SPATIAL PATTERN OF ADULT TREES AND SEEDLING SURVIVORSHIP IN *PENTASPADON MOTLEYI* IN A LOWLAND RAIN FOREST IN PENINSULAR MALAYSIA

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OKUDA, T., KACHI, N., YAP, S.K. & MANOKARAN, N. 1995. Spatial pattern of adult trees and seedling survivorship in *Pentaspadon motleyi* in a lowland rain forest in Peninsular Malaysia. The spatial pattern of seedling survival was studied in a lowland rain forest in Peninsular Malaysia. The studies included 1) the distribution of adult trees and saplings (> 1 cm in dbh) of *Pentaspadon motleyi* locally known as pelong, based on data obtained in 1987 in a 50-ha plot where all trees > 1 cm dbh are mapped; 2) the survivorship of ca. 1-year-old seedlings in relation to distance from the nearest adult of pelong, seedling density and presence of light-gaps in a 1-ha plot for 78 weeks from August 1991. A total of 738 adult trees and saplings were found in the 50-ha plot. There were no saplings (1 - 2.5 cm dbh) within 6 m of conspecific adult trees more than 40 cm in dbh, but they did occur under non-conspecific adult trees. During the census, ca. 45% seedlings died. The mortality rate of seedlings close to the conspecific adult (0 - 2 m) was significantly greater than that away from it (> 2 m). Transplanted seedlings growing in 4% full sunlight within a light-gap and in the nursery showed much higher survival and growth rates than those growing in 2 - 2.5% full sunlight under the canopy. The spatial distribution patterns of saplings in the 50-ha plot and seedling survivorship within the 1-ha plot indicate that seedling survivorship is affected to some extent by nearby conspecific adult trees. It also suggests that seedlings in the shade die before they grow to sapling size, unless they encounter light-gaps outside the crown area of the mother tree. The study suggests the importance of light-gaps which minimize the effects of distance- responsible-mortality agents on the seedlings.

Key words: Distance-dependent mortality - Malaysian lowland forest - *Pentaspadon motleyi* - seedling recruitment

OKUDA,T., KACHI,N., YAP, S.K. & MANOKARAN, N. 1995.Corak ruang pokok-pokok dewasa dan kemandirian bijibenih *Pentaspadon motleyi* di dalam hutan hujan tanah pamah di Semenanjung Malaysia. Corak ruang kemandirian bijibenih dikaji dalam hutan hujan tanah pamah di Semenanjung Malaysia. Kajian yang dijalankan termasuk 1) taburan pokok-pokok dewasa dan anak-anak pokok (diameter aras dada > 1 cm) *Pentaspadon motleyi* (nama tempatan ialah pelong), berdasarkan pada data yang diperoleh pada tahun 1987 dari plot 50-ha di mana semua pokok-pokok yang mempunyai diameter aras dada > 1 cm dipetakan; 2) kemandirian anakbenih yang berumur kira-kira satu tahun yang berkaitan dengan jarak dari pokok pelong dewasa yang terdekat, ketumpatan anak benih dan kewujudan ruang cahaya dalam plot 1 ha selama 78 minggu dari bulan Ogos 1991. Sejumlah 738 pokok-pokok dewasa dan anak pokok didapati dalam plot 50 ha. Tidak ada anak pokok (diameter aras dada 1-2.5 cm) dalam jarak 6 m dari pokok-pokok dewasa spesies yang sama yang mempunyai diameter aras dada melebihi 40 cm tetapi terdapat anak pokok di bawah pokok-pokok dewasa yang berlainan spesies. Semasa bancian, kira-kira 45% anakbenih telah mati. Kadar kematian biji benih yang berdekatan dengan pokok dewasa dari spesies yang sama (0 - 2 m) adalah lebih tinggi daripada bijibenih yang berada jauh daripadanya (> 2 m). Bijibenih-bijibenih alih yang tumbuh dalam 4% cahaya matahari penuh dalam jarak ruang cahaya dan dalam tapak semaian menunjukkan kemandirian dan kadar pertumbuhan yang lebih tinggi daripada bijibenih alih yang tumbuh dalam 2-2.5% cahaya matahari penuh di bawah sudur. Corak-corak taburan ruang anak-anak pokok dalam plot 50 ha dan kemandirian bijibenih dalam plot 1 ha menunjukkan bahawa kemandirian bijibenih dipengaruhi sehingga had tertentu oleh pokok-pokok dewasa dari spesies yang sama yang berdekatan. Ini juga menandakan bahawa bijibenih-bijibenih dalam tempat teduh akan mati sebelum ia membesar pada saiz anak pokok kecuali ia bertemu dengan ruang-ruang cahaya luar dari ruang silara pokok induk. Kajian ini menunjukkan kepentingan ruang-ruang cahaya yang mengurangkan kesan-kesan agen-agen jarak-penyebab-kematian pada bijibenih-bijibenih.

Introduction

The spatial distribution pattern of dispersed seeds and saplings has important implications for the fitness of the mother tree, spatial and genetic structure of populations and ultimately the species diversity within a community (Augspurger 1983a). According to the escape hypothesis (Howe & Smallwood 1982) originally proposed by Janzen (1970) and Connell (1971), seeds or seedlings suffer high mortality in close vicinity to their mother tree as a result of predators or parasites common under this tree, while they enjoy higher survivorship away from the mother tree. That is, a new adult will not be produced in the immediate vicinity of the mother tree where most seeds fall and consequently the adults are more regularly distributed than expected from seed-fall pattern (Janzen 1970). This hypothesis has been regarded as an explanation on how a tropical forest can maintain high tree species richness. Many biologists have examined the hypothesis; some studies were affirmative, but most failed to show strong supporting evidence. The affirmative data were normally published while negative data may be under-represented in the literature (Clark & Clark 1984). These authors found that only 8 of the total 24 reviewed reports showed strong evidence that distance from adults influenced the seedling survival (e. g. Augspurger 1983a, b, De Steven & Putz 1984). These conflicting results appear to be largely due to the research methods, species chosen for the study and locality (Schupp 1988). Considering the higher species richness in the tropics, relatively few published data are available to evaluate the escape hypothesis (Howe & Smallwood 1982). Most of these case studies were conducted in neotropical regions, particularly in central America, either Panama or Costa Rica. Only a few (e.g. Chan 1980, Becker & Wong 1985) were conducted in Asian tropical forests where the vegetation structure and species composition differ from those in neotropical regions.

Recent tree census studies in large-scale plots (e.g. 50 ha), where many individual trees have been recorded systematically, allow the affinity of mature and immature trees to be determined (Hubbell 1979, Condit *et al.* 1992) and these results usually demonstrated negative evidence for the escape hypothesis. Analysis based upon many data obtained in such plots appears to provide higher accuracy concerning the affinity of juveniles and adults, but overlooks the survivorship of early-stage seedlings, as this database usually consists of trees 1 cm or more in dbh (diameter at breast height). The results of short-term studies, e.g. mortality, during a defined period, or fragmentary information based on spatial patterns of large size saplings and adults, often lead to the failure to detect increased spacing of progeny and adults over a longer time scale (Augspurger 1983b, Clark & Clark 1984). Strong spatial changes with time can result from very early progeny mortality (Augspurger 1983b) and thus, study on the early stage of seedling establishment is indispensable to examine the escape hypothesis.

On the other hand, seedling survivorship in relation to herbivory, pathogens or other biological factors is strictly dependent on the age of the seedlings and type of species (Augspurger 1984a). In addition to the effects of host specific enemy in close vicinity to the adults, there are interfering effects of the adult tree, such as allelopathy, a higher frequency of destructive litter fall from the adult canopy, local depletion of critical nutrients within the adult's root zone or particularly effective shading by the adult crown; these are important because such effects can also produce apparent distance or density-dependent progeny mortality (Clark & Clark 1984).

In addition to testing the escape hypothesis, documenting the dynamics of seedling recruitment of individual tree species is important for understanding tropical forest dynamics (Schupp 1990). In our study, one of the common species in a lowland rain forest in Peninsular Malaysia, *Pentaspadon motleyi* Hook f. (Anacardiaceae), locally known as "pelong", was studied to determine 1) whether seedling survival is enhanced as a result of their escape from the parents, and 2) how the future spatial pattern of this species is related to seedling recruitment.

Pelong is widely distributed in lowland forests of Malaysia, Indonesia, Philippines, Papua New Guinea and Solomon Islands. It flowers twice (from March to May and from October to November) but no flowering was observed during the present study (Ng 1989). The fruits are ovoid to ovoid-oblong shape, 3 - 5 × 2 - 2.75 cm, and contain one large seed (Corner 1988, Ng 1989). Thus these large fruits, when not carried away by dispersal animals, fall mostly within or very near the zone of the tree crown.

Materials and methods

Study area

The study area was located in the Pasoh Forest Reserve (2°58 'N, 102°18 'E), Negeri Sembilan, about 70 km southwest of Kuala Lumpur, Malaysia. The mean annual precipitation measured at this reserve from 1970 to 1974 was 2054 mm with two distinct peaks in April/May and November/December (Soepadmo & Kira 1977). The soils in the study area are derived from a parent material of shale, granite and fluviatile granitic alluvium (Allbrook 1973). Broadly the vegetation type at Pasoh Forest Reserve is lowland dipterocarp forest, characterized by a high proportion of Dipterocarpaceae (Symington 1943, Wyatt-Smith 1961, 1964).

The 50-ha plot was established and enumerated by the Forest Research Institute Malaysia (FRIM) between 1985 and 1989 in primary forest at this Reserve. All woody plants of 1 cm dbh and larger were measured, identified and mapped to the nearest 10 cm (Manokaran *et al.* 1991). The methodology for establishing these plots is described in Manokaran *et al.* (1990).

Methodology

Pelong is one of the ten most common species in the Pasoh Forest Reserve, with a density of 6.5 ha^{-1} and basal area of 0.52 m^2 ha^{-1} (Manokaran & Kochummen 1990). The mature trees in the Pasoh Forest Reserve in most cases reach the main canopy layer, which was estimated to be from 20 to 30 m high (Manokaran & Kochummen 1990).

For a preliminary study concerning the distribution of mature and immature trees in the Pasoh Forest Reserve, we used the tree census data obtained in 1987 within the 50-ha plot (Manokaran *et al.* 1990). The total number of pelong trees was 738, 75% of which ranged from 1 to 10 cm in dbh. In this study, plants 1 to 2.5 cm in dbh were termed saplings.

In order to examine the density of immature trees around mature trees, distances between all trees, regardless of their size, were obtained from the database for the 50-ha plot. Then, the total number of saplings within a 20-m radius of each tree (target tree) was counted. The number of saplings was pooled in every 1-m increment from the target tree and sapling density (m^{-2}) was obtained.

A separate census for seedling survivorship was conducted within an area of 1 ha, 1.6 km southwest of the 50-ha plot (hereafter termed the 1-ha plot) where selective logging was conducted in the mid-1950s. Nine adult trees with dbh ranging from 16 to 35 cm were found. Distances from one adult to the next nearest adult ranged from 3 to 18 m. Since seedling density was high underneath all these trees, all were presumed to have been reproductively active in the previous fruiting year.

In August 1991, 20 quadrats were placed with sizes of 1 × 1 m^2, 1.5 × 1.5 m^2, 2 × 2 m^2, 2.5 × 2.5 m^2 and 3 × 3 m^2 at a distance ranging from 0 to 12 m from the nearest conspecific adult tree. The larger quadrats were placed further from the adult trees to accommodate the lower number of seedlings. All seedlings were identified as one cohort emerging after the seed flush one year prior to the census. Few saplings were found in the plots.

All seedlings in each quadrat were tallied using consecutive numbers and the heights (cm) were measured every month from August 1991 to December 1992 and every two months from December 1992 to March 1993. The total seedlings tallied was 562.

All the tagged seedlings growing in the 1-ha plot were shaded by the canopy. In addition to the dispersal distance, differences in light and associated micro-climatic factors found in gaps have been known to influence seedling survival (e.g. Augspurger 1983a, 1984a). Since the seedling density and the distance from adults are correlated, a definite distance or density effect can only be investigated by controlling one of these variables and varying the other (Augspurger 1983a, Clark & Clark 1984). To partly solve this problem, a transplanting experiment was conducted. Approximately 300 seedlings were dug out randomly on 19 August 1991 and potted in black plastic pots (10 cm diameter) with soil excavated from the 1-ha study site and nursed until they recovered from the transplanting effects. On 2 September 1991, 200 of the surviving seedlings were selected and replanted in four 2 x 2 m quadrats with 50 plants in each quadrat. One of the 4 transplant quadrats (T-4) was under a light-gap (ca. 3 x 5 m in size, 4% of photon flux intensity relative to an open site 19 m from the nearest adult), while the others were under shade conditions (ca. 2 to 2.5 % in photon flux density). Two of the shaded quadrats (T-2, T-3) were placed in 20 and 33 m distance from the adults and the other (T-1) was placed 1 m from the bole of the adults. Of the remaining seedlings, 42 were planted in a nursery outside the forest with ca. 4% of the light intensity of the open site to determine the growth of these seedlings under a higher light intensity than in the forest floor. Photon flux density was measured using the photons scensor (LI-190SA, LI-COR). Since there were no light-gaps close to the adults, it was not possible to use a similar quadrat with more light near the adult tree. Seedlings of other species found in the transplant quadrats were dug out prior to the start of experiment. Thus interspecific competition was reduced in comparison to the quadrats with naturally growing seedlings. The limited number of seedlings available prevented an experiment on the mortality response to density. All seedlings in the transplant quadrats were tallied and the number of surviving plants and their height were checked every month until September 1992 similar to the naturally growing seedlings. After this, measurements were conducted every other month until March 1993.

Results

Spatial pattern of saplings and adult trees in the 50-ha plot

Trees of pelong are unevenly distributed in the 50-ha plot, being congregated at the western edge and southeastern corner of the plot, both areas being low-lying and swampy (Figure 1). Their distribution corresponds therefore to the topographic variations in the plot. A few trees were present on a hill-top located in the middle of the plot or on the gentle hill-slopes towards the edge of the plot.

Although the overall distribution of pelong is related to topographic features, the abundance of saplings appears to be related to the distance from the nearest adult pelong trees. The data show that many saplings occurred around an immature tree, while less were found around a big adult tree. This becomes apparent when the density of saplings (1-2.5 cm dbh) was determined around target trees of various diameters (Figure 2). When the size of the target tree was less than 20 cm, there was at least one sapling per m^2 for every 1 m increment of radius up to 9 m from the target tree. However, when the size of a target tree was

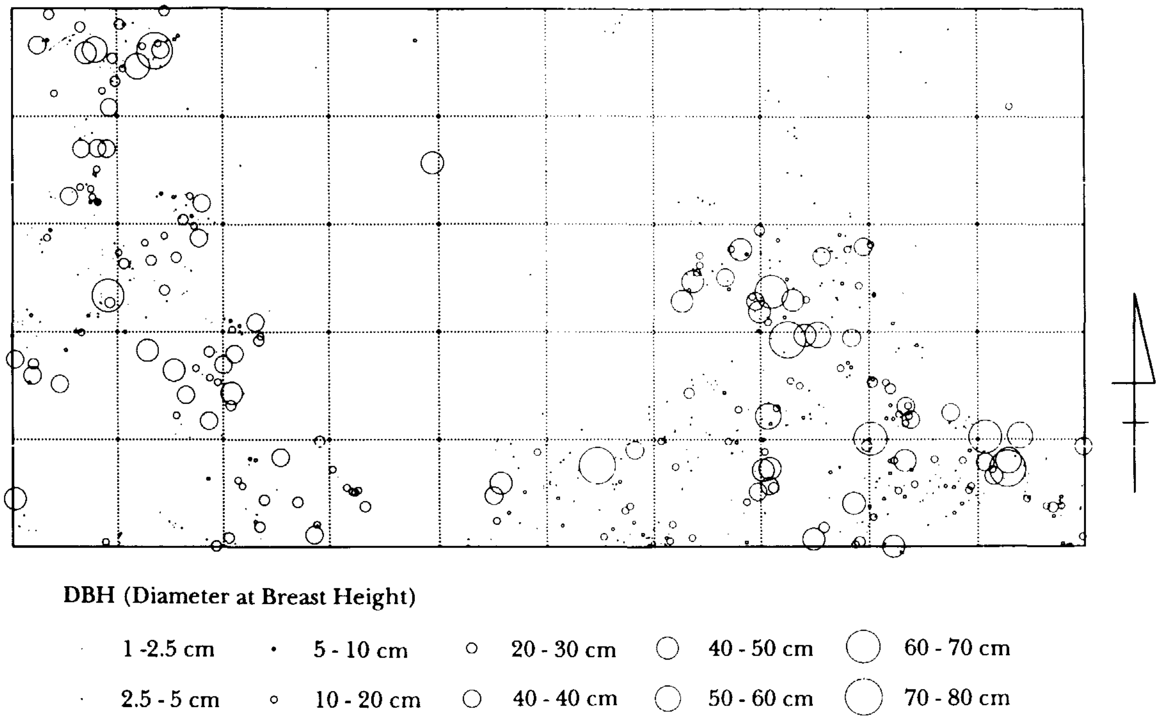


Figure 1. Spatial pattern of *Pentaspadon motleyi* (pelong) in 50-ha plot. Each tree bole is located at the center of a circle 30 times as large as the dbh (diameter at breast height). Each mesh size in the plot is 100 × 100 m

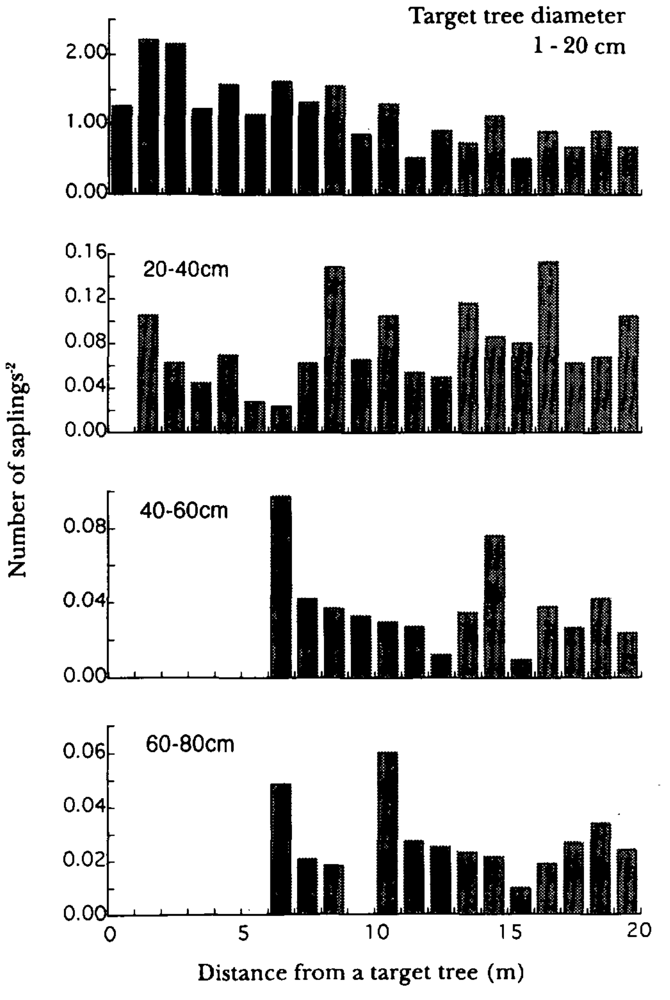


Figure 2. Sapling (1-2.5 cm dbh) density (m^{-2}) within 20-m radius of various sized target trees

more than 40 cm dbh, no sapling was found within a radius of 6 m from the target tree. Saplings were present in the close vicinity of non-conspecific adult trees more than 40 cm in dbh (Figure 3).

Survivorship of natural seedlings

The number of seedlings in a quadrat was totaled at each interval of 2 m from the nearest adult tree (Figures 4 and 5). Total seedlings at each distance at the beginning of the census were: 75 (5 quadrats placed 0-2 m from the nearest adult tree, 5 m^2 in total area of quadrats), 286 (4 quadrats, 2-4 m, 22.5 m^2, ditto), 71 (3 quadrats, 4 - 6 m, 8.5 m^2, ditto), 59 (2 quadrats, 6 - 8 m, 8 m^2, ditto), 53 (3 quadrats, 8 - 10 m, 19 m^2, ditto), 18 (3 quadrats, 10 - 12 m, 19 m^2, ditto).

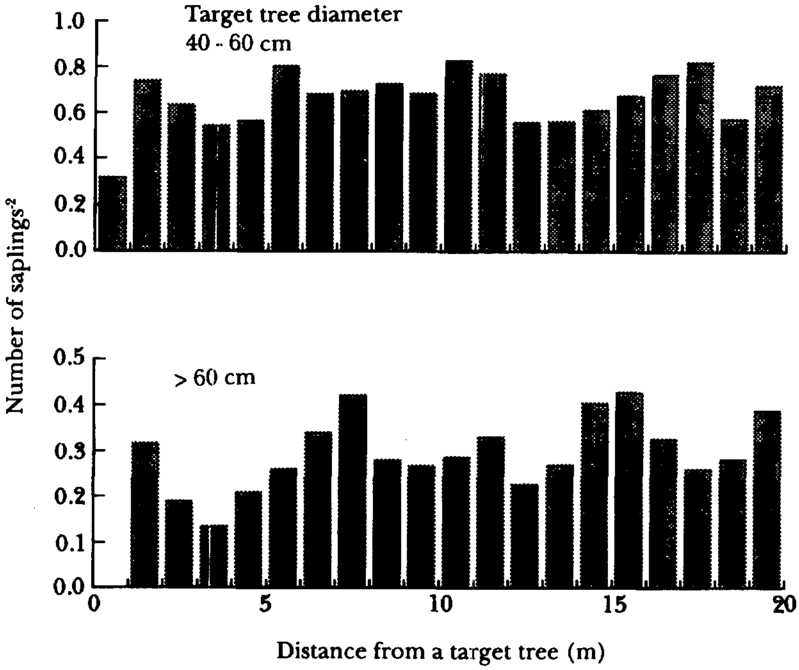


Figure 3. Sapling (1-2.5 cm dbh) density (m^{-2}) within 20-m radius of non-specific trees

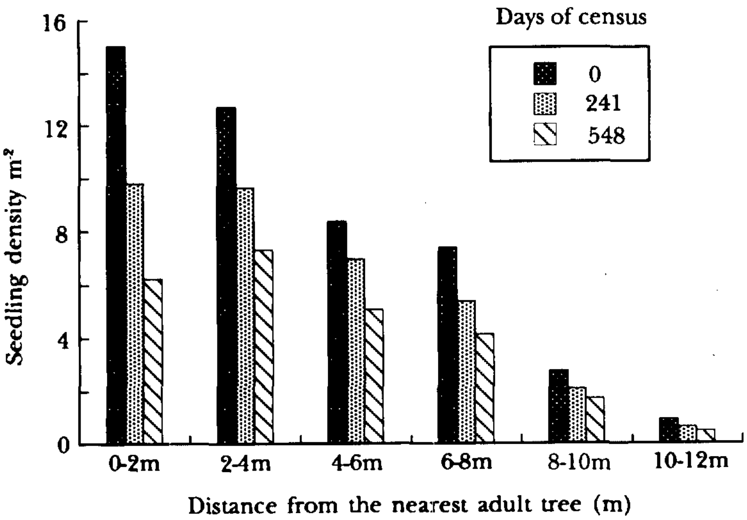


Figure 4. Seedling density in relation to distance from the nearest adult tree at the beginning of the census(day 0), the middle (day 241) and end (day 548) of the census

Seedling density generally decreased with increasing distance from the nearest adult tree (Figure 4). The zone with most abundant seedlings showed a distinct outward shift throughout the experiment; the highest peak was found in the area of 0 - 2 m on day 0, but shifted to the area of 2- 4 m on day 584. The decrease in the number of surviving seedlings over time was exponential and can be expressed as a linear regression line in semi-logarithmic plots (Figure 5). The decrease rates in the range 0 - 2 m from the adult trees were significantly higher ($p < 0.01$) than in any other distance range (Table 1). In addition, the decrease rate in the 2- 4 m area was also higher than in the 4 - 6 m area. There is an exceptional case in the 10 - 12 m area, where the decrease rate was significantly higher than in any other area ranging from 2 - 10 m. However, this may be due to the fact that the number of seedlings is very limited in the quadrats in this range (total number of samples was 18).

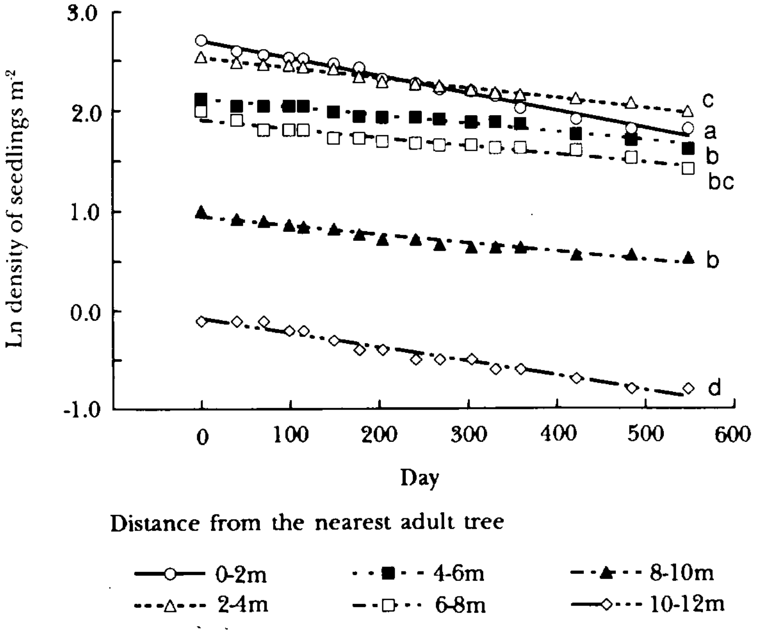


Figure 5. Survivorship of *Pentaspadon motleyi* seedlings during the period August 1991 to February 1993 (548 days) at different distances from the nearest adult tree. Regression lines with different letters are significantly different ($p < 0.01$). See Table 1 for details

Survivorship of transplanted seedlings

The seedlings in the nursery and the light-gap showed higher survivorship, while those in one of the shaded conditions (T-3) were all dead at the end of the experiment (Figure 6). The survival ratio in the other shaded conditions (T-1, T-2) was more or less similar to that of seedlings growing naturally. Comparison of the survival ratios in T-1 and T-2, (both shaded, but the former closer to the adults) showed no significant difference, indicating that there was no distance effect on transplanted seedlings.

Table 1. Results of t-test to examine diferences in regression slopes of survivorship of naturally growing seedling among the different positions from the nearest adult trees. The regression lines of the survivorship are shown in Figure 5 ($n = 16$; $df = 28$; ***, $p < 0.001$; **, $p < 0.005$; *, $p < 0.01$). The minus values indicate that regression slopes for survivorship in the distance from adult trees (A) is greater (steeper) than that in the distance shown in the left column (B)

Distance from nearest tree (B)	Distance from the nearest tree (A) 0-2 m	2-4 m	4-6 m	6-8 m	8-10 m
2 - 4 m	- 11.022 ***				
4 - 6 m	- 12.693 ***	- 3.115 **			
6 - 8 m	- 10.330 ***	- 2.103	0.257		
8 - 10 m	- 11.279 ***	- 2.218	0.493	0.166	
10 - 12 m	- 2.847 *	5.768 ***	7.534 ***	6.376 ***	6.739 ***

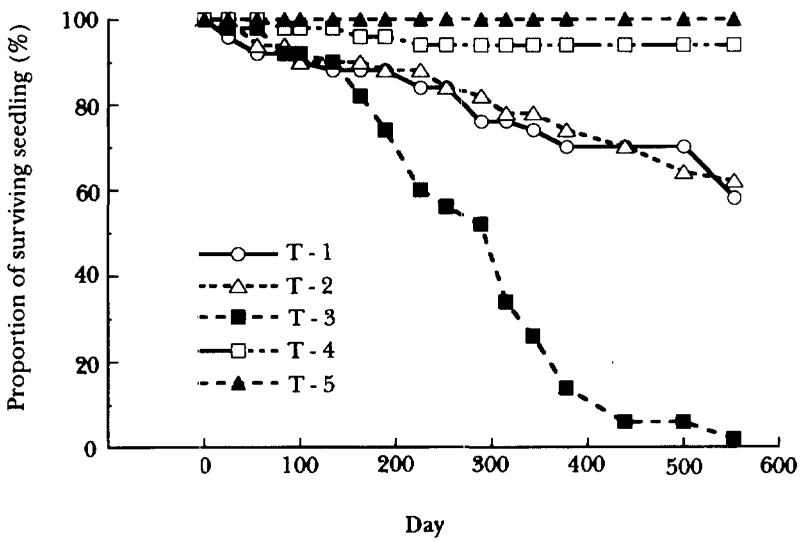
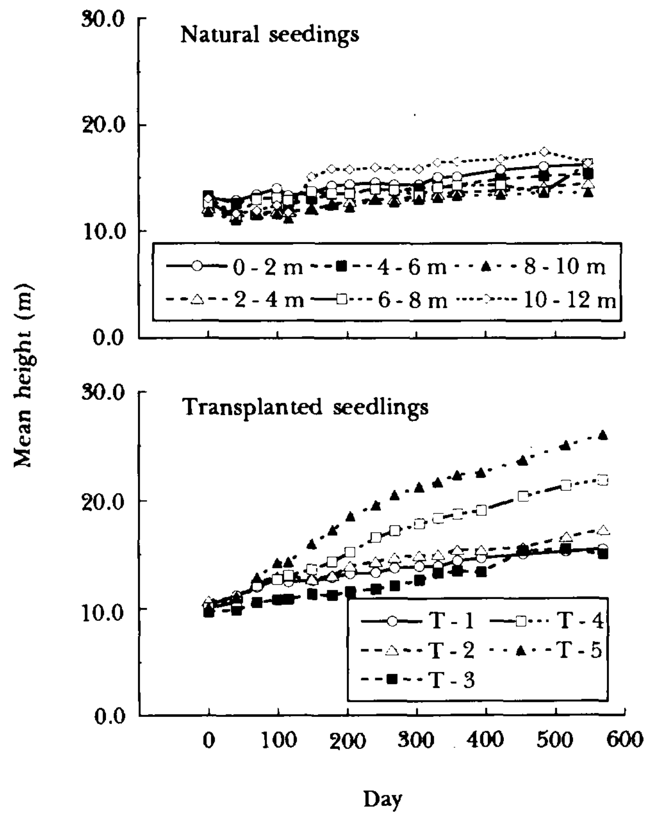


Figure 6. Proportion of surviving seedlings of *Pentaspadon motleyi* from September 1991 to March 1993 in transplant experiment

Variation of plant height

There was no significant difference in the height of the surviving naturally growing seedlings between quadrats at different distances from the nearest adult (p>0.05) (Figure 7). The height of transplanted seedlings showed no significant differences (p>0.05) among the quadrats in shaded conditions but there were significant differences (p < 0.01) between the quadrats under shaded (T-1, T-2) and light-gap (T-4) conditions. Growth of these transplanted seedlings under shade was low and their height was similar to that of the natural growing seedlings.



Figurer 7. Mean height of surviving seedlings of *Pentaspadon motleyi* growing naturally and transplanted

Mortality factor in natural and transplanted seedlings

There were no seedlings damaged by insect or vertebrate herbivores. The cause of mortality for the 37% of dead seedlings both naturally growing and transplanted is unknown. These seedlings died suddenly, although they did not show any apparent diagnostic symptom during the previous month; 45% of total dead seedlings died either of wilting or uprooting after developing necrotic symptoms on leaves, main stems or shoot apices. These seedlings usually shed all their leaves after changing colour from light green to yellow and then brown. Five per cent of seedlings died due to a physical break in the stem. In addition, about 22% of dead seedlings appeared to be damaged by fungus, probably by *Fusarium semitectum* which was isolated from seedlings showing necrotic symptoms. This fungus can cause damping-off (Claire Elouard, pers. comm.). There were no distinctive differences in mortality factors of dead seedlings found at different distances from the adult tree.

Discussion

Analysis of data from the 50-ha plot showed no pelong saplings around the crown area of their adult trees. This phenomenon apparently agrees with the Janzen-Connell model which predicts that progeny recruitment would begin at some "minimum critical distance" away from the parent, because high mortality of the progenies caused by species specific pests at a closer distance would preclude any recruitment (Augspurger & Kitajima 1992). Clark and Clark (1984), however, reported that only 4 of the 24 studies reviewed showed supporting evidence for "the minimum critical distance" prediction. The range of this critical area probably depends upon the way the seeds are dispersed. Lighter seeds or seed with wings may have a wider range of critical area. Our results indicate that the critical area appeared to be 6 m from the adults and this "minimum critical distance" appeared to be true only for saplings (1 - 2.5 cm dbh) .

Analysis of the data from the 1-ha plot indicate that there is no minimum critical distance for seedling distribution. However, seedling survivorship close to the bole of adult trees was significantly lower than that away from adults (Figure 5). Furthermore, the peak in seedling density showed an outward shift at the end of the experiment in comparison with that at the beginning (Figure 4). These results suggest that, although some seedlings survive under the adult tree (< 6 m from adult tree) in the 1-ha plot, they will die eventually, as shown for the sapling distribution in the data for the 50-ha plot. The fact that there were no saplings under the conspecific adult, although there were some under non-conspecific adults, implies that a host-specific enemy was involved in determining the seedling and sapling distribution.

However, transplanted seedling survival was not affected markedly by the distance from the mother tree. This may due to the soil microbial flora being changed after the soil excavation and transplantation. The difference between the survival of naturally growing seedlings and that of transplanted seedlings implies that pathogens in soils influenced seedling survival. Since the soils for transplanted seedlings originated from one place in the experimental plot, the effects of light intensity on the survival of transplanted seedlings have been amplified rather than the effects of soil origin.

The transplant experiment indicates that almost all the seedlings emerging after the most recent seed flush will die unless they encounter suitable conditions for growth such as light-gaps. Pelong has a high demand for light. Seedlings probably require light-gaps or sun flecks to grow to sapling stage and better light conditions away from the adult trees may allow them to develop to saplings. This is supported by the following observations: 1) the seedlings grown at a nursery or in transplant quadrats in light-gaps showed 30 to 40 % greater height growth than those under closed canopies; 2) no seedlings died at the nursery after the plants had been transplanted; 3) few saplings were found in the 1-ha plot under closed canopy. The absence of saplings in shaded forest leads to the assumption that the species requires a light-gap for successful regeneration (Brokaw 1980, Augspurger 1984a). This may also be supported by the clumped distribution of pelong in the 50-ha plot data.

The overall importance of canopy gaps for successful forest regeneration has been widely recognized (Schultz 1960, Hartshorn 1978, Whitmore 1984, Denslow 1987, Augspurger 1984a, Schupp *et al.* 1989), but there are few detailed studies of influences of light-gaps on seedling survivorship. Augspurger (1983a) and Augspurger and Kelly (1984) stated in their series of the studies on seedling survival of *Platypodium elegans* in BCI, Panama, that the probability of the seedling encountering light-gaps will increase with increased dispersal distance from their parents. Although some seedlings which locate away from their parents are in the shade of non-conspecific parent canopies, others may benefit from slight irregularities in canopy structure which increase the light level (Augspurger & Kelly 1984). It has often been reported that the number of damages caused by fungal pathogens was lower under light-gaps compared with those under shade (e.g. Augspurger 1984b, Augspurger & Kelly 1984). Consequently, the increased probability of encountering light-gaps has a similar effect on the seedling and sapling distribution as host-specific enemies eliminate the progeny in close vicinity to their conspecific adult. In this sense, the result obtained from the present study partly supports the "colonization hypothesis" (Augspurger 1984b), which emphasizes the enhanced seedling survival by increased probability that some offspring land in light-gaps in the forest.

It is generally understood that pathogens causing fatal damage to seedlings have low host specificity and can exist in soils in dormant form when there are no available resources (e.g. Walker 1969, Garrett 1970). However, large fruit crops and a high seedling density which periodically occurs intensively under the conspecific adult possibly cause an aggregation of non-host specific enemy (pathogens) that eventually accounts for the distance and density dependent effects (Janzen, 1971, Augspurger & Kelly 1984, Schupp 1988).

Increased mortality due to insufficient light was apparently independent of the seedling density and the distance from the mother tree. However, as the spatial pattern of the pelong saplings implies, their distribution is possibly regulated by distance or density dependent mortality factors. The mortality of pelong seedlings may have been caused by a combination of physiological response to the light conditions and pathogen effects. In order to prove this hypothesis, further experiments are needed to examine whether the seedlings maintain higher survivorship in light-gaps located very close to adult trees.

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References

ALLBROOK, R. F. 1973. The soils of Pasoh Forest Reserve, Negeri Sembilan. *Malaysian Forester* 36 : 22 - 33.

AUGSPURGER, C.K. 1983a. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71 : 759 - 771.

AUGSPURGER, C. K. 1983b. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40 : 189 - 196.

AUGSPURGER, C. K. 1984a. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72 : 777 - 795.

AUGSPURGER, C. K. 1984b. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65 : 1705 - 1712.

AUGSPURGER, C. K. & KELLY, K. K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, and light conditions. *Oecologia* 61 : 211 - 217.

AUGSPURGER, C. K. & KITAJIMA, K. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. *Ecology* 73 : 1270 - 1284.

BECKER, P. & WONG. M. 1985. Seed dispersal, seed predation, and juvenile mortality of *Aglaia* sp. (Meliaceae) in lowland dipterocarp rain forest. *Biotropica* 17 : 230 - 237.

BROKAW, N. 1980. Gap-phase regeneration in a neotropical forest. Ph.D. thesis, University of Chicago.

CHAN, H. T. 1980. Dipterocarps II. Fruiting biology and seedlings studies. *Malaysian Forester* 43 : 438 - 451.

CLARK, A.C. & CLARK, D. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Natualist* 124 : 769 - 788.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist* 140 : 261 - 286.

CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298 - 310 in Den Boer, P. J. & Gradwell, G.R. (Eds.) *Dynamics of Populations. Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations.* Oosterbeek, 1970. Center for Agricultural Publishing and Documentation, Wageningen.

CORNER, E.J. H. 1988. *Wayside Trees of Malaya.* Volume 1. Malayan Nature Society, Kuala Lumpur, 476 pp.

DENSLOW, J.S. 1987. Tropical rain forest gaps and tree diversity. *Annual Review of Ecology and Systematics* 18 : 431 - 451.

DE STEVEN, D. & PUTZ, F.E. 1984. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* 43 : 207 - 216.

GARRETT, S. D. 1970. *Pathogenic Root-Infecting Fungi.* Cambridge University Press, Cambridge, 294 pp.

HARTSHORN, G. S. 1978. Tree falls and tropical forest dynamics. Pp. 617 - 638 in Tomlinson, P.B. & Zimmerman, M. H. (Eds.) *Tropical Trees As Living Systems.* Cambridge University Press. Cambridge.

HOWE, H. F. & SMALLWOOD, J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13 : 201 - 228.

HUBBELL, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203 : 1299 - 1309.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104 : 501 - 528.

JANZEN, D. H. 1971. Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. *American Naturalist* 105 : 97 - 112.

MANOKARAN, N. & KOCHUMMEN, K. M. 1990. A re-examination of data on structure and floristic composition of hill and lowland dipterocarp forest in Peninsular Malaysia. *Malayan Nature Journal* 44 : 61 - 75.

MANOKARAN, N., LAFRANKIE, J.V., KOCHUMMEN, K. M., QUAH, E. S., KLAHN, J. E., ASHTON, P. S. & HUBBELL, S. P. 1990. *Methodology for the 50-ha Research Plot at Pasoh Forest Reserve.* Research Pamphlet No. 104. Forest Research Institute Malaysia. 69 pp.

MANOKARAN, N., LAFRANKIE, J.V. & ISMAIL, R. 1991. Structure and composition of the Dipterocarpaceae in a lowland rain forest in Peninsular Malaysia. *Biotrop Special Publication* 41 : 317 - 331.

NG, F.S.P. (Ed.). 1989. *Tree Flora of Malaya. A Manual for Foresters.* Volume 4. Longman Malaysia, Petaling Jaya.

SCHULTZ, J. P. 1960. *Ecological Studies on Rain Forest in Northern Suriname.* NV Noord-Hollandsche Uitgevers Maatschappij, Amsterdam.

SCHUPP, E.W. 1988. Seed and early seedling predation in the forest understory and in tree fall gaps. *Oikos* 51 : 71 - 78.

SCHUPP, E. W. 1990. Annual variation in seedfall, postdispersal predation, and recruitment of a neotropical tree. *Ecology* 71 : 504 - 515.

SCHUPP, E.W., HOWE, H.F., AUGSPURGER, C.K. & LEVEY, D.J. 1989. Arrival and survival in tropical treefall gaps. *Ecology* 70 : 562 - 564.

SOEPADMO, E. S. & KIRA, T. 1977. Contribution of the IBPP-PT research project to the understanding of Malaysian forest ecology. Pp. 63 - 94 in Sastry, C. B., Srivastava, P. B.L. & Abdul Manap, A. (Eds.) *A New Era in Malaysian Forestry.* Universitii Pertanian Malaysia Press, Serdang.

SYMINGTON, C. F. 1943. *Foresters' Manual of Dipterocarps.* Malayan Forest Records No. 16. Penerbit Universiti Malaya, Kuala Lumpur.

WALKER, J. C. 1969. *Plant Pathology.* McGraw-Hill, New York. 819 pp.

WHITMORE, T.C. 1984. *Tropical Rain Forests of the Far East.* 2nd edition. Oxford University Press, Oxford. 352 pp.

WYATT-SMITH, J. 1961. A note on the fresh-water swamp, lowland and hill forest types of Malaya. *Malayan Forester* 24 : 110 - 121.

WYATT-SMITH, J. 1964. A preliminary vegetation map of Malaya with description of the vegetation types. *Journal of Tropical Geography* 18 : 200 - 213.