Journal of Tropical Ecology (2002) 18:645–658. With 3 figures. Copyright © 2002 Cambridge University Press
DOI:10.1017/S0266467402002420 Printed in the United Kingdom

A decade of canopy-tree seedling survival and growth in two Bornean rain forests: persistence and recovery from suppression

LISA J. DELISSIO*[1], RICHARD B. PRIMACK†, PAMELA HALL‡ *and* H. S. LEE§

**Salem State College, Department of Biology, 352 Lafayette Street, Salem, MA 01970, USA*
†Boston University, Department of Biology, Boston, MA 02215, USA
‡Aarhus University Herbarium, Building 137, Universitesparken, DK-8000 Aarhus C, Denmark
§Forest Department, 93660 Kuching, Malaysia

(Accepted 3rd September 2001)

ABSTRACT. The population dynamics of 8500 shade-tolerant tree seedlings of 13 tree species were followed for 10 years at rain forests in Lambir Hills National Park and Bako National Park, Malaysian Borneo. Since these dipterocarp forests have lower rates of canopy gap formation than do rain forests elsewhere, tree seedling biology was predicted to differ. Approximately 50% of seedlings present in 1986 were still alive in 1996. Seven out of thirteen had seedling populations composed predominantly of individuals that were at least 10 years old. These seedlings can undergo alternating periods of relatively rapid and slow growth. Many seedlings that grew rapidly in the first census interval survived through a period of suppression in the second census interval, and conversely many seedlings with a history of suppression had exceptionally high growth in the final census interval. Seedlings of South-East Asian forest tree species are long-lived and appear to be adapted to long periods of suppression in the understorey.

KEY WORDS: age structure, dipterocarps, growth, Lambir Hills National Park, mortality, population dynamics, resilience, Sarawak, shade-tolerant tree seedlings, tropical rain forest

INTRODUCTION

In the species-rich, aseasonal, lowland forests of Borneo, shade-tolerant trees of the Dipterocarpaceae, the dominant tree family, as well as canopy trees of several other families, display gregarious flowering events at intervals of approximately 2–11 y (Appanah 1985, Ashton 1988, Curran *et al*. 1999, Wich & van Schaik 2000, Wood 1956). Mast-fruiting, the supra-annual production of

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[1] Corresponding author. Email: lisa.delissio@salemstate.edu

fruits, follows. This masting yields large numbers of seeds, up to 115 000 per individual dipterocarp (Ashton 1988). The seeds that survive germinate within weeks resulting in dense seedling populations with clumped distributions (Ashton 1969, Curran & Webb 2000, Fox 1967, Itoh 1995). Seedling mortality rates tend to be high initially, decreasing over 3–4 y (Barnard 1956, Curran & Webb 2000, Delissio 2000, Itoh *et al*. 1995, Wyatt-Smith 1958).

Most shade-tolerant tree seedlings require light from canopy gaps for survival and growth into canopy-sized trees (Platt & Strong 1989, Swaine & Whitmore 1988). For example, at La Selva tropical rain forest in Costa Rica, approximately 75% of canopy tree species must experience canopy gaps in order to reach maturity (Hartshorn 1978). Periodic large-scale disturbances such as hurricanes and cyclones, earthquakes, fires and volcanism are important determinants of forest dynamics and structure in the rain forests of the Caribbean region, Panama, Hawaii, New Guinea, Australia, the Solomon Islands, and many parts of South-East Asia, including northern and eastern Borneo (Adams 1992, Arriaga 2000, Beaman *et al*. 1985, Brokaw & Walker 1991, Clark 1990, Crow 1980, Garwood *et al*. 1979, Putz & Milton 1982, Vitousek *et al*. 1993, Walker 1991, Whitmore 1989, 1998). These disturbances result in snapped trunks and uprooted trees which create gaps in the forest canopy that allow light to penetrate into the understorey.

In contrast to other South-East Asian or neotropical forests, the primary rain forests of Sarawak in north-west Borneo have a lower incidence of large-scale natural disturbances. While fires and dry periods do occur (Baillie 1976, Brünig 1969), extended droughts are rare (Nakagawa *et al*. 2000, Walsh 1996). Trees in these forests are more likely to die standing and fall apart in place (Ashton & Hall 1992, Gale 2000, Hall 1991), creating smaller, shorter-lived gaps (Whitmore 1978). Moreover, in at least one of two forests considered in this investigation (Lambir Hills National Park), gaps form at a relatively slow rate, 0.1% of the total area y^{-1} (Ohkubo *et al*. submitted), compared with rates of 0.7–2.9% y^{-1} in neotropical forests and in the forests of French Guiana (Clark 1990, van der Meer 1995). The most important form of disturbance in Lambir is likely to be the rare catastrophic landslides that occur on steep slopes as a result of heavy rains (Ohkubo *et al*. 1995).

The relative rarity of treefall events in the forests of north-west Borneo, and the subsequent rarity of canopy gaps, may have important implications for the evolution of life history characteristics in shade-tolerant tree species, and for the maintenance of high species diversity in these forests. Moreover, the lowland dipterocarp forests of South-East Asia are of interest to evolutionary ecologists because of their unusually high numbers of coexisting, closely related tree species (Ashton 1969, Whitmore 1984, 1995) which also form the basis of the South-East Asian timber industry. Therefore, the information from long-term census work has important ecological and economic implications.

METHODS

Study sites

The research sites for our study are located within two large forest reserves in the Malaysian state of Sarawak: Lambir Hills National Park and Bako National Park. In 1965, Ashton (Ashton & Hall 1992), established these sites for an on-going long-term study of mature trees. Each site has four permanent 0.6-ha plots numbered 1–4 at Lambir and 2–5 at Bako. The plots at Lambir are situated on a mosaic of sandy humult ultisols to udult clay ultisols (Ashton & Hall 1992, Palmiotto 1998). The plots at Bako are on sandy humult ultisols (Ashton & Hall 1992, Hall 1991). The research plots at Lambir and Bako span altitudinal ranges of 360–450 m asl, and 30–75 m asl respectively (Hall 1991).

The research plots were established in mature forest in 1965. Data collected from these plots over the 1965–1985 period were used to analyse forest structure and community composition (Ashton & Hall 1992, Hall 1991, Primack & Hall 1992). Since 1965, they have accumulated gaps (Ashton & Hall 1992). The plots at Bako appear to be recovering from a large-scale disturbance, perhaps a drought (Hall 1991, Primack & Hall 1992), and Plots 3 and 4 appear to be recovering from more recent smaller-scale disturbances (L. Delissio, *pers. obs.*). Bako is a relatively low-stature forest with a high density of smaller trees, and the number of smaller trees is declining as the canopy increases in biomass. The forest at Lambir is of higher stature, and is relatively stable in stand structure compared with Bako. No large-scale disturbances occurred in the research plots during this study.

The Lambir plots are now embedded in a 52-ha long-term research plot, established for the investigation of tree demographics and reproductive ecology (Davies *et al*. 1998, Itoh *et al*. 1997, Lee *et al*. 1995, Yamakura *et al*. 1995). For trees $\geqslant$ 10 cm in diameter at breast height (dbh), this forest is among the most species-rich forests in the world (Condit 1995).

Study species

The 13 study species (seven at Bako and six at Lambir) selected in 1986, are shade-tolerant climax species as defined by Swaine & Whitmore (1988). Four dipterocarp species were included because of their importance to the ecology of these forests. The following criteria were applied to select species: (1) trees of the species were common within the site; (2) seedlings of the species could be identified in the field; and (3) the species was of ecological or silvicultural importance (Hall & Primack 1987).

The focal species at Bako included *Artocarpus odoratissimus* Blanco, *Cotylelobium melanoxylon* (Hook. f.) Pierre, *Dryobalanops beccarii* Dyer, *Gonocaryum minus* Sleum., *Pimelodendron griffithianum* (Muell. Arg.) Benth. and *Swintonia schwenkii* (Teijsm. & Binn.) Teijsm. & Binn. (Table 1). The focal species at Lambir included *Allantospermum borneensis* Form., *Dipterocarpus globosus* Vesq., *Elateriospermum tapos* Bl., *Mangifera parvifolia* Boerl. & Koord., *Mangifera pentandra* Hook., *Shorea beccariana* Burck, and *Whiteodendron moultonianum* (W.W. Sm.) Steen. (Table 1). Fieldwork showed that some *S. beccariana* juveniles are morphologically indistinguishable from those of *Shorea amplexicaulis* Ashton (see Ashton 1969). The two species are combined in this analysis and referred to as *Shorea beccariana*. In previous reports, *M. parvifolia* was referred to by its synonym, *Mangifera havilandii*.

Census

In six 100-m × 60-m plots (three at Lambir and three at Bako), four 2-m × 100-m seedling transects spaced 10 m apart were established (Hall & Primack 1987). Two plots that were irregular in shape (Plot 4 which runs along a ridge at Lambir and Plot 2 at Bako) had a different arrangement of 2-m-wide transects, but the same total transect area as the 100-m × 60-m plots. Each transect was divided into 10-m sections marked by permanent pegs. Both sites had transects that were offset to avoid trails. The total census area at Lambir was 3200 m^2. At Bako, some transects were shortened to avoid trails for a total census area of 3000 m^2. All eight plots were sampled at each of the four censuses (1986, 1988, 1990 and 1996).

Seedlings were defined as individuals with a main stem $<$ 1 cm dbh and $\geqslant$ 20 cm in height. All seedlings of the study species within the transects were censused. Each seedling was mapped and labelled with a permanent nursery tag. Seedlings within the sampling area that had recently attained 20 cm were added at each census. Positive growth was recorded, as was lost height due to dieback and breakage. *Dryobalanops beccarii* recruits only were subsampled within three of the plots at Bako in 1996 due to their large numbers. The total area sampled for *D. beccarii* recruits in 1996 was 1970 m^2.

Analysis

Growth rates were calculated as the difference in height divided by the difference in the decimal dates of the censuses. Median and maximum annualized growth rates (cm y^{-1}) were calculated for seedlings present in 1986 that survived to 1996 and that had a net positive change of height over that interval. The proportion of seedlings surviving was calculated as the difference between the number of seedlings present in 1986 and the number of this set that had died as of 1996 divided by the number of seedlings present in 1986. Seedlings that had advanced to the sapling size class ($>$ 1 cm dbh) were counted as surviving.

RESULTS

At the 1986 census 4622 seedlings were tagged. Of this initial set, 2373 were alive and seedling-sized at the 1996 census. For all species from both sites

Table 1. Study species, sample sizes and population densities of seedlings of each species present at the 1986 census, and sample sizes and population density of recruits of each species at the census in which they were initially tagged (1988, 1990 or 1996). Most species did not occur in all plots.

Species/Family			N	Population density (seedlings per m^2) by plot			
Lambir				2	3	4	5
Allantospermum borneensis	Recruits:	1986	205	—	0.070	0.158	0.029
Ixonanthaceae		1988	18	—	0.010	0.008	0.006
		1990	3	—	0.000	0.001	0.003
		1996	301	—	0.150	0.093	0.033
Dipterocarpus globosus	Recruits:	1986	1881	—	0.334	1.095	0.923
Dipterocarpaceae		1988	105	—	0.026	0.04	0.056
		1990	22	—	0.001	0.018	0.009
		1996	51	—	0.014	0.026	0.009
Elateriospermum tapos	Recruits:	1986	17	—	0.003	0.009	0.010
Euphorbiaceae		1988	137	—	0.008	0.004	0.160
		1990	2	—	0.000	0.000	0.003
		1996	2	—	0.000	0.000	0.003
Mangifera parvifolia	Recruits:	1986	232	—	0.091	0.093	0.106
Anacardiaceae		1988	15	—	0.009	0.003	0.008
		1990	37	—	0.006	0.035	0.005
		1996	44	—	0.009	0.039	0.005
Mangifera pentandra	Recruits:	1986	78	0.098	—	—	—
Anacardiaceae		1988	2	0.003	—	—	—
		1990	0	0.000	—	—	—
		1996	0	0.000	—	—	—
Shorea beccariana	Recruits:	1986	536	—	0.170	0.205	0.295
Dipterocarpaceae		1988	89	—	0.035	0.024	0.006
		1990	18	—	0.000	0.008	0.015
		1996	290	—	0.193	0.024	0.015
Whiteodendron moultonianum	Recruits:	1986	359	—	0.329	0.018	0.103
Myrtacaceae		1988	72	—	0.048	0.000	0.043
		1990	15	—	0.008	0.001	0.010
		1996	33	—	0.025	0.000	0.010
Bako				1	2	3	4
Artocarpus odoratissimus	Recruits:	1986	21	0.005	0.003	0.007	0.014
Moraceae		1988	13	0.005	0.001	0.004	0.007
		1990	4	0.000	0.004	0.001	0.000
		1996	1	0.000	0.000	0.001	0.000
Cotylelobium melanoxylon	Recruits:	1986	186	0.064	0.024	0.030	0.132
Dipterocarpaceae		1988	46	0.036	0.000	0.008	0.017
		1990	33	0.010	0.003	0.004	0.028
		1996	8	0.005	0.000	0.001	0.004
Dryobalanops beccarii	Recruits:	1986	458	0.051	0.284	—	0.289
Dipterocarpaceae		1988	41	0.009	0.007	—	0.040
		1990	17	0.001	0.012	—	0.010
		1996	1162	1.034	0.444	—	3.975
Gonocaryum minus	Recruits:	1986	148	0.123	0.061	—	0.010
Icacinaceae		1988	37	0.036	0.012	—	0.000
		1990	18	0.015	0.004	—	0.004
		1996	8	0.003	0.007	—	0.001
Pimelodendron griffithianum	Recruits:	1986	20	0.001	0.003	0.012	0.011
Euphorbiaceae		1988	8	0.001	0.005	0.000	0.004
		1990	3	0.000	0.000	0.001	0.003
		1996	0	0.000	0.000	0.000	0.000
Swintonia schwenkii	Recruits:	1986	480	—	—	0.395	0.249
Anacardiaceae		1988	88	—	—	0.070	0.043
		1990	18	—	—	0.014	0.010
		1996	201	—	—	0.158	0.113

At Lambir, 800 m^2 was sampled in each plot in every census. Transect areas sampled at Bako were as follows: Plot 1 = 780 m^2; Plot 2 = 740 m^2; Plot 3 = 760 m^2; and Plot 4 = 720 m^2, with the exception of *D. beccarii* recruits in 1996 which were sampled in Plot 3 as above and subsampled in Plots 1 (580 m^2), 2 (550 m^2) and 4 (80 m^2).

combined, the probability of survival by 10 y was 52% (Figure 1, Table 2). An additional 2962 recruits were tagged in 1988, 1990 and 1996. Fifty seedlings progressed to the sapling size-class (> 1 cm dbh) in the intervening 10 y, representing a promotion rate of around 1%. The proportion of seedlings present in 1986 that survived to 1996 was significantly greater in Lambir (57%) than at Bako (43%) ($\chi^2 = 64.7$, $P < 0.0001$) (Table 2). The proportions of seedlings surviving in each plot also differed significantly within each site (Lambir: $\chi^2 = 75.4$, $P < 0.001$; Bako: $\chi^2 = 36.3$, $P < 0.0001$). Likewise the proportions of seedlings of each species surviving differed significantly within each site (Lambir: $\chi^2 = 208$, $P < 0.0001$; Bako: $\chi^2 = 94.0$, $P < 0.0001$).

By 1996, large numbers of seedlings were at least a decade old, and probably many were much older. For seven of the 13 species (three at Bako and four at Lambir), 65–96% of seedlings present in 1996 were at least 10 y old (Figure 2).

Across sites, five of the 13 species had large seedling establishment events during the course of the 10 y study that were evident from the census work (Table 1). *Elateriospermum tapos* had a large number of new seedlings at the 1988 census. *Allantospermum borneensis*, *D. beccarii*, *S. beccariana* and *S. schwenkii* had large numbers of new seedlings at the 1996 census.

To determine if fast-growing seedlings continue to grow rapidly in successive time periods, and whether seedlings with poor growth performance can recover to grow rapidly again, we used census records of the five study species that had the largest population sizes at the initiation of the study: *Dipterocarpus globosus*, *D. beccarii*, *S. beccariana*, *S. schwenkii* and *W. moultonianum*. For each species, seedlings were ranked by their growth performance at each census. Six categories of seedling performance were described: (1) advanced to sapling: the seedling achieved 1 cm dbh; (2) rapid growth: annual growth rate (the 90th percentile of growth rates for seedlings of the same species in the census interval of interest); (3) moderate growth: annual height growth rate > 2 cm y^{-1}. (The measurement error for height was approximately ± 2 cm. The 2 cm cut-off was at the 50th percentile of positive growth for all species combined in all census intervals combined.); (4) suppressed: $|\text{change in height}| \leqslant 2$ cm y^{-1}; (5) height loss: annual height loss > 2 cm y^{-1}; (6) dead: seedling died during the census interval (Figure 3).

The fastest-growing seedlings from the 1986–1988 census interval were selected for an examination of their performance in 1988–1990. Seedlings were capable of surviving through periods of suppression or height loss after a period of fast growth (Figure 3). Of the fast-growing seedlings from the initial census interval, 25–60% showed poor performance in 1988–1990, but these seedlings survived to the end of the second census interval. Of this set of seedlings, a subset was selected that was composed of those initially fast-growing seedlings that were then suppressed or that lost height in 1988–1990. These seedlings were assessed for their performance in the 1990–1996 census interval. Of these fast-growing seedlings that had become suppressed or lost height, 21–63%

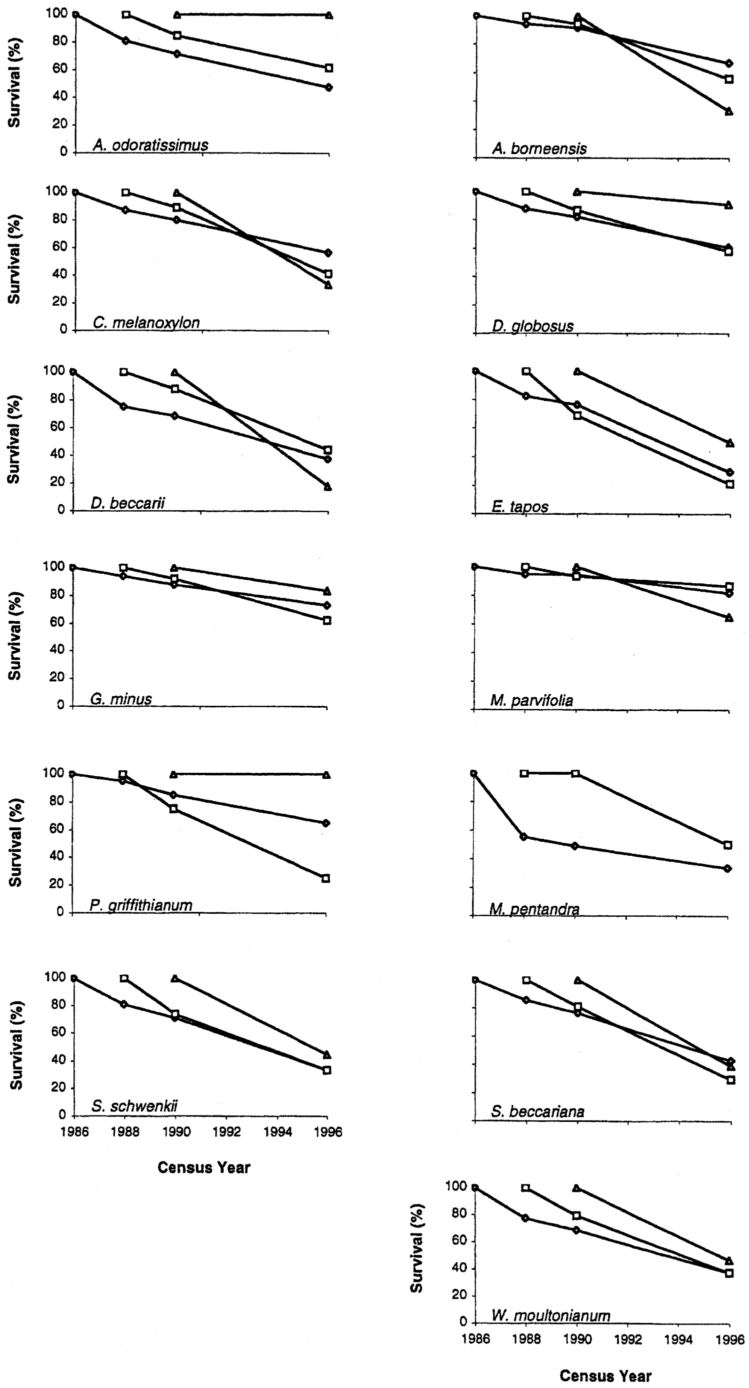

Figure 1. Survivorship of 13 shade-tolerant species in two mixed dipterocarp forests. Survival is shown as the percentage of seedlings surviving. Initial sample sizes are the same as those given in Table 1. Diamonds represent seedlings present in 1986. Squares represent seedlings that were new in 1988. Triangles represent seedlings that were new in 1990.

Table 2. Seedling performance over 10 y as shown by proportion surviving (%), and median and maximum annualized growth rates (cm y^{-1}) for seedlings present in 1986. N for growth rates reflects only surviving seedlings with positive height change.

	Survival		Growth rate		
	N	%	N	Median	Max
Lambir					
Total	3308	56	1680	1.8	22.5
Plot 2	78	33	24	0.9	7.5
3	797	48	326	1.5	22.5
4	1261	55	632	1.7	11.0
5	1172	65	698	2.1	12.0
Allantospermum borneensis	205	67	113	1.4	14.2
Dipterocarpsu globosus	1881	61	1059	2.0	22.5
Elateriospermum tapos	17	29	5	1.0	3.2
Mangifera parvifolia	232	81	176	1.4	6.8
Mangifera pentandra	78	33	24	0.9	7.5
Shorea beccariana	536	43	184	2.0	12.0
Whiteodendron moultonianum	359	37	119	1.0	15.8
Bako					
Total	1314	43	433	2.0	20.0
Plot 1	191	42	70	1.8	20.0
2	277	65	59	1.6	7.5
3	338	64	104	1.5	13.9
4	507	53	200	2.5	15.9
Artocarpus odoratissimus	21	48	8	2.9	9.4
Cotylelobium melanoxylon	186	55	73	2.4	20.0
Dryobalanops beccarii	458	38	129	3.0	15.3
Gonocaryum minus	148	73	66	1.8	6.9
Pimelodendron griffithianum	20	65	6	4.7	6.5
Swintonia schwenkii	480	33	151	1.7	15.9

began to grow again in the third census interval, some moving into the sapling size-class, and as much as 15% rejoined the rapid-growth category.

DISCUSSION

Many tropical trees, particularly in South-East Asia, have supra-annual fruiting events (Ashton 1988, Corlett 1990, Yap 1987, Yasuda *et al*. 1999), and the newly germinated seedlings have a high mortality rate (Itoh 1995, Itoh *et al*. 1995, Turner 1990). However, this high mortality rate obscures the fact that those seedlings that do become established after the initial die-off of most of their cohort are resilient and long-lived. The long-term survival of the seedlings of shade-tolerant canopy tree species in tropical forests has also been documented in Australia (Connell & Green 2000, Connell *et al*. 1984), Panama (DeSteven 1994), French Guiana (Forget 1992, 1997) and Zaire (Hart 1995). For many tree species at Bako and Lambir, the majority of seedlings are a decade or more in age, and some seedlings may even be $\geqslant$ 50 y old.

In these forests, the seedling bank is a multi-aged stand composed of individuals from multiple fruiting events, in which a seedling's height is a poor

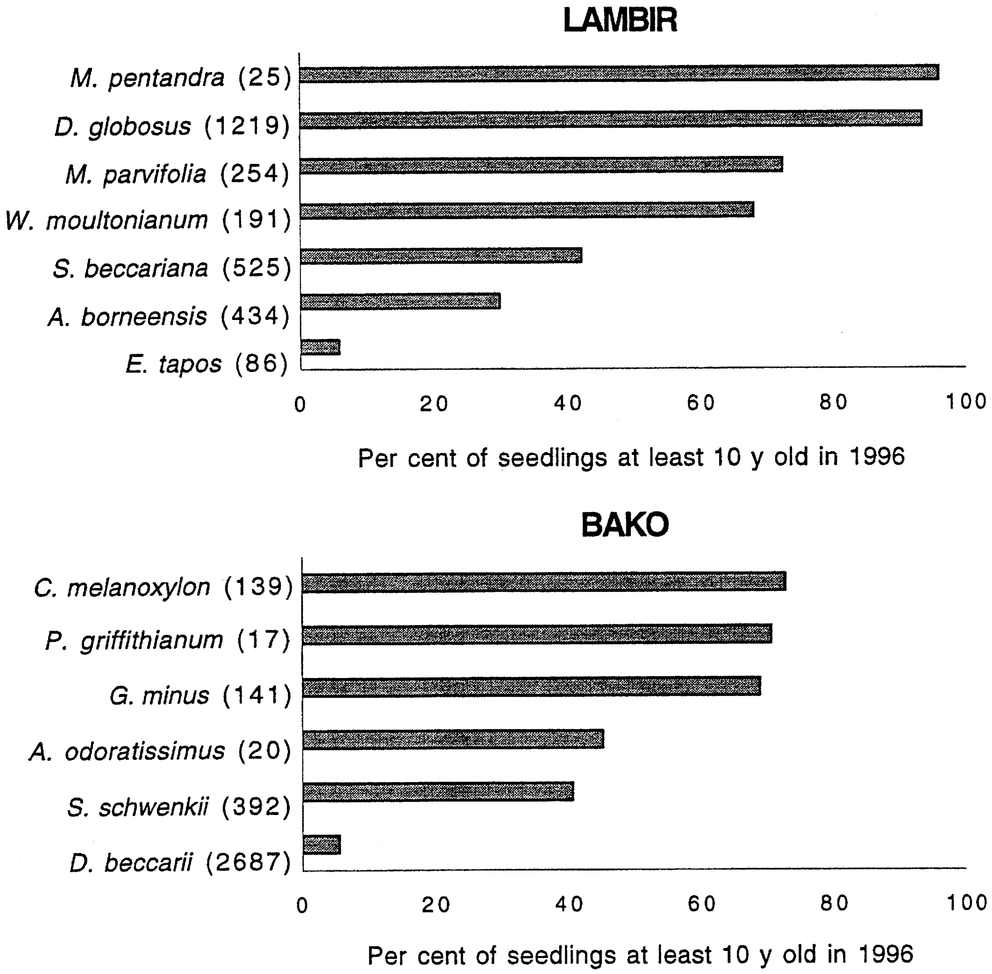

Figure 2. Per cent of all seedlings from each species that were at least 10 y old in 1996. The total number of seedlings of each species present in 1996 is given in parentheses.

predictor of its age. A small seedling that has never experienced a light gap might be from the same cohort of several decades ago as a canopy tree that germinated in a large gap and grew more quickly. The processes that take place in the understorey community determine the set of seedlings present at the time and location of gap formation (Brokaw & Scheiner 1989), and thus are critical for the regeneration of mixed dipterocarp forests.

The tree seedlings in these populations that have the fastest initial growth rates can become suppressed and survive for months or years with slow growth. The ability of seedlings to persist and grow slowly in the shaded understorey may confer a great advantage as height is a strong determinant of seedling survival and competitive ability at the time of gap formation (Brown & Whitmore 1992, Connell 1989). Furthermore, old, previously suppressed seedlings in these forests can recover from suppression to achieve short-term growth

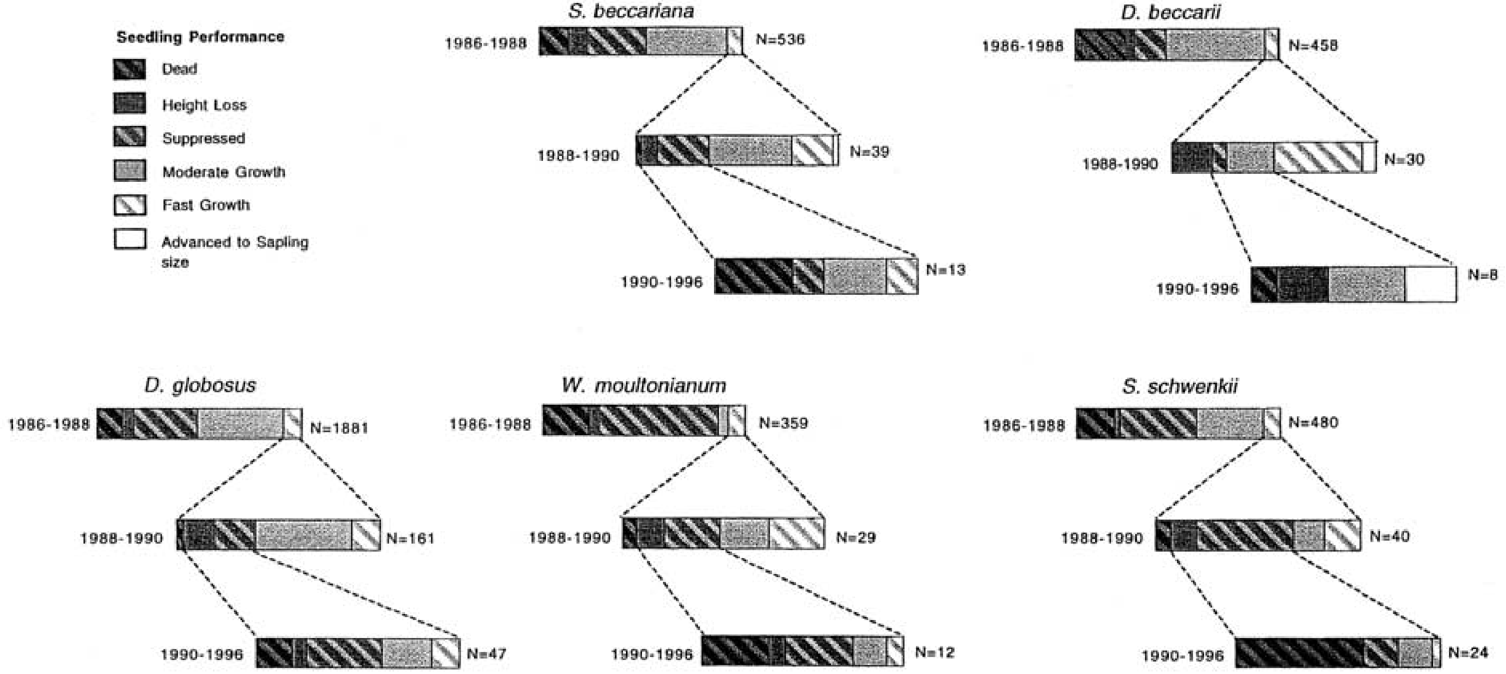

Figure 3. Alternating performance across three consecutive census intervals of seedlings tagged in the initial 1986 census. Each bar represents the relative proportions of seedlings in each of six performance rankings in census intervals ending in 1988, 1990 and 1996. The dotted lines indicate the subset of seedlings in each census interval that were examined for performance rank in the subsequent census interval. Seedlings with the highest performance rank (Rapid growth) in the first census interval were followed into the second census interval. Of these, seedlings with the poor performance ranks (Height loss or Suppressed) were followed into the third census interval.

rates equivalent to those of the fastest-growing seedlings in the population. A similar plasticity of growth rates has been noted for dipterocarp seedlings and saplings in Sabah in northern Borneo, and in Sri Lanka (Ashton & de Zoysa 1990, Moad 1992). This capacity to survive through alternating periods of fast and slow growth facilitates the persistence of seedlings over time, allowing access to a greater number of small, temporary gaps, and so should be selectively advantageous if these seedlings have a chance of reaching maturity.

These results have implications for forestry methods that require an assessment of the vigour of pre-existing seedlings before harvest and that are based on the untested assumption that older individuals in low-light environments lose their ability to respond to improved growing conditions (Ashton 1990, Poore 1968, Tang 1987). Our study provides evidence that 10-y-old seedlings that have persisted through periods of poor performance can return to rapid growth, and supports the idea that nearly all seedlings can respond to an opening in the canopy regardless of age (Liew & Wong 1973).

Space for establishment, in this case canopy gaps, allocated at random and paired with environmental variability may facilitate species coexistence (Chesson & Warner 1981, Hubbell & Foster 1986, Sale 1977). The rarity and small size of canopy gaps in these forests may enhance the importance of recruitment limitation, in this case failure to have seedlings at the site of a gap, as a controlling factor in community diversity and composition (Brokaw & Busing 2000, Hubbell *et al*. 1999, Hurtt & Pacala 1995). The ability of seedlings to persist in a suppressed state under deep shade has been cited as a possible mechanism for the maintenance of high levels of diversity in the tropical rain forest (Uhl *et al*. 1988). This ability would allow weak competitors access to gaps inaccessible to stronger competitors that happen to be recruitment limited (Brown *et al*. 1999, Wright 2002). An adaptation for the long-term persistence of seedlings could help to explain the unusually high levels of species diversity in the relatively stable forests of north-west Borneo.

ACKNOWLEDGEMENTS

We gratefully acknowledge the Forest Department of Sarawak for their kind assistance with this project. In particular, we would like to acknowledge the great contribution of Sylvester Tan in the management of census work and data. We also thank Peter S. Ashton, Adrien Finzi, Thomas Kunz and Gillian Cooper-Driver, and three anonymous reviewers for their invaluable comments on various versions of this manuscript. This work was supported by NSF Grant DEB - 9974133, in-kind support from the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute, and a grant from the Sarawak Timber Association.

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