PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

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Phil. Trans. R. Soc. Lond. B 1992 **335**, 369-378
doi: 10.1098/rstb.1992.0028

Do dipterocarp seedlings really partition tropical rain forest gaps?

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SUMMARY

The theory of gap regeneration dynamics proposes that different species of tree partition canopy gaps because they are preferentially adapted to a particular gap size class. A variety of gap sizes would therefore favour the regeneration of a range of species. The theory has been used to explain the extraordinarily high tree species diversity of tropical rain forests. A test was mounted in lowland evergreen dipterocarp rain forest in the Danum Valley, Sabah, East Malaysia by the creation of ten, artificial canopy gaps ranging in size from 10 m^2 to 1500 m^2 (6 to 30% canopy openness). The responses of established populations of seedlings of three dipterocarp species (*Hopea nervosa*, *Parashorea malaanonan* and *Shorea johorensis*) with contrasting silvicultural reputations were monitored for 40 months in these gaps and under closed forest. There were significant differences in survival and growth under closed forest between these three species. However, in gaps, the most important determinant of seedling survival and growth was seedling size at the time of gap creation, regardless of species. An ability to persist for long periods under closed forest and slowly accumulate growth may bestow an enormous size advantage on seedlings when gaps occur. Generalizations on the regeneration dynamics of dipterocarp rain forests need to be modified in the light of this result. Further observations for several years are important to see whether forest recovery eventually converges on predictions from the original paradigm.

1. INTRODUCTION

The management of the lowland dipterocarp rain forests of western Malesia dates back to the early years of the 20th century. Foresters, especially in British territories, developed an empirical understanding of the ecology of the main timber producing species and, building on silvicultural knowledge of European forests, learned how to manipulate the forest canopy to encourage the regeneration of favoured species. They learned by experience how species would respond and when and where to carry out treatments to ensure good regeneration. Frustratingly, this knowledge was rarely formally recorded.

Although there have been advances in our understanding of short term plant growth responses at the physiological level, integrating these processes over larger timescales is problematic. The problem of making the connection between short-term response and long-term performance is particularly acute in forest ecology where the appropriate timescale may be several decades. The result is that ecological theory often outruns the capacity to test it. The theory of forest gap-phase regeneration dynamics is a case in point.

Richards (1952) made explicit the basic precept of rain forest silviculture when he highlighted the role of canopy disturbance in regeneration. He suggested that seedlings of light-demanding tree species respond more quickly to gaps created by tree falls than those of the climax species. Both Whitmore (1975, 1978) and Hartshorn (1978) recognized that many tropical rain forest trees are dependent on canopy gaps for successful regeneration. Given the enormous species diversity of tropical rain forest it is a tempting supposition that if many species are competing for the scarce gap resource, then different species must be successful in different gaps to avoid competitive exclusion. Hartshorn (1978) proposed several possible reasons for differential success. These include species differences in seed dormancy and seedling shade tolerance, the time of gap occurrence relative to seed and seedling availability, seed dispersal, substrate conditions, plant–herbivore relations and the size of gaps. Whitmore (1978) emphasized the importance of gap size in influencing the species composition of gap regeneration. The larger the gap the more its microclimate differs from that of closed forest. He proposed that pioneer (or light-demanding) species are only able to establish in large gaps under conditions which inhibit growth of the climax seedlings of primary forest trees.

This simple theory of gap regeneration dynamics has since been much discussed and elaborated (e.g. Whitmore 1983, 1989; Pickett 1983; Brokaw 1985). The theory has been used to account for the extraordinarily high tree species diversity of tropical rain forests. It has been suggested that different species of tree partition gaps because they are preferentially

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Phil. Trans. R. Soc. Lond. B (1992) **335,** 369–378
Printed in Great Britain

adapted to gaps of particular size ranges (Denslow 1980; Pickett 1983; Augspurger 1984; Coley *et al.* 1985). Specialization would bestow competitive superiority in one particular gap size but would involve adaptive compromises that would restrict success in gaps of differing sizes. Gap size is therefore seen to constitute an important axis of variation for niche differentiation thereby maintaining the species richness of tropical rain forests by competitive interactions (Orians 1982).

Although conceptually neat, it has proved extremely difficult to test the theory of gap phase regeneration in practice. Two problems in particular have frustrated attempts to assess the degree of gap-size partitioning among tropical rain forest tree seedlings. The first is the problem of measuring gap size. Without an objective and repeatable measure of gap size any hypothetical relationship between seedling growth and gap size must remain pure speculation. In an attempt to introduce a standard method for the quantification of gap size Brokaw (1982) suggested it should be measured as the area of a vertical projection down to the ground of the innermost point reached by the foliage at any level on the perimeter. This definition has proved both practically and theoretically inadequate (Popma *et al.* 1988; Whitmore *et al.* 1992). It is in practice difficult to make accurately the vertical projection Brokaw advocates and no allowance is included for holes in the canopy other than the main gap. Secondly, the microclimatic effects of a canopy gap and hence its effects on plant growth are not restricted to that area immediately beneath it. The size and orientation of a gap controls the amount of solar radiation that will reach the forest understory (Mitchell & Whitmore 1992; Whitmore *et al.* 1992). The greater the amount of radiation received the more the microclimate will be altered. Plants respond to the microclimatic change rather than to gap size *per se*. A measure of gap size therefore needs to reflect the magnitude of microclimate change rather than human perceptions of gap geometry. It needs to take account of radiation arriving from any direction, not solely from directly above. In this paper gap size is measured from vertical hemisphere photographs of the forest canopy taken at the start of the experiment, and correlated with measures of microclimate made in each experimental plot over one year (Whitmore *et al.* 1992).

The second major problem that frustrates attempts to test theories of gap-size partitioning is that of the heterogeneity of natural seed and seedling banks. To investigate the relationship between gap size and seedling growth ecologists need to compare the growth of wild seedlings of several tree species in a range of different gap sizes. Despite the fact that the theory of gap dynamics has been a focus of academic debate in tropical rain forest ecology for over a decade there are remarkably few studies of interspecific differences in growth and survival under differing degrees of canopy openness. This is in no small part due to the difficulty of finding a large seedling bank of sufficient different species growing simultaneously in a large number of canopy gaps of different sizes. Consequently several studies have reported observations from very small numbers of gaps or for very few species (Fox 1973; Tomboc & Basada 1978; Becker 1983). More comprehensive studies have provided little evidence to support the hypothesis of gap-size partitioning. Thompson *et al.* (1988) found some tree species in a Queensland rain forest had the capacity to acclimate and dominate in a wide range of gap sizes. Barton (1984) found no difference in the regeneration of five climax species between large and small gaps in lowland rain forest at Finca La Selva, Costa Rica and suggested that there was little evidence for the existence of tree species that regenerate almost exclusively in small gaps, where pioneers do not thrive. Brokaw (1985) found that the density of seedlings of climax species on Barro Colorado Island, Panama was unrelated to gap size. Brokaw & Scheiner (1989) found that whilst saplings of pioneer tree species occurred in significantly greater density in large (greater than 150 m^2) gaps there was no significant variation in species composition associated with gap size for climax species.

The publications on tropical gap phase dynamics are confusing because there is a wide variety in the nomenclature used to describe tree species with different seedling shade tolerance. In an attempt to clarify matters Swaine & Whitmore (1988) proposed that there are two ecologically distinct classes. Pioneer species are those whose germination and seedling establishment requires exposure to full radiation. Climax (or non-pioneer) species have seeds that can germinate and seedlings that establish below a closed canopy. They further proposed that within both of these classes there are various ecological groups but that these merge into each other. Much of the confusion in the literature concerns the names given to the various groups of climax species which range from strong light-demanders to strong shade-tolerants, although all differ from pioneers in being able to germinate and then establish in canopy shade.

It is of little surprise to discover that empirical observations of natural gap regeneration have confirmed the inability of pioneer species to grow or survive for long periods in shade. This is a consequence of a method of regeneration which is adaptively keyed to colonizing areas of major canopy disturbance and which makes these species physiologically distinct from climax species (Oberbauer & Strain 1984; Oberbauer & Donnelly 1986). Pioneer species occur at low densities, and have poor growth and survival in small gaps. Brokaw (1987) found considerable overlap in the size of gaps colonized by three pioneer species in Costa Rica.

In all parts of the humid tropics pioneer species only constitute a very small proportion of the tree flora (Whitmore, 1984). Most tree species are in the climax class. If the concept of gap-size partitioning is to have a value over and above a mere re-expression of well-established differences between a pioneer and climax species it must demonstrate that sympatric climax tree species have distinct and largely non-overlapping gap size ranges for optimum seedling growth and survival.

2. METHODS

Ten artificial gaps, ranging in size from 10 m^2 to 1500 m^2 and two closed forest control plots were created in lowland dipterocarp evergreen rain forest in the Danum Valley Conservation Area, Sabah, East Malaysia (4°58′N, 117°48′E, altitude less than 200 m ASL, see Marsh & Greer, this symposium). Gaps were made by felling all trees and non-dipterocarp saplings taller than 2.0 m over mapped and tagged seedling populations. All brash was cut up and removed to the edges of the plots to reduce damage to seedlings and to allow access. Large trees were mostly felled so as to fall away from the seedling plots but where this was not possible fallen trunks were left *in situ* (see also Kennedy & Swaine, this symposium).

West Malesian Dipterocarpaceae are characterized by gregarious flowering and fruiting two or three times a decade (Burgess 1972). At these events up to about half of all the trees flower and fruit. The seeds germinate immediately and the forest floor becomes covered in mixed-species carpets of seedlings at densities of several million per hectare (ha)† (Barnard 1956; Fox 1972).

In early 1987, when canopy gaps were created, there was no record of any major dipterocarp fruiting having occurred in the study area for over four years. Under closed forest the dipterocarp seedling bank was sparse and patchy. Fox (1972) has highlighted both the temporal and spatial heterogeneity of dipterocarp seedling populations in Sabah forests. Variation in seedling numbers over time results from differential recruitment and mortality. Spatial patchiness is the result of poor dispersal of the relatively large and heavy fruits of Dipterocarpaceae (Burgess 1970). Seedling densities were low, so our sample plots were positioned in patches of relatively high seedling density to obtain a sufficiently large seedling sample size. As a consequence, if patch density is inversely related to time since fruiting, young seedlings may be over-represented in the plots.

Over 1500 dipterocarp seedlings were identified, measured, mapped and tagged before gaps were made. After gap creation seedling heights and survival were recorded at frequent intervals throughout the 40-month study reported here.

Microclimate was monitored at the subjectively judged centre of all gap and closed forest plots for over a year after the gaps were made (Brown 1990). Hemisphere photographs were used to measure gap size at the beginning of the experiment (Whitmore *et al.* 1992). On the basis of both microclimatic and gap size measurements gaps were grouped into five size classes against which dipterocarp seedling growth and survival is compared (table 1).

The hypothesis of niche differentiation of gap size suggests that each species is competitively inferior outside a specific gap-size range (e.g. Denslow 1980). This may be because it grows sub-optimally or because, whereas it still maintains optimum growth, a competing species has superior growth. The difference is of both theoretical and practical importance. In the first case gap size specialization is intrinsic to a particular species. The gap size range in which it is able to achieve maximum growth is physiologically determined. Dipterocarps, for instance, are often reported to fail in large canopy gaps (Whitmore 1984). It would be possible to determine the optimum gap size for a given species by controlled growth trials in a range of gap sizes. In the latter case gap size specialization is extrinsic to a particular species. The gap size range in which it is able to achieve maximum growth is determined by the other species present in each gap. It would only be possible to determine the optimum gap size for a given species by observing seedling growth in competition with all other components of gap regrowth. The underlying reasons for gap size specialization are of particular interest to silviculturists. If seedlings of timber trees achieve optimum growth in a distinct gap size range, levels of timber harvesting and hence canopy opening could be attuned to select for commercially desirable species, If, however, species selection in different sizes of gap is on the basis of competitive interactions, the silviculturist may be able to select desirable species by weeding out competitors.

To establish the relative importance of these two factors a 'weeding' treatment was introduced. One half of the four largest gaps and three of the six smallest gaps were cut and weeded free of all non-dipterocarp regrowth. This included non-dipterocarp seedlings, resprouts from cut stumps and seedlings which germinated from seeds after gap creation. In all other areas, apart from the initial cutting of the gap, no treatment of any sort was used.

3. RESULTS

In early 1987, at the start of this study, the dipterocarp seedling bank in the experimental plots consisted of ten different species. Only three of these occurred as more than isolated individuals.

1. *Hopea nervosa* King. Medium hardwood (Burgess 1966). Typically a species of flat or undulating lowlands (Symington 1943). A rather small-sized, non-emergent tree, seldom exceeding 25 m tall and 2 m girth, which is not important for timber (Meijer & Wood 1964).
2. *Parashorea malaanonan* (Blco.) Merr. Light hardwood (Burgess 1966), the most commercially important timber species of Sabah, where it is widely distributed, normally common, locally abundant, and gregarious in forest at low and medium altitudes. A big emergent tree. Seedlings are usually abundant and regenerate profusely in moderate shade (Meijer & Wood 1964).
3. *Shorea johorensis* Foxw. Light hardwood (Burgess 1966). Meijer and Wood (1964) report that quantities of suppressed seedlings averaging 30 cm are found in primary forest which provide among the most vigorous and fastest growing dipterocarp seedlings in canopy openings. A big emergent tree.

These three dipterocarp species are common as adults and grow sympatrically in the Danum forest

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† 1 ha = 10^4 m^2.

Table 1. *Analyses of hemisphere photographs and results of 12 months of microclimatic measurements in the centre of ten artificial canopy gaps and two closed forest control plots*

		mean daily temperature/°C				
size classes	canopy openness (%)	max. air	min. air	max. soil at 10 mm	max. soil at 50 mm	mean daily photosynthetically active radiation (PAR)/(μmol^{-2} d^{-1})
Closed forest	2			27.0	25.2	1.0
	4	28.4	21.2	25.2	24.4	1.1
tiny	8	33.5	21.5	30.0	25.6	4.9
	6	31.1	21.3	29.4	25.8	3.1
	8	33.6	21.5	29.4	26.0	3.1
	7	34.2	21.3	28.9	25.9	6.4
	6	30.3	21.2	29.5	25.6	2.3
	13	35.4	21.4	31.3	25.4	9.9
	11	34.9	21.3			10.6
medium	17	35.3	21.5	31.5	27.0	14.4
	18	34.6	21.3	27.4	27.4	13.5
large	30	38.2	21.6	33.4	29.0	19.2

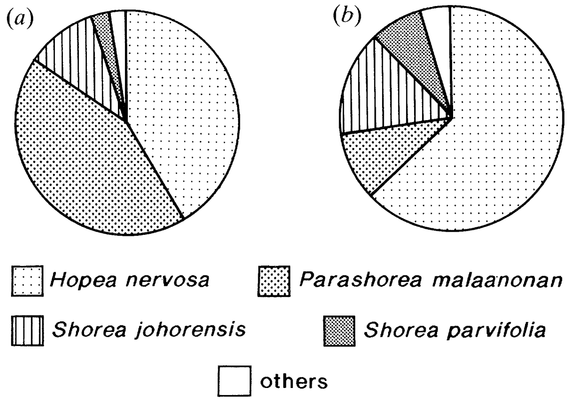

Figure 1. The species composition of (*a*) the total dipterocarp seedling bank and (*b*) dipterocarp seedlings taller than 1.0 m in 12 plots under closed forest, Danum Valley, February 1987.

(see Newbery *et al.*, this symposium). It can be seen that they have differing timber characteristics and silvicultural reputations. We may therefore expect that if gap size is an important axis for niche differentiation these three species will show distinct differences in their gap size range for optimum growth and survival.

Hopea nervosa seedlings were ubiquitous whereas those of *Parashorea malaanonan* occurred in dense patches. There were also sparse patches of *Shorea johorensis*. Figure 1*a* shows the relative contributions of these three species to the total dipterocarp seedling bank in the experimental plots. There were important differences in the population size structure between these species. Figure 1*b* shows their relative contributions to the total of seedlings taller than 1.0 m.

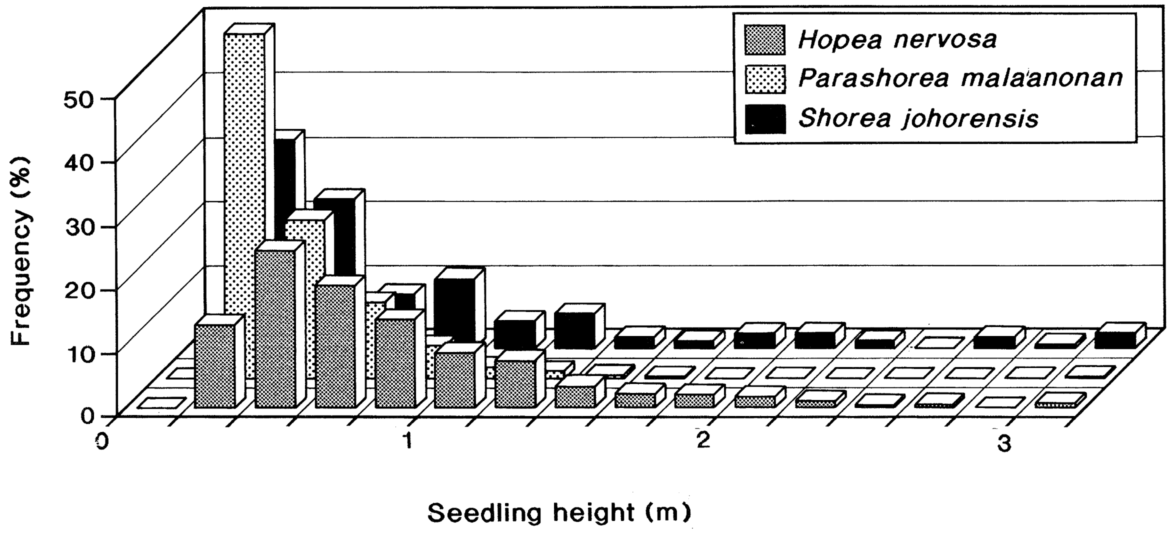

Figure 2. Frequency distribution of seedling heights for the three most common dipterocarp species in twelve closed forest plots, Danum Valley, February 1987.

Although *Parashorea malaanonan* seedlings comprised 43% of the total seedling bank they comprised only 10% of seedlings greater than 1.0 m tall. In contrast *Hopea nervosa* seedlings comprised 42% of the total seedling bank but 65% of the seedling bank taller than 1.0 m.

Figure 2 shows the size–percent. frequency distributions for the three most common seedling species. It confirms that most *Parashorea malaanonan* seedlings were very small; over 50% of them were shorter than 0.3 m. Over 50% of *Hopea nervosa* seedlings were taller than 0.7 m. *Shorea johorensis* occupied an intermediate position. More than 30% of its seedlings were shorter than 0.3 m but another 30% were taller than 0.8 m. The very small size of most *Parashorea malaanonan* seedlings is either the result of severe suppression of growth under a closed forest canopy or because the seedling population of this species is dominated by new recruits which die off rapidly before putting on much height growth. Either explanation would indicate that *Parashorea malaanonan* is less tolerant of closed forest shade than *Hopea nervosa*.

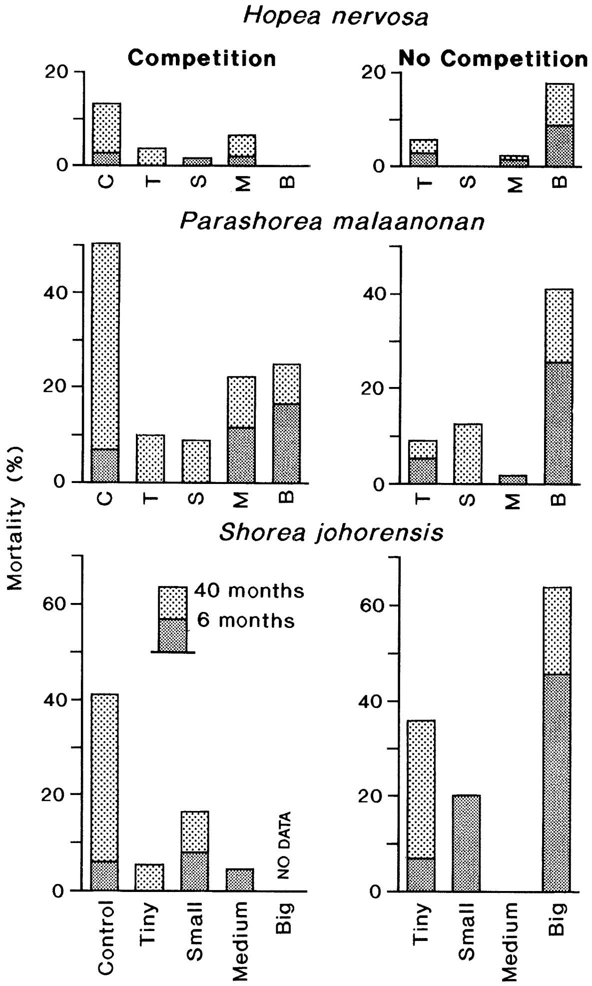

Figure 3. Cumulative seedling mortality 6 and 40 months after gaps were created, for the three most common dipterocarp species (all seedling sizes). Results are divided into those plots where competition from non-dipterocarp species was removed and those where seedlings were left to compete with all other regrowth.

There were significant differences in mortality between these three species. Figure 3 shows mortality in different sizes of gap as a percentage of the original seedling number. Figures are divided into those plots where non-dipterocarp competition was weeded out (no competition) and those left untouched (competition). Total mortality is divided into those seedling deaths which occurred in the first 6 months and those which occurred thereafter. Considerable seedling mortality occurred in the 6 months immediately after gap creation, particularly in the largest gap size. This effect was more pronounced in plots where non-dipterocarp competitors were weeded out. Gap-size differences in mortality crudely reflect the magnitude of environmental change that occurred on gap creation. For both *Parashorea malaanonan* and *Shorea johorensis* seedlings these early deaths constituted a substantial proportion of the total that occurred throughout the study. In contrast *Hopea nervosa* suffered very little mortality in this first 6 month period except in the big gap, no competition plot where 50% of the total mortality occurred during this time.

After the initial 6 month period of high mortality gaps of all sizes enhanced dipterocarp seedling survival compared with the closed forest control plots. Mortality for all three common species was greatest under closed forest. *Parashorea malaanonan* and *Shorea johorensis* suffered considerably higher mortality than *Hopea nervosa* under closed forest, confirming their lower level of persistence in forest shade.

Hopea nervosa showed low mortality in all sizes of gap and under closed forest throughout the 40 month study. *Parashorea malaanonan* showed high mortality under closed forest but survived well in tiny and small gaps. *Shorea johorensis* suffered high mortality under closed forest but survived well in tiny, small and medium sized gaps. For all three species mortality in big gap plots weeded free of non-dipterocarp competition (i.e. where canopy shade and mutual shading by gap regrowth was at a minimum) was higher than in all other gap plots.

Seedling size clearly played an important role in determining mortality levels, irrespective of species. Small seedlings were considerably less likely to survive both the shock of gap creation and 40 months of growth. Figure 4 shows the mean initial height (t_0) of seedlings which survived throughout the 40 month study compared with the mean initial height of seedlings which died during that period. In all plots seedlings which died were, on average smaller, and mostly considerably smaller, than those that survived.

Small seedlings may have been more vulnerable for several reasons. Small seedlings have fewer leaves. In fact most *Parashorea malaanonan* seedlings less than 300 mm tall had fewer than six leaves at the time of gap creation. Sudden exposure to high irradiance when canopy gaps are created may cause damage to dipterocarp seedlings through excessive heating of leaves, photo-oxidation of photosynthetic pigments and induced water stress. Many of the seedlings monitored in these artificial canopy gaps manifested severe chlorotic and necrotic injury to exposed leaves shortly after gap creation. The frequency of such damage declined

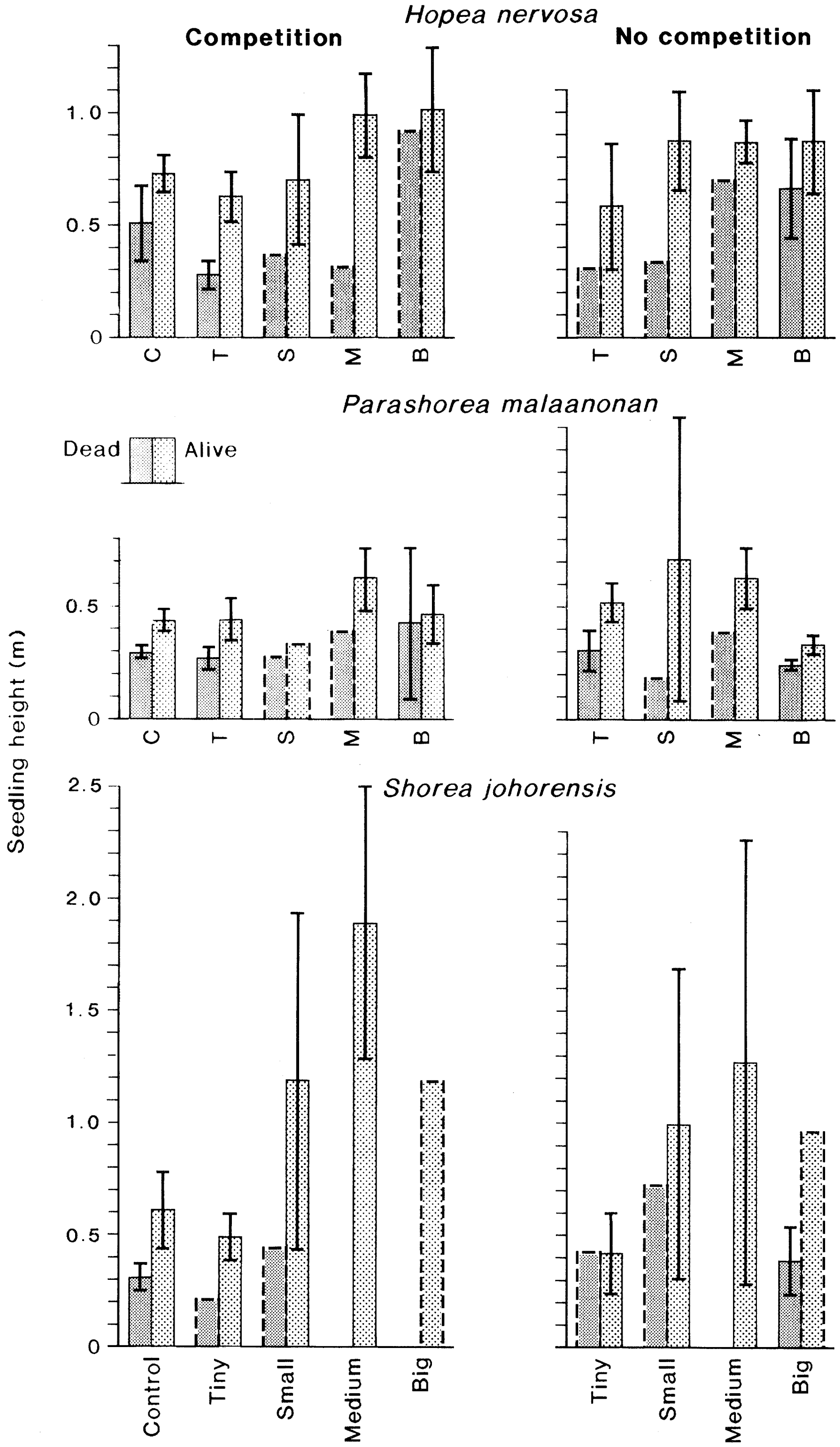

Figure 4. Mean initial height (mm) (t_0), with 95% confidence intervals, of seedlings which survived throughout the 40 month study compared with the mean initial height (t_0) of seedlings which died during that period.

with decreasing gap size (Brown 1990). Damage was more serious for small seedlings because damaged leaves constituted a greater proportion of their total leaf area. Small seedlings had little self-shading. Newly created gaps had little ground cover. The soil surface in the larger gaps became desiccated (Kennedy 1991). Suppressed seedlings under a closed forest canopy may have a poorly developed root system relative to a large leaf area (Sasaki & Mori 1981). Such seedlings may succumb to water shortage when suddenly exposed to high temperatures and soil surface desiccation. Small *Parashorea malaanonan* and *Shorea johorensis* seedlings were observed to be severely wilted before they died in the largest gap.

It is possible that there are differences between species in physiological sensitivity to sudden environmental change, especially to a substantial increase in irradiance. Despite this, these results indicate that one of the most important determinants of seedling survival lies in the size of seedlings when gaps are made. An ability to persist for long periods under closed forest shade and slowly accumulate growth may

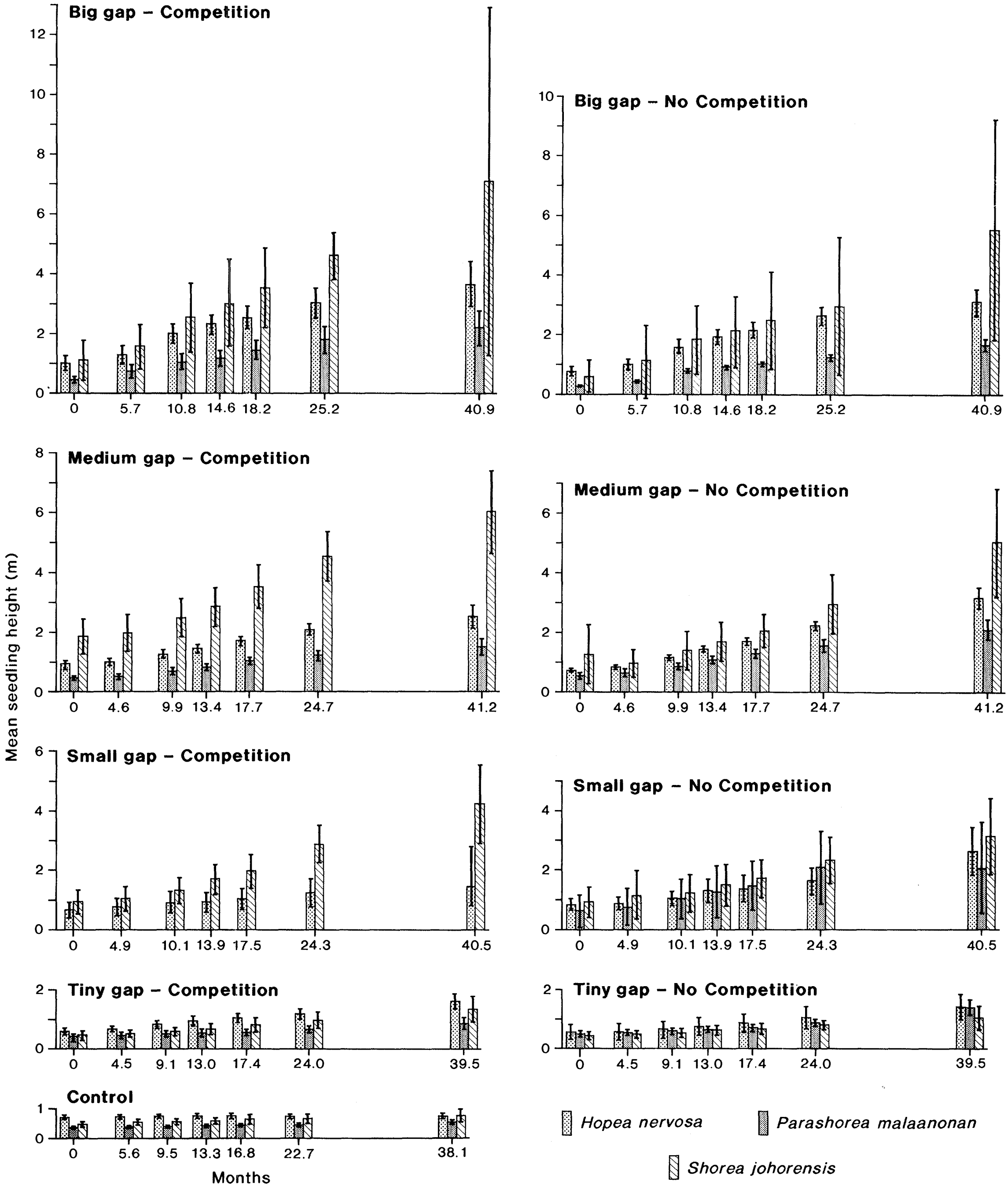

Figure 5. Mean height (mm) of surviving seedlings and 95% confidence limits at successive remeasurements throughout the 40 month study. Results are divided by species, gap size and into those plots where competition from non-dipterocarp species was removed and those where seedlings were left to compete with all other regrowth.

bestow an enormous size advantage on seedlings when gaps occur. Large seedlings have better developed root systems to withstand soil surface desiccation and large numbers of leaves with considerable self-shading. The consequence of this is that species such as *Hopea nervosa* which have a substantial proportion of large seedlings in the seedling bank have a big competitive advantage, irrespective of gap size.

Figure 5 shows mean seedling heights by species and gap size-class at each remeasurement period throughout the study. Whereas gap size clearly influenced total growth for all three dipterocarp species it had little influence on their relative growth performances. In almost every case the species with the tallest seedlings at the time of gap creation remained the tallest throughout the study period. Seedlings which were large at the beginning of the experiment were better able to survive the shock of gap creation and had a larger leaf area (Brown 1990) and probably a larger root system for more rapid growth. As a consequence large seedlings grew more rapidly than small ones, amplifying initial height differences.

It could be argued that the mean performance of a large number of seedlings of a species in a particular gap size does not accurately reflect the growth of the most vigorous individuals. Because canopy gaps will

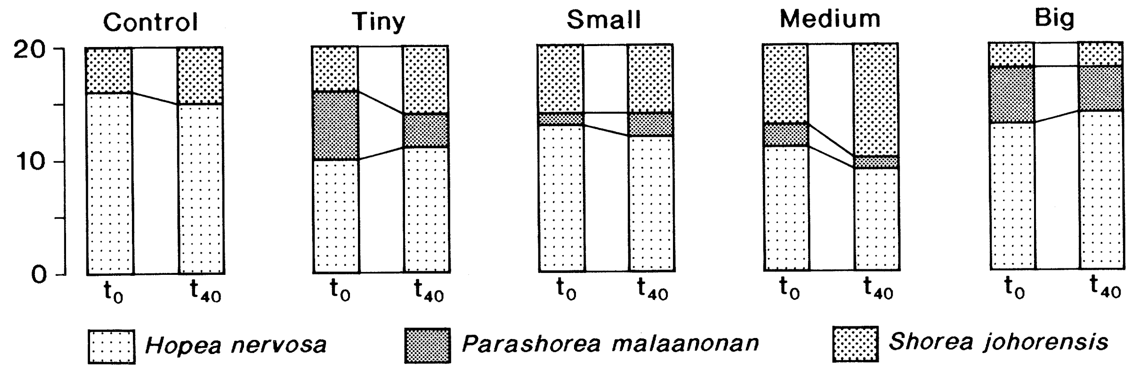

Figure 6. Relative species contributions to the tallest 20 seedlings of the three common dipterocarp species at the time of gap creation and 40 months later, divided by gap size class.

Table 2. *Results of an analysis of variance by multiple regression of growth of Hopea nervosa, Parashorea mallanonan, and Shorea johorensis seedlings over 40 months against initial seedling height and dummy variables representing the three species*

(R^2 = the percentage of the total variance accounted for by the regression. p = the probability of no relationship between seedling growth and the two predictors. p_{ht} = the probability of no relationship between seedling growth and initial seedling height. p_{sp} = the probability of no relationship between seedling growth and seedling species.)

Gap Size	p_{ht}	p_{sp}	R^2 (%)	p
control	0.787	0.006	5.5	0.017
tiny	< 0.001	0.001	27.8	< 0.001
small	< 0.001	< 0.001	75.1	< 0.001
medium	< 0.001	< 0.001	46.2	< 0.001
big	< 0.001	0.944	45.1	< 0.001

ultimately be filled by only one or a few adult trees most seedlings will perish, even of the most well-adapted species. We should therefore focus our attention on the largest seedlings and see which species leads in the race to monopolise space and radiation. Figure 6 shows relative contributions to the tallest 20 seedlings of these three common species in each gap size class both at the start and finish of the 40 months of observation. There was remarkably little change in composition. *Hopea nervosa* seedlings which dominated at the time of gap creation still dominated over three years later in all gaps, irrespective of size.

Table 2 shows the results of an analysis of variance by multiple regression of seedling growth of the three common species over 40 months against initial seedling height and dummy variables representing species (Draper & Smith 1981). Values of R^2 give the percentage of the total variance accounted for by the regression and p values give the probability of no relationship between seedling growth and the two predictors. This is broken down in the analysis into two components, p_{ht}, the probability of no relationship between seedling growth and initial seedling height and p_{sp}, the probability of no relationship between seedling growth and seedling species. Interestingly, there is a very weak but significant relationship ($p < 0.01$) between species and height growth under closed forest, but no relationship with intial seedling height. The conclusions this points to are that large size appears to be of little competitive advantage at closed forest of photosynthetically active radiation (PAR), which are close to the compensation point, but that there are differences between species in their ability to grow under a closed forest canopy. In combination with observed differences in mortality this observation supports the hypothesis of differential adaptation to the closed forest environment. Once gaps occur in the canopy large size bestows a clear growth advantage. There were strong and significant relationships between initial seedling size and seedling growth in all sizes of gap (table 2). There were strong and significant relationships between species and seedling growth in tiny, small and medium sized gaps but no relationship at all in the largest gap size where the environmental change was most extreme and subsequent seedling growth rates most rapid.

4. DISCUSSION

The evidence from this study of the growth of three common species of dipterocarp in a Bornean rain forest does not indicate any clear partitioning of canopy gaps by preferential adaptation of each species to a particular size range. Height growth of all three species was enhanced by increasing gap size. Although there were species differences in growth in some gap sizes there was no evidence of species specializations on a narrow gap size range. Height growth was proportional to original seedling size in all gaps, and thus initial height differences became amplified. *Hopea nervosa* seedlings were particularly favoured in all of the gaps created in this study because of their large size at the time gaps were made.

Hopea nervosa is well known by foresters to be more shade tolerant than the other species studied. We have found that this is because its seedlings are able to persist significantly longer below closed canopy. Its seedlings are not specialized for rapid height growth only in tiny gaps. In fact it is a generalist with seedlings capable of growing fast in a wide range of gap sizes.

These observations raise an important question as to what conditions favour the regeneration of the less shade-tolerant (i.e. more light-demanding) climax species. It has been shown that for the species of this group which were studied seedlings are less persistent than *Hopea nervosa* below a closed canopy. Their seedlings have little opportunity for slow growth and are therefore always relatively small under closed forest. When a gap forms, they are only likely to succeed in filling it in the absence of larger seedlings of another species. Such a condition is unlikely to occur in the Danum forest at present, as larger *Hopea nervosa* seedlings are both common and ubiquitous.

Light-demanding, climax dipterocarp species, principally *Parashorea malaanonan* and *Shorea johorensis* (but also *Shorea parvifolia*, *Shorea leprosula*, *Shorea fallax*, see Brown (1990)) are prevalent as adult trees in the Danum forest. Species known by foresters to be shade-tolerant (e.g. species of *Shorea* section Shorea, known locally as *balau* or *selangan batu*) are rare at Danum. The results of this study indicate that gaps in the Danum forest are presently favouring the growth of seedlings of shade-tolerant species such as *Hopea nervosa*. If the Danum forest is not to undergo substantial change in its species composition towards one in which shade-tolerant dipterocarp species are common there will need to be future dramatic change in the growth performance of seedlings of the two light-demanding species discussed here, reversing the patterns observed during the first 40 months of gap regeneration. The alternative implication is that there has been significant change in forest conditions. Some time in the past these light-demanding species were favoured but today they are not.

It is only possible to speculate as to circumstances which would favour the regeneration of light-demanding, climax, dipterocarp species. At present their seedlings are out-competed in canopy gaps because they are unable to withstand long periods of shade suppression. However, we have shown that even the tiniest canopy gap results in a conspicuous increase in seedling survival and permits slow growth. The Danum forest canopy is currently too dense for the long-term survival of healthy *Parashorea malaanonan* and *Shorea johorensis* seedlings. But if canopy gaps developed more frequently as a result of a change in the disturbance regime the strongly shade-tolerant species such as *Hopea nervosa* would lose the advantage that their long shade persistence gives them. Under such conditions both light-demanding and shade-tolerant climax species would survive well. The more frequent the occurrence of gaps the more the two groups would approach competititve equality. Thus we can see that the frequency of canopy disturbance may be of great importance in determining which species of climax tree seedling is favoured. This conclusion corroborates Canham's (1989) suggestion that the regeneration success of different climax species may depend on the frequency of disturbance and the duration of periods of release versus suppression more strongly than on gap size or radiation levels *per se*. The gap regeneration hypothesis must be adapted to incorporate a time dimension in addition to the existing preoccupation with space.

We are grateful to the Malaysian Socio-Economic Research Unit and the Danum Valley Management Committee for permission to carry out this study. The work was carried out from Oxford Forestry Institute and was financed by a grant from the U.K. Natural Environment Research Council. This paper is Number A/044 of the Royal Society's South-east Asian Rain Forest Research Programme.

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