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**Regeneration Processes and Coexistence Mechanisms
of
Two Bornean Emergent Dipterocarp Species**

1995

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INTRODUCTION

TREE DIVERSITY OF TROPICAL RAIN FORESTS

Tropical rain forests are distinguishable by their extraordinary richness of species. It is the mechanisms maintaining the high species richness which many tropical ecologists have tried to elucidate. For the richness of tree species alone, various theoretical hypotheses have been proposed. In general, these hypotheses can be divided into two groups, i.e. equilibrium and non-equilibrium hypotheses. The former predicts that floristic composition is stabilized by intrinsic biotic interactions under the given environmental regime of the site. It tends to return, therefore, to original composition, if the species mixture is altered by disturbances (Ashton 1989a, Hubbell & Foster 1986). By contrast, the latter holds that floristic structure continually changes, dependent on the balance between immigration, or speciation, and extinction. The latter also suggests that generalists are superior to specialists in such unpredictable conditions, so that many of the coexisting tree species in the same guild have generalized rather than diverged their niches (Hubbell 1979, Hubbell & Foster 1983, 1986).

In the first category, many mechanisms maintaining tree species richness have been proposed. I do not review all of them here, but will mention some examples. Ashton (e.g. 1964, 1969, 1976) reported that species-specific requirements for soil properties are related to tree richness. Connell (1971, 1978) argued that species richness is determined by the disturbance regime of a site. Grubb (1977) emphasized the importance of 'regeneration niche' for coexistence of morphologically similar tree species. Tilman (1982) predicted that micro-spatial heterogeneity in resources enhanced species richness (but originally for herbaceous plants). Janzen (1970) and Connell (1971) speculated that the remarkable mortality of juveniles near mother trees prevent monodominance of certain species. Nevertheless, when comparing the large number of theoretical hypotheses, there is still insufficient field data required to evaluate these hypotheses. It is necessary to accumulate further field data in various regions and different forests.

For such field studies, it is ideal to consider all species coexisting in a focal forest. However, study species are often limited due to the restricted time and man power for a field study. In such cases, choice of study species is a substantial problem. Rogstad (1989) recommends closely related, sympatric species, or species in a small monophyletic group. One of the significant features of the high species diversity of tropical rain forests is the presence of closely related, morphologically similar, sympatric species (cf. Ashton 1982, Fedrov 1966, Richards 1954, Whitmore 1984). Such species are most likely to have relatively similar niches, because most of them have the same ecological and physiological heritage via their common ancestral lineage (Rogstad 1989). The maintenance mechanisms may therefore appear typically in the coexistence of such species. Moreover, monophyletic groups are more

informative for evolutionary processes of tropical trees (Rogstad 1989).

Spatial scale is another important matter in evaluating the hypotheses for the species richness. The hypotheses mentioned above are not necessarily contradictory to each other; they are possibly operating simultaneously in a particular forest. However, the relative importance of each mechanism may differ depending on focal spatial scale; i.e. different mechanisms might be working in different scales. For example, on a regional scale, it is known that different species are found in different habitats with different topography or soils, resulting in various formations (cf. van Steenis 1957, Whitmore 1984). Habitat effects may be less important within each habitat or formation, however. The relative importance of working mechanisms may also be related to the degree of environmental heterogeneity, which varies from place to place. Mechanisms working in a relatively homogeneous area might be different from those in a more heterogeneous area, even though the spatial scales considered are similar in both areas. The species richness and its supporting mechanisms in a particular forest may have a hierarchical nature in terms of spatial scale. It is, therefore, important to elucidate the relationships among various working mechanisms across different spatial scales in the same site which have not yet been well understood.

A sound understanding of the maintenance mechanisms of species richness is crucial not only for tropical ecology but also for conservation and uses of tropical rain forests. We cannot conserve or properly manipulate tropical rain forests without a knowledge of its species richness.

OBJECTIVES AND FORMAT OF THE THESIS

In this study, coexistence mechanisms of two emergent dipterocarp species, i.e. *Dryobalanops aromatica* and *D. lanceolata*, was examined. Although they have not been proved to be monophyletic, they are congeneric, hence probably sister species (P. S. Ashton *pers. comm.*). They are found in sympatric at the study site, where the topography and soils are spatially complex and very heterogeneous. The main objectives of this study are (1) to understand their regeneration processes and (2) to elucidate the mechanisms of their coexistence in the study forest. This is a case study on the coexistence mechanisms of ecologically similar, sympatric species in a tropical rain forest including highly heterogeneous environments. By using a large study plot of 52 ha in area, this study also intends to discuss the multi-scale mechanisms affecting the regeneration and coexistence of the two study species.

Following to the descriptions of the study site and species (Chapter 2), their regeneration processes and coexistence mechanisms are speculated on, based on the static data of their populations in Chapters 3 to 5. To evaluate their status in the study forest, I will first analyze their population structure using a large permanent plot (52 ha in area) consisting of highly

heterogeneous environments (Chapter 3). Then, I will estimate the effects of environmental factors, especially topography, on their spatial distributions and coexistence (Chapter 4). In Chapter 5, I focus on the regeneration process on a smaller scale, where environments are relatively homogeneous and suitable for the two species. The factors that may affect their regeneration on this scale are estimated from the spatial relations between their juvenile distributions and site factors such as light conditions and local tree densities.

The regeneration processes and coexistence mechanisms shown in Chapters 3-5 should be considered hypothetical, because they are speculated on only from the static data. They should be evaluated from more dynamic view points. The latter half of the thesis (Chapters 6-8), therefore, treats more dynamic phases, especially the seed and seedling dynamics.

The seed and seedling dynamics during a 2.5-year period following seed dispersal have been studied (Chapter 6). In this chapter, the features in seedling dynamics of the two study species are discussed by comparing them to two other dipterocarp species. Next, I argue the possibility of coexistence through the differences in seedling growth response to light conditions (Chapter 7). A shading experiment was conducted to evaluate the differences. In Chapter 8, the importance of topography and relating forest floor conditions for their coexistence is examined by a transplanting experiment. Seeds of the two species were sown together under various forest floor conditions, and the effects of the forest floor environment to their germination and establishment were examined.

In the last chapter (Chapter 9), I summarize the regeneration processes and relating factors for the two study species on the basis of the preceding chapters. Moreover, the importance of environmental heterogeneity on the maintenance of tree species richness in the study forest is discussed.

STUDY SITE AND SPECIES

STUDY SITE: Lambir Hills National Park

This study was conducted in a lowland tropical rain forest of Lambir Hills National Park in northern Sarawak (Fig. 2.1). The Park is located on undulating low hills (ca. 60-450 m a.s.l.) about 30 km south of Miri city. The following descriptions of the National Park depend primarily on an excellent review by Watson (1985).

Vegetation

The Park is a fragment of natural vegetation, which is surrounded by secondary forests, oil palm plantations and cultivated fields. The size is approximately 7000 ha, of which ca. 85% was originally covered with mixed dipterocarp forests (*sensu* Ashton 1964), while the other ca. 15%, mostly at the higher altitude area around Bukit Lambir, was heath forests or kerangas forests. Approximately 30% of the Park, however, has been modified by human activities such as logging or shifting cultivation (Fig. 2.2)

The flora of mixed dipterocarp forests on the coastal hills in North West Borneo, where the Park is located, is exceptionally rich and contains many endemic species (Ashton 1990). More than 1000 species of trees larger than 1 cm diameter have been recorded in a 52-ha area of the mixed dipterocarp forest in Lambir (Chai *et al.* 1995, Lee *et al.* 1995).

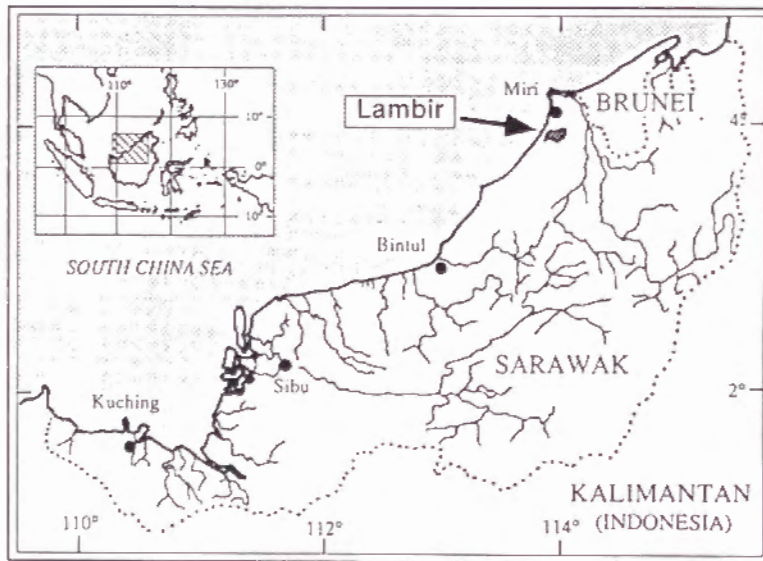


Fig. 2.1 Location of Lambir Hills National Park.

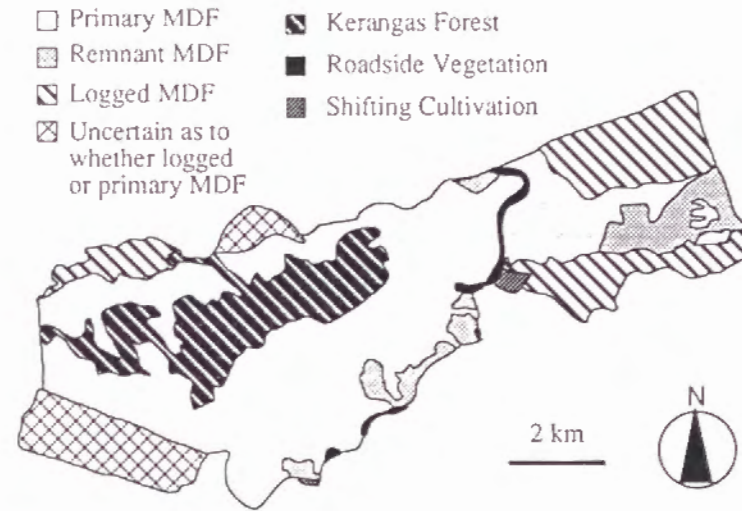


Fig. 2.2 Vegetation map of Lambir Hills National Park (after Watson 1987). MDF: mixed dipterocarp forest.

The mixed dipterocarp forests on the upper slopes and the ridges are dominated by trees of Dipterocarpaceae, especially *Shorea spp.*, *Dryobalanops aromatica* and *Dipterocarpus spp.*. Other common tree families are Burseraceae, Anacardiaceae, Euphorbiaceae, Myristicaceae, Lauraceae and Sterculiaceae. The ground flora consists of various palms (Palmae), such as *Licuala*, *Borassodendron borneense* and *Eugeissona minor*. Along the lower slopes and in the valley bottoms, however, the dominance of Dipterocarpaceae is less obvious, while the ground flora is generally more dense with herbaceous species of Araceae, Zingiberaceae, Melastomataceae and Polygalaceae. Epiphytes and lianas are also more abundant in the forests on the lower slopes and in the valleys.

More details of the flora of the mixed dipterocarp forests in the Park were described by Ashton (1973), Chai *et al.* (1995), Hall (1990), Soepadomo *et al.* (1984) and Watson (1985).

Kerangas forests are characterized by low stature, dense pole size trees, small, sclerophyllous leaves and thick litter layer (Brunig 1974, Whitmore 1984). They are dominated by *Gymnostoma nobile* (Casuarinaceae), *Dacrydium spp.* (Podocarpaceae), *Podocarpus neriifolius* (Podocarpaceae), *Calophyllum spp.* (Guttiferae), *Tristania obovata* (Mrytaceae) and *Ploiarium alternifolium* (Theaceae). The ground flora includes shrubs such as *Euthemis minor* (Ochnaceae), the rare fern *Matonia foxworthyi*, various pitcher plants (*Nepenthes spp.* (Nepenthaceae)) and ant plants such as *Hydnophytum formicarium* (Flacourtiaceae) and *Clerodendrum spp.* (Verbenaceae).

Climate

The climate of Lambir is relatively dry and less seasonal compared to other regions in Sarawak. The average annual rainfall is 2764 mm (1967-1993) at Miri Airport *ca.* 20 km north of the Park (Momose *et al.* 1994). There is no distinct dry season, though the periods February-March and July-August have relatively little rainfall, while the period of the northeast monsoon ('landas season': October-January) has heavier rainfall (Fig. 2.3). Although the year to year fluctuation in rainfall is large, and distinct spells of wet and dry weather sometimes occur throughout the year (Fig. 2.4). Dry months with less than 50 mm rainfall occurred 18 times (6 times each in February and March; twice each in January and August; once each in May and July) in 27 years (1967-1993) at Miri Airport.

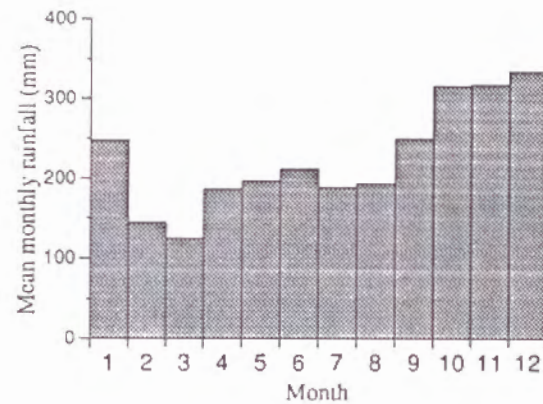


Fig. 2.3 Mean monthly rainfall at Miri Airport (1967-1993) (after Momose *et al.* 1994).

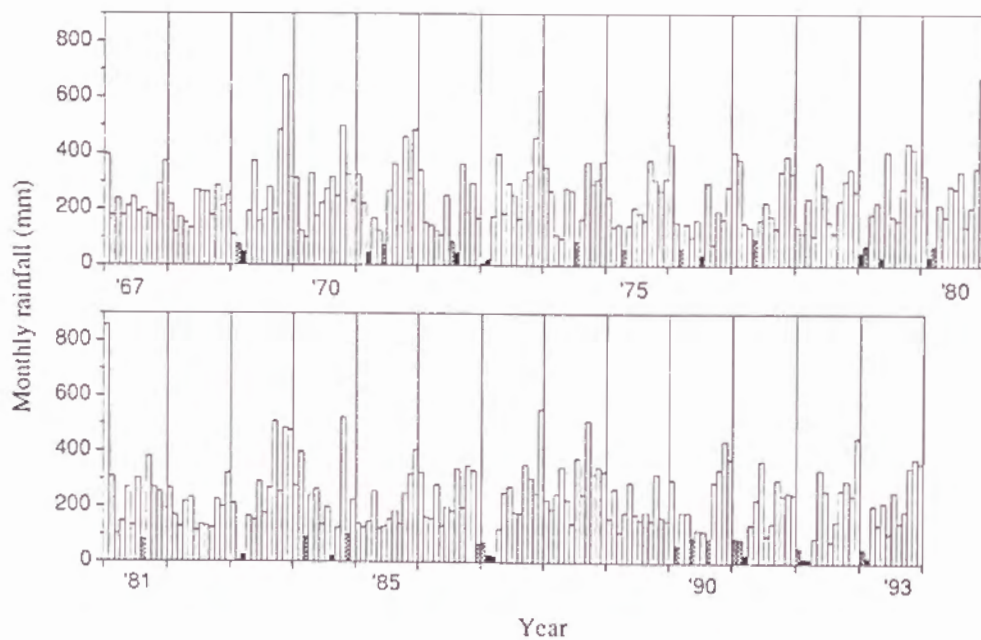


Fig. 2.4 Monthly rainfall at Miri Airport (after Momose *et al.* 1994). Shaded columns are months with less than 100 mm. Solid columns are months with less than 50 mm.

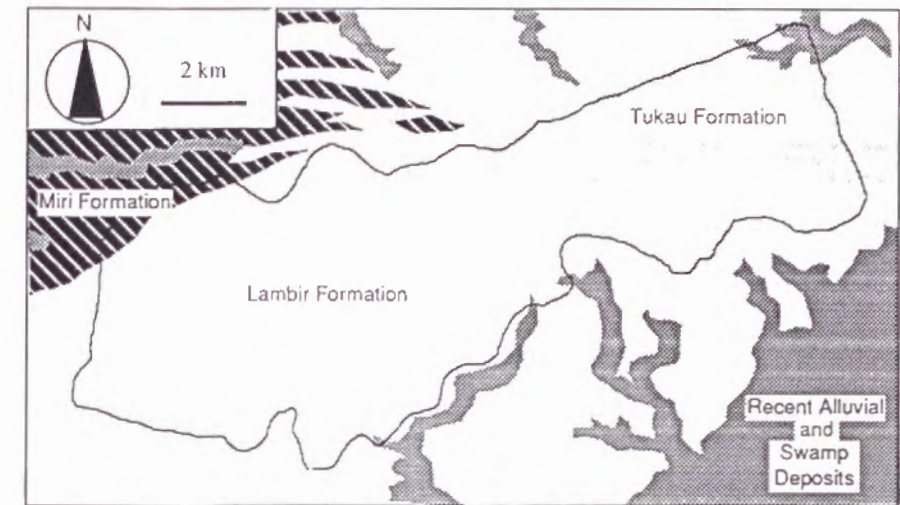


Fig. 2.5 Geological map of Lambir Hills National Park (after Watson 1987). Solid line indicates national park boundary.

Geology, Topography and Soils

The Lambir Hills are composed entirely of Tertiary sedimentary rocks. Three formations are found within the park: 1) the Lambir Formation, 2) the Tukai Formation and 3) the Miri Formation (Fig. 2.5). The Lambir Formation, which covers most of the park, consists of sandstones alternating with silt and silty clay. The Lambir Formation is thought to have developed as coastal plain deposits with strong fluvial influences during Miocene (*ca.* 10-25 million years ago) (Mulock Hower 1967).

The topography of the Lambir Hills National Park is very complex, having the long ridge of the Lambir Hills cuesta in northeast direction with many subsidiary dip-faultings (Fig. 2.6). Landslides probably play an important role in the erosion processes in the Lambir Hills (Ohkubo *et al.* 1995). They may occur only when the soil becomes extremely saturated during periods with prolonged heavy rainfall. In the early landas season of 1963, a large number of landslides took place due to the exceptionally heavy rainfall (P. S. Ashton *pers. comm.*).

No detailed soil survey has been conducted in the Lambir Hills, except for some preliminary soil research mainly in the mixed dipterocarp forest area (*e.g.* Andriess 1972, Ashton 1973, Hirai *et al.* 1994, Matsumura 1994, Wall 1962). Tie (1982) classified the soils in the Park into three types: 1) Podzols, 2) Red-Yellow Podzolic Soils and 3) Skeletal Soils.

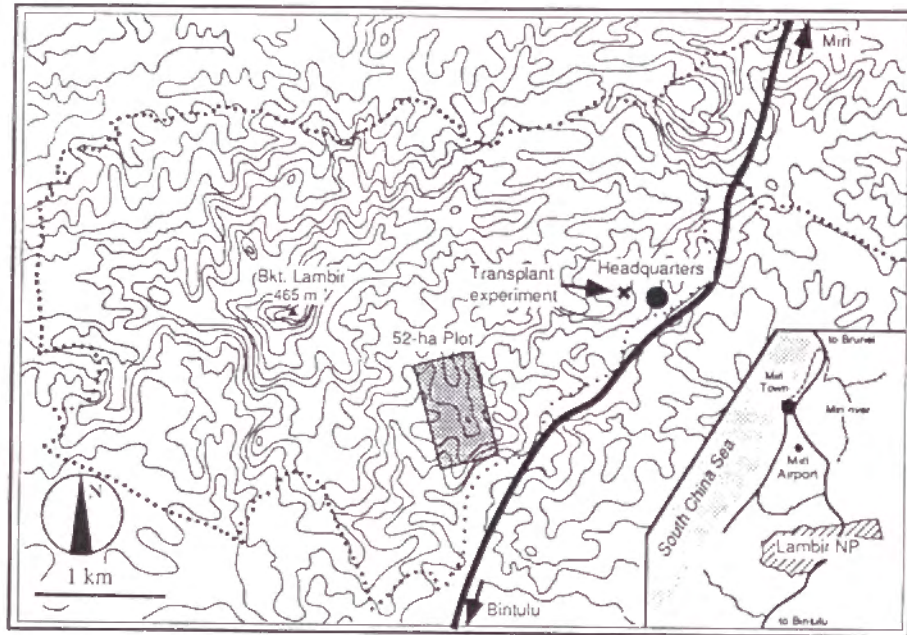


Fig. 2.6 Topography of Lambir Hills National Park. Contours are at 100 ft. intervals. The dotted line indicates national park boundary. The positions of the 52-ha plot (see Chapter 3) and the transplant experiment (see Chapter 8) are also shown.

Podzols occur on the north slope of the main ridge of the cuesta, and their distribution is assumed to coincide with that of kerangas forests (Fig. 2.2).

Red-Yellow Podzolic Soils cover most of the rest of the Park, where fine mixed dipterocarp forests have developed. In general, they have a moderately thick A_0 , and thin A_1 horizon, overlying a deep yellow sandy loam B horizon, and they are susceptible to gully erosion and landslides (Wall 1962). Their chemical properties are generally poor, having a low level of cation exchange capacity and nutrients. However, their properties vary considerably from place to place even within small areas depending on topography, clay content, mother rock (sandstone or shale) and maturity (Hirai *et al.* 1995, Palmiotto 1995). Ashton & Hall (1992) classified the soils into two types based on the soil properties, especially clay content: *adult ultisol* and *humult ultisol*. Therefore, an area covered by this soil type is highly heterogeneous in terms of soil properties, and it should be considered as a complex mosaic of different soil patches.

Skeletal soils are found on solid rock or fragmented rock of steep slopes. They are very shallow (< 50 cm) and stony.

STUDY SPECIES: *Dryobalanops aromatica* and *D. lanceolata*

Taxonomy and Distribution

Dipterocarpaceae is divided into three subfamilies: *Pakaraimoideae*, *Monotoideae*, and *Dipterocarpoideae* (Ashton 1984). The subfamily *Pakaraimoideae* consists of the monotypic genus, *Pakaraimaea*, which is distributed in British Guyana, South America. *Monotoideae*, most of which species are small trees or shrubs, is represented in Africa and Madagascar. *Dipterocarpoideae* is the most divergent subfamily, comprising 13 genera and about 470 species, which range from the Seychelles through Sri Lanka, India, Bangladesh, Myanmar, Thailand, Indochina, South China, to Malesia (including Malaysia, Indonesia, the Philippines and Papua New Guinea).

Dryobalanops Gaertn. *f.* is a small and homogeneous genus, comprising seven species (*D. aromatica* Gaertn. *f.*, *D. lanceolata* Burck, *D. oblongifolia* Dyer, *D. keithii* Sym., *D. beccarii* Dyer, *D. fusca* Sloot. and *D. rappa* Becc.). The genus is endemic in West Malesia; two species (*D. aromatica* and *D. oblongifolia ssp. occidentalis* Ashton) are distributed in the Malay Peninsular and Sumatra, and all seven species in Borneo (Fig. 2.7). *Dryobalanops* formerly had a wider distribution also in South India, Kampuchea, South Sumatra, West Java, and the Moluccas, judging from the fossil wood records (Ashton 1982).

Each species has its own distribution and habitat preference (Fig. 2.7 and Table 2.1). *Dryobalanops fusca* and *D. keithii* are distributed locally in kerangas forests of west Borneo and on river banks of northwest Borneo, respectively. Malayan subspecies of *D. oblongifolia* occurs by streams or in swampy areas, though its Bornean subspecies (*D. oblongifolia ssp. oblongifolia* Dyer) is found mainly on hillsides (Ashton 1964, Ashton 1982, Symington 1943, van Steenis 1931). Distributions of *D. aromatica*, *D. lanceolata*, *D. beccarii* and *D. rappa* overlap at northern Sarawak and Brunei, where the study site (Lambir Hills National Park) is located (Fig. 2.1). This study was thus conducted at the center of diversity of the genus *Dryobalanops*.

Table 2.1 Proportions (%) of specimens collected from various habitat, based on the site descriptions in labels of *Dryobalanops* specimens kept at the Kuching Herbarium. *N*: total number of specimens which had site description.

Species	<i>N</i>	Ridge	Slope & flat land	Swamp	Kerangas
<i>D. aromatica</i>	10	70	30	0	0
<i>D. lanceolata</i>	18	28	72	0	0
<i>D. beccarii</i>	26	50	42	8	0
<i>D. oblongifolia</i>	4	50	50	0	0
<i>D. keithii</i>	1	0	100	0	0
<i>D. rappa</i>	14	0	0	71	29
<i>D. fusca</i>	7	0	14	0	86

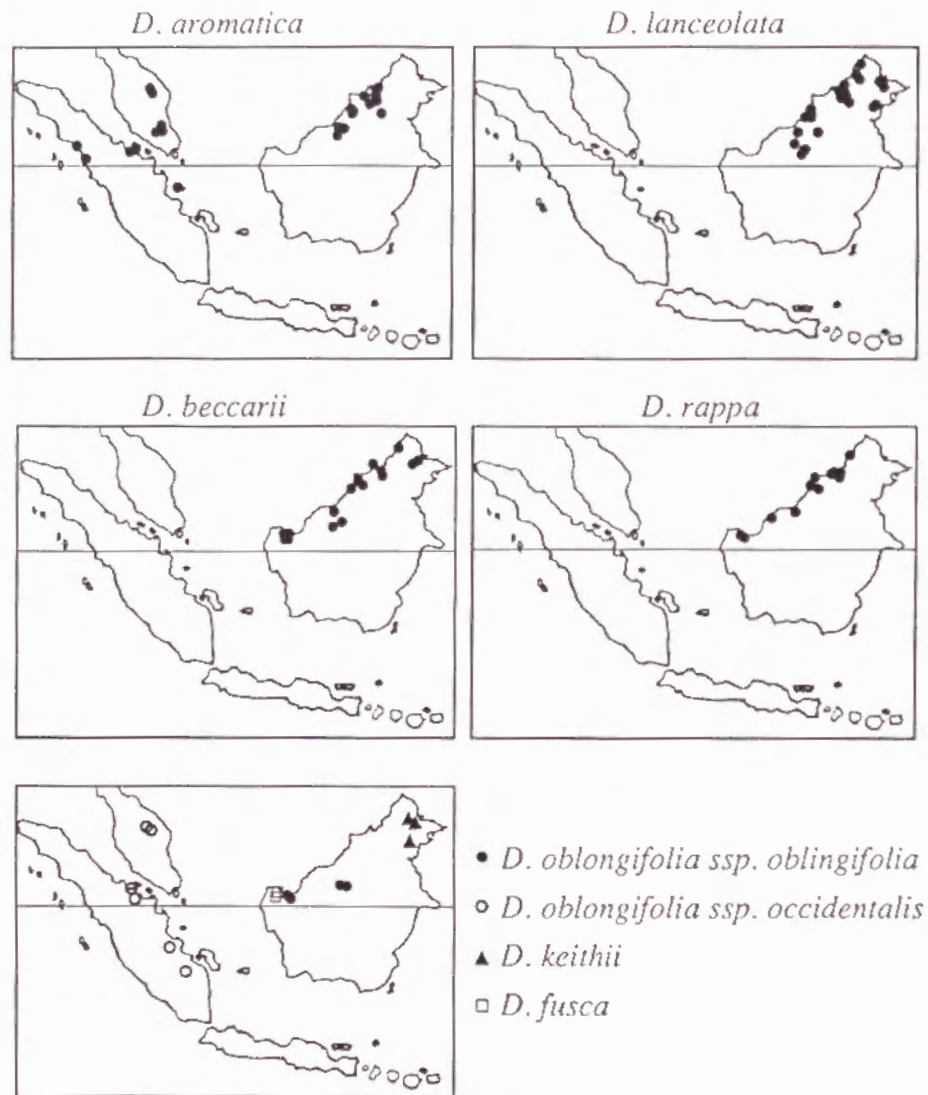


Fig. 2.7 Distributions of *Dryobalanops* species. Data from specimens of the Kuching Herbarium, Ashton (1982), Symington (1974) and van Slooten (1931). No available data for Indonesian Borneo (Kalimantan).

Since *D. rappa* is a mixed peat swamp species (Table 2.1, Ashton 1964, 1982), it was not found in the study plots, all of which were established on a hilly area. Although there have been some records of *D. beccarii* from Lambir (e.g. Hall 1990, Watson 1985), distribution of *D. beccarii* in the study forest could not be confirmed during this study. The morphological features of *D. aromatica* and *D. beccarii* are very similar (Ashton 1964), and they are often indistinguishable, especially for juveniles, in the study area (A. Itoh pers. observation, P. S. Ashton pers. comm., S. Kobayashi pers. comm.). So far, there has been no morphological evidence which suggest that the trees which were identified as *D. aromatica* consist of two different species. Therefore, it was tentatively concluded that only two species, *D. aromatica* and *D. lanceolata*, were distributed in the study site, and trees which might be *D. beccarii* were treated as *D. aromatica* in this study.

Ecology

Dryobalanops aromatica and *D. lanceolata* are among the tallest trees in West Malesia: up to 60-70 m in height and 1.5-2 m in diameter (P. S. Ashton pers. comm., Corner 1988, Foxworthy 1927, van Slooten 1931). On account of their huge size, they play an important part in the structure of the forest where they occur. They are always found very abundantly or growing gregariously, often predominating the upper canopy and emergent trees (Ashton 1964, 1982, Meijer 1970, Symington 1943, van Slooten 1931, Whitmore 1984, Wyatt-Smith 1963).

Both species produce large one-seeded (2-3 g dry weight) fruits which have five sepal wings (7-10 cm in length) (Fig. 2.8). The fruits will be referred to as "seeds" hereafter. The

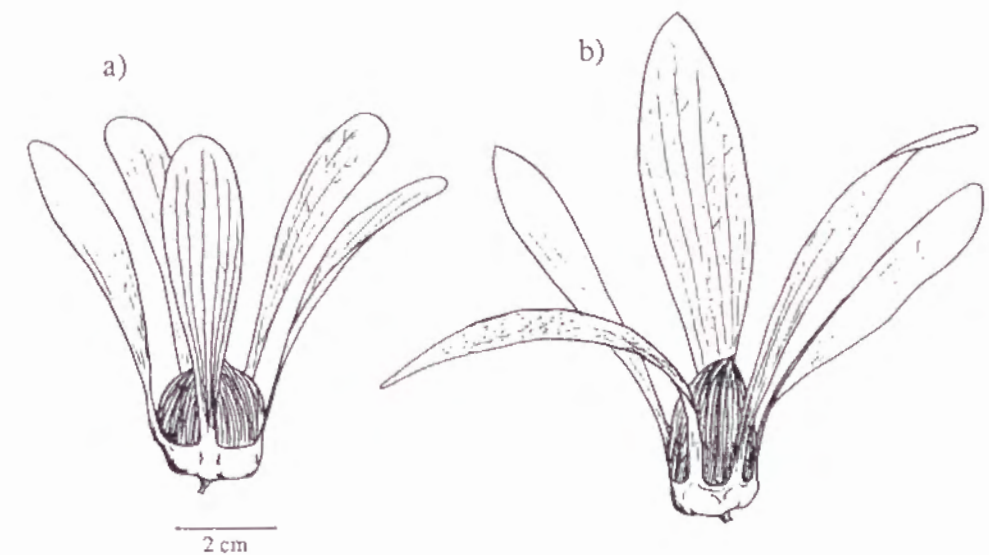


Fig. 2.8 Fruits of *Dryobalanops lanceolata* (a) and *D. aromatica* (b).

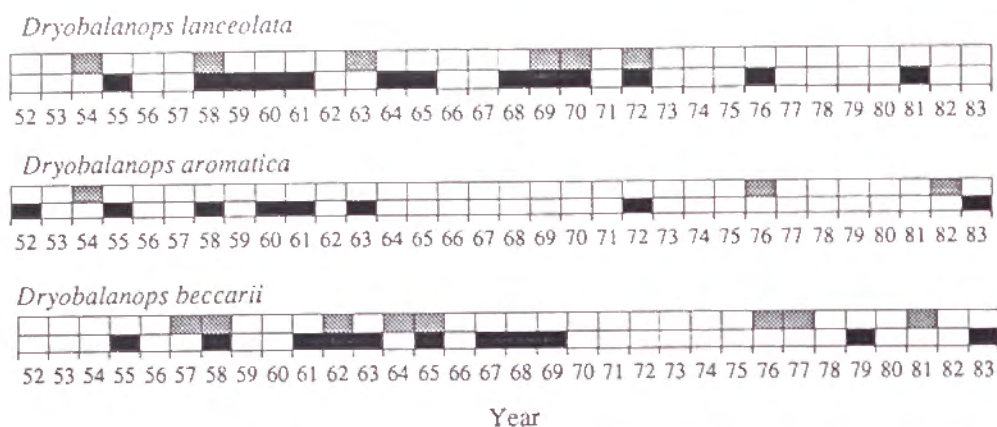


Fig. 2.9 Collecting years of *Dryobalanops* specimens with flowers or fruits at the Kuching Herbarium. Black columns: years with fruiting specimens; Shaded columns: years with flowering specimens; open columns: years with infertile specimens or no collection.

interval of heavy fruiting has been reported to be relatively short (ca. 2-4 years), compared to other dipterocarp species (Chan 1977 and Appanah 1979 in Ashton 1989, Cockburn 1975). Specimens at the Kuching Herbarium also suggest that both species fruited frequently in northern Borneo as a whole (Fig. 2.9), though there were many years without collection of *Dryobalanops* specimens. Their flowering or fruiting month varied year to year (Fig. 2.10) as well as place to place. Whether these phenological features in the whole of northern Borneo can be applied to a certain small area such as the Lambir Hills has yet to be studied.

The seeds of *D. aromatica* and *D. lanceolata* have no dormancy and germinate promptly after dispersal. Development and morphology of seedlings of the two species were similar, and described well by Edelin (1990), Ng (1991) and de Vogel (1983). The tap root and hypocotyl emerge from the apex of the fruit. The tap root grows upwards at first, then curves downward to enter the soil (Fig. 2.11a). The distinctly unequal fleshy cotyledons are pulled out of the fruit wall (Fig. 2.11b). The first internode strongly elongates to produce one or two pair of opposite oblong leaves (hereafter "primary leaves") (Fig. 2.11b). Next leaves are arranged spirally on the main stem, and a lateral plagiotropic branch is produced at every few nodes (Fig. 2.11c). Stipules are small and fall early.

Juveniles of *D. aromatica* show Roux's architecture model, having an orthotropic trunk with slender plagiotropic lateral branches which are drooping due to their own weight (Halle *et al.* 1978, Edelin 1990). When the trees become taller, *D. aromatica* suddenly changes its architecture, and all the branches, including first order branches, tend towards orthotropy (Halle & Ng 1981, Edelin 1990). At the mature stage, the leaves are confined to the edge of the crown, and the crown and crownlets develop mutual avoidance, resulting in a spherical crown showing crown-shyness (Halle & Ng 1981, Whitmore 1984). The morphological

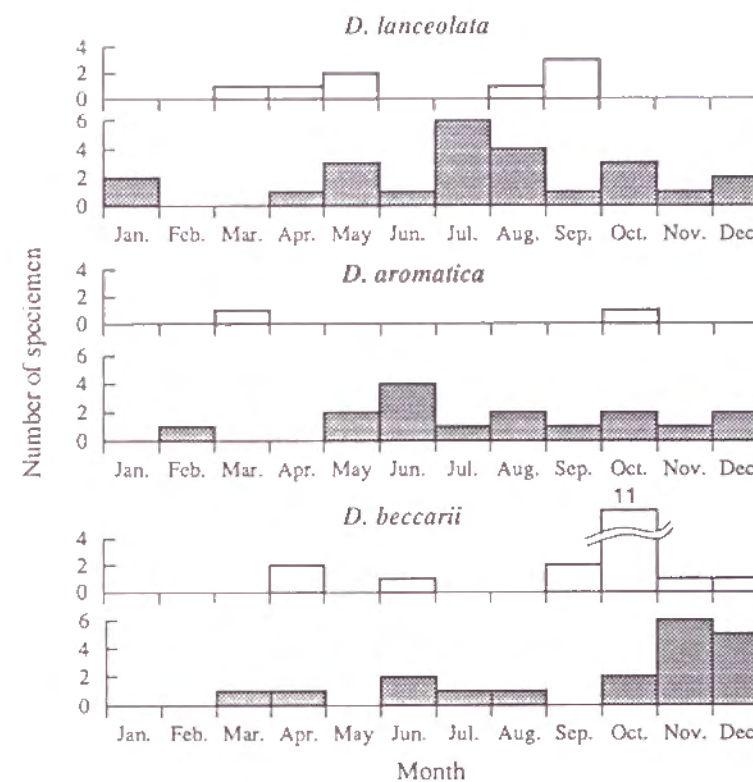


Fig. 2.10 Number of *Dryobalanops* specimens with flowers (open columns) or fruits (shaded columns) in each month. Data from specimens at the Kuching Herbarium (collected in Sarawak, Brunei and Sabah during the period 1952-1983).

features of *D. lanceolata* are generally similar to those of *D. aromatica*, though lateral branches of *D. lanceolata* juveniles are thicker, hence less drooping, and the shape of the mature crown is more crowded by crownlets and leaves, showing less clear crown-shyness (A. Itoh pers. observation).

Uses and Silviculture

The vernacular names in Sarawak are 'Kapur peringgi' or 'Keladan' (Iban name) for *D. aromatica* and 'Kapur paji' or 'Paji' (Iban name) for *D. lanceolata*. They are important timber species of medium hardwood for construction and plywood (Sarawak Timber Industry Development Corporation 1987). Their timbers share similar properties, containing much silica and having a specific gravity of 0.5-0.8.

Formerly, crystalline camphor (Borneo camphor) and oleo-resin were collected from mature trees of *D. aromatica* (Beccarii 1904, van Slooten 1931), but they have not been collected in the twentieth century due to the appearance of cheaper camphor from *Cinnamomum*

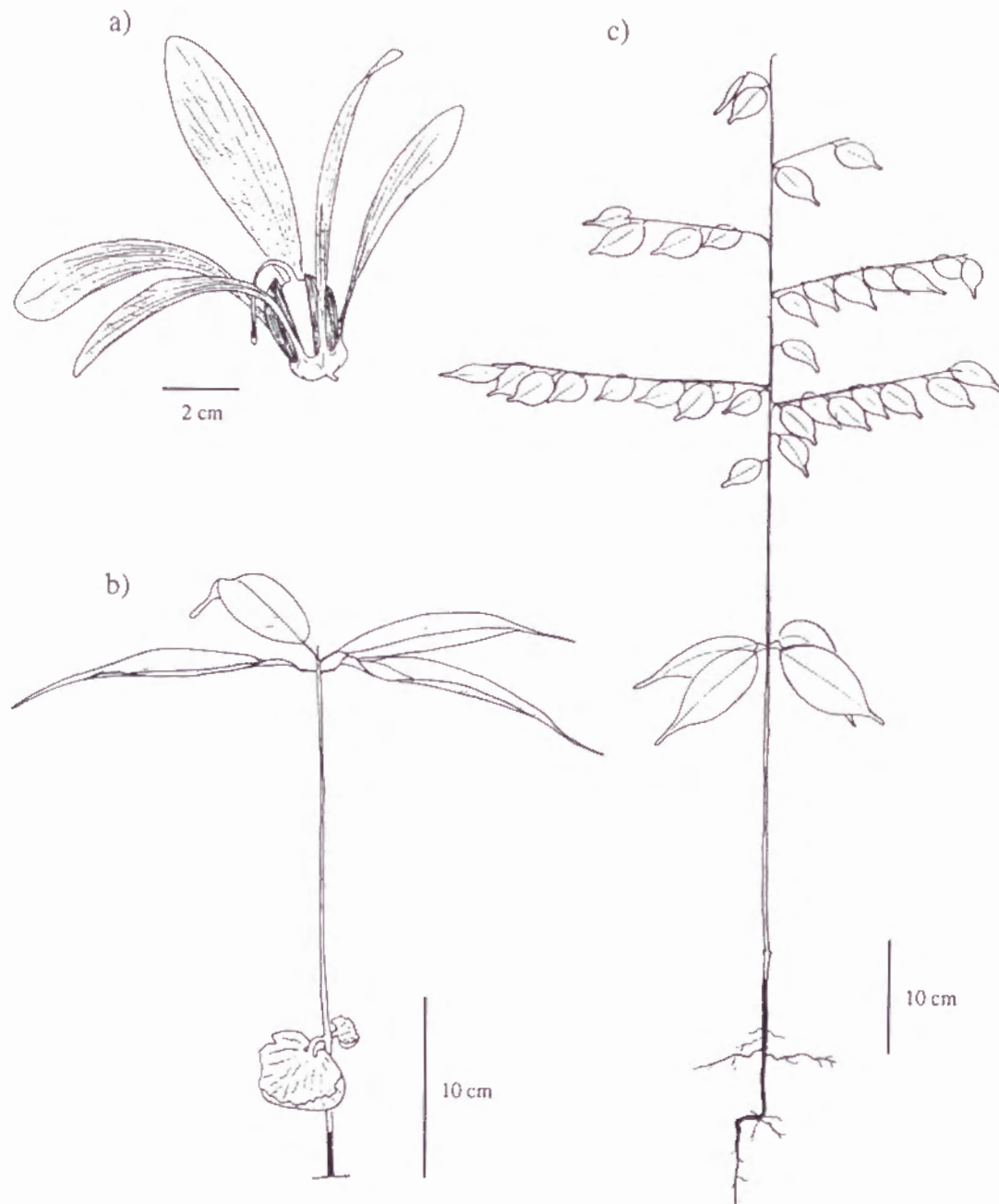


Fig. 2.11 Seedling development of *Dryobalanops aromatica*: a) a germinating fruit; b) a seedling at the primary leaf stage; c) a 2-year old seedling.

comphora (Lauraceae) (Burkill 1935).

Because of the frequent fruiting, high germination rate and rapid growth of the juveniles, *D. aromatica* and *D. lanceolata* are important and hopeful species for plantation in logged over forests in Malaya and Borneo. *Dryobalanops aromatica* has been a major species for line planting in secondary forests of Malaya from the 1940's (Appanah & Weinland 1993a). Studies and applications of *D. lanceolata* and *D. aromatica* for planting have recently started in various regions in Borneo: Sabah (Mura-Costa *in prep.*, Mura-Costa & Lundoh *in prep.*), Sarawak (O. K. Earnest Chai *pers. comm.*, J. J. Kendawang *pers. comm.*, A. Itoh *pers. observation*), Brunei (Ochiai *et al.* 1994, Shiraishi & Mohsin 1994, Ishii *et al.* 1994, Kitamura *et al.* 1994) and Kalimantan (Y. Okimori *pers. comm.*, S. Sasaki *pers. comm.*).

STATUS OF *DRYOBALANOPS* IN THE STUDY FOREST

INTRODUCTION

Tropical rain forests are generally the most diverse plant communities in the world without any dominant species (Leigh 1982, Richards 1952, Whitmore 1984). However, tropical forests dominated by one or a few species (hereafter, monodominant forests) have been reported in Africa (e.g. Eggleing 1947, Hart *et al.* 1989, Moutsambote *et al.* 1994), South America (e.g. Beard 1946, Connell & Lowman 1989, Davis & Richards 1934), and Southeast Asia (e.g. Richards 1952, Whitmore 1984). Early studies on monodominant forests in the tropics were reviewed by Connell & Lowman (1989) and Hart *et al.* (1989).

Dryobalanops aromatica has often been referred to as an example in the making of monodominant forests in South East Asia (Connell & Lowman 1989, Hart *et al.* 1989, Richards 1952). In the east of Malaya, *D. aromatica* formerly dominated rain forests in patches over several thousand square kilometers (Foxworthy 1927, Whitmore 1984, Wyatt-Smith 1963). Rain forests dominated by *D. aromatica* were also reported in Sumatra (van Zon 1916 in van Slooten 1931) and Labuan Island, Sarawak (Low 1848 in van Slooten 1931).

Other species of the genus *Dryobalanops* have also been reported to make monodominant forests. Abundant stands of *D. lanceolata* have been found in central Sarawak (Beccarii 1904) and Sabah (Meijer 1970). *Dryobalanops beccarii* also dominated some lowland forests in Brunei (Yamada 1991) and west Kalimantan (Kaji & Suzuki 1994). In secondary forests of peat swamp area in Brunei, pure stands of *D. rappa* have been reported by Ashton (1964) and Yamada (1991).

In this chapter, to understand the status of *D. aromatica* and *D. lanceolata* in the study forest, their population structure and canopy dominance were analyzed using a large scale (52 ha) permanent plot. Two questions were addressed: (1) Do *D. lanceolata* and/or *D. aromatica* dominate the canopy of the study forest in a large scale (52 ha) and/or in a small scale (1 ha)? (2) If so, does their dominance reduce the diversity of other canopy or subcanopy species?

METHODS

A permanent plot of 52-ha (1040 m x 500 m) was established in the forest during the period 1990-1993. The plot was divided into 1300 squares of 20 m x 20 m in size. Each square was further divided into 25 quadrats of 5 m x 5 m. The demarcation of the plot, squares and quadrats was done by a theodolite and compass survey. Aluminum pipes and plastic pegs

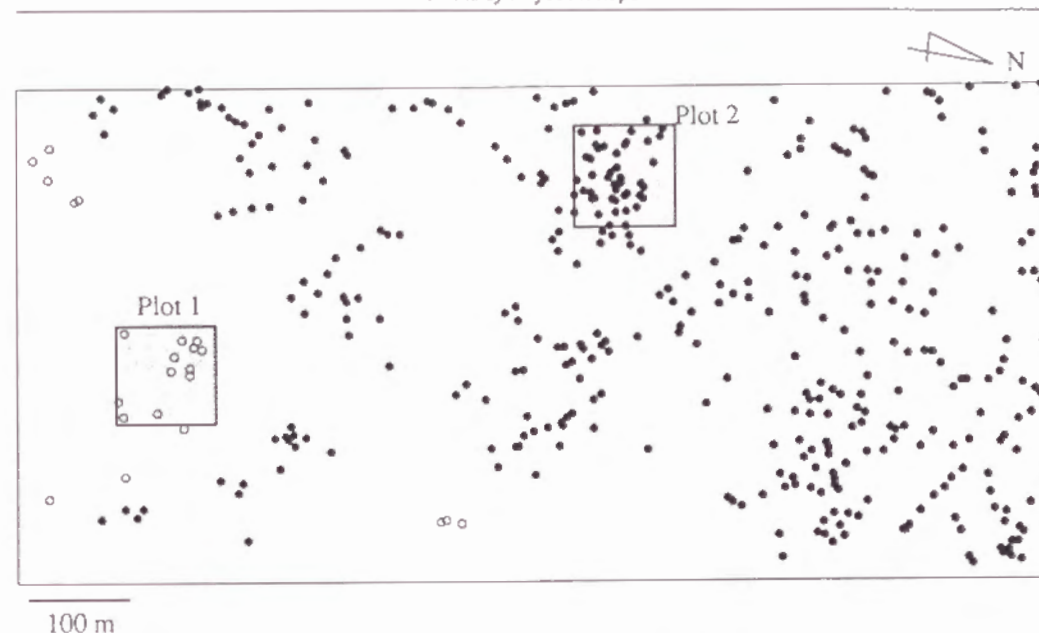


Fig. 3.1 Distributions of *Dryobalanops aromatica* (●) and *D. lanceolata* (○) trees (≥ 30 cm in DBH) in the 52-ha plot. Shaded areas are plots for analysis of local dominance (see text).

were put at the corners of all the squares and quadrats, respectively.

All trees equal to and larger than 1 cm DBH (diameter at breast height or 1.3 m above the ground) were tagged with aluminum number plates and measured in DBH using a diameter tape to the nearest 0.1 cm. Trees with buttress higher than 1.3 m were measured at just above the buttress height. Positions of the base of all trees were mapped on a sheet of section paper for each 5 m x 5 m quadrat. Species identification of the tagged trees were done after the enumeration. Tree species were identified in the field if possible, however, specimens were collected by tree climbers from all trees which could not be identified in the field.

Dominance of *Dryobalanops* in the small scale was analyzed using two 1-ha subplots (Plot 1 and Plot 2) established within the 52-ha plot. The positions of Plot 1 and Plot 2 were chosen to include many large trees (DBH ≥ 30 cm) of *D. lanceolata* and *D. aromatica*, respectively (Fig. 3.1).

RESULTS AND DISCUSSION

Status in the 52-ha plot

Dryobalanops aromatica ($N = 8,419$) was the most abundant canopy species in the 52-ha plot, and it distributed widely in the whole area of the plot (Fig. 3.1). *D. lanceolata* ($N =$

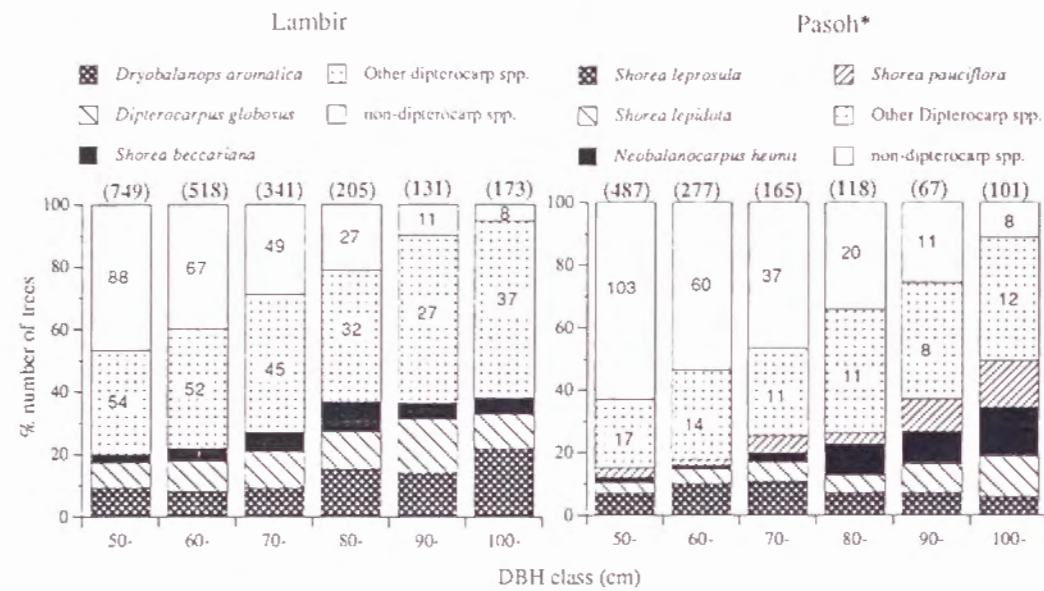


Fig. 3.2 Proportions of common canopy tree species in various size classes. Numerals in parenthesis are total tree number in each size class. Numerals in columns are number of species in each category (for Lambir, tentative number of taxa which had been identified by August 1993). *: Data for Pasoh was calculated from Appanah & Weiland (1993).

954), however, was restricted to the southeastern side of the plot, and was not common in the plot as a whole. The spatial distribution patterns of the two species were segregated between species, but aggregated within species. Details of their spatial patterns will be discussed in the next chapter.

Figure 3.2 shows the proportions of common canopy species and other dipterocarp species to total tree number at various DBH classes larger than 50 cm. For comparison, data of the 50-ha plot in Pasoh forest, Peninsular Malaysia (Appanah & Weiland 1993b) are also shown. The data indicates that the proportion of *D. aromatica* in the main canopy of the Lambir plot was not exceptionally high compared to other common canopy species of Lambir and Pasoh forests. In Lambir, *D. aromatica* occupied 8-20% of any size classes, and the proportion was higher in larger size classes. *Dipterocarpus globosus*, the second most abundant canopy species ($N = 2,405$) in the Lambir plot, was less than 10% of the largest size class (DBH ≥ 1 m), though its proportions were comparable to those of *D. aromatica* in the size classes 50-100 cm. In Pasoh, *Neobalanocarpus heimii*, *Shorea parviflora* and *S. lepidota* occupied 12-15% each at the largest size class. *Shorea leprosula* occupied ca. 10% in 60-80 cm DBH classes. Therefore, though *D. aromatica* was the most abundant canopy species, it did not dominate the canopy of the 52-ha plot as a whole.

DBH frequency distributions of *D. aromatica*, *D. lanceolata* and *Dipterocarpus globosus*

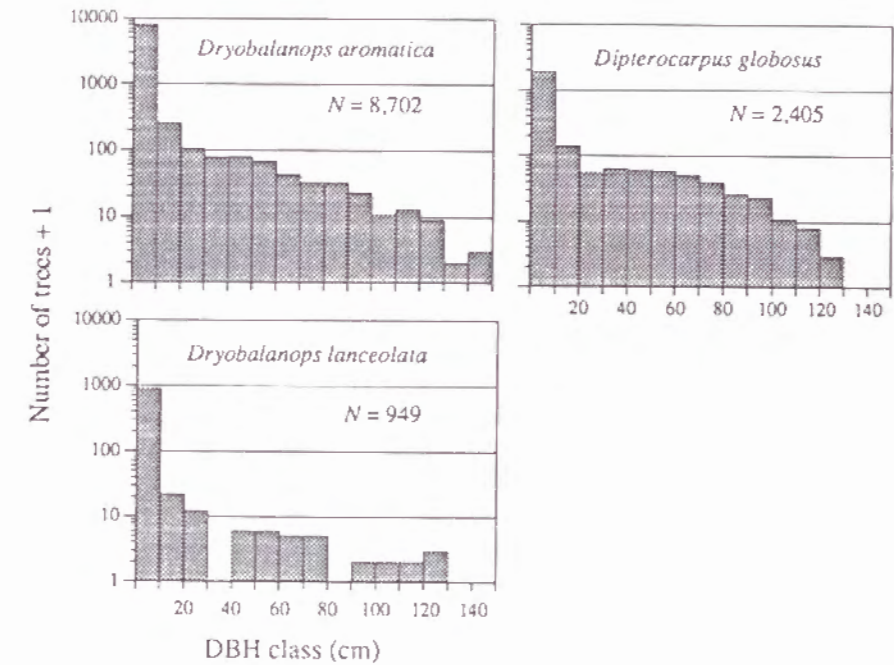


Fig. 3.3 DBH frequency distributions of *Dryobalanops aromatica*, *D. lanceolata* and *Dipterocarpus globosus* in the Lambir 52-ha Plot. DBH classes are at 10-cm intervals except for the smallest class (1-10 cm). N : total number per 52 ha.

are shown in Fig. 3.3. Both of the two *Dryobalanops* had slightly decreasing patterns in a semi-log scale, having abundant small size trees. The proportions of trees 1-5 cm DBH were 87.6% and 89.9% for *D. aromatica* and *D. lanceolata* respectively. *D. lanceolata* had a higher proportion in smaller individuals than did *D. aromatica*. The ratios of adult trees (DBH ≥ 30 cm) to poles (5 cm \leq DBH $<$ 30 cm) to saplings (1 cm \leq DBH $<$ 5 cm) were 1 : 2.0 : 18.4 and 1 : 4.3 : 36.2 for *D. aromatica* and *D. lanceolata*, respectively. *Dipterocarpus globosus* was comparable to *D. aromatica* in the number of middle size trees (cf. 40-100 cm DBH classes), however there were fewer trees of both the smaller and larger size classes. The ratio of adult:pole:sapling was 1 : 1.1 : 5.1. Assuming that the populations were in a state of equilibrium, the probability of a sapling becoming an adult would only be 1/18 and 1/36 for *D. aromatica* and *D. lanceolata* respectively, and 1/5 for *D. globosus*. This suggests that there is a continuous mortality in juveniles of the two *Dryobalanops* before they mature. By contrast, the mortality of established juveniles may be less severe for *D. globosus*.

Dominance of *Dryobalanops* in the small scale

D. aromatica and *D. lanceolata* were the most abundant canopy species in each 1-ha subplot (Table 3.1). The proportions of *Dryobalanops* were higher in large size classes than in small size classes. *Dryobalanops aromatica* and *D. lanceolata*, respectively, occupied 23% and 15% of trees larger than 30 cm DBH in number, and 30% and 27% in basal area. This indicates that the upper canopy and emergent trees of both subplots were dominated by *Dryobalanops*, however, the lower canopy and subcanopy included many other tree species.

The species diversity of the lower canopy and subcanopy was very high in both subplots (Table 3.1). Total numbers of 177 and 125 taxa have been identified in trees larger than 10 cm DBH in Plot 1 and Plot 2, respectively. These figures may be highly underestimated, since the identification have not yet completed at the species level, especially for Bruseraceae, Lauraceae, Myrtaceae, Myristicaceae and Sapotaceae, which may include many different species. The numbers of tree species per hectare above 10 cm DBH were *ca.* 140 in Andulau,

Table 3.1 Tree number and basal area in various DBH classes in Plot 1 and Plot 2. *Dr* represents *Dryobalanops lanceolata* in Plot 1, and *Dryobalanops aromatica* in Plot 2.

DBH class (cm)	No. / ha		Basal area (m ² / ha)		
	<i>Dr</i> (%)	other spp. (NT**)	<i>Dr</i> (%)	other spp.	
Plot 1					
10 - 20	5 (2)	292 (130)	0.09 (2)	4.50	
20 - 30	4 (5)	80 (52)	0.17 (4)	3.70	
30 - 40	0 (0)	32 (28)	0 (0)	2.98	
40 - 50	2 (10)	18 (17)	0.37 (11)	2.91	
50 - 60	2 (33)	4 (4)	0.52 (37)	0.89	
60 - 70	3 (50)	3 (3)	0.93 (50)	0.92	
70 - 80	1 (20)	4 (4)	0.43 (21)	1.60	
80 - 90	0 (0)	2 (2)	0 (0)	1.19	
90 - 100	1 (25)	3 (3)	0.69 (25)	2.11	
100 -	3 (60)	2 (2)	3.20 (43)	4.25	
Plot 2					
10 - 20	12 (3)	433 (111)	0.18 (5)	6.62	
20 - 30	15 (10)	130 (61)	0.77 (11)	6.19	
30 - 40	6 (9)	63 (30)	0.56 (9)	5.67	
40 - 50	16 (32)	34 (23)	2.58 (32)	5.41	
50 - 60	4 (21)	15 (10)	0.89 (19)	3.69	
60 - 70	6 (43)	8 (7)	1.90 (40)	2.83	
70 - 80	3 (33)	6 (6)	1.40 (36)	2.53	
80 - 90	2 (25)	6 (4)	1.09 (24)	3.41	
90 - 100	0 (0)	4 (4)	0 (0)	2.89	
100 -	3 (100)	0 (0)	2.80 (100)	0	

* Proportion to total value of each DBH class.

** NT: tentative number of taxa identified before August 1993, excluding *Dryobalanops*.

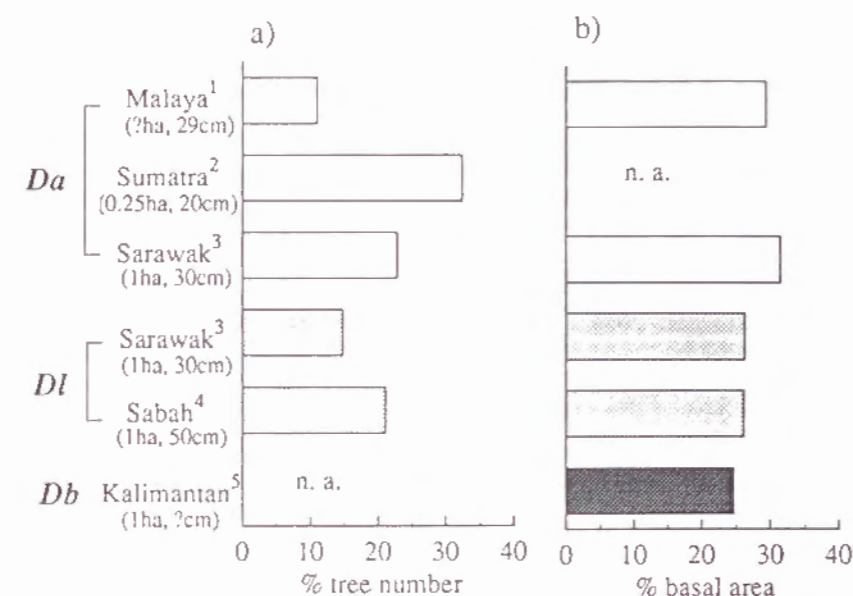


Fig. 3.4 Canopy dominance of *Dryobalanops* in tree number (a) and basal area (b). *Da*: *Dryobalanops aromatica*; *Dl*: *D. lanceolata*; *Db*: *D. beccarii*. Figures in parenthesis are plot size and lower DBH limit of canopy. Data sources are 1: Wyatt-Smith (1969); 2: van Zon (1916); 3: current study; 4: Meijer (1970); 5: Kaji & Suzuki (1994). n.a.: data not available.

Brunei (Ashton 1964), *ca.* 150 in Sungei Menyala, Malaya (Wyatt-Smith 1949), *ca.* 180 in East Kalimantan (Kartawinata *et al.* 1981), *ca.* 210 in Pasoh (Kouchummen *et al.* 1990), and 225 and 210 in an alluvial forest and a dipterocarp forest, respectively, in Gunung Mulu, Sarawak (Proctor *et al.* 1983). The actual species diversity of the subplots, therefore, may be comparable to or rather higher than other aseasonal lowland rain forests in South East Asia. The dominance of the upper canopy and emergent trees by *Dryobalanops* may have little influence on the diversity of the lower canopy and subcanopy. Based on the data from Wyatt-Smith (1963), Kachi *et al.* (1993) also suggested that the canopy dominance of *D. aromatica* has little effect on the diversity of the other tree species in Peninsular Malaysia.

Figure 3.4 shows the canopy dominance by three species of *Dryobalanops* in various regions. Dominance in terms of tree number varied among species and regions, probably because the value was largely influenced by the sample size and the lower limit of the canopy tree in the forest investigations, while dominance of basal area was not much different in all

species and regions with values of 25-30%. In a small scale of 1 ha, the degree of dominance by *D. aromatica* and *D. lanceolata* in the study site was comparable to other *Dryobalanops* dominant forests that have been reported in other regions.

However, the degree of canopy dominance by species of *Dryobalanops* (25-30%) is smaller than those of other monodominant forests in the humid tropics. Connell & Lowman (1989) defined a monodominant forest as a forest more than 50% (by number) of which canopy was occupied by one species. Therefore, most *Dryobalanops* forests might not be monodominant forests on the basis of their definition, although several authors referred to *Dryobalanops aromatica* as an example of monodominant species in the South East Asian tropics (Connell & Lowman 1989, Hart *et al.* 1989, Richards 1954, Whitmore 1984). The dominance of *Dryobalanops* may be between monodominant forests and typical mixed tropical rain forests (*sensu* Richards 1954).

In conclusion, *D. aromatica* and *D. lanceolata* predominated the upper canopy and emergent trees very locally (*e.i.* in a small scale of 1 ha) in the study forest. However, since their distributions were highly clumped, they were not dominant species in the 52-ha plot as a whole. Even at places predominated by the two *Dryobalanops*, their dominance was not extremely high, and the lower canopy and subcanopy showed great diversity in tree species. It would be of interest to study why they do not become more abundant and dominate the whole canopy. What are the mechanisms that maintain the diversity of other canopy trees in *Dryobalanops* predominant stands?

EFFECTS OF TOPOGRAPHY ON LARGE SCALE SPATIAL PATTERNS

INTRODUCTION

Tropical rain forest communities show variation on a range of scales. Whitmore (1984, 1990) attempted to rank the factors influencing rain forest composition. Availability of flora is the primary factor which determines the species composition of a local area. Major disturbances, such as cyclones, and major habitat differences are the next important factors resulting in differences between formations. Species specific features of reproductive behavior ('reproductive pressure') and difference in topography and soil are related to less obvious variations within formations. The relative importance of the latter two factors, however, is variable among species as well as place (Ashton 1964, 1976, Austin *et al.* 1972, Baillie *et al.* 1987, Hubbell & Foster 1983, Poore 1968, Wong & Whitmore 1970).

The importance of the topography and soil difference leads to an equilibrium view, in which the community composition is more or less stable according to the environmental mosaic in the community. On the other hand, the importance of reproductive behavior supports an unequilibrium view, in which the composition is more unstable and fluctuates stochastically because there is a large element of chance in this hypothesis (Wong & Whitmore 1970, Hubbell & Foster 1983, Whitmore 1990).

The first step for checking the relative importance of the two factors is to analyze the relationship between species distribution and topography and/or soil in a community. A strong relationship between them suggests that environmental factors play an important role in determining the community composition.

It was shown in the previous chapter that *Dryobalanops aromatica* and *D. lanceolata* predominated the main canopy very locally (\approx 1-ha scale). However, the dominance was not high in the 52-ha plot as a whole because of their highly clumped distributions (Fig. 3.1). Therefore, the spatial distribution pattern and its causes in the whole 52-ha plot scale should be clarified to understand the mechanisms of their co-existence in the plot. The question addressed in this chapter was whether the spatial distributions of *Dryobalanops aromatica* and *D. lanceolata* have a significant relation with topography in the 52-ha permanent plot. If so, their distributions in the plot must be determined mainly by topography. The influence of soil, another important environmental factor, was also discussed.

METHODS

Calculation of topographic features

Mean slope inclination and surface relief of each quadrat were calculated from the 20 m x 20 m grid data of altitude. For each quadrat, a plane which is expressed by Eq (4.1) was calculated from the three dimensional coordinate data at each corner of the quadrat by a mean least square method.

$$z = b_1 + b_2x + b_3y \quad (4.1)$$

Mean slope inclination (s) were calculated from the coefficients of Eq (4.1) as,

$$s = \tan^{-1}(b_2^2 + b_3^2). \quad (4.2)$$

Surface relief of a quadrat was evaluated by "convexity index (CI)". CI was calculated as,

$$CI = h - h_s \quad (4.3)$$

where h is the mean altitude of focal quadrat and h_s is the mean altitude of a surrounding 60 m x 60 m quadrat. Values of h and h_s were calculated by following Eqs:

$$h = \frac{z_{i,j} + z_{i+20,j} + z_{i,j+20} + z_{i+20,j+20}}{4}, \quad (4.4)$$

$$h_s = (z_{i-20,j-20} + z_{i-20,j} + z_{i-20,j+20} + z_{i-20,j+40} + z_{i,j-40} + z_{i+20,j-40} + z_{i+40,j-40} + z_{i+40,j+20} + z_{i+20,j+20} + z_{i,j+20}) / 12, \quad (4.5)$$

where $z_{i,j}$ is the altitude of the left bottom corner ($(x, y) = (i, j)$) of a focal quadrat.

Quantitative analysis of spatial patterns

The data of DBH and position for all *D. aromatica* and *D. lanceolata* trees (DBH \geq 1 cm) in a southern 50-ha area (500 m x 1000 m) of the 52-ha plot was used for analysis. Morishita's $I\delta$ index (Morishita 1959) was used for evaluation of spatial pattern. The value of $I\delta$ takes a negative value down to -1 for uniform distribution of individuals, 0 for random distribution and a positive value up to 1 for clump distribution. The analysis was applied independently for three size classes (large tree : DBH \geq 30 cm; pole : 5 cm \leq DBH < 30 cm; sapling : 1 cm \leq DBH < 5 cm).

The ω index of Iwao (1977) was used for analysis of spatial association between size classes of each species or between the two species. The ω index takes from the maximum value of +1 for complete overlapping, through 0 for independent occurrence, to the minimum of -1 for complete exclusion.

The values of $I\delta$ and ω were calculated for various quadrat sizes, as the 50 ha area was divided into 8, 32, 128, 512, 2048, 8192 or 32768 quadrats.

RESULTS

Spatial pattern

D. aromatica was distributed wider in the plot than was *D. lanceolata*, which was mostly restricted to the south-east side (Fig. 4. 1).

Spatial distribution patterns of large trees, poles and saplings of *D. lanceolata* were highly clumped (Fig. 4. 2). The values of $I\delta(s)/I\delta(2s)$ had a peak at 62.5 m x 62.5 m in poles and saplings of *D. lanceolata*, indicating that they had a mean clump size on this scale (Fig. 4. 2). Large trees of *D. lanceolata* showed a wide peak between 62.5 m x 62.5 m and 125 m x 125 m, suggesting a larger mean clump size than those of saplings and poles.

The $I\delta$ index also showed aggregated distribution in all size classes of *D. aromatica*, though larger size classes were less aggregated (Fig. 4. 2). Saplings and poles had two peaks at 31.2 m x 31.2 m and 125 m x 125 m in $I\delta(s)/I\delta(2s)$. This suggests that they had double-clumped distributions: small clumps of 31.2 m x 31.2 m mean size within large clumps of 125 m x 125 m mean size. Large trees showed no clear peak, suggesting that they were aggregated individually and that the mean clump size could not be detected.

The values of ω index were positive at all quadrat sizes used in poles and saplings of *D. lanceolata*, indicating that distributions of large trees and saplings or poles were segregated on all scales (Table 4. 1). In *D. aromatica*, ω index took positive values at large quadrat sizes, but took negative values at a 3.9 m x 3.9 m quadrat size both in poles and saplings. This suggests that distributions of smaller trees were aggregated in larger scales, but segregated from large trees in fine scales.

Table 4.1 Values of ω index between large trees (dbh \geq 30 cm) and poles (5 cm \leq dbh < 30 cm) or saplings (1 cm \leq dbh < 5 cm) of *Dryobalanops aromatica* and *D. lanceolata* in a 52-ha plot.

Quadrat size (m x m)	<i>D. aromatica</i>		<i>D. lanceolata</i>	
	Pole	Sapling	Pole	Sapling
3.9 x 3.9	-0.653	-0.072	0.015	0.026
7.8 x 7.8	0.009	0.027	0.047	0.074
15.6 x 15.6	0.092	0.094	0.137	0.127
31.2 x 31.2	0.249	0.174	0.285	0.277
62.5 x 62.5	0.443	0.199	0.787	0.770
125 x 125	0.533	0.256	0.857	0.887
250 x 250	0.559	0.122	0.822	0.887

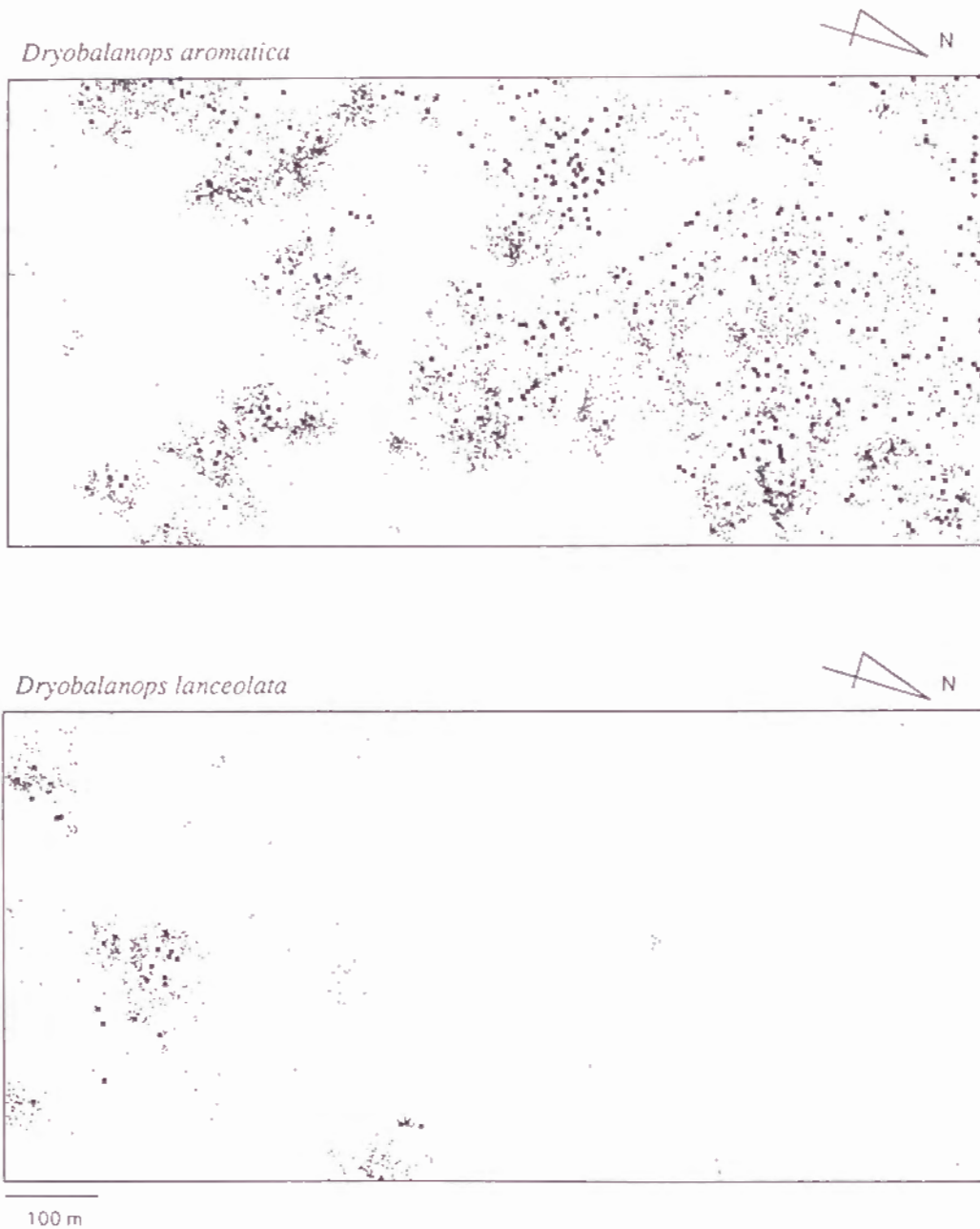


Fig. 4.1 Spatial distributions of two *Dryobalanops* trees larger than 1 cm DBH in the 52-ha plot. Large squares indicate trees larger than 30 cm DBH.

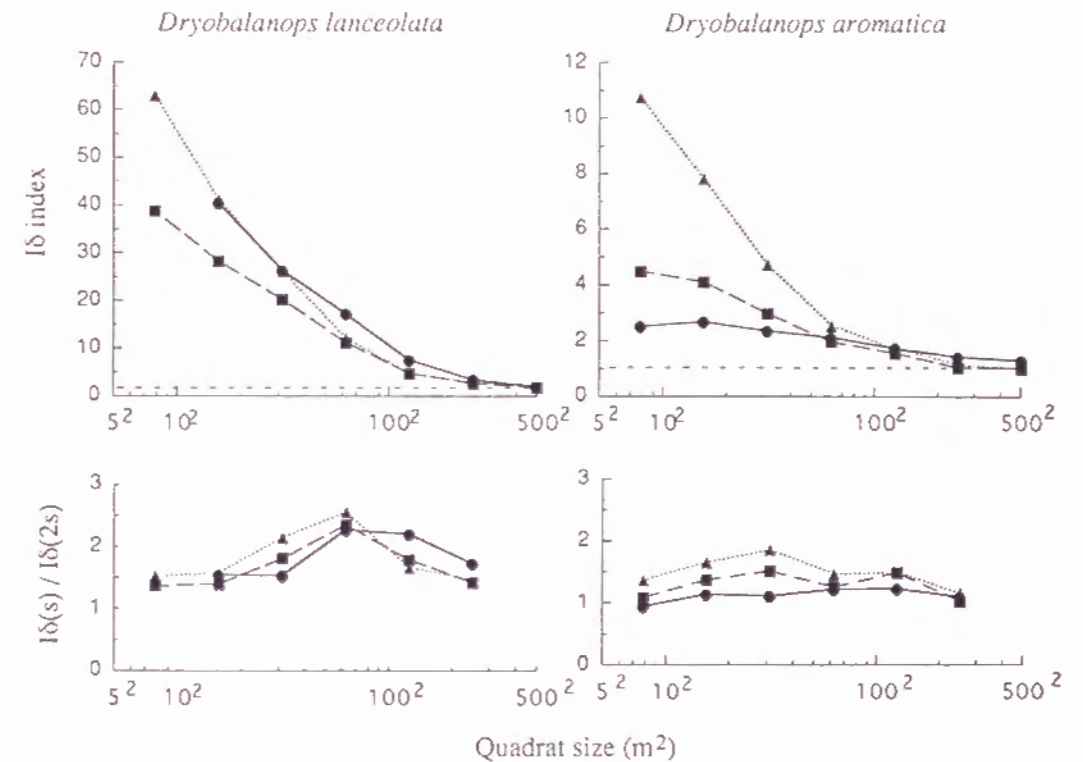


Fig.4.2 Morishita's $I\delta$ index and $I\delta(s)/I\delta(2s)$ for large trees (\bullet ; dbh ≥ 30 cm), poles (\blacksquare ; $5 \leq$ dbh < 30 cm) and saplings (\blacktriangle ; $1 \leq$ dbh < 5 cm) of two *Dryobalanops*. Dotted lines ($I\delta = 1$) indicate random distribution.

Distributions of *D. aromatica* and *D. lanceolata* were highly segregated even for small individuals (Table 4. 2). For large trees, values of ω index in smaller scales than 31.2 m x 31.2 m were -1, indicating complete segregation of the two species.

Relationship between distribution and topography

In order to see the interactive effects of slope inclination and surface relief on the density of the two species, all quadrats (20 m x 20 m) were classified by their topographic features into six categories. First, they were divided into two categories by their mean slope inclination as steep slope (mean inclination $\leq 30^\circ$) or gentle slope (mean inclination $< 30^\circ$). Then, each slope was classified into three more categories based on its surface relief as concave (CI ≤ -1.5), flat ($-1.5 < CI < 1.5$) or convex (CI ≥ 1.5).

The topography of the 52-ha plot and spatial distribution of each category are shown in Figs. 4. 3 and 4.4. Variation of topography within the plot was large and highly heterogeneous. Gentle slopes with convex surface relief were found along main ridges. Between the main

Table 4.2 Values of ω index between *Dryobalanops aromatica* and *Dryobalanops lanceolata* in a 52-ha plot.

Quadrat size (m x m)	Large trees (dbh \geq 30 cm)	All trees (dbh \geq 1 cm)
7.8 x 7.8	-1	-0.760
15.6 x 15.6	-1	-0.792
31.2 x 31.2	-1	-0.849
62.5 x 62.5	-0.969	-0.813
125 x 125	-0.888	-0.463
250 x 250	-0.719	-0.144

ridges, gentle slopes with flat or concave relief were distributed. Steep slopes were mostly on the south to east side of the main ridges.

There were significant positive relationships between the values of convexity index (CI) and the mean density of *D. aromatica* in all size classes (Fig. 4. 5). On the other hand, the mean density of *D. lanceolata* was negatively correlated with CI.

All size classes of *D. aromatica* showed a higher mean density in quadrats of convex surface relief than in those of concave surface relief on either steep slopes or gentle slopes (Table 4. 3). Large trees of *D. aromatica* had a higher mean density on gentle slopes than on steep slopes. On the other hand, the mean density of saplings was higher on steep slopes. In contrast to *D. aromatica*, the mean density of *D. lanceolata* was higher in quadrats of flat or concave surface relief than in those of convex relief on gentle slopes. Although some poles and saplings of *D. lanceolata* were distributed on the steep slopes having convex surface relief, no large tree was found on those quadrats.

DISCUSSION

The results clearly indicate the habitat segregation of *D. aromatica* and *D. lanceolata* in terms of topography. They showed opposite preferences to surface relief. *Dryobalanops aromatica* was distributed more on convex places such as ridges, while *D. lanceolata* was found more on concave places such as valleys. The linear relationships between the mean densities and CI values (Fig. 4. 3) suggests that they respond even to small differences in topography. Similar relationships between the distributions of the two species and topography were also found in tropical rain forests of Brunei by Ochiai *et al.* (1994).

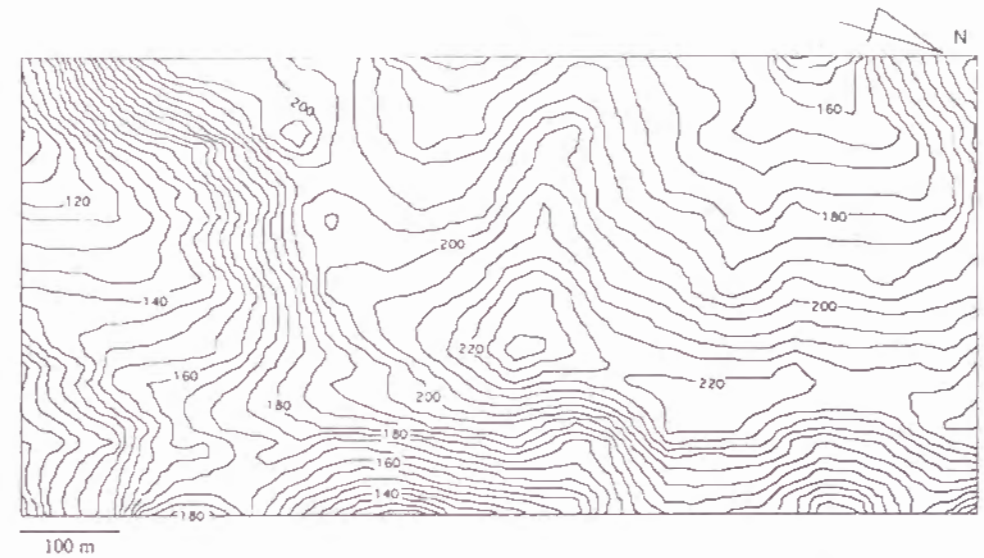


Fig. 4.3 Topography of the 52-ha plot. Contours are at 5 m intervals. Numerals on contours show the altitude in meters.

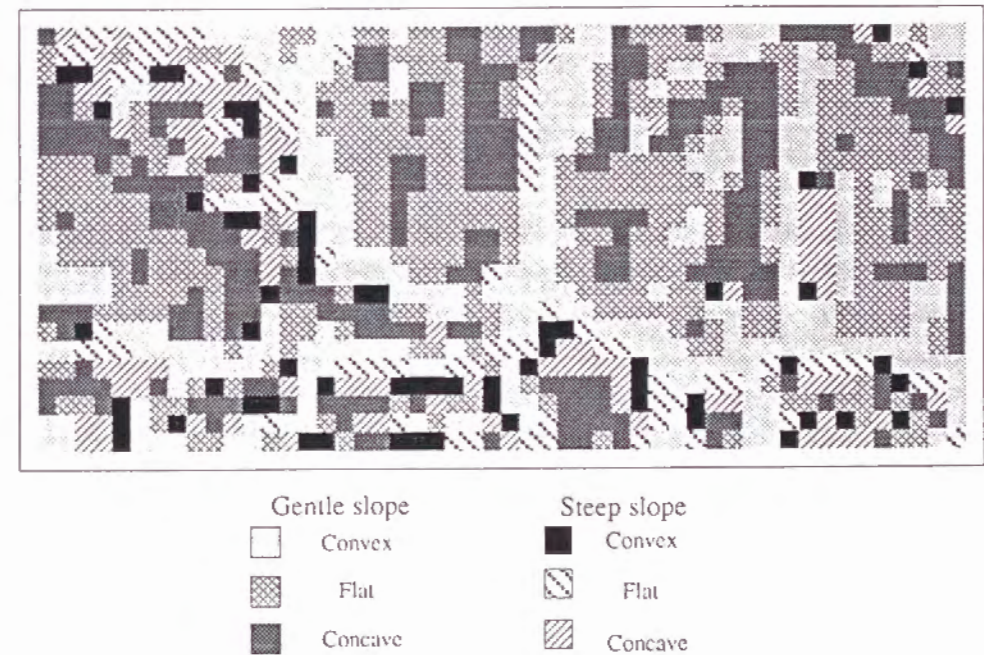


Fig. 4.4 Spatial distributions of topographic categories in the 52-ha plot (see text for topographic categories).

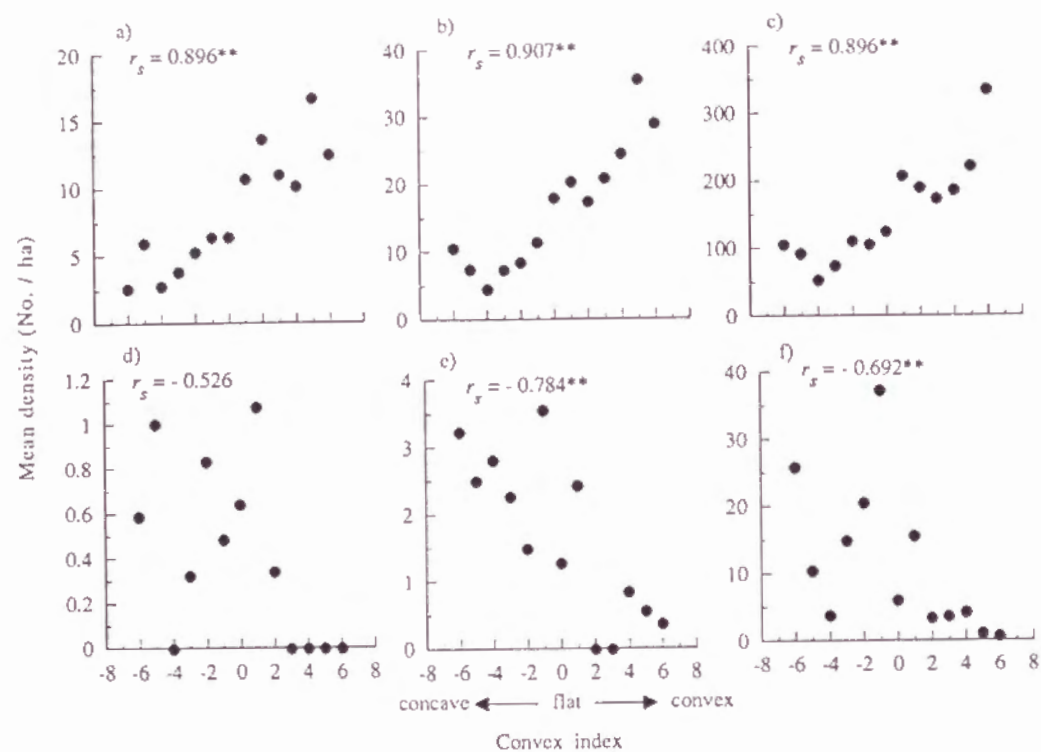


Fig. 5.5 Relationships between convex index (see text) and mean density of *Dryobalanops aromatica* (a: large trees, b: poles, c: saplings) and *D. lanceolata* (d: large trees, e: poles, f: saplings). r_s : Spearman's rank correlation (**: significant at $p < 0.01$).

Topography, however, may not be the only factor for determining their distributions. Hirai *et al.* (1995) found some differences in soil characteristics sampled from under *D. aromatica* and *D. lanceolata* trees on larger scales than in this study in the Lambir Hills. *Dryobalanops aromatica* were distributed only on upper slopes or ridges of sandy soils, while *D. lanceolata* were found in a variety of soil and topographic conditions, such as valleys of sandy or clay soils as well as ridges of heavy clay soils (Hirai *et al.* 1995, Matsumura 1994). They speculated that soil moisture condition was the most important soil factor which influenced the distributions of the two *Dryobalanops*. The restriction of *D. lanceolata* distribution on the southeast side of the plot (Fig. 4. 1) was probably because only that the area was covered by clay-rich soils, while the other part was mostly covered by sandy soils (Palmiotto 1995). It is likely that topography and soil, therefore, have an interactive effect on the distribution of the two *Dryobalanops*, and topography shows clear effects within the same soil type.

The results suggest that *D. aromatica* and *D. lanceolata* are coexisting in the study forests by occupying patches of different topography and/or soil, although the effects of soil

Table 4.3 Mean density of *Dryobalanops aromatica* and *Dryobalanops lanceolata* in quadrats (20 m x 20 m) of various topographic categories (see text for details) in a 52-ha plot. Figures in parenthesis are total number of trees found in each category. Large tree: dbh ≥ 30 cm; Pole: 5 cm \leq dbh $<$ 30 cm; Sapling: 1 cm \leq dbh $<$ 5 cm.

Topographic category	Area (ha)	Mean density (No. ha ⁻¹)				
		<i>Dryobalanops aromatica</i>		<i>Dryobalanops lanceolata</i>		
		Large tree	Pole	Sapling		
Gentle slope	Concave	4.4 (48)	7.3 (80)	0.6 (6)	2.7 (30)	17.2 (190)
	Flat	6.2 (91)	14.0 (202)	1.0 (14)	12.8 (41)	26.0 (377)
	Convex	13.9 (155)	24.7 (275)	0.1 (1)	0.3 (3)	2.3 (26)
Steep slope	Concave	2.6 (9)	8.9 (31)	0.3 (1)	0.9 (3)	1.4 (5)
	Flat	8.0 (21)	15.5 (41)	0 (0)	0.8 (2)	9.1 (24)
	Convex	8.5 (27)	24.4 (78)	0 (0)	1.25 (16)	8.75 (182)
Uncategorized	6	7.0 (42)	15.5 (93)	0.2 (1)	2.7 (16)	28.0 (182)
Total	52	7.6 (393)	15.4 (800)	0.4 (23)	1.9 (99)	16.0 (832)

and topography may have a complex interrelationship. This would allow their spatial patterns to be more or less stable on a local scale, and the highly heterogeneous topography and soil of the study forest (Yamakura *et al.* 1995a, Palmiotto 1995; see also Chapter 2) then takes an important role in maintaining their coexistence.

The segregated distributions of saplings and poles of *D. aromatica* to large trees (Table 4. 2) suggest that *D. aromatica* has some density-dependent or distance-dependent seeds or seedling mortality (Janzen 1970, Connell 1971) as is found in some tropical rain forest species (Augsburger 1983a, b, Clark & Clark 1984). The scale of juvenile inhibition (< 7.8 m x 7.8 m), however, seems too small to effectively maintain species richness in the local community, because the diameters of emergent trees in the forest were usually larger than 15 m. On a small scale (*ca.* < 1 ha), spatial distributions of the two species, especially those of juveniles, may be influenced more by reproductive features of each species such as fruiting frequency, seed dispersal, seedling establishment and growth of established juveniles (Whitmore 1984). The aggregated distributions of saplings and poles to large conspecific trees are probably caused by inadequate seed dispersal, which will be shown in the next chapter. Details of spatial distributions on the small scale will be discussed in the next chapter.

FACTORS INFLUENCING SMALL SCALE SPATIAL PATTERNS

INTRODUCTION

In the previous chapters I showed that *Dryobalanops aromatica* and *D. lanceolata* were distributed segregatedly in relation to topography and soils in the large scale of whole 52-ha plot in the study forest (Chapter 4), and that they predominated the main forest canopy in patches in the smaller scale (\approx 1 ha) (Chapter 3). The dominance of *Dryobalanops*, however, was not so extreme as other dominant species in tropical wet forests; the species diversity of the canopy trees in *Dryobalanops* dominant stands was comparable to that of non-dominant tropical rain forests in the same region (Chapter 3; see also Hart *et al.* 1989, Connell *et al.* 1989, Kachi *et al.* 1993, Richard 1954).

The aims of this chapter are 1) to compare the stand structure of the patches in which *D. aromatica* and *D. lanceolata* were predominant, 2) to estimate the regeneration process of the two species and 3) to estimate the factors influencing their regeneration and spatial patterns in this small scale. I established two 1.6-ha subplots where respective species were predominant in the 52-ha plot. The spatial relations between their juvenile distributions and four site factors (*i.e.* forest floor light condition, local tree density, total basal area and distance from mother tree) were analyzed within these subplots. Mechanisms of the intermediate canopy dominance by the two *Dryobalanops* are also discussed.

METHODS

Census of juvenile distributions

Inside the 52-ha plot mentioned in Chapter 3, two 1.6-ha subplots (100 m x 160 m) were chosen to include many *Dryobalanops* trees (Fig. 5.1). One plot (Plot L), which had many *D. lanceolata*, was on a gentle slope along a small creek. The other plot (Plot A), in which many *D. aromatica* appeared, included a wide ridge and the upper part of a steep slope.

Each subplot was divided into 640 quadrats (5 m x 5 m) by theodrite and compass. All trees larger than 1 cm DBH were counted and measured for the DBH in each quadrat. The number of trees less than 1 cm DBH were also counted for *Dryobalanops*. Individual trees of *Dryobalanops* were categorized into five groups according to the developmental stage and DBH, *i.e.* 1) seedling at the primary leaf stage (PLS): individuals which had primary leaves on the stem, 2) seedling: DBH < 1 cm, 3) sapling: 1 \leq DBH < 5 cm, 4) pole: 5 \leq DBH < 30 cm and 5) adult: DBH \geq 30 cm. These categories were chosen only for convenience, but the lower DBH limit of reproductive trees appeared to be approximately 30 cm for both species (A. Itoh *pers. observation*).

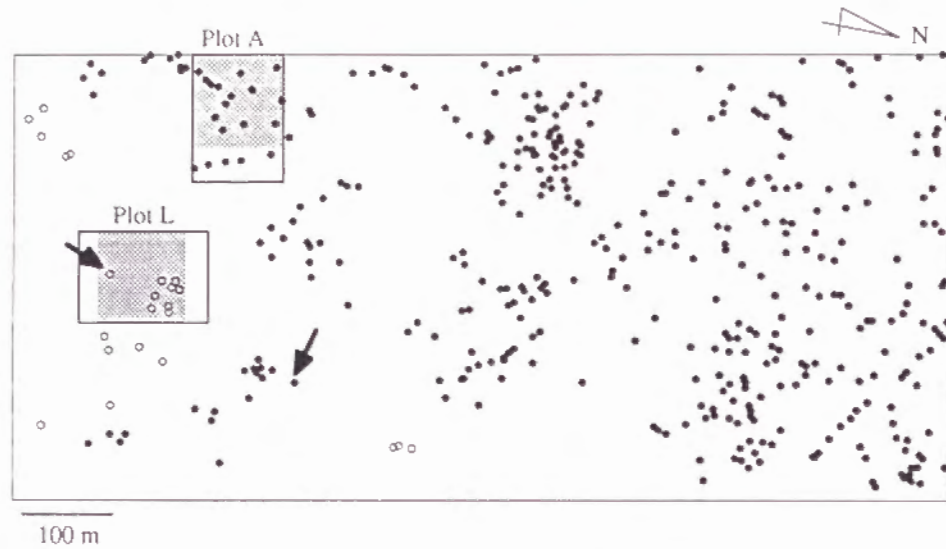


Fig. 5.1 Positions of Plot A and Plot L. Shaded areas represent plots for the analysis of the relationships between juvenile distributions and site factors (see text). Open and solid circles indicate large trees (≥ 30 cm DBH) of *Dryobalanops lanceolata* and *D. aromatica*, respectively. Arrows indicate the mother tree for the study of seed dispersal (see text).

Spatial pattern of forest floor light environment

Diffuse site factor (DSF) (Anderson 1964) was used for evaluation of the forest floor light environment. DSF indicates the average condition of a forest floor light environment very well (Whitmore *et al.* 1993). Hemispherical photographs were taken 50 cm above the ground at the center of each 5 m x 5 m quadrat with a fisheye lens (Nikon Fisheye Nikkor 8 mm). The photographs were taken in a 1.2-ha area of each 1.6-ha subplot (Fig. 5.1); a total of 960 photos were taken in September-October and November 1992 in Plot L and Plot A, respectively. The value of DSF was calculated by the manual method of Anderson (1964).

Distribution of newly established seedlings

To evaluate the seed dispersal patterns, the distribution of newly established seedlings around a solitary fruiting tree of each species was studied. The fruiting trees were at least 40 m apart from other fruiting conspecific trees (Fig. 5.1). A 80 m x 80 m plot was established around each mother tree, and the plot was divided into 5 m x 5 m quadrats ($N = 256$). The number of newly established seedlings in each quadrat was counted. The census was carried out in March 1991 (14 months after seed dispersal) and November 1992 (4 months after seed dispersal) for *D. aromatica* and for *D. lanceolata*, respectively. Since primary leaves attached on the seedlings for more than two years (see Chapter 6), newly established seedlings were easily distinguished from advanced seedlings by the presence or absence of their primary

leaves. Because the germination and mortality rates of seedlings did not correlate to the distance from the mother trees during the observation periods (see Chapter 6), the distribution patterns of newly established seedlings were assumed to be affected only by seed dispersal

Statistical analysis

To analyze the spatial pattern of the DSFs, a geostatistical techniques summarized as a set of semivariograms was used (Robertson 1987). The semivariogram is a plot of how the mean square deviation changes as a function of distance within the sampled area.

To evaluate the effects of site factors on the juvenile density, the multiple regression analysis was used. Dependent variables were the density of seedlings or saplings in each quadrat; four site factors were calculated for each quadrat as independent variables, *i.e.* 1) number of all trees larger than 1 cm in DBH, 2) total basal area of all trees larger than 1 cm in DBH, 3) DSF value at the center of the focal quadrat and 4) the distance from the nearest adult *Dryobalanops* tree to the center of the focal quadrat. The statistical analysis was conducted by SYSTAT (Wilkinson 1992).

RESULTS

Stand structure of each plot

The stem density in Plot A was two times denser than in Plot L; but the maximum DBH was much larger in Plot L (194 cm) than in Plot A (124 cm) (Fig. 5.2). The differences in the tree density and basal area (BA) were larger in the smaller size classes than in the larger size classes (Figs. 5.2 and 5.3); the total basal area was 12.5 m²/ha and 19.5 m²/ha for trees larger than 51 cm DBH, but 18.9 m²/ha and 42.3 m²/ha for smaller trees in Plot L and Plot A, respectively. These results indicated that Plot A was a very dense stand, especially with abundant small trees, but Plot L consisted of very large trees with relatively sparse small trees.

D. aromatica and *D. lanceolata* were the most abundant canopy species in each

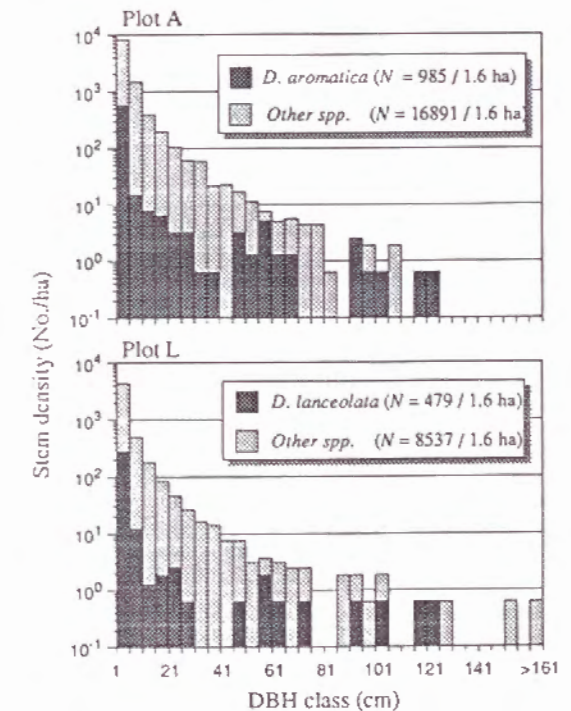


Fig. 5.2 DBH frequency distributions in Plot A and Plot L.

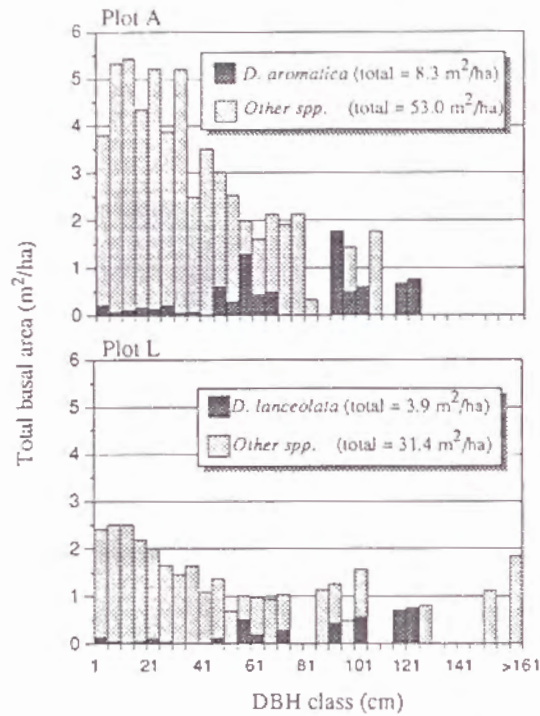


Fig. 5.3 Total basal area in various DBH classes in Plot A and Plot L.

regardless of the between-quadrate distance. Therefore, it was concluded that the DSFs were spatially patterned across the plots.

The contour maps of the DSF distribution supported the conclusion of the geostatistical analysis (Fig. 5.5). Plot L contained several large patches (*ca.* 300-400 m²) of strongly shaded forest floor (DSF < 1%). In Plot A, strongly shaded quadrats were mostly restricted to the northwestern side, where the slope was gentle; there was a large patch with very bright conditions (DSF > 5%) at the center, where a relatively new scar of a small land slide was observed. As a result, the forest floor was more shaded on average in Plot L (2.1% DSF) than in Plot A (2.6% DSF) (*t*-test, *p* < 0.001).

Distribution of new seedlings around mother tree

Newly established seedlings of *D. aromatica* and *D. lanceolata* showed similar distributions (Fig. 5.6). There was no correlation between seedling density and distance from the mother trees within 10 m of the mother trees. The density was more or less constant among the quadrats which were under the canopy of the mother trees. At a distance of more than 10 m from the mother trees, seedling density decreased rapidly with distance, and negative linear regressions were fitted well on a double logarithmic scale. No seedling was found in quadrats farther than 40 m from the mother trees.

plot; they occupied 19.5% and 17.3% of total basal area of trees larger than 31 cm DBH respectively (Figs. 5.2 and 5.3). There were abundant juveniles of both species including individuals smaller than 1 cm DBH (Fig. 5.7).

The between-quadrate autocorrelation in the DSFs was strongest in the scales < *ca.* 20 m in both species (Fig. 5.4). The correlation decreased with distance within this scale, but rather stable in the larger scales (*ca.* 20-100 m). These results indicate that the DSFs of quadrats apart < 20 m from each other were more similar than those of the quadrats farther apart, and that the difference in the DSFs of any pair of quadrats apart as far as 20-100 m was similarly predictable by the variance of the whole 1.2-ha area,

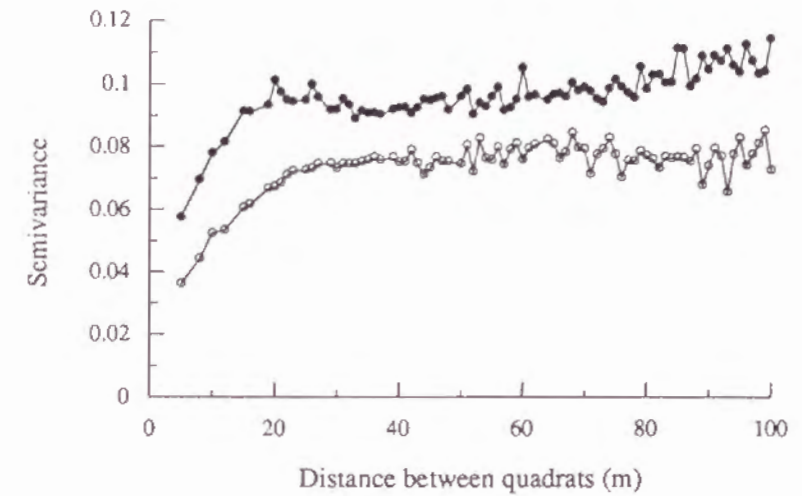


Fig. 5.4 Semivariograms of the diffuse site factors in Plot L (●) and Plot A (○).

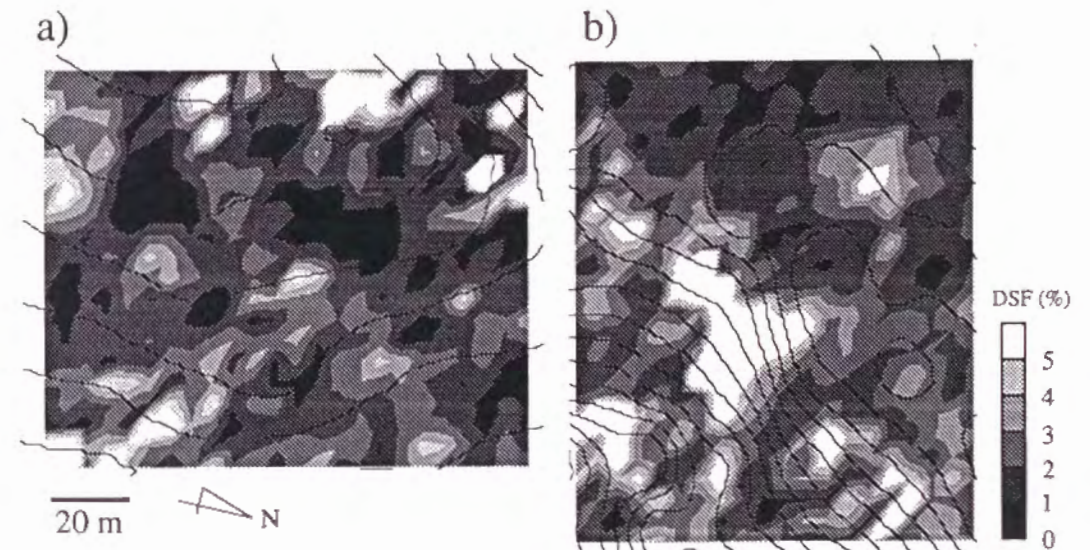


Fig. 5.5 Spatial distributions of forest floor light intensity (%DSF) in Plot L (a) and Plot A (b). Solid lines are topographic contours at 2 m intervals.

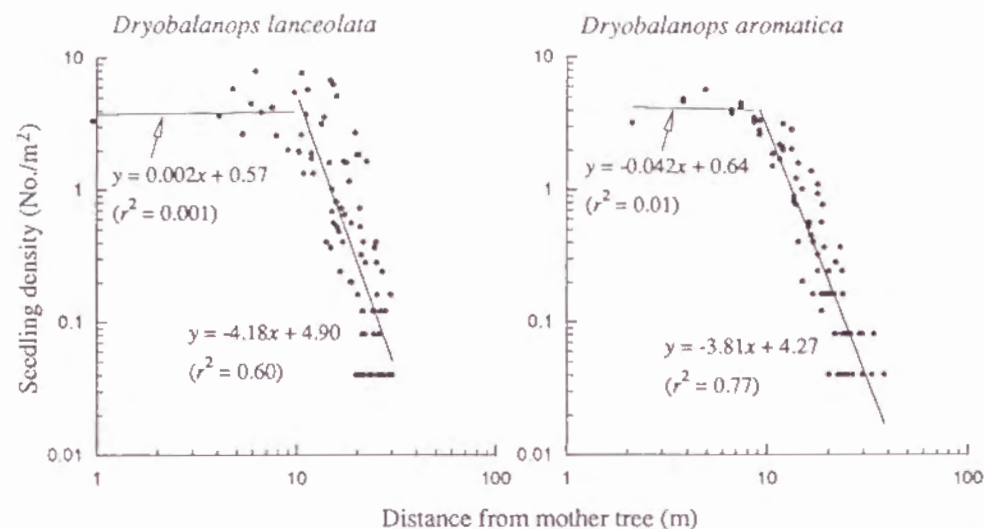


Fig. 5.6 Relations between the distance from the mother trees and density of newly established seedlings of *Dryobalanops lanceolata* (a) and *D. aromatica* (b). Solid lines are regression lines on a log-log scale for 0-10 m and > 10 m from mother trees, respectively.

Spatial pattern of juvenile distribution

In Plot L, PLSs were dense near the trees that had fruited within two years before the census (Fig. 5.7). Seedlings were abundant in any quadrat within 40 m from conspecific adults. The mean density of seedlings was highest within 5 m of the nearest conspecific adult, and decreased with distance (Fig. 5.8). By contrast, few saplings and poles were found under canopies of conspecific adults (Fig. 5.7). The mean density of saplings and poles had a peak of 15-20 m (Fig. 5.8). The peak of frequency shifted outward as the size increased; the peaks were at 5-10 m, 15-20 m and 15-25 m for seedlings, saplings and poles, respectively.

In Plot A, PLSs were not so abundant as those of *D. lanceolata* in Plot L (Fig. 5.7). They were not necessarily most abundant at the nearest quadrats to conspecific adults, though the mother trees were not identified. Seedlings were widely distributed all over the plot; the density was not highest at the nearest distance interval (< 5 m) but a distance of 5-10 m (Fig. 5.8). The distribution of saplings was more patchy; there were few saplings on the northwestern side of the plot, where the slope was gentle and the forest floor was strongly shaded (Fig. 5.6). The mean density of saplings decreased slightly with distance from the nearest conspecific adult; that of poles had a low peak at 15-20 m (Fig. 5.8). The peaks of frequency were 5-10 m for seedlings and saplings, and 10-15 m for poles.

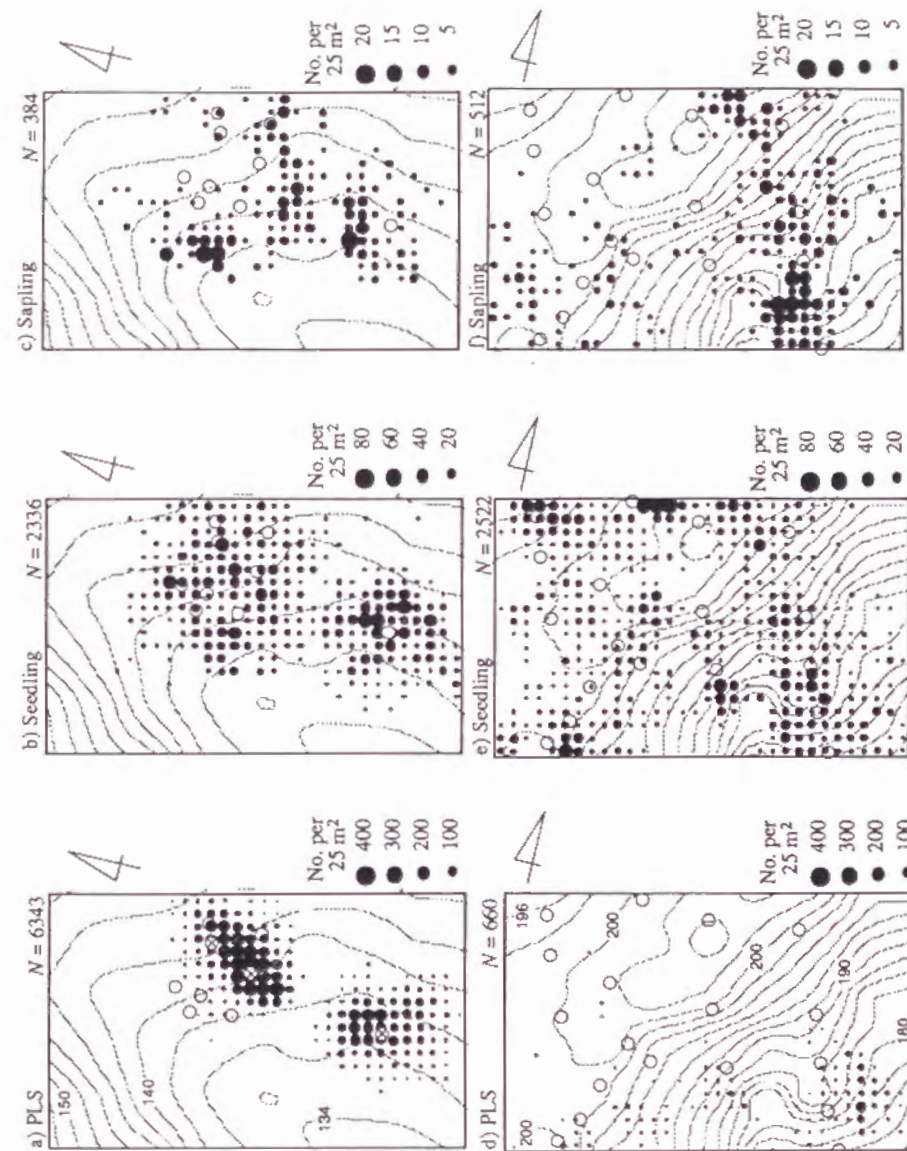


Fig. 5.7 Spatial distributions in the density of primary-leaf seedlings (PLS), seedlings (DBH < 1 cm) and saplings (15 < DBH < 5 cm) of *Dryobalanops lanceolata* (a-c) and *D. aromatica* (d-f). Dotted lines are topographic contours at 2 m intervals. O: adult *Dryobalanops* trees (DBH ≥ 30 cm); ○ in (a): trees fruited within two years before enumeration.

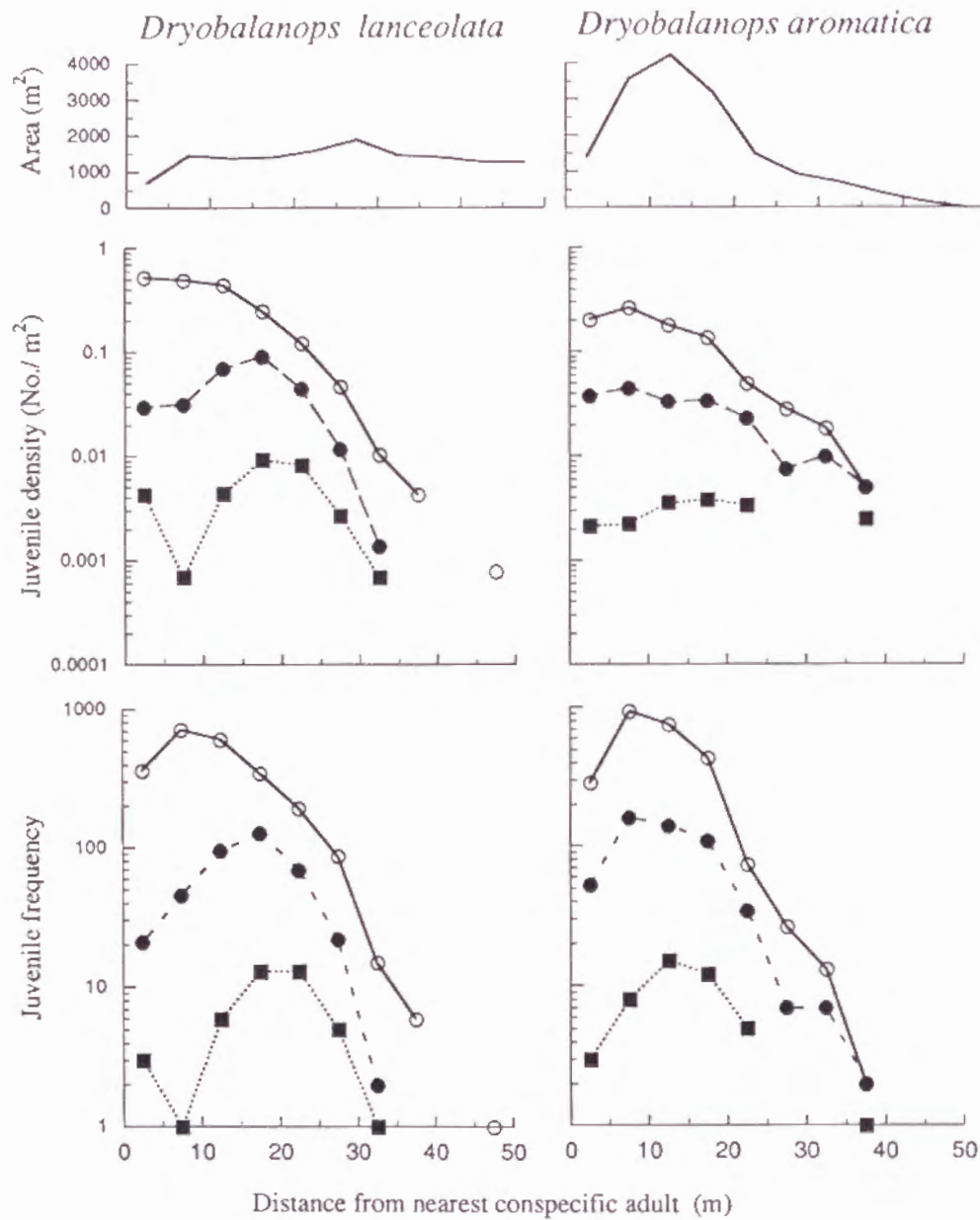


Fig. 5.8 Relations between the distance from the nearest conspecific adult and density or frequency of seedlings (○: DBH < 1 cm), saplings (●: 1 ≤ DBH < 5 cm) and poles (■: 5 ≤ DBH < 30 cm). The distance was categorized into 5-m intervals; each point was plotted at the middle of each 5-m interval. The upper figures show the total area (m²) of each distance interval in the 1.6-ha plot.

Relationship between juvenile distribution and site factors

Table 5.1 shows the results of a multiple regression analysis between seedling or sapling density pre quadrat and four site factors. The quadrats with more than 5% DSF were excluded from the analysis. This is because such quadrats often occurred in places which had recently been strongly disturbed by a land slide or a large tree fall, and included very few trees. BA and DSF were log-transformed, and NLT was root-transformed for normalization. The frequency distributions of all site factors were no different than the normal distribution in both plots after the transformation (F -test, $p > 0.1$).

The seedling density of *D. lanceolata* correlated significantly only to NLT (Table 5.1), implying that its spatial distribution was affected only by the positions of mother trees and the seed dispersal pattern (see Fig. 5.6). By contrast, the seedling density of *D. aromatica* correlated positively to DSF, and negatively to BA as well as to NLT. That is to say, its seedlings tended to be more dense at the quadrats with larger DSF up to 5% and smaller BA, if the distance from the nearest adult was the same. The density of saplings correlated positively to DN, and negatively to BA for both species. Since DN and BA positively correlated to each other in both plots ($r = 0.233$ and 0.254 , $p < 0.0001$), the opposite correlations to these site factors suggest a strong tendency for their saplings to have been distributed in the quadrats with higher DN and smaller BA. In other words, the quadrats with many small trees but no large trees. The effect of NLT on the sapling density was significant for *D. lanceolata* but

Table 5.1 Results of multiple regression analysis between *Dryobalanops* juvenile density and four site factors. PCC: partial correlation coefficient; MCC: multiple correlation coefficient. DN: density (No./ 25 m² quadrat) of trees ≥ 1 cm DBH; BA: total basal area (m²/ 25 m²) of trees ≥ 1 cm DBH; DSF: diffuse site factor (%) at the center of focal quadrat; NLT: distance (m) from the nearest adult *Dryobalanops* (DBH ≥ 30 cm) to the center of focal quadrat.

DBH class (cm)	PCC				MCC
	DN	BA	DSF	NLT	
<i>Dryobalanops aromatica</i>					
- 1*	-0.019	-0.202†	0.098*	-0.187†	0.272†
1 - 5	0.255†	-0.110*	0.041	-0.046	0.249†
<i>Dryobalanops lanceolata</i>					
- 1*	0.053	0.042	0.063	-0.570†	0.579†
1 - 5	0.369†	-0.108*	-0.028	-0.239†	0.405†

* excluding seedlings at the primary-leaf stage.

* significant at $p < 0.05$

† significant at $p < 0.001$

of suppressed juveniles, other species which can grow in more shaded conditions would be more competitive under canopies of large trees. *Dryobalanops* may not regenerate without large gaps, even though they have more seedlings awaiting under the forest canopy. Occurrence of proper size gaps may be infrequent for the two *Dryobalanops* to dominate the whole canopy in the study forest. To evaluate this hypothesis, it is necessary to study the gap regime of the study forest and the effects of gap formation on regeneration of many co-occurring canopy species.

SEEDLING DYNAMICS

INTRODUCTION

Tropical rain forests of West Malesia are dominated by various species of Dipterocarpaceae in a sympatric manner (Ashton 1982, Whitmore 1989). Previous studies have shown that many dipterocarps share general features in their regeneration processes (reviewed in Ashton 1982, 1988, 1989, Whitmore 1984, 1989). However, there have been only a few quantitative field studies on the seedling demography at the species level (Burgess 1969, Fox 1973, Turner 1990).

Species-specific differences in regeneration processes, or differences in regeneration niche, are one of the important mechanisms for maintaining species richness in tropical rain forests (Grubb 1977). Even a number of tree species which share the same ecological requirement at maturity could coexist if they have different requirements at their juvenile stages. Another possible mechanism promoting the tree diversity is the escape hypothesis (Janzen 1970, Connell 1971). Remarkably high mortality of seeds or seedlings near mother trees, where the seed and seedling densities are mostly high, prohibits a certain species from dominating the forest, thus promoting the species diversity. Such distance- and density-dependent seed or seedling mortality has been found in some neotropical tree species (e.g. Augspurger 1983a, b, 1984, Augspurger & Kelly 1984, Clark & Clark 1984), however few studies have been conducted in Malesian rain forests (Chan 1980). To understand the high diversity of dipterocarps in the forests of west Malesia, further studies on seedling dynamics at the species level are necessary.

The analysis of population structures of *Dryobalanops aroamtica* and *D. lanceolata* in the study site (Chapters 3, 4 and 5) suggested the importance of seedling banks for their regeneration and maintenance of their populations. Therefore, it is necessary to clarify the seedling dynamics of the two species in the natural conditions to understand the regeneration processes and the mechanisms of their coexistence. In this chapter, their seedling survivorship and growth were studied for 2.5 years after mass fruiting. Two other dipterocarp species, *Dipterocarpus actangulus* Vesque and *Dipterocarpus globosus* Vesque, were also studied by the same methods in order to make the features of *Dryobalanops* as a genus more clear. The subject of this chapter is to analyze (1) quantitative differences in seedling mortality and the mortality factors among the four species to evaluate their regeneration niche divergence and (2) the effects of distance from mother trees and initial density on the mortality of seeds and seedlings to test the escape hypothesis. I also discuss the relationships between the obtained features of seedling demography and the population structures of each species in the study forest.

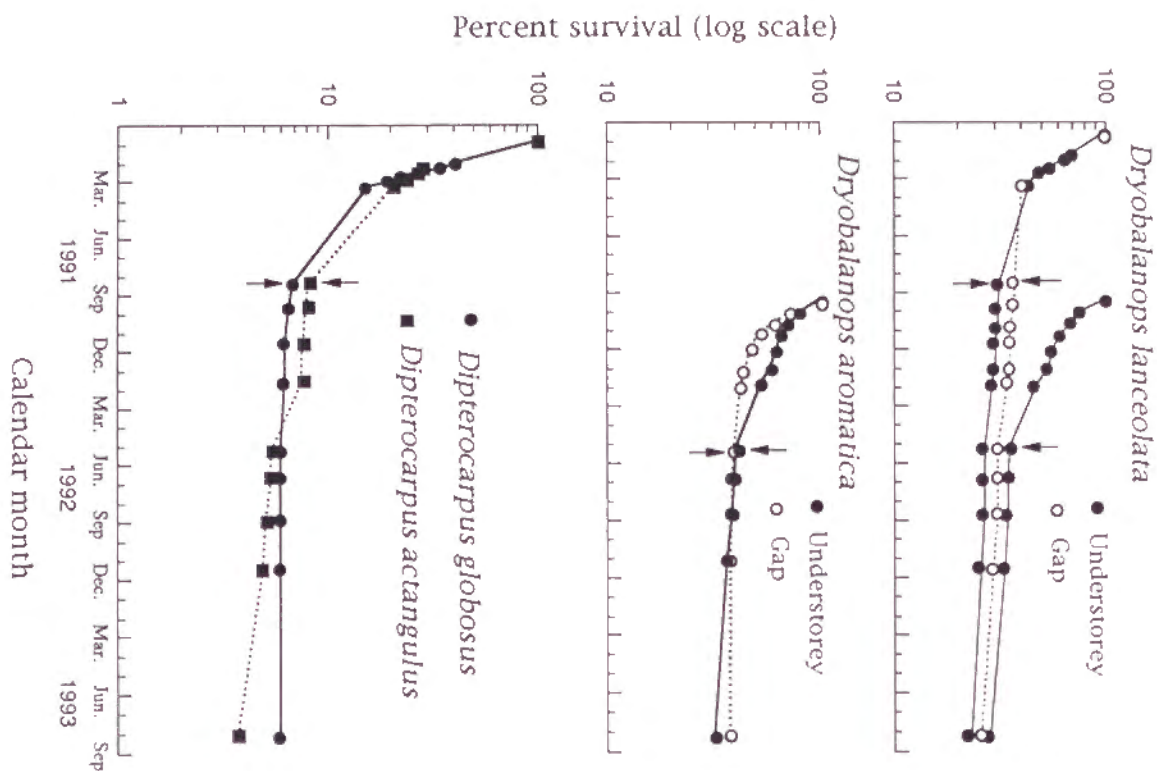


Fig. 6.2. Survivorship of four dipterocarps in a mixed dipterocarp forest of Sarawak, east Malaysia. Survival is indicated by the proportion of living seeds or seedlings to the total number of initially marked mature seeds. Sample sizes are the same as in Table 6.3. Arrows indicate the census dates when all living seedlings had shed the cotyledons.

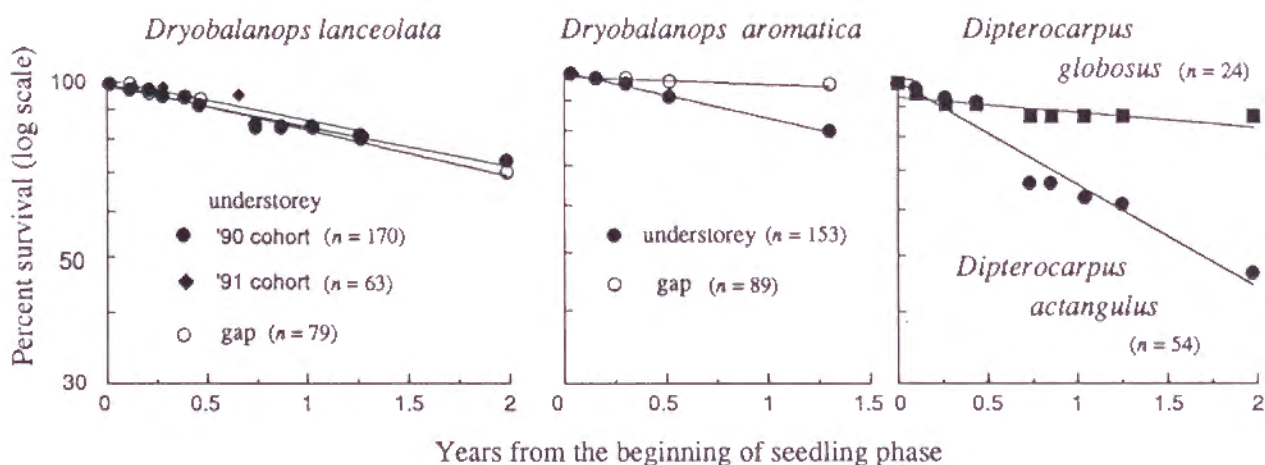


Fig. 6.3. Survivorship of seedlings of four dipterocarps during the seedling phase (see text for the definition of the phase). n = initial number of seedlings. Solid lines indicate calculated linear regressions in a semi-logarithmic scale: *Dry. lanceolata* : (●) $y = -0.071x + 2.0$, $r^2 = 0.969$; (◆) $y = -0.075x + 2.0$, $r^2 = 0.952$; (○) $y = -0.082x + 2.0$, $r^2 = 0.972$; *Dry. aromatica* : (●) $y = -0.083x + 2.0$, $r^2 = 0.996$; (○) $y = -0.017x + 2.0$, $r^2 = 0.891$; *Dip. actangulus*: $y = -0.181x + 2.0$, $r^2 = 0.948$; *Dip. globosus*: $y = -0.026x + 2.0$, $r^2 = 0.612$.

Growth of seedlings

Seedlings of the four species grew little in the understory after the initial rapid growth when they used the reserve stored in the seed (Fig. 6.5). In the gaps, leaf production of the two *Dryobalanops* was continuous, and about three times better than that at the understory at the last census. At the beginning, *Dryobalanops* seedlings in the gaps were significantly smaller in height than those in the understory. They caught up and surpassed the understory seedlings afterwards.

Only a few leaves were lost during the study period (*Dry. lanceolata* in understory: 1.2 (mean) ± 0.12 (S.E.) leaves/seedling, *Dry. lanceolata* in gap: 2.7 ± 0.35 , *Dry. aromatica* in understory: 0.3 ± 0.06 , *Dry. aromatica* in gap, 0.9 ± 0.20 , *Dip. globosus*: 1.5 ± 0.26 , *Dip. actangulus*: 1.0 ± 0.18). Main leaf mortality factors were physical damage by limb or litter fall and herbivory by insects. The majority of primary leaves were still attached at the last census regardless of species and sites, suggesting a longer leaf life span than two years.

For all species, the mean number of produced leaves by the seedlings which were alive at the time of the last census was positively correlated to the diffuse site factor of the quadrats where they had grown (Fig. 6.6).

DISCUSSION

Seed and seedling dynamics of the four dipterocarp species were quantitatively different even within the pairs of congeneric species, whose juvenile morphology appears very similar. This result suggests that they have diverged in their regeneration niches and that these differences may affect the structure of the seedling community in the study forest.

Relations of seedling dynamics to seedling populations

The most interesting finding of this study is that the observed seed and seedling dynamics are consistent with the seedling population densities of the four species in the study forest. *Dip. actangulus*, which had the lowest seedling population density among these species, showed the lowest germination rate, low survival during the cotyledon phase, and the highest mortality rate during the seedling phase. The highest seedling population densities of *Dry. aromatica* and *Dry. lanceolata* are consistent with the higher germination rates and the relatively low seedling phase mortality in the understory. The intermediate seedling population density of *Dip. globosus* is also consistent with the comparatively low germination rate and the lowest seedling phase mortality, which may compensate the low germination.

The difference in the seedling phase mortalities of *Dry. aromatica* and *Dry. lanceolata* is also consistent with the observed spatial patterns of their seedlings in the forest. The local

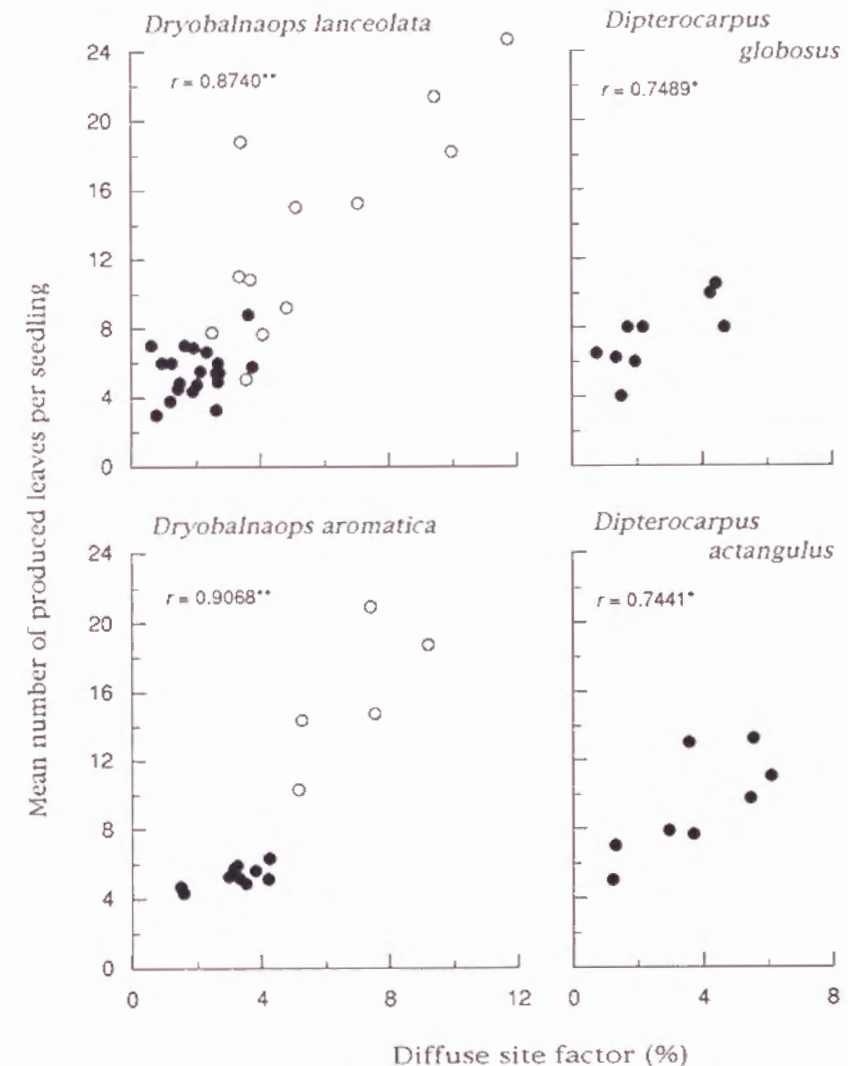


Fig. 6.6. Relationships between the mean total leaf production and diffuse site factor of each quadrat for seedlings of four dipterocarps. Leaf production was the mean value of total number of produced leaves during a 32-month period (22-month for *Dry. aromatica*) by the seedlings that were alive at the last census. Filled circles are quadrats in understory. Open circles are quadrats in gaps. Correlation coefficients (r) were calculated from pooled data of understory and gap for two *Dryobalanops*. Significance level: * $p < 0.05$; ** $p < 0.01$.

density of seedling population of *Dry. lanceolata* correlated significantly only to the distance from adult trees, while that of *Dry. aromatica* had a positive correlation to the light intensity of the forest floor as well (Chapter 5). These situations probably reflect the different and indifferent seedling phase survival between the understorey and the gap for *Dry. aromatica* and *Dry. lanceolata*, respectively. The initial spatial pattern of established seedlings, which is positively correlated to the distance from the fruited adult trees (Chapter 5), would be maintained for a long period in *Dry. lanceolata*; in *Dry. aromatica*, however, it would be changed gradually depending on the light conditions which are affected by the occurrence of gaps. More dense seedling populations of *Dry. aromatica* would then be found in less shaded places.

Effects of predation on seedling dynamics

During the period from germination until all seedlings had shed the cotyledons (cotyledon phase), seedling survival was largely influenced by various kinds of predation. The germination rates were probably determined mostly by the predispersal seed predation (Tables 6.2 and 6.3). Some of the dispersed seeds may have been damaged by vertebrates on the forest floor before they germinated (Fig 6.1). For germinated seeds, predation by insects and vertebrates was an important mortality factor in all species studied, though large proportions of mortality factors were unidentified (Fig. 6.4). As is mentioned in Chapter 8, root predation in the litter and soil, which was not checked in this study, was the major mortality factor of *Dry. aromatica* and *Dry. lanceolata* during the period from germination to primary leaf production. Thus considerable number of seedlings which died from unidentified factors were probably killed by root predation, at least for the two *Dryobalanops*. The survivorship at this phase, therefore, was affected not only by one specific type of predation but by various kinds of predation.

Moreover, the relative importance of each predation was not the same among the four species; for example, predispersal predation rates were lower in *Dip. globosus* and possibly in *Dip. actangulus*, which had the lowest germination rate, than in the two *Dryobalanops*. Therefore, differences in density and activity of each predator may affect the cotyledon phase survival of these species differently.

The density of mammals in the study forest was lower than other lowland rain forests in Malaysia possibly due to hunting pressure, as well as the rarity of fruit trees which vertebrates favor, such as *Ficus spp.* (Watson 1985). The relatively low predation rates (9-17%) by vertebrates found in the two *Dryobalanops* were likely due to this low mammal density. In the Malay Peninsular, about 90% of *Dry. aromatica* seeds were damaged by rodents on the forest floor of a plantation (Kachi *et al.* 1993). Many *Dry. lanceolata* seeds were also observed being eaten by wild pigs in East Kalimantan (Y. Okimori, personal communication).

Under this low vertebrate predation, the two *Dryobalanops* should have an advantage over the *Dipterocarpus* in terms of seedling establishment because the probability of establishment largely depends on the predispersal predation rates, which were lower in the two *Dryobalanops* (Table 6.2). Under a higher vertebrate density, hence severe vertebrate predation, however, more *Dryobalanops* seeds would be damaged by vertebrates before they are established, even though they can escape from predispersal predation. On the other hand, establishment of the two *Dipterocarpus* may be less affected because a majority of the seeds which would be eaten by vertebrates may have already been damaged by insects if the vertebrates consume dispersed seeds regardless whether the seeds have been infected with insects or not. Thus, the advantage of the two *Dryobalanops* over the two *Dipterocarpus* may be lessened under severe vertebrate predation. Dirzo & Miranda (1991) pointed out the possibility that differences in herbivorous vertebrate density affect the structure and diversity of understorey vegetation in Mexican rain forests.

Density- and distance-effect on seedling mortality

Density- and distance-dependent mortality was not observed in any of the four species under the conditions examined (< 20 m from the mother trees and without canopy gaps). This is not surprising for the seedling phase because the major mortality factors were fallen branches and water stress, both of which may correlate little to the distance from the mother trees and the initial density. The interesting fact is, for mortality at the seedling phase, neither showed significant correlation in spite of the importance of predation at this phase. This suggests that the predators did not act density- nor distance-dependently, which is hypothesized in the Janzen-Connell model (Connell 1971, Janzen 1970). Chan (1980) also failed to find significant correlations between the seed/seedling survival and the distance from the mother tree nor the initial density for *Shorea leprosula* in Peninsular Malaysia.

By contrast, the spatial patterns of seedling mortality, hence seedling distributions, are likely to be influenced by the occurrence of gaps. The activity of the predators appeared to be promoted in gaps (Fig. 6.1, Shupp 1989), but the seedling phase mortality of *Dry. aromatica* was lower in the gap. The positive correlations between seedling growth and light intensity (Fig. 6.6) also suggest the importance of forest floor light environment for seedling growth, which is largely dependent on the positions of gaps. The degree of the gap influence, however, may differ among the four species. For example, the gap affected the mortality at the seedling phase for *Dry. aromatica* but not for *Dry. lanceolata*. In this study, I cannot discuss the influence of gaps for the two *Dipterocarpus* because none of their seedlings was studied in gaps. Further information about the mortality and growth of seedlings of the two *Dipterocarpus* in gaps are required.

In conclusion, though the four dipterocarp species shared general features in seedling

demography and growth, these features were quantitatively different among the species. These results suggest that they have diverged in their regeneration niches, however the differences were larger between species of different genus than those within the same genus. It is interesting to note that *Dry. aromatica* and *Dry. lanceolata* showed more or less similar features in seedling dynamics in spite of the large differences in the environments where they were distributed (Chapter 5). These results suggest that their similar performance in seedling dynamics may be the results of different responses to the environment. Experimental studies, in which environmental factors are controlled, are required to understand the physiological and ecological differences of the two *Dryobalanops*, and to clarify the mechanisms of the segregated distributions.

SEEDLING GROWTH RESPONSE TO DIFFERENT LIGHT INTENSITIES

INTRODUCTION

It was shown in Chapters 5 and 6 that seedlings of *Dryobalanops aromatica* and *D. lanceolata* did not grow well under the deep shade of the forest floors, and gap formation was required for release of the suppressed seedlings to become large trees. The light level for the release is often different among various dipterocarp species, thus the suitable gap size for regeneration appears to be different (Mori 1980, Sasaki & Mori 1981, Nicholson 1960, Turner 1989, 1990a, b).

Differentiation of optimum light conditions for regeneration among species results in different distributions and relative frequency of the species under various regimes of gap formation (cf. Brokaw & Sheiner 1989, Denslow 1980a,b, 1984, Denslow *et al.* 1990). A species that needs a large gap may be more prevalent in a forest where large gaps are often produced, however less frequent or even non-existent in a forest where only small gaps occur.

The stands on sandy ridges, where *D. aromatica* was distributed, and those in clayey valleys, in which *D. lanceolata* was grown, showed different spatial patterns of forest floor light environment in the study site (Chapter 5). Ashton & Hall (1992) suggested that the spatial pattern and size of gap formation in the two stands were remarkably different. These spatial and temporal differences in light conditions may affect the distributions and population structures of the two *Dryobalanops*, if there is a remarkable difference between the two species in the optimum light conditions for regeneration.

The aims of this chapter are: 1) to compare the seedling growth responses of the two *Dryobalanops* in different light intensities by a shading experiment and 2) to discuss the effects of the different gap regimes on regeneration and distributions of the two species.

METHODS

Shading experiment Mature seeds of the two *Dryobalanops* were collected from under the canopy of a mother tree of each species during the 1991 fruiting period (late September) in the study forest. Seed dry weight was not significantly different between the species (*t*-test, $p > 0.1$, $N = 20$ per species). Six conspecific seeds were sown in a cylindrical pot (34 cm diameter and 20 cm deep) filled with peat soil and forest top soil after their wings were detached. Four pots (two for each species) were placed at the center of every four shading chambers (1 m x 1 m x 80 cm height) and outside of the chambers ('open treatment'). The

positions of pots were randomized several times at irregular intervals (1-3 weeks) within each treatment. The chambers were covered with black nylon mesh-cloth, and the inside light intensity were controlled by changing the number of cloths and/or the mesh size to ca. 7%, 11%, 27% and 48% relative light intensity (RLI) respectively. The RLI was calculated from the simultaneous measurement by a pair of photometers (Minolta T-1H) at 30 min. intervals inside and outside of each chamber from 0700h to 1800h on 14 January 1992, a fine but occasionally cloudy day (Fig. 7.1b). There were no differences in air temperature among the chambers, but the temperature in the open was higher than that in the chambers (Fig. 7.1a).

The shading experiment was conducted at the ground of our field house in Miri city, ca. 20 km north of Lambir, from 23 September 1991 to 22 January 1992 (a 4-month period). The pots were well watered two times every day, 0800h and 1600h, throughout the experiment, except for rainy days. Height, diameter at the base of cotyledons, number of branches and number of produced and lost leaves were measured monthly for all living seedlings. The seedlings were harvested at the end of the experiment. All the leaves were photocopied to transparent plastic sheets individually, and the leaf area was measured by an automatic area meter from the sheets. The seedlings were divided into leaf, stem (including branches) and root fractions, dried at 80°C for 48 hours and then weighed.

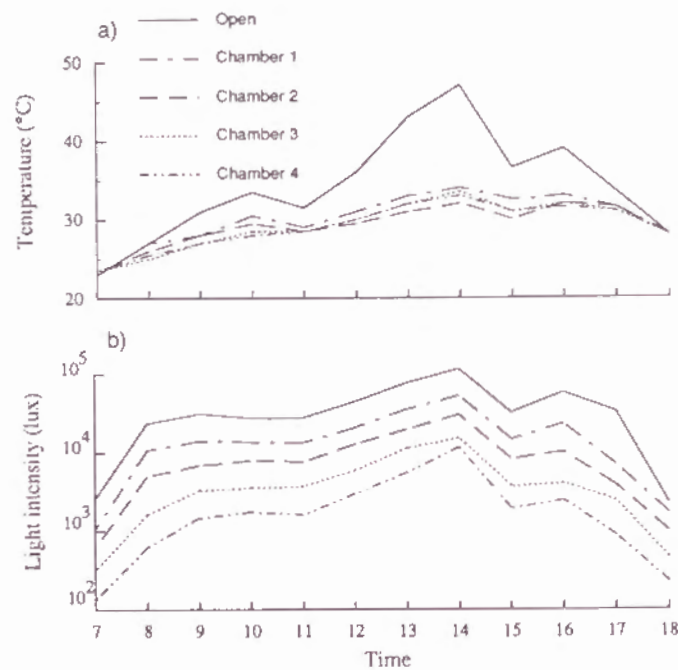


Fig. 7.1 Daily changes in temperature (a) and light intensity (b) in shading chambers on 14 January 1992.

Data analysis

The results were analyzed by a two-way analysis of variance (ANOVA) with shading and species as the two factors using SYSTAT (Wilkinson 1992). Eight largest seedlings in each treatment were used for the statistical analysis because several individuals (1-4 in each treatment) had died or grown poorly at the end of the experiment.

The optimum growth model proposed by Hozumi *et al.* (1960) was applied for quantitative analysis of the relationships between the mean part or total weight and RLI. They formulated the effect of 'optimum factor' on plant growth as

$$\frac{1}{w} = \frac{A_1}{f} + A_2 f + B \quad (7.1)$$

where w is mean weight, f is the amount of factor (RLI(%) in this study) and A_1 , A_2 , and B are coefficients specific to the period of growth. Equation (7.1) gives an optimum curve with maximum values of w (w_{max}) at an optimum level of f (f_{opt}). The values of f_{opt} and w_{max} are respectively given by

$$f_{opt} = \sqrt{\frac{A_1}{A_2}} \quad (7.2)$$

and

$$w_{max} = \frac{1}{2\sqrt{A_1 A_2} + B} \quad (7.3)$$

Coefficients of Eq (7.1) were determined by a linear least squares method using a computer program written by T. Yamakura in BASIC.

RESULTS

The results were summarized in Tables 7.1 and 7.2. Shading had a highly significant effect on all growth parameters measured. All parameters except mean height were significantly different between the two species. *Dryobalanops lanceolata* grew better than *D. aromatica* in any treatment. The interaction effect of shading and species was significant for growth of above ground parts (*e.g.* leaf weight, stem weight, leaf area), but not significant for root weight and morphological parameters (*e.g.* leaf size, T/R ratio, leaf weight ratio, specific leaf area). This suggests the two species responded differently to changes of RLI only in the growth of above ground parts.

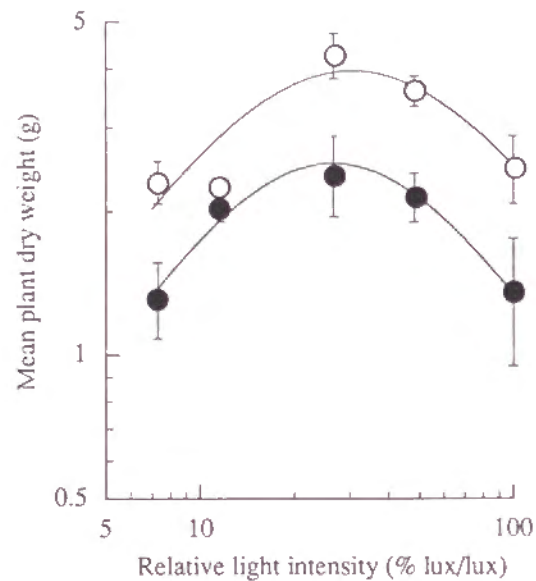


Fig. 7.2 Relationships between relative light intensity and seedling dry weight of *Dryobalanops aromatica* (●) and *D. lanceolata* (○). Vertical bars indicate standard errors. Solid lines are estimated optimum curves formulated by Eq (7.1), of which coefficients are shown in Table 7.3.

more rapid increase and decrease around the optimum values of RLI, hence a more sensitive response to changes of RLI in the above ground growth. The significant interaction effects found in above ground parts (Table 7.2) were probably due to this species-specific response to change of RLI.

Morphological features of the two seedling species were significantly different, though their responses to changes of RLI were similar. The higher values of leaf number, leaf size, T/R ratio, leaf weight ratio and SLA for *D. lanceolata* (Table 7.2) indicate that seedlings of *D. lanceolata* produced more, larger and thinner leaves than did *D. aromatica*. T/R ratio and leaf weight ratio decreased with RLI in both species, suggesting more photosynthetic substances were allocated to root in brighter conditions. Specific leaf area of both species also decreased with RLI.

The relationships between height and total dry weight of the two seedling species were significantly different, however the difference in those between diameter and weight were insignificant ($F = 0.003$, $df = 1,76$, $p = 0.956$) (Fig. 7.4). The significantly smaller slope ($F = 8.89$, $df = 1,76$, $p = 0.004$) of the regression line in the height-weight relation of *D. aromatica* (Fig. 7.4a) suggests that *D. aromatica* promoted more height growth than did *D. lanceolata*

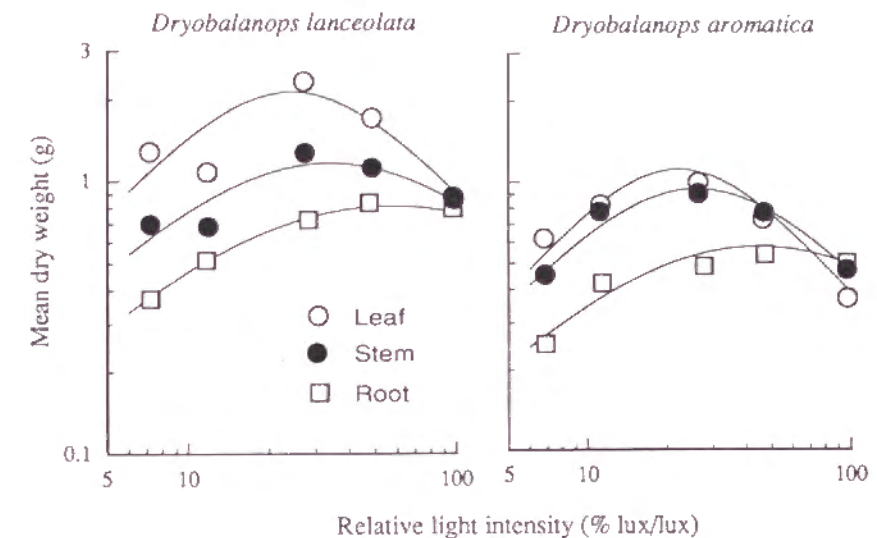


Fig. 7.3 Relationships between relative light intensity and leaf, stem or root weight of *Dryobalanops aromatica* and *D. lanceolata* seedlings. Solid lines are estimated optimum curves formulated by Eq (7.1), of which coefficients are shown in Table 7.3.

under suitable light conditions.

The mean weights of shoot and root did not show a linear relationship on a double logarithmic scale (Fig. 7.5), which is expected from the simple hypothesis of relative growth of the two parts. In more shaded conditions than the optimum RLI (f_{opt}), the relationship was estimated to be more or less linear for both species. However, in brighter conditions, the root weight was kept at a constant level, though the total seedling weight decreased with RLI (Fig. 7.2). The shoot weight therefore decreased rapidly with RLI, resulting in a line bent around f_{opt} .

DISCUSSION

The optimum seedling growth under partial shade, as found in this experiment, has also been reported in some other shade tolerant tropical rain forest species (e.g. Ashton & de Zoya 1989, Chazdon & Pearcy 1986, Nicholson 1960, Mori 1980, Sasaki & Mori 1981). The previously reported optimum light conditions, however, were mostly brighter than those found in *D. aromatica* and *D. lanceolata* seedlings in this experiment. Even the optimum

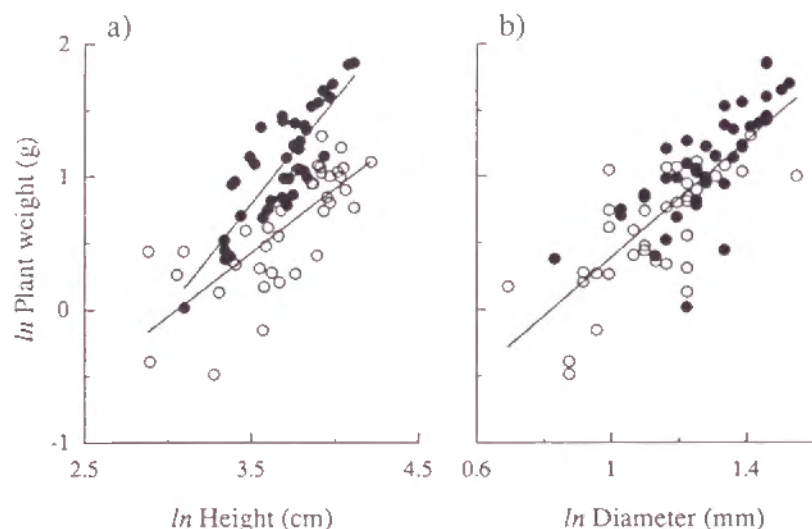


Fig. 7.4 Relationships between seedling weight and (a) height or (b) diameter of *Dryobalanops aromatica* (○) and *D. lanceolata* (●). Solid lines are linear regression lines on a double logarithmic scale. Data of both species were pooled in height for the calculation of the regression line due to no significant interspecific differences.

light conditions for *D. aromatica* (27% RLI) and *D. lanceolata* (31% RLI) may be just comparable to, or rather brighter than those found at the center of a medium size gap in natural tropical rain forests (cf. Chazdon 1986, Chazdon & Fetcher 1984, Oberbauer *et al.* 1988, 1989, Raich 1989, Smith *et al.* 1992, Whitmore *et al.* 1993, see also Chapter 4). Therefore, light levels may rarely be excessive on the forest floors for *D. aromatica* and *D. lanceolata* seedlings, except in extraordinarily large gaps produced by landslides or logging. The species-specific responses within lower light levels are probably more meaningful than the optimum light levels in considering their ecological features at the seedling phase. However, since light level increases rapidly with height from the ground (Kira & Yoda 1989, Smith *et al.* 1992, Yoda 1974), growth responses to brighter light levels may also be important for the growth of larger individuals or saplings.

The most remarkable difference in responses to RLI was the promoted height growth of *D. aromatica*, especially under suitable conditions. Similar differences were observed in two-year seedlings which had grown under the closed canopy and in small gaps of the Lambir forests (A. Itoh unpublished data; see also Fig. 6.5). This difference may indicate the different strategies of the two *Dryobalanops* to the different gap regimes found in each distribution stand.

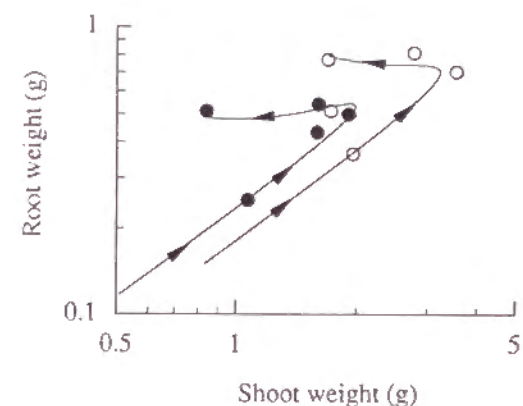


Fig. 7.5 Relationships between mean shoot and root weight of *Dryobalanops aromatica* (●) and *D. lanceolata* (○) seedling grown under various light intensities. Solid lines are expected relations from the calculated optimum curves of Eq (7.1) for each part weight. Arrows indicate the direction of increasing light intensity.

Kohyama (1987) hypothesized two strategies for sapling growth under the shaded forest floors based on the differentiations of allometrical relations in shade-tolerant saplings. Saplings of the species that favored height growth rather than expansion of assimilative area were 'optimists', who would win between-sapling competition as soon as light conditions improved. In contrast, the species which expanded their leaves in a wider area with well-developed lateral branches were 'pessimistic' about the early formation of a gap, and rather suitable for survival on the dark forest floor. *D. aromatica* might therefore have some advantage over *D. lanceolata* in the forests with more frequent gap formations, while *D. lanceolata* might be more suitable for the forests with highly shaded forest floors and less frequent gap formations.

Ashton & Hall (1992) speculated that gap regimes were different in the forests on the sandy hills and on the clayey soils of the Lambir Hills. On the sandy dip slopes, most trees appeared to die standing, gradually losing their leaves and limbs, and thus small gaps may have been produced at an even rate. On the gentle clayey slopes, however, wind-throw may have been a major cause of canopy tree mortality, resulting in larger gaps. Although the overall frequency of gap formation in each stand is not clear, it is likely that the gap formation is more frequent and predictable on the sandy parts, and unpredictable but with a larger gap on the clayey parts. It is suggested therefore that *D. aromatica* and *D. lanceolata* are superior in terms of seedling growth strategy to each other under the gap regimes of the presently distributing stands.

It is interesting to note that *D. lanceolata* grew better than *D. aromatica* in any light

condition used in the experiment. The growth conditions used in the experiment, except light intensity (e.g. enough soil water and relatively high contents of soil nutrients), were similar to environments of clay-rich valleys of the study site, where *D. lanceolata* was distributed. *D. lanceolata* may, therefore, be superior to *D. aromatica* in terms of early seedling growth in such an environment regardless of light conditions. The differences in spatial and temporal patterns of forest floor light conditions, which were found between sandy ridges and clayey valleys, may not be able to explain the mechanisms of segregated distributions of *D. aromatica* and *D. lanceolata*, at least from the view point of seedling growth. Other environmental factors than light may be more important. Does *D. aromatica* grow better in poor nutrient soils and/or under deficit of water, which are the characteristics of the sandy ridge environment? We need more experiments controlling other environmental factors. It is essential to know the performance of their seedlings under various soil water and nutrient conditions.

EFFECTS OF FOREST FLOOR ENVIRONMENT ON GERMINATION AND SEEDLING ESTABLISHMENT

INTRODUCTION

A number of authors have reported species-specific correlations between canopy tree distributions and topography and soils in tropical rain forests (e.g. Ashton 1969, Austin *et al.* 1972, Baillie *et al.* 1987, Lescure & Boulet 1985, Rogstad 1990). The distributions of *D. aromatica* and *D. lanceolata* also showed significant correlations with topography and soils in the Lambir Hills (Chapter 3). These relations suggest that there is niche divergence among the species and that their distributions are determined at least partly by the physical environment. However, from such relationships only, the mechanisms which control the spatial distribution of these species cannot be clarified. Experimental studies are indispensable for understanding of the mechanisms (Grub 1989, Silvertown 1987).

The field study on the seedling dynamics (Chapter 6) and the shade experiment (Chapter 7) failed to find the mechanisms of their segregated distributions. They showed quite similar features in seedling dynamics despite the differences in environmental conditions of their natural habitats (Chapter 4). Further experimental studies are required to evaluate the effects of environment on their regeneration, and to understand its mechanisms. In this chapter, a transplant experiment was conducted using the seeds of *D. aromatica* and *D. lanceolata*. The effects of forest floor environment such as litter accumulation, soil conditions and light intensity on the different seedling species were studied.

In order to clarify the effects of environment on survivorship and growth of tropical rain forest seedlings, numerous transplant experiments have been conducted using seedlings grown in green houses (e.g. Augspurger 1984a, Bongers & Popma 1990, Popma & Bongers 1988, Denslow *et al.* 1990, Howe 1990, Osunkoya *et al.* 1992, 1993). However, these experiments gave little information on seed germination and the early phase of establishment. The period from germination to establishment is the most critical phase for many plant populations, when they are susceptible to disturbance and environment effects (Harper 1977, Silvertown 1987). Species-specific strategies are liable to evolve at this phase (McCarthy & Facell 1990). Therefore, I focused only on the germination and early establishment phase in the current experiment.

The questions addressed in this chapter were as follows; 1) How does the forest floor environment affect the germination and seedling establishment of the two species?; 2) Is there a difference between the species in the mechanisms and/or the degree of environment effects on the germination and seedling establishment?; 3) Is seedling establishment a critical phase in their regeneration process, regulating mature tree distribution?

probability of survival through development stage II.

Seedling development was slower on the ridge than in the valley. Most seeds had germinated at 10 days after both in the valley and the ridge. At 20 days, more than 90% of living individuals had attained development stage III or IV in the valley, however, on the ridge, 94-98% were still at development stage II. Many seedlings died in the 20-30-day period on the ridge.

Effects of forest floor environment

In the valley, the proportions of seedlings opening primary leaves (development stage IV) were significantly larger for *D. lanceolata* than *D. aromatica* both in the understory (G -test, $\chi^2 = 5.476$, $p = 0.0193$) and in the gap ($\chi^2 = 8.064$, $p = 0.0045$), but the proportions were not different between the understory and the gap within each species (*D. aromatica*: $\chi^2 = 0.003$, $p = 0.987$; *D. lanceolata*: $\chi^2 = 0.290$, $p = 0.590$) (Fig. 8.1). On the ridge, on the other hand, the proportions were larger for *D. aromatica* than *D. lanceolata* within each canopy cover (understorey: $\chi^2 = 8.372$, $p = 0.0038$; gap: $\chi^2 = 4.143$, $p = 0.0418$), and larger in the gap than in the understory within each species (*D. aromatica*: $\chi^2 = 4.290$, $p = 0.038$; *D. lanceolata*: $\chi^2 = 8.520$, $p = 0.0035$) (Fig. 8.1).

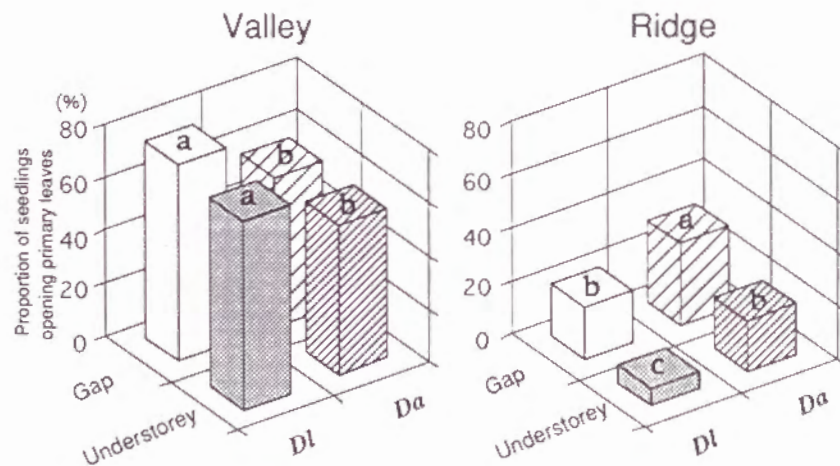


Fig. 8.1 Proportions (%) of seedlings surviving to the stage of primary leaves (development stage IV; see text) for *Dryobalanops aromatica* (Da) and *D. lanceolata* (Dl) in different forest floor environments. Different letters indicate significant differences within the same topography (valley or ridge) by G -test ($p < 0.05$).

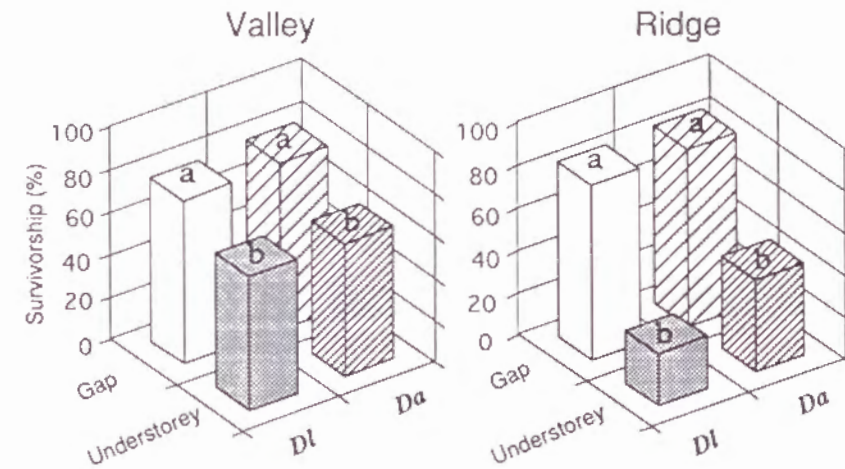


Fig. 8.2 Survivorship (%) at one year of seedlings of the stage of primary leaves (development stage IV; see text) for *Dryobalanops aromatica* (Da) and *D. lanceolata* (Dl) in different forest floor environments. Different letters indicate significant differences within the same topography (valley or ridge) by G -test ($p < 0.05$).

One year survivorship of seedlings which attained development stage IV was significantly larger in the gap than in the understory within each topography and species ($\chi^2 = 3.949$ - 10.218 , $p = 0.0014$ - 0.0469) (Fig. 8.2). The survivorship was not different between species within each topography and canopy cover ($\chi^2 = 0.0052$ - 0.891 , $p = 0.345$ - 0.942).

Factors of seedling death

On the ridge, the most important mortality factor until development stage IV was root predation (Fig. 8.3). Root predation occurred only for seedlings whose root was still inside the litter layer (development stage II). The predators could not be specified. Scars of predation were intense near the root tip in most cases. Mortality by root predation was higher on the ridge than in the valley for both species, especially for *D. lanceolata* (mortality on the ridge was 51-59%).

Mortality by desiccation was found only on the ridge for seedlings at development stage II. The mortality was significantly higher in the understory than in the gap for *D. aromatica* on the ridge ($\chi^2 = 4.596$, $p = 0.032$) (Fig. 8.3).

Cotyledon damage was mostly done by unidentified tiny bark beetles (Scolytidae). There was no environmental effect on mortality by cotyledon damage (Fig. 8.3). Vertebrate predation

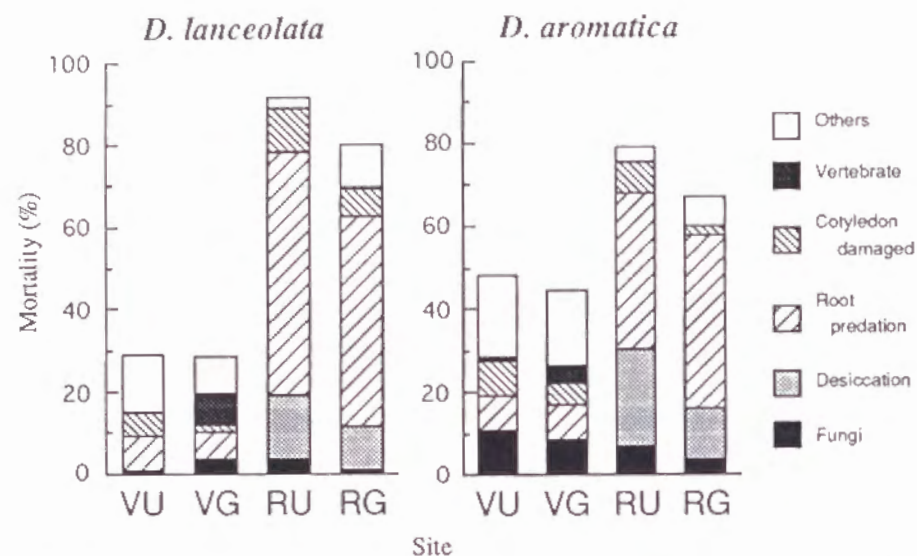


Fig. 8.3 Mortality of seeds and seedlings before primary leaf production for *Dryobalanops aromatica* and *D. lanceolata* in various forest floor environments. Total mortality is divided into six categories based on mortality factors (see text for details). VU: valley understorey, VG: valley gap, RU: ridge understorey, RG: ridge gap.

was found only in some quadrats in the valley gap, where some seeds, seedlings and plastic markers were found broken up. More *D. aromatica* seedlings were killed by fungi than *D. lanceolata*, especially in the valley (Fig. 8. 3).

Most of the dead seedlings after development stage IV were found standing and intact with wilted leaves, suggesting that they had suffered water stress.

DISCUSSION

Effects of forest floor environment on seedling establishment

This study showed the complex effects of forest floor environment on seedling establishment of *D. aromatica* and *D. lanceolata*.

Forest floor environment showed no effect on the germination rates of both species. Seeds of two dipterocarp species (*Dipterocarpus grandiflorus* (Blco) Blco, *Shorea multiflora* (Burck) Sym.) also showed similar germination rates in forest understorey and in a gap (50% canopy cover), but less in a clearing (2% canopy cover), in a Malaysian rain forest (Raich & Gong 1990). However, seeds of *Shorea crutisii* Dyer ex King (Turner 1990a) and *Vatica nitens* King (Raich & Gong 1990) germinated better in understorey than in the same gap. Turner (1990a) speculated that excessive temperature was an important cause of seed death in the gap. Size of the gaps in the current study was probably not large enough to damage the

seeds of *Dryobalanops* by extreme changes of environment, such as high temperature.

At the primary phase of establishment, *D. aromatica* and *D. lanceolata* showed higher survivorship in the valley than on the ridge. In addition to the direct effect of desiccation, root predation was important in reducing establishment rates on the ridge. On the ridge, seedling development, especially root elongation, was delayed during the first 20-day period. This was most likely due to the effect of drying litter, because there were only three days with good rain (> 1 mm/day) (J. V. RaFrankie, unpublished data), and the litter on the ridge was drying during the period. The dry litter led a longer duration of development stage II for the seedlings on the ridge, and probably increased the root predation rate, because seedlings of this phase were most susceptible to root predation. Therefore, the physical effect of dry litter was amplified by root predation.

The amount of litter accumulation influences plant establishment, though the magnitude and mechanisms are variable among species (Ahlgren & Ahlgren 1981, Fowler 1988, Molofsky & Augspurger 1992, Sydes & Grime 1981). Litter amount may have some effect on the establishment of *D. aromatica* and *D. lanceolata* through the mechanisms mentioned above. A large amount of litter accumulation increases the degree of dryness on the surface of a forest floor, because it is separated by a thick litter layer from the humus layer and soil surface, which usually have relatively high and stable water contents. Furthermore, it takes longer for roots to penetrate the thicker litter layer (Facelli & Pickett 1991). Thus the establishment rate is probably smaller in a micro-site with larger litter accumulation within a local site of the same soil and topography. On the ridge studied, establishment rates were higher in the gap than in the understorey (Figs. 8. 1 and 8. 2). This was probably due to the lower accumulation of litter in the gap site, though the relation between litter accumulation and canopy cover was not clear. In persistently wet environments such as the valley studied here, the influence of the amount of litter may be small.

The magnitude of the effects of forest floor environment, especially dry litter, on seedling establishment differed between the two species. The higher establishment rate of *D. aromatica* on the ridge appeared to be the result of its lower root predation rate. Root predation can be reduced by two ways as 1) effective defence against root predation by chemical compounds and 2) capacity for faster root elongation, which shorten the crucial period for root predation.

Dipterocarp species differ in their tolerance of dry conditions at germination (Ashton 1982). Size of seeds is related to the degree of desiccation tolerance. The seeds of larger seed species were less tolerant than those of smaller seed species within *Dipterocarpus* and *Shorea* (Thompsett 1985, 1987). Although seed sizes of *D. aromatica* and *D. lanceolata* were not different, Thompsett (1991) indicated that *D. aromatica* seeds have a smaller value of "lowest-safe moisture content (LSMC)", below which seeds are damaged by desiccation, than *D. lanceolata* seeds. This suggests that *D. aromatica* seeds are more desiccation-tolerant than those of *D. lanceolata*. However, there has been no study of the relationship between desiccation-tolerance

and capacity for root elongation under dry conditions, which may be more important in reducing the rate of root predation. In general, larger seeds can provide more nutrient reserves for production of root systems required for faster penetration of litter (Foster 1986, Garwood 1983). More detailed studies on the process of germination and seedling development are required in order to fully understand the mechanisms of establishment.

Influence of establishment phase on mature tree distribution

This study provides some evidence of the divergence in regeneration niches (Grubb 1977, Turner 1990a) between *D. aromatica* and *D. lanceolata*. The mechanisms for the fine-scale spatial separation of the two species can be partly explained by this niche divergence.

Forest floor dryness during the early establishment phase was fatal to *D. lanceolata*. Total mortality of *D. lanceolata* during the one-year experiment was 98.3% in the understorey on the ridge. This value, however, must be an underestimate, because the mortality by predispersal predation was excluded in this study. In a mast fruiting year (1990), the mature seed production of an emergent *D. lanceolata* was estimated to be 7276 in the study forest, of which 43.8% did not germinate mostly due to predispersal predation (see Chapter 6). Given this estimation, only 82 seedlings per adult tree would survive in the understorey on the ridge one year after mast fruiting. In the natural distribution area, however, more than 2000 *D. lanceolata* seedlings per fruited trees were surviving two years after heavy seed dispersal (see Chapter 5). Therefore, the early phase of seedling establishment seems to be a bottleneck for regeneration of *D. lanceolata* and a limit to its mature tree distribution in relatively dry sites.

Even in the humid aseasonal tropics, soil water deficit can frequently occur (Whitmore 1984). Vegetation on the shallow soils in coastal Sarawak is subject to severe moisture stress almost every year (Baillie 1972, 1976; Brunig 1969). In Sarawak persistently wet forest floor sites may be restricted to locations with clay-rich soils which have good water-holding capacity, or to topographically wet places such as valleys, even on sandy soils. The absence of *D. lanceolata* from upper slopes and ridges having sandy soils is probably due to the difficulty of seedling establishment on such relatively dry forest floors.

The distribution pattern of *D. aromatica*, however, which is not found in valleys with sandy soils or on clay-rich soils, cannot be explained from the view point of establishment phase dynamics, because *D. aromatica* can establish both on ridges and in valleys. Spatial distribution of mature trees of certain species is dependent not only on seedling establishment, but also on seed dispersal and spatial effects on survival and growth of established seedlings (Augspurger 1984a, Brokaw & Sheiner 1989, Grubb 1977, Oldeman & Dijk 1991). This latter process is likely to be more important in determining the mechanisms influencing the mature tree distribution of *D. aromatica*.

GENERAL DISCUSSION

In this chapter, I firstly summarize the regeneration processes of *Dryobalanops aromatica* and *D. lanceolata* based on the results of the previous chapters. Then, I discuss the role of habitat heterogeneity in maintaining the canopy tree richness of the study forest.

REGENERATION PROCESSES OF TWO DRYOBALANOPS

The regeneration processes of the two *Dryobalanops* studied are summarized as following, based on the current and previous studies.

Flowering to seed maturity

At the population and regional level, both species appear to flower at a relatively short intervals (1-4 yr.?) compared to other dipterocarp species (Chapter 2, Chan & Appanah 1980). The flowering intervals of each individuals, however, may be longer than those at the population level. In the study forest, at least one fruiting tree of each species was found every year during the 4-year study period; both species fruited in December 1990, September 1991, August 1992, July 1993 and August 1994 (only one fruiting tree of *D. aromatica* was found in 1994). But no individual was observed to fruit more than twice during the period. Thus, individual trees may not be able to flower annually or at a very short intervals of a few years.

Reproductive biology of *D. lanceolata* during the period from flowering to seed dispersal has been well known thanks to the study by Momose *et al.* (*in prep.*). They observed the reproductive process in the tree canopy using a tree tower and walk way system constructed around an emergent tree of *D. lanceolata* (ca. 70 m in height) in the Lambir forest. Flowers of *D. lanceolata* were pollinated by medium sized stingless bees (*Trigona spp.*). All flowers observed were successfully pollinated, but 93% were aborted within three weeks after flowering. They did not show complete self incompatibility, although selfed fruits appeared to be selectively aborted based on the result of a bagging experiment. It took about four months until the fruits matured, and during this period 40% of the remaining fruits were damaged by insect seed-predators, mainly weevils (*Mecynolobus crassus*), on the tree canopy. It was concluded that about 4-5% of flowers became intact mature seeds at the time of seed dispersal.

Although there is no detailed study on reproduction biology of *D. aromatica*, it may not be much different from that of *D. lanceolata* judging from the observations about the pollinators, seed-predators (Chapter 6, Momose *et al. in prep.*, A. Itoh *pers. observation*), and predation and germination rates (Chapter 6).

Besides the insect seed predators, giant squirrels (*Ratufa affinis*) were some times observed to eat the fruits on the canopy (A. Itoh *pers. observation*), though it was not known how much they affected the seed survivorship before dispersal.

Seed dispersal to seedling establishment

Mature fruits having five long sepal-wings are dispersed by wind, but their dispersal distance was relatively short and rarely over 30 m from the base of mother trees (Chapter 5). Most of the dispersed fruits are likely to fall directly under the canopy of mother trees, which are ca. 10-15 m in radius, while the few remaining fruits are dispersed over 15-20 m out of the canopy. Longer distance dispersal (ca. > 100 m) of *D. lanceolata* fruits was observed once in the study forest (A. Itoh, pers. observation), nevertheless, this was probably an unusual case. The fruiting tree (ca. 70 m tall) was standing on top of a ridge near the national park boundary; there was no large tree out of the park, hence no obstacle to seed dispersal.

For both species, about 10-20% of the dispersed seeds were eaten by vertebrates (e.g. rodents) within one week after dispersal (Chapter 6). However, as was discussed in Chapter 6, some of the seeds which were eaten by vertebrates probably had been damaged by insects before dispersal. Thus, actual seed loss by vertebrate-predation may have been smaller. The predation rates were higher in gaps probably due to the higher activity of predators in gaps (Chapter 6, Shupp 1986).

In addition to the vertebrate predation, 1.5-7% of the germinated seeds were attacked by insects (e.g. *Xyleborus* spp.; Chapter 6, Momose *et al. in prep.*) on the forest floor. However, Momose *et al. (in prep.)* reported that this was a secondary predation and most of the attacked seeds had already been damaged by weevils on the tree canopy before dispersed. Therefore, the loss of seeds by this factor alone might be smaller.

Another 3-9% of germinated seedlings died before rooting due to the poor root development (Chapter 6). Combining all mortality factors (e.g. vertebrate or insect predation, up-rooted, fallen branches, etc.), approximately 40-60% of the germinated seeds were killed during the period from seed dispersal to the time when the seedlings shed cotyledons. This means about 3-4% of flowers survived until they established and shed cotyledons.

The survivorship at this period may be slightly better in gaps, where postdispersal predation by vertebrate is less severe. However, gap was not required for their germination, and the seedlings could establish even under deep shade (Chapters 5 and 6). Newly established seedlings of 3185 and 2171 in number were found around one mother tree of *D. lanceolata* and *D. aromatica*, respectively at 0.5 year (*D. lanceolata*) and 1 year (*D. aromatica*) after seed dispersal (Chapter 5). It is thus concluded that both species have an ability to accumulate a large number of seedlings around the mother trees even under the shaded forest understorey.

These high establishment rates, however, may be attained only within the environments of the currently distributed places, i.e. sandy ridges for *D. aromatica* and clayey soils for *D. lanceolata* (Chapter 4). They do not always establish well under conditions out of their natural distributions. The transplanting experiment (Chapter 8) showed that few seedlings of *D. lanceolata* (< 2% of germinated seeds) established and survived one year on a sandy ridge because of the dry forest floor. Thus, the dry conditions are possible obstacle to regeneration

of *D. lanceolata* on sandy ridges. By contrast, seedlings of *D. aromatica* established even on the dry ridge. This higher tolerance of *D. aromatica* to dry conditions, in terms of seedling establishment, may be responsible for its distribution on sandy ridges. The transplanting experiment however failed to explain why *D. aromatica* was not distributed in valleys or on clayey soils, because it also established well in the valley. The reason may lie in the period after seedling establishment, such as the survivorship and growth of juveniles.

Survival and growth of established seedlings

Seedling mortality declined after the established seedlings shed the cotyledons (Chapter 6). The mortality rates were 15-16% and 17% in the understorey for *D. lanceolata* and *D. aromatica*, respectively. Supposing that these mortality rates continue, around the above mentioned mother trees, ca. 1400-1500 and 1000 seedlings would survive until 5 years after seed dispersal for *D. lanceolata* and *D. aromatica*, respectively. At 10 years post-dispersal, ca. 600-700 (*D. lanceolata*) and 400 (*D. aromatica*) seedlings would still be surviving. This implies that they can maintain persistent seedling populations in the understorey even if the fruiting intervals are > 10 years.

The high ability to maintain a dense seedling population itself, however, does not necessarily indicate their successful regeneration *in situ*. The seedlings were suppressed and grew little in the shaded understorey; for rapid growth, they needed relatively high light intensities, which were obtained by gap-formation (Chapters 5, 6 and 7). Therefore, only the seedlings that are growing in or near canopy gaps may grow into a larger size class, or saplings. Consequently, the spatial distributions of saplings were restricted to the small patches which had recently experienced gap-formation (Chapter 6).

From the view point of seedling growth, the two *Dryobalanops* do not seem to be the strongly shade-tolerant climax species, which usually grow relatively slowly even in gaps (Swaine & Whitmore 1988). By contrast, seedlings of the climax species that grow relatively fast in gaps usually die quickly in deep shade (Whitmore 1990). This was not the case for either of the two *Dryobalanops* species. Therefore, the seedlings of *D. aromatica* and *D. lanceolata* are unique in having a high shade-tolerance and very fast growth in high light intensities simultaneously.

Saplings to adult trees

The current studies focused mainly on the dynamics of seedlings. We do not have sufficient data on the dynamics of larger juveniles, such as saplings and poles, for discussion. However, this latter process also seems to be important in the regeneration processes of the two *Dryobalanops* species.

Tabel 9.1 Sapling, pole and adult tree numbers of emergent species in the 50-ha plots of Pasoh and Lambir (data for Pasoh species are from Manokaran et al. 1992)

Family	Species	Number per 50 ha				Sapling/Pole	Pole/Adult
		Sapling*	Pole*	Adult*	Total		
Anacardiaceae							
	<i>Mangifera griffithii</i>	46	87	11	144	0.5	7.9
	<i>Pentaspadon motleyi</i>	475	196	67	738	2.4	2.9
Apocynaceae							
	<i>Dyera costulata</i>	126	141	29	296	0.9	4.9
Burseraceae							
	<i>Canarium megalantyum</i>	123	70	7	200	1.8	10.0
	<i>Triomma malaccensis</i>	351	104	39	494	3.4	2.7
Celastraceae							
	<i>Kokoona reflexa</i>	199	35	7	241	5.7	5.0
	<i>Lophetalum floribundum</i>	83	36	14	133	2.3	2.6
Dipterocarpaceae							
	<i>Anisoptera laevis</i>	73	52	12	137	1.4	4.3
	<i>Dipterocarpus cornutus</i>	972	407	96	1475	2.4	4.2
	<i>Dipterocarpus costulatus</i>	506	96	24	626	5.3	4.0
	<i>Dipterocarpus crinitus</i>	165	56	15	236	2.9	3.7
	<i>Dipterocarpus globosus</i> **	1691	381	333	2405	4.4	1.1
	<i>Dryobalanops aromatica</i> **	7410	909	383	8702	8.2	2.4
	<i>Dryobalanops lanceolata</i> **	829	97	23	949	8.5	4.2
	<i>Neobalanocarpus heimii</i>	2800	416	75	3291	6.7	5.5
	<i>Parashorea densiflora</i>	78	71	9	158	1.1	7.9
	<i>Shorea acuminata</i>	1780	335	96	2211	5.3	3.5
	<i>Shorea bracteolata</i>	892	212	31	1135	4.2	6.8
	<i>Shorea guiso</i>	659	51	10	720	12.9	5.1
	<i>Shorea lepidota</i>	866	196	110	1172	4.4	1.8
	<i>Shorea leprosula</i>	2405	458	154	3017	5.3	3.0
	<i>Shorea macroptera</i>	1221	330	46	1597	3.7	7.2
	<i>Shorea maxwelliana</i>	4484	1048	150	5682	4.3	7.0
	<i>Shorea ochrophloia</i>	382	48	12	442	8.0	4.0
	<i>Shorea ovalis</i>	1026	247	35	1308	4.2	7.1
	<i>Shorea parvilolia</i>	1230	359	96	1685	3.4	3.7
	<i>Shorea pauciflora</i>	1928	358	84	2370	5.4	4.3
Fagaceae							
	<i>Quercus argentata</i>	657	295	98	1050	2.2	3.0
Guttiferae							
	<i>Calophyllum macrocarpum</i>	188	42	6	236	4.5	7.0
Irvingiaceae							
	<i>Irvingia malayana</i>	135	81	15	231	1.7	5.4
Leguminosae							
	<i>Cynometra malaccensis</i>	776	334	87	1197	2.3	3.8
	<i>Dialium maingayi</i>	66	40	2	108	1.7	20.0
	<i>Dialium platysepalum</i>	866	186	32	1084	4.7	5.8
	<i>Intsia palembanica</i>	369	85	66	520	4.3	1.3
	<i>Koompassia malaccensis</i>	348	193	123	664	1.8	1.6
	<i>Sindora coriacea</i>	1040	172	20	1232	6.0	8.6
Meliaceae							
	<i>Dysoxylum carolinea</i>	78	25	5	108	3.1	5.0
Rosaceae							
	<i>Atuna excelsa</i>	304	109	32	445	2.8	3.4
Sterculiaceae							
	<i>Heritiera simplicifolia</i>	211	223	24	458	0.9	9.3

* Sapling: 1 ≤ DBH < 5 cm; Pole: 5 ≤ DBH < 30 cm; Adult: DBH ≥ 30 cm

** Species in the Lambir plot (No./52 ha)

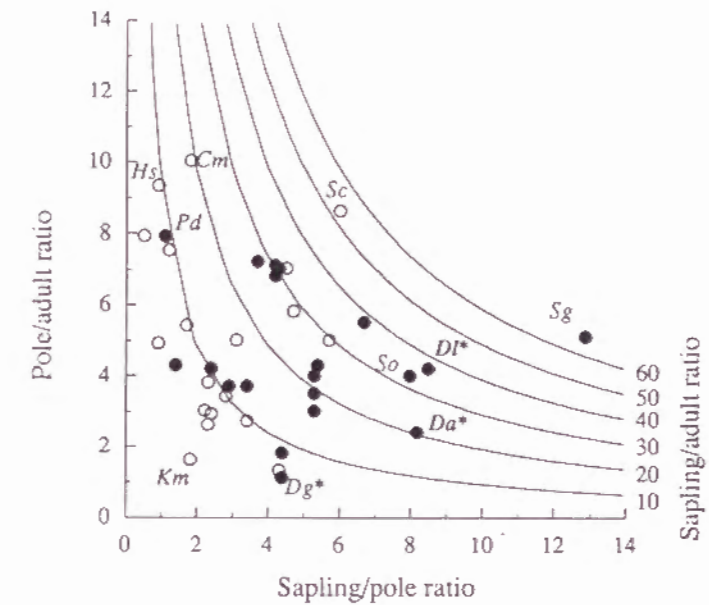


Fig. 9.1 Relations between sapling/pole ratio and pole/adult ratio for emergent tree species in the 50-ha plots of Pasoh (after Appanah et al. 1992) and Lambir. Black circles show species of Dipterocarpaceae; open circles are species of other families. Sapling: 1 ≤ DBH < 5 cm; pole: 5 ≤ DBH < 30 cm; adult: DBH ≥ 30 cm Cm: *Canarium megalantyum*; Da: *Dryobalanops aromatica*; Dg: *Dipterocarpus globosus*; DI: *Dryobalanops lanceolata*; Hs: *Heritiera simplicifolia*; Km: *Koompassia malaccensis*; Pd: *Parashorea densiflora*; Sc: *Sindora coriacea*; Sg: *Shorea guiso*; So: *Shorea ochrophloia*. Asterisks indicate Lambir species.

The diameter frequency distributions of the two *Dryobalanops* (cf. Fig. 3.3, Table 5.1) suggest that mortality continues after they become saplings (DBH ≥ 1 cm). This was also supported by a comparison of population structure among the two *Dryobalanops* and all emergent species of the Pasoh 50-ha plot (Table 9.1 and Fig. 9.1). The two *Dryobalanops* populations in the Lambir plot showed higher ratios of saplings (1 ≤ DBH < 5 cm) to poles (5 ≤ DBH < 30 cm) than most of the Pasoh emergent species, though the ratios of poles to adults (DBH ≥ 30 cm) are intermediate. This implies that the probability of the *Dryobalanops* saplings to grow into the pole size is relatively small, even though they maintain very dense sapling populations in the forest understorey. The period from sapling to pole is, thus, probably more critical for the regeneration of the two *Dryobalanops* in the Lambir forest than it is for most of the emergent trees in the Pasoh forest. Otherwise, the higher proportions of

saplings suggest that the populations of the two *Dryobalanops* might not be stable, but increasing in the Lambir forest.

To fully understand the process of regeneration of the two *Dryobalanops*, it is necessary to monitor the population dynamics of the larger size classes, *i.e.* saplings, poles and adults. This will be attained from an ongoing project of the population dynamics and growth of all trees larger than 1 cm DBH in the 52-ha plot (Lee *et al.* 1995).

IMPORTANCE OF ENVIRONMENTAL HETEROGENEITY FOR LOCAL SPECIES RICHNESS

One of the interesting findings of this study is that factors which affected spatial distribution patterns of the two *Dryobalanops* species had a hierarchy in terms of spatial scale. Their spatial distributions were largely affected by topography and soil in the whole plot scale (Chapter 4). However, in a smaller scale (≈ 1 ha), they were not affected by these factors but by the forest growth cycle (*sensu* Whitmore 1984) (Chapters 5, 6 and 7). Therefore, their spatial patterns can be described as a mosaic of small patches resultant from the spatial arrangement of various phases of the forest growth cycle, superimposed on patches resultant from the differences in topography and soil. This suggests that factors affecting species compositions may differ according to focal spatial scales; the habitat heterogeneity was most responsible for their coexistence in the larger scale, but the forest growth cycle may be more important for their coexistence with other canopy species in the smaller scale. The forest growth cycle regulates regeneration of the two *Dryobalanops* and may prevent them from dominating the whole canopy.

The hierarchy of factors mentioned above was probably observed so clearly because the study plot included a great diversity of habitats. It was established on a hilly area with a highly complex topography, including two distinct soil types (Chapter 2, Hirai *et al.* 1995, Yamakura *et al.* 1995). The environmental heterogeneity within the plot was therefore remarkably high; small fragments of various habitats were mixed finely in the plot. This is in sharp contrast to other 50-ha plots in Pasoh and Barro Colorado Island (BCI), which were established in a flat area (Fig. 9.2). Their plot layouts intend to make environments within the plot as homogeneous as possible. This is because they mainly address the question of how tree diversity can be maintained even within a homogeneous habitat in a tropical rain forest. Their environmental homogeneity might, however, bias the relative importance of the environmental heterogeneity for the local tree diversity.

This study was not able to reveal all the mechanisms that promote coexistence of the two *Dryobalanops*, though it pointed to soil water conditions as a possible mechanism (Chapter 8). Nevertheless, this study suggests various direct or indirect mechanisms that may promote

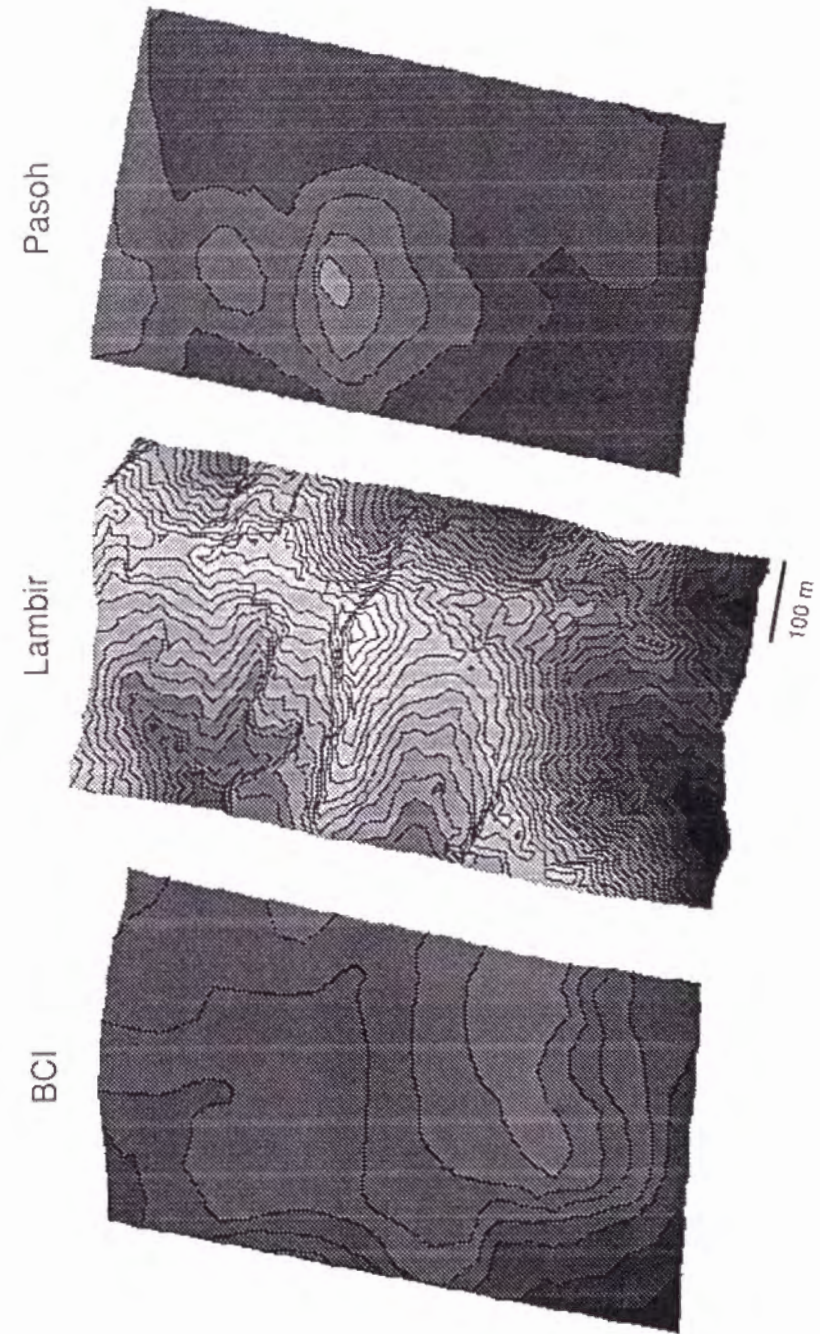


Fig. 9.2 Bird's-eye views of three 50-ha plots in Barro Colorado Island (BCI; after Hubbell & Foster 1984), Lambir and Pasoh (after Manokaran *et al.* 1992). Contours are at 5 m intervals for all three figures.

coexistence through topographical differences. Besides the physical and chemical properties of soil (Hirai *et al.* 1995), forest stand structure and gap regime seem to be largely affected by topography. Yamakura *et al.* (1995a, b) suggested that above ground biomass, tree density, maximum tree size, forest stratification, and possibly proportion of gap area are all correlated to topography within the Lambir 52-ha plot (see also Chapter 5). Ashton & Hall (1992) observed the differences in gap regime between sandy ridges and clayey lower slopes in the same site. Poorter *et al.* (1994) also found a correlation of gap formation to topography in a tropical moist forest of the Ivory Coast; the gap densities, sizes and total areas were higher on the upper and middle slope than on the crest or lower slope. Since disturbance regime, including gap formation, is one of the most important factors for determining species compositions (cf. Denslow 1980a,b, 1984, Whitmore 1984), topography might affect the species composition indirectly by influencing gap regime. For example, topography affected the effects of gaps on seedling establishment and survival of the two *Dryobalanops* in a complex manner (Chapter 8). This implies that topography (a larger scale factor) may interact with gap regime (a smaller scale factor) in affecting the regeneration processes and local species compositions. Therefore, it is important to elucidate the factors affecting regeneration of tree species at various hierarchical or spatial scales, and to clarify their interactions across different scales in illustrating the coexistence mechanisms of rain forest tree species.

In conclusion, the environmental heterogeneity of the Lambir 52-ha plot is undoubtedly one reason for the remarkable tree species richness expected in the Lambir forest, which might be higher than Pasoh and BCI (Chai *et al.* 1995, J. LaFrankie & P. S. Ashton *pers. comm.*). However, the current study considered only two of the more than 1000 tree species found in the 52-ha plot (Lee *et al.* 1995). We should study the coexistence mechanisms for many more tree species coexisting in the plot.

Moreover, studies of environmentally heterogeneous forests are also helpful for conservation of tropical rain forests. Today, most of the easily accessible tropical rain forests have been already exploited; in such areas, undisturbed forests, if any, are fragmented. There are few undisturbed tropical rain forests which are environmentally homogeneous over a wide area. Large undisturbed rain forests are mostly restricted to the hilly areas where exploitation has been difficult due to its complex topography (cf. Apannah & Weiland 1993b, Harcour 1992). The situation of the Lambir plot, therefore, may not be an unusual case among the present conservation areas. It will give us useful information about rain forest conservation to study the mechanisms of maintaining the remarkable tree diversity of the Lambir forest.

SUMMARY

CHAPTER 1

Coexistence of closely related, sympatric tree species is one of the remarkable features of species rich tropical rain forests. This study aims to reveal the regeneration processes and coexistence mechanisms of two congeneric emergent tree species, which are distributed in sympatric in a Bornean rain forest.

CHAPTER 2

The study site was a mixed dipterocarp forest in the Lambir Hills National Park (= 7000 ha) located in eastern Sarawak, east Malaysia. The park is in an aseasonal wet tropical climate with an average annual rainfall of *ca.* 2800 mm. Its topography and relating soil properties are highly complex, making a fine mosaic consisting of various habitats.

The study species, *Dryobalanops aromatica* Gaertn. f. and *D. lanceolata* Burck (Dipterocarpaceae), are emergent species, growing up to > 60 m tall at maturity. They have been reported to make dominant stands in Asian tropics.

CHAPTER 3

The degree of their dominance and their status in the study forest were evaluated using a large scale permanent plot (52 ha: 500 m x 1040 m).

D. aromatica (total number of trees larger than 1 cm DBH (*N*) = 8419) was the most abundant canopy species in the 52-ha plot; *D. lanceolata* was not so abundant (*N* = 954). Even the dominance of *D. aromatica*, however, was not extremely high among the common canopy species at the whole plot scale (52 ha). The spatial distributions of the two *Dryobalanops* species were highly clumped; they predominated the main canopy very locally at the scale of *ca.* 1 ha. In their most dense 1-ha stands, *D. aromatica* and *D. lanceolata*, respectively, occupied 23% and 15% of trees larger than 50 cm DBH in number, and 30% and 27% in basal area. Their dominance was comparable to other *Dryobalanops* dominant forests previously reported (25-30% in basal area). Nevertheless, this was much lower than the dominance of other mono-dominant tropical rain forests in which dominant species often occupied > 50% of the canopy trees in number. Species richness of the canopy trees in the 1-ha stands was very high, comparable to those reported in typical mixed tropical lowland rain forests of the Asian tropics.

CHAPTER 4

Since the spatial distributions of *D. aromatica* and *D. lanceolata* were shown to be clumped (Chapter 3), their spatial distributions in the 52-ha plot and the effects of topography in this large scale were analyzed statistically. *D. lanceolata* had clumps (*ca.* 1 ha in size) consisting of large trees and many juveniles. *D. aromatica* juveniles showed double clumping as larger

clumps (ca. 1 ha) around large trees and smaller clumps (ca. 0.1 ha) within the larger ones. *D. aromatica* juveniles, however, were segregated from larger conspecific trees on a fine scale (ca. 4 m x 4 m). Distributions of the two species were highly segregated from each other in relation to the topography. The mean local density (No. / 400 m²) of *D. aromatica* was positively correlated to the degree of concaveness of surface relief, while that of *D. lanceolata* was negatively correlated. Besides topography, soils appeared to affect their segregated distributions. It was concluded, therefore, that they were co-occurring in the plot by occupying different patches of the heterogeneous habitat mosaic.

CHAPTER 5

Factors influencing the spatial distributions of the two species were estimated in the scale of predominant clumps. Two 1.6-ha subplots whose canopy were predominated by *D. aromatica* or *D. lanceolata* were established in the 52-ha plot; they occupied 19.5% (*D. aromatica*) and 17.3% (*D. lanceolata*) of the total basal area of trees ≥ 30 cm DBH. Forest structure of the two subplots were largely different from each other; the subplot predominated by *D. aromatica* was two times larger in the total number of trees ≥ 1 cm DBH, however it had a less shaded forest floor in average, compared to that of *D. lanceolata*.

Both species had abundant juveniles of various sizes. Newly established seedlings (< 14-month old) were concentrated around mother trees for both species, suggesting their relatively poor seed dispersal (< 40 m). Spatial distribution of seedlings (DBH < 1 cm) negatively correlated to distance from the nearest conspecific adult (DBH ≥ 30 cm) in both species, indicating that seedling distribution was affected mostly by seed dispersal. However, that of *D. aromatica* positively correlated to light intensity at the forest floor as well. Spatial distribution of saplings (1 \leq DBH < 5 cm) correlated positively to local density of all tree species and negatively to total basal area for both species. Sapling distribution may therefore be concentrated in the patches of the late gap phase or early building phase of the forest growth cycle, where many small trees but no large trees exist.

It is concluded that both species had a generally similar regeneration process in spite of the large differences between their predominant stands: *i.e.* 1) they may not require gap-formation for germination, establishment and survival resulting in a persistent seedling/sapling bank around mother trees, but 2) formation of proper gap may be required for rapid growth of their suppressed juveniles, hence for the later phase of their regeneration. Their intermediate local dominance of forest canopy is also discussed in terms of this regeneration process.

CHAPTER 6

To evaluate the regeneration process of the two *Dryobalanops* species estimated in Chapter 5, especially for the seedling phase, survivorship and growth of their seedlings were observed for 2.5 years after seed dispersal. Two other dipterocarp species, *Dipterocarpus globosus*

Vesque and *Dipterocarpus actangulus* Vesque, were also included for comparison.

Predispersal seed predation rates were 75, 27-34 and 18-26% for *Dip. globosus*, *Dry. lanceolata* and *Dry. aromatica*, respectively. Less than 20% of the two *Dryobalanops* seeds were damaged by vertebrates after seed dispersal. During the period from seed dispersal to the time when the seedlings had shed cotyledons, about 90 and 60-70% of dispersed seeds died for the two *Dipterocarpus* and the two *Dryobalanops*, respectively. The major mortality factors during this period were up-rooted and seed/seedling predation by insects or vertebrates. Thereafter, all species showed constant mortality rates of 34, 15-16, 17 and 6 %/yr at the forest understorey for *Dip. actangulus*, *Dry. lanceolata*, *Dry. aromatica* and *Dip. globosus*, respectively. Mortality rate was lower in a gap (4 %/yr) than in the understorey for *Dry. aromatica*, while not different between gap (17 %/yr) and understorey for *Dry. lanceolata*. A majority of dead seedlings were killed by fallen branches or were found standing with wilted leaves, suggesting water stress. No significant correlation was found between seed/seedling mortality and distance from mother trees or initial density for all four species. The seedlings showed little height growth and leaf production in the understorey, but grew better in gaps; for all species, the mean leaf production was positively correlated to the cumulative diffuse light intensity of their habitats.

These results supported the estimated regeneration process: *i.e.* they may make a dense seedling bank around mother trees, the spatial pattern of which may be affected mostly by seed dispersal; the effect of gap on spatial pattern of seedlings may be larger in *D. aromatica* than in *D. lanceolata*; their seedlings may be suppressed under forest canopy and released by gap formation to grow rapidly.

CHAPTER 7

To evaluate the possibility that the two *Dryobalanops* were segregated from each other through the difference in seedling growth response to light conditions, a shading experiment was conducted. Four-month shading from germination resulted in both species showing an optimum light conditions for seedling growth. The relations between 4-month old seedling weight and light condition were expressed by the optimum growth model of Hozumi *et al.* (1960), formulated as

$$\frac{1}{w} = \frac{A_1}{f} + A_2f + B,$$

where w is mean weight of seedlings, f is relative light intensity (RLI) and A_1 , A_2 , and B are coefficients. Estimated optimum RLIs were 27% and 31% for *D. lanceolata* and *D. aromatica*, respectively. Seedlings of *D. aromatica* tended to promote height growth rather than diameter growth and leaf production, compared to *D. lanceolata*. It is concluded that the differences in

seedling response to light conditions were not large enough to explain their segregated distributions alone.

CHAPTER 8

To evaluate the effects of forest floor environments on germination and establishment, seeds of the two *Dryobalanops* were sown in gaps and understorey on a ridge and a valley. Germination rates were 92-100% regardless of site and species. On the ridge, the proportion of seedlings that opened primary leaves was larger in *D. aromatica* (19-30%) than *D. lanceolata* (7-19%), mostly due to higher root predation in *D. lanceolata*. In the valley, by contrast, the proportion was larger in *D. lanceolata* (71-74%) than *D. aromatica* (56%). After primary leaf production, seedlings of both species had higher survivorship in the gaps than in the understorey. It is concluded that the absence of *D. lanceolata* on sandy ridges was at least partly because of its poor establishment on such dry forest floors, and that the explanation of the absence of *D. aromatica* in valleys must lie in the latter period rather than during seedling establishment.

CHAPTER 9

The regeneration processes of the two *Dryobalanops* were summarized, and the effects of habitat heterogeneity in the study forest on its species richness were discussed. It was suggested that factors affecting tree species diversity have a hierarchy in terms of spatial scale. In the large scale of the whole 52-ha plot, coexisting of the two *Dryobalanops* was maintained by complex arrangement of topography and soils of the plot. In the smaller scale (≈ 1 ha), however, their regeneration was affected more by forest growth cycle. The remarkably high species richness in the Lambir 52-ha plot was at least partly due to its highly heterogeneous environments. It is of importance to study the coexistence mechanisms for many more co-occurring tree species in various spatial scales.

ACKNOWLEDGMENTS

This study was carried out at the Forest Resource Laboratory, Division of Tropical Agriculture, Graduate School of Kyoto University, under the supervising of Dr. H. Watanabe, to whom I am grateful for helpful guidance and encouragement during this study. This study is part of a cooperative ecological project among the Forest Department of Sarawak, Harvard University, and several Japanese Universities. Without the project, I could not have conducted the field research. I thank all the members who participated in the project, especially Dr. S. Tamura and Datuk C. L. Leo Chai for their general direction of the project. Drs. T. Yamakura, K. Ogino, I. Yamada, K. Kyuma, and Mr. H. S. Lee kindly arranged for me to participate in the project and encouraged me both in Sarawak and in Japan. The Sarawak Government and the Forest Department of Sarawak permitted me to study in Sarawak. Mr. O. K. Earnest Chai and the staff of the Silvicultural Research Office, Sibuluan, mainly carried out the enormous field and computer work for the 52-ha plot. Drs. J. V. LaFrankie and J. K. Jarvie, and Mr. S. S. Tan headed the difficult work for identification of all trees in the 52-ha plot.

Drs. T. Ohkubo, T. Inoue, T. Yumoto, I. Ninomiya, A. Komiyama, H. Hirai, H. Hirotsu, M. Kato, K. Sakurai, T. Itino, H. Nagamasu, R. Terauchi, K. Kimura, H. Kawaguchi, and Mrs. S. J. Davis, B. Perumal, H. Matsumura, K. Momose, T. Nagamitsu, P. A. Palmiotto, and members of the Laboratory of Forest Resources and the Laboratory of Forest Ecology, Kyoto University, gave me fruitful advice and helped me in writing the thesis. Dr. M. Kanzaki permitted me to use the results of topography analysis in Chapter 4. Drs. T. Yamakura, P. S. Ashton, T. Kohyama, N. Kachi, T. C. Whitmore, D. M. Newbery, and S. Takeda read parts of early drafts critically and made helpful comments. Mrs. A. A. Hamid, J. J. Kendawang, O. T. Braken and F. Okitsu helped me during my stay in Sarawak. Many local people assisted the field work, and they also gave me great hospitality.

This study was financially supported partly by the Ministry of Education, Science and Culture, Japan, the Forest Department of Sarawak, and Fellowships of the Japan Society for the Promotion of Science for Japanese Junior Scientists.

And last, I want to thank my wife Masayo, my parents, and my parents-in-law very much for their understanding and wholehearted support.

This thesis could not have been completed without help of so many people, all of whom I cannot mention here. Again, I would like to express my sincere gratitude to all of them.

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