Plant Ecology **132:** 121–136, 1997.

Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia

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Received 21 July 1995; accepted in revised form 27 November 1996

Key words: Coexistence, Dipterocarpaceae, *Dryobalanops aromatica*, *Dryobalanops lanceolata*, Gap dynamics, Janzen-Connell hypothesis

Abstract

Spatial distribution patterns of two emergent tropical rainforest tree species (*Dryobalanops aromatica* & *D. lanceolata*) were examined in where they were dominant (17–20% of total basal area of canopy trees) in Sarawak, East Malaysia. Newly established seedlings ($<$ 2 years old) were restricted to areas $<$ 40 m from mother trees for both species, suggesting a limited seed dispersal. Seedling ($<$ 1 cm in dbh) density was highest around conspecific adults ($\geq$ 30 cm in dbh). Negative spatial patterns were observed between larger juveniles (1–5 cm in dbh) and conspecific adults for both species; the most dense populations of sapling (1–5 cm in dbh) and poles (5–30 cm in dbh) were found at a distance of 15–20 m from the nearest conspecific adult. Seedlings of both species were distributed randomly with respect to light conditions evaluated by a forest floor diffuse site factor and a canopy closure index. Saplings of both species, and poles of *D. lanceolata*, were distributed under more open conditions than expected from spatially random distributions, and from average light conditions of all species of the same size classes. Possible mechanisms for the observed distribution patterns and intermediate canopy dominance of *Dryobalanops* were discussed from the viewpoints of gap-dynamics and distance-dependent mortality.

Nomenclature: P.S. Ashton (1982).

Introduction

Tropical rainforests generally have no distinctly dominant tree species. Monodominant rainforests, which are dominated by one or a few species, however, have been reported in the wet tropics (cf. Connell & Lowman 1989; Hart et al. 1989). *Dryobalanops aromatica* Gaertn. f. and *Dryobalanops lanceolata* Burck (Dipterocarpaceae) are known to occur as dominant species in some forests of southeast Asia (Foxworthy 1927; Richards 1952; Wyatt-Smith 1963; Whitmore 1984). The degree of dominance of the two species, however, is not so high (usually $<$ 30% of canopy trees, Kachi et al. 1993; Itoh et al. 1995b) as to regard these as monodominant forests, that is, forests in which the dominant species occupy $>$ 50% of canopy trees (Connell & Lowman 1989). Though canopy tree diversity is generally low in monodominant forests, the *Dryobalanops*-dominant forests seem to have as many canopy tree species as mixed rainforests in the same region (Kachi et al. 1993; Itoh et al. 1995b). Tree species diversity of small plots (0.6 ha), however, decreased with increase in *D. lanceolata* dominance in the plots in Sarawak (P.S. Ashton unpubl. data). It is of interest to know the mechanisms that prevent dominant members from becoming more abundant and dominating the whole canopy. To understand the mechanisms, we must know the regeneration processes of the species in a particular forest.

The present spatial pattern of a particular species, especially the adult-juvenile relationship, provides useful information of regeneration process of the species (e.g., Hubbell 1979; Hamill & Wright 1986; Sterner et al. 1986; Kohyama et al. 1994). A negative spatial correlation between adults and juveniles suggests density- and/or distance-dependent mortality of the offspring, which can promote species diversity (Janzen 1970; Connell 1971). Requirement of light-gaps for regeneration may also result in a negative correlation between adults and offspring (Hamill & Wright 1986). Poor seed dispersal and specialization for particular habitats generally result in a clumped distributions of adults and juveniles (Hamill & Wright 1986). We must be careful, however, in interpreting the spatial patterns, because different processes could lead to the same pattern as is mentioned above. Other information than spatial distributions of the focal species, such as distributions of other tree species, the relationship between spatial patterns and light conditions, and reproductive properties (e.g. fecundity, seed dispersal patterns, seed and seedling survival, juvenile growth, response of juveniles to canopy gaps), are helpful in interpreting the working processes behind the present dispersion patterns.

In this study, we examine spatial distribution patterns of two *Dryobalanops* species in the stands in which they are dominant members. The juvenile distributions are analyzed from the viewpoints of distance from adults and light conditions. We discuss (1) the processes that produced the observed distribution patterns and (2) the possible mechanisms that prevent *Dryobalanops* from dominating the whole canopy.

Study site and methods

Study site and species

The study site is a tropical rainforest in Lambir Hills National Park (4°12′ N, 114°00′ E) in Sarawak, East Malaysia (Figure 1). The park is situated on undulating lowland hills (ca. 60–450 m a.s.l.). Approximately 85% of the area is covered with mixed dipterocarp forests (*sensu* Ashton 1964) (Watson 1985). The average annual rainfall is 2764 mm (1967–1993) at Miri Airport, located about 20 km north of the study site (Momose et al. 1994). There is no distinct dry season, though the period February–August has relatively little rainfall.

Dryobalanops aromatica and *D. lanceolata* are emergent evergreen trees of lowland tropical rainforest in Borneo; *D. aromatica* also occurs in Sumatra and the Malay Peninsula (Ashton 1982). In the study forest, the distributions of the two species were spatially segregated from each other with respect to topography and soils (Figure 2; Hirai et al. 1995; Itoh et al. 1995c). *D. aromatica* is the most abundant canopy species on upper slopes and ridges with sandy soils with an organic surface horizon, but rare in valleys or clay-rich soils without an organic horizon. *D. lanceolata* is, in contrast, mostly found on clay-rich soils or in valleys if on sandy soils. Apart from the habitat difference, population structure is generally similar for both species in the study forest. Each species is a dominant member of the upper canopy and emergent strata in patches on the scale of a few hectares (Itoh et al. 1995b, c). There are always various sizes of juveniles around adult trees. The two species also share similar reproductive properties. They have relatively short fruiting intervals among dipterocarp species (Chan & Appanah 1980; Itoh 1995); they produce a wind dispersed fruit with a large seed (2–3 g dry weight) and five equal sepal wings; both species have high germination and establishment rates regardless of forest floor light condition (Itoh et al. 1995a); the established seedlings are shade-tolerant (Itoh et al. 1995a). We expected, therefore, similar regeneration processes and spatial patterns between the two species in spite of their apparently different habitat preference.

Spatial distribution

Two 1.6-ha plots (100 × 160 m) were established within stands where each species was abundant. They were located in a 52-ha permanent plot which had been established in the study site (Chai et al. 1995; Yamakura et al. 1996a, b) (Figure 2). One plot was on a gentle slope along a small creek having clay-rich soils, including many *D. lanceolata* trees (hereafter the lower-slope plot); the other plot included a wide ridge and the upper part of a steep slope on sandy soils, having a dense population of *D. aromatica* (hereafter the ridge-top plot).

Each plot was divided into 640 quadrats of 5 m × 5 m in size by theodolite and compass. Trees of all species $\geq$ 1.0 cm dbh (diameter at breast height, or at 1.3 m above the ground) were measured by dbh using a diameter tape to the nearest 0.1 cm; diameters were measured at just above buttresses for trees with

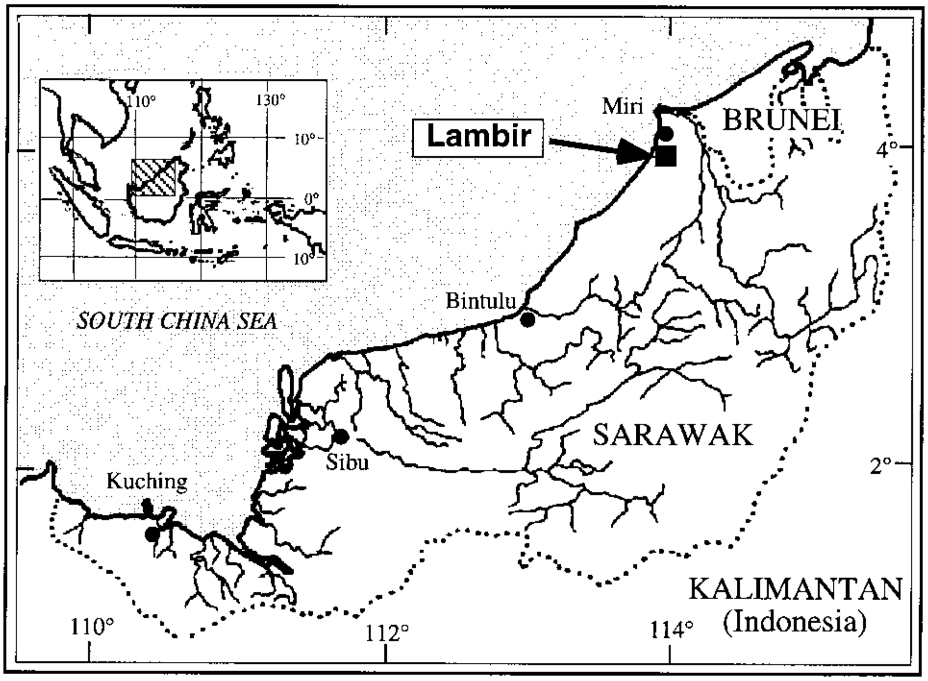

Figure 1. Location of Lambir Hills National Park.

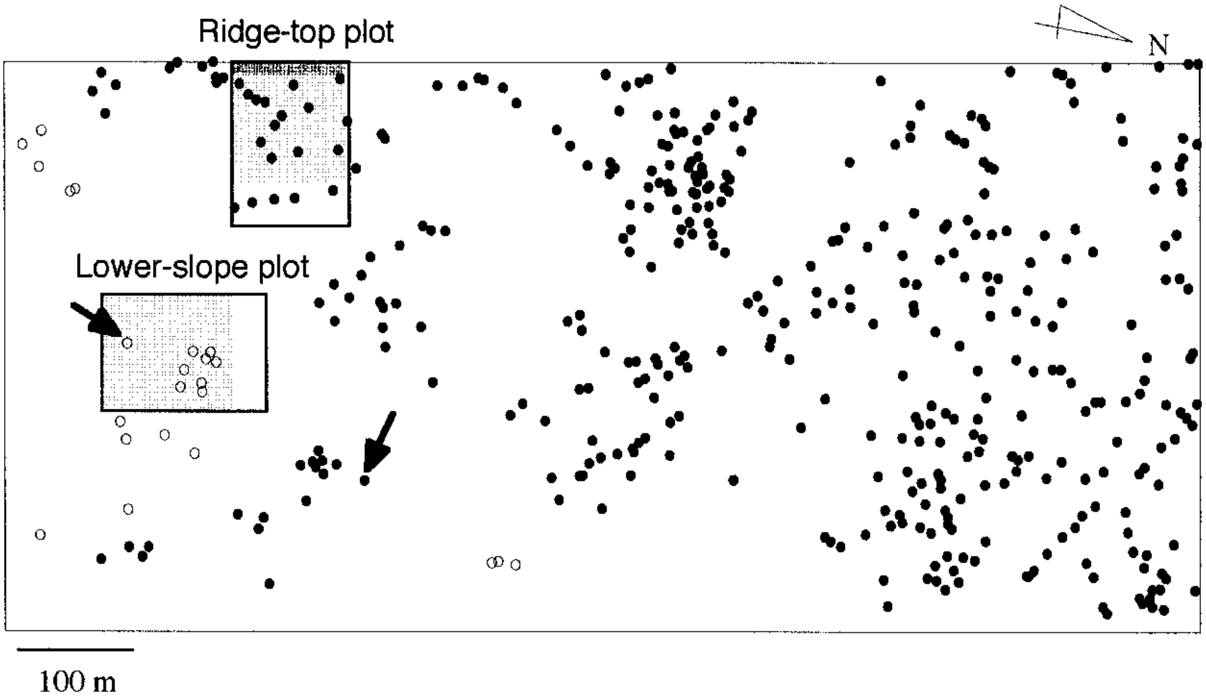

Figure 2. Positions of two 1.6-ha study plots in a 52-ha permanent plot (after Itoh et al. 1995b). Open and solid circles represent large trees ($\geq$ 30 cm in dbh) of *Dryobalanops lanceolata* and *D. aromatica*, respectively. Shaded areas were used for measurement of diffuse site factors (DSF), and the deeply shaded area was excluded for calculation of a canopy closure index (CCI) (see text for details). Arrows indicate the mother trees for the study of the distribution of newly established seedlings (see text).

buttresses. The base positions were mapped on a sheet of section paper for each quadrat. The coordinates of individual trees in the plots were calculated from the maps using a digitizer to the nearest 10 cm. The number of *Dryobalanops* trees < 1.0 cm dbh was counted for each quadrat. The census was conducted in May and September–October 1992 for the upper-ridge plot and the lower-slope plot, respectively.

Individual trees of *Dryobalanops* were categorized into five size classes according to their developmental stage and dbh, i.e., (1) seedlings at the primary leaf stage (PLS): individuals which had primary leaves on the stem, (2) seedlings: dbh < 1 cm without primary leaf, (3) saplings: $1 \leq$ dbh < 5 cm, (4) poles: $5 \leq$ dbh < 30 cm, and (5) adults: dbh ≥ 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 in the study forest, because the smallest flowering tree observed during the period 1990–1994 was about this size (A. Itoh, pers. obs.).

Distribution of newly established seedlings

To evaluate seed dispersal patterns, the distribution of newly established seedlings was determined around a solitary fruiting tree of each species. A 80 m × 80 m plot was established around each mother tree (Figure 2). There were no other fruiting conspecific trees within 40 m outside of the plots. The plot was divided into 5 m × 5 m quadrats ($N = 256$). The number of newly established seedlings in each quadrat was counted in March 1991 (4 months after seed dispersal) and in November 1992 (14 months after seed dispersal) for *D. lanceolata* and *D. aromatica*, respectively. Since primary leaves remained attached to the seedlings for more than two years (Itoh et al. 1995a), newly established seedlings were easily distinguished from advanced ones by the presence of their primary leaves.

The original seed-dispersal patterns may have been different from those of established seedlings because the processes just after germination are generally critical for seedling survival. Therefore we compared the density of dispersed seeds and that of surviving seedlings on the census dates using 1 m × 1 m quadrats ($N = 10$ and 21 for *D. aromatica* and *D. lanceolata*, respectively) in the plots.

Spatial correlation among size classes

To evaluate the spatial correlation between different size classes, we used the ω index of Iwao (1977). The ω index takes a maximum value of $+1$ for complete overlapping, through zero for independent occurrence, to a minimum of -1 for complete exclusion. The ω index was calculated between all possible pairs of the four different size classes mentioned above, except for PLS, using three different sampling unit size, i.e. 5 m × 5 m, 10 m × 10 m, and 20 m × 20 m in both the ridge-top and lower-slope plots.

Relationship between light conditions and juvenile distribution

To evaluate the effects of shading, we analyzed whether *Dryobalanops* juveniles were distributed under more open or closed conditions than expected from random distributions with respect to light conditions. The median light conditions of juveniles were compared to those of 5 m × 5 m gird data at four height levels: forest floor (50 cm above ground), seedling level (2.1 m), sapling level (9.2 m), and pole level (32.0 m). The latter three height levels were equivalent to the maximum height of each size class which was estimated by a hyperbolic equation of height to dbh (Ogawa et al. 1965):

$$\frac{1}{H} = \frac{1}{A \times D} + \frac{1}{H^*}, \tag{1}$$

where H is tree height in m, D is dbh in cm, and A and H^* are coefficients specific to a forest. We used the coefficients ($A = 2.162$ m cm^{-1}, $H^* = 63$ m) estimated from 112 sample trees in the study forest using the least squares method (Yamakura et al. 1996b). The maximum heights were calculated using the maximum dbh of each size class: 1 cm, 5 cm and 30 cm for seedling, sapling and pole size classes, respectively.

For evaluation of light conditions at the forest floor, we used a diffuse site factor (DSF), which is the percentage of diffuse light at a given site compared with total light in the open (Anderson 1964). DSF indicates the average light condition of a measured point (Mitchell & Whitmore 1993; Whitmore et al. 1993). Hemispherical photographs were taken 50 cm above the ground at the center of each 5 m × 5 m quadrat with a fisheye lens (Nikon Fisheye Nikkor 8 mm) in a 1.2-ha area of each study plot (Figure 2). A total of 960 photos were taken in September–October and November 1992 in the lower-slope and ridge-top plots, respectively. The value of DSF was calculated by the manual method of Anderson (1964).

A modified canopy closure index (Lieberman et al. 1989, 1995) (CCI) was used for the shading conditions at the other three height levels. CCI of Lieberman et al. (1989) uses the following measures: the horizontal distance (d) between the focal point in the-three dimensional space and each taller tree within a given radius; the height difference (h) between the focal point and each taller tree; and the distance (Δh) from the focal point to the top of each taller tree, calculated from d and h. The ratio $\Delta h/h$ is the sine of the included angle θ. CCI is defined as the sum of these ratios for all taller trees within the specified radius (10 m in thus study):

$$\mathrm{CCI} = \sum_{i=1}^{n} \sin\theta. \tag{2}$$

Though their CCI calculation assumed flat topography, the difference in ground height was not negligible in the current study plots. Thus we adjusted the value of h as:

$$h^{*} = (H + a_t) - (l + a), \tag{3}$$

where H is the height of the focal tree, a_t is the relative altitude at the center of the quadrat in which the tree is located, l is the focal height level, and a is the relative altitude at the center of focal quadrat. H was estimated by Equation (1) independent of species. The value of a and a_t were estimated to the nearest 1 m from a 1-m-interval contour map, which was made on the basis of land-survey data of 20 m × 20 m gird in the 52-ha plot.

We used the data of tree positions and dbh of all species $\geq$ 1 cm dbh in the study plots and the areas 10 m outside of the plots, which were from the data set of the 52-ha tree census (Chai et al. 1995; Yamakura et al. 1995; 1996). We did not calculate CCI in a western side area (10 m × 100 m) of the ridge-top plot because this area is on the margin of the 52-ha census plot and no tree position and diameter data was available outside of the area (Figure 2). CCI was thus calculated for all quadrats at three height levels within 1.6-ha and 1.5-ha areas in the lower-slope plot and the ridge-top plot, respectively.

Then, we calculated the light conditions of individual juveniles for all species in the plots. We assumed that all juveniles within a particular quadrat had the same light condition of the equivalent height levels: DSF at forest floor or CCI at 2.1 m high for the seedling size class (dbh $<$ 1 cm), CCI at 9.3 m high for the sapling size class ($1 \leq$ dbh < 5 cm), and CCI at the 32.0 m high for the pole size class ($5 \leq$ dbh < 30 cm). For the seedling size, we only calculated for *Dryobalanops* because we had no seedling data for other species.

If individual juveniles are distributed at random with respect to light conditions, the probability of juveniles being included in a particular quadrat is same among the quadrats. Thus, we expect an insignificant difference between the median light conditions calculated for the quadrats and those for the juveniles. If more juveniles are distributed under more open conditions, we expect larger median light conditions for juveniles than quadrats. To evaluate the light conditions of all juvenile species, we compared the medians of the sapling and pole size class trees of all species, including *Dryobalanops*, with those of quadrats at the equivalent height levels, separately, using the Mann–Whitney U-test. This indicates if light conditions affect the spatial distributions of all juveniles. Then we compared the median light conditions of Dryobalanops seedlings, saplings and poles, respectively, with those of quadrats. This indicates the effects of light conditions on the spatial distributions of only *Dryobalanops* juveniles.

The statistical analysis was conducted by SYSTAT (Wilkinson 1992).

Results

Stand structure

The two plots apparently differed in forest structure (Figure 3). The ridge-top plot was 1.4 times denser in the number of stems than the lower-slope plot. The maximum dbh was larger in the lower-slope plot (194 cm) than in the ridge-top plot (124 cm). The differences in the tree density and basal area were greatest in the smaller size classes; the total basal area was 11.3 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ and 15.7 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ for trees larger than 51 cm dbh; but 18.6 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ and 31.2 $\mathrm{m}^2\ \mathrm{ha}^{-1}$ for the smaller trees, in the lower-slope and ridge-top plots, respectively.

D. aromatica and *D. lanceolata* were the most abundant canopy species in the ridge-top plot and the lower-slope plot, respectively. They occupied 19.7% (*D. aromatica*) and 16.9% (*D. lanceolata*) of the total basal area of trees $\geq$ 31 cm dbh, and 29.6% (*D. aromatica*) and 23.1% (*D. lanceolata*) of that of trees $\geq$ 51 cm dbh (Figure 3). Both species had abundant juveniles

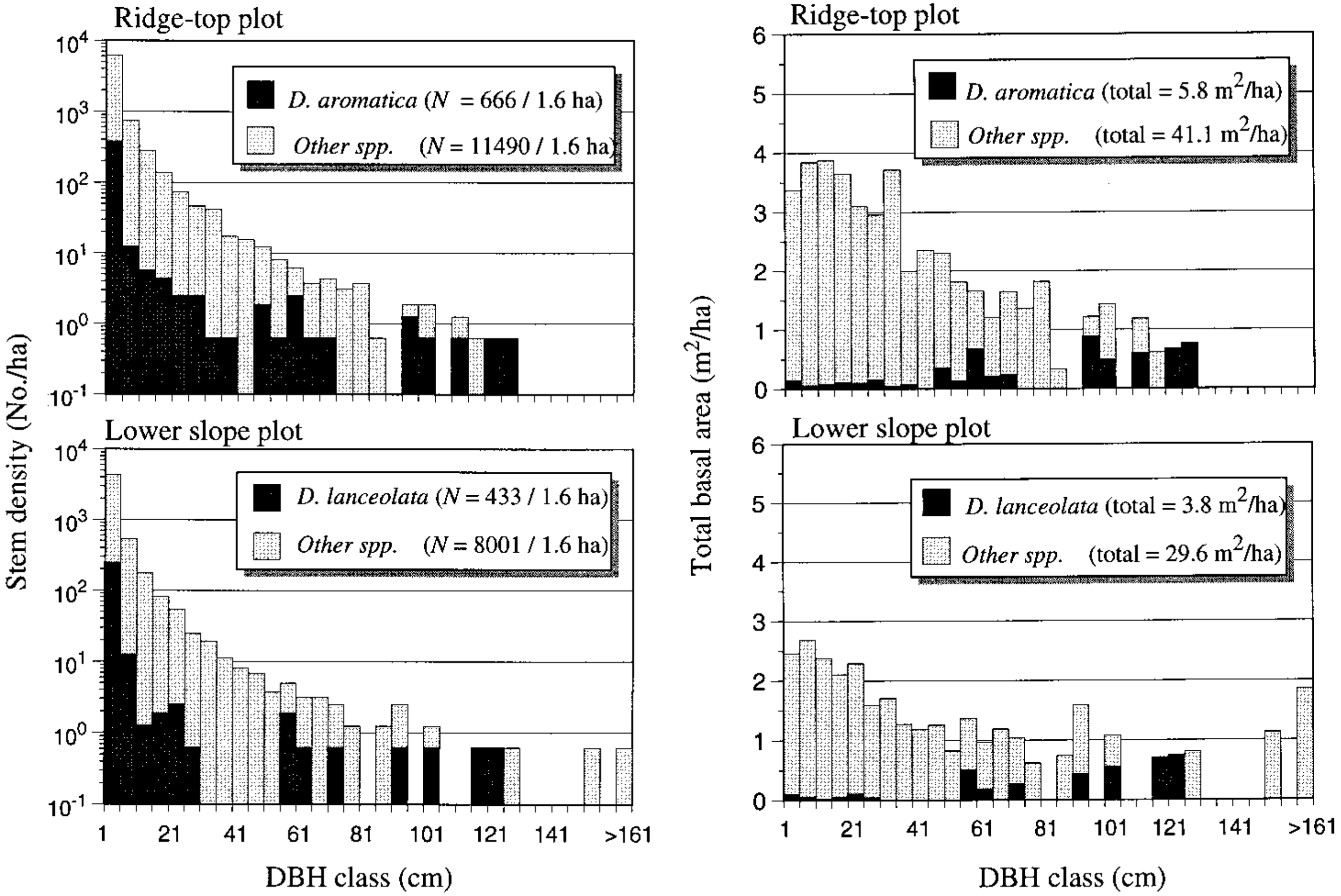

Figure 3. Stem density (right) and total basal area (left) at various dbh classes in two 1.6-ha plots of *Dryobalanops*-dominant strands. Each column is divided into *Dryobalanops* and other species. Values of total density and basal area of other spp. exclude those of *Dryobalanops*.

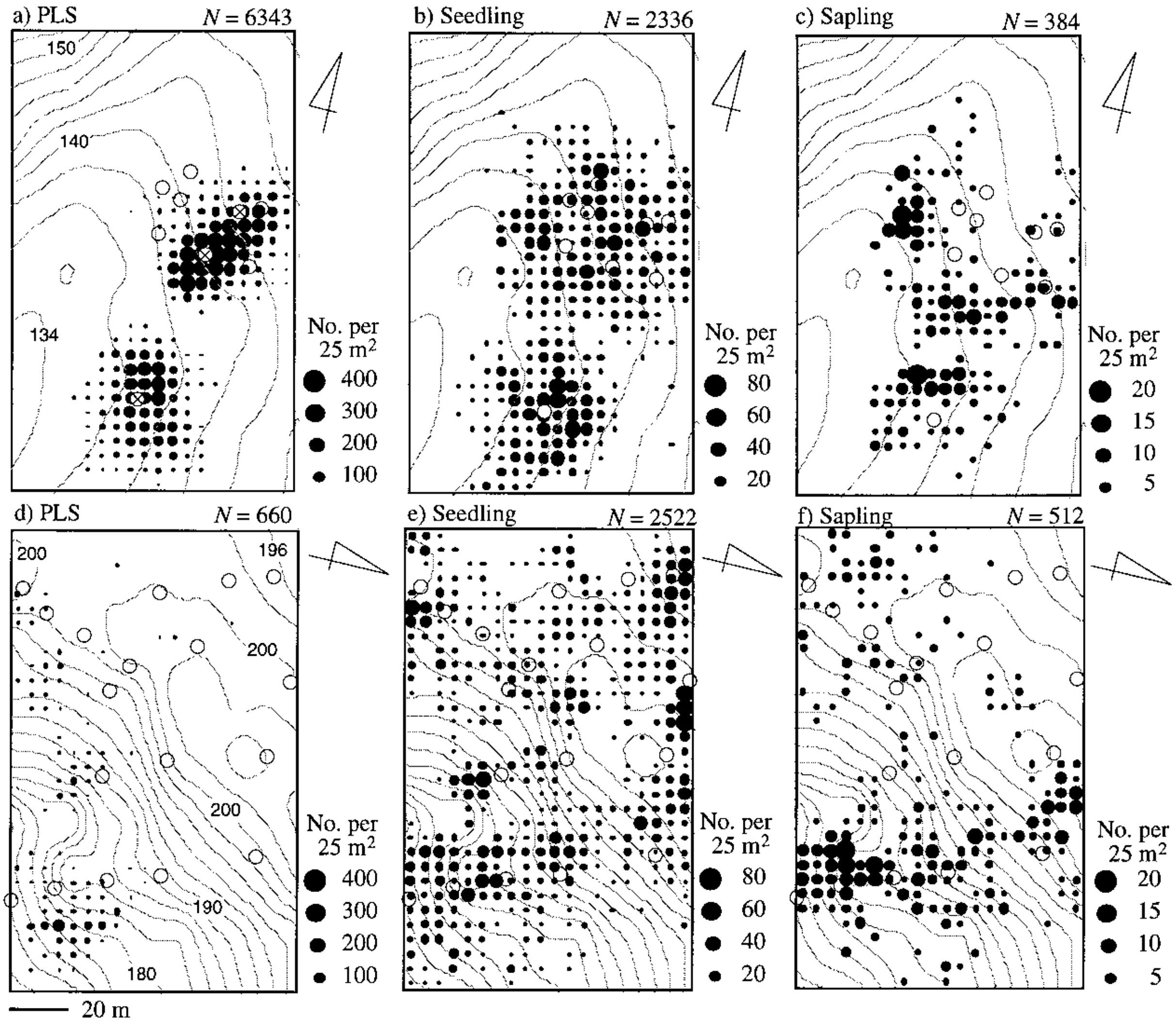

Figure 4. Spatial distributions of the density of primary-leaf seedlings (PLS), other seedlings (dbh $<$ 1 cm), and saplings (1 $\leq$ dbh $<$ 5 cm) of *Dryobalanops lanceolata* (a-c) and *D. aromatica* (d–f). Dotted lines are topographic contours at 2 m intervals. Open circles represent *Dryobalanops* trees with dbh $\geq$ 30 cm. Open circles with × inside in (a) indicate trees which had fruited within two years before enumeration.

including individuals smaller than 1 cm dbh (Figures 3 and 4).

Distribution of new seedlings around mother trees

The mortality of seeds/seedlings in 1 m × 1 m quadrats during the period from seed dispersal to the census dates was spatially at random without significant relationship to initial seed density or distance from mother trees (see also Itoh et al. 1995a). The density of seedlings in the quadrats at the census dates was significantly correlated to initial seed density in both species ($r = 0.68$–$0.89, p = 0.001$–0.03). We, therefore, concluded that there were little difference in spatial patterns between the dispersed seeds and the established seedlings.

Newly established seedlings of *D. aromatica* and *D. lanceolata* showed similar distributions (Figure 5). The seedling density had no correlation with distance from mother trees within 10 m, where most quadrats were under the canopies of the mother trees. At a distance of more than 10 m from the mother trees, the seedling density decreased rapidly with distance, and negative linear regressions were fitted well on a double logarithmic scale.

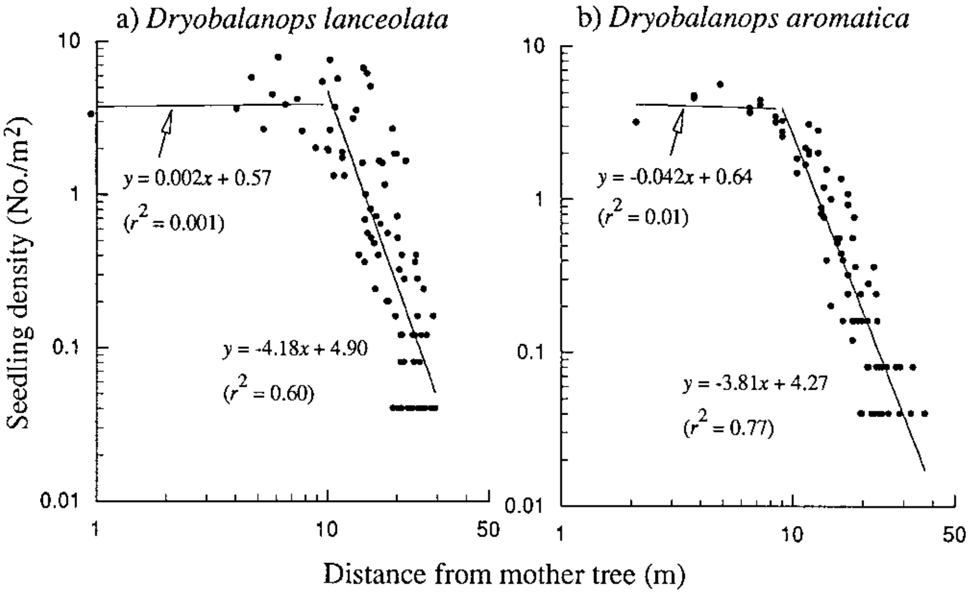

Figure 5. Relationships between the distance from mother trees and density of newly established seedlings of two *Dryobalanops* species. Solid lines are separated regression lines on a log-log scale for 0–10 m and $>$ 10 m from the mother trees.

Spatial pattern of juvenile distribution

In the lower-slope plot, PLSs were dense near the trees that had fruited within two years before the census; one of them fruited in December 1990 (21 months before the census) and the other two in September 1991 (13 months before the census) (Figure 4a). Seedlings were abundant in quadrats within 40 m of conspecific adults. The mean density of seedlings was highest within 5 m of the nearest conspecific adult, and decreased with distance (Figure 6c). By contrast, relatively few saplings were found under canopies of conspecific adults (Figure 4c). The mean density of saplings and poles had a peak at 15–20 m (Figure 6c). 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 (Figure 6e).

In the ridge-top plot, PLSs were not as abundant as those in the lower-slope plot (Figure 4d). They were not necessarily most abundant in the nearest quadrats to conspecific adults, though the mother trees were not identified; fruiting was observed in December 1990 (15 months before the census). Seedlings were widely distributed all over the plot (Figure 4e); the density had a peak at 5–10 m (Figure 6d). The distribution of saplings was more patchy than that of seedlings; there were few saplings on the northwestern site of the plot, where the slope was gentle and the forest floor was strongly shaded (Figure 4f). 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 (Figure 6d). The peaks of frequency were 5–10 m for seedlings and saplings, and 10–15 m for poles (Figure 6f).

The distribution of *D. lanceolata* seedlings was aggregated with conspecific adults at all three unit sizes (Table 1). The distributions of saplings and poles of *D. lanceolata* were independent to that of adults at smaller quadrat sizes, but positively correlated at the largest unit size (20 m × 20 m). It is suggested that saplings and poles were distributed within those 20 m × 20 m units which include conspecific adults, but that their density was not always high near adults within the unit area. Seedlings and adults of *D. aromatica* also aggregated at larger unit sizes, but segregated at the small unit size (5 m × 5 m), suggesting a negative distribution pattern between adults and seedlings at a very local scale. The saplings and poles of *D. aromatica* showed negative correlations to adults at the larger quadrat sizes, indicating they tended to be distributed far from conspecific adults at these scales.

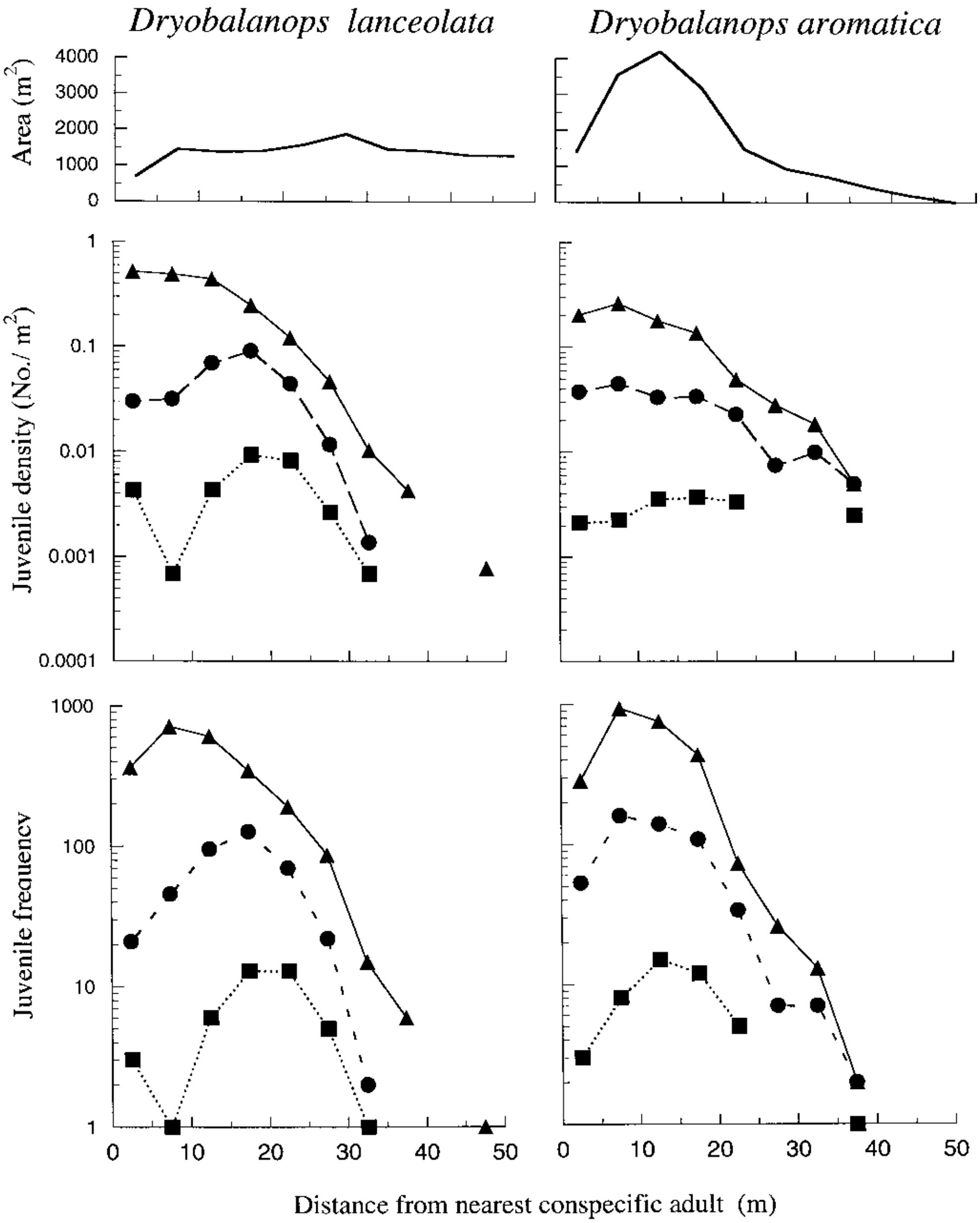

Figure 6. Relationships between the distance from the nearest conspecific adult (dbh $\geq$ 30 cm) and density (c–d) or frequency (e–f) of seedlings (triangles: dbh $<$ 1 cm), saplings (circles: 1 $\leq$ dbh $<$ 5 cm) and poles (squares: 5 $\leq$ dbh $<$ 30 cm) of two *Dryobalanops* species. The distance was categorized into 5-m intervals; each point was plotted at the middle of each 5-m interval. The upper figures (a–b) show the total area of each distance interval, which was calculated from the number of 5 m × 5 m quadrats in each interval.

Relationship between light condition and juvenile distribution

Light conditions were correlated with the distance from nearest *Dryobalanops* adult in both plots (Table 2). The relationships were different between the two plots; CCI at 2.1 m and 9.1 m were negatively correlated to the adult distance in the lower-slope plot, but positively in the ridge-top plot. The negative correlations in the lower-slope plot may be due to the bias of the north-eastern corner of the plot (ca. 40 × 40 m^2), where forest structure was different from other part of the

Table 1. The ω-index (Iwano 1977) in three unit sizes between different size classes of two *Dryobalanops* species. Numerals in parenthesis are total stem number per 1.6 ha.

Size class*	Unit size (m × m)								
	5 × 5			10 × 10			20 × 20		
	Seedling	Sapling	Pole	Seedling	Sapling	Pole	Seedling	Sapling	Pole
Dryobalanops lanceolata									
Seedling (2336)									
Sapling (384)	**0.24**			**0.38**			**0.55**		
Pole (42)	**0.10**	**0.35**		**0.24**	**0.57**		**0.33**	**0.74**	
Adult (9)	**0.20**	0.04	0.02	**0.33**	0.03	0.06	**0.67**	**0.31**	**0.16**
Dryobalanops aromatica									
Seedling (2519)									
Sapling (512)	**0.24**			**0.34**			**0.37**		
Pole (44)	0.01	**0.19**		0.05	**0.30**		**0.21**	**0.46**	
Adult (18)	*−0.15*	0.01	0.03	**0.18**	0.02	*−0.19*	**0.38**	−0.04	*−0.14*

Positive values $\geq +0.1$ are shown by bold letters; negative values ≤ -0.1 are shown by italic letters.
* Seedling: dbh $<$ 1 cm; sapling: $1 \leq$ dbh $<$ 5 cm; pole: $5 \leq$ dbh $<$ 30 cm; adult: dbh $\geq$ 30 cm

plot. Tree density was much higher and CCI was larger in that area. The area was far ($>$ 40 m) from present *Dryobalanops* adults and no *Dryobalanops* occurred there. If we consider only the seed dispersal range ($<$ 40 m from nearest adult; cf. Figure 5), the distances were correlated to light conditions similarly for both plots: there were insignificant correlations for DSF and negative correlations for CCI at all height levels. This indicates that, within the seed dispersal range, locations near adult *Dryobalanops* were more shaded than those farther at the height levels 2–32 m.

The lower-slope plot had smaller medians both for DSF and CCI than the ridge-top plot at the same height levels (Table 3). This is curious because the results suggest that the lower-slope plot was more shaded at the forest floor level but less shaded at the higher levels. This may be explained that CCI is based on the tree heights estimated from dbh, and takes no account of variation in the height-dbh relationship and the size of crowns. Trees on sandy and ridge sites tend to be shorter and to have smaller crowns that those which have the same dbh on clay and downslope sites (A. Itoh pers. obs.). Therefore, CCI is inappropriate for a comparison of light conditions between sites, but it is useful for a comparison within a site where the relationships between dbh and height or crown size vary little. On the other hand, DSF can use for comparisons both between and within sites, because it takes account of the actual light penetrating crowns.

Medians of DSF and CCI for seedlings of both species were not different from those for the quadrats which located at 5 m × 5 m grid within the plots (Table 3). This suggests that their seedlings were distributed at random in the study plots with respect to light conditions. Medians of CCI were significantly smaller for saplings of both species and poles of *D. lanceolata* than expected from random distributions, indicating that their distributions were inclined to more open conditions. Poles of *D. aromatica* had, on the other hand, a significantly larger median CCI than expected from random distributions; they were located under more shaded conditions than expected by chance.

Medians of CCI for all juvenile species including *Dryobalanops* were not significantly different from the quadrats' medians for all size classes except for the sapling size class in the lower-slope plot (Table 3). Sapling size trees of all sapling species had a larger median CCI than those of *D. lanceolata* in the lower-slope plot. Thus the above mentioned median differences from random distributions in *Dryobalanops* juveniles were species specific features rather than features of the whole stand structure.

Results were the same if we considered only the seed dispersal range ($<$ 40 m from nearest adult) in the lower-slope plot, except that the median CCI of all species at the sapling level (9.1 m above ground) was not different from expected random distributions ($p = 0.166$ by Mann-Whitney U-test).

Table 2. Correlation coefficients between distance from nearest adult of *Dryobalanops aromatica* (ridge-top plot) or *D. lanceolata* (lower-slope plot) and shading conditions. Shading conditions are evaluated by diffuse site factor (DSF) at 50 cm above ground and by a canopy closure index (CCI) at 2.1 m, 9.1 m and 32.0 m. Smaller CCI and larger DSF indicate more open conditions. See text for CCI calculation. Maximum distances from nearest *Dryobalanops* adult are 41.4 m and 78.1 m for the ridge-top and lower-slope plots, respectively. Values calculated for the seed dispersal range ($<$ 40 m from nearest *D. lanceolata* adult) are also shown for the lower-slope plot. Numerals in parenthesis are sample sizes.

	Lower-slope plot		Ridge-top plot
	Whole plot	$<$ 40 m from adult	
$\log_{10}$(%DSF)	0.118^{**} (480)	0.081 (406)	-0.047 (480)
CCI at 2.1 m	0.227^{***} (640)	-0.179^{**} (466)	-0.161^{***} (600)
CCI at 9.1 m	0.112^{**} (640)	-0.242^{***} (466)	-0.357^{***} (600)
CCI at 32.0 m	-0.289^{***} (640)	-0.434^{***} (466)	-0.344^{***} (600)

Significance level: $^{**}p < 0.01$; $^{***}p < 0.001$.

Table 3. Median light conditions of *Dryobalanops aromatica* and *D. lanceolata* juveniles. Light conditions are evaluated by a diffuse site factor (DSF) at 50 cm above ground and a canopy closure index (CCI) at 2.1 m for seedlings (dbh $<$ 1 cm), and by CCI at 9.1 m and 32.0 m for saplings ($1 \leq$ dbh $<$ 5 cm) and poles ($5 \leq$ dbh $<$ 30 cm), respectively. Medians of all tree species (including *Dryobalanops*, are also shown for the sapling and pole size classes. E: medians for 5 m $\times$ 5 m grid data, which are expected from random distribution with respect to DSF and CCI values (see text.). Smaller CCI and larger DSF than those of E within each size class and plot indicate that juveniles are distributed under more open conditions than expected from random distributions. Numerals in parenthesis are sample sizes.

Size class	Lower-slope plot			Ridge-top plot		
	D. lanceolata	All species	E	*D. aromatica*	All species	E
Seedling						
$\log_{10}$(%DSF)	0.230 (2307)	–	0.224 (480)	0.366 (2077)	–	0.317 (480)
CCI at 2.1 m	47.65 (2336)	–	48.02 (640)	71.10 (2431)	–	71.30 (600)
Sapling						
CCI at 9.1 m	14.86^{*} (384)	16.10^{*} (6529)	15.65 (640)	23.44^{**} (497)	25.41 (8631)	25.23 (600)
Pole						
CCI at 32.0 m	0.353^{**} (42)	0.798 (1782)	0.843 (640)	1.789^{*} (41)	1.469 (2418)	1.451 (600)

Significance level of difference from random distributions (E): $^{*}p < 0.05$; $^{**}p < 0.01$.

Discussion

Mechanisms affecting observed spatial patterns

Although seedlings of the two *Dryobalanops* species, including newly established ones, were dense around the present mother trees, negative distribution patterns were observed between larger juveniles and conspecific adults (Figures 4 and 6, Table 1). Saplings and poles were denser at some distance (10–20 m) from

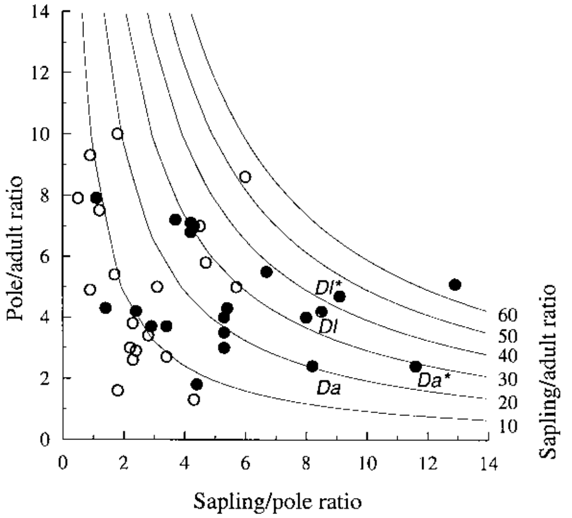

Figure 7. Relationships among sapling/pole, pole/adult and sapling/adult ratios for emergent tree species in a 50-ha plot in Pasoh and for Dryobalanops in a 52-ha plot and its dominant stands (1.6-ha) in Lambir. Closed circles are species of Dipterocarpaceae; open circles are species of other families. *Da*: *D. aromatica*; *Dl*: *D. lanceolata*; asterisks indicate the dominant stands (1.6-ha plots of the current study). Sampling: $1 \leq$ dbh < 5 cm; pole: $5 \leq$ dbh < 30 cm; adult: dbh ≥ 30 cm. Values for Pasoh species are calculated from Manokaran et al. (1992).

the present nearest adult (Figure 6). There are two possible explanations for this result: (1) there were other adults, which produced some of the present saplings and poles, and are now dead; (2) the negative distribution patterns were produced during the period from seedlings through saplings to poles.

In the former case, most offsprings may not mature under their mother trees before the adults die. This may happen if juvenile growth is very slow under the adult canopies and adults' mortality rate is high. We expect, in this case, two distinct patches in a population: patches including adults with small juveniles, and patches of large juveniles without adults or small juveniles. Such a population structure was found for a canopy species, *Calophyllum* cf. *soulattri* Burm., in tropical rainforests in Sumatra, Indonesia (Mukhtar et al. 1992). In the current study, however, all juveniles of *Dryobalanops* were found within the possible dispersal area ($<$ 40 m) of the present adults, and there were no areas which had only saplings or poles without any seedlings (Figure 4). Thus, we cannot reject the possibility that all the juveniles were offsprings of the present adults.

In the latter case, several mechanisms could produce the observed patterns. One possibility is density- and/or distance-dependent mortality of seedlings as proposed by Connell (1971) and Janzen (1970). Hervibores or pathogens have been found to cause such mortality in some neotropical rainforest tree species, though most cases were found in seed or early seedling mortality (*e.g.* Augspurger 1983a, b; 1984; Burkey 1994; Clark & Clark 1984; Condit et al. 1992, 1994). Another possible mechanism is requirement of canopy gaps for regeneration (Augspurger et al. 1983a; Hamill & Wright 1986; Condit et al. 1992; Kohyama et al. 1994). If seedlings require open conditions to survive and grow into saplings and poles, distributions of saplings and poles may be concentrated in less shaded sites, which are not under the present mother trees.

The light-condition analysis (Table 3) supports the importance of canopy gaps to the survival of saplings and poles. It suggests that shading has no effect on seed survival, germination and seedling establishment but that established seedlings may need more open conditions to become saplings than do most of the other species. They may be able to survive and/or grow to saplings within canopy gaps, but they may be less competitive to more shade-tolerant species under shaded conditions. Itoh et al. (1995a) also found little effect of shade on seed survival, germination and seedling establishment of the two species in the study forest.

However, poles of *D. aromatica* had more shaded conditions than expected from random distributions (Table 3). This is inconsistent with the gap preference hypothesis mentioned above. A possible explanation is that poles of *D. aromatica* were excluded from the extremely open areas which were found within small land slides (ca. 200–600 m^2 in size) on the steep slope of the ridge-top plot. If we exclude the quadrats of < 1 CCI at the pole level, the median CCI of *D. aromatica* poles was 1.980, slightly smaller than those of all quadrats (1.985) and pole size trees of all species (2.062), though the differences were insignificant ($p = 0.59 - 0.86$ by Mann–Whitney U-test). *D. aromatica* may not be able to regenerate under severely disturbed areas such as land slides, probably because its advanced seedlings and saplings are killed by the severe disturbance and outcompeted by pioneers.

In spite of the suggested importance of gaps, we cannot conclude which of the two possible mechanisms, gap requirement and distance-dependent mortality, is more important. Since CCI and distance from adults were negatively correlated (Table 2), both seedling mortality by shading and that by distance-dependent factor(s) can result in the observed negative distribution patterns. It is also possible that both mechanisms are working simultaneously. Moreover, we cannot reject the above-mentioned possibility that dead adults influenced the present juvenile distributions. We need to continue to monitor juvenile mortality and its cause(s) to understand the working mechanisms underlying the observed patterns. The ongoing studies on population dynamics of trees $\geq$ 1 cm dbh of all species, including *Dryobalanops*, in the 52-ha plot (cf. Chai et al. 1995; Yamakura et al. 1996a) and on juvenile dynamics of *Dryobalanops* $<$ 1 cm dbh in the current study plots will help answer this question.

Intermediate dominance of Dryobalanops

Whitmore (1984) hypothesized that 'regeneration pressure' was the cause of the canopy dominance by *D. aromatica* in some Malayan rainforests. He suggested that 'there were more likely to be small (*D. aromatica*) individuals awaiting release than other species' due to its relatively frequent fruiting and the high shade-tolerance of its juveniles (see also Kachi et al. 1993).

Empirical evidence suggests that *Dryobalanops* has relatively short intervals of fruiting among dipterocarp species (Chan & Appanah 1980; Itoh 1995). In the Lambir forest, the two *Dryobalanops* species were among the most frequently fruiting canopy species during the period 1990–1996; they fruited in 1990, 1991, 1992, 1993, 1994 (only few *D. aromatica*) and 1996 (A. Itoh pers. obs.). Most of the trees which fruited were different individuals in each year. 1990, 1992 and 1996 were mast fruiting years which included many other species. Besides these observations, the high germination (66–84% of fallen mature seeds), establishment (42–64% of fallen mature seeds) and early seedling phase survival (83–85%/yr of established seedlings) rates (Itoh et al. 1995a) are likely support the regeneration pressure hypothesis.

However, if this high survival in the early seedling phase is a factor contributing to canopy dominance, the trend of high survival must be maintained thorough subsequent size classes (Hart 1995). We must check if *Dryobalanops* actually has more juveniles than other canopy species.

Unfortunately, we do not have data of juvenile abundance for other individual species in the study forest, because species identification has not yet been completed and we did not count seedlings ($<$ 1 cm dbh) of other species. Therefore, we compared the juvenile abundance of *Dryobalanops* in Lambir (the 52-ha plot) to that of emergent species in Pasoh, West Malaysia (a 50-ha plot). The Pasoh forest is dominated by Dipterocarpaceae, but there is no dominant species like *Dryobalanops* in the Lambir plot (Kochummen et al. 1990; Manokaran et al. 1992).

The sapling to adult ratios of *D. lanceolata* and *D. aromatica* were the 4th and 15th largest among the 38 emergent species (Figure 7, Appendix 1). The pole to adult ratios were among the lower group: 21st and 35th for *D. lanceolata* and *D. aromatica*, respectively. The results were similar if we used the data of dominant stands (the current study plots) for *Dryobalanops*, except that the ratios of saplings to poles were slightly larger than those for the whole 52-ha (Figure 7, Appendix 1). Therefore, there is no evidence at present that *Dryobalanops* in the study forest has more pole size trees awaiting release than emergent species in the Pasoh forest, though *Dryobalanops* has relatively abundant saplings. We do not yet know whether *Dryobalanops* has more seedlings than other species, since we have no data of seedling abundance except for *Dryobalanops*.

The remarkable feature of *Dryobalanops* population structure is the high sapling to pole ratio (Figure 7, Appendix 1). This suggests two possible explanations: (1) mortality during the period from saplings to poles is higher in *Dryobalanops* than in most of the other emergent species; (2) *Dryobalanops* populations in Lambir are increasing. In the former case, the intermediate canopy dominance of *Dryobalanops* can be interpreted as a stable condition. In the latter case, however, the degree of dominance may increase and *Dryobalanops* may dominate the whole canopy, cyclically or permanently, at least in their appropriate habitats.

The current study supports the former interpretation. The negative correlations between adults and saplings or poles suggest existence of some mechanisms that inhibit survival and growth of seedlings in the vicinity of conspecific adults. This possibly prevents *Dryobalanops* from dominating the whole canopy, whatever the mechanism is. If a species has better ability in seedling establishment than other species and its post-establishment survival is worse than others when near adults, its population would increase under low adult abundance but it could not come to dominate the whole canopy. The larger sapling to pole ratios in the dominant stands than in the whole 52-ha plot (Figure 7, Appendix 1) might suggest that survival of saplings in the dominant stands is lower than that is the average in the 52-ha plot, where dominant stands of *Dryobalanops* were patchily distributed (Figure 2).

It is interesting to note that this result is in contrast to the findings in a monodominant forest of *Gil-*

bertiodendron dewevrei (De Wild.) Léonard, in Zaïre (Hart 1995). *Gilbertiodendron* had a lower establishment rate (0.3% of fallen seeds) and a higher seedling survival rate in the understorey (49% per 10 years) than a subdominant species, *Julbernardia seratii* (De Wild.) Troupin. Population structure also suggested higher survival of sub-canopy size class juveniles of *Gilbertiodendron*. Hart (1995) concluded that *Gilbertiodendron* maintains canopy dominance by the high juvenile survival that compensates for the high seed mortality.

Nonetheless, it remains to be evaluated whether the observed negative patterns are actually working to prevent the two *Dryobalanops* species from dominating the whole canopy. The above-mentioned monitoring of the population dynamics in the study plot (cf. Chai et al. 1995; Yamakura et al. 1995; 1996) should eventually shed light on the problem of the intermediate dominance of *Dryobalanops*.

Acknowledgements

We thank Datuk Leo Chai C.L. and Dr S. Tamura for their general direction of a long term ecological study project in Sarawak, of which the present research was a part, the Forest Department of Sarawak and the Sarawak State Government for permission to do this research, Mr E. O. K. Chai and the staff of the Silvicultural Research Office, Sibu for field work and data processing, and Dr J. V. LaFrankie and Mr S. S. Tan for species identification. We also thank Drs H. Watanabe and I. Yamada for their encouragement during the research. This research was partly funded 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.

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Appendix 1. Number of trees in three size classes of emergent species in a 50-ha plot in Pasoh and *Dryobalanops* in a 52-ha plot and in dominant stands (1.6-ha) in Lambir. S: Sapling ($1 \leq$ dbh < 5 cm); P: pole ($5 \leq$ dbh < 30 cm); A: adult (dbh ≥ 30 cm). Juvenile ratios calculated between all pairs of the size classes are also shown. Pasoh species are ranked according to the sapling to adult ratio (S/A). Values for Pasoh species are calculated from Manokaran et al. (1992). Values for all species in Pasoh are estimated from Manokaran & LaFrankie (1990).

Species	Family	Size class				Juvenile ratio		
		S	P	A	Total	S/P	P/A	S/A
		Lambir						
1.6-ha plot (current study)								
Dryobalanops aromatica	Dipterocarpaceae	512	44	18	574	11.6	2.4	28.4
All species		9380	2564	211	12155	3.7	12.2	44.5
Dryobalanops lanceolata	Dipterocarpaceae	384	42	9	435	9.1	4.7	42.7
		6529	1782	121	8432	3.7	14.7	54.0
All species								
52-ha plot								
Dryobalanops aromatica	Dipterocarpaceae	7410	909	383	8702	8.2	2.4	19.3
Dryobalanops lanceolata	Dipterocarpaceae	829	97	23	949	8.5	4.2	36.0
All species		282578	70161	6192	358931	4.0	11.3	45.6
		Pasoh						
50-ha plot								
Shorea guiso	Dipterocarpaceae	659	51	10	720	12.9	5.1	65.9
Sindora coriaceae	Leguminosae	1040	172	20	1232	6.0	8.6	52.0
Neobalanocarpus heimii	Dipterocarpaceae	2800	416	75	3291	6.7	5.5	37.3
Dialium maingayi	Leguminosae	66	40	2	108	1.7	20.0	33.0
Shorea ochrophloia	Dipterocarpaceae	382	48	12	442	8.0	4.0	31.8
Calophyllum macrocarpum	Guttiferae	188	42	6	236	4.5	7.0	31.3
Shorea maxwelliana	Dipterocarpaceae	4484	1048	150	5682	4.3	7.0	29.9
Shorea ovalis	Dipterocarpaceae	1026	247	35	1308	4.2	7.1	29.3
Shorea bracteolata	Dipterocarpaceae	892	212	31	1135	4.2	6.8	28.8
Kokoona reflexa	Celastraceae	199	35	7	241	5.7	5.0	28.4
Dialium platysepalum	Leguminosae	866	186	32	1084	4.7	5.8	27.1
Shorea macroptera	Dipterocarpaceae	1221	330	46	1597	3.7	7.2	26.5
Shorea pauciflora	Dipterocarpaceae	1928	358	84	2370	5.4	4.3	23.0
Dipterocarpus costulatus	Dipterocarpaceae	506	96	24	626	5.3	4.0	21.1
Shorea acuminata	Dipterocarpaceae	1780	335	96	2211	5.3	3.5	18.5
Canarium megalantyum	Burseraceae	123	70	7	200	1.8	10.0	17.6
Shorea leprosula	Dipterocarpaceae	2405	458	154	3017	5.3	3.0	15.6
Dysoxylum carolinea	Meliaceae	78	25	5	108	3.1	5.0	15.6
Shorea parvifolia	Dipterocarpaceae	1230	359	96	1685	3.4	3.7	12.8
Dipterocarpus crinitus	Dipterocarpaceae	165	56	15	236	2.9	3.7	11.0
Dipterocarpus cornutus	Dipterocarpaceae	972	407	96	1475	2.4	4.2	10.1
Atuna excelsa	Rosaceae	304	109	32	445	2.8	3.4	9.5
Irvingia malayana	Irvingiaceae	135	81	15	231	1.7	5.4	9.0
Triomma malaccensis	burseraceae	351	104	39	494	3.4	2.7	9.0
Cynometra malaccensis	Leguminosae	776	334	87	1197	2.3	3.8	8.9
Heritiera simplicifolia	Sterculiaceae	211	223	24	458	0.9	9.3	8.8
Parashorea densiflora	Dipterocarpaceae	78	71	9	158	1.1	7.9	8.7
Shorea lepidota	Dipterocarpaceae	866	196	110	1172	4.4	1.8	7.9
Pentaspadon motleyi	Anacardiaceae	475	196	67	738	2.4	2.9	7.1
Quercus argentata	Fagaceae	657	295	98	1050	2.2	3.0	6.7
Anisoptera laevis	Dipterocarpaceae	73	52	12	137	1.4	4.3	6.1
Lopopetalum floribundum	Celastraceae	83	36	14	133	2.3	2.6	5.9
Intsia palembanica	Leguminosae	369	85	66	520	4.3	1.3	5.6
Dyera costulata	Apocynaceae	126	141	29	296	0.9	4.9	4.3
Mangifera griffithii	Anacardiaceae	46	87	11	144	0.5	7.9	4.2
Koompassia malaccensis	Leguminosae	348	193	123	664	1.8	1.6	2.8
All species		270050	65100	3750	338900	4.1	17.4	72.0