

Dispersal and survival of juveniles of dominant tree species in a tropical rain forest of West Sumatra

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ABSTRACT Adult trees of a given species distribute sparsely in tropical rain forests due to high tree species diversity, and dispersal and survival of juveniles are important processes to form such a pattern. Dispersal and juvenile survival of seven tree species were studied over 13 years in a 1-ha plot of tropical rain forest in Ulu Gadut, West Sumatra, Indonesia. All individuals of juveniles were marked and examined in 1989, 1998 and 2002. Estimation of dispersal kernel was successful for *Calophyllum soulattri* having the highest juvenile density among 7 species. Although dispersal kernel was significant in *Gonystylus forbesii* and *Mastixia trichotoma*, actual juvenile density was lower than expected in some subplots having high expected sapling density. Significant reduction of the sapling survival rate by neighboring conspecific saplings was detected in *Calophyllum soulattri* and *Hopea dryobalonoides*, and that by conspecific trees was detected in *Swintonia schwenkii* and *Cleistanthus glandulosus*. The negative effect of conspecific plants on juvenile survival was a more important factor than topography, and may be common in tropical rain forest trees. Aggregated distribution of saplings around mother trees might be formed just after seed dispersal; however, such patterns might be obscured by high mortality around mother trees, and relatively uniform tree distribution may be formed. Since regeneration is a rare phenomenon due to gregarious reproduction, we might be able to observe only limited stages of these processes simultaneously.

Key Words: dispersal, survival, juveniles, tropical forest

INTRODUCTION

Adult trees of a given species distribute sparsely in tropical rain forests, reflecting high tree species diversity, and dispersal and survival of tree juveniles are important processes in biodiversity conservation (Trakhtenbrot et al. 2005). Various studies on seed dispersal have been reported applying recent parameterization techniques (Ribbens et al. 1994; Clark et al. 1999). Most attention has been paid to measure the distribution of dispersal distance (Nathan et al. 2003; Nathan & Casagrand, 2004; Greene et al. 2004; Komuro & Koike 2005; Skarpaas et al. 2005; Ohtani & Koike, 2005).

Spatial variation in juvenile survival is another important factor determining distribution patterns of adult trees. Ground surface relief may affect the survival of juveniles through water condition and resource availability (Russo et al. 2005). Aggregated distribution of juveniles and the existence of large trees may prohibit the survival of conspecific juveniles (Mukhtar et al. 1998; Clark et al. 1999).

Several ecological studies in a foothill rain forest in Ulu Gadut, West Sumatra have been carried out since 1980, including growth and death of trees (Kohyama et al. 1989), spatial distribution pattern of representative tree species (Kohyama et al. 1994), dynamics of above ground big woody organs (Yoneda et al. 1990), horizontal variance of stand structure (Yoneda et al. 1994), impact of dry weather on the stand dynamics (Yoneda et al. 2006), canopy structure (Koike & Syahbuddin, 1993), and soil quality characterization in relation to tree species diversity (Kubota et al. 2000). Although the dispersal pattern of *Swintonia schwenkii* seeds (Suzuki & Kohyama, 1991) and survival of *Calophyllum soulattri* (Mukhtar et al. 1992, 1998) were studied, dispersal and survival of other species have not yet been studied, and general patterns in tree species there are still unknown.

In this study, we investigated whether dispersal

limitation could be detected in common tree species, and evaluated effects of neighboring conspecific plants and topography on the survival of juveniles of these species.

METHODS

Study site

This study was carried out at a 1.00 ha permanent plot, named Pinang–pinang plot in a foothill forest of Mt. Gadut (Lat. 0°55' S, Long. 100°30' E, elevation ranged from 575 m to 605 m), 18 km east from Padang, West Sumatra, Indonesia. This plot is covered primarily by mature trees occurring in patches with sporadic gap and regrowth patches. Detailed description of the vegetation can be found in the previous papers (Kohyama et al. 1989; Yoneda et al. 1990).

The plot was set up in 1981 consisted of 115 subplots of approximately equivalent areas. In this research, topographic environments (slope inclination, laplacian representing concavity, and logarithm of specific catchment area representing wetness) were calculated using a free GIS (Koike, 2005) from 1 m mesh DEM based on a contour map drawn by Ogino et al. (1984). The average value for each subplot was used for analysis.

Studied species

We chose seven tree species having many saplings. Saplings of these species are common and dominant on the forest floor. These include emergent tree species (*Swintonia schwenkii* T & B), canopy tree species (*Calophyllum soulattri* Burm, *Hopea dryobalanoides* Miq.), and sub-canopy tree species (*Cleistanthus glandulosus* Jabl., *Mastixia trichotoma* Bl., *Grewia florida* Miq. and *Gonystylus forbesii* Gilg). The characteristics of the selected seven tree species are shown in Table 1.

Field survey for juveniles and trees

The position of target tree species (DBH > 9 cm) was

mapped in 1981, and diameter measurement data from 1989 and 1996 were used for analysis. The saplings (0–100 cm in height) and young trees (101–1000 cm in height) of the seven species were marked in September 1989, and re-examined in September 1998 and September 2002. Positions and plant height were measured in these surveys.

Dispersal kernel

The dispersal kernel is a mathematical function that represents the expected density of juveniles from one mother tree. Various dispersal kernel calculations have been proposed (Clark et al. 1999; Nathan et al. 2003; Nathan & Casagrand, 2004; Skarpass, 2005; Ohtani & Koike, 2005). We employed the dispersal kernel, assuming the exponential decrease of sapling density with the distance from a mother tree. Since we could not obtain the minimum tree size for reproduction, the number of saplings produced by a mother tree was assumed to be proportional to the basal area of each mother tree. The dispersal kernel we employed is thus :

$$D_j = \sum_{i=1}^n aB_i e^{-rx_{ij}} \quad (1)$$

where D_j is the density of saplings (m^{-2}) in the j -th subplot, B_i is the basal area (m^2) of the i -th mother tree, x_{ij} is the distance from the i -th mother tree to the center of j -th subplot, and n is the number of mother trees considered. Regression coefficient a represents the sapling density just under the mother tree of $1 m^2$ in basal area. Regression coefficient r is always negative, and a large absolute value of r represents a steep decline of sapling density in relation to the distance from the mother tree. Since we considered all sizes of trees as potential mother trees, much effort would have been required to obtain the distribution of all mother trees outside of the plot. We however considered mother trees only in the plot as target tree species are abundant in the plot, and the plot located on the ridge top is somewhat of an "island" of

Table 1. Tree species studied. Dispersal agents were estimated from propagule morphology and personal observations.

Species	Family	Maximum DBH	Dispersal agents	Latest mass reproduction before 1989
<i>Calophyllum soulattri</i>	Guttiferae	65.4	Bats	1981
<i>Cleistanthus glandulosus</i>	Euphorbiaceae	29.1	Birds	Not known
<i>Gonystylus forbesii</i>	Thymelaceae	43.7	Animal?	Not known
<i>Grewia florida</i>	Tiliaceae	29.7	Bird	Continuous
<i>Hopea dryobalanoides</i>	Dipterocarpaceae	61.5	Wind	Not known
<i>Mastixia trichotoma</i>	Cornaceae	40.1	Animal?	Not known
<i>Swintonia schwenkii</i>	Anacardiaceae	132.0	Wind	Continuous

remnant old-growth forest. We assume that the effect of omitting outside mother trees is not large.

Parameters a and r were determined by the maximum likelihood method assuming Poisson error function. The log likelihood was:

$$\ln L = \sum_{j=1}^m \ln \left[\frac{e^{-\lambda_j} \lambda_j^{z_j}}{z_j!} \right] \quad (2)$$

λ_j is the expected number of saplings in the j -th subplot as

$$\lambda_j = A_j D_j$$

where, A_j is area (m^2) of the j -th subplot, z_j is actual number of saplings (0–100 cm in height) in 1989 in the j -th subplot, and m is the number of subplots. Tree diameter in 1989 was used for B . $\log L$ was maximized by Solver of Microsoft Excel. Significance of the model was tested by the likelihood ratio test using the null model of uniform sapling density.

Topographic environments may have an affect on the success of plant at germination and establishment stages. To detect such effects, the correlation between residuals ($z_j - \lambda_j$) of the dispersal model and topographic environments (slope inclination, laplacian representing concavity, and logarithmic specific catchment area representing wetness) were calculated.

Analysis of survivorship

Survivorships from 1989 to 1998 of seven species were analyzed. Slope inclination, laplacian, and logarithmic specific catchment area were considered as topographic environments, and juvenile density of the same species in subplots in 1989, the total basal area (BA) of the same species in subplots in 1996, and the total BA of all species in subplots in 1996 were considered as biological environments. Logistic regression with a stepwise variable selection procedure (SPSS 12.0J) was used to detect significant environmental factors on survival. Survival (value=1) or death (value=0) of juveniles in 1998 was assumed as a dependent variable, and topographical and biological environmental variables as independent variables.

RESULTS

Juvenile and adult tree distribution of seven tree species is shown in Fig. 1. Trees distributed almost evenly in *Cleistanthus glandulosus*, *Swintonia schwenkii* and *Grewia florida*, whereas aggregated in *Hopea dryobalanoides* and *Gonystylus forbesii*. *Calophyllum soulattri* had few adults and many juveniles.

The number of juveniles of seven tree species

decreased during the research period (Fig. 2), representing lesser recruitment than mortality. *Calophyllum soulattri* had the highest sapling density (0–100 cm in height) throughout the research period, whereas saplings of *Gonystylus forbesii* and *Grewia florida* were not abundant. The most abundant species in young trees (101–1000 cm in height) was different from those of saplings. *Gonystylus forbesii* and *Cleistanthus glandulosus* were abundant species, and *Grewia florida* and *Mastixia trichotoma* had a few young trees.

Dispersal kernel

Dispersal kernels were significant for three species having large number of juveniles such as *Calophyllum soulattri*, *Gonystylus forbesii* and *Mastixia trichotoma* (Table 2, $P < 0.001$). In contrary these were not significant in *Grewia florida*, *Hopea dryobalanoides* and *Swintonia schwenkii* (Table 2, $P > 0.1$). Estimation of sapling density was successful for *Calophyllum soulattri*, however, juvenile densities in *Gonystylus forbesii* and *Mastixia trichotoma* were lower than expected in some subplots having high expected sapling density (Fig. 3). No significant correlation was found ($P > 0.05$) between residuals (actual sapling number in subplot – predicted number) and environmental factors (slope, laplacian, and log catchment area), except for slightly more juveniles than expected in subplots of large catchment area in *Mastixia trichotoma* ($P < 0.05$).

Survivorship

The survivorship rate of saplings (0–100 cm in height) over nine years (1989–1998) was high in *Swintonia schwenkii*, *Gonystylus forbesii* and *Mastixia trichotoma* (62.3%, 60.7% and 52.2% respectively) (Table 3). *Grewia florida* and *Hopea dryobalanoides* had low survivorship rates (35.7% and 33.1%, respectively). The survivorship rates of young trees (101–1000 cm in height) over nine years were generally higher than those of saplings except for *Swintonia schwenkii* (Table 4). Survivorship rates were high in *Hopea dryobalanoides* and *Gonystylus forbesii* (76.4% and 65.6% respectively). *Grewia florida* had a low survivorship rate of 47.1%.

In saplings, conspecific plants caused negative effects in four species, whereas topography showed less importance than conspecific plants (Table 3). The high density of conspecific saplings reduced the survival rate in *Calophyllum soulattri* and *Hopea dryobalanoides*, and large conspecific basal areas reduced the survival rate in *Cleistanthus glandulosus* and *Swintonia schwenkii* (Fig. 4). Topography was significant in *Mastixia trichotoma*,

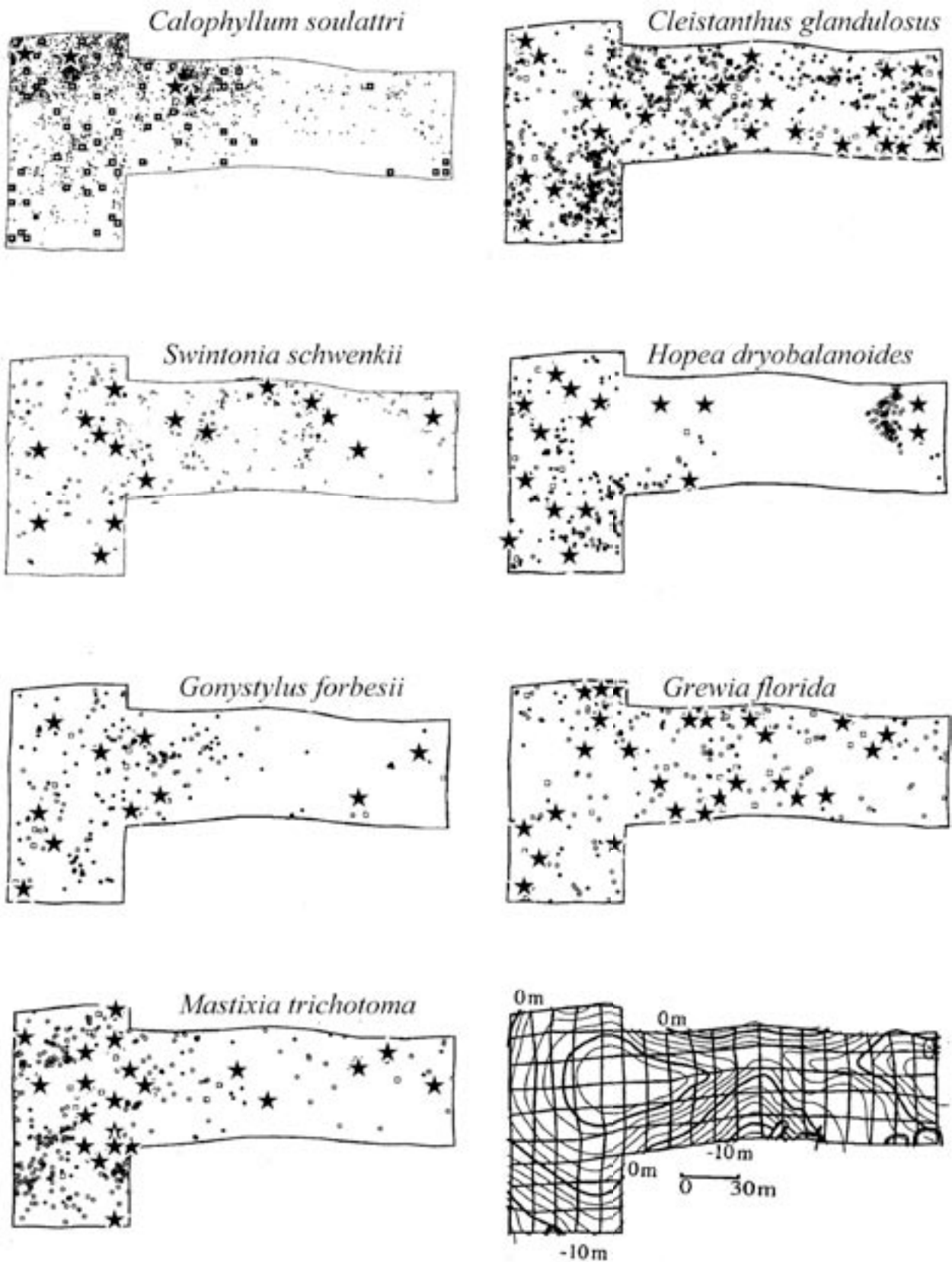


Fig. 1. Distribution map of juveniles and adult trees, and topography with 2 m contour. Cited and modified from Suzuki and Kohyama, 1991; Mukhtar *et al.*, 1992; Kohyama *et al.*, 1994.

○ saplings < 100 cm; ● young trees 101-1000 cm; □ > 1001 cm in high and DBH < 9 cm; ★ tree (DBH > 9 cm)

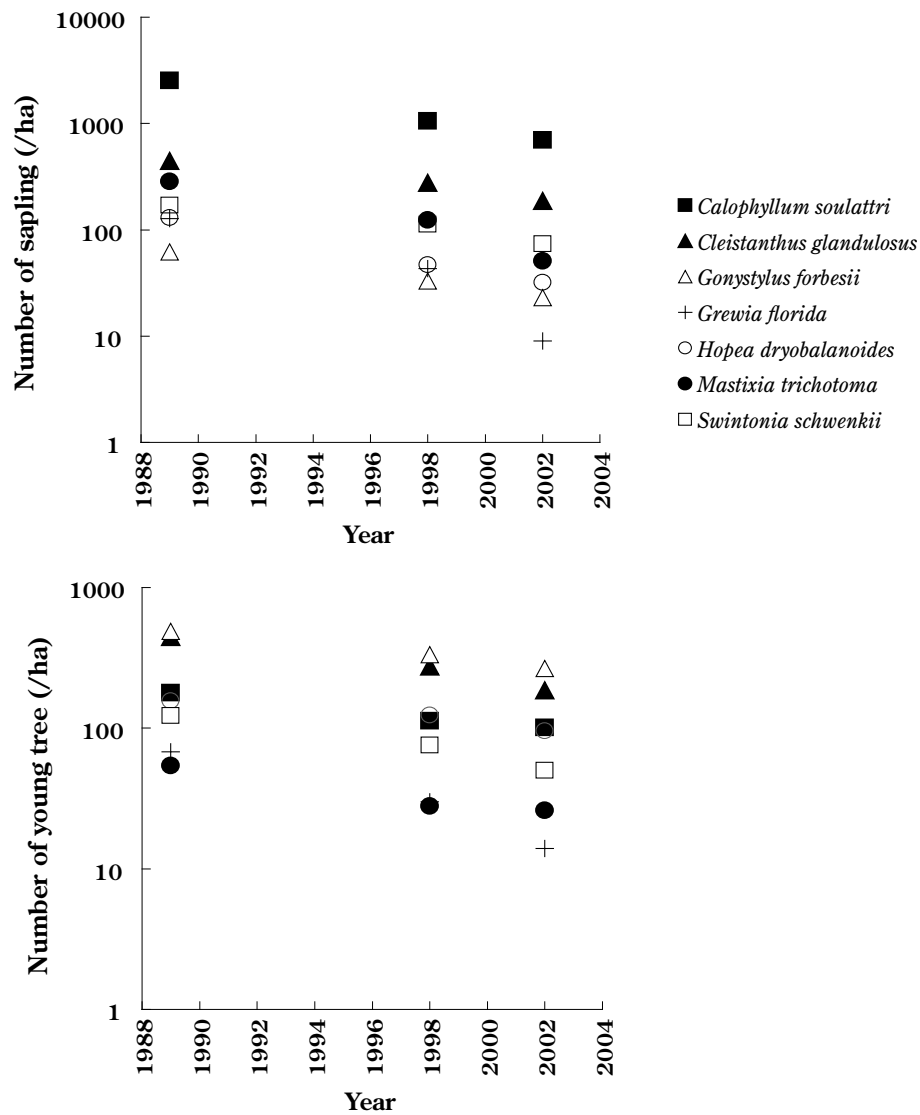


Fig. 2. Number of saplings and young trees in the research period. Note that the numbers in 1998 and 2002 include new recruits, and the graph is not survivorship curve.

Table 2. Dispersal kernels for saplings (height 0–100 cm). B is basal area of the mother tree in m^2 .

Species	Sapling density (m^{-2}) from a single mother tree standing x m distant	Significance
<i>Calophyllum soulattri</i> .	$3.78 B e^{-0.0733x}$	$P < 0.001$
<i>Cleistanthus glandulosus</i>	$0.443 B e^{-0.00812x}$	$P < 0.1$
<i>Gonystylus forbesii</i>	$0.430 B e^{-0.0533x}$	$P < 0.001$
<i>Grewia florida</i>	–	ns
<i>Hopea dryobalanoides</i>	–	ns
<i>Mastixia trichotoma</i>	$0.175 B e^{-0.0357x}$	$P < 0.001$
<i>Swintonia schwenkii</i>	–	ns

ns: not significant

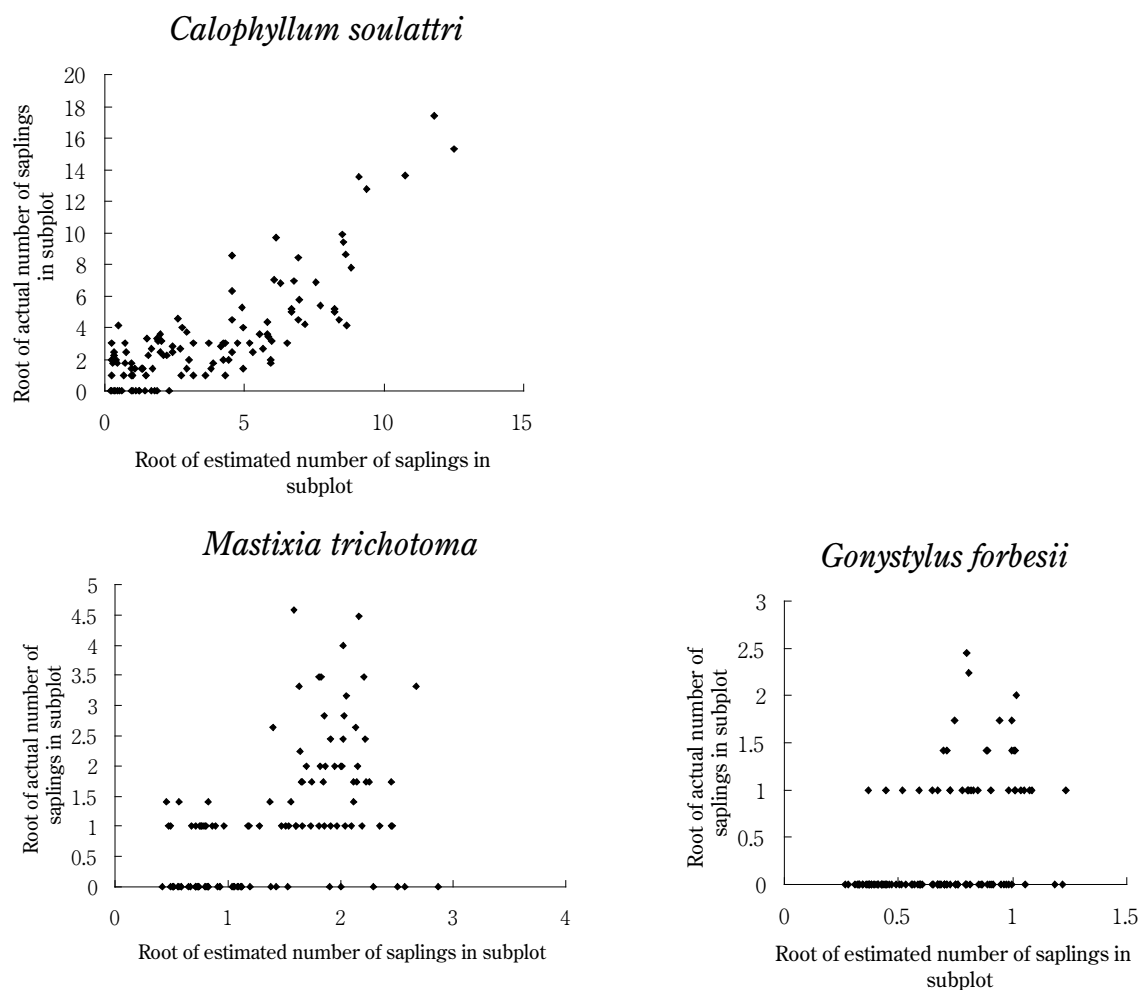


Fig. 3. Number of actual and estimated sapling numbers in subplots. Estimated number was λ_j in the equation 2.

and was the second or third significant variable in *Calophyllum soulattri*.

In young trees, conspecific plants also caused negative effects in three species, and topography generally showed less importance than conspecific plants (Table 4). The effect of conspecific young tree density was significant in *Mastixia trichotoma*, and conspecific basal area was significant in *Calophyllum soulattri* and *Swintonia schwenkii*. Another significant variable was total basal area in *Cleistanthus glandulosus*. Topography was significant only for *Cleistanthus glandulosus* as the second variable.

DISCUSSION

Seed limitation caused by the dispersal process was detected in three species (*Calophyllum soulattri*, *Gonystylus forbesii* and *Mastixia trichotoma*) among seven

examined and neighboring conspecific plants caused sapling mortality in four species. Aggregated spatial patterns of saplings will be produced by the seed dispersal process, but density dependent mortality decreases the aggregated spatial heterogeneity. Relatively uniform tree distribution will be formed through these processes. It might be one reason for sparse distribution of many tree species in tropical rain forests.

Since reproduction is rarely observed due to gregarious reproduction of this region (Inoue & Nakamura, 1990), we might be able to observe only limited stages of these processes in a given snapshot survey. *Calophyllum soulattri* in 1989 might be close to the first stage just after the mass reproduction. *Mastixia trichotoma* in 1989 might be in the following stage after the mortality process. Species with continuous reproduction (*Swintonia schwenkii* and *Grewia florida*) may not form quite an aggregated sapling distribution,

Table 3. Results of survival analysis for saplings (0–100 cm in height). Environmental variables used in logistic regression with stepwise variable selection procedure were basal area of all species, basal area of the own species, sapling density of the own species, slope inclination, log catchment area, and laplacian of each subplot. Laplacian represents concavity of ground relief and was calculated as second deliberative.

Species	Number of saplings in 1989 (survival rates for nine years)	One variable model	Two variables model	Three variables model	Significant variables in single variable analysis
<i>Calophyllum soulattri</i>	2600 (42.20%)	-Sapling density**	-Sapling density** +Slope**	-Sapling density** +Slope** +Laplacian**	-Sapling density** -Own BA** -Total BA* +Slope** +Laplacian**
<i>Cleistanthus glandulosus</i>	442 (48.9%)	-Own BA**	ns	ns	-Own BA** -Slope*
<i>Gonystylus forbesii</i>	61 (60.7%)	ns	ns	ns	ns
<i>Grewia florida</i>	126 (35.7%)	ns	ns	ns	ns
<i>Hopea dryobalonoides</i>	127 (33.1%)	-Sapling density**	ns	ns	-Sapling density** +Catchment area*
<i>Mastixia trichotoma</i>	278 (52.2%)	-Laplacian**	ns	ns	-Laplacian** -Catchment area**
<i>Swintonia schwenkii</i>	168 (62.3%)	-Own BA**	ns	ns	-Own BA** -Total BA*

**P<0.01, *P<0.05, ns: not significant

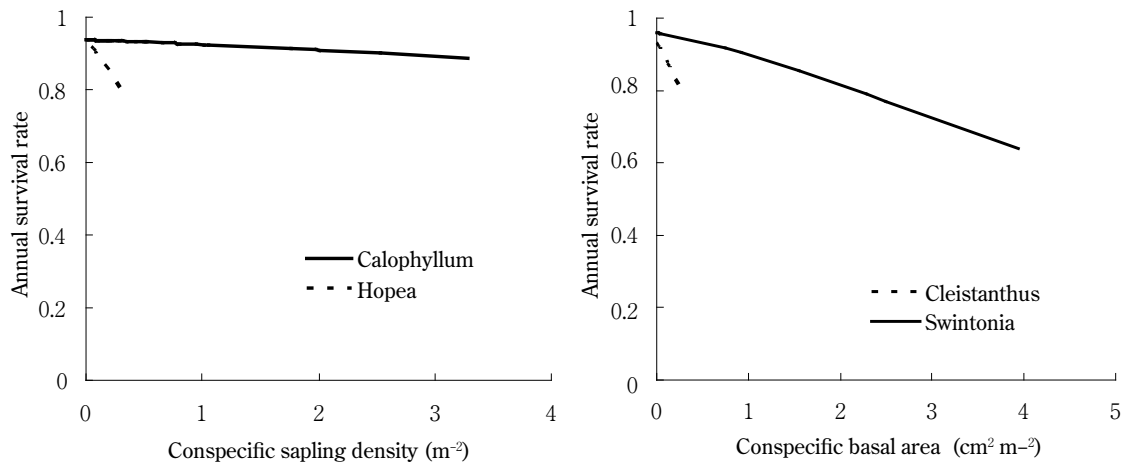


Fig. 4. Effect of sapling density and basal area (BA) of the own species on survivorship of saplings (0–100 cm in height). Estimated curves are shown.

due to the larger contribution of old saplings than in the case of having many one-year-old seedlings in species with mass reproduction.

Density dependent mortality has been reported in many cases. Tomita et al. (2002) found intensive

seed predation in high seed density sites of beech. The mechanism of density dependent mortality for species studied in this study is not known (Janzen, 1970).

Seed dispersal kernel could not be detected in about half of the studied species. We used saplings of 0–100 cm

Table 4. Results of survival analysis for young trees (101–1000 cm in height). Environmental variables used in logistic regression with stepwise variable selection procedure were basal area of all species, basal area of the own species, sapling density of the own species, slope inclination, log catchment area, and laplacian of each subplot.

Species	Number of young trees in 1989 (survival rates for nine years)	One variable model	Two variables model	Three variables model	Significant variables in single variable analysis
<i>Calophyllum soulattri</i>	180 (63.9%)	–Own BA**	ns	ns	–Young tree density* –Own BA**
<i>Cleistanthus glandulosus</i>	490 (60.8%)	+Total BA*	+Total BA* +Catchment area*	ns	+Total BA* +Catchment area*
<i>Gonystylus forbesii</i>	122 (65.6%)	ns	ns	ns	ns
<i>Grewia florida</i>	68 (47.1%)	ns	ns	ns	ns
<i>Hopea dryobalanoides</i>	161 (76.4%)	ns	ns	ns	ns
<i>Mastixia trichotoma</i>	47 (53.2%)	–Young tree density*	ns	ns	–Young tree density*
<i>Swintonia schwenkii</i>	125 (56.8%)	–Own BA*	ns	ns	–Own BA*

**P<0.01, *P<0.05, ns: not significant

height in this research. However, clearer dispersal kernel may be obtained using seeds or one-year-old seedlings. Other reasons such as the relatively longer dispersal distance compared to distance among mother trees, non-synchronous reproduction of large trees, significant number of mother trees outside the plot, and the death of large mother trees just before the research period might cause the failure of dispersal kernel estimation. While we considered mother trees only within the plot, the half decrease distance of *Calophyllum soulattri* sapling density was 9.5 m (Table 2), and the effect caused by mother trees outside the plot should be limited.

Although a model simultaneously including both dispersal and survival processes is possible, we could not determine optimum parameters as inverse problems, because there were many possible parameter sets having similar likelihoods. Thus we analyzed both processes separately.

Although soil condition may have an effect on tree distribution (Masunaga et al. 1997; Kubota et al. 2000; Hermansah et al. 2002; Palmiotto et al. 2004), topography was a less important environmental factor for sapling survival compared to the negative effects by conspecific plants in this study. Soil condition had effects on sapling survival in cases of large environmental difference. Russo et al. (2005) found that *Hopea dryobalanoides* had

significantly higher survival rates in adult soil than in low-fertile humul soil in gap areas of Lambir National Park, Sarawak, Malaysia. Whereas *Swintonia schwenkii* had no significant differences in survival rates between soils in their research site. Our research site was limited to a ridge area of small spatial scale (Fig. 1), and a narrow environmental range might be a reason for the small effect of topography. Studies in larger topographic gradients is required to clarify the importance of topography on sapling survival and to evaluate the importance of the sapling stage on the development of spatial distribution patterns of adult trees. In other words, the pattern of species dispersion is mainly regulated by intraspecific density dependence at a local (< 1 ha) spatial scale.

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