Relationship between Topography and Distributions of Two Emergent Species, *Dryobalanops aromatica* and *D. lanceolata* (Dipterocarpaceae), in a Tropical Rain Forest, Sarawak

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ABSTRACT

Dryobalanops aromatica and *D. lanceolata* (Dipterocarpaceae) are co-occurring emergent species in the mixed dipterocarp forest of Lambir Hills National Park, Sarawak. Their spatial distributions were studied in a large permanent plot (52 ha in size), whose topography was highly heterogeneous. *D. lanceolata* had clumps (ca. 1 ha) consisting of large trees and 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. aromanca* juveniles, however, were segregated from large 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 density of *D. aromatica* was positively correlated to the degree of concaveness of surface relief, while that of *D. lanceolata* was negatively correlated. It was concluded that they were co-occurring in the plot by occupying different patches of the heterogeneous habitat mosaic.

INTRODUCTION

Tropical rain forest communities show variation at 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, Hubble & 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, Hubbel & 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. In this paper, we studied the spatial patterns of two emergent tree species, *Dryobalanops aromatica* Gaertn. *f.* and *Dryobalanops lanceolata* Burck (Dipterocarpaceae) in a mixed dipterocarp forest of northeast Borneo, and the relationship between their distributions and topography was analyzed.

METHODS

Study site and study species

This study was conducted in a mixed dipterocarp forest of Lambir Hills National Park (4°12'N, 114°00'E) in Sarawak, east Malaysia. The average annual rainfall is 2764 mm (1967-1993) at Miri Airport ca. 20 km north of the study site, and there is no distinct dry season.

D. aromatica and *D. lanceolata* are large evergreen trees growing up to more than 70 m in height. *D. aromatica* is distributed in the Malay Peninsula, Sumatra and Borneo, while *D. lanceolata* is endemic to Borneo (Ashton 1982). They are common emergent trees in the study site.

Field survey

A permanent plot of 52 ha in size (1040 m x 500 m) was established in the study forest. The plot was divided into 20 m x 20 m quadrats (1300 quadrats in total). Demarcation of the quadrats was done by theodolite and compass survey. Positions of all trees of 1 cm dbh (diameter at breast height) and larger in each quadrat were mapped, and their dbh were measured with a diameter tape measure (for more details, see Chai et al. and Yamakura et al. in this volume).

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. (1) was calculated from the three dimensional coordinate data at each corner of the quadrat by the mean least square method.

$$z = b_1 + b_2x + b_3y \ . \qquad (1)$$

Mean slope inclination (s) were calculated from the coefficients of Eq (1) as,

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

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

$$CI = h - hs , \quad (3)$$

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

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

$$hs = (z_{i-20,j-20} + z_{i-20,j} + z_{i-20,j+20} + z_{i-20,j+40} + z_{i,j+40} + z_{i+20,j+40} + z_{i+40,j+40} + z_{i+40,j+20} + z_{i+40,j} + z_{i+40,j+20} + z_{i+20,j-20} + z_{i,j-20}) / 12, \quad (5)$$

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

Morishita's Iδ index (Morishita 1959) was used for evaluation of spatial pattern. The value of Iδ 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 ≥30 cm; pole: 5 cm≤ dbh < 30 cm; sapling: 1 cm ≤ dbh < 5 cm).

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

Fifty hectares of the 52-ha plot was used for the analysis. The values of Iδ 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

Diameter distribution

Both species had an abundance of small trees. The proportions of trees smaller than 5 cm in dbh were 87.6% and 89.9% in *D. aromatica* and *D. lanceolata*, respectively (Fig. 1). *D. lanceolata* had a higher proportion in smaller individuals than did *D. aromatica*. The ratios of large trees (dbh ≥ 30 cm) to poles (5 cm ≤ dbh < 30 cm) to saplings (1 cm ≤ dbh < 5 cm) were 1:2.0:18.4 in *D. aromatica* and 1:4.3:36.2 in *D. lanceolata*.

Spatial pattern

D. aromatica was distributed wider in the plot than was *D. lanceolata*, which was mostly restricted on the southest side (Fig. 2).

Spatial patterns of large trees, poles and saplings of *D. lanceolata* were highly clumped (Fig. 3). The value of $I\delta(s)/I\delta(2s)$ had a peak at 62.5 m x 62.5 m in *X* ploles and saplings of *D. lanceolata*, indicating that they had a mean clump size on this scale (Fig. 3). 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. 3). 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 ca. 31.2 m x 31.2 m mean size within large clumps of ca. 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 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.

Distributions of *D. aromatica* and *D. lanceolata* were highly segregated even for small individuals (Table 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 $\geq 30^{\circ}$) or gentle slope (mean inclination $< 30^{\circ}$). Then, each slope was classified into three more categories based on its surface relief as concave ($CI \leq -1.5$), flat ($-1.5 < CI < 1.5$) or convex ($CI \geq 1.5$).

The topography of the 52-ha plot and spatial distribution of each category is shown in Fig. 4 and 5. 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 ridges, gentle slopes with flat or concave relief were distributed. Steep slopes were mostly on the south to east side of the main ridges.

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 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.

Since surface relief appeared to be more important than slope inclination, we analysed more details of the effects of surface relief (Fig. 6). There were significant positive, more or less linear, relationships between the values of convex index (CI) and the mean density of *D. aromatica* in all size classes. On the other hand, the mean density of *D. lanceolata* was negatively correlated with CI.

DISCUSSION

This study clearly indicates 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. 6) suggests that they respond even to small differences in topography.

Topography, however, may not be the only factor for determining their distributions. Hirai et al. (in this volume) found some differences in soil characteristics sampled from *under D. aromatica* and *D. lanceolata*. Thus, soil may also influence their spatial patterns. The restriction of *D. lanceolata* distribution on the south-east side of the plot was probably because only that area may be covered by clay-rich soils (cf. Palmiotto in this volume), on which *D. lanceolata* tends to be distributed (Hirai et al. in this volume). It may be within the same soil types that topography has a clear effect on the distributions of the two species. The effects of soil and topography, however, may have a more complex interrelationship. It is likely that the two *Dryobalanops* are coexisting in Lambir by occupying patches of different topography and/or soil, and that their spatial patterns would be more or less stable on the whole-plot scale, i.e. 52 ha. The highly heterogeneous topography and soil of Lambir forests (Yamakura et al. in this volume, Palmiotto in this volume) takes an important role in maintaining their coexistence.

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. The aggregated distributions of saplings and poles to large conspecific trees are probably caused by inadequate seed dispersal. Most of their fruits are dispersed under the canopy of mother trees, and the number of dispersed fruits rapidly decreases outside of the canopy. Almost all fruits are dispersed within 40 m from mother trees (Itoh 1995). Small scale disturbances, such as tree fall gaps and small land slides, seem to be related to the spatial patterns of their juveniles on this scale (Itoh 1995).

The segregated distributions of saplings and poles of *D. aromatica* to large trees (Table 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 (Augspurger 1983, Clark & Clark 1984). The distance from mother tree and seedling density, however, had no significant effect on seedling mortality of *D. aromatica* during a 2.5-year period from seed dispersal in the study forest (Itoh *et al.* 1995). The later phase mortality and growth of established seedlings may be important for the observed juvenile inhibition from large trees. The scale of juvenile inhibition (< 7.8 m x 7.8 m), though, seems too small to effectively maintain species richness in the local community, because the diameters of emergent trees in the forest were often larger than this scale.

CONCLUSION

The importance of environmental heterogeneity for coexistence of two *Dryobalanops* was clearly shown in the current study, however, they are only two of more than 1,000 tree species in the Lambir forest. Further research including more species is required before concluding how the environmental heterogeneity is important for the determination of community composition and the maintenance of species richness in the forest. Research on the ecological behavior of each species, such as reproduction biology, seed dispersal, seedling establishment and juvenile response to environment, are also required to clarify the mechanisms of environmental effects on species richness.

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Discussion for Itoh *et al.*'s paper

Ashton Mr Itoh's presentation is really exciting for me. I didn't realise that he has done so much analysis with the data from the plot as well as those from his seedling studies. In my own day as a graduate student instead of having one plot with a full range of topography, I worked in two different sites, one of which was predominantly represented by shales and clays much the same as those in Lambir, and the other one by sandstone also largely of the same geological formation. The two species of Dryobalanops, aromatica and lanceolata, were completely separated, one species on one site and the other species only in the other site. My results show that both of them were predominant as large trees on the ridge, but the soils and topography separate them out. This demonstrates that one can get a lot of useful information from a 50 ha plot but that it is necessary also to work at a larger scale, the landscape scale, to test the generality of the conclusions.

Ogino How big was the size of your seedling experiment?

Itoh The area was quite small. Two study sites were chosen, one on the ridge and the other in the valley. There were six plots per site each 2 m by 2 m in dimension.

Ogino How many seedlings were planted?

Itoh 240 seedlings were planted per species per site.

Ogino Is this number of seedlings enough to study the effect of sites?

Itoh Even with 240 seedlings per site we were able to detect significant differences. It would be better to have a larger number of seedlings but 240 seedlings, I think, may be the minimum.

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

Quadrat size (m x m)	*D. aromatica* Pole	*D. aromatica* Sapling	*D. lanceolata* Pole	*D. lanceolata* 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

Table 2. Values of ω index between *Dryobalanops aromatica* and *Dryobalanops lanceolata* in a 52-ha plot.

Quadrat size (m x m)	Large trees (dbh ≥ 30 cm)	All trees (dbh ≥ 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

Table 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 ≤ dbh < 30 cm; Sapling: 1 cm ≤ dbh < 5 cm.

Topographic category	Area (ha)	Mean density (No. ha $^{-1}$)					
		Dryobalanops aromatica			*Dryobalanops lanceolata*		
		Large tree	Pole	Sapling	Large tree	Pole	Sapling
Gentle slope							
Convcave	11.0	4.4 (48)	7.3 (80)	88.3 (974)	0.6 (6)	2.7 (30)	17.2 (190)
Flat	14.5	6.2 (91)	14.0 (202)	99.5 (1442)	1.0 (14)	12.8 (41)	26.0 (377)
Convex	11.2	13.9 (155)	24.7 (275)	202.8 (2263)	0.1 (1)	0.3 (3)	2.3 (26)
Steep slope							
Convcave	3.5	2.6 (9)	8.9 (31)	101.8 (354)	0.3 (1)	0.9 (3)	1.4 (5)
Flat	2.6	8.0 (21)	15.5 (41)	203.0 (536)	0 (0)	0.8 (2)	9.1 (24)
Convex	3.2	8.5 (27)	24.4 (78)	317.0 (1014)	0 (0)	1.25 (16)	8.75 (182)
Uncategorised	6	7.0 (42)	15.5 (93)	7.3 (643)	0.2 (1)	2.7 (16)	28.0 (182)
Total	52	7.6 (393)	15.4 (800)	139.0 (7226)	0.4 (23)	1.9 (99)	16.0 (832)

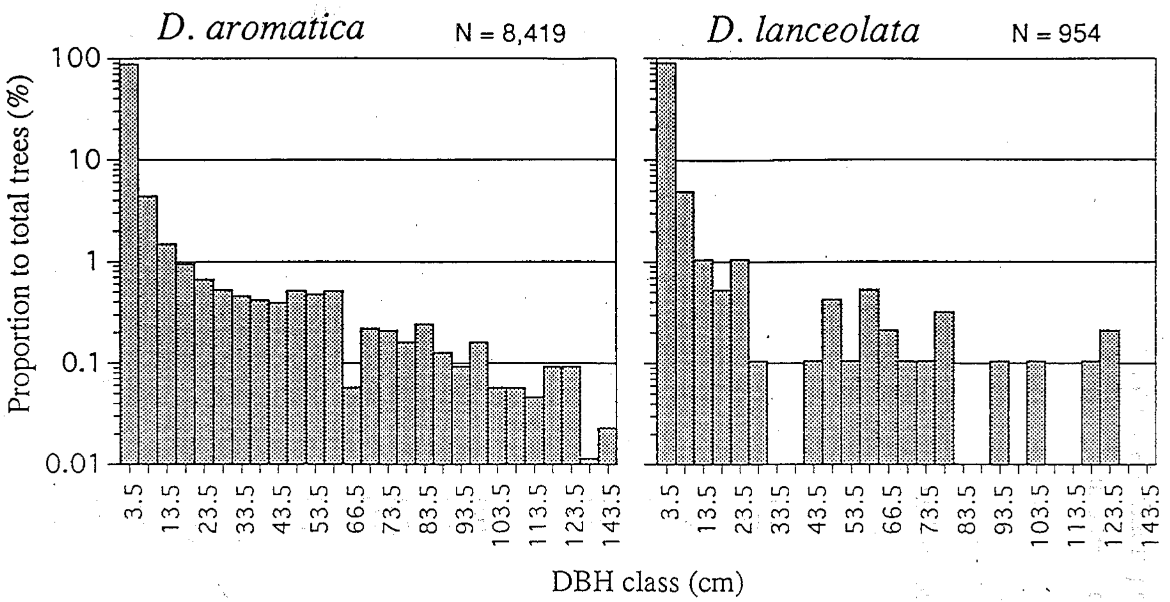

Fig. 1. Diameter frequency distribution of two *Dryobalanops* species. Proportions to total trees of 1 cm dbh and larger are shown. Dbh class is indicated by the middle value of each 5-cm intervals. *N*: total number of trees in the 52-ha plot.

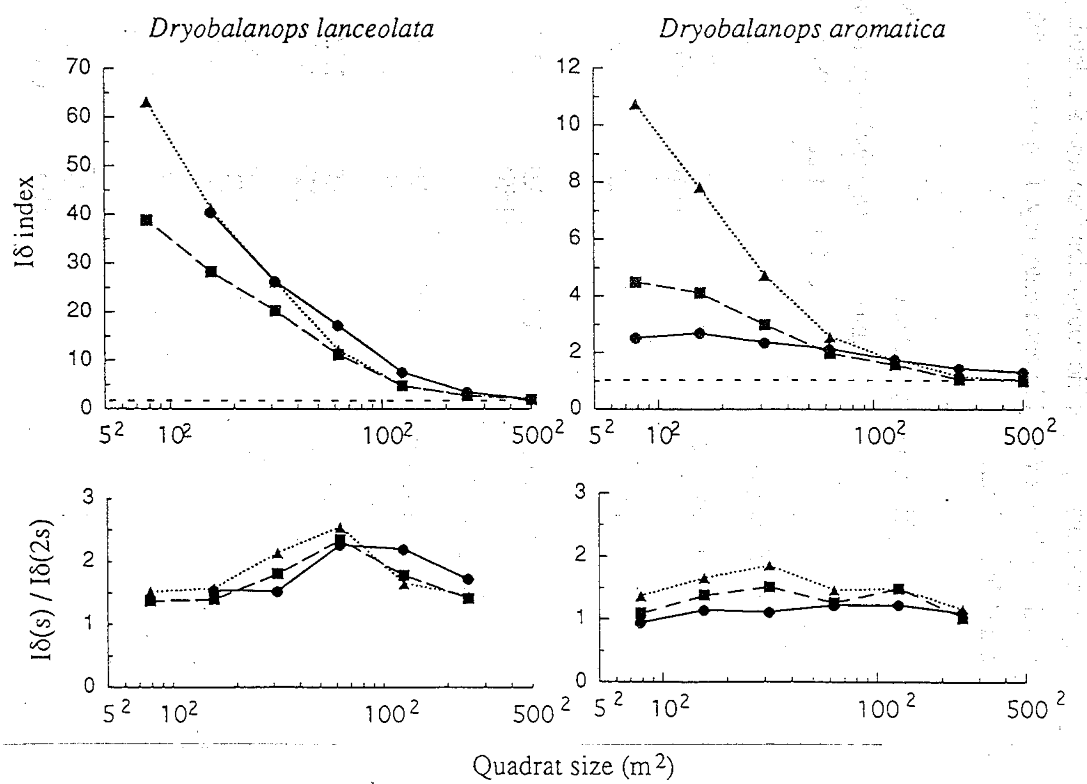

Fig. 3. Changes in Morishita's Iδ index and Iδ(s)/Iδ(2s) with changing quadrat size *for Dryobalanops lanceolata* and *D. aromatica*. Circles indicate large trees: dbh ≥ 30 cm. Squares indicate poles: 5 ≤ dbh < 30 cm. Triangles indicate sapling: 1 ≤ dbh < 5 cm. Dotted lines (Iδ = 1) indicate random distribtuion.

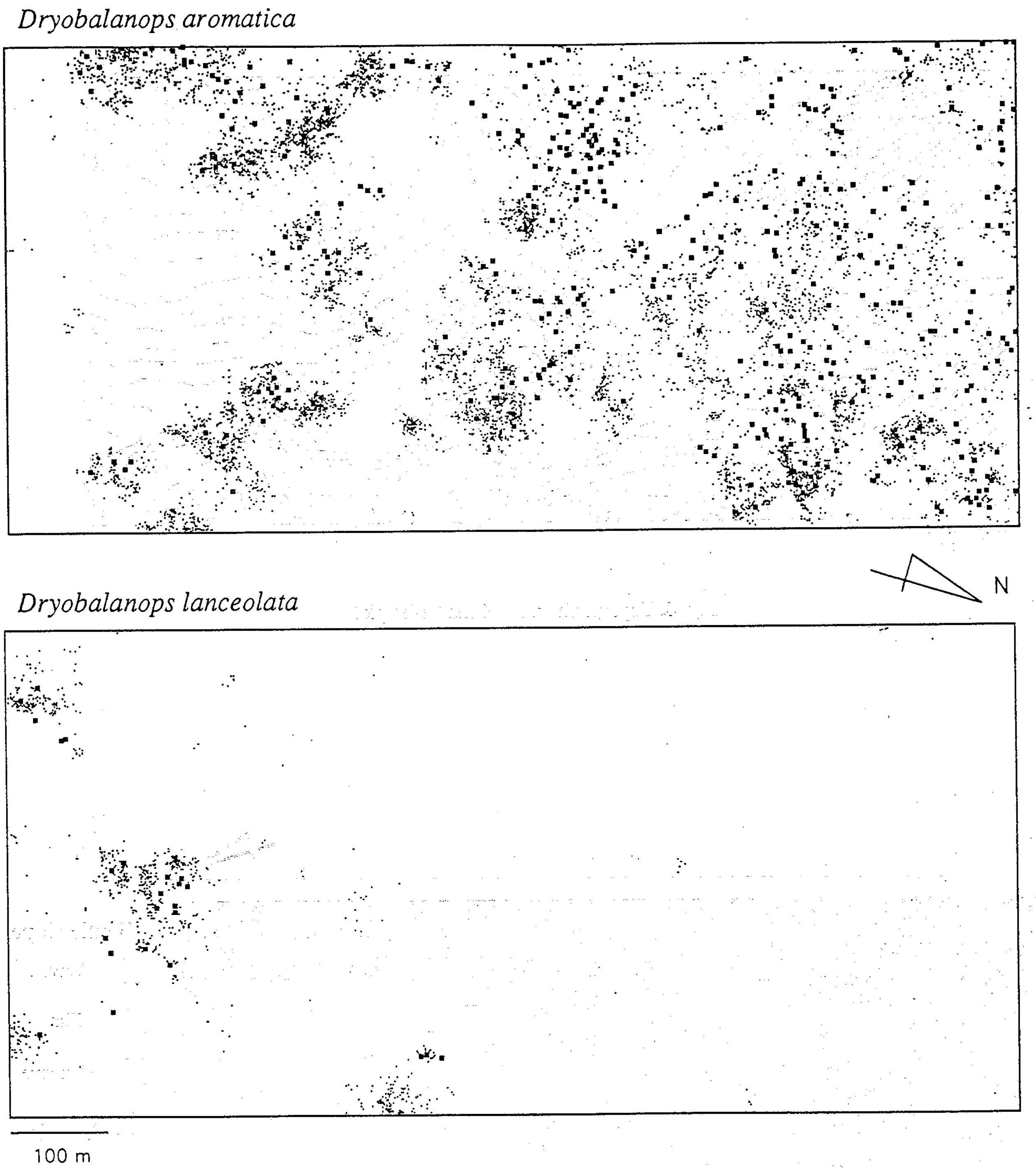

Fig. 2. Spatial distributions of two *Dryobalanops* species (dbh $\geq$ 1 cm)in the 52 ha plot. Large squares indicate trees larger than 30 cm dbh.

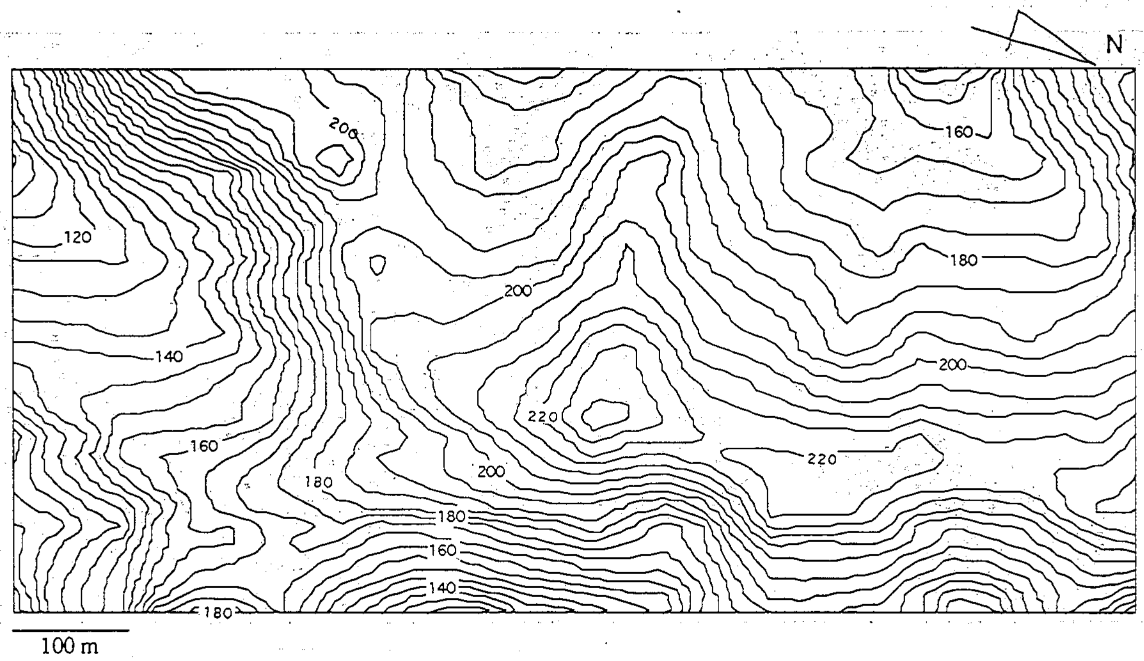

Fig. 4. Topography map of the 52-ha plot.

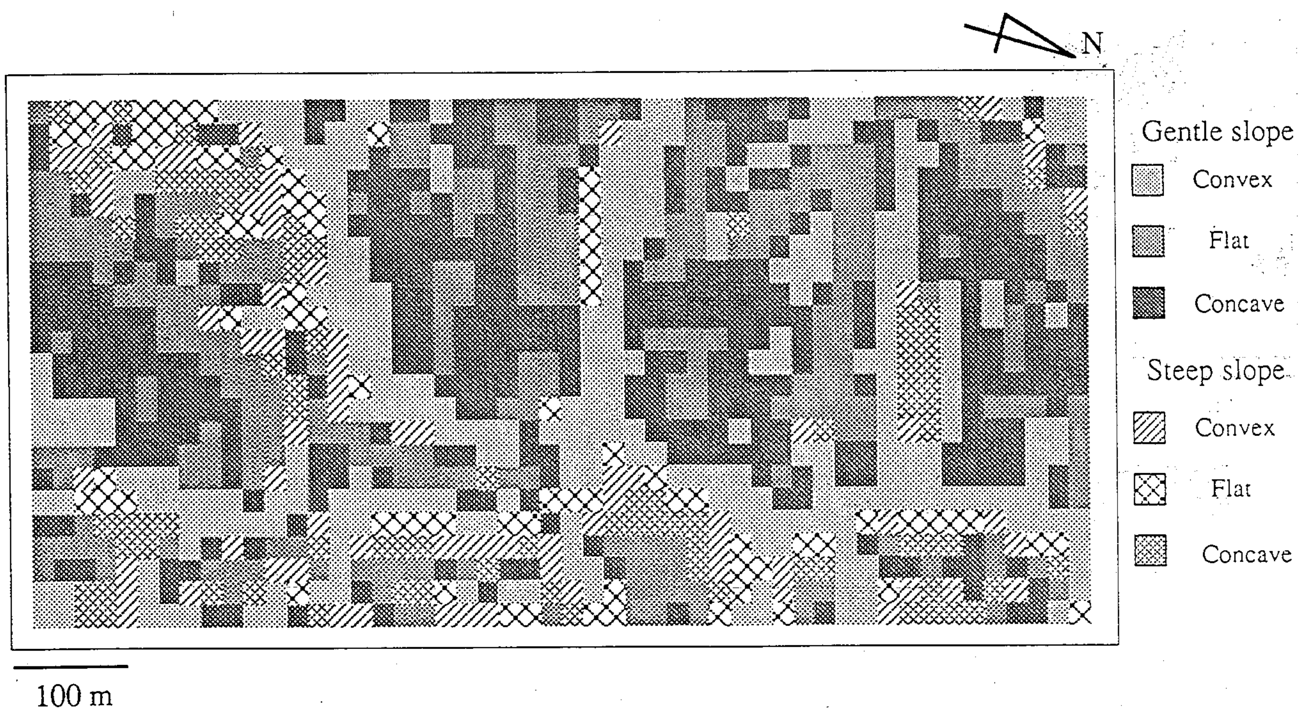

Fig. 5. Spatial distribtuions of topographic categories (see text for details).

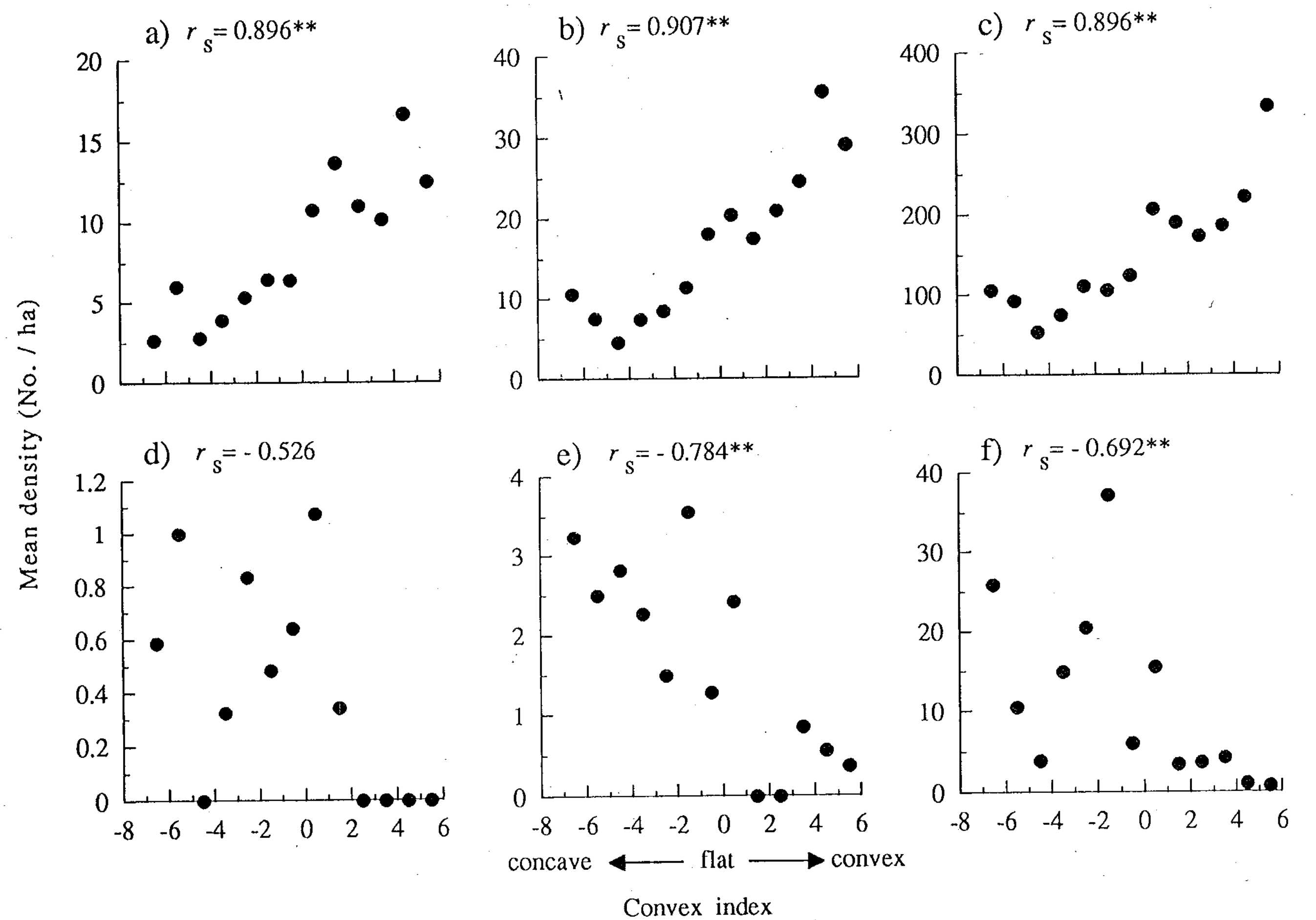

Fig. 6. Relationships between convex index (see text) and mean density of *Dryobalanops aromatica* (a: dbh ≥ 30 cm; b: 5 ≤ dbh < 30 cm; c: 1 ≤ dbh < 5 cm) and *D. lanceolata* (d: dbh ≥ 30 cm; e: 5 ≤ dbh < 30 cm; f: 1 ≤ dbh < 5 cm). r_s indicate Spearman's rank correlation coefficient (*: significant at $P < 0.05$; **: significant at $P < 0.01$).