

The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest

Lisa J. Delissio^{*†1} and Richard B. Primack[†]

^{*}Salem State College, Department of Biology, Salem, MA 01970, USA

[†]Boston University, Department of Biology, Boston, MA 02215, USA

(Accepted 30th August 2002)

Abstract: In the first 3 mo of 1998, an aseasonal tropical rain forest at Lambir Hills National Park on the north-west coast of Borneo suffered an unusually severe drought. Extreme climatic events such as this one are expected to influence tree population structure and community dynamics through differential effects on growth and mortality. The demographics of seedlings of seven shade-tolerant tree species, including two dipterocarps, during this severe drought were contrasted with baseline demographic data from two earlier census intervals, one of which included a slight drought, and one of which included no drought. Hemispherical photographs were used to document an opening of the canopy that resulted from the dieback and mortality of large trees during the severe 1998 drought. Seedlings that experienced an increase in canopy openness were less likely to die than other seedlings. Rates of mortality and height loss were significantly increased in association with drought. The overall mortality rates during the severe drought and slight drought census intervals were $8.2\% \text{ yr}^{-1}$ and $7.3\% \text{ yr}^{-1}$ respectively, compared with $4.9\% \text{ yr}^{-1}$ for the non-drought census interval. The incidence of height loss during the severe drought census interval was 27.5%, compared with rates of 11.7% and 20.1% for earlier census intervals. Dipterocarp species were less affected than some non-dipterocarp species, and the smallest seedlings suffered the greatest impact. If droughts in this region continue to increase in intensity and severity, they may ultimately cause a change in the species population densities and stand structure of the understorey seedling community of this rain forest.

Key Words: Dipterocarps, El Niño Southern Oscillation Event, height loss, Lambir Hills National Park, mortality, population dynamics, Sarawak, shade-tolerant tree seedlings, tropical rain forest

INTRODUCTION

Local and global land-use transformations, habitat fragmentation, greenhouse gas emissions, and alterations to the hydrogeological cycle are all expected to contribute to a change in climate characterized by increasingly extreme weather (Intergovernmental Panel on Climate Change Working Group I 2001). In the context of concerns over global climate change and its impact on tropical rain forests (Markham 1998, Primack & Hall 1992, Whitmore 1989), it is noteworthy that the El Niño Southern Oscillation (ENSO) droughts in South-East Asia have been increasing in frequency and intensity over recent decades (Salafsky 1998, Walsh 1996). ENSO-associated events, including droughts, are likely to become more frequent and more extreme (Meehl 1997, Timmerman *et al.* 1999). Non-drought years may be essential for the production of a substantial population of seedlings to supply the replacements for canopy trees when they die (Becker *et al.* 1998).

Therefore, seasonality, a change in the climate, or an extreme climatic event can have a measurable impact on tree population density, biomass turnover rates, stand structure, species distributions, phenology, or community composition (Bawa & Dayanandan 1998, Burgess 1969, Corlett & LaFrankie 1998, Goldammer & Price 1998, Kudo & Kitayama 1999, Phillips & Gentry 1994, Tang & Chong 1979, Turner & Whitmore 1991, Veenendaal & Swaine 1996, Woods 1989).

From mid-January to mid-April 1998 the lowland dipterocarp rain forest at Lambir Hills National Park (LHNP) in the Malaysian state of Sarawak on the island of Borneo suffered one of the most severe droughts that it has experienced this century (Harrison 2000, Nakagawa *et al.* 2000). The lowland dipterocarp forests of South-East Asia are important ecologically and economically because these forests have unusually high numbers of coexisting, closely related tree species, many of which are timber trees in the dipterocarp family (Ashton 1964, Whitmore 1984, 1995). In terms of trees, the forest at LHNP may be the most species-rich forest in the world (Condit 1995). In this ENSO-associated drought, total

¹ Corresponding author: Department of Biology, Salem State College, 352 Lafayette St., Salem, MA 01970, USA. Email: lisa.delissio@salem-state.edu

rainfall at LHNP from January–March 1998 was less than a quarter of the mean rainfall for these 3 mo (Nakagawa *et al.* 2000). As a result of the 1998 drought, there was an increase in the mortality rates of trees in this forest (Nakagawa *et al.* 2000). During the drought, tree mortality rates were 5–7 times the tree mortality rates during a pre-drought period. Dipterocarp trees at LHNP were disproportionately affected by the severe 1998 drought, with mortality rates 12–30 times higher than during the earlier non-drought period. In addition, the drought also caused the local extinction of insect pollinators of *Ficus* spp. (Harrison 2000). The effects of this drought were also evident in Bornean heath forest and in summit vegetation on Mt. Kinabalu (Kudo & Kitayama 1999).

Tree seedlings in neotropical rain forests have shown increased mortality rates after only 1 mo with rainfall < 100 mm (Hartshorn 1992). Moreover, the seedlings (by our size-class definition) of some tree species in Bornean heath forest showed evidence of water stress during the same 1998 drought (Cao 2000). Additionally, the mortality of large trees can cause an opening in the forest canopy, allowing light into the understorey, possibly affecting natural regeneration processes (Hartshorn 1978).

The effect of an extended dry period on seedling demographics in aseasonal tropical forest has remained for the most part uninvestigated (Whitmore 1998). Most studies of the impact of drought on tropical tree seedlings lack pre-drought demographic data, creating difficulty in the interpretation of post-drought data (Becker & Wong 1994, Leighton & Wirawan 1986). In the study reported here, we had collected 10 y of data on seedling growth and mortality prior to the 1998 drought for seven shade-tolerant tree species, and performed assessment of understorey light availability. This 10-y study period included two census intervals of comparable length to the census interval that included the severe 1998 drought. One of these census intervals included a slight drought, and the other had no drought. An additional seedling census and a second set of light measurements taken after the severe 1998 drought were used in combination with these baseline data to determine the effects of drought on natural regeneration processes in this forest. Long-term studies such as this one are important because they can show whether a forest is affected by changes in climate, changes that do not respect a forest's protected status (Primack 1992). In this study, drought takes the form of a natural experiment, making it possible to evaluate the impact of drought on a set of shade-tolerant seedlings.

STUDY SITE AND SPECIES

History of the plots

The study focused on the population dynamics of tree seedlings before and during a severe drought at a forest

reserve at Lambir Hills National Park (LHNP) ($4^{\circ}20'N$, $113^{\circ}50'E$) near the north-coast town of Miri, in the Malaysian State of Sarawak, Borneo. Droughts of this severity are uncommon in this region, and the 1998 drought was expected to affect the rates of seedling growth and mortality.

In 1965, the Sarawak Forest Department established research sites in Borneo for an on-going long-term study of trees ≥ 10 cm diameter at breast height (130 cm above the point of emergence from the ground) (Ashton & Hall 1992). The LHNP research site has four permanent plots, numbered 2–5, each 0.6 ha in area. Plots 2, 3 and 5 are 100 m \times 60 m, and Plot 4 is 20 m \times 300 m (Hall & Primack 1987).

A large amount of background material on the soils, hydrology, vegetation, tree demography and systematics of this forest has been published (Ashton 1969, Ashton & Hall 1992, Baillie *et al.* 1987, Hall 1991, Palmiotto 1998, Primack & Hall 1992). Data collected from the 0.6-ha plots over the 1965–1985 period were used to analyse forest structure and community composition (Ashton & Hall 1992, Hall 1991, Primack & Hall 1992). The forest canopy is 35–40 m in height, and the forest itself is moderately stable in stand structure in comparison with other mixed dipterocarp forests in Sarawak. A 52-ha long-term research plot at the site is producing extensive information on reproductive ecology and tree demographics (for example Ashton 1996, Davies 2001, Davies *et al.* 1998, Itoh *et al.* 1997, Lee *et al.* 1995, Yamakura *et al.* 1995). The 52-ha plot was superimposed on the long-term research plots described here, so that Plots 2, 3 and 5 and approximately half of Plot 4 are included in the larger plot.

Climate

The climate in this region is considered aseasonal, but has annual variation in rainfall, with the wettest season normally beginning in September and ending in January (Brünig 1969). It rains almost every day, even during the drier months. While annual rainfall totals are typically high, the temporal distribution of rainfall can be quite variable leading to moderate, or less frequently, severe water stress for plants (Baillie 1976). While north-west Borneo has a history of short and infrequent seasonal and periodic droughts (defined as < 100 mm mo^{-1} rainfall in Brünig 1969), dry periods in Sarawak are rarely ≥ 3 mo (Walsh 1996, Walsh & Newbery 1999, Whitmore 1984). In north-west Borneo, mild moisture stress is expected to occur 30–90 d y^{-1} , and short-term severe droughts occur almost annually.

Topography and soils

The topography at LHNP is hilly and complex, with many steep slopes and occasional landslips (Yamakura *et al.*

1995). The research plots span an altitudinal range of 120 m asl. A portion of Plot 4 runs along a ridge. Palmiotto (1995, 1998) performed a detailed analysis of soil types for the 52-ha plot at this site. In his study, Palmiotto (1998) defined humult soils as those with a root-mat depth ≥ 1 cm and a soil texture of loam to sandy loam, and ultid soils as clay to loam soils without a measurable root mat. The soils in the 52-ha plot range in texture from clay loam to sandy loam. Plot 2 is dominated by deep ultid clay loam soils, with a mixture of soil types ranging from ultid to humult. Plots 3 and 5 are on a mixture of soil types that range from an intermediate type, between ultid and humult, to humult. Plot 4 is on humult ultisol (Ashton & Hall 1992). Soil texture is likely to affect floristic composition in mixed dipterocarp forests through its influence on water availability (Newbery *et al.* 1996, Palmiotto 1998). However, although seedling locations by plot were considered in the analysis, soil type itself was not considered due to the patchwork nature of the soil type distributions and our lack of knowledge concerning the soil types for individual seedlings.

Study species

Seven shade-tolerant tree species, including two species of the ecologically and economically important Dipterocarpaceae were included in the study (Table 1). All of the

study species are shade-tolerant 'climax species' as defined by Swaine & Whitmore (1988). The study species were selected such that trees of each were common within the plots, and the seedlings were easily identifiable in the field (Hall & Primack 1987). The study species 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.) V. Steen. (Table 1). Nomenclature follows Delissio *et al.* (2002).

The long-term demographics of the seedlings of the study species (1986–1996) were described in Delissio *et al.* (2002). Seedlings of the study species are exceptionally long-lived and have the ability to recover rapid growth following periods of suppression. That investigation also showed evidence of seedling establishment events. *Elateriospermum tapos* had large numbers of new seedlings at the 1988 census, and *A. borneensis* and *S. beccariana* had large numbers of new seedlings at the 1996 census. However, all of the seedlings present in 1986 were of unknown age, the ages of the new seedlings present in 1988 were known to ± 1 y, and the ages of the new seedlings present in 1996 were known to ± 3 y. Therefore, the age structures of these samples were not comparable in this analysis.

Table 1. Study species and their sample sizes for the 1986–1988 census interval (SLD), the 1988–1990 census interval (ND), the 1996–1998 census interval (SVD), and for light assessment. N is the entire sample. SN is the subset sample.

Species		N=	Number of seedlings by plot			SN=
			2	3	4	
<i>Allantospermum borneensis</i>	SLD	201	2	53	126	22
	ND	190	—	52	113	25
	SVD	64	—	22	20	22
	Light	18	—	3	9	6
<i>Dipterocarpus globosus</i>	SLD	1855	—	262	859	734
	ND	1690	—	244	734	712
	SVD	73	—	22	27	24
	Light	18	—	3	4	11
<i>Elateriospermum tapos</i>	SLD	17	—	2	7	8
	ND	807	—	9	29	769
	SVD	37	—	3	1	33
	Light	—	—	—	—	—
<i>Mangifera parvifolia</i>	SLD	229	—	72	73	84
	ND	226	—	69	68	89
	SVD	68	—	20	27	21
	Light	18	—	1	11	6
<i>Mangifera pentandra</i>	SLD	78	78	—	—	2
	ND	45	45	—	—	5
	SVD	26	26	—	—	14
	Light	—	—	—	—	—
<i>Shorea beccariana</i>	SLD	530	—	134	161	235
	ND	526	—	134	149	243
	SVD	66	—	19	24	23
	Light	20	—	—	13	7
<i>Whiteodendron moultonianum</i>	SLD	354	—	260	14	80
	ND	341	—	224	12	105
	SVD	58	—	23	9	26
	Light	10	—	—	3	7

Total area censused was 800 m², except for *E. tapos* in ND, which was sampled in 2.4 ha. The seedlings censused in ND were a subsample within the same area.

METHODS

Census

The seedlings were censused in four 0.6-ha study plots. Three of the study plots, numbered 2, 3 and 5, each had four seedling transects, measuring 2 m × 100 m. Plot 4 had three seedling transects, one 2 m × 100 m, one 2 m × 240 m, and one 2 m × 60 m, for the same total length in all plots. The plots were also divided into 10-m × 10-m quadrats. At each census, seedlings of the study species were mapped and labelled with permanent identification tags. Seedlings were defined as individuals ≥ 20 cm in height and < 1 cm in stem diameter at 130 cm above the ground. Height, and survival or mortality, were recorded at each census. New recruits were added to the study at each census.

To increase sample size, the seedlings of *E. tapos* only were censused in the quadrats in 1988 and 1990 only. The seedlings of all study species were censused in the transects in 1988, 1990 and 1996. The 1996–1998 census included 392 seedlings randomly selected from the seven study species, with the objective of sampling 25–75 seedlings per species (Table 1). Due to the subsampling procedure used in 1998, it was impossible to examine changes in seedling densities that may have resulted from the 1998 drought. Seedlings from this set were also assessed for rates of herbivory, leaf life spans and changes in above-ground biomass for the 1996–1998 census interval (Delissio & Primack, in preparation).

Canopy assessment

Light environments were assessed for 84 seedlings randomly selected from the five study species with the largest population sizes (*A. borneensis*, *D. globosus*, *M. parvifolia*, *S. beccariana* and *W. moultonianum*). These species did not occur in Plot 2, so light measurements refer to Plots 3, 4 and 5 only. These 84 seedlings were randomly selected from the set of seedlings described above, with the objective of sampling 10–20 seedlings per species (Table 1).

Each seedling's light environment was recorded through the use of hemispherical photography during the 1996 and 1998 field seasons. For seedlings that were dead at the 1998 census, a light measurement was recorded at the seedling's former location and height. A Pentax K1000 camera with a Sigma hemispherical lens was mounted on a tripod directly over the apex of each seedling. The digitized images were analysed using Solarcalc software for the Macintosh (Chazdon 1992, Chazdon & Field 1987).

Weighted canopy openness (WCO) and the length of direct irradiance per day (min d⁻¹) (LDI, also referred to as MDIR in Chazdon 1992, Chazdon & Field 1987, Nicotra *et al.* 1999) were calculated. WCO is a measure of

diffuse light that is more sensitive to gaps that are directly overhead (Nicotra *et al.* 1999). LDI represents the amount of light received by a seedling as a weighted average over 10 d (solar tracks). Neither of these measures accounts for a likely decrease in light availability caused by hazy conditions that occurred in this region during the end of the drought (Cao 2000, Laumonier & Legg 1998).

Census dates and drought

Seedlings were censused on the following dates: 23–18 August 1986, 23–27 July 1988, 24–28 June 1990, 10 March–29 May 1996, and 30 May–21 June 1998. The 1986, 1988 and 1990 censuses were carried out by P. Hall, R. Primack and the Sarawak Forest Department. L. Delissio and the Sarawak Forest Department performed the 1996 census. L. Delissio carried out the 1998 census.

One slight drought (3-mo shifting average rainfall (SAR) < 100 mm) occurred during the 1986–1988 census interval. The 3-mo SAR for December 1986–February 1987 was 86 mm mo⁻¹, and the 3-mo SAR for January 1987–March 1987 was 93 mm mo⁻¹ (M. Nakagawa, unpubl. data; Nakagawa *et al.* 2000). The 1986–1988 census intervals for individual seedlings included 4 mo with drought and 19–20 mo without drought. There were no periods of slight or severe drought during the 1988–1990 census interval (Nakagawa *et al.* 2000).

A slight drought plus a severe drought (3 mo SAR < 50 mm) both fell within the 1996–1998 census interval. The slight drought (3 mo SAR = 95 mm) occurred from March–May 1997 (Nakagawa *et al.* 2000). The severe drought (mean monthly rainfall = 46 mm) occurred from January–March 1998 (Nakagawa *et al.* 2000). In contrast, the mean monthly rainfall for January–March, based on 14 y of data prior to the drought, was 192 mm (Nakagawa *et al.* 2000). The severe 1998 drought was associated with an El Niño Southern Oscillation (ENSO) event. The census intervals for individual seedlings from 1996–1998 included 3 mo with slight drought, 3 mo with severe drought and 18–21 non-drought months.

Analytical techniques

In order to address issues of repeated measures while comparing mortality and incidence of height loss across census intervals, the data set was subsetted such that a unique set of transect segments was considered for each census interval. For example, for the 1986–1988 census interval, seedlings in the 1st, 4th and 7th sections of the first transect of each plot were included, while for the 1988–1990 census interval the 2nd, 5th and 8th sections of the first transect were included (Table 1). The order of the sections selected for a census interval alternated

between transects within a plot. Regression analyses that contrasted parameters across census intervals employed these subsets, as did calculations of these parameters by census interval for pooled data. After subsetting, the 1986–1988 and 1996–1998 census intervals had low sample sizes of *E. tapos*. For this reason, *E. tapos* was excluded from regression equations that predicted mortality or height loss across census intervals when species was included as an independent variable. The entire sample (not subsetted) was used for comparisons and calculations within census intervals.

Mortality rates for heterogeneous populations have been shown to decrease artificially with increasing duration of census intervals (Sheil & May 1996). The artificial decrease occurs because high-risk individuals tend to die early in the census interval, leaving those individuals with a lower risk of mortality. For this reason, only census intervals of roughly equal lengths were employed for comparisons involving mortality. Mortality rates were calculated as mortality per year, m , where m is defined as:

$$m = 1 - (N_1/N_0)^{1/t}$$

in which N_0 and N_1 are respectively the number of seedlings of a given species that are alive at the beginning and end of a time interval, t . This formula provides the most appropriate measure of annual mortality rates for situations in which mortality rates are high, as would be expected for seedlings, especially during a drought (Sheil *et al.* 1995). The time interval t was defined as the arithmetic mean of the time between census measurements for the individual seedlings of each species (cf. Condit *et al.* 1995). Exact census dates were recorded for each seedling and were utilized in the calculation of t . Values of t within a set of seedlings did not differ by more than 44 d. The normal approximation to the binomial variance was used to calculate 95% confidence limits for the absolute number of seedlings that died, which was then used to calculate limits for mortality rates (cf. Condit *et al.* 1995).

Standard least-squares regression was used to predict the natural logarithm of WCO or the natural logarithm of LDI from census year, plot, species and the natural logarithm of seedling height ($\ln \text{height}$). A Wilcoxon signed-rank test for paired differences was used to test for changes in WCO and LDI from 1996–1998, for all plots combined, and on a plot by plot basis. In addition to mortality, the incidence of height loss was examined because it could be a more sensitive indicator of water stress or breakage caused by falling debris. Nominal logistic regression models were used to predict mortality or the incidence of height loss from multiple factors, including species, plot, $\ln \text{height}$, and change in WCO. Nominal regression is a method of maximum likelihood estimation where the basic random variable of interest is a dichotomous variable with a binomial distribution. Chi-square tests were used to compare the frequency of mortality across

census intervals, and to predict mortality or the occurrence of height loss within census intervals from the categorical variables of species and plot. All statistical tests were performed using JMP statistical software package for the Macintosh (SAS Institute Inc. 1998).

RESULTS

Seedling canopy environment

The least-squares regression predicting the natural logarithm of weighted canopy openness (ln WCO) from census year, plot, species and the natural logarithm of seedling height ($\ln \text{height}$) was highly significant ($R^2 = 0.173$, $n = 168$, $df = 7$, $P < 0.0001$). Similarly, the regression predicting the natural logarithm of min direct irradiance d^{-1} in 1996 (ln LDI 1996) from census year, plot, species, and $\ln \text{height}$ was highly significant ($R^2 = 0.293$, $n = 168$, $df = 7$, $P < 0.0001$). In both cases, census year and plot were the only significant independent variables. The increases in each of these measures indicate a potential increase in light availability from 1996–1998. For all species in all plots combined, the median WCO in 1998 was 1.23 times the median WCO in 1996, and the median LDI 1998 was 1.28 times the median LDI in 1996 (Figure 1). For individual seedlings, the values for WCO in 1996 and in 1998 lay in the range 5–18% and 3–27% respectively. LDI in 1996 and in 1998 was 27–118 min, and 28–366 min, respectively. In both 1996 and 1998, median values for WCO and LDI were highest in Plot 4, which runs along a ridge and along a trail in places (Table 2).

Seedling demographics

Mortality rates The logistic regression model predicting seedling mortality from census interval, plot, species and $\ln \text{height}$, was statistically significant ($\chi^2 = 114$, $df = 8$, $P < 0.0001$), with all independent variables making a significant contribution to the model. *Mangifera pentandra* was considered separately because it occurred only in Plot 2. The logistic regression model predicting *M. pentandra* seedling mortality from $\ln \text{height}$ and census interval was not statistically significant ($\chi^2 = 5.47$, $df = 3$, $P = 0.141$).

Both the 1996–1998 census interval that included both a slight and a severe drought (SVD), and the 1986–1988 census interval that included a slight drought (SLD), had a significantly greater frequency of mortality than did the 1988–1990 census interval that included no drought (ND) (ND vs. SVD: $\chi^2 = 4.27$, $df = 1$, $P = 0.039$; ND vs. SLD: $\chi^2 = 10.3$, $df = 1$, $P = 0.001$) (Figure 2a). There was no difference between mortality in the SLD and SVD census intervals ($\chi^2 = 0.80$, $df = 1$, $P = 0.362$). The SLD, ND and SVD census intervals had overall mortality rates of 7.3% y^{-1} , 4.9% y^{-1} and 8.2% y^{-1} respectively (Table 2).

Mortality differed by plot in the SLD census interval

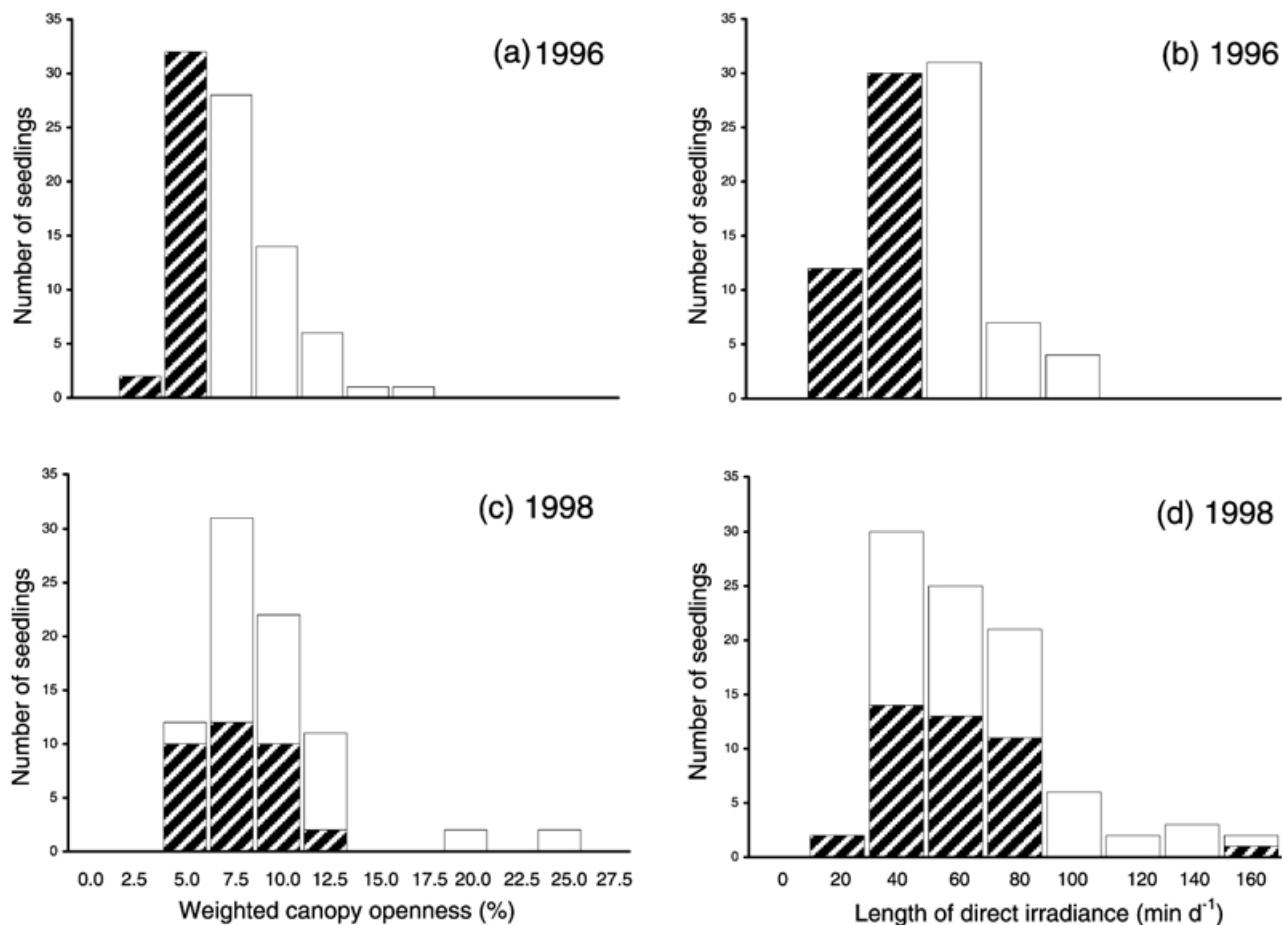


Figure 1. Distribution of weighted canopy openness (%) (WCO) and length of direct irradiance (min d^{-1}) (LDI) before (a, b) and after (c, d) a 1998 drought at Lambir Hills National Park. The first set of canopy photographs was taken in the summer of 1996. The second set of canopy photographs was taken in the summer of 1998. Individuals in diagonal stripes in 1996 are also in diagonal stripes in 1998 to demonstrate the change in the spread of WCO or LDI for those seedlings which were under relatively closed canopy in 1996. The numbers on the x-axis indicate the beginning of each interval. For example '2.5' indicates 2.5–2.9% WCO.

Table 2. Median weighted canopy openness (%) and median length of direct irradiance (min d^{-1}) by plot before and after the 1998 drought, with results of one-sided Wilcoxon Paired-Sample tests.

Plot	N	WCO (%)			LDI (min d^{-1})		
		1996	1998	Wilcoxon test estimate	1996	1998	Wilcoxon test estimate
3	7	8.4	8.6	3.9*	65	65	27
4	40	8.7	10.6	2.3**	69	84	21**
5	37	7.3	8.8	1.2**	51	59	11**

N is the number of hemispherical photographs taken both years in each plot.

* $P \leq 0.05$, ** $P \leq 0.01$

($\chi^2 = 83.3$, $df = 3$, $P < 0.0001$), and in the ND census interval ($\chi^2 = 95.2$, $df = 3$, $P < 0.0001$). However, the proportion of seedlings surviving the SVD census interval was not significantly different by plot ($\chi^2 = 3.65$, $df = 3$, $P = 0.301$). Mortality rates by plot ranged from 5% (Plot 5) to 26% (Plot 2) in the SLD census interval, from 4% (Plot 4) to 10% (Plot 5) in the ND census interval, and

from 9% (Plots 3, 4 and 5) to 19% (Plot 2) in the SVD census interval (Figure 3a).

Mortality differed by species within the SLD and ND census intervals (SLD: $\chi^2 = 101$, $df = 6$, $P < 0.0001$; ND: $\chi^2 = 410$, $df = 6$, $P < 0.0001$) (Figure 4a). However, the proportion of seedlings surviving the SVD interval was not significantly different by species ($\chi^2 = 10.0$, $df = 6$,

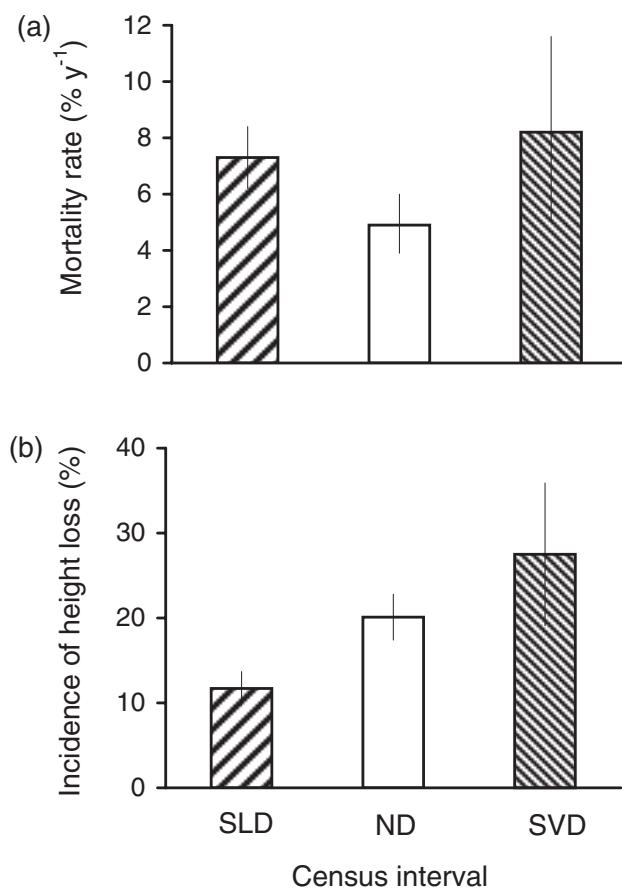


Figure 2. (a) Mortality rates ($\% \text{ y}^{-1}$) with 95% confidence intervals for all seedlings combined across three census intervals. (b) Proportion of seedlings with height loss (%) with 95% confidence intervals for all seedlings combined across three census intervals. See Table 1 for census interval abbreviations.

$P = 0.123$). The ranges of mortality rates within each census interval were SLD: 3% (*A. borneensis* and *M. parvifolia*) to 26% (*M. pentandra*); ND: 1% (*M. parvifolia*) to 21% (*E. tapos*); and SVD: 6% (*A. borneensis*) to 18% (*M. pentandra*).

Mortality differed by \ln height within each of the three census intervals (SLD: $\chi^2 = 123$, df = 1, $P < 0.0001$; ND: $\chi^2 = 355$, df = 1, $P < 0.0001$; SVD: $\chi^2 = 34.6$, df = 1, $P < 0.0001$). For nearly every species, regardless of census interval, the median initial height of the seedlings that survived was greater than the median initial height of the seedlings that died (Table 3). For every species, the proportional difference in height between seedlings that survived and seedlings that died during the SVD census interval was at least as great as that during the SLD or ND census intervals, indicating a disproportionate advantage for the tallest seedlings in the severe 1998 drought.

As the change in WCO from 1996–1998 and the change in LDI over the same time interval were correlated ($r = 0.824$, df = 1, $P < 0.0001$), only change in WCO was

used as an independent variable in equations predicting seedling mortality or height loss over the SVD census interval. For the set of seedlings with WCO measurements, the logistic model predicting mortality from change in WCO ($\text{WCO}_{1998} - \text{WCO}_{1996}$), plot, species and \ln height was statistically significant ($\chi^2 = 28.4$, df = 7, $P = 0.0001$). Only change in WCO and \ln height were significant independent variables; seedlings that had an increasingly positive change in WCO or greater initial height also had an increased likelihood of seedling survival. For the seedlings that survived, the seedling that showed the greatest loss in WCO from 1996–1998 had a decrease in WCO of 5.2%. The surviving seedling that showed the greatest increase in WCO from 1996–1998 had an increase in WCO of 17.9%. For those seedlings that died, the change in WCO ranged from a decrease of 5.9% to an increase of only 8.8%.

Occurrence of height loss The logistic regression predicting height loss from census interval, plot, species and \ln height was statistically significant ($\chi^2 = 59.6$, df = 8, $P < 0.0001$), with census interval, species and \ln height making significant contributions to the model. *Elateriospermum tapos* was not considered in this model because no *E. tapos* seedlings lost height in the SLD census interval. *Mangifera pentandra*, which occurred only in Plot 2, was considered separately. The nominal regression model predicting the occurrence of height loss for *M. pentandra* seedlings from \ln height and census interval was statistically significant ($\chi^2 = 8.98$, df = 3, $P = 0.030$) with only census interval making a significant contribution to the model.

The proportions of seedlings suffering height loss were 12% (SLD), 20% (ND) and 28% (SVD) (Figure 2b). The proportion of surviving seedlings showing height loss was significantly greater in the SVD census interval than in the SLD census interval at the $P = 0.05$ level ($\chi^2 = 17.5$, df = 1, $P < 0.0001$), and significantly greater than the proportion of seedlings showing height loss during the ND census interval at the $P = 0.01$ level ($\chi^2 = 3.08$, df = 1, $P = 0.080$) (Figure 2b). Other non-drought factors and interactions were also important, as the incidence of height loss was significantly greater in the ND census interval than in the SLD census interval ($\chi^2 = 24.7$, df = 1, $P < 0.0001$).

The proportion of seedlings exhibiting height loss differed significantly across plots in the SLD and ND census intervals (SLD: $\chi^2 = 61.5$, df = 3, $P < 0.0001$; ND: $\chi^2 = 16.4$, df = 3, $P = 0.001$). In the SLD census interval, the incidence of height loss ranged from 9% in Plots 2 and 4 to 22% in Plot 3. During the ND census interval, it ranged from 13% (Plot 3) to 23% (Plot 2). It did not differ by plot in the SVD census interval ($\chi^2 = 4.0$, df = 3, $P = 0.256$). In the SVD census interval, the lowest incidence

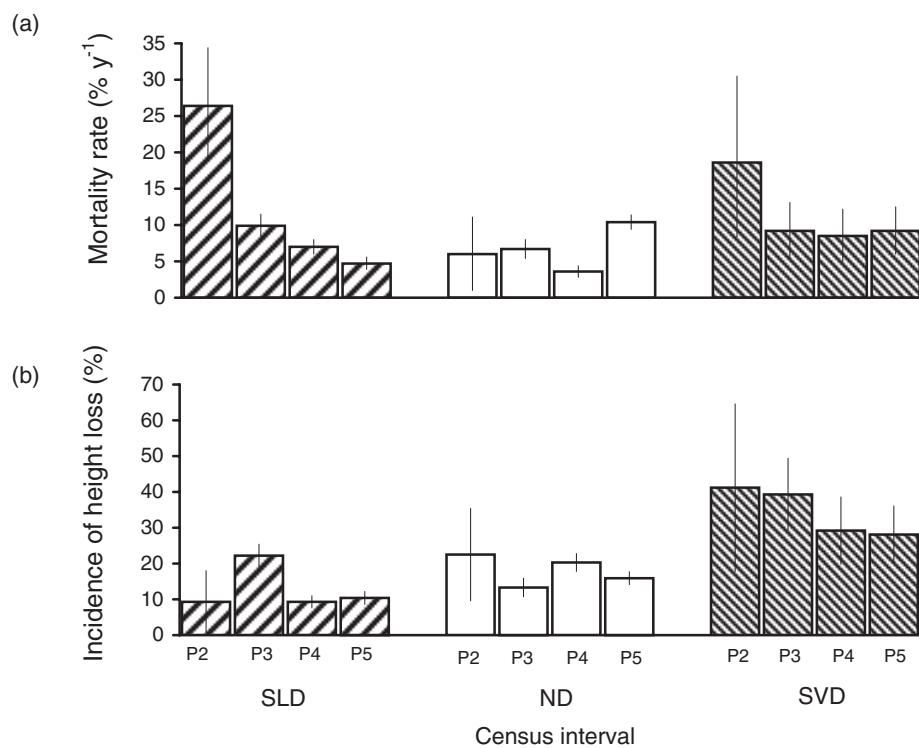


Figure 3. (a) Mortality rates ($\% y^{-1}$) with 95% confidence intervals for seedlings by plot across three census intervals. (b) Proportion of seedlings with height loss (%) with 95% confidence intervals for seedlings by plot across three census intervals. See Table 1 for census interval abbreviations.

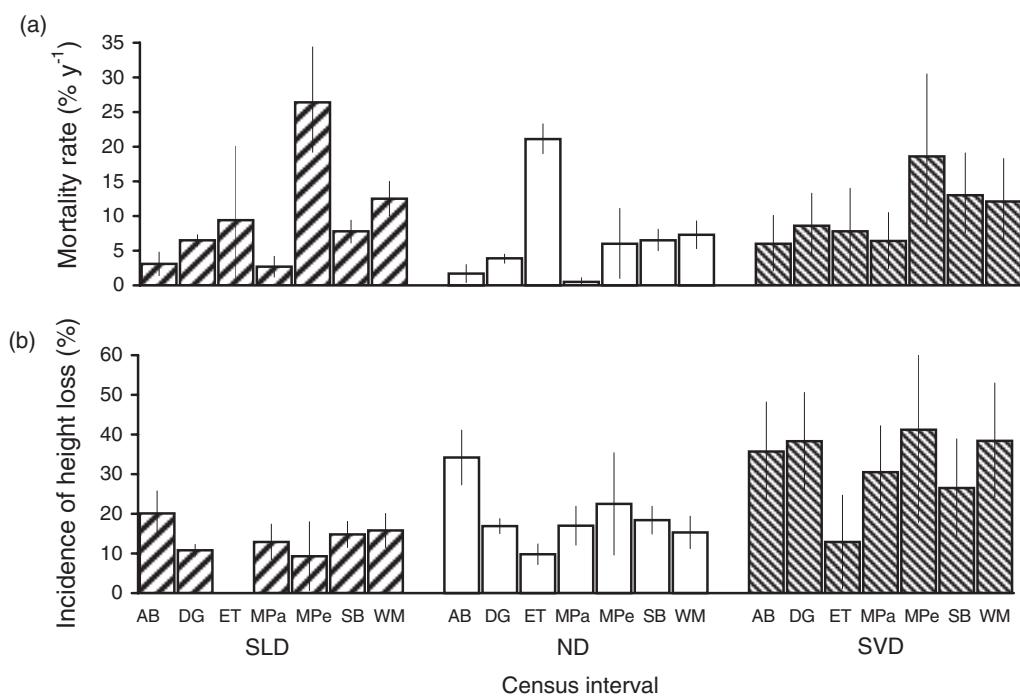


Figure 4. (a) Mortality rates ($\% y^{-1}$) with 95% confidence intervals by species across three census intervals. (b) Proportion of seedlings with height loss (%) with 95% confidence intervals by species across three census intervals. See Table 1 for census interval abbreviations. Species names abbreviations are as follows: *Allantospermum borneensis* = AB; *Dipterocarpus globosus* = DG; *Elateriospermum tapos* = ET; *Mangifera parvifolia* = MPa; *Mangifera pentandra* = MPe; *Shorea beccariana* = SB; and *Whiteodendron moultonianum* = WM.

Table 3. Median initial height (cm) for seedlings that survived (Alive) or died (Dead), or lost height (Loss) or gained height (Gain) during each of three census intervals at Lambir Hills National Park. The number of seedlings in each set is given in parentheses.

	SLD				ND				SVD			
	Alive	Dead	Gain	Loss	Alive	Dead	Gain	Loss	Alive	Dead	Gain	Loss
<i>Allantospermum borneensis</i>	44 (189)	31 (12)	40 (151)	55 (38)	45 (184)	33 (6)	50 (121)	41 (63)	79 (56)	23 (8)	58 (36)	102 (20)
<i>Dipterocarpus globosus</i>	40 (1625)	30 (230)	40 (1450)	50 (175)	47 (1567)	35 (123)	47 (1303)	50 (264)	71 (60)	35 (13)	70 (37)	76 (23)
<i>Elateriospermum tapos</i>	64 (14)	70 (3)	64 (14)	—	28 (512)	25 (295)	27 (463)	35 (49)	76 (31)	41 (6)	71 (27)	88 (4)
<i>Mangifera parvifolia</i>	70 (217)	55 (12)	70 (189)	79 (28)	71 (224)	72 (2)	70 (186)	75 (38)	64 (59)	50 (9)	64 (41)	74 (18)
<i>Mangifera pentandra</i>	39 (43)	26 (35)	40 (39)	31 (4)	42 (40)	32 (5)	42 (31)	48 (9)	66 (17)	37 (9)	56 (10)	76 (7)
<i>Shorea beccariana</i>	60 (452)	45 (78)	56 (385)	79 (67)	59 (462)	45 (64)	57 (377)	68 (85)	75 (49)	56 (17)	71 (36)	87 (13)
<i>Whiteodendron moultonianum</i>	29 (272)	26 (82)	28 (229)	30 (43)	28 (295)	24 (46)	28 (250)	32 (45)	51 (44)	36 (14)	48 (27)	52 (17)

See Table 1 for census interval abbreviations.

of height loss was in Plot 5 (28%) and the greatest incidence of height loss in Plot 2 (41%) (Figure 3b).

The proportion of seedlings surviving with height loss differed between species within the first two census intervals (SLD, *E. tapos* excluded: $\chi^2 = 18.3$, df = 5, P = 0.003; ND: $\chi^2 = 59.9$, df = 6, P < 0.0001) but not in the final census interval ($\chi^2 = 10.3$, df = 6, P = 0.114) (Figure 4b). For every species, the greatest incidence of height loss occurred in the SVD census interval. The proportion of seedlings with height loss ranged from 0% (*E. tapos*) to 20% (*A. borneensis*) in the SLD census interval, 10% (*E. tapos*) to 34% (*A. borneensis*) in the ND census interval and from 12% (*E. tapos*) to 41% (*M. pentandra*) in the SVD census interval.

During all three census intervals, incidence of height loss differed by ln height (SLD: $\chi^2 = 36.3$, df = 1, P < 0.0001; ND: $\chi^2 = 31.3$, df = 1, P < 0.0001; SVD: $\chi^2 = 5.82$, df = 1, P = 0.016). During all census intervals, the seedlings that lost height tended to be taller initially, except for the seedlings of *M. pentandra* during the SLD census interval, and *A. borneensis* during the ND census interval, for which the opposite was true (Table 3).

DISCUSSION

One of the most severe droughts of the twentieth century in an aseasonal tropical rain forest at LHNTP caused an opening of the forest canopy, and had a significant impact on the performance of the shade-tolerant seedlings of canopy trees. This 1998 drought was associated with increased seedling mortality, and an increased incidence of seedling height loss. Through differential effects on seedlings of differing species and sizes, drought may affect the species population densities and stand structure of the seedling bank in this forest.

Significant increases in weighted canopy openness and length of direct irradiance occurred during the severe

1998 drought, a drought that also caused increased tree mortality (Nakagawa *et al.* 2000). Increasingly positive changes in canopy openness were associated with an increased likelihood of seedling survival. However, as there was a net increase in seedling mortality during this period, the positive impact of canopy die-back on seedling success was probably counteracted to some extent by the otherwise poorer growing conditions created by the drought, probably water stress. Also, falling debris from a canopy that was dying back may have caused increased seedling stem breakage, as indicated by the high incidence of height loss in the 1996–1998 census interval. This height loss may also have contributed to increased seedling mortality (Clark & Clark 1992).

It could be expected that the regrowth of trees and saplings would soon reduce canopy openness again. This type of transition was recorded for the forest at Barro Colorado Island where a severe El Niño dry season opened the canopy in 1983. The forest at BCI was fully recovered by the time of the following year's rainy season (Leigh *et al.* 1990, Smith *et al.* 1992). The trees completely recovered their ability to produce and hold leaves (Leigh *et al.* 1990), closing the canopy within 1 y of the drought (Smith *et al.* 1992).

Our results indicate that the relative ranks of the study species on mortality and the incidence of height loss differ in response to drought. However, in contrast to the mature trees in this forest (Nakagawa *et al.* 2000), the seedlings of dipterocarp seedlings did not show a greater proportional increase in mortality as compared with the non-dipterocarp seedlings. Rather, the *M. parvifolia* suffered a disproportionate increase in mortality during the 1996–1998 census interval, with a mortality rate nearly 13 times that in the 1988–1990 (non-drought) census interval. The dipterocarp species, on the other hand, showed mortality rates only 2–4 times those of the non-drought census interval. Similarly, the proportion of seedlings with height

loss after the 1998 drought was greatest for *M. pentandra* with more than a four-fold increase over this measure for the 1986–1988 census interval. This result, therefore, is more similar to that of Cao (2000) who found that in the Bornean heath forest during the 1998 drought, water stress in tree seedlings was more evident in the non-dipterocarp than in the dipterocarp species.

In this forest, tree species distributions are related to small scale differences in soil types, in some cases apparently due to differences in soil moisture (Palmiotto 1998). These distributions may be the result of differential mortality at the seedling stage. However, although the plots differed by soil types, there was no clear trend in mortality rates or height loss to tie the effects of drought to plot.

While shorter seedlings were less likely to survive, they were also less likely to lose height. This apparent contradiction may be explained if shorter seedlings are more likely to die as a result of the height loss, and so are counted as dead rather than alive with height loss. During dry periods, plants are thought to rely on water available from deep within the soil profile (Jipp *et al.* 1998). Smaller individuals are expected to be more sensitive to water stress than would be larger tree-sized individuals. The relatively shallow and less extensive root systems of seedlings may limit access to soil water in a patchy environment (Hartshorn 1992). From the results of our study, it appears that the disadvantage of small size is accentuated during severe drought.

Even during the 1996–1998 census interval, which included both slight and severe droughts, seedling mortality rates were well within seedling mortality rates reported for this and other mixed dipterocarp rain forests in periods of slight or no drought. In another study at LHNP, Itoh *et al.* (1995) showed a mortality rate of 6% y^{-1} for *D. globosus* seedlings, and mortality rates of 15–34% y^{-1} for the seedlings of other dipterocarps, for the period of 1991–1993 which included a slight drought (Nakagawa *et al.* 2000). In our study, *D. globosus* seedlings had mortality rates of 3.9–8.6% y^{-1} . Another study showed mortality for shade-tolerant tree seedlings in Peninsular Malaysia of approximately 5–18% (Turner 1990), and dipterocarp seedlings under closed forest in northern Borneo had mortality rates of up to approximately 15% y^{-1} (Brown & Whitmore 1992). Across census intervals, mortality rates in our study species ranged from 1–31% y^{-1} . The relatively low mortality rates observed during the drought may indicate that these long-lived and resilient seedlings are adapted to survive through rare climatic events (Brünig 1969, Delissio *et al.*, 2002).

Multiple factors complicated the analysis of the impact of the drought. It is possible that unobserved seedling establishment events just prior to the initiation of this study were associated with the relatively high mortality rates for *M. pentandra* and *W. moultonianum* in the initial census interval. The relatively high mortality rate for *E.*

tapos in the non-drought census interval was likely to be due to the high mortality of new seedlings that were established prior to the 1988 census. Likewise, some of the increased mortality for *A. borneensis* and *S. beccariana* in the severe drought census interval can be attributed to their large numbers of new seedlings at the 1996 census. Haze during the latter part of the drought may have reduced the loss of water through evapotranspiration and thus reduced water stress (Cao 2000). Moreover, approximately 83% of the 1986–1988 census interval, and 76% of the 1996–1998 census interval were composed of non-drought months. Our results suggest that non-drought factors that were not quantified in this study also play an important role in the performance of seedlings in the understorey. More studies of the impact of drought on tree seedlings will be required in order to clarify these points. The fact that we were able to show significant effects in spite of these confounding factors suggests that the actual effect of drought on seedling demographics was substantial. Tree seedlings may be sensitive indicators of the impact of global climate change on tropical forests.

ACKNOWLEDGEMENTS

We gratefully acknowledge the Forest Department of Sarawak for their participation in this project. In particular, we would like to acknowledge the great contribution of Sylvester Tan in management of the 1986–1990 census work and data. Special thanks are due to Pamela Hall for setting up these seedling quadrats, and for her willingness to share the data. This work was supported by grants from the U.S. National Science Foundation, a J. and J. Ruinen Fellowship in Tropical Botany (Harvard University), Boston University, and by in-kind support from the Centre for Tropical Forest Science of the Smithsonian Tropical Research Institute, and the University of Malaysia, Kuching. Peter Ashton, Adrien Finzi, Tom Kunz, Gillian Cooper-Driver, Peter Palmiotto, Tatsuhiro Ohkubo and four anonymous reviewers provided valuable comments on the manuscript. Robin Chazdon provided valuable advice on methods. Many thanks to Michiko Nakagawa who supplied unpublished analyses of the 1997 drought.

LITERATURE CITED

- ASHTON, P. S. 1964. *Ecological studies in the mixed dipterocarp forests of Brunei State*. Oxford Forestry Memoirs, No. 25, Oxford. 75 pp.
- ASHTON, P. S. 1969. Speciation among tropical forest trees: some deductions in the light of recent evidence. *Biological Journal of the Linnean Society* 1:155–196.
- ASHTON, P. S. 1996. Niche specificity among tropical trees: a question of scales. Pp. 491–514 in Newbery, D. M., Prins, H. H. T. & Brown, N. D. (eds.). *Dynamics of tropical communities*. Blackwell Science, Oxford.

- ASHTON, P. S. & HALL, P. 1992. Comparisons of structure among mixed dipterocarp forests of north-western Borneo. *Journal of Ecology* 80:459–481.
- BAILLIE, I. C. 1976. Further studies on drought in Sarawak, East Malaysia. *Journal of Tropical Geography* 43:20–29.
- BAILLIE, I. C., ASHTON, P. S., COURT, M. N., ANDERSON, J. A. R., FITZPATRICK, E. A. & TINSLEY, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on Tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3:201–220.
- BAWA, K. S. & DAYANANDAN, S. 1998. Global climate change and tropical forest genetic resources. *Climate Change* 39:473–485.
- BECKER, P. & WONG, M. 1994. Drought-induced mortality in tropical heath forest. *Journal of Tropical Forest Science* 5:416–417.
- BECKER, P., LYE, O. C. & GOH, F. 1998. Selective drought mortality of dipterocarp trees: no correlation with timber group distributions in Borneo. *Biotropica* 30:666–671.
- BROWN, N. D. & WHITMORE, T. C. 1992. Do dipterocarp seedlings really partition tropical rain forest gaps? *Philosophical Transactions of the Royal Society of London, Series B* 335:369–378.
- BRÜNIG, E. F. 1969. On the seasonality of droughts in the lowlands of Sarawak (Borneo). *Erdkunde* 23:127–133.
- BURGESS, P. F. 1969. Ecological factors in hill and mountain forests of the States of Malaya. *Malayan Nature Journal* 22:119–128.
- CAO, K.-F. 2000. Water relations and gas exchange of tropical saplings during prolonged drought in a Borean heath forest, with reference to root structure. *Journal of Tropical Ecology* 16:101–116.
- CHAZDON, R. L. 1992. Photosynthetic plasticity of two rain forest shrubs across natural gap transects. *Oecologia* 92:586–595.
- CHAZDON, R. L. & FIELD, C. B. 1987. Photographic estimation of photosynthetically active radiation: evaluation of a computerized technique. *Oecologia* 73:525–532.
- CLARK, D. A. & CLARK, D. B. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. *Ecological Monographs* 62:315–344.
- CONDIT, R. 1995. Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution* 10:18–22.
- CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1995. Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419–439.
- CORLETT, R. T. & LAFRANKIE, J. V. 1998. Potential impacts of climatic change on tropical Asian forests through an influence on phenology. *Climatic Change* 39:439–453.
- DAVIES, S. J. 2001. Tree mortality and growth in 11 sympatric *Macaranga* species in Borneo. *Ecology* 82:920–932.
- DAVIES, S. J., PALMIOTTO, P., ASHTON, P. S., LEE, H. S. & LAFRANKIE, J. V. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* 86:662–673.
- DELISSIO, L. & PRIMACK, R. In prep. Two years of growth in Malaysian tree seedlings: allocation of above-ground biomass and survival in the understory.
- DELISSIO, L., PRIMACK, R. B., HALL, P. & LEE, H. S. 2002. A decade of canopy tree seedling survival and growth in two Bornean rain forests: persistence and recovery from suppression. *Journal of Tropical Ecology* 18:645–658.
- GOLDAMMER, J. G. & PRICE, C. 1998. Potential impacts of climate change in fire regimes in the tropics based on MAGICC and a GISS GCM-derived lightning model. *Climate Change* 39:273–296.
- HALL, P. 1991. *Structure, stand dynamics, and species compositional change in three mixed dipterocarp forests of northwest Borneo*. Ph.D. Dissertation. Department of Biology, Boston University, Boston. 701 pp.
- HALL, P. & PRIMACK, R. B. 1987. *Long-term ecological studies in three contrasting mixed dipterocarp forests*. Unpublished report, Boston University. 65 pp.
- HARRISON, R. D. 2000. Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London: Biological Sciences Series B* 267:911–915.
- HARTSHORN, G. S. 1978. Tree falls and tropical forest dynamics. Pp. 617–630 in Tomlinson, P. B. & Zimmermann, M. H. (eds). *Tropical trees as living systems: the proceedings of the Fourth Cabot Symposium held at Harvard Forest, Petersham, Massachusetts, on April 26–30, 1978*. Cambridge University Press, Cambridge.
- HARTSHORN, G. S. 1992. Possible effects of global warming on the biological diversity in tropical forests. Pp. 137–146 in Peters, R. L. & Lovejoy, T. E. (eds). *Global warming and biological diversity*. Yale University Press, New Haven.
- INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE WORKING GROUP I 2001. *Climate change 2001: the scientific basis, technical summary*. UNEP, Geneva. 63 pp.
- ITOH, A., YAMAKURA, T., OGINO, K. & LEE, H. S. 1995. Survivorship and growth of seedlings of four dipterocarp species in a tropical rainforest of Sarawak, East Malaysia. *Ecological Research* 10:327–338.
- ITOH, A., YAMAKURA, T., OGINO, K., LEE, H. S. & ASHTON, P. S. 1997. Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. *Plant Ecology* 132: 121–136.
- JIPP, P. H., NEPSTAD, D. C., CASSEL, D. K. & DECARVALHO, C. R. 1998. Deep soil moisture storage and transpiration in forests and pastures of seasonally-dry Amazonia. *Climate Change* 39:395–412.
- KUDO, G. & KITAYAMA, K. 1999. Drought effects on the summit vegetation on Mount Kinabalu by an El Niño event in 1998. *Sabah Nature Parks Journal* 2:101–110.
- LAUMONIER, Y. & LEGG, C. 1998. Le suivi des feux de 1997 en Indonésie. *Bois et Forêts des Tropiques* 258:5–18.
- LEE, H. S., ASHTON, P. S. & OGINO, K. 1995. *Long term ecological research of tropical rain forest in Sarawak*. Ehime University, Matsuyama. 228 pp.
- LEIGH, E. G. H., WINDSOR, D. M., RAND, A. S. & FOSTER, R. B. 1990. The impact of the ‘El Niño’ drought of 1982–83 on a Panamanian semideciduous forest. Pp. 473–486 in Glynn, P. W. (ed.). *Global ecological consequences of the 1982–1983 El Niño-southern oscillation event*. Elsevier Press, New York.
- LEIGHTON, M. & WIRAWAN, N. 1986. Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982–1983 El Niño

- southern oscillation event. Pp. 75–102 in Prance, G. T. (ed.). *Tropical rain forests and the world atmosphere*. Westview Press American Association for the Advancement of Science, Boulder.
- MARKHAM, A. 1998. Potential impacts of climate change on tropical forest ecosystems. *Climate Change* 39:141–142.
- MEEHL, G. A. 1997. Pacific region climate change. *Ocean and Coastal Management* 37:137–147.
- NAKAGAWA, M., TANAKA, K., NAKASHIZUKA, T., OHKUBO, T., KATO, T., MAEDA, T., SATO, K., MIGUCHI, H., NAGAMASU, H., OGINO, K., TEO, S., HAMID, A. A. & LEE, H. S. 2000. Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16:355–367.
- NEWBERRY, D. M., CAMPBELL, E. J. F., PROCTOR, J. & STILL, M. J. 1996. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and patterns in the understorey. *Vegetatio* 122:193–220.
- NICOTRA, A. B., CHAZDON, R. L. & IRIARTE, S. V. B. 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. *Ecology* 80:1908–1926.
- PALMIOTTO, P. A. 1995. Preliminary characterization of soil texture and organic matter thickness in 52 ha of lowland mixed dipterocarp forest, Lambir Hills National Park, Sarawak, Malaysia. Pp. 61–67 in Lee, H. S., Ashton, P. S. & Ogino, K. (eds). *Long term ecological research of tropical rainforest in Sarawak*. Ehime University, Matsuyama.
- PALMIOTTO, P. A. 1998. *The role of specialization in nutrient-use efficiency as a mechanism driving species diversity in a tropical rain forest*. Doctor of Forestry Dissertation. School of Forestry and Environmental Studies, Yale University, New Haven, Connecticut. 282 pp.
- PHILLIPS, O. L. & GENTRY, A. H. 1994. Increasing turnover through time in tropical forests. *Science* 263:954–958.
- PRIMACK, R. B. 1992. Tropical community dynamics and conservation biology: long-term data on community dynamics are a necessary part of research studies. *BioScience* 42:818–821.
- PRIMACK, R. B. & HALL, P. 1992. Biodiversity and forest change in Malaysian Borneo. *BioScience* 42:829–837.
- SALAFSKY, N. 1998. Drought in the rain forest, Part II: an update based on the 1994 ENSO event. *Climate Change* 39:601–603.
- SAS INSTITUTE INC. 1998. JMP Statistical Discovery Software, Version 3. SAS Institute, Cary.
- SHEIL, D. & MAY, R. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84:94–100.
- SHEIL, D., BURSLEM, D. F. R. P. & ALDER, D. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83:331–333.
- SMITH, A. P., HOGAN, K. P. & IDOL, J. R. 1992. Spatial and temporal patterns of light and canopy structure in a lowland tropical moist forest. *Biotropica* 24:503–511.
- SWAINE, M. D. & WHITMORE, T. C. 1988. On the definition of ecological species groups in tropical rain forests. *Vegetatio* 75:81–86.
- TANG, H. T. & CHONG, P. F. 1979. ‘Sudden’ mortality in a regenerated stand of *Shorea curtisii* in Senaling Inas Forest Reserve, Negeri Sembilan. *The Malaysian Forester* 42:240–248.
- TIMMERMAN, A., OBERHUBER, J., BACHER, A., ESCH, M., LATIF, M. & ROECKNER, E. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398: 694–696.
- TURNER, I. M. 1990. Tree seedling growth and survival in a Malaysian rain forest. *Biotropica* 22:146–154.
- TURNER, I. M. & WHITMORE, T. C. 1991. The northern limit of Red Meranti in the Malay Peninsula. *Proceedings of the 4th Dipterocarp Round Table Conference, BIOTROP Special Publication* 41:295–305.
- VEENENDAAL, E. M. & SWAINE, M. D. 1996. Limits to tree species distributions in lowland tropical rainforest. Pp. 163–191 in Newbery, D. M., Prins, H. H. T. & Brown, N. D. (eds). *Dynamics of tropical communities*. Blackwell Science, Oxford.
- WALSH, R. P. D. 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12:385–407.
- WALSH, R. P. D. & NEWBERRY, D. M. 1999. The ecoclimatology of Danum, Sabah, in the context of the world’s regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society of London* 354:1869–1883.
- WHITMORE, T. C. 1984. *Tropical rain forests of the Far East*. (Second Edition). Clarendon Press, Oxford. 352 pp.
- WHITMORE, T. C. 1989. Southeast Asian tropical forests. Pp. 195–218 in Lieth, H. & Werger, M. J. A. (eds.). *Tropical rain forest ecosystems*. Elsevier, New York.
- WHITMORE, T. C. 1995. Comparing southeast Asian and other tropical rain forests. Pp. 5–15 in Primack, R. B. & Lovejoy, T. E. (eds). *Ecology, conservation, and management of Southeast Asian rainforests*. Yale University Press, New Haven.
- WHITMORE, T. C. 1998. Potential impact of climate change on tropical rain forest seedlings and forest regeneration. *Climate Change* 39:429–438.
- WOODS, P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21:290–298.
- YAMAKURA, T., KANZAKI, M., ITOH, A., OHKUBO, T., OGINO, K., CHAI, E. O. K., LEE, H. S. & ASHTON, P. S. 1995. Forest architecture of Lambir Rain Forest revealed by a large-scale research plot I. Topography of the plot. Pp. 227–228 in Lee, H. S., Ashton, P. S. & Ogino, K. (eds). *Long term ecological research of tropical rain forest in Sarawak*. Ehime University, Matsuyama.