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Growth and survivorship of dipterocarp seedlings: differences in shade persistence create a special case of dispersal limitation

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A series of growth experiments and observations on natural populations have been carried out on dipterocarp species of contrasting ecology growing in artificial gaps and the forest understorey. These studies have demonstrated that although differences exist between species in photosynthetic and growth responses to the high-light environment, competition for light in canopy gaps is highly asymmetrical and tends to reinforce any pre-existing dominance hierarchy. We propose that differences in seedling persistence in forest canopy shade are highly influenced by species-specific biotic and abiotic interactions. Our experiments suggest that as seedlings, dipterocarp species trade off traits which enhance persistence and growth in shade against those that enhance their ability to exploit gaps. Less competitive species survive for progressively longer periods of time after a gregarious fruiting event. This leads to significant shifts with time in the number of species present in the seedling bank and hence in the importance of interspecific competition in determining which species dominates regrowth in gaps. We propose that this special case of dispersal limitation is more likely to account for coexistence of dipterocarp species than differences in growth responses to gaps of different size, with stochastic and environmental variables interacting to determine species distribution and abundance.

Keywords: Dipterocarpaceae; seedling regeneration; mast fruiting; niche differentiation; species coexistence

1. INTRODUCTION

One of ecology's most challenging problems remains the determination of the relative importance of factors controlling coexistence in species-rich communities. The debate, so far, has centred on the degree to which communities are structured by competitive interactions between species as opposed to being accidental collections of individuals in which competition has little importance in regulating species richness and abundance (Hubbell 1998).

Fedorov (1966) noted that species-rich tropical rainforest communities were characterized by groups of closely related taxa. He proposed that very low population densities in combination with irregularity of flowering would lead to speciation through random genetic drift rather than natural selection. Thus, he maintained, series of closely allied species might differ physiognomically, but rarely ever compete in ways leading to ecological differentiation. Fedorov cites the genus *Shorea* within the Dipterocarpaceae as a prime example of non-adaptive differentiation in a large group of very closely related species. An alternative viewpoint was put forward by Ashton (1969), who concluded from studies of the Dipterocarpaceae in Brunei and Sarawak that species were highly specialized to different niches as a consequence of evolution in a relative stable environment over long periods of time. Ashton (1998) suggests that as species within large congeneric series (such as *Shorea*) are most similar, these groups should experience the most stringent diversifying selection. It is, therefore, within these groups of closely related species that we should search most carefully for evidence of interspecific competition. Studies of niche differentiation in closely related species also have the advantage of being able to attribute observed differences in ecology to adaptive divergence rather than the conservation of ancestral traits in descendant species. It is not surprising to discover that species from different clades differ in their ecological range (e.g. Popma & Bongers 1988). What is far from clear is to what extent such differences can be attributed to niche differentiation.

The Dipterocarpaceae, therefore, provides a valuable test of any proposed mechanisms for species coexistence. Big trees of this family dominate lowland rainforests in western Indonesia, Malaysia, Brunei and the Philippines. The Dipterocarpaceae is remarkable for the number of sympatric species within the same genus. Newbery *et al.* (1996) found five species of *Shorea* to be among the 38 most abundant species $\geqslant 10$ cm girth at breast height (gbh) in two 4-ha plots in the lowland forest at Danum Valley, Sabah. In a subsample of these plots, Still (1996) found densities of 1061 and 860 seedlings per hectare of six *Shorea* species in section *Mutica*. At Sungei Menyala in peninsular Malaysia, Manokaran & Swaine (1994)

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found ten species of *Shorea* in 2 ha of forest and individuals of these species comprised nearly 11% of the total number of stems >10 cm diameter at breast height (dbh). The same study found 13 species of *Shorea* in an 8-ha plot in Pasoh Forest, Malaysia.

A small number of studies have compared dipterocarp species and revealed evidence for niche differentiation. Ashton *et al.* (1988) reported sequential flowering in trees in the Dipterocarpaceae that have a common insect pollinator. Ashton (1964) found patterns in the landscape-scale distribution of dipterocarp trees in Brunei reflected soil fertility. However, a similar study of a topographically more uniform forest in Pasoh, Peninsular Malaysia, by Wong & Whitmore (1970) found little evidence for high niche specificity for most dipterocarp species. Although their ordination of species data showed a gradual shift in forest composition from plot to plot they concluded that this was due to limited dispersal leading to patchy species distributions. Manokaran & Swaine (1994) suggested that there are site differences across the Pasoh forest and that these may well be responsible for the floristic variation seen between plots. Newbery *et al.* (1996) found no relationship between the spatial distribution of individuals between 10 and <50 cm gbh of any dipterocarp species and either topography or soil chemistry in two 4-ha plots at Danum Valley, Sabah. Eschenbach *et al.* (1998) found striking similarity in the light response curves of net photosynthesis for crown leaves from adult trees of five species of dipterocarp from four different genera. Gunatilleke *et al.* (1998) report that nine *Shorea* species within the endemic section *Doona* from Sri Lanka are naturally distributed across an elevation gradient. However, they found that seedlings of all but one of the species tested grew best in a shade house at low elevations.

In the last decade, the search for evidence of niche differentiation in tropical rainforest trees has focused, to a large extent, on the environmental gradients created by natural treefall gaps. There are a number of reasons why this may have occurred.

(i) It is commonly observed that plant growth is light-limited in the forest understorey. Most tree species depend on gaps for rapid growth beyond the seedling stage and some species require high irradiance for germination and establishment (Swaine & Whitmore 1988). Competition for light is more likely to lead to competitive exclusion than competition for any other resource (Weiner 1986). Gaps are perceived to be the loci for interspecific competition for light, and the outcome of biotic interactions at this life-stage may play a fundamental role in determining the future composition of the forest.

(ii) The failure, so far, to find any clear evidence for habitat or phenological niche differentiation among adults of many climax tropical rainforest tree species has led to the hypothesis that for many species differences may only exist in the regeneration niche (*sensu* Grubb 1977).

(iii) Chesson & Warner (1981) have demonstrated theoretically how highly variable juvenile recruitment and survival can lead to coexistence in species with overlapping generations and relatively unvarying adult survival. Stochastic variation in the environment (such as unpredictable formation of treefall gaps) does not merely disrupt the process of competitive exclusion but will have different effects on the reproductive success of differently adapted species. This model has focused attention on recruitment and in particular variation in recruitment success from year to year as a process that is potentially crucial in population regulation (Leigh 1996).

(iv) Seedlings are typically more abundant and their growth responses can be measured more easily than those of adult trees. Hence they are more amenable to experimentation by short-term research projects. Seedling growth and survival may also be more responsive to environmental variation than that of large trees (Zagt & Werger 1998).

Nevertheless, it has proved singularly difficult to identify significant variation in seedling traits of climax tree species that would permit niche differentiation in gap environments (Brown & Jennings 1998). Ashton & Berlyn (1992) measured net photosynthesis under contrasting levels of irradiance in single leaves of four species of *Shorea* growing in Sri Lanka. One species, *Shorea megistophylla*, showed the highest rates at all levels of irradiance between 350 and 1600 mmol $m^{-2}\,s^{-1}$ and the second highest at 50 μmol $m^{-2}\,s^{-1}$. A comparison of light-saturated rates of photosynthesis in the youngest fully expanded leaves of seedlings of ten species of dipterocarp growing at Danum Valley showed species were very similar (Press *et al.* 1996; Barker *et al.* 1997). Whitmore & Brown (1996) concluded that they could find no evidence for fundamental niche differentiation between 11 species of dipterocarp seedling growing in a range of canopy gaps of different sizes. All species showed increasing rates of growth with increasing gap size. They judged that the patterns that they had observed were better explained by a shifting competitive hierarchy model (*sensu* Keddy 1989) whereby there is a trade-off between minimum resource requirements for survival and maximum level of response to unlimited resource supply. This model implies that species shift position in the competitive hierarchy along a resource gradient even though all or most may show increasing response to increasing resource supply.

A failure to identify adequate evidence for niche differentiation on gap light environments is far from a conclusive test of the regeneration niche hypothesis for at least three reasons.

First, a suite of both abiotic and biotic factors impacts on seedling fitness and survival and relatively few studies have examined the responses of seedlings to such interactions. Further, even with one variable, such as irradiance, the scale of temporal changes in light quantity (e.g. sunflecks) and quality may exert important effects on seedlings. Sunflecks are an important source of light energy for understorey plants and the photosynthetic responses to dynamic light are complex and may be species specific. For example, dipterocarp seedlings differ in rates of photosynthetic induction and loss of induction (Zipperlen & Press 1997). Watling *et al.* (1997) demonstrated that Australian rainforest species responded individualistically to flecked radiation with regard to both their photsynthetic and growth characteristics.

Second, our ability to measure plant responses to perturbations of the atmospheric and edaphic environment often limits our ability to establish causal relationships between plant performance and environmental manipulation. For example, few studies have addressed whole plant carbon exchange under field conditions, instead opting for more straightforward measurements of gas exchange at the leaf level. With respect to growth, many studies have placed too great an emphasis on seedling height at the expense of determining the three-dimensional space that seedlings occupy (Zipperlen & Press 1996). The architecture of seedlings may be particularly important in the shade, where investment in horizontal growth rather than vertical growth may enhance the capture of sunflecks (Kohyama 1987; King 1990, 1996; Henry & Aarssen 1997). In the longer term this trait may offset the apparent advantage of preferential investment in vertical growth (Zipperlen & Press 1996).

Third, predicting responses to environmental variables is difficult because of adaptations to environmental change, which themselves can be highly species specific. For example, interspecific differences in dipterocarp responses to flecked light were found to be smaller than the impact of light environment under which the seedlings were growing. Thus, the complexity of plant responses, the role of interacting factors and the ability of species to adapt to changes in environment have all affected the quality of evidence that has been sought in an attempt to support the niche differentiation hypotheses.

Furthermore, studies of gap-phase regeneration dynamics have examined only a part of the regeneration niche as originally defined by Grubb (1977). Important aspects that have received little attention include the processes that influence the abundance and condition of seedlings in the forest understorey prior to gap formation. Studies of niche differentiation along a light gap gradient are invariably carried out on experimental seedling populations in which differences in seedling size and condition are minimized. However, in natural treefall gaps differences between individuals in these variables may override any interspecific differences in adaptation. Nevertheless, seedling abundance and condition in the forest understorey will be affected by species-specific differences in physiology and allometry. As competition for light in gaps is likely to be asymmetrical (*sensu* Begon *et al.* 1986), dominance patterns in gaps may be strongly influenced by seedling size at the time of gap creation (Brown & Whitmore 1992). Gap formation, rather than creating the environment in which strong interspecific competition takes place, may merely reinforce patterns of selection that took place in the forest understorey. There is a need for a more detailed examination of the relative roles of chance and species adaptation in controlling the composition and condition of seedling banks at the time of gap formation.

The idea that many species of adult tree are ecologically equivalent and that chance may play an important role in determining which grows where is not a new one. Symington (1943, p. xiii), describing the distribution of dipterocarps in the Malaysian peninsula, hypothesized that 'Obscure local climatic or edaphic variations may influence the distribution of species but it is more probable that the main determining factors are chance and opportunity'. Richards (1969) doubted the existence of sufficient niches to accommodate the diversity of species found in tropical rainforests and asked if it was possible that 'Whether species A, B, C... occupies a given niche when it becomes vacant is determined to a large extent by chance?' Whitmore (1975) attempted to reconcile the roles of chance and competitive interactions by suggesting that there exists a hierarchy of variation in tropical forests with the relative importance of different mechanisms changing with the scale of study. Whitmore proposed that 'the manifold roles of chance' were extremely important at the very local scale, in determining which species colonized vacant space in a treefall gap, but that at larger scales ecological differentiation and then the availability of flora became increasingly important. A very similar idea was subsequently put forward by Ricklefs (1987).

Studies of forest dynamics in the New World have lent support to the idea that chance rather than niche differentiation may be the principal determinant of which species grows where. Hubbell & Foster (1986) have emphasized the importance of dispersal limitation in constraining the extent of competitive interactions between species. There has been a tendency, in theoretical ecology, to assume that species are uniformly mixed in communities and hence the survival of any one species is influenced by its interactions with all others, simultaneously. This is clearly not the case; dispersal of most tropical rainforest tree species is limited. Hubbell & Foster (1986) have argued that where dispersal is limited in a species-rich community, individuals of one species will compete, from place-to-place and time-to-time, with an unpredictable subset of other species. These competitive interactions will take place in an environment that is also unpredictable. As very few individuals within a species' population will be subject to the same selective pressures, the result will be the evolution of generalist tree species rather than niche specialists. They propose that being in the right place at a propitious time may be more important to a tree's success in growing to maturity than competitive superiority in that particular environment.

Tilman (1994) has developed a theoretical model in which he has shown that if species exhibit a trade-off between their competitive and dispersal abilities then an infinite number of species may coexist. Vacant sites are not necessarily occupied by the species that is best adapted to the local environment. If the most competitive species are the least well dispersed, they will fail to colonize many potentially suitable sites. Such sites may be colonized, by default, by any species that happens to be present. Well dispersed but competitively inferior species are able to maintain a population by colonizing vacant sites. If dispersal limitation is an important constraint on biotic interactions then it is unlikely that any correlation will be found between resource availability and patterns of species abundance and growth.

Like many tropical rainforest trees, reproductively mature dipterocarps occur at low population densities. Their seeds are heavy and they are primarily dispersed by gravity. It is therefore likely that interspecific competition will show strong spatial structure. The consequences of

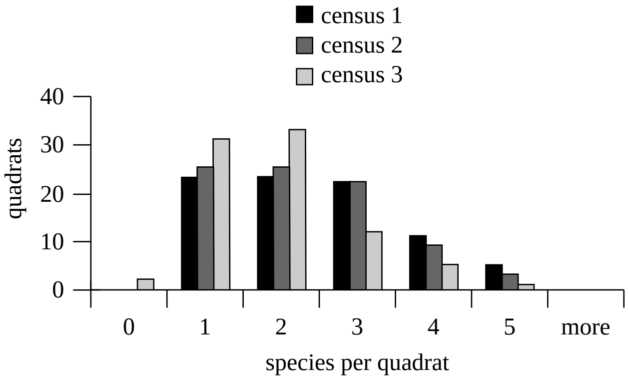

Figure 1. Dipterocarp species density in 24 randomly positioned 1 m^2 quadrats surveyed at six-month intervals following the 1997 mast fruiting event at Danum Valley.

dispersal limitation for dipterocarp population dynamics need to be explored.

2. MAST FRUITING IN THE DIPTEROCARPACEAE AND THE SEEDLING BANK

A characteristic of non-seasonal lowland dipterocarp rainforest is supra-annual gregarious fruiting events in which many individuals across a wide range of dipterocarp species disperse fruit simultaneously (Burgess 1972). Yap & Chan (1990) have shown that although most species flower annually the proportion of individuals that are involved in each flowering event varies considerably from year to year. Seed viability and seedling establishment appear to be highest in gregarious fruiting years. It has not yet been established whether this is as a consequence of the favourable environmental conditions that may have triggered gregarious fruiting or due to the satiation of dipterocarp seed predators (Ashton *et al*. 1988; Kelly 1994; Toy *et al*. 1992). As a consequence, at intervals varying typically between three and 11 years, there is substantial multi-species recruitment to the dipterocarp seedling bank. Fox (1972) recorded up to 57 000 dipterocarp seedlings per hectare following mast fruiting in Sabah. This pattern of mast fruit production exacerbates the degree to which seedlings of dipterocarp species are likely to be subject to interspecific competition. In a series of 24 quadrats placed at random at three sites, each one stratified into ridge-top, mid-slope and valley-bottom and surveyed immediately after a mast fruiting event at Danum in 1997 we found up to five species of dipterocarp seedling per square metre (see figure 1). Gregarious fruiting and simultaneous establishment of large mixed-species populations of seedlings may mean that interspecific competition is less limited by dispersal than in other tropical rainforest communities with asynchronous phenologies. Furthermore, synchronous establishment and the comparatively small range of seed sizes may mean that seedling size variability within and between species is less than is found elsewhere. The greater the size disparity between individuals the greater the likelihood that gap creation will result in asymmetrical competition for light and merely reinforce pre-existing dominance hierarchies. When seedlings are of approximately equal height and have similar architectures, differences in seedling adaptation may play an important role. We may therefore conclude that mast fruiting may result in more intense interspecific competition between dipterocarp species and this may have lead to more extreme diversifying selection.

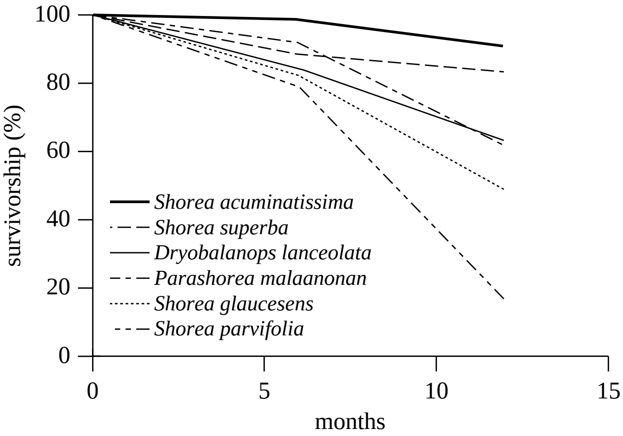

Figure 2. Survivorship of six species of dipterocarp seedling over one year following the 1997 mast fruiting event at Danum Valley in 84 randomly positioned 1 m^2 quadrats in the forest understorey.

Fox (1976) has shown that the density of the dipterocarp seedling bank declines rapidly with time after a gregarious fruiting, until the next fruiting event. He monitored population density of ten species in the red meranti group of the genus *Shorea* (Dipterocarpaceae) for 12 years and found periods of gregarious fruiting to be followed by high seedling mortality. Species differed significantly in their mortality and recruitment rates and hence in the number of individuals present at any one time. Fox (1976) pointed out that felling of canopy trees at different times would, as a consequence, have resulted in regrowth of differing composition. We have found similar differences in the survival of six species of dipterocarp seedling over one year following the 1997 mast fruiting event at Danum Valley in 84 randomly positioned 1 m^2 quadrats in the forest understorey (figure 2). Turner (1990) found significant differences in mortality between seedling populations of three species of *Shorea* growing in the forest understorey in coastal hill dipterocarp forest in peninsular Malaysia. Whitmore & Brown (1996) found significant differences in the survival of three dipterocarp species in closed forest. Over 60% of the seedling population of *Hopea nervosa* survived six-and-a-half years compared with less than 35% of *Shorea johorensis* seedlings. Still (1996) found a close relationship between mean rates of growth and mortality among six dipterocarp species growing in 2 ha of forest at Danum Valley.

Differential mortality implies that the number of species found in the seedling bank at any point on the forest floor declines as time passes (see figure 1). We propose that this constitutes a special case of dispersal limitation. The longer a species population is capable of persisting in forest shade the greater the probability that when gaps form, competitively superior species will not be present. If there is a trade-off between traits that enhance persistence and growth in the forest understorey and those that enhance competitiveness in gap environments then this may provide a mechanism for species

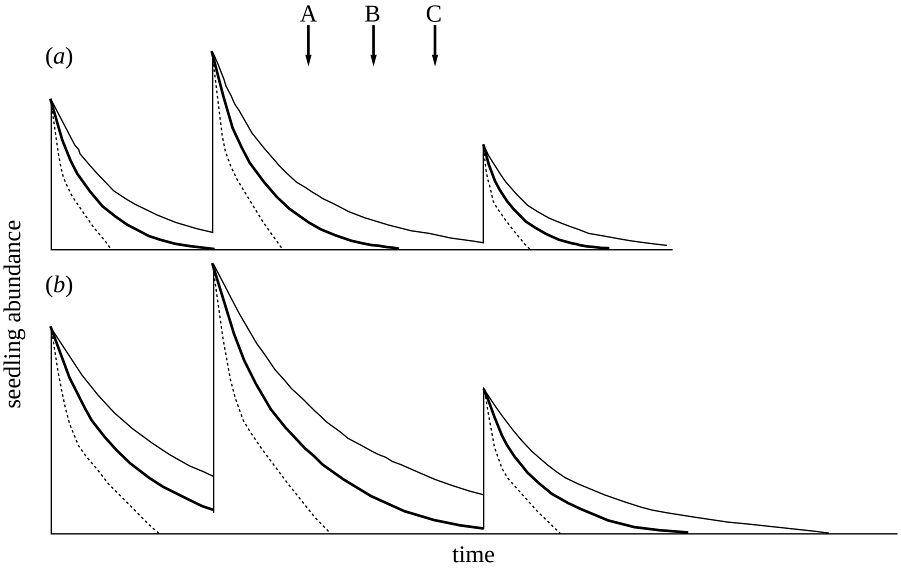

Figure 3. Simultaneous creation of canopy gaps over sites with contrasting canopy cover would result in quite different outcomes. The most competitive but least persistent species would dominate gaps formed at time *A* at sites with previously relatively open canopies. At time *C* gaps formed in dense canopies will be dominated, by default, by the most persistent species. (*a*) Dark site; (*b*) light site.

coexistence. Growth of four sympatric species of *Shorea* was compared, in the Singharaja forest in three natural treefall gaps of contrasting size (Ashton *et al.* 1995). Two out of the four species examined, *Shorea megistophylla* and *Shorea trapezifolia* showed superior growth in gap environments but much lower survival in shade. Treefall gaps that form soon after a gregarious fruiting event will occur over a dense, species-rich seedling bank in which most individuals are small and when there will be little interspecific variation in seedling size. Interspecific competition will be intense and traits which enhance competitiveness in gaps such as a high relative growth rate, will maximize the chances of successful seedling regeneration. Shade-persistent species are likely to experience poor seedling recruitment during such periods. In contrast, when gaps are formed some considerable time after the last gregarious fruiting event, the seedling bank will consist of a few shade-persistent species. Interspecific competition will be weak and recruitment will be by default rather than by superior adaptation. Highly competitive species are likely to experience poor recruitment at such times due to low abundance and poor condition. As Chesson & Warner (1981) have demonstrated, survival from periods of good recruitment can more than compensate for periods of poor recruitment (the so-called 'storage effect'), leading to species coexistence.

Persistent species that are able to grow slowly in the forest understorey will further increase their advantage with time by ensuring that they are in a dominant position when any future gaps form. Brown & Whitmore (1992) suggested that, at the time of their study, gaps in the Danum forest were likely to be colonized by *Hopea nervosa* as seedlings of this shade-persistent species were large and relatively abundant. They concluded that 'If the Danum forest is not to undergo substantial change in its species composition, towards one in which shade-tolerant species of dipterocarp are common, there will need to be future dramatic change in the growth performance of seedlings of light-demanding species'. We now propose that this observation was a consequence of there having been no gregarious dipterocarp fruiting for at least four years before this study. Extrapolation from short-term observations of regeneration dynamics may be misleading when there is long-term variability in recruitment probabilities for different species.

In the following section we describe interspecific differences in responses to environmental variables. While these occur both pre- and post-gap formation, we propose that understorey environments exert greater selective pressure on seedlings because they will determine the presence or absence of species at the time of gap creation. Thus it is the complex, but ultimately predictable, interactions between species and environment and the unpredictable timing of gap creation with its associated change in micro-environment that act in unison to control niche differentiation.

3. SITE FACTORS AND SPECIES TRAITS AFFECTING SEEDLING PERSISTENCE

Foxworthy (1932) commented that in certain very dark places, where the canopy cover is very dense, little or no regeneration survives. In other places seedlings of many species may persist for a number of years in a state of arrested development. As a consequence, the simultaneous creation of canopy gaps over two such contrasting sites would result in quite different outcomes (see figure 3). Where the seedling bank had been eroded to a very small number of individuals, competition would be negligible and the gap would be occupied, by default, by whichever species had survived. In contrast, in sites where many species have persisted interspecific competition will continue to play an important role. At any one time, seedling traits that enhance persistence in shade and those that improve competitive ability may both be successful strategies in different parts of the forest. Brown (1996) examined growth and survival of three species of dipterocarp seedling on a light gradient from the centre of a tropical rainforest canopy gap into the surrounding forest. He found that seedlings of *Shorea johorensis* grew tallest everywhere but ultimately almost all seedlings died beneath the forest canopy, allowing slower growing species to dominate. These observations are in accordance with those made on seedlings of 13 species of tree on

Barro Colorado Island, Panama, by Kitajima (1994) where species with the highest relative growth rates in shade over the first few months after germination also suffered highest rates of mortality. Augspurger (1984) demonstrated that the main causes of mortality in the shaded understorey are fungal pathogens and herbivory. Kitajima (1994) proposed that survival in shade is likely to depend on a morphology that will enhance defence against herbivores and pathogens. Traits such as tough leaves and a well-developed root system, will carry substantial construction costs and as a consequence should result in a lower leaf-area ratio and lower rates of whole-plant carbon gain. Shade-tolerant plants will therefore grow more slowly than light-demanding species even in shaded environments. Grime (1977) maintained that species dominant in productive sites are better competitors regardless of site conditions, but that they will suffer higher mortality in resource-poor sites. This contention would appear to be supported by these observations from tropical rainforests.

Grubb (1996) has proposed that root competition may be as important as competition for light in influencing patterns of establishment in tropical rainforest. Nutrient supply rates and interspecific differences in their modes of acquisition may exert important impacts on both seedling survival and growth. Almost all published accounts of experimental manipulation of nutrient supply explore the response of seedlings to an increase in putatively limiting nutrients. Experiments designed to determine the impact of nutrient additions on the performance of dipterocarp seedlings have been equivocal (Sundralingham *et al*. 1985; Turner *et al*. 1993). Although some pot studies have shown seedlings to be unresponsive, there is increasing evidence to support the view that nutrient addition can exert important impacts on not only dipterocarps but also seedlings of neotropical climax species. Addition of nutrients under field conditions in Sabah (slow-release pellets, plants grown in short collars to prevent initial root invasion and rooted in forest) stimulated both the relative increase in seedling height and branch length of *Shorea johorensis* and *Dryobalanops lanceolata* (figure 4). These responses were observed within six months of nutrient addition and were sustained over a subsequent three-year period (S. Jackson, J. Scholes and M. C. Press, unpublished data). Also, nutrient addition affected a suite of other variables, including a stimulation of leaf turnover rates and higher foliar nitrogen concentrations. These responses may have profound and sometimes unpredictable consequences for survivorship. For example, while the additional nitrogen may be used for the construction of photosynthetic pigments and proteins, ultimately stimulating carbon gain, more nutrient-rich leaves may be subjected to greater predation by invertebrate and vertebate herbivores.

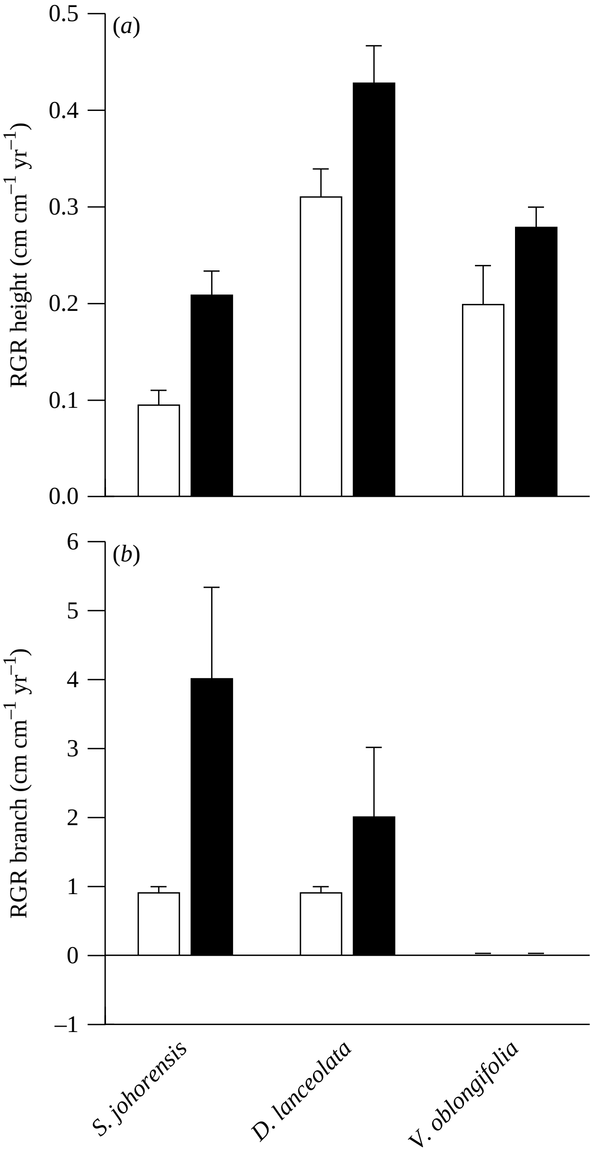

Figure 4. Relative height growth rates (*a*) and relative branch length growth rates (*b*) for three species planted under secondary forest canopy (the ML site of Zipperlen & Press (1996) was *ca*. 10% canopy openness), after nine months growth. Filled bars show the response of seedlings to nutrient additions.

Regrettably, there is little information on the impact of root competition or nutrient depletion on the survival and growth of seedlings in the forest understorey. Even in the absence of any change in the pool size or flux of nutrients following gap formation, lower densities of fine absorptive roots may mean that nutrient availability is greater at these sites (Denslow *et al*. 1998; Ostertag 1998). Root competition and soil resource depletion may not only be widespread but may have a much greater impact on population dynamics through driving patterns of differential survival than occasional pulses of nutrient enrichment or root gaps (Vitousek 1984). Gunatilleke *et al*. (1996) have demonstrated significant difference in the performance of eight sympatric dipterocarp species in soils differing in pH, bulk density, organic matter content and elemental composition. It is difficult to assess which aspects of the soil induced these differing responses as so many aspects of soil structure and composition varied independently. An important aspect of assessing the relative importance of competition for soil resources versus tolerance of soil resource scarcity is a detailed picture of resource dynamics (Goldberg & Novoplansky 1997). Although much is known about the spatial and temporal patterns of nutrient availability in the forest understorey, information is rarely available at an appropriate scale of resolution. Further, as Silver (1994) points out, such data are rarely integrated in an ecologically meaningful way with other measures of nutrient cycling. Even less is known about plant responses to specific nutrients, both individually and in combination. Burslem and co-workers (Burslem *et al*. 1996; Gunatilleke *et al*. 1997) suggested that magnesium ions may limit the growth of dipterocarp seedlings. However, it is not possible from their manipulation studies to disentangle the effects of the cation from the counterion sulphate, thus raising the possibility that sulphate ions may limit the growth of dipterocarp seedlings in the field.

Seedlings growing in the understorey will almost always experience competition with adult trees and shrubs for scarce soil resources. Shortly after a gregarious fruiting event, while seedling densities remain high, they will also compete with each other. Just as patchiness in canopy cover may alter the relative survival probabilities of different species of tree seedling, patchiness in the availability of soil resources may also produce a mosaic of differential survival. The zones of depletion (*sensu* Huston & DeAngelis 1994) surrounding adult plants will differ in both the degree and type of nutrient depletion. In addition to looking for differential responses to nutrient additions, ecologists should turn their attention to differences in the ability of species to survive and grow in the face of nutrient deficits and the mechanisms that they might employ. All dipterocarp seedlings are ectomycorrhizal and in heavily shaded environments the relative benefits of enhanced nutrient capture and costs of carbon supply to the symbiont may be finely balanced. Furthermore, not all interactions in the forest understorey should be considered to be competitive. It has been demonstrated in northern boreal forests that ectomycorrhizal networks are capable of transferring nutrients and carbon between species (Simard *et al*. 1997). It is not known whether or not such processes occur in dipterocarp forests, but if they do, then facilitation as well as competition may play a role in determining the dynamics of seedling banks.

The effects of herbivory on dipterocarp seedling survival in the forest understorey are also poorly described. Relatively low levels of leaf area loss are observed on natural seedlings, however, this disguises the highly skewed distribution of damage among leaves. Furthermore, other types of herbivory may have greater impact than leaf area loss. Herbivory may be highly variable in space and time, and only long-term monitoring of seedling banks is likely to reveal its true importance. We have monitored seedling survival after the gregarious fruiting of dipterocarps at Danum Valley in 1996–1997 and have found a significant relationship (Mann–Whitney, $p < 0.01$) between leaf-area loss and seedling survival in two out of four forest sites. Furthermore, a root-boring beetle (Coleoptera: Platypodidae) was found to attack between 9 and 85% of all seedlings of *Parashorea malaanonan*. A significantly greater proportion of *P. malaanonan* seedlings that died during our survey had been attacked than in the population of this species in general. The study was undertaken at the height of the 1998 El Niño Southern Oscillation. It is possible that only those seedlings of *P. malaanonan* that were drought stressed were vulnerable to pin-hole borer attack. The interaction of this extreme climatic event with an essentially unpredictable and spatially heterogeneous insect pest outbreak has had a large influence on the structure of the seedling bank in this part of the forest.

4. CONCLUSIONS

We propose that when gaps are formed shortly after a gregarious fruiting event then the outcome of interspecific competition in the gap environment will be determined both by intrinsic competitive ability and initial seedling size. However, the longer the period before gap creation, the fewer the species remaining in the seedling bank and the less important competitive interactions will become. As Brown & Whitmore (1992) reported, the dominant species in the seedling bank will simply be those that are able to persist in the forest understorey. If the rate of forest turnover does not change over time and the intervals between gregarious fruiting events are unpredictable but typically exceed the persistence of the most competitive species, this provides a special case of dispersal limitation that will enhance species coexistence. Our observations and experiments suggest that small interspecific differences amongst sympatric dipterocarp seedlings lead to substantial differences in survival probabilities in the forest understorey. In gaps they are often obliterated by the asymmetry of competition for light.

We have provided a range of examples of how differences in seedling persistence in forest canopy shade are highly influenced by species-specific biotic and abiotic interactions. Ashton (1998) has called for greater research effort to integrate leaf-level physiology, whole-plant life-history attributes and population dynamics. We reiterate the need for such research, particularly in the context of stress-tolerance in the forest understorey.

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