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T. C. Whitmore and N. D. Brown

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Dipterocarp seedling growth in rain forest canopy gaps during six and a half years

T. C. WHITMORE[1] AND N. D. BROWN[2]

[1] *Geography Department, Downing Place, Cambridge CB2 3EN, U.K.*
[2] *Department of Plant Sciences, South Parks Road, Oxford OX1 3RB, U.K.*

SUMMARY

The growth of seedlings of 11 species of Dipterocarpaceae in artificial canopy gaps of different sizes in a lowland evergreen dipterocarp rain forest in Sabah has been followed for 77 months. Three species were abundant and studied in most detail. The main objective was to analyse the foresters' observation, on which silviculture is based: as gap size increases, species that are more light-demanding win the race to fill the gap.

Hopea nervosa seedlings had higher survival in closed forest than those of the other two well represented species, *Parashorea malaanonan* and *Shorea johorensis*. From seedling demography these two species groups can be called shade-tolerants and light-demanders respectively.

At 40 months the seedlings tallest at gap creation had increased their height advantage in all gap sizes. These were mainly *H. nervosa*. By 53 months, seedlings of *Shorea johorensis* had grown ahead of *H. nervosa* in all but closed forest and tiny gaps of 6% and 8% canopy openness (1 and 4 mol m^{-2} day^{-1} photosynthetically active radiation (p.a.r.) respectively). By 77 months they were even further ahead. Thus *S. johorensis* has a more flexible response. It is better able to use the extra p.a.r. of larger gaps (*ca.* 10% openness or more; 10 mol m^{-2} day^{-1} p.a.r. or more), and is a light-demander in a second sense, whereas *H. nervosa* is light-indifferent in this sense. Seedlings of *P. malaanonan* unexpectedly failed to show rapid height growth in the larger gaps at 53 and 77 months. This species alone suffered very serious apical damage by herbivory.

The 11 species under study occurred in various mixtures. To analyse success in gap-filling in the forest they were grouped by timber density into two classes. With increasing gap size, one group, six light hardwood species, known to be light-demanders, grow progressively ahead of the other group, four medium hardwood species, known to be shade-tolerant. *P. malaanonan*, also a light hardwood, grows only slowly because of herbivory.

We find no evidence for fundamental niche differentiation. All species showed increasing rates of growth with increasing gap size. Species that responded more slowly might succeed in situations where they alone occur.

1. INTRODUCTION

Perception of the dynamics of the tropical rain forests of southeast Asia and the ecology of the common big tree species has been acquired as a result of many decades of observation on growth and performance by foresters who have needed this knowledge to develop silvicultural systems. Understanding has advanced furthest for the dipterocarp rain forests of western Malesia, whose silviculture is now well known (Wyatt-Smith 1963; Nicholson 1979; Whitmore 1984). In these forests Dipterocarpaceae are abundant in terms of both species and numbers, and most are big trees that reach the canopy top or are emergent from it. Within the Dipterocarpaceae there are species that are regarded as extremely shade-tolerant to strongly light-demanding. All are climax species in the sense of Swaine & Whitmore (1988) (that is, they can (i) germinate and establish below closed forest canopy and (ii) maintain seedling banks below closed forest). As commonly occurs among climax tree species, shade-tolerant dipterocarps have high-density timber and light-demanders have lighter timber (Whitmore 1990). Canopy opening, by logging or other means, releases seedlings and it is observed that with a small degree of canopy disturbance shade-tolerant species (for example *Hopea*) grow up to fill the gaps, whereas with progressively greater disturbance progressively more light-demanding species are released. Dipterocarp rain forest silviculture is based on this property (Wyatt-Smith 1963). The formerly extensively practised Malayan Uniform silvicultural system involves removing all commercial trees over 45 cm diameter at one operation and poisoning the rest over 5 cm diameter unless commercial and of good form. This drastic canopy opening releases the most light-demanding group of species with timber of the lowest density (for example *Parashorea* and Light Red Meranti *Shorea* spp.).

The biological differences between species that lead

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to the release of successively more light-demanding dipterocarp seedlings in progressively larger canopy gaps are not known (Whitmore 1984). In 1987 we began to address this problem by observing growth of naturally established seedlings in artificial canopy gaps of different sizes created over mixed populations of shade-tolerant and light-demanding species.

The experiment is taking place in the Ulu Segama Forest Reserve, eastern Sabah, Borneo, in the Danum Valley Research Centre forest, at 4° 54′, 117° 48′ E. Twelve plots were established in natural mixed-species populations of seedlings. Two were retained as closed-canopy controls and artificial canopy gaps were created over the other ten. The gaps were made by cutting off and removing all plants except dipterocarp seedlings taller than 2 m from roughly rectangular areas, leaving the forest floor intact, to create gaps of area projected between tree crowns (Brokaw 1982) of 0–200 m^2 and with a percentage canopy openness (Whitmore *et al.* 1993) of 6–26 %. Most dipterocarp seedlings were shorter than 1.5 m; a few were 1.5–3.2 m tall. Gap definition and microclimate have been described in detail in Brown (1990, 1993), Brown & Whitmore (1992) and Whitmore *et al.* (1993). Table 1 gives a summary.

There are three main dipterocarp species under study, all with seedling populations occurring in all of the twelve plots, plus eight less common species with unevenly distributed seedlings. Of the three main species *Hopea nervosa* is shade-tolerant (our nomenclature follows Ashton (1982)). At the start of the study it had 42 % of all seedlings studied; 65 % of those were 1 m or more tall (figure 1 in Brown & Whitmore 1992). *Parashorea malaanonan* is a light-demander and had numerous small seedlings, 43 % of the total number studied but only 10 % of seedlings 1 m or more tall. *Shorea johorensis* is a light-demander. It had 11 % of all seedlings and 15 % of those taller than 1 m.

Brown & Whitmore (1992) described what happened during the first 40 months after gap creation, and full details are not repeated here. It was observed that tall seedlings better survived the shock of gap creation and grew faster in all gap sizes, thus amplifying their initial height advantage. As mentioned above, a large proportion of the tallest seedlings in the seedling bank below the closed forest canopy were of the shade-tolerant species *H. nervosa*. This is because in the absence of a canopy gap very few seedlings of light-demanding species persist long enough in this environment to grow tall. Once gaps develop, shade-tolerant species such as *H. nervosa*, which comprise a substantial proportion of the tall seedlings in the seedling bank, have a big competitive advantage, irrespective of gap size. At 40 months after gap creation *H. nervosa* still dominated the total seedling community and was also the most common species among the 20 tallest seedlings at all gap sizes (figures 5 and 6 in Brown & Whitmore 1992). The conclusion was that at 40 months canopy gaps had favoured seedlings of *H. nervosa* and similar shade-tolerant species and, unless a dramatic change was yet to occur in the relative performances of shade-tolerants and light-demanders, the forest would lose its present dominance by light-demanding dipterocarp species. More generally, however, the first 40 months of growth present a dilemma. If the growth trends observed are typical, and if they were to continue, all dipterocarp rain forests would in time have their upper canopy full of shade-tolerant members of the family. This is manifestly not so. Indeed, the Danum forest itself has light-demanding *Parashorea* and *Shorea* species as the most abundant dipterocarps in the upper part of the canopy.

Now we take the study forward and report on the next 37 months, doubling the time since gap creation.

2. RESULTS

The dipterocarp seedlings were not alone in the gaps; pioneer and other tree species grew up with them but by 40 months had been overtopped and by 77 months had disappeared.

For the analyses, seedling plots have been grouped into five gap size classes (table 1). One medium gap is omitted because its initial size was considerably enlarged by a natural treefall during the study period, which also damaged many of its seedlings. Seedlings grow in response to gap microclimate. We were able to show (table 4 in Whitmore *et al.* 1993) a strong correlation ($r = 0.930$, $P < 0.001$) between percentage canopy openness and a composite index of four microclimatic variables (mean daily photosynthetically active radiation (p.a.r.), mean maximum monthly soil temperature 0–5 cm, mean daily minimum percentage relative humidity, and mean daily maximum air temperature). For this analysis therefore we analysed seedling growth against mean percentage canopy openness of each gap size class. This was measured by hemispherical photography a few months after gap creation. The gaps closed to some extent by lateral crown growth during the 77 months of the study but the changes do not affect the analyses because the rank order and relative differences between the gap size classes did not alter. There are also gradients across the gaps in microclimate, with extreme values in the centre where measurements were made (Brown 1993). The seedling plots were central in each gap and the mean figures used to express growth of several or all seedlings in the population compensate for unevenness in microclimate.

(*a*) *Seedling survival*

For each species, seedlings from each size class of gap were pooled to calculate seedling survival, after confirming with a heterogeneity χ^2 analysis (Zar 1984) that there were no significant differences in mortality between gaps within a size class. Figure 1 shows seedling survival at 77 months since gap creation plotted against mean canopy openness for each gap size class. The 95 % confidence interval for each survival estimate was generated by using the inverse F distribution (Sheil & May 1996). It can be seen on figure 1 that for all three species the lowest survival occurred beneath closed forest and in the largest gap. Closer examination was then made of differences in survival between the species in each of the five different

Table 1. *The canopy gaps created in this study, grouped by size class and measures of irradiance*

(Mean values for the parameters of each gap size class are rounded to an appropriate number of significant figures.)

gap size class	gap number	felled area[a] m^2	projected opening[a] m^2	mean daily p.a.r.[b] mol m^{-2}	canopy openness[c] (% (s.d.))
closed forest	C1	0	0	1.0	
	C2	0	0	1.1	
	mean	0	0	1	6 (0.6)
tiny	2	143	73	4.9	
	3	107	4	3.1	
	8	104	50	6.4	
	10	56	0	2.3	
	mean	100	32	4.2	8 (1.0)
small	5	204	140	9.9	
	7	—[d]	200	10.6	
	mean	—	170	10.3	10 (1.6)
medium	1	1057	706	14.4	
	6	154	37[e]	13.5	
	mean	600	370	14	17 (2.6)
large	4	1200	970	19	26 (3.0)

[a] Whitmore *et al.* (1993), tables 1 and 2.

[b] Brown (1990) table 2.1.

[c] Computed from six or more hemisphere photographs per gap or control plot that include the one to three positions at which p.a.r. was measured; WINPHOT 4 (ter Steege 1994) was used, which corrects for lens distortion (see Mitchell & Whitmore 1993, figure 6).

[d] Gap 7 is natural, not created by felling.

[e] Gap 6 is on a steep slope, open to the east but overhung by trees upslope. It has a small projected opening but high p.a.r. owing to side light.

gap size classes by using the χ^2 test (table 2). Differences between species were significant under closed forest and in medium-sized gaps. Under closed forest, *H. nervosa* showed the highest survival. Over 60% of its seedling population enumerated before gap creation were still alive at 77 months compared with less than 35% of *S. johorensis* seedlings. Both *H. nervosa* and *S. johorensis* showed high levels of survival in medium-sized gaps whereas *P. malaanonan* seedlings suffered high mortality (figure 1). We attribute this to high levels of herbivory, described below.

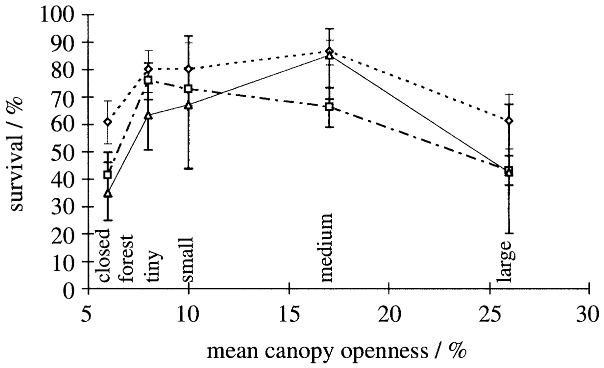

Figure 1. Seedling population survival in canopy gaps of different sizes after 77 months: ◇, *H. nervosa*; □, *P. malaanonan*; △, *S. johorensis*.

(*b*) *Mean height growth*

Figure 2*a* shows mean seedling height after 53 months in relation to gap size. Mean height is calculated only for those seedlings that survived the full 77 months of the experiment. This was done because the mean height of all seedlings will increase, regardless of seedling growth, solely as a consequence of the fact that there is higher mortality among small seedlings (Brown & Whitmore 1992). At 53 months in the closed forest all three species are *ca.* 1 m tall and in the tiny gaps they are *ca.* 2 m tall with no significant differences between species. It can be seen in figure 2*a* that in the three larger gap sizes, small, medium and large, *S. johorensis* has grown progressively faster and is significantly taller, with mean heights *ca.* 4.4, *ca.* 7.5 and *ca.* 8.5 m respectively. In contrast, *H. nervosa* and *P. malaanonan* have only responded very weakly to increasing gap size. Figure 2*b* shows the situation at 77 months. In the closed forest and tiny gaps none of the species has yet grown much. In the three larger gap

Table 2. *Results of five* χ^2 *tests for difference in seedling survival over 77 months among* H. nervosa (*Hn*), P. malaanonan (*Pm*) *and* S. johorensis (*Sj*) *in four sizes of gap and under closed forest*

(*n* = sample size at start.)

gap size	*n* Hn	Pm	Sj	d.f.	χ^2	*P*
large	73	244	14	2	3.60	0.165
medium	172	131	27	2	14.74	< 0.001
small	40	111	22	2	1.47	0.480
tiny	85	125	49	2	3.58	0.167
closed forest	115	111	63	2	6.62	0.037

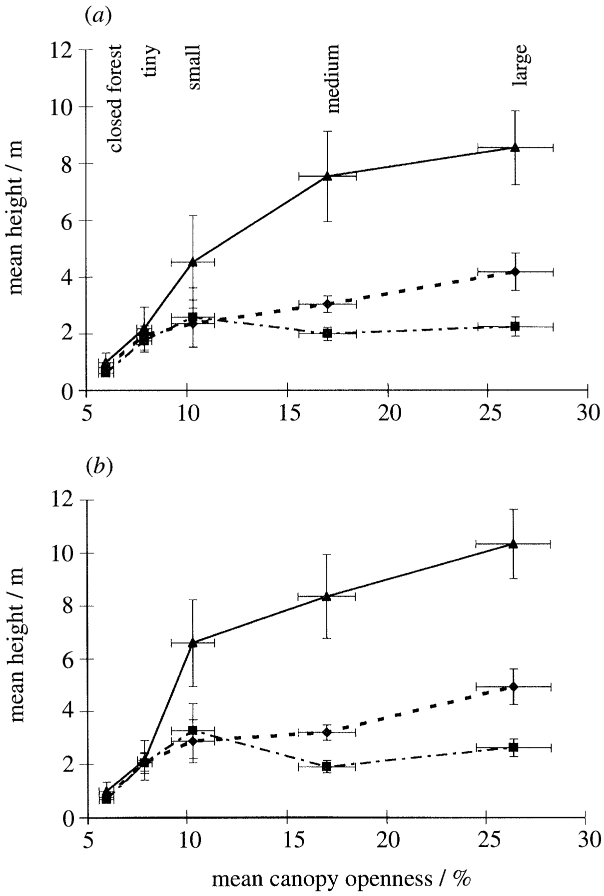

Figure 2. Mean height of all individuals of the three common species in gaps of increasing size at (*a*) 53 months and (*b*) 77 months: ◆, *H. nervosa*; ■, *P. malaanonan*; ▲, *S. johorensis*. Only seedlings that survived the full 77 months of the experiment are used to calculate means. Error bars represent 95% confidence intervals around the mean values.

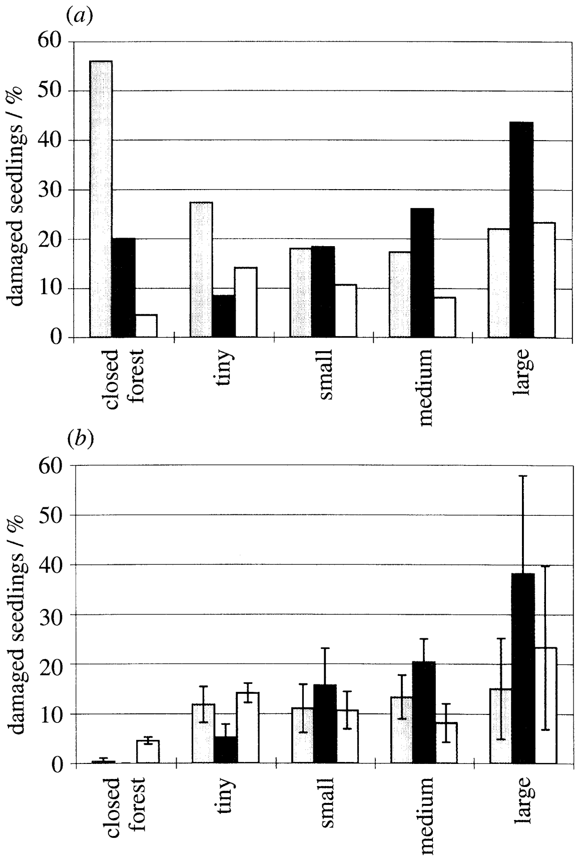

Figure 3. Seedling apex damage over the first two years to the three common species in gaps of increasing size, expressed as the mean percentage, at each of five censuses, of damaged seedlings and seedlings newly damaged since the last census: grey bars, *H. nervosa*; black bars, *P. malaanonan*; white bars, *S. johorensis*. Error bars represent the 95% confidence intervals around the mean values for newly damaged seedlings. (*a*) Total damage; (*b*) new damage.

sizes all three species have grown even taller, with the difference from the situation at 53 months that *S. johorensis* has grown much more and at *ca.* 6, 8.3 and 10 m in height has got even further ahead of the other two species.

(*c*) ***Herbivory***

During the first two years of this study every seedling was examined approximately every four months. The condition of the apical bud and the area removed by herbivores of the ten most recently expanded leaves were recorded (Brown 1990). All species lost leaf area to herbivores in all gaps but no significant differences were detected. However, significant differences were found in the proportion of seedlings with dead or missing apices. Figure 3*a* shows the average proportion (over five censuses) of seedlings of the three common species with dead or missing apices in every gap size class. The total number of damaged seedlings will consist of some which were recently damaged and some damaged in previous periods that have been unable to grow a new apex so successive censuses cannot be used as independent samples of the proportion of seedlings with apical damage. Figure 3*b* therefore shows only that proportion of seedlings in each gap size class which had lost their apices since the previous census. When only this new damage is considered, successive samples are independent. The rate of damage is higher in gaps than beneath closed forest for all species, and increases with gap size for both *P. malaanonan* and *S. johorensis*.

In the large gaps there were significant differences between species in the number of seedlings damaged by herbivory between censuses (Kruskal–Wallis analysis of variance, $P < 0.05$). A larger proportion of *P. malaanonan* seedlings were being damaged between censuses than of the other species. On average, in the large gap over 40% of all seedlings of this species had dead or damaged apices. This damage was observed to be caused mainly by insects, and in the large gap particularly by *Nisitrus vittatus* (de Haan) (Gryllidae, Eneopterinae) a widespread cricket of open, sunny locations. Repeated removal and regrowth of the apical bud caused seedlings of *P. malaanonan* to have a stunted form in the medium and large gaps.

Under closed forest a significantly larger proportion of *H. nervosa* seedlings had dead or missing apices than of the other species. However, the proportion of newly damaged seedlings at each census was very small and there were no significant differences between species. On average *H. nervosa* seedlings were much older than those of *S. johorensis* and *P. malaanonan*. Old seedlings accumulate damage over a long period in the forest understorey where a damaged apex is not rapidly replaced. Seedlings under closed forest are frequently damaged by debris falling from the canopy (see Clark & Clark 1989).

(*d*) *The tallest seedlings*

Only the tallest seedlings grow up to fill a gap and form the building and mature phases of the growth cycle. Thus mean seedling height (figure 2), although useful for an analysis of differences between species, does not tell us which species actually wins the race. That depends on which individual seedlings are actually present in each gap. In addition to the three common species our gaps had eight rarer ones. These need to be included in an examination of winners and losers.

Species of Dipterocarpaceae vary in density of their timber from *ca*. 450–1120 kg m^{-3} at 15% moisture content (so-called air dry) (Desch 1941). Among the many species whose autecology is well known (Wyatt-Smith 1963), low-density timber is associated with light-demanding, fast-growing seedlings and high-density timber with shade-tolerant, slower-growing seedlings. The experience of foresters working on silviculture is that for all rain forest dipterocarp species timber density can be used as a surrogate measure of how light-demanding their seedlings are. We have therefore grouped together the three medium hardwood and seven light hardwood species that had seedlings on our plots. These have mean timber densities of 850 and 540 kg m^{-3} respectively (Burgess 1966). The mean height of the tallest three individuals in these groups is shown for each gap size class, at 40 and 77 months, in figure 4. *P. malaanonan* (a light hardwood) is shown separately because its growth alone was severely affected by herbivory. At 40 months (figure 4*a*) there is little difference in height between the tallest individuals in the medium and light hardwood groups across the whole range of gap sizes. However, by 77 months (figure 4*b*) the light hardwood species group are tallest, that is, they have collectively grown fastest, and *P. malaanonan* has been left seriously behind all other species in small, medium and big gaps. By 77 months light hardwoods collectively have won the race, with different species dominant in different gaps, depending on which happened to be present at the outset of our study.

Table 3 shows the results of an analysis of variance by multiple regression of the height of the seedlings of the three common species at 77 months against initial seedling height and a dummy variable representing the three species (Draper & Smith 1981). Values of R^2 give the amount of total variance accounted for by the regression, and P values give the probability of no relationship between seedling growth and the two predictors (initial height and species). Brown & Whitmore (1992) showed that there was a significant relationship between initial seedling height and seedling growth over the first 40 months in all sizes of gap. Table 3 shows that at 77 months the effect of initial size remains significant only in large and small gaps. In contrast, there is now a significant relationship between *species* and growth under closed forest and in small, medium and large gaps. The general conclusion is that the advantage bestowed on seedlings by large initial size has declined over time as species differences in growth have developed.

The initial advantage of large seedling size is lost most rapidly at the larger gap sizes. This is shown in figure 5 by the length of time taken (in months) from the start of the experiment for the mean height of *S. johorensis* seedlings to become significantly taller ($P < 0.05$) than the mean height of *H. nervosa* seedlings (Student's 1-tailed, unequal variance test of difference between means). Figure 5 shows that, ultimately, *S. johorensis* has overtaken *H. nervosa* even in the closed forest and tiniest gaps and with increasing gap size it has overtaken progressively earlier. In the largest gap, however, *S. johorensis* seedlings were severely affected by the shock of gap creation (Brown & Whitmore 1992) and here they have taken longer to overtake seedlings of *H. nervosa*.

(*e*) *Summary of results*

There were differences in seedling survival between species under closed forest and in gaps (figure 1). The study of seedling growth in gaps of increasing size demonstrates that by 53 months (figure 2*a*) in the tiny gaps, at low p.a.r., all three common species have grown to about the same height but with increasing gap size *S. johorensis* is now much taller, that is, it has grown progressively faster. These differences had hardly developed by 40 months, the time of the previous analysis. Over the next two years, to 77 months (figure 2*b*), *S. johorensis* increased its height lead.

Foresters know *P. malaanonan* as a light-demanding dipterocarp similar to *S. johorensis*, whose seedlings, saplings and poles grow fast. In our study *P. malaanonan* occurred at high density and its height growth was as slow as, or slower than, the known shade-tolerant species *H. nervosa* (figures 2 and 4). It was much more severely damaged by herbivory than any other species (figure 3). We suggest that these very dense populations rendered its seedlings susceptible to apical herbivory, which reduced its height growth.

3. DISCUSSION

We are now, at 77 months after gap creation, in a position to interpret the foresters' observation, which originally triggered this research, that shade-tolerant dipterocarp species are released in small gaps and light-demanders in bigger ones.

H. nervosa can be described as a shade-tolerant species in the sense that its seedling populations survive longer in closed forest conditions (figure 1). *Hopea beccariana*, another abundant known shade-tolerant species, whose seedlings we monitored elsewhere at

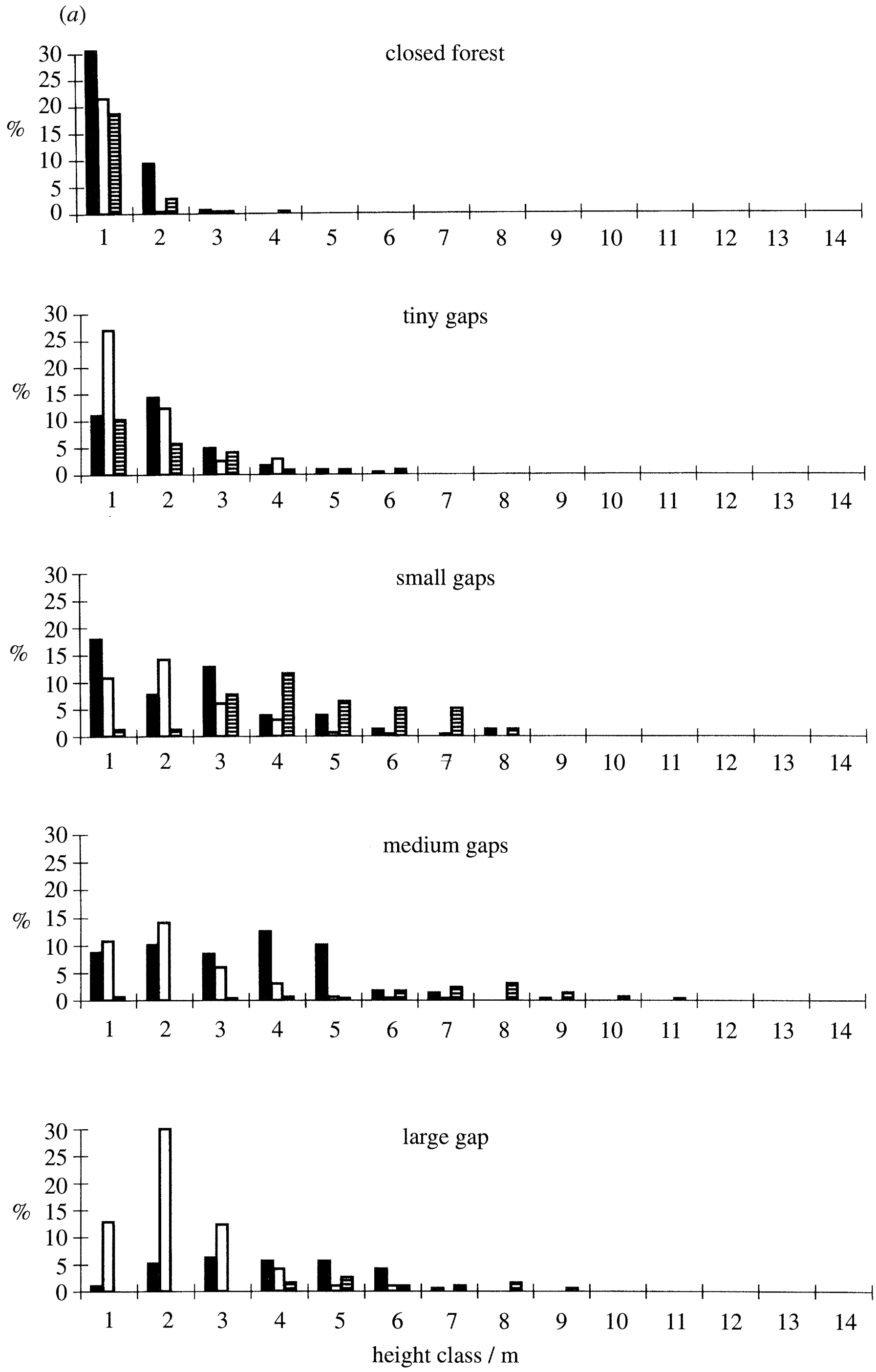

Figure 4. For description see facing page.

Danum, behaves similarly (results not shown). *H. nervosa* shows only a small height-growth response to increasing amounts of p.a.r. either as gap size increases or in a given gap size with increasing time (figure 2). *H. nervosa* can therefore be well described as 'light-indifferent'.

S. johorensis, by contrast, has light-demanding seedlings in the sense that in the dense shade conditions of closed forest there is high mortality (figure 1). In tiny gaps its growth is similar to that of *H. nervosa* but as p.a.r. increases either with gap size, or over time in a given gap (figure 2), so does its height advantage. Thus *S. johorensis* is able to use increasing amounts of p.a.r. In this progressive response to p.a.r., *S. johorensis* is a light-demander, although in a different sense from its high seedling mortality at low p.a.r. below a closed canopy (figure 1).

If timber density is used as a surrogate measure of shade tolerance the same result is obtained (figure 4). Light hardwoods as a group gain dominance in larger gap sizes, those with p.a.r. of 10 mol $\mathrm{m^{-2}\ day^{-1}}$ or more in our study (that is, small gaps and larger).

The greater height growth of light-demanders becomes increasingly manifest with time. Our first analysis, made at 40 months (Brown & Whitmore 1992), was too early for differences to have developed, and the picture was still determined by the greater initial height of shade-tolerant *H. nervosa* seedlings.

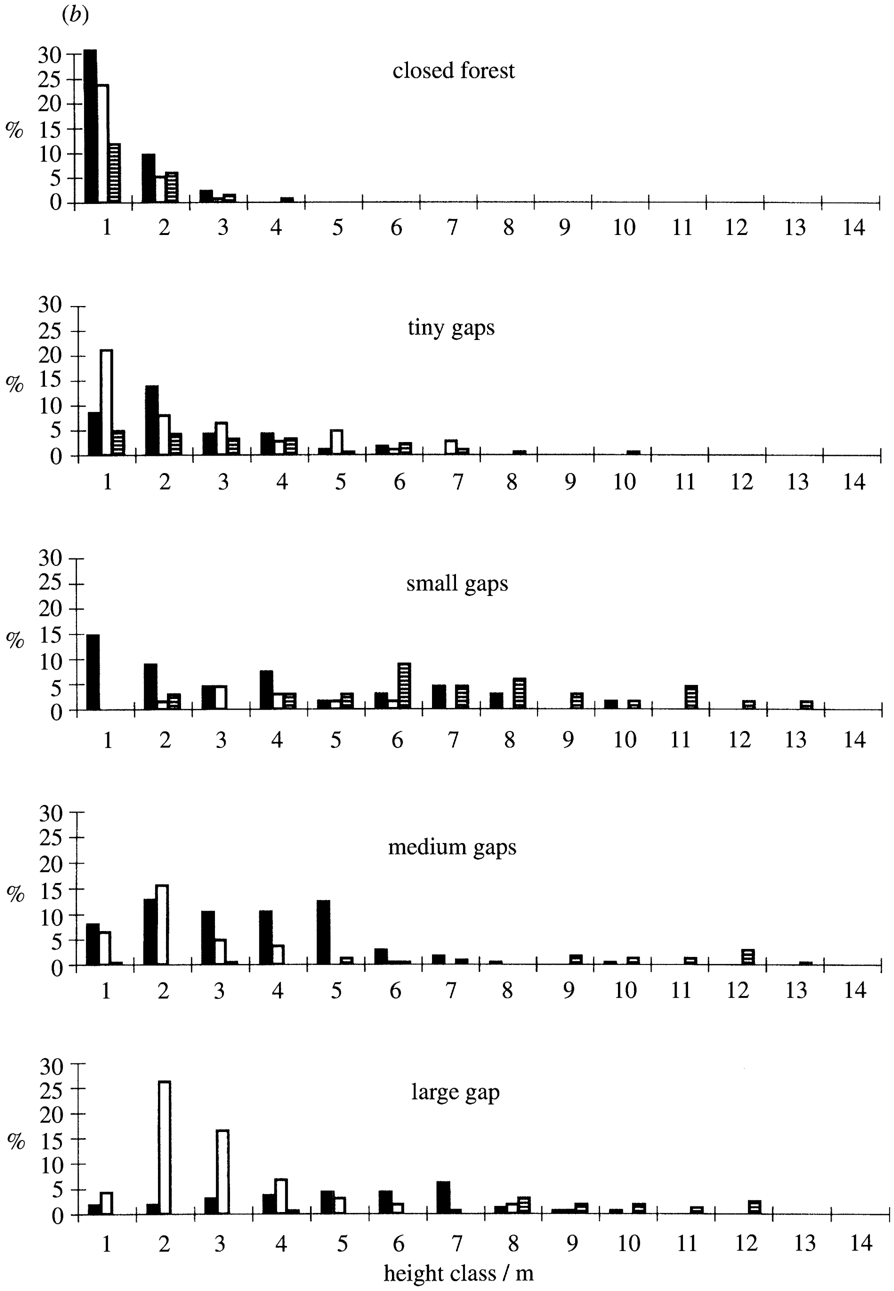

Figure 4. Population structure of all seedlings of medium hardwoods (black bars, three species) and light hardwoods (hatched bars, seven species) and of *P. malaanonan* (white bars) in 1 m height classes in the different gap sizes at (*a*) 40 months and (*b*) 77 months. Medium hardwood species: *H. beccariana*, *H. nervosa*, *S. superba*; light hardwood species: *S. argentifolia*, *S. bracteolata*, *S. fallax*, *S. johorensis*, *S. leprosula*, *S. parvifolia*, *S. virescens*.

Table 3. *Results of an analysis of variance by multiple regression of growth of seedlings of the three common species over 77 months against initial seedling height and dummy variables representing the three species*

		initial height		species		total		
gap size	*n*	*f*	*P*	*f*	*P*	r^2	*f*	*P*
closed forest	129	0.02	0.899	10.9	< 0.001	0.15	7.3	< 0.001
tiny	176	6.8	0.811	0.21	0.101	0.041	2.4	0.068
small	54	10.2	0.002	12.2	< 0.001	0.414	11.5	< 0.001
medium	244	0.98	0.323	51.7	< 0.001	0.391	51.2	< 0.001
large	151	50.5	< 0.001	36.8	< 0.001	0.459	41.4	< 0.001

The exception to the general pattern is *P. malaanonan*, a light hardwood (timber density 510 kg m^{-3}), a known fast grower and a light-demander in the sense that seedling populations have low survival below closed forest (figure 1). In our experiment it occurs at very high population density and is so seriously attacked by herbivores (more so than any other species) that its height growth is reduced to that of shade-

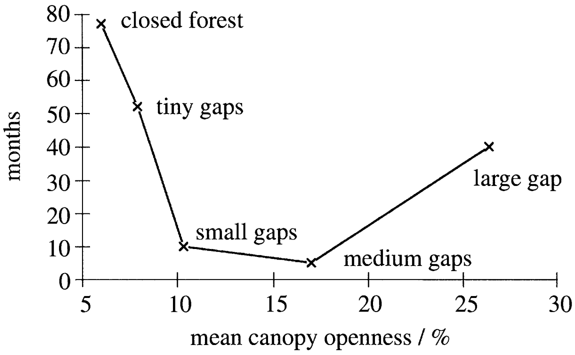

Figure 5. Months taken for seedlings of *S. johorensis* to grow significantly taller than those of *H. nervosa* in gaps of different size.

tolerant *H. nervosa* (figure 2) and the medium hardwood species group (figure 4). *P. malaanonan* is common as a big tree in the Danum forest and over a large part of eastern Sabah (Fox 1972). Until they were felled for timber progressively from the 1960s onwards these were the most valuable commercial forests in the country. We suggest that *P. malaanonan* achieved its status by successful release of seedlings from low-density populations that did not attract devastating levels of herbivory.

Thus our study suggests that, among Dipterocarpaceae, light-demanding species are usually the winners in all but the smallest canopy gaps, but that debilitating herbivory can in certain circumstances cause such a species to lose. Shade-tolerant species win mainly in some tiny gaps. At the low irradiances of such gaps they grow in height at about the same rate as light-demanders but have the competitive advantage, arising from their low mortality, of larger populations of taller seedlings in the closed-forest seedling bank. Seedlings of this ecological group also occasionally succeed in larger gaps, also because of the initial advantage of greater height.

All these dipterocarp species grow faster in height as gap size increases (figures 2 and 4). There is no evidence to support the hypothesis that each species grows optimally in a particular size of gap (Denslow 1980); that is to say, the species do not show fundamental niche differentiation. Instead there is a shifting competitive hierarchy (Keddy 1989) whereby all species respond to an increase in p.a.r., but the rate of change of response differs between species resulting in changes in rank in the competitive hierarchy. Among the three species we have studied in detail (figure 2), *P. malaanonan* has its expected position in the hierarchy reduced by herbivory, and the other two change in rank position after different periods in gaps of different sizes (figure 5).

Foresters have discovered that if a forest is opened beyond a certain amount, dipterocarp regeneration is unsatisfactory. In the biggest gap that we studied (canopy openness 26%, p.a.r. *ca.* 19 mol m^{-2} day^{-1}) mortality was greater than in the smaller gaps (figure 1) and also apical damage was higher (figure 3), which suggests that the canopy has been opened beyond the optimum for dipterocarp seedling release. Our second discovery of practical significance to foresters is that if it is desired to favour the regeneration of light hardwood species after logging, the canopy gaps need to be at least our 'small gap' size (figure 2), with canopy openness 10% and p.a.r. *ca.* 10 mol m^{-2} day^{-1} (*ca.* 30% of the amount in the open) and that medium gaps (canopy openness 17%, p.a.r. *ca.* 14 mol m^{-2} day^{-1}: *ca.* 40% of the amount in the open) are better.

Over the past few years there have been several studies on the ecophysiological attributes of shade-tolerant and light-demanding tropical tree species (recently reviewed by Whitmore (1996); see also Oberbauer *et al.* (1993) and Poorter & Oberbauer (1993)). It has emerged from this work that a general characteristic is that light-demanding species are more flexible, in the sense that they are better able variously to adjust architecture, morphology, leaf anatomy and several ecophysiological attributes. In particular, light-demanders increase their rates of light-saturated photosynthesis as p.a.r. increases much more than do shade-bearers (Fetcher *et al.* 1994; Raaimakers 1994, figure 6.1; Press *et al.* 1996) to different conditions. These studies have been on individual leaves or plants.

Our studies of seedling growth at Danum demonstrate the ecological significance of the greater flexibility of light-demanding species at the level of whole populations out in the forest. We have shown that the light-demanders have a greater capacity to adjust to and benefit from the changing microclimate of larger gaps. This results in their greater success than shade-bearers in the larger canopy gaps.

Although there is no evidence that individual species are finely tuned to particular gap sizes, as a broad generalization shade-bearers are more likely to succeed in small gaps and light-demanders in larger ones. In our closed forest control plots and tiny gaps (figures 2 and 4), shade-bearers and light-demanders showed similar height growth but in larger gaps with their much higher p.a.r. shade-bearers grew only slightly faster, whereas light-demanders grew much faster. This lack of response suggests that shade-bearers are perhaps better described as light-indifferent species.

The question then arises: In which of the various ecophysiological attributes listed above is *S. johorensis* more flexible than *H. nervosa*? Studies on rates of light-saturated photosynthesis and stomatal conductance of dipterocarps by Koyama (1981) and Press *et al.* (1996) showed that all of the dozen or so species that they investigated were very similar and were markedly different from pioneer tree species and a strongly shade-tolerant herb (*Begonia* sp.). Thus the difference between our two dipterocarp species is unlikely to lie at this basic level. As part of the present study we recorded various measures of plant architecture and morphology. These show (results not shown) that the increase in height growth with increasing gap size (figure 2) is closely paralleled by increases in leaf number, leaf area, and total length of branches. It seems that it is at this level, the allocation of resources, that *S. johorensis*, the light-demander under study, is more flexible.

By 77 months the regrowing forest has reached the building phase of the growth cycle in the larger gaps. These have filled with a dense stand of young trees, some approaching the size of telegraph poles, 12–14 m tall. The observations at Danum will continue, changing now to diameter, not height, measurements. It will be of interest to see whether rapid growth continues or stagnates.

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