# Spatially aggregated fruiting in an emergent Bornean tree

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**Abstract:** We investigated the spatial distribution of fruiting in *Dryobalanops aromatica* (Dipterocarpaceae), a mast-seeding emergent tree that is found in the tropical rain forests of Borneo. Of 393 adults (diameter at breast height (dbh) > 30 cm) in a 52-ha area, 143 (36.4%) individuals fruited. A second-order spatial analysis, based on Ripley's *K*-function, revealed that fruiting trees were significantly (P < 0.05) aggregated with respect to the total population over distances of 15–115 m. Thus, the spatial distribution of fruiting trees was more aggregated than expected from the adult tree distribution, which itself was aggregated within the study plot. Logistic regression analysis showed that fruiting trees had a significantly greater dbh and were surrounded by more conspecific adults per ha than non-fruiting individuals. Moreover, fruiting trees were found at higher elevations, on steeper slopes, and on sandy rather than clayey soils. In contrast, annual diameter growth, adult density over areas < 1 ha, and slope convexity did not significantly affect fruiting probability. The ratio of seedling (20 cm ≤ h < 60 cm) and sapling (60 cm ≤ h < 300 cm) density to adult density was higher in sites at higher elevations, on steeper slopes, and on sandy soils than that for lower elevations, flat slopes and clayey soils. This suggests that the aggregation of fruiting trees occurred not only at the time of the study, but that it had occurred repeatedly in the past, at the high-elevation, steep-sloped, sandy sites. Thus, site conditions probably affect the dynamics and spatial structure of local populations through differences in fruiting frequency among trees experiencing different site conditions.

**Key Words:** Borneo, Dipterocarpaceae, *Dryobalanops aromatica*, general flowering, masting, spatial distribution

## INTRODUCTION

Since a shortage of seed input strongly limits the recruitment of trees, seed limitations can contribute to species coexistence in forest communities by regulating the recruitment of otherwise dominant species (Hubbell *et al.* 1999, Hurtt & Pacala 1995). Spatial seed limitation is caused by clumped distributions of reproductive individuals, coupled with limited seed dispersal. However, if fruiting individuals are not a random set of the whole population but are a subset of spatially aggregated individuals, then seed limitation can occur even when adult trees are distributed randomly over the population. Therefore, spatial variation in fruiting within a population is an important factor in the spatial dynamics of tree populations. There have been few studies, however, that have reported population-scale spatial variation in flowering and fruiting among tropical forest trees (Burgess 1972, Chan & Appanah 1980). It is not clear what proportion of individuals flower and fruit at the population scale, nor whether the occurrence of flowering and fruiting is spatially random or aggregated, nor what factors affect the flowering and fruiting of individual trees.

Tropical rain forests in South-East Asia share a unique reproductive phenomenon, termed 'general flowering' (Appanah 1985): the majority of plant species (including canopy and understorey trees, climbers and epiphytes) flower and fruit synchronously at intervals of 2–10 y (Appanah 1985, Ashton *et al.* 1988, Burgess 1972, Medway 1972, Ng 1977). Many studies have investigated variations in the occurrence of general flowering at a regional scale (Ashton *et al.* 1988, Burgess 1972, Curran & Leighton 2000, Sakai *et al.* 1999, Sasaki *et al.* 1979, Wich & van Schaik 2000, Yasuda *et al.* 1999). To our knowledge, however, no quantitative studies have considered population-scale variations in the flowering and fruiting of canopy trees during each general-flowering event (Burgess 1972, Chan & Appanah 1980).

In this study, we investigated the population-scale (≈ 0.5 km²) spatial pattern of fruiting individuals for an

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emergent tree, *Dryobalanops aromatica* (Dipterocarpaceae), in a general-flowering year. We examined: (1) whether the occurrence of fruiting was randomly distributed or spatially aggregated at the population scale; (2) what factors related to the fruiting probability of individual trees; and (3) whether the observed spatial patterns in fruiting showed a long-term tendency in the study population.

## METHODS

### Study site

This study was conducted in a permanent plot ($500 \times 1040$ m), established in a lowland mixed dipterocarp forest at Lambir Hills National Park ($4°20'$N, $114°0'$E) in the Malaysian state of Sarawak, on the island of Borneo. All trees in the plot $\geq 1$ cm in diameter at breast height (dbh) were labelled, mapped and identified to species. Dbh was measured twice, once between 1991 and 1993 and again in 1997 (Yamakura *et al*. 1995, 1996). The climate at the study site is generally wet, although less rainfall is recorded between February and August. The average annual rainfall from 1968 to 1998 at Miri Airport, about 20 km north of the study site, was 2725 mm. The soils comprise two types of ultisol (udult and humult) that are distributed side by side in the study site. Udult soils contain more clay and are more fertile than humult soils (Ashton & Hall 1992, Baillie *et al*. 1987, Palmiotto 1998). The topography is characterized by hilly terrain with steep slopes, including scars caused by small landslides (Yamakura *et al*. 1995).

### Study species

*Dryobalanops aromatica* Gaertn. f. (Dipterocarpaceae) is an emergent tree that grows up to 60 m tall and 2 m in diameter. It is distributed in parts of the Malay Peninsula, as well as Sumatra and Borneo (Ashton 1982). This species was the most common in the 52-ha study plot, with 10 503 individuals (3% of the total number of trees $\geq 1$ cm dbh) comprising 152.8 m$^2$ of basal area (6.9% of the total basal area; Itoh *et al*. 1995*a*). *Dryobalanops aromatica* produces wind-dispersed fruit (5–7 g fresh weight) with five sepal wings (about 4–7 cm long) and one seed (Itoh *et al*. 1995*b*). This species flowers and fruits more frequently than do most dipterocarp species. Fruiting *D. aromatica* trees were observed at Lambir every year between 1990 and 1998, except in 1995 (Itoh *et al*. 1997). Considerable *D. aromatica* fruiting occurred only from 1991 to 1992, and from 1996 to 1997, when many other species also fruited heavily after periods of mass flowering (Sakai *et al*. 1999). Frequent reproduction of *D. aromatica* was also observed in Peninsular Malaysia (Appanah & Weinland 1993).

We observed all *D. aromatica* > 30 cm dbh in the plot (n = 393) from the ground with binoculars from 6–14 February 1997, when mature fruit had started to fall. To assess whether a tree had fruited, we looked for fruit in the canopy. If none was seen from the first observation point, we checked for canopy fruit from several different observation points and searched for fallen fruit on the ground under the canopy. We may, however, have missed the fruiting of trees that had a very small number of fruit. Thus, our results reflect only those individuals with relatively heavy fruiting.

### Statistical analysis

The spatial distribution of fruiting trees was analysed by Ripley's *K*-function (Diggle 1983, Ripley 1976), which is defined as:

$K(t) = \lambda^{-1}E$ [number of other fruiting trees within distance $t$ of an arbitrary fruiting tree],

where $E$ represents the expected value and $\lambda$ is the mean number of fruiting trees per unit area. The unbiased estimate of $K(t)$ is defined as:

$$\hat{K}(t) = \frac{A}{n^2}\sum_{i \neq j}\sum w_{i,j}^{-1}I_t(u_{i,j}), \tag{1}$$

where $n$ is the number of fruiting trees in the plot; $A$ is the plot area; $u_{i,j}$ is the distance between the $i$th and $j$th fruiting trees; $I_t(u)$ is equal to 1 if $u < t$ and 0 otherwise; $w_{i,j}$ is the proportion of the circumference of a circle whose centre is the $i$th tree and whose radius, $u_{i,j}$, lies within the plot; and the summation is for all pairs of fruiting trees not more than $t$ apart (Diggle 1983, Ripley 1976). As recommended by Besag & Diggle (1977), we used a square-root transformation of $K(t)$:

$$\hat{L}(t) = \sqrt{\frac{\hat{K}(t)}{\pi}} - t \tag{2}$$

The value of $\hat{L}(t)$ is 0 for a random spatial distribution at distance $t$, whereas positive and negative values of $\hat{L}(t)$ indicate aggregated and regular distributions, respectively. Because the spatial distribution of all adult trees was clumped, the $\hat{L}(t)$ of fruiting trees would be positive even if they were randomly selected (Sterner *et al*. 1986). Thus, we used Monte Carlo simulations to examine whether the $\hat{L}(t)$ of fruiting trees was significantly larger or smaller than would be expected if the fruiting trees were a random set of all adult trees. We randomly selected the same number of trees as there were fruiting adults in the plot and calculated $\hat{L}(t)$ for each of 1000 simulations. Then, the 25th largest and the 25th smallest values at each distance t were used for 95% confidence intervals. We used the statistical package *R* (Free Software Foundation, Inc., USA) with the add-on Splancs package (Rowlingson & Diggle 1993) for spatial analyses.

Logistic regression was used to analyse how the prob-

ability of fruiting ($P_f$) was associated with the size, growth and site conditions of each tree. The binary variable (fruiting or non-fruiting) was regressed against the independent variables dbh, annual diameter growth, site condition (four variables: elevation, slope inclination, slope convexity and soil texture), and density of conspecific adults at each of three scales ($20 \times 20$ m, $50 \times 50$ m, $100 \times 100$ m). Conspecific densities were included to handle the statistical problem of spatial autocorrelation of fruiting, which will be shown later in the results. Because conventional logistic regression assumes that the fruiting probability of a focal tree is independent of the fruiting of its neighbours, the results are violated when fruiting is spatially autocorrelated (Hubbell *et al*. 2001, Legendre 1993). By adding conspecific densities, we can separate the effect of spatial autocorrelation from the effects of other factors (Hubbell *et al*. 2001).

The analysis was run using the logistic model:

$$P_f = \frac{1}{1+e^{-z}}, \tag{6}$$

where

$$z = b_0 + b_1x_1 + b_2x_2 + \ldots + b_nx_n, \tag{7}$$

$x_1, x_2, \ldots x_n$ are independent variables, and $b_0, b_1, \ldots b_n$ are coefficients. Independent variables were added stepwise to each model, and log-likelihood ratio tests were used to assess the significance of the contribution of each variable to the model (Trexler & Travis 1993). Adding independent variables in the reverse order yielded identical results. The Hosmer–Lemeshow test was applied to analyse the goodness-of-fit of the model that contained only significant variables. We divided the adult trees into 10 groups of approximately equal size according to the predicted probability of fruiting, and calculated Pearson's $\chi^2$ value from the observed and predicted numbers of fruiting trees per group. This value was compared to a chi-square value with eight degrees of freedom (Hosmer & Lemeshow 1989). To evaluate the degrees of effect, we calculated the odds ratios based on the range of values observed in the *D. aromatica* population for each significant independent variable. Calculated in this way, the odds ratio is the ratio of the odds of a tree having the smallest probability of fruiting, and the odds of it having the greatest probability, in the study population with regard to a given variable. Therefore, the odds ratio indicates the difference between the minimum and maximum fruiting probabilities predicted by each variable within the observed range. Because the minimum and maximum values can be extremes, we also calculated the odds ratio using the difference between the first and third quartiles. We used the Regression Models option in SPSS ver. 10.0 (SPSS Inc., USA) for logistic regression analyses.

To calculate the density of conspecific adults at different scales, the 52-ha plot was divided into quadrats of the

three sizes used in regression analyses: 1300 $20 \times 20$-m quadrats, 200 $50 \times 50$-m quadrats, and 50 $100 \times 100$-m quadrats. The southernmost 2-ha area ($40 \times 500$ m) of the plot was removed from the calculation because it contained no *D. aromatica* adults. The density of conspecific adults was determined by counting the number of *D. aromatica* adults per quadrat. The annual diameter growth (*DG*) of each tree was calculated by the equation:

$$DG = \frac{D_1 - D_0}{\Delta t,} \tag{8}$$

where $D_0$ and $D_1$ are the dbh (cm) at the first and second census, respectively, and $\Delta t$ is the time (in years, from 4.4 to 5.7) between the first and second census. The site-condition variables were determined for each of the 1300 $20 \times 20$-m quadrats in the plot (Palmiotto 1998, Yamakura *et al*. 1996). We described soil texture using four categories, ranging from 1 (high sand content) to 4 (high clay content), based on a field evaluation of apparent sand content, slipperiness and stickiness, following Kimmins (1987). We then pooled categories 2–4 into one 'clay' category, because *D. aromatica* adults were rarely found on category-3 and -4 soils. Therefore, soil texture was an unordered categorical variable (sand or clay) that was treated as a dummy variable in logistic regression. The other variables (elevation, slope inclination and slope convexity) were calculated from the elevation data at each corner of each $20 \times 20$-m quadrat using the methods of Yamakura *et al*. (1996). Each tree in the plot was assigned the site variables of its quadrat. Dbh was $\log_e$-transformed prior to analyses, as described in Thomas (1996).

## Long-term effects of site conditions on fruiting

To assess whether the observed spatial pattern of fruiting in 1997 showed a long-term tendency or was restricted to the single fruiting episode of 1997, we compared the average number of juveniles per adult between two areas within the 52-ha plot that had larger and smaller fruiting probabilities in 1997. If the effects of site conditions were consistent over the long term, and if fruiting tended to be spatially aggregated to the area where more fruiting was observed in 1997, we would expect a larger number of juveniles per adult in that area.

The number of *D. aromatica* juveniles (20 cm $\leq$ h < 300 cm) was counted in 1300 $2 \times 2$-m subplots placed at the north-east corner of each $20 \times 20$-m quadrat in the 52-ha study plot. The juvenile census was conducted from September–December 2000, nearly 4 y after the observed fruit fall (February–March 1997). Because the initial height of established seedlings is about 20 cm for *D. aromatica* (Itoh *et al*. 1995*b*), almost all juveniles in the subplots were included in the census. We divided the juveniles into two categories: seedlings (20 cm $\leq$ h < 60 cm) and saplings (60 cm $\leq$ h < 300 cm). Because the max-

imum height of 4-y-old seedlings in the forest understorey is 60 cm (Itoh *et al*. 1995*b*), most individuals that originated from the 1997 fruiting were seedlings according to the definition.

We classified the 1300 20 × 20-m quadrats into two categories, which will be referred to as the more-reproductive and the less-reproductive sites, based on the fruiting probabilities of the trees surrounding the quadrats, as follows. First, we estimated the fruiting probability of each adult tree in the plot (n = 393) using the logistic regression model obtained by the method described above. We used constant values for dbh (54.7 cm, i.e. the median of the 393 trees) and adult density per ha (13 ha$^{-1}$) for all trees, and we used observed values for significant site variables, i.e. elevation, slope inclination and soil texture, as discussed below. Since no cross effects are included in our regression model, the difference in dbh and adult density does not affect the rank of fruiting probability of each tree if the same values are used for all of them. We then ranked the 393 trees in order of their fruiting probability based on site differences. Quadrats in which the juvenile plots were within 30 m of any of the trees that had a higher fruiting probability than the calculated median probability were then considered to be the more-reproductive sites. We used 30 m because the maximum distance of fruit dispersal was 30 m for one of the largest *D. aromatica* (dbh = 148 cm) in the study forest (Itoh *et al*. 1997). The less-reproductive sites were quadrats that had no adults, or only individuals that had a lower fruiting probability than the median probability within 30 m of the juvenile plots.

## RESULTS

Of 393 adult trees, 143 (36.4%) individuals fruited. Fruiting trees were significantly more aggregated than expected from a random selection of all adult trees at *t* = 15–115 m (Figures 1 and 2).

The proportion of fruiting trees was positively related to dbh (Figure 3). Logistic regression also indicated that dbh was positively related to fruiting probability (Table 1). In addition to dbh, fruiting probability was significantly related to elevation, slope inclination, soil texture and conspecific adult density within 1-ha quadrats (Table 1). Trees found at a greater conspecific density over an area of 1 ha, and those at higher elevations, on steeper slopes, and on sandy soils, were more likely to fruit than other trees. The Hosmer–Lemeshow test indicated that observed fruiting probabilities were not significantly different from those predicted by the model that included only these significant variables ($\chi^2$ = 5.17, df = 8, P = 0.740). Table 2 shows the odds ratios based on the range and the quartile differences. Because soil texture was a categorical variable of two levels, its odds ratio was compared with those based on the range of values for the other

variables. The odds ratios, whether based on ranges or on quartile differences, were ordered among the variables as follows: dbh > elevation > slope inclination > conspecific density > soil texture.

Because the size-dependence in fruiting probability seemed less clear for trees ≥ 60 cm in dbh (Figure 3), logistic regression analysis was also conducted for these trees only (n = 165). Only elevation (P < 0.01) and soil texture (P = 0.06) were selected as factors that significantly related to the fruiting probability. This suggests that dbh, slope and conspecific density were not important for the fruiting of the larger trees, although they may have affected the fruiting of smaller individuals.

The more-reproductive sites occupied 17.5 ha (33.7%) of the plot and consisted of several patches on the major ridges (Figure 1 and Table 3). The proportions of individuals in the more- and less-reproductive sites significantly differed between adults and seedlings (chi-square test, $\chi^2$ = 73.4, df = 1, P < 0.01) and between adults and saplings ($\chi^2$ = 38.4, df = 1, P < 0.01), but differences were insignificant between seedlings and saplings ($\chi^2$ = 2.1, df = 1, P = 0.15). Densities of adults, seedlings and saplings were 4.1, 8.7 and 7.6 times larger in the more-reproductive sites than in the less-reproductive sites, respectively (Table 3). On average, adult trees in the more-reproductive sites had 2.1 and 1.8 times more seedlings and saplings, respectively, than those in the less-reproductive sites.

## DISCUSSION

The results clearly show that fruiting of *D. aromatica* in 1997 was not spatially random but was aggregated with respect to the total population (relative spatial aggregation). As a result, the spatial distribution of fruiting trees was more aggregated with respect to the framework of the plot (absolute spatial aggregation) than that of all adults, which was also spatially aggregated (see Figure 1). In addition, fruiting was biased in favour of tree size and certain site conditions, i.e. elevation, slope inclination and soil texture. Tree size, however, was not significant for trees ≥ 60 cm dbh. Trees at high elevations, on steep slopes and in sandy soils were more likely to fruit. The relative spatial aggregation of fruiting may be due to site effects on fruiting probability. Since these site conditions are spatially aggregated in the study plot (A. Itoh, *pers. obs*.), the sites with high elevations, steep slopes and sandy soils are aggregated (see also Figure 1). This leads the relative spatial distribution of fruiting trees to be aggregated. The size-effect may not have contributed to the relative spatial aggregation because trees larger than 60 cm dbh are a random set of the whole population at the scales *t* < 80 m by *K*-function analysis (data not shown). The larger trees even showed significant spatial repulsion with respect to the total population (P < 0.05)
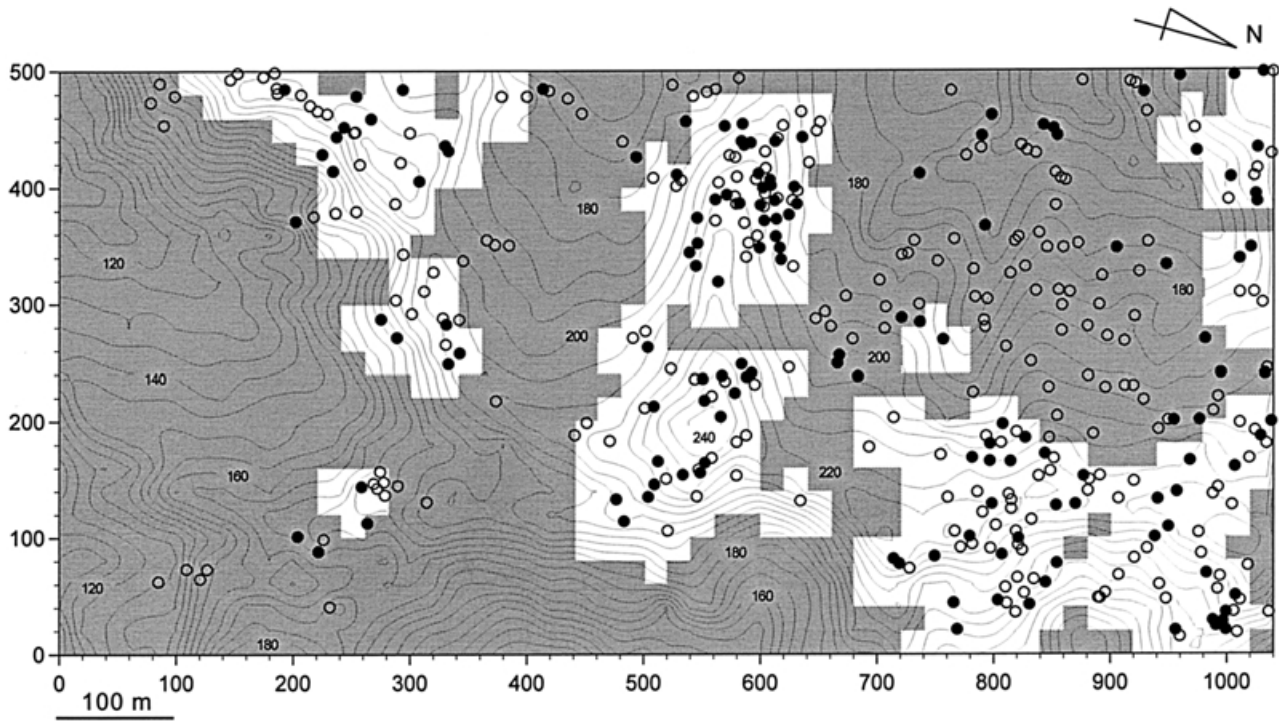
**Figure 1.** Spatial distribution of fruiting (●) and non-fruiting (○) *Dryobalanops aromatica* trees (dbh > 30 cm) in a 52-ha plot at Lambir. Topographic contours are shown at 5-m intervals. Shaded areas are the quadrats within 30 m of which had no adults, or only individuals that had a lower fruiting probability than the median probability based on a site-dependent logistic regression model (see text for details).
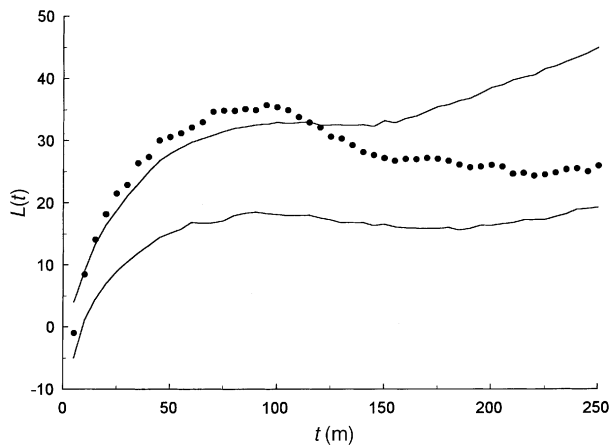


**Figure 2.** Spatial aggregation function $L(t)$ for fruiting *Dryobalanops aromatica* trees. Solid lines are 95% confidence intervals obtained by Monte Carlo simulations under the null hypothesis that fruiting trees are a random set of the total population.
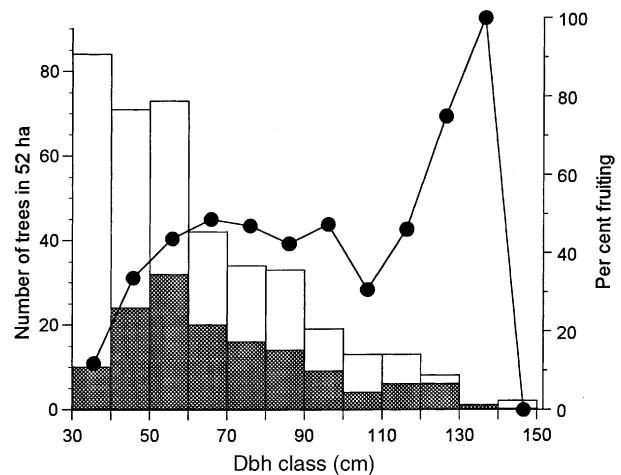


**Figure 3.** Distribution of fruiting (shaded columns) and non-fruiting (open columns) *Dryobalanops aromatica* trees by dbh. Proportion of fruiting trees per dbh class is also shown.

at larger scales ($t > 80$ m), which can drive relative spatial repulsion but not aggregation.

Spatially aggregated fruiting, if coupled with seed dispersal, will have consequential effects on the dynamics and spatial patterns of tree populations by limiting recruitment in sites with low seed input. Seed dispersal distances depend on tree height and are generally < 30 m for *D. aromatica* (Itoh *et al.* 1997). Using the height-dependent

seed-dispersal curves and the positions of fruiting trees, we estimated that seed input in 1997 was restricted around fruiting trees in the study plot (A. Itoh, *pers. obs.*). Thus, the aggregated fruiting observed in our study would probably affect the spatial distribution of this *D. aromatica* population. If trees in high-elevation, steep-sloped, sandy sites produce seeds more frequently over the long term, then the population of *D. aromatica* would gradually shift

**Table 1.** Results of logistic regression analysis for fruiting probability of *Dryobalanops aromatica*. Factors were selected by forward stepwise selection with log-likelihood ratio tests.

| Factors | Coefficient | (SE) | P[1] |
|---|---|---|---|
| **Significant factors** | | | |
| $\log_e$(dbh(cm)) | 1.66 | 0.314 | < 0.001 |
| Elevation (m) | 0.016 | 0.007 | 0.016 |
| Slope inclination (degree) | 0.028 | 0.013 | 0.027 |
| Density in 1ha (ha$^{-1}$) | 0.037 | 0.016 | 0.019 |
| Soil texture (sand) | 0.633 | 0.311 | 0.037 |
| Constant | −12.1 | 2.00 | < 0.001 |
| **Non-significant factors** | | | |
| Slope convexity (m) | | | 0.597 |
| Diameter growth (cm y$^{-1}$) | | | 0.452 |
| Density in 0.25 ha (ha$^{-1}$) | | | 0.399 |
| Density in 0.04 ha (ha$^{-1}$) | | | 0.896 |

log-likelihood (LL) of the selected model = −231
−2(LL(model)−LL(constant only model)) = 53.2, df = 5, P < 0.001

[1] Obtained by log-likelihood ratio test by removing or adding the focal factor from/to the selected model for significant and non-significant factors, respectively.

to these sites. In the study plot, tree density of *D. aromatica* was positively related to elevation, slope inclination and soil sand content (Itoh 1995*a*).

The effect of fruiting aggregation on long-term population dynamics was partly supported by the fact that the high-elevation, steep-sloped, sandy sites, where more fruiting was expected from the logistic regression model, had a higher juvenile-to-adult ratio than did those sites in which less fruiting was expected (Table 3). This result suggests that the aggregation of fruiting happened not only in 1997 but that it also occurred, repeatedly, in the

past. However, this finding should be confirmed by long-term observations, as lower mortality of seeds or small seedlings on the more-reproductive sites could also explain this result. This is however inconsistent with the fact that the mortality of seeds and seedlings was higher on a sandy ridge than in a wet gully during a 1-y field experiment (Itoh 1995*b*).

It is noteworthy that the fruiting intensity of *D. aromatica* was not very high in 1997 (36% of trees > 30 cm dbh). The intensity of flowering, and therefore fruiting, varies greatly between general-flowering episodes (Appanah 1985). Nearly all adults of a given population can produce fruit in a very heavy general-flowering year. The general-flowering event of 1996–1997 at Lambir may have been a moderate one (Sakai *et al.* 1999). Thus, our study should be considered a case of moderate flowering and fruiting. If almost all adults bear fruit during heavy general-flowering episodes, the site effects on fruiting observed in this study may be less obvious because most trees may fruit, even those in low-elevation, flat-sloped, clayey sites. Site effects may be more important during moderate fruiting episodes than during heavy ones.

Our study suggests the possibility that spatial variation in fruiting affects the dynamics and spatial patterns of an emergent tree population. We are not aware of any other studies on population-scale variation in the fruiting of tropical canopy trees during a given reproductive episode; however, Gibson & Menges (1994) and Nanami *et al.* (1999) reported that the spatial limitations of seed input affect the spatial patterns of dioecious temperate populations because only female trees produce seeds. Our results

**Table 2.** Odds ratios of fruiting probability of *Dryobalanops aromatica* based on the range and the difference between the 1st and 3rd quartiles observed in the study population. Soil texture is a categorical variable with two levels (sand/clay).

| | $\log_e$(dbh, cm) | Elevation (m) | Slope (degree) | Density (ha$^{-1}$) | Soil texture |
|---|---|---|---|---|---|
| Minimum | 3.40 | 129 | 3.5 | 1 | – |
| Maximum | 5.00 | 238 | 54.1 | 31 | – |
| Range | 1.60 | 109 | 50.6 | 30 | – |
| 1st quartile (Q1) | 3.75 | 185 | 12.9 | 9 | – |
| 3rd quartile (Q3) | 4.34 | 210 | 25.4 | 18 | – |
| Q3 − Q1 | 0.59 | 25 | 12.5 | 9 | – |
| **Odds ratio** | | | | | |
| Range | 14.1 | 5.74 | 4.12 | 3.03 | 1.88 |
| Q3 − Q1 | 2.65 | 1.49 | 1.42 | 1.40 | – |

**Table 3.** Densities of adults, seedlings and saplings of *Dryobalanops aromatica* at two edaphically different sites within a 52-ha plot. Numerals in parentheses are relative values to the adult densities of the same site. Seedling and sapling densities were calculated from the data of 2 × 2-m subplots at all 20 × 20-m grid points. More-reproductive sites are generally located at higher elevations, on steeper slopes, and on more sandy soils comparing to less-reproductive sites (Figure 1; see text for the definition of the sites).

| | Area (ha) | Density (ha$^{-1}$) | | |
|---|---|---|---|---|
| | | Adult[1] | Seedling[1] | Sapling[1] |
| More-reproductive sites | 17.5 | 15.3 (1) | 4000 (261) | 2903 (190) |
| Less-reproductive sites | 34.5 | 3.7 (1) | 458 (124) | 383 (104) |

[1] Adult: dbh > 30 cm; seedling: 20 ≤ h < 60 cm; sapling: 60 ≤ h < 300 cm.

suggest that similar processes may be working for monoecious species through site-dependence in fruiting.

Logistic regression analysis suggested that some site conditions, i.e. elevation, slope inclination and soil texture, are possibly responsible for the population-scale variation in fruiting of *D. aromatica*. At the moment, it is difficult to confirm the mechanisms of how these factors affect fruiting because the physiology of flowering and fruiting in *D. aromatica*, as well as in many other tropical trees, is virtually unknown.

It is possible that drought conditions on sandy ridges promote flowering, and hence fruiting, of *D. aromatica*, if flowering is initiated by prolonged drought (Appanah 1985, Burgess 1972, Curran *et al*. 1999, Medway 1972). Higher elevation, sandy sites are generally drier in Lambir (Hirai *et al*. 1997, Ishizuka *et al*. 1998). However, there is no evidence that drought stimulates flowering in *D. aromatica*.

Some circumstantial evidence suggests that the general-flowering episode of 1996–1997 in Lambir was triggered by a drop in minimum temperatures, as hypothesized by Ashton *et al*. (1988). Sakai *et al*. (1999) reported that daily minimum temperatures at the canopy level (35 m above the ground) were unusually low (< 21 °C) during January and February 1996 at a site *c*. 4 km from the current study plot. Ishizuka *et al*. (1998) observed no water stress during the period 1996–1997 at the same site. Dry sites on sandy ridges may have experienced sharp drops in temperature, whereas wet soils may have buffered the temperature dips at night (S. Appanah, *pers. comm.*). It is therefore possible that spatial variation in minimum temperature at the canopy level resulted in the aggregation of fruiting *D. aromatica*. Monitoring of spatial variations in canopy temperature and soil water conditions at the population scale is needed to determine whether small-scale variations in environmental cues affect flowering and fruiting.

Soil fertility is another possible factor that can affect individual flowering by altering the responsiveness of individual trees to flowering cues. The internal conditions of a tree, such as its nutritional status, may affect flowering and fruiting. Burgess (1972) speculated that even mature trees could not respond to external cues for general flowering if they had insufficient carbohydrates. Thus, site fertility may affect the flowering and fruiting of individual trees. However, our results are inconsistent with Burgess's hypothesis, because fruiting was concentrated in less-fertile sites, i.e. sandy ridges and steep slopes (Ashton & Hall 1992, Hirai *et al*. 1997, Ishizuka *et al*. 1998, Palmiotto 1998), where better productivity is unexpected. In Sumatra, van Schaik (1986) also reported that mast fruiting within a stand occurred on the less fertile higher terraces but not on the more fertile lower terraces. The effects of soil fertility on the flowering and fruiting of tropical rain-forest species therefore warrant further study, both in the laboratory and in the field.

## ACKNOWLEDGEMENTS

## LITERATURE CITED

APPANAH, S. 1985. General flowering in the climax rain forests of South-East Asia. *Journal of Tropical Ecology* 1:225–240.

APPANAH, S. & WEINLAND, G. 1993. *Planting quality timber trees in Peninsular Malaysia*. Malayan Forest Record No. 38, FRIM, Kepong. 247 pp.

ASHTON, P. S. 1982. *Dipterocarpaceae*. Flora Malesiana, series 1, vol. 9. Martinus Nijhoff Publishers, The Hague.

ASHTON, P. S. & HALL, P. 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology* 80:459–481.

ASHTON, P. S., GIVNISH, T. J. & APPANAH, S. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132:44–66.

BAILLIE, I. C., ASHTON, P. S., COURT, M. N., ANDERSON, J. A. R., FITZPATRICK, E. A. & TINSLEY, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on Tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3:201–220.

BESAG, J. & DIGGLE, P. J. 1977. Simple Monte Carlo tests for spatial pattern. *Applied Statistics* 26:327–333.

BURGESS, P. F. 1972. Studies on the regeneration of the hill forests of the Malay Peninsula. The phenology of dipterocarps. *Malaysian Forester* 35:103–123.

CHAN, T. T. & APPANAH, S. 1980. Reproductive biology of some Malaysian dipterocarps I. Flowering biology. *Malaysian Forester* 43:132–143.

CURRAN, L. M. & LEIGHTON, M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs* 70:101–128.

CURRAN, L. M., CANIAGO, I., PAOLI, G. D., ASTIANTI, D., KUS-NETI, M., LEIGHTON, M., NIRARITA, C. E. & HAERUMAN, H. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 286:2184–2188.

DIGGLE, P. J. 1983. *Statistical analysis of spatial point patterns*. Academic Press, London. 148 pp.

GIBSON, D. J. & MENGES, E. S. 1994. Population structure and spatial pattern in the dioecious shrub *Ceratiola ericoides*. *Journal of Vegetation Science* 5:337–346.

HIRAI, H., MATSUMIRA, H., HIROTANI, H., SAKURAI, K., OGINO, K. & LEE, H. S. 1997. Soils and the distribution of *Dryobalanops aromatica* and *D. lanceolata* in mixed dipterocarp forest – a case study at Lambir Hills National Park, Sarawak, Malaysia. *Tropics* 7:21–33.

HOSMER, D. W. & LEMESHOW, S. 1989. *Applied logistic regression*. John Wiley & Sons, New York. 307 pp.

HUBBELL, S. P., FOSTER, R. B., O'BRIEN, S. T., HARMS, K. E., CONDIT, R., WESCHLER, B., WRIGHT, S. J. & LOO DE LAO, S. 1999. Light gap disturbances, recruitment limitation, and tree diversity in neotropical forest. *Science* 283:554–557.

HUBBELL, S. P., AHAUMADA, J. A., CONDIT, R. & FOSTER, R. B. 2001. Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research* 16:859–875.

HURTT, G. C. & PACALA, S. W. 1995. The consequences of recruitment limitation: reconciling change, history and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.

ISHIZUKA, S., TANAKA, S., SAKURAI, K., HIRAI, H., HIROTANI, H., OGINO, K., LEE, H. S. & KENDAWANG, J. J. 1998. Characterization and distribution of soils at Lambir Hills National Park in Sarawak, Malaysia, with special reference to soil hardness and soil texture. *Tropics* 8:31–44.

ITOH, A. 1995a. *Regeneration processes and coexistence mechanisms of two Bornean emergent dipterocarp species*. Doctoral dissertation, Kyoto University, Kyoto.

ITOH, A. 1995b. Effects of forest floor environment on germination and seedling establishment of two Bornean rainforest emergent species. *Journal of Tropical Ecology* 11:517–527.

ITOH, A., YAMAKURA, T., OGINO, K., LEE, H. S. & ASHTON, P. S. 1995a. Population structure and canopy dominance of two emergent dipterocarp species in a tropical rain forest of Sarawak, East Malaysia. *Tropics* 4:133–141.

ITOH, A., YAMAKURA, T., OGINO, K. & LEE, H. S. 1995b. Survivorship and growth of seedlings of four dipterocarp species in a tropical rain forest of Sarawak, East Malaysia. *Ecological Research* 10:327–338.

ITOH, A., YAMAKURA, T., OGINO, K., LEE, H. S. & ASHTON, P. S. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak Malaysia. *Plant Ecology* 132:121–136.

KIMMINS, J. P. 1987. *Forest ecology*. Macmillan, New York. 531 pp.

LEGENDRE, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673.

MEDWAY, Lord 1972. Phenology of a tropical rain forest in Malaya. *Biological Journal of Linnean Society* 4:117–146.

NANAMI, S., KAWAGUCHI, H. & YAMAKURA, T. 1999. Dioecy induced spatial patterns of two dominant tree species, *Podocarpus nagi* and *Neolitsea aciculata*. *Journal of Ecology* 87:678–687.

NG, F. S. P. 1977. Gregarious flowering of dipterocarps in Kepong, 1976. *Malaysian Forester* 40:126–136.

PALMIOTTO, P. A. 1998. *The role of specialization in nutrient-use efficiency as a mechanism driving species diversity in a tropical rain forest*. Doctoral dissertation. Yale University, New Haven.

RIPLEY, B. D. 1976. The second-order analysis of stationary point processes. *Journal of Applied Probability* 13:255–266.

ROWLINGSON, B. & DIGGLE, P. 1993. Splancs: spatial point pattern analysis code in S-Plus. *Computers and Geosciences* 19:627–655.

SAKAI, S., MOMOSE, K., YUMOTO, T., NAGAMITSU, T., NAGAMASU, H., HAMID, A. A., NAKASHIZUKA, T. & INOUE, T. 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany* 86:1414–1436.

SASAKI, S., TAN, C. H. & ZULFATAH, R. R. 1979. Some observations of unusual flowering and fruiting of dipterocarps. *Malaysian Forester* 42:38–65.

STERNER, R. W., RIBIC, C. A. & SHATZ, G. E. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. *Journal of Ecology* 74:621–633.

THOMAS, S. C. 1996. Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. *OIKOS* 76:145–154.

TREXLER, J. C. & TRAVIS, J. 1993. Nontraditional regression analyses. *Ecology* 74:1629–1637.

VAN SCHAIK, C. P. 1986. Phenological changes in Sumatran rain forest. *Journal of Tropical Ecology* 2:327–347.

WICH, S. A. & VAN SCHAIK, C. P. 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology* 16:563–577.

YAMAKURA, T., KANZAKI, M., ITOH, A., OHKUBO, T., OGINO, K., CHAI, E. O. K., LEE, H. S. & ASHTON, P. S. 1995. Topography of a large-scale research plot established within the Lambir rain forest in Sarawak. *Tropics* 5:41–56.

YAMAKURA, T., KANZAKI, M., ITOH, A., OHKUBO, T., OGINO, K., CHAI, E. O. K., LEE, H. S. & ASHTON, P. S. 1996. Forest structure of a tropical rain forest at Lambir, Sarawak with special reference to the dependency of its physiognomic dimensions on topography. *Tropics* 7:1–18.

YASUDA, M., MATSUMOTO, J., OSADA, N., ICHIKAWA, S. E., KACHI, N., TANI, M., OKUDA, T., FURUKAWA, A., NIK, A. R. & MANOKARAN, N. 1999. The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology* 15:437–449.