forest. Similar studies must be done in several sites in the same forest and in other forests, from temperate to tropical forests. By comparing these results, the importance of the regeneration process and stratification of different forests can be understood well. To understand the regeneration process of the tropical rain forest is critical to manage it.

## **Objectives of the Study**

The present study aimed to understand how the complex stratification is maintained by many species in a tropical rain forest. Crown dynamics of some species of several heights were examined whether or not their crowns were expanding. According to the present study, one example of the dynamic condition of the complex stratification will be presented.

## **Scope and Limitation**

Since the crowns which could be studied were limited to the position of the tree tower and canopy walk-way system, only one individual could be examined for every species surveyed in the present study. It is desirable to study many individuals of one species to understand the species specific growth patterns. Since the present study was restricted to the crown dynamics of trees around the tower system, it was impossible to extend to all other sites, even in the same forest, because there was no other tower system.



## **CHAPTER II**

### **LITERATURE REVIEW**

#### **Stratification**

Many researchers (Ashton 1964, Kira 1978, Richards 1983) have paid attention to the complex stratification of tropical rain forests. The stratification of forests has been shown by profile diagrams of the structures. Richards (1952) recognized five strata in most types of Mixed and Single-dominant rain forest and grouped them into A, B, C, D and E layers. The A stratum comprises the top layer of the biggest trees which commonly stand as isolated or grouped emergents above a continuous B layer, which is the main canopy. C layer is a lower story of trees and D layer is woody treelets. Forest floor herbs and small seedlings belong to the E layer. The densest layer is the B layer at about 20-30 m in height (Richards 1983).

Kira (1978) showed the vertical distribution of leaf area, leaf biomass and woody organ biomass after felling a 0.2 Peninsular Malaysia. The pattern of leaf distribution indicated the existence of a main canopy at 20-35 m above the ground which was formed by the dense crowns of large trees. Kira (1978) also reported the profile of light inside the forest. Leaf area density was almost homogeneous between 10 m and 30 m above the ground. The wide space of the main canopy was fairly evenly filled with leaves despite the apparent stratification. However, these studies examined only mature phases, and they did not pay attention to gap and building phases (Whitmore 1984).

Recently, Koike and Syahbuddin (1993) measured a two-dimensional distribution of foliage density by using photographs in a forest at Bukit Pinang Pinang, West Sumatra. They found that there was a significant stratification with a dense foliage layer below 15 m in height, but there was no significant continuous upper canopy layer. This unstratified upper canopy structure might be caused by a mixture of species with different potential for height growth.

Kohyama (1992) and Kohyama (1993) proposed a size-structured multi-species model to describe the coexistence of various tree species. The competition for capturing light is normally one-sided, that is, although taller trees suppress smaller trees around them, smaller trees do not affect taller trees. The model took into account the effect of this one-side competition. The model suggests that the trade-offs between the potential maximum size and potential recruitment rate, and between potential size growth rate and susceptibility to suppression of size growth rate, provide stable coexistence of several species. He concluded that the vertical and horizontal structure of forest is important to maintain the tree species diversity.

### Allometry

The difference in growth rate among plant parts, such as diameter, height, crown depth and leaf area indicates allocation patterns of organic matter within species. This relative growth pattern is termed allometry (Kira 1978). The allometry model has been used to estimate the biomass of tree organ. Recently allometry has been applied to express the architecture of trees. Therefore, it is important to compare the allometric relations between species. Many allometric characteristics have been compared for several species. (Aiba and Kohyama 1996, King 1990, 1991, Kohyama and Hotta 1990, O'Brien et al. 1996, Thomas 1996).

King (1990) compared allometries of understory trees and of saplings of subcanopy-canopy trees in Barro Colorado Island, Panama and found that understory

species had larger diameters at breast height and wider, heavier, leafier crowns than similar height saplings of canopy species. The understory species also showed greater increases in trunk diameter and crown mass per height increment. He concluded that understory species have the crowns which increase light interception and persistence in the understory, while saplings of overstory species allocate their photosynthetic products to height growth.

Kohyama and Hotta (1990) compared allometric relationships of understory saplings among subcanopy, canopy and emergent trees on the equatorial foothill forest in Ulu Gadut Valley, West Sumatra. They also showed that the differences resulted from a trade-off between height growth and leaf area extension.

King (1991) compared the relative growth rates (RGR) and patterns of aboveground biomass allocation between gap-associated and shade tolerant species at La Selva Biological Station, Costa Rica. A significant negative correlation was found between the natural logarithm of the percent leaf allocation and RGR for shade-tolerant species, but such correlation could not be found for gap-associated species. Although shade-tolerant saplings invest most of their aboveground growth to leaves when they are heavily shaded, gap-associated species allocate constant aboveground growth to the stem and branches irrespective of the light conditions. He considered that the difference of the plasticity was supposed to be an important factor which determines the shade tolerance and successional status of the species.

Aiba and Kohyama (1996) examined allometries of several species and compared the maximum height of the species and the height of each species at two diameter classes, 2 cm and 10 cm, on a primary warm-temperate rain forest in Yakushima Island, southern Japan. The average height was larger for the species which could attain a higher maximum height when their dbhs were 10 cm. By contrast, no correlation was found between the average height at diameter 2 cm and the species maximum height. This appeared to reflect a trade-off between height growth and lateral growth of crowns. From these results, they concluded that the architecture of saplings of canopy and understory species is not necessary to be different, but are

likely to be related to the strategies of waiting for regeneration opportunities under the canopy.

O'Brien et al. (1995) compared the relationships among diameters, heights, and crown shapes of eight species ranging in size from saplings to large adults in a neotropical forest on Barro Colorado Island, Panama. Understory species forage for light and their crowns became very irregular. On the contrary, saplings of canopy species have to grow straight because they have to become large sizes.

Many allometric relationships have been examined as mentioned earlier. However, most of these studies made use of small trees to measure several precise indices after cutting, such as leaf area (King 1990,1991, Kohyama and Hotta 1990). The studies which involved tall trees measured the indices which could be made easily without cutting, such as heights, diameters and crown areas (Aiba and Kohyama 1996, O'Brien et al. 1995). In this connection, it is important to examine crown dynamics which directly reflect the competition for the light resource. It is indispensable to study the crown dynamics of several trees which constitute several strata to understand how the complex structure is maintained.

### **Crown Dynamics**

Plants do not have the ability of movement, consequently plants forage for the resources by changing their sizes and shapes and individually consisting of an assemblage of repeating units. According to this construction, plants have the plasticity to grow and occupy space in heterogenous environments. This repeating unit was referred to as module by Harper and White (1974). They considered a module as a leaf and its axillary bud. Since then, various researchers have used the word 'module' in various definitions. Room et al. (1994) readjusted the definition. They defined several repeating units such as 'metamer', 'module' and ramet. Accordingly, 'metamer' is an internode, the axillary buds at its proximal end and the leaf or leaves at

its distal end. 'Module' is the product of a single apical meristem, a set of metamers originating from one axillary/apical bud, or the smallest unit of morphology capable of producing daughter units and/or seeds.

A plant grows by regulating the number and locations of modules to receive the light resource (Takeda 1994) and a tree structure is an accumulation of module dynamics of the past. As a result, locations of existing modules are restricted by the arrangement of past modules. Species specific structures of trees are formed as a result of the modular characteristics, that is, the difference of resource acquiring capacities among them (Takeda 1994).

It has been established that in temperate forests, trees elongate current-year shoots in the growing season between spring and autumn, and stop growing in winter. A current-year shoot consists of a young shoot, leaves and buds which develop from a winter bud. This current-year shoot corresponds to the 'module' in a temperate forest.

Crown dynamics can be described through modular characteristics such as modular length or modular phenology, and through the increase or decrease rate of the number of modular units (Ardhana 1988, Bazzaz and Harper 1977, Kikuzawa 1983, Koike 1989, Maillette 1982a, Maillette 1982b, Wilson 1991). Bazzaz and Harper (1977) analyzed plant growth as a demography of leaves (modules) in a glasshouse at Pen-y-ffridd Field Station, Bangor. This was the first study of module demography. Subsequently, Maillette (1982a) attempted to analyze the structural dynamics of the growth of silver birch using demographic techniques at the Botanic Gardens of U.C.N.W., Treborth. She analyzed the fates of buds in relation to leaf dynamics and shoot elongation, and discussed that the leader shoot played an important role in determining the growth and form. Furthermore, Maillette (1982b) made a matrix model to describe the bud number in the crown.

A similar analysis was made by Koike (1989) on the mechanisms of foliage-crown development and crown-to-crown interactions mediated by light conditions at the Kamigamo Experimental Forest Station of Kyoto University. He developed transition matrices for shoot lengths in 10 cm class for two *Quercus* species and compared with the actual shoot population dynamics.

Wilson (1991) described the crown development based on the shoot length. When he measured the shoot length of 8- to 10-year-old black birch (*Betula lenta*), he found that older branches had more short shoots and shorter long shoots than younger branches. Later, he developed a growth model and simulated individual branch growth. Simulation studies based on this model showed that predicted shoot numbers and total shoot lengths close to those of the actual branches.

Kikuzawa (1983) studied the seasonal change in mean numbers of leaves per shoot for 41 tall tree species in deciduous broad-leaved forests in Hokkaido, northern Japan. Leaf emergence patterns were classified into three types. The first was a succeeding type, the second was an intermediate type and the last was a flush type. These types were recognized from the ecological status of the species. From this point of view, Kikuzawa (1986) proposed that pioneer species would elongate their shoots non-seasonally and late-successional species would elongate their shoots seasonally even in tropical rain forests.

Kikuzawa et al. (1996) correlated these leaf phenology and shoot architecture in sapling trees of four species which are common in the deciduous broad-leaves forest of Hokkaido. The inclination of the terminal shoot from the vertical in species with a flushing type leaf emergence was greater than that of species with successive leafing. A large inclination of the terminal shoot would minimize self-shading among leaves that emerge simultaneously. This was considered an advantage in maximizing carbon gain. A small inclination would lead to more self-shading but would allow a sapling to attain a greater height within a shorter period. This was considered an advantage in situations where shading by adjacent plants was a greater potential problem than self-shading.

According to these analyses, growth conditions of a target tree will be recognized precisely by a short-term study compared to the study of the diameter measurement. Furthermore, the life history strategy of the species will be recognized by the differences and plasticity of modular characteristics inside the crown (Harper 1974, 1990, Room et al. 1994, White 1979).

### **Phenology**

Leaf flushing phenologies have been observed by many researchers in south-east Asian tropical rain forests (Koriba 1958, Medway 1972, Ng 1981, 1984, Ogawa 1978, Putz 1979, Yamashita et al. 1995). All these studies related phenology with rainfall seasonality. Koriba (1958) pointed out that even in the tropics of uniform climate, there were various types of growth patterns of tree species.

Medway (1972) recorded flushing, flowering and fruiting phenology of 61 canopy trees in Ulu Gombak from 1960 to 1969. Despite specific variations in phenology, the community as a whole exhibited regular seasonality, with single annual peaks of flowering and fruiting and a double peak of leaf production. These seasons were consistent with the heavy rainfall seasons.

Ng (1981) studied leaf flushing and flowering phenology of 86 trees of dipterocarp species in the arboretum of Forest Research Institute, Malaysia from 1972 to 1980 and found that flowering had only one peak per year in April, while leaf flushing had two peaks per year, in April and October. The flowering peak coincided with the first flushing peak and the leaf flushing peaks coincided with the two rainfall peaks.

Seasonal fluctuations of litterfall in Pasoh Forest Reserve was studied by Ogawa (1978) from May 1971 to February 1974. Annual rhythm was observed in the leaf litterfall, with two peaks in February - May and in October. This trend coincided with the two-peaked rainfall seasonality.

Yamashita et al. (1995) studied seasonal variations in litterfall in a plantation of *Dipterocarpus baudii* at the campus of Forest Research Institute, Malaysia from July 1991 to July 1993. Seasonal variations of leaf and stipule litter of *D. baudii* exhibited two peaks a year. These variations were significantly correlated with the precipitation. Since the stipule litter indicates the flush of new leaves, seasonalities of leaf flushing and falling were also correlated.

Phenological activities of canopy trees in the Sungei Buloh Forest Reserve, Malaysia was studied by Putz (1979) from January 1972 to March 1976. It appears that strong seasonality in flower, fruit and leaf production was not apparent and phenological activities proceeded uninterrupted throughout the year. The result did not coincide with Medway (1972), Ng (1981), Ogawa (1978) and Yamashita et al. (1995).

Earlier study by Ng (1984) on shoot elongation patterns of saplings of many species found that there were two distinctive elongation patterns, continuous growth type and intermittent growth type.



## CHAPTER III

### MATERIALS AND METHODS

#### Study Site

The study was carried out at Pasoh Forest Reserve, Peninsular Malaysia. The location of the Pasoh Forest Reserve is shown in Fig. 1. This reserve is surrounded by oil palm plantations on three sides and by a virgin hill dipterocarp forest on the north-eastern side. The Pasoh Forest Reserve is a lowland dipterocarp forest and is a part of the lowland evergreen rain forest formation. This forest formation is characterized by the dominance of the Dipterocarpaceae (Manokaran et al. 1992a), especially the reserve belongs to the Red Meranti - Keruing type where the species of *Dipterocarpus* (Keruing) and *Shorea* (Red Meranti group) dominate.

In 1985, a 50 ha permanent plot was established in the center of the reserve by Forest Research Institute, Malaysia in collaboration with the National Science Foundation and the Smithsonian Tropical Research Institute. Within the 50 ha plot, a total of 335,256 stems of 1 cm dbh and above has been recorded, which belongs to 814 species, 294 genera and 78 families. The most common families were the Euphorbiaceae and Annonaceae among the smaller trees, and the Dipterocarpaceae, Leguminosae and Burseraceae among the bigger trees. The most common species is *Xerospermum noronhianum* (Sapindaceae) which accounts for 2.5 % of the total number (Manokaran et al. 1992a, Appanah and Weinland 1993b, Lee 1995).