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# Population Structure and Canopy Dominance of Two Emergent Dipterocarp Species in a Tropical Rain Forest of Sarawak, East Malaysia

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**ABSTRACT** Population structure and canopy dominance of *Dryobalanops aromatica* and *D. lanceolata* were studied in a tropical rain forest of Sarawak, East Malaysia, using a large permanent plot (52 ha in size). *D. aromatica* was the most abundant canopy species (number of trees ≥ 1 cm DBH per 52-ha ($N$) = 8702), while *D. lanceolata* was much less abundant ($N$ = 949). Neither species was dominant in the whole plot scale (52 ha), but they predominated the main canopy and emergent trees very locally in a scale of ca. 1 ha. In their most dense 1-ha subplots, *D. aromatica* and *D. lanceolata* occupied, respectively, 23% and 15% of trees ≥ 30 cm DBH in number, and 30% and 27% in basal area. These values were comparable to the dominance of *Dryobalanops* species reported in other regions (25-30% in basal area), but much lower than the dominance of other typical monodominant tropical rain forest species (often > 50% in tree number). The total number of canopy tree species in each 1-ha subplot was similar to those of typical mixed tropical rain forests in the Asian tropics, suggesting little effect of *Dryobalanops* predominance on the species diversity of other canopy trees.

**Key Words**: *Dryobalanops aromatica* / *Dryobalanops lanceolata* / population structure / canopy dominance / monodominant forest / tropical rain forest / Sarawak

Tropical rain forests are generally the most diverse plant communities 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 various regions, e.g. Africa (Eggeling, 1947; Hart *et al.*, 1989; Moutsambote *et al.*, 1994), South America (Beard, 1946; Connell & Lowman, 1989; Davis & Richards, 1934), and South East Asia (Richards, 1952; Whitmore, 1984). *Dryobalanops aromatica* Gaertn. f. have 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). Rain forests dominated by *D. aromatica* were found in the southeast part of the Malay Peninsula (Foxworthy, 1927; Whitmore, 1984; Wyatt-Smith, 1963) and in Sumatra (van Zon, 1916 in van Slooten, 1931). Dominant forests of other species of the genus *Dryobalanops* have also been reported, e.g. *D. lanceolata* Burck in Sarawak (Beccarii, 1904) and Sabah (Meijer, 1970), *D. beccarii* Dyer in Brunei (Yamada, 1991) and West Kalimantan (Kaji & Suzuki, 1994), *D. rappa* Becc. in Brunei (Ashton, 1964; Yamada, 1991).

In this study, the population structure of *D. aromatica* and *D. lanceolata* and their canopy dominance were analyzed using the data set of a large scale (52 ha) permanent plot

established in a tropical rain forest of northeastern Borneo. Two questions were addressed: (1) Do *D. lanceolata* and/or *D. aromatica* dominate the canopy of the study forest in the whole plot scale (52 ha) and/or in a smaller scale (1 ha)? (2) If so, does their dominance reduce the diversity of other canopy or subcanopy species?

## STUDY SPECIES, SITE AND METHODS

*Dryobalanops aromatica* and *D. lanceolata* are among the tallest trees in the West Malesia: up to 60-70 m in height and 1.5-2 m in diameter (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 main canopy and emergent trees as was mentioned above (Ashton, 1964, 1982, Meijer 1970, Symington 1943, van Slooten 1931, Whitmore 1984, Wyatt-Smith 1963). They are important timber species of medium hardwood for construction and plywood. Crystalline camphor (Borneo camphor) and oleo-resin were formerly 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 comphora* (L.) Seib. (Lauraceae) (Burkill, 1935).

This study was conducted in a mixed dipterocarp forest (Ashton, 1964) of Lambir Hills National Park (4°12' N, 114°00' E) in Sarawak, East Malaysia. The park is situated on undulating low hills (ca. 60-450 m a.s.l.), and ca. 85% of the area is covered with mixed dipterocarp forests (Watson, 1985). At Miri Airport, located about 20 km north of the study site, the average annual rainfall was 2764 mm for the years 1967-1993 (Momose *et al.*, 1993). There is no distinct dry season, though the period of February to August has relatively less rainfall than the rest of the year.

A permanent plot of 52-ha (1040 m × 500 m) was established in the forest during the period 1990-1993. The plot was divided into 1300 squares of 20 m × 20 m in size. Each squares was further divided into 25 quadrats of 5 m × 5 m. The demarcation of the plot and

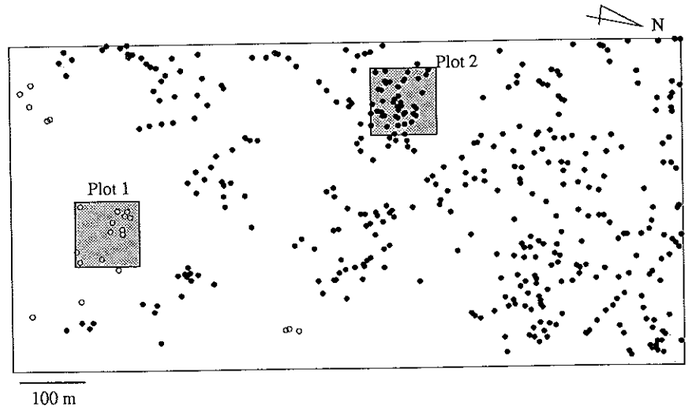


**Fig. 1. Spatial distributions of *Dryobalanops aromatica* (●) and *D. lanceolata* (○) trees (≥ 30 cm in DBH) in the 52-ha plot.** Shaded areas are plots for analyses of local dominance.



the division into squares and quadrats were done by a tacheometer and compass survey. Aluminum pipes and plastic pegs 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 by 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 for all 5 m × 5 m quadrats. 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. More details of the plot establishment and tree assessment are described elsewhere (e.g. Yamakura *et al.*, in prep.; Chai *et al.*, in prep.).

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*as, respectively (Fig. 1).

## RESULTS AND DISCUSSION

### Status in the 52-ha plot

*Dryobalanops aromatica* ($N$ = 8702 per 52 ha) was the most abundant canopy species in the 52-ha plot, and it distributed widely in the plot (Fig. 1). *Dryobalanops lanceolata* ($N$ = 949), 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 elsewhere (e.g. Itoh *et al.* in prep.).

Figure 2 shows the proportions of common canopy species and other dipterocarp species

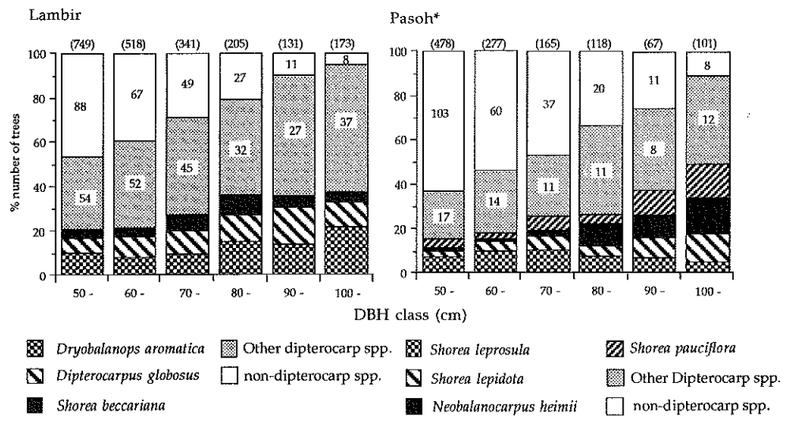


**Fig. 2. Proportions of common main canopy tree species in various size classes.** Numerals in parenthesis represents total stem number in each size class. Numerals in columns are number of species in each category: for the Lambir plot, tentative number of taxa which had been identified by August 1993 (Chai *et al.* in prep). *: Data for Pasoh were calculated based on Appanah & Weinland (1993).

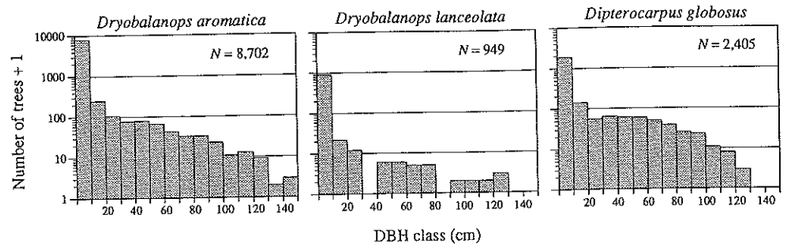


**Fig. 3. Diameter frequency distributions of *Dryobalanops aromatica*, *D. lanceolata* and *Dipterocaprpus globosus*.** DBH classes are at 10-cm intervals except for the smallest class (1 ≤ DBH < 10 cm). *N*: total stem numbers of trees ≥ 1 cm DBH in the 52-ha plot.

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, 1993) is 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 the Lambir and Pasoh forests. In Lambir, *D. aromatica* occupied 8-20% in any size class ≥ 50 cm DBH, and the proportion was higher in larger size classes. *Dipterocarpus globosus* Vesque, the second most abundant canopy species in the Lambir plot (N = 2405), was less than 10% of the largest size class (DBH ≥ 1 m), though its proportions were comparable to those of *D. aromatica* in the smaller size classes of 50-100 cm DBH. In Pasoh, *Neobalanocarpus heimii* (King) Ashton, *Shorea parviflora* Dyer and *S. lepidota* (Korth) Bl. occupied 12-15% each in the largest size class. *Shorea leprosula* Miq. occupied about 10% in 60-80 cm DBH classes. Therefore, it cannot be concluded that *D. aromatica* dominated the main canopy of the 52-ha plot as a whole, although it was the most abundant canopy species.

Frequency distributions of DBH for *D. aromatica* and *D. lanceolata* are shown in Fig. 3, and that for *Dipterocarpus globosus* is also shown for comparison. Both *Dryobalanops* species had abundant small size individuals; the proportions of trees 1-5 cm DBH were 87.6% and 89.9% for *D. aromatica* and *D. lanceolata*, respectively. In the DBH classes larger than 10 cm, they showed frequency patterns slightly decreasing with DBH in a semi-log scale. The ratios of adult trees (DBH ≥ 30 cm) to poles (5 cm ≤ DBH < 30 cm) to saplings (1 cm ≤ 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 (40-100 cm DBH), however there were fewer trees in 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 mortality would continue for juveniles of the two *Dryobalanops* species until they mature. By contrast, the mortality of juveniles may be less severe for *D. globosus* after they reach sapling size.

### Dominance of *Dryobalanops* in the small scale

*Dryobalanops aromatica* and *D. lanceolata* were the most abundant canopy species in each 1-ha subplot (Table 1). The proportions of *Dryobalanops* were higher in large size classes than in small size classes. *Dryobalanops aromatica* and *D. lanceolata*, respectively, occupied



Table 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 *Dr* | (%*) | Basal area ($m^2$ / ha) other spp. | (NT**) | *Dr* | (%*) | 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*.

23% and 15% of trees of 30 cm DBH and larger in number, and 30% and 27% in basal area. This indicates that the upper canopy and emergent trees of both plots were predominated by *Dryobalanops* species, however, the lower canopy and subcanopy included many other tree species.

In spite of the dominance of the main canopy by *Dryobalanops*, the species diversity of the lower canopy and subcanopy was still high in both plots (Table 1). Total numbers of 177 and 125 taxa had been tentatively identified by August 1993 (Chai *et al.* in prep.) in trees larger than 10 cm DBH in Plot 1 and Plot 2, respectively. These figures must be highly underestimated, because the identification had not yet been completed at the species level for many genera and families. The numbers of tree species per hectare above 10 cm DBH were ca. 140 in Andulau, 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). Therefore, the actual species diversity of the current subplots may be comparable to or rather higher than other lowland tropical 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 little effect of the canopy dominance on the diversity of other tree species in a *D. aromatica* dominant forest

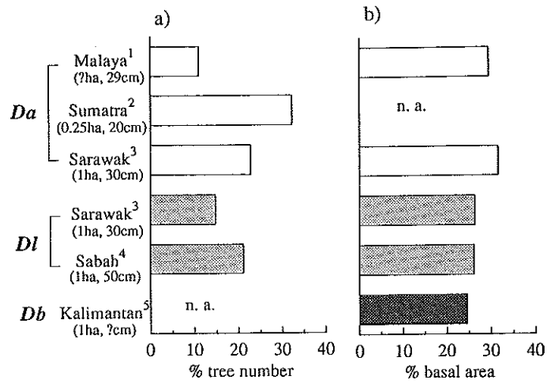


**Fig. 4. Canopy dominance of *Dryobalanops* in tree number (a) and basal area (b).** Species abbreviations are: *Da: Dryobalanops aromatica; Dl: D. lanceolata; Db: D. beccarii.* Figures in parenthesis are plot size and lower DBH limit of canopy tree used in the study. Data sources are: 1: Wyatt-Smith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

of Peninsular Malaysia.

Figure 4 shows canopy dominance by three species of *Dryobalanops* in various regions. Dominance in terms of tree number varied among the species and regions, probably because the value was largely influenced by the sample size and the lower limit of the canopy tree used in the forest investigations, while dominance of basal area was less variable among the species and regions with values of 25-30%. In a small scale of 1 ha, the canopy dominance of *D. aromatica* and *D. lanceolata* found in the current study was comparable to those in other *Dryobalanops* dominant forests that have been reported in other regions.

The degree of canopy dominance by *Dryobalanops* (25-30%), however, is smaller than those in 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 are not monodominant forests on the basis of their definition. Nevertheless, several authors referred to *D. 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 moderate between typical 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 (i.e. in a small scale of 1 ha) in the study forest. They were not the dominant species in the 52-ha plot as a whole, however, mainly because their spatial distributions were highly clumped. Moreover, even at places where *Dryobalanops* species predominated the main canopy, their dominance was not extreme, 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, and to clarify the mechanisms which maintain the diversity of other canopy trees in *Dryobalanops* predominate stands.

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## 東マレーシア，サラワク州の熱帯雨林におけるフタバガキ科リュウノウジュ属２種（***Dryobalanops aromatica***，***D. lanceolata***）の個体群構造と林冠優占度

東マレーシア，サラワク州の熱帯雨林に設置した大面積調査区（面積 52 ha）の毎木調査データを用いて，２種のリュウノウジュ（*Dryobalanops aromatica*と*D. lanceolata*）の個体群構造と林冠優占度を解析した。*D. aromatica* は 52 haあたりの胸高直径１cm以上の個体数（N）が 8702で，調査区内で最も個体数の多い林冠樹種であった。*D. lanceolata*はN = 949であった。プロット全体の平均で考えると，２種ともに優占樹種とはいえなかった。しかし，２種の空間分布が集中分布であったため，面積１ha程度の大きさで局所的に各々の種に林冠が擬優占されている場所があった。それぞれの種が擬優占する１haずつのサブプロットでは，*D. aromatica*と*D. lanceolata*各々が胸高直径 30 cm以上の林冠木に占める割合は，本数率で23%と15%，胸高断面積で30%と27%であった。これらの林冠優占度は，これまでに他の地域の*Dryobalanops*優占林で報告された優占度（断面積で25-30%）と同じであるが，その他の樹種による典型的な熱帯雨林の優占群落における優占度（本数率で50%以上）よりもずっと小さい。したがって，*Dryobalanops*優占林は典型的な単独種優占熱帯雨林 (monodominant tropical rain forest) と典型的な混交熱帯雨林 (mixed tropical rain forest) の中間的なものであると考えた。また，２種の擬優占するサブプロットでこれまでに同定された林冠樹種数は，熱帯アジア地域の典型的な混交多雨林のものと同等であった。これは，*Dryobalanops* の擬優占が他の林冠構成樹種の多様性に与える影響が小さいことを示唆するものである。