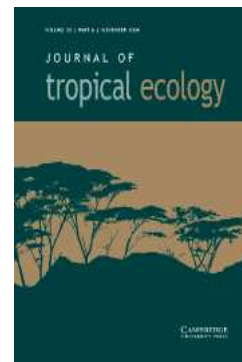


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# Resistance of a lowland rain forest to increasing drought intensity in Sabah, Borneo

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**Abstract:** Occasional strong droughts are an important feature of the climatic environment of tropical rain forest in much of Borneo. This paper compares the response of a lowland dipterocarp forest at Danum, Sabah, in a period of low (LDI) and a period of high (HDI) drought intensity (1986–96, 9.98 y; 1996–99, 2.62 y). Mean annual drought intensity was two-fold higher in the HDI than LDI period (1997 v. 976 mm), and each period had one moderately strong main drought (viz. 1992, 1998). Mortality of ‘all’ trees  $\geq 10$  cm gbh (girth at breast height) and stem growth rates of ‘small’ trees 10–< 50 cm gbh were measured in sixteen 0.16-ha subplots (half on ridge, half on lower slope sites) within two 4-ha plots. These 10–50-cm trees were composed largely of true understorey species. A new procedure was developed to correct for the effect of differences in length of census interval when comparing tree mortality rates. Mortality rates of small trees declined slightly but not significantly between the LDI and HDI periods (1.53 to 1.48%  $y^{-1}$ ); mortality of all trees showed a similar pattern. Relative growth rates declined significantly by 23% from LDI to HDI periods (11.1 to 8.6  $mm\ m^{-1}\ y^{-1}$ ); for absolute growth rates the decrease was 28% (2.45 to 1.77  $mm\ y^{-1}$ ). Neither mortality nor growth rates were significantly influenced by topography. For small trees, across subplots, absolute growth rate was positively correlated in the LDI period, but negatively correlated in the HDI period, with mortality rate. There was no consistent pattern in the responses among the 19 most abundant species ( $n \geq 50$  trees) which included a proposed drought-tolerant guild. In terms of tree survival, the forest at Danum was resistant to increasing drought intensity, but showed decreased stem growth attributable to increasing water stress.

**Key Words:** Borneo, drought, forest dynamics, interval correction, mortality, tree growth, understorey

## INTRODUCTION

The climate of the world’s rain-forest regions is rarely constant over scales of decades to centuries. Considering rainfall, periods of equable climate are characteristically punctuated by unpredictable events in the form of droughts and floods. These can last for a few days to several weeks but their effects on the vegetation are often much longer (Whitmore 1984, Whitmore & Burslem 1998). Furthermore, such events are usually masked when climatic variables are summarized in the form of monthly and annual means (Brünig 1969, 1971). On well-drained sites drought is probably the potentially most stressful factor, one which leads to disturbance, and exerts a strong natural selective force on the species composition of the vegetation.

Climate models suggest that the frequency and strengths of extreme climatic events are likely to increase in the coming decades as a result of planetary warming combined with continuing regional-scale changes in land-use (Hulme & Viner 1998, Timmermann *et al.* 1999). The term ‘drought intensity’, introduced in the present paper, can express a combination of the frequency and strengths of droughts within a period. Droughts are expected to have major impacts on the dynamics of tropical forests (Condit 1998), and regions in which the vegetation is presently well-adjusted to a defined regime may suffer from increases in drought intensity in the future.

Knowledge of what a forest has experienced in terms of past climate is critically dependent, however, on the length of records of direct measurements, this being at most *c.* 120 y in the tropics (Walsh 1996a). More extreme prior events may have occurred with still considerable consequences for present-day vegetation. Therefore,

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whilst anecdotal historical records of notable major events are valuable, recent climate records alone may not be too reliable a guide to the past. Further insights must come from considering forest species composition and structure, and the evolved morphological and ecophysiological characteristics of the trees.

In this paper one lowland dipterocarp forest in Borneo is considered. Several general questions arise that set the broader context. How adapted to drought are tree species in the various forest types of this formation, and to what extent are the corresponding forest ecosystems resistant or resilient to changes in drought intensity? What are the thresholds of drought intensity below which the forests must remain to avoid severe damage and a long period of recovery? Can the type of vegetation at a particular site, now under a moderate drought regime, be expected to change to one of a more extreme regime?

Droughts are an acknowledged integral part of the environment of the rain forest in Borneo (Walsh 1996a). Walsh (1996b) has shown that over the last century strong droughts have occurred on average 1.54 times per 20 y (range 0–4.7 times). This estimate was based on just nine sites with rainfall records of 35 to 105 y. A strong drought was defined as an event with a cumulative rainfall deficit (CRD) of  $\geq 200$  mm, i.e. a deficit which accumulated over a set of successive months each having  $< 100$  mm of rainfall. Moderate droughts with CRDs of  $100 < \text{CRD} < 200$  mm occurred more frequently at 3.25 per 20 y (Walsh & Newbery 1999). Trees growing for 200 y would therefore be expected to experience about 15 strong and 30 moderate droughts on average, and their first 20 y of sapling growth would be likely subject to at least one drought. Some forests in Borneo very rarely or never experience a drought, whilst others experience as many as 40 in 200 y. Thus, important ecological information is given by the *spectrum* of frequencies and strengths of the droughts to which a site is subject, and not simply the monthly climate variables averaged over several years.

Responses to drought disturbance and stress may be measured in terms of tree mortality, recruitment and growth. A forest that shows no response to an increase in drought intensity is resistant to this factor, because the species are well adapted. However, if droughts have been part of the 'normal' long-term climatic environment in which tree species were selected then the patterns in species composition of Bornean forests should be determined, at least in part, by intensity of droughts. Newbery *et al.* (1999) have proposed the hypothesis that understorey species play a critical role in determining a forest ecosystem's resistance and resilience to drought; and when this very numerous group of small trees is damaged or removed it will lead to a lowland dipterocarp forest becoming more vulnerable to such events. The precise effect of drought is expected to vary with the local

topography at a site, because ridges are more prone to water stress than lower slopes (Gibbons & Newbery 2003, Newbery *et al.* 1996).

Long-term studies of the dynamics of two permanent 4-ha plots at Danum (Newbery *et al.* 1992, 1996, 1999) have allowed the effects of recent droughts to be assessed. This was difficult because no period was completely free of some form of drought effect (be it immediate, recent or possibly lagged) but rather there existed relatively more or less drought intensive periods. In this paper, a comparison between a period of relatively low (1986–96) and a period of relatively high (1996–99) intensity of droughts is presented. The aims were (1) to measure the immediate effect of increasing drought intensity on tree mortality and stem growth, (2) to compare these variables on ridge and lower-slope sites, and (3) to test whether there were differential species' responses to increasing drought intensity.

## STUDY SITE

The Danum Valley Conservation Area ( $117^{\circ} 8' \text{ E}$ ,  $5^{\circ} 0' \text{ N}$ ), lies *c.* 60 km inland of the East Coast of the Malaysian state of Sabah, Borneo. The site is located *c.* 1.2 km NW of the Danum Valley Field Centre (DVFC) in undisturbed primary forest, on gently undulating topography at an elevation of *c.* 200 m asl (Marsh & Greer 1992). Danum has a 'normally' aseasonal tropical climate (in non-drought years) that is intermediate between the drier east coast of Borneo and the wetter inland parts of southern Sabah.

Meteorological records exist for Danum since 1985 and include two moderate El Niño Southern Oscillation (ENSO)-related droughts, one in 1992 (CRD = 123 mm) spread over the 4 mo of January to April, and the other in 1998 (CRD = 102 mm) concentrated in March and April (87 and 11 mm rainfall respectively) but preceded in November 1997–February 1998 by lower-than-average rainfall ( $123\text{--}151 \text{ mm mo}^{-1}$ ) in what is normally a wet part of the year (Walsh & Newbery 1999). An earlier very strong ENSO-related drought in 1982–83 occurred widely in Sabah and may have affected Danum. Historical records show Borneo-wide droughts of great intensity in 1877–78 and 1915 that probably had larger and longer-lasting effects on the forest at Danum than those of 1982–83, 1992 and 1998 (Walsh 1996b). The long-term average annual rainfall at Danum between 1986 and 2002 was 2783 mm.

In 1985 two 4-ha permanent plots were set up, each of them 100 m wide (W–E) and 400 m long (S–N), lying parallel to one another and *c.* 300 m apart. Both plots intentionally included topographic gradients from lower slope to ridge with elevation differences of *c.* 35 m (Newbery *et al.* 1992, 1996). The lower SW corners

of the plots are 208 and 220 m asl. The soils are a mixture of orthic acrisols and dystric cambisols and lie on sandstone, mudstone, and miscellaneous rocks (Wright 1975).

## METHODS

### First and second enumerations in period 1

In the first enumeration from 1985–1986, every living tree  $\geq 10$  cm gbh (girth at breast height, 1.3 m; 3.18 cm diameter at bh) in the plots was mapped to the nearest 0.1 m, numbered with an aluminium tag, paint-marked, and measured for gbh at the mark. Almost every tree was identified to the species level (Newbery *et al.* 1992, 1996).

In the second enumeration from 1995–1996, all numbered trees were censused for alive/dead status, and the gbh of each survivor was measured. Stem condition at the point of measurement was recorded in one of 17 nominal classes (e.g. measured above buttresses, stem deformed, fluted, cracked, fused with liana, bark stripped, etc.; see Newbery *et al.* 1999), and the condition of the whole tree was scored according to one of seven classes (*viz.* alive 'AA', alive but top broken 'AB' and alive but coppiced 'AC', plus four others). Trees that were leafless with dead branches, or fallen, rotten or disintegrating were recorded as dead: a few were missing but since the exact locations were known these certainly had also died. Trees that had grown into the size class of  $\geq 10$  cm gbh since the first enumeration were tagged, paint-marked and measured as new recruits. Vegetative specimens of recruits were collected and matched with the reference collection from the first enumeration in Leiden (Newbery *et al.* 1999). Authorities for species used in the present paper are given in Newbery *et al.* (1996, 1999).

### Selection of the subplots for period 2

As resources did not allow for a full re-enumeration, sixteen 40-m  $\times$  40-m subplots within the two main plots were chosen to sample the upper and lower parts of the local topographic gradient. Eight subplots within each main plot were chosen from a regular grid using a stratified random sampling procedure. From the mean elevations at the 20-m  $\times$  20-m grid points, a weighted average for each possible 40-m  $\times$  40-m area was calculated. All such areas with mean elevations  $\geq 25$  m or in the range 3–12 m were numbered and taken as ridge and lower slope subsets respectively. Contour diagrams are given elsewhere (Gibbons & Newbery 2003, Newbery *et al.* 1996).

From each of these subsets four subplots were selected at random for each main plot, allowing neighbouring

subplots to border by up to 20 m on just one side, but with no overlap in area. This ensured as many subplots per plot as possible yet maintaining independence of the sampling units. The subplots covered 2.56 ha, or 32% of the total area of the main plots placed within a forest block of *c.* 20 ha. The mean ( $\pm$  SE) relative within-plot elevations for the ridge subplots were  $26.7 \pm 0.9$  m and  $28.4 \pm 1.6$  m ( $n = 4$ ) for plots 1 and 2 respectively, with corresponding lower-slope subplot elevations of  $8.8 \pm 1.4$  m and  $7.3 \pm 1.6$  m ( $n = 4$ ). The mean differences in elevation between ridge and lower-slope subplots were therefore 17.9 and 21.1 m. In 1996 these 16 subplots had 403 species of tree  $\geq 10$  cm gbh, and 368 species of tree 10–< 50 cm gbh.

### Remeasurement of subplots in period 2

All trees  $\geq 10$  cm gbh in the chosen subplots were revisited between 20 December 1998 and 29 April 1999 and scored for alive-dead status. Subplots were measured in a random order to avoid confounding time with topographic effect. The gbh of each living small tree (10–<50 cm gbh) was remeasured either with a thin steel tape or with calipers where tape measurements were impossible due to fused lianas or damage to the stem at the height of the paint mark. The coding system for the classification of stem condition at the point of measurement, and of tree status at the time of remeasurement, were adopted from the second enumeration of the main plots (Newbery *et al.* 1999). Codes were revised where a condition or status had changed since the first re-enumeration. On checking the subplots in 2001 some (mostly very small) trees which were recorded as missing and presumed to be dead in 1999 were found alive. Several were damaged and still below 10 cm gbh. Their status in 1999 was corrected. The mean lengths ( $\pm$  SE) of periods 1 and 2 were  $9.983 \pm 0.006$  and  $2.616 \pm 0.004$  y respectively, based on the dates of measurements of individual trees.

### Calculations of mortality and growth rates

Annualized mortality ( $\% y^{-1}$ ) was calculated for all ( $\geq 10$  cm gbh) and for small (those 10–< 50 cm gbh) trees as:  $m_a(t) = 100 \times [1 - (1 - (n_d/n_o))^{1/t}]$ , where  $n_d$  trees died in an original population of  $n_o$  over a census interval of  $t$  y (Alder 1995, Sheil *et al.* 1995). Sheil & May (1996) have shown that  $m_a$  is dependent on the time interval. Using the approach described in Appendix 1, subplot mortality rates in period 2 were corrected for time interval differences using individual species' mortality rates to estimate the between-group (species) heterogeneity in the forest. The resulting correction is conservative, *i.e.*

the difference in  $m_a$  between the two intervals was likely to have been slightly underestimated and thus the probability of finding a significant difference was reduced.

Growth was calculated as absolute ( $agr = [gbh_2 - gbh_1]/t$ ) and relative ( $rgr = [\ln(gbh_2) - \ln(gbh_1)]/t$ ) girth increment per year for small trees ( $10 < gbh < 50$  cm), with  $gbh$  in mm and  $t$  in y. The latter rate was expressed in units of  $mm\ m^{-1}\ y^{-1}$ . Trees that were difficult to measure because of fused lianas or a damaged stem at the point of measurement, or because they had broken stems (sometimes with coppicing) were removed from the data set. Of the trees so retained, those with absolute growth rates of  $\leq -4.0\ mm\ y^{-1}$  were excluded. Newbery *et al.* (1999) associated these mainly with changes in the bark loss, tree damage, unusually large shrinkages or errors of measurement.

### Species' comparisons

Values of  $m_a$  and  $rgr$  were found in the two periods separately for those species with  $\geq 50$  trees  $10 < gbh < 50$  cm  $gbh$  alive at the start of both periods, samples sizes  $< 50$  being unreliable with large binomial errors (see Newbery *et al.* 1999). Time intervals corresponding to each species' measurements were used, but subplot-level corrections for the effect of time interval difference between periods on  $m_a$  were not applied because the species were taken to be relatively homogeneous (see Appendix 1).

### Statistical analysis

Rates at the subplot level were subject to analysis of variance using GenStat (Version 6, Payne 2000). The effect of plot was estimated in stratum 1; then topography (at the subplot level), nested within plots, in stratum 2; and lastly period and topography  $\times$  period, nested within subplots, in stratum 3. In all cases residuals satisfactorily met the conditions of the normal error distribution. For tests of significance between the two topographic levels, repeated-measures analysis was not feasible because there were only two times (Payne 2000, Winer *et al.* 1991).

Using all 16 subplots, however, did not allow statistical independence of the two periods. To achieve this two randomization procedures were used: (1) Plot and topography terms were ignored. Eight of the 16 subplots were selected at random for the LDI period, leaving the other eight for the HDI period. This allowed a simple analysis of variance for the period effect. The procedure was repeated 50 times for each of the mortality and growth variables. (2) Plot and topography terms were retained. Two of the four subplots per plot  $\times$  topography

combination were randomly selected for the LDI period, leaving the other two of the four for the HDI period. This led to a two-factor analysis of variance of topography and period (with plots as 'blocks'). The procedure was repeated as for (1). Randomizations were achieved with Fortran77/Nag library routines.

## RESULTS

### Droughts at Danum

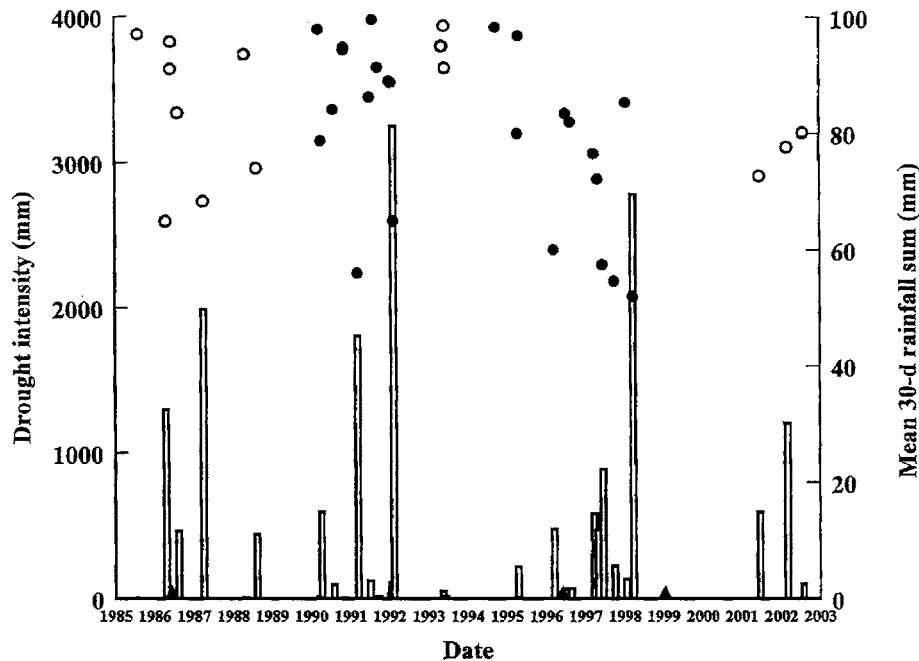
Analysis of the daily rainfall records since August 1985 allows a better quantification of the frequency and intensity of dry periods than calculating CRD on monthly totals. A drought was defined as a period in which the running 30-d rainfall total fell below 100 mm (Brüning 1969, Walsh 1996a); the 30-d rainfall deficit was the difference between rainfall and 100 mm during a drought. Between July 1985 and December 2002 there were 38 droughts ranging in duration from 1–93 d (Figure 1); 32 of these droughts fell between the mean start and end dates of periods 1 and 2 (Table 1). Period 1 had three times as many droughts as period 2, but on an annual basis droughts were more frequent in the second period. Means of drought duration were similar between periods although the number of drought days per annum was *c.* 1.5-fold higher in period 2 than 1.

Mean 30-d rainfall deficit was over two-fold higher in period 2 than 1 with the lowest 30-d rainfall minima reaching 8–9 mm once in each of the periods (Table 1). Rainfall deficit per annum was *c.* 2.6-fold greater in period 2 than 1. Total intensity of drought per period was expressed as

$$\sum_{i=1}^m \text{mean deficit}(i) \times \text{duration}(i),$$

for  $i = 1, m$  drought events per period. This resulted in a mean drought intensity per annum in period 2 that was twice that in period 1 (Table 1).

Periods 1 and 2 each experienced one main drought of intensity  $> 2500$  mm, the first being from 12 February to 14 May 1992 (93 d) and the second 26 March to 22 May 1998 (58 d) (Figure 2). In period 1 this main event came roughly midway and was the end drought of a small cluster of increasingly stronger events starting around 20 March 1990. In period 2, the main event, together with a cluster of again increasingly stronger events, occurred from 21 March 1996 to 22 May 1998 and overlapped with much of period 2 (Figure 1). The beginning and end of period 1 and the start of period 2 were both at times of mild droughts, whilst the end of period 2 was free of droughts. This means that neither period could be differentiated with the labels 'drought' or 'non-drought'. The largest 'drought-free' period in the rainfall series was



**Figure 1.** Drought events at Danum Valley, Sabah, in the period 1 August 1985 to 31 December 2002. A drought occurred when the running 30-d sum of rainfall fell below 100 mm. Open bars are drought intensity (see text) and points are the mean 30-d sums of rainfall within each event (closed circles, within each of two clusters of droughts; open circles, outside of these clusters). Some drought events were of such low intensity (typically <5 mm) that they do not show above the x-axis. The triangles on the x-axis indicate the mean start and end dates of the 1986–1996 and 1996–1999 enumeration periods 1 and 2.

from 23 May 1998 to 22 June 2001 (3 y 1 mo), and the next one – broken by four very short mild events – was 14 May 1992 to 26 September 1994. An interesting feature of the cluster of droughts overlapping period 2 (26 September 1994 to 22 May 1998; Figure 1), was the linear decline in rainfall (i.e. increasing deficit) over time ( $r = -0.705$ ,  $df = 10$ ,  $P = 0.010$ ). This feature was not apparent, however, for the cluster in period 1 (20 March 1990 to 14 May 1992;  $r = -0.156$ ,  $df = 10$ ,  $P = 0.63$ ). Periods 1 and 2 were accordingly labelled as low-(LDI)

and high-(HDI) drought-intensity periods respectively, and will be referred to as such hereafter.

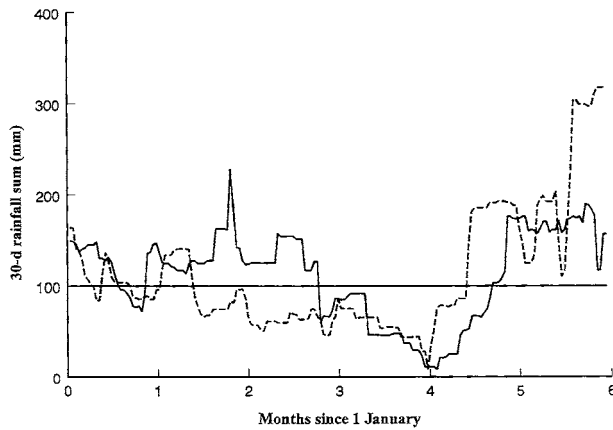
#### Mortality and growth at the subplot level

In 1986 and 1996 there were 5727 and 5509 trees  $\geq 10$  cm gbh ('all' trees) in the 16 subplots, of which 818 died between 1986 and 1996 and 280 between 1996 and 1999. For the trees 10–<50 cm gbh ('small' trees) the

**Table 1.** Frequency and intensity of drought in the two enumeration periods 1986–96 and 1996–99 at Danum, Sabah, Malaysia.

	Period		Ratio 2:1
	1	2	
Dates	09.06.86 –03.06.96	03.06.96 –14.01.99	
Interval (y)	9.98	2.62	
Number of droughts	24	8	
Mean number of drought events per y	2.40	3.03	1.26
Mean duration per event (d) (range)	14.0 (1–93)	17.9 (4–58)	
Mean number of drought days per y	35.2	54.6	1.55
Mean of mean 30-d sum of rainfall per event (mm)	85.9	70.4	
Mean of mean 30-d rainfall deficit per event (mm)	14.1	29.6	2.10
Mean of min. 30-d sum of rainfall per event (mm) (range)	75.8 (9–100)	50.4 (8–79)	
Mean deficit per y (mm)	34.87	90.22	2.59
Total intensity (mm)*	9735	5233	
Mean intensity per y (mm)	975	1997	2.05

\* See text for definition of total intensity.



**Figure 2.** Running 30-d sums of rainfall in the periods 1 January – 30 June of 1992 (dashed line) and of 1998 (solid line), at Danum Valley, Sabah, with the threshold for water stress drawn at 100 mm. These years contain the strongest events within the low (LDI) and high (HDI) drought intensity periods.

corresponding numbers were 5190 and 4960, with 741 and 254 dying; sample sizes per subplot ranged from 264–386 and 262–360 trees in 1986 and 1996 respectively. The numbers of small trees for which growth rates were valid were 3927 in 1986–96 and 4319 in 1996–99; subplots had ranges of 175–298 and 219–324 trees for the two periods respectively. Mean gbh increased from 18.8 to 21.2 cm between 1986 and 1996, and from 19.1 to 19.5 cm between 1996 and 1999 (based on means of the 16 subplots). The difference between the first and second gbh values for 1996 was because (1) recruits were added in 1996, and (2) trees that lost their paint marks in the first period could be measured at moved points of measurement in the second period. Tables of small-tree mortality and growth rates in the 16 subplots are available on request from the corresponding author.

Mortality rates of all and small trees were not significantly correlated between periods across the 16 subplots ( $r = -0.050$ ,  $df = 14$ ,  $P = 0.853$ ;  $r = -0.044$ ,  $P = 0.871$ ; respectively), but agr and rgr of small trees were significantly positively correlated ( $r = 0.644$ ,  $P = 0.007$ ;  $r = 0.663$ ,  $P = 0.005$ ; respectively). Interestingly, in the HDI period, the mortality rate of small trees was significantly negatively correlated with agr and rgr ( $r = -0.583$ ,  $P = 0.018$ ;  $r = -0.522$ ,  $P = 0.038$ ; respectively) whereas in the LDI period there was a marginally positive correlation with agr ( $r = 0.481$ ,  $P = 0.059$ ) although for rgr it was not significant ( $r = 0.275$ ,  $P = 0.303$ ).

Mortality rates of all trees were insignificantly 5.2% lower in the HDI than LDI period (Table 2;  $F = 0.27$ ;  $df = 1, 14$ ;  $P = 0.61$ ). For small trees the decrease was similarly small at 3.3%, and also insignificant ( $F = 0.17$ ;  $df = 1, 14$ ;  $P = 0.687$ ). Differences in growth of small trees, however, were highly significant. Absolute growth

**Table 2.** Mean mortality and growth rates ( $\pm 1$  SE) of trees in two topographic classes, and these combined, for low (LDI) and high (HDI) drought intensity periods (1986–96, 1996–99) for two main plots ( $n = 8$  subplots per class) at Danum, Sabah for two tree size classes (all,  $\geq 10$  cm gbh; and small,  $10 < 50$  cm gbh). Values of  $m_a$  in the HDI period have been corrected for the difference in interval-effect (see text).

	Size class	LDI period	HDI period
Mortality, $m_a$ (% $y^{-1}$ )	All		
Ridge		$1.37 \pm 0.08$	$1.47 \pm 0.12$
Lower slope		$1.70 \pm 0.21$	$1.44 \pm 0.16$
Combined		$1.54 \pm 0.12$	$1.46 \pm 0.09$
Mortality, $m_a$ (% $y^{-1}$ )	Small		
Ridge		$1.38 \pm 0.07$	$1.51 \pm 0.12$
Lower slope		$1.69 \pm 0.19$	$1.44 \pm 0.15$
Combined		$1.53 \pm 0.11$	$1.48 \pm 0.10$
Absolute growth rate (mm $y^{-1}$ )	Small		
Ridge		$2.39 \pm 0.28$	$1.60 \pm 0.17$
Lower slope		$2.51 \pm 0.24$	$1.94 \pm 0.31$
Combined		$2.45 \pm 0.18$	$1.77 \pm 0.17$
Relative growth rate (mm $m^{-1} y^{-1}$ )	Small		
Ridge		$11.20 \pm 1.29$	$7.73 \pm 1.02$
Lower slope		$11.08 \pm 1.02$	$9.44 \pm 1.50$
Combined		$11.14 \pm 0.80$	$8.59 \pm 0.90$

rate in the HDI period was 28% lower than in the LDI period (Table 2;  $F = 19.7$ ,  $df = 1, 14$ ;  $P < 0.001$ ). Relative growth rate was 23% lower in the HDI than LDI period (Table 2;  $F = 13.8$ ,  $df = 1, 14$ ;  $P = 0.002$ ). The effect of topography on  $m_a$ , agr and rgr of small trees was not significant ( $F = 0.73$ ,  $0.55$  and  $0.28$ , respectively;  $df = 1, 13$ ;  $P > 0.41$ ); nor was the interaction between period and topography significant ( $F = 1.89$ ,  $0.47$  and  $1.79$ , respectively;  $df = 1, 14$ ;  $P > 0.19$ ). Nevertheless, rgr decreased by 14.8% on lower slopes and 31.0% on the ridges. The result was similar for  $m_a$  of all trees (topography,  $F = 1.19$ ; and interaction  $F = 1.46$ ;  $P > 0.25$ ). One-sample t-tests showed that mean differences between periods (HDI – LDI) were not significantly different from 0 for all- and small-tree mortality rates ( $t = -0.40$ ,  $P = 0.695$ ;  $t = -0.52$ ,  $P = 0.613$ ; respectively) but were highly significantly different for agr and rgr of small trees ( $t = -4.52$ ,  $P < 0.001$ ;  $t = -3.63$ ,  $P = 0.002$ ; respectively).

From randomization procedure 1, mortalities of all and small trees did not differ significantly (for  $P \leq 0.05$ ) between periods in any run, but for agr and rgr of small trees 19 and 15 respectively of the 50 runs were significant ( $F$  with  $df = 1, 14$ ). In all significant cases, the mean agr or rgr in the LDI period was greater than that in the HDI period (overall 48 and 45/50 runs respectively). From randomization procedure 2, neither period nor topography was significant in any run for mortalities of all and small trees, although the period  $\times$  topography interaction was significant in correspondingly five and four runs. By contrast, agr and rgr differed between

**Table 3.** Mean mortality,  $m_a$ , and relative growth, rgr, rates for small trees (10–<50 cm gbh) of 19 species with  $n \geq 50$  trees (at start of both intervals for mortality) for the low (LDI; 1986–96) and high (HDI; 1996–99) drought intensity periods at Danum. Intervals for individual species ranged from 9.83 to 10.21 y for LDI, and from 2.38 to 2.96 for HDI, periods (means 10.01 and 2.62 y).

Species	Mortality rate (% $y^{-1}$ )					Relative growth rate ( $mm\ m^{-1}\ y^{-1}$ )				
	LDI period		HDI period			LDI period		HDI period		
	$n_{86}$	$m_{a86-96}$	$n_{96}$	$m_{a96-99}$	ratio <sup>1</sup>	$n_{86}$	rgr <sub>86-96</sub>	$n_{96}$	rgr <sub>96-99</sub>	ratio <sup>2</sup>
<i>Aporosa falcifera</i>	74	0.84	73	1.59	1.89 a	57	12.80	69	5.52	0.43 B-
<i>Ardisia colorata</i>	166	1.28	179	1.12	0.88	125	12.35	152	8.18	0.66 b-
<i>Baccaurea stipulata</i>	76	1.26	68	1.08	0.85	57	8.38	61	4.74	0.57 b-
<i>Cleistanthus glaber</i>	117	1.25	109	1.17	0.93	84	7.87	90	4.16	0.53 b-
<i>Dacryodes rostrata</i>	59	0.71	59	3.28	4.62 A	52	7.68	52	7.50	0.98
<i>Dimorphocalyx muricatus</i>	275	0.95	255	1.74	1.83 a	226	5.22	223	3.96	0.76
<i>Fordia splendissima</i>	156	1.00	160	1.94	1.95 a	118	9.59	132	8.12	0.85
<i>Litsea caulocarpa</i>	105	2.32	99	6.15	2.65 A	66	18.20	74	16.38	0.90
<i>Lophopetalum beccarianum</i>	71	0.57	81	0.00	0.00	64	15.11	75	13.62	0.90
<i>Madhuca korthalsii</i>	112	0.55	123	0.92	1.67 a	97	10.35	110	8.84	0.85
<i>Mallotus penangensis</i>	58	1.44	67	1.02	0.71	49	11.87	60	11.91	1.00
<i>Mallotus wrayi</i>	712	1.49	701	1.74	1.17	568	9.09	622	7.12	0.78
<i>Maschalocorymbus corymbosus</i>	120	3.86	105	3.03	0.79	65	8.44	85	7.26	0.86
<i>Polyalthia cauliflora</i>	123	1.28	113	1.35	1.05	104	4.77	105	2.86	0.60 b-
<i>Polyalthia rumphii</i>	52	1.02	50	0.00	0.00	45	8.62	48	8.16	0.95
<i>Polyalthia sumatrana</i>	51	1.04	50	2.30	2.21 A	46	17.43	42	16.73	0.96
<i>Polyalthia xanthopetala</i>	59	3.05	55	7.60	2.49 A	41	11.17	44	6.66	0.60 b-
<i>Reinwardtiidendron humile</i>	76	3.18	60	3.70	1.16	49	4.97	52	-1.04	-0.21 B-
<i>Shorea fallax</i>	84	2.13	97	3.47	1.63 a	61	17.71	84	8.03	0.45 B-
Totals	2546		2504			1974		2180		
Weighted means		1.49		2.01			9.65		7.30	

<sup>1</sup> For mortality rate: 'A' indicates that the ratio of HDI period/LDI period  $m_a$  was  $\leq 2.0$  (100% increase), and 'a' the ratio was  $\leq 1.5$  (50% increase).

<sup>2</sup> For relative growth rate: 'B-' indicates that the ratio of HDI period/LDI period rgr was  $< 0.50$  (50% decrease), and 'b-' the ratio was  $< 0.25$  (25% decrease).

periods in 17 and 15 runs respectively, topography was not significant in any run, and the interaction was significant in just two runs for rgr. Differences between periods were consistently in the same direction, as in procedure 1 for all significant runs (overall 47 and 45/50 respectively). Clearly, the power of the randomization tests, with  $n = 8$  subplots, was lower than that of the analysis of variance, with all  $n = 16$  subplots.

### Species' responses

Relative differences between species in  $m_a$  and rgr showed strong agreement between periods. The  $m_a$  values in the LDI and HDI periods were significantly positively correlated ( $r = 0.671$ ,  $df = 17$ ,  $P = 0.002$ ) as were the values of rgr ( $r = 0.818$ ,  $df = 17$ ,  $P < 0.001$ ). Annualized mortality and rgr were not correlated with one another in either the LDI or HDI periods ( $r = -0.040$  and  $0.063$ ,  $df = 17$ ,  $P \geq 0.78$ ), indicating no 'trade-off' in responses across species.

Of the 19 species with  $\geq 50$  trees in both periods, 12 exhibited increases and seven decreases in  $m_a$  between the LDI and HDI period (Table 3). Four species, *Dacryodes rostrata*, *Litsea caulocarpa*, *Polyalthia sumatrana* and *P. xanthopetala*, had  $\geq 100\%$  higher values of  $m_a$  in the

HDI period compared with the LDI period: their values were also substantially higher than those for other species in the HDI period. Five further species had increases in  $m_a$  of between  $\geq 50$  and 100% (Table 3). Two species had zero mortality rates in the HDI period.

Eighteen species had decreases in rgr from the LDI to HDI period, and one (*Mallotus penangensis*) showed no change (Table 3). Three species, *Aporosa falcifera*, *Reinwardtiidendron humile* (with negative rgr in HDI) and *Shorea fallax*, had decreases in rgr of  $\geq 50\%$ , and five other species decreased by 25–< 50% (Table 3). For the 51 species with  $\geq 20$  trees in both periods, 40 decreased and 11 increased their rgr from LDI to HDI periods.

Four species of particular interest from previous work are the ubiquitous and highly dominant understorey species, *Mallotus wrayi*; and the proposed guild of drought-tolerant/avoiding understorey species *Dimorphocalyx muricatus*, *Cleistanthus glaber* and *Lophopetalum beccarianum* (Newbery *et al.* 1996). Mortality rate and rgr of *M. wrayi* changed little between the two periods (Table 3). For *D. muricatus*,  $m_a$  increased by *c.* 80% whilst rgr decreased by *c.* 25% from the LDI to HDI period. *Cleistanthus glaber* showed little change in  $m_a$  from the LDI to HDI period, but its rgr decreased by almost 50%. For *L. beccarianum*,  $m_a$  fell to zero in the HDI period but the rgr remained similar for the periods. These proposed drought



tolerant/avoiding species therefore showed a mixed set of responses to increasing drought intensity, a set not readily distinguishable from that of the other species in Table 3.

## DISCUSSION

### Intensity of droughts at Danum

The 1998 drought was a significant and strong event for NW Sabah in terms of cumulative rainfall deficit (Kota Kinabalu, Labuan Island and Kudat) but of more moderate intensity in SE Sabah (Tawau and Lahad Datu). The rainfall pattern at Danum is generally better correlated with the SE than NW sites (Walsh & Newbery 1999). This 1998 event ranked reasonably highly among the recent Bornean droughts of ecological significance (cf. Beaman *et al.* 1985, Brünig 1969, 1971; Goldammer & Siebert 1990, Harrison 2001, Leighton & Wirawan 1996, Mori 2000); it was not as intense as that in 1982–83 judging by the Tawau and Lahad Datu records (Walsh 1996b, Walsh & Newbery 1999). During the 1998 main event many of the canopy and emergent trees became defoliated (G. Reynolds & R. P. D. Walsh, *pers. comm.*)

The rainfall data for Danum showed important site-specific features in that there was also a moderate drought in 1992 at Danum, one which was not remarked upon elsewhere in Sabah. This 17.5-y record was essential for defining the drought intensities of the two enumeration periods and understanding the contingent forest dynamics. Whilst the definition of drought relied on the general threshold of 100 mm for the 30-d rainfall sum, this still needs to be confirmed by evapotranspiration estimates for the forest at Danum. It is furthermore likely that different species and size classes would have been affected at earlier or later times. The timing of enumerations with regard to droughts is problematic because at almost any time the forest is subject to some immediate, recent or lagged effects. For instance, the first enumeration in 1985–86 was at the time of a minor drought, and it was 3 y after the strong 1982–83 event.

Rainfall deficit alone may not accurately reflect soil water potential and the limitation of water supply to trees in a period of drought. A further important consideration is the replacement of depleted soil water reserves with depth between droughts (R. P. D. Walsh, *pers. comm.*). It is possible that the much lower-than-normal rainfall in November 1997 to February 1998 led to a relatively greater stress for trees during the main 1998 event, compared with the one in 1992 (Figure 1), than is suggested by the drought intensity values. The effect of clustering of droughts may therefore need to consider the between-drought rainfall more carefully, and a dynamic

hydrological model for Danum is required to better estimate changing soil water deficits.

### Effect of droughts on the forest at Danum

Mortality levels of 1.5%  $y^{-1}$  (Table 2) at Danum were below the pan-tropical average of *c.* 1.8%  $y^{-1}$  (Phillips *et al.* 1994, Swaine *et al.* 1987). The forest appeared to be resistant to droughts of the 1992 and 1998 intensity in terms of  $m_a$  but this was not so for agr and rgr. The decrease in growth rates can be explained parsimoniously by the HDI period having proportionally more days of growth-limiting water stress than the LDI period. It is unknown whether those trees that died had lower growth rates than those which survived to be measured.

Understorey species (forming *c.* 85% of small trees 10–<50 cm gbh) are seen as a protective layer for saplings of the more drought-sensitive canopy species, many of which are dipterocarps (Newbery *et al.* 1999). Whilst the results of the present analysis do not directly test this hypothesis,  $m_a$  in the understorey remained almost constant despite the increasing drought intensity. Analysis at the species level revealed no interpretable patterns: there were no obvious differences between the postulated drought-tolerant/avoiding guild (Newbery *et al.* 1996) and other species. The present study did indicate some species which could be interpreted as being 'drought-sensitive'. Possibly a much stronger drought would have shown greater differentiation in dynamics between guild and non-guild species.

Comparisons with other sites in the same region around 1998 are limited. A more severe drought than at Danum occurred in Lambir National Park, Sarawak (Nakagawa *et al.* 2000), with January–March having a CRD of 160 mm, and the 30-d running totals fell below 100 mm for 89 d (Potts 2003). Nakagawa *et al.* (2000) recorded trees  $\geq 10$  cm dbh (31.4 cm gbh) in a 1.38-ha plot. In their 'non-drought' period of 1993–97,  $m_a$  was 0.89%  $y^{-1}$  whilst in the 'drought' period of 1997–98 it was 6.37%  $y^{-1}$ . Potts (2003) recensused 2.1 ha of forest for trees  $\geq 1$  cm dbh (3.14 cm gbh) at similar times in another site at Lambir and found corresponding values of  $m_a$  of 2.40 and 7.63%  $y^{-1}$ . In neither case was a correction for difference in intervals made, nor were growth rates estimated.

### Role of droughts in ecosystem dynamics

The findings support the notion that the trees  $\geq 10$  cm gbh forming the forest at Danum are largely well-adapted to droughts of the 1992/98 intensity (Newbery *et al.* 1992, 1999) and the various species tolerate and/or avoid

the stress where they grow on the topographic gradient (Gibbons & Newbery 2003, Newbery *et al.* 1996). The full re-enumeration of the main plots in 2001 (authors' unpubl. data) will allow for lagged mortality and the effect of reduced rgr on  $m_a$  to be tested. The 17.5-y record at Danum is possibly not long enough to say with confidence that the spectrum of frequency and intensity shown in Figure 1 is representative of the last 1–2 centuries: historical records elsewhere indicate that much stronger droughts may occur unpredictably once in several decades (Walsh 1996a, b).

The forest at Danum showed an intriguing compensation effect in its dynamics between the LDI and HDI periods. In the LDI period, subplots with relatively high agr had *higher*  $m_a$ -values than those with relatively low agr suggesting that subplots with fast growth created more light competition and then mortality rose. However, in the HDI period the opposite occurred: subplots with relatively high agr had *lower*  $m_a$ -values than those with relatively low agr, probably because high-agr subplots had more light as a result of the defoliation in the canopy caused by the higher drought intensity and this allowed better survival. Nevertheless, agr was strongly positively correlated across subplots whilst  $m_a$  was not, so generally high- and low-agr subplots switched  $m_a$  levels in opposite ways over time. The net result was little change in  $m_a$  between periods, although average agr and rgr declined from the LDI to HDI period.

Droughts as strong as the one in 1998 may also have affected trees < 10 cm gbh at Danum, as was shown for seedlings at Lambir in the same year by Delissio & Primack (2003). This would obviously have short-term consequences for recruitment. Nevertheless, if such droughts are part of the 'normal' environment, a stable species composition of trees  $\geq 10$  cm gbh would be expected in the long-term. A rather prosaic conclusion is that the present forest at Danum is simply composed of species that are adapted to this regime of repeated disturbances: what appears 'extreme' within a short-term study of 10–20 y is but a small part of a much larger spectrum of events of varying intensity leading to many immediate, lagged and overlapping effects on the forest.

Important questions for future work are: (1) Above what intensity of drought are the present species at Danum unable to tolerate the stress imposed, and when that threshold is passed what are the long-term consequences for the forest? (2) If the frequency of medium/low intensity droughts increases further in the coming decades, will the forest be sufficiently resilient in the necessarily shorter between-drought intervals? (3) Given that the forest at Danum is probably still aggrading after the very strong disturbing drought of 1878, do the dynamic processes allow greater resistance/resilience to moderate droughts compared with when the forest is at maximum site biomass?

Droughts are thought to be a major factor determining the structure and composition of Bornean rain-forest ecosystems (Brünig 1969, 1971). The response of a forest to drought involves many complex processes, however. It occurs over several time scales, is contingent on the climate at a given site, and is dependent in detail on the species and size classes of the trees present. Unless very severe (see Leighton & Wirawan 1996), droughts do not normally have immediate impact in terms of mortality, although a long period of increasingly severe water stress would be expected to lead to tree death sooner or later, either directly by xylem cavitation or indirectly by reduced growth rates (Walsh & Newbery 1999).

Continued long-term measurement of the permanent plots at Danum is an empirically reliable way of detecting any lag effects of reduced rgr on tree mortality, showing possible compensatory growth (recovery) after a drought, and determining whether these resilience mechanisms, in the understorey especially, lead to long-term ecosystem stability. Understanding how this stability might be maintained is a major prerequisite of conservation and wise management of the tropical rain forest.

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#### LITERATURE CITED

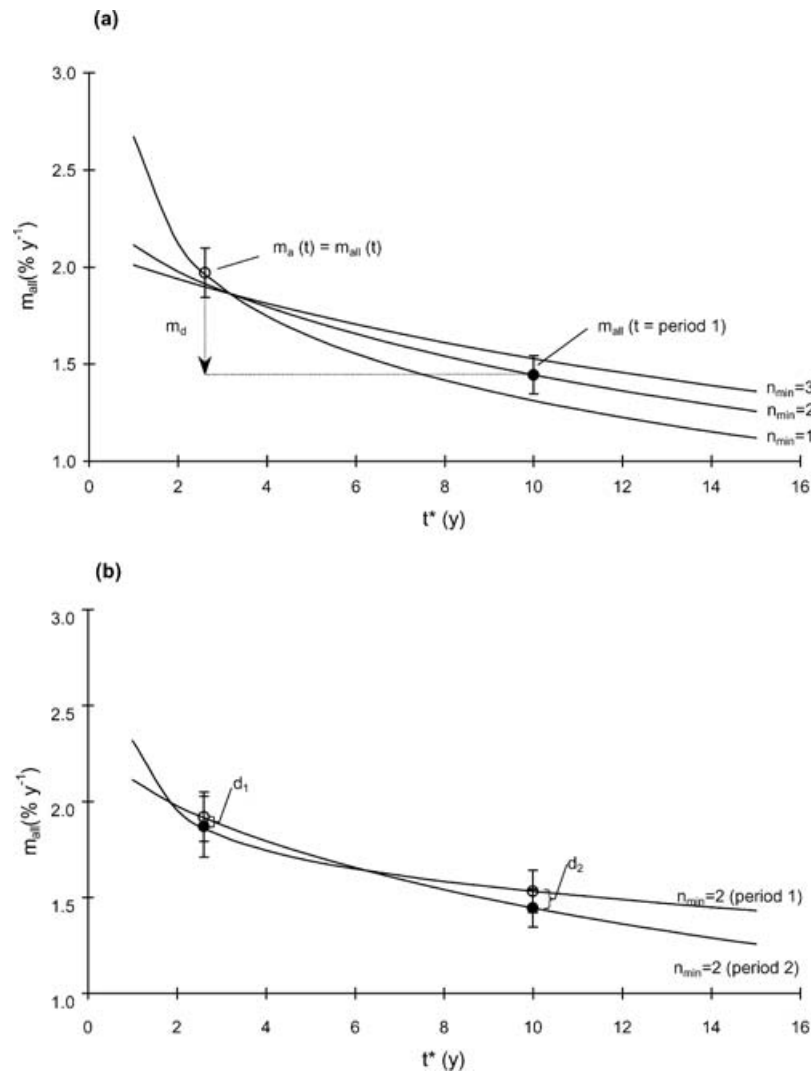
- ALDER, D. 1995. *Growth modelling for mixed tropical forests*. Forestry Papers No. 30. Oxford Forestry Institute, 231 pp.
- BEAMAN, R. S., BEAMAN, J. H., MARSH, C. W. & WOODS, P. V. 1985. Drought and forest fires in Sabah in 1983. *Sabah Society Journal* 10:10–30.

- BRÜNIG, E. F. 1969. On the seasonality of droughts in the lowlands of Sarawak (Borneo). *Erdkunde* 2:127–133.
- BRÜNIG, E. F. 1971. On the ecological significance of drought in the equatorial wet evergreen (rain) forest of Sarawak (Borneo). Pp. 66–97 in Flenley, J. R. (ed.). *Transactions of the 1st symposium on Malesian ecology*, Department of Geography, Hull University, UK.
- CONDIT, R. 1998. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change* 39:413–427.
- DELISSIO, L. J. & PRIMACK, R. B. 2003. The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest. *Journal of Tropical Ecology* 19:489–500.
- GIBBONS, J. M. & NEWBERY, D. M. 2003. Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. *Plant Ecology* 164:1–18.
- GOLDAMMER, J. G. & SEIBERT, B. 1990. The impact of droughts and forest fires on tropical lowland rain forest of East Kalimantan. Pp. 11–31 in Goldammer, J. G. (ed.). *Fire in the tropical biota*. Springer-Verlag, Berlin.
- HÄMMERLI, A. 1999. *The effect of drought on mortality and growth of trees in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia*. Diploma thesis. University of Bern, Switzerland.
- HARRISON, R. D. 2001. Drought and the consequences of El Niño in Borneo: a case study of figs. *Population Ecology* 43:63–75.
- HULME, M. & VINER, D. 1998. A climate change scenario for the tropics. *Climatic Change* 39:145–176.
- LEIGHTON, M. & WIRAWAN, N. 1996. Catastrophic drought and fire in Borneo tropical rain forest associated with 1982–1983 El Niño southern oscillation event. Pp. 75–102 in Prance, G. T. (ed.). *Tropical rain forest and world atmosphere*. AAAS, New York.
- MARSH, C. W. & GREER, A. G. 1992. Forest land-use in Sabah, Malaysia: an introduction to the Danum Valley. *Philosophical Transactions of the Royal Society, London, B* 335:331–339.
- MORI, T. 2000. Effects of drought and forest fires on dipterocarp forest in East Kalimantan. Pp. 31–45 in Guhardja, E., Fatawi, M., Sutisna, M., Mori, T. & Ohta, S. (eds), *Rainforest ecosystems of East Kalimantan: El Niño, fire and human impacts*. Springer-Verlag, Berlin.
- 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.
- NEWBERY, D. M., CAMPBELL, E. J. F., LEE, Y. F. & RIDSDALE, C. E. 1992. Primary lowland dipterocarp forest at Danum Valley, Sabah, Malaysia: structure, relative abundance and family composition. *Philosophical Transactions of the Royal Society, London, B* 335:341–356.
- NEWBERY, 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.
- NEWBERY, D. M., KENNEDY, D. N., PETOL, G. H., MADANI, L. & RIDSDALE, C. E. 1999. Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah, Malaysia, and the role of the understorey. *Philosophical Transactions of the Royal Society, London, B* 354:1763–1782. [See also Erratum. *Ibid.* 355: 1865.]
- PAYNE, R. W. (Ed.) 2000. *The guide to Genstat*. Vols 1 and 2. Lawes Agricultural Trust, Rothamsted.
- PHILLIPS, O. L., HALL, P., GENTRY, A. H., SAWYER, S. A. & VASQUEZ, R. 1994. Dynamics and species richness of tropical rain forests. *Proceedings of the National Academy of Sciences, USA* 91:2805–2809.
- POTTS, M. D. 2003. Drought in a Bornean everwet rain forest. *Journal of Ecology* 91:467–474.
- SHEIL, D. & MAY, R. M. 1996. Mortality and recruitment rate evaluations in heterogeneous tropical forests. *Journal of Ecology* 84:91–100.
- SHEIL, D., BURSLEM, D. F. R. P. & ALDER, D. 1995. The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology* 83:331–333.
- SWAINE, M. D., LIEBERMAN, D. & PUTZ, F. E. 1987. The dynamics of tree populations in tropical forest: a review. *Journal of Tropical Ecology* 3:359–69.
- TIMMERMANN, 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* 398:694–697.
- WALSH, R. P. D. 1996a. Climate. Pp. 159–205 in Richards, P. W. *The tropical rain forest*. (Second edition). Cambridge University Press, Cambridge.
- WALSH, R. P. D. 1996b. 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. & NEWBERY, D. M. 1999. The ecoclimatology of Danum, Sabah, in the context of the world's rain forest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society, London, B* 354:1869–1883.
- WHITMORE, T. C. 1984. *Tropical rain forests of the Far East*. (Second edition). Clarendon Press, Oxford.
- WHITMORE, T. C. & BURSLEM, D. F. R. P. 1998. Major disturbances in tropical rainforests. Pp. 549–565 in Newbery, D. M., Prins, H. H. T. & Brown, N. D. (eds), *Dynamics of tropical communities*. Blackwell Science, Oxford.
- WINER, B. J., BROWN, D. R. & MICHELS, K. M. 1991. *Statistical principles in experimental design*. (Third edition). McGraw-Hill, New York.
- WRIGHT, P. S. 1975. *The Soils of Sabah. Volume 3: Western Parts of Tawau and Lahad Datu Districts*. Land Resource Study 20, Ministry of Overseas Development, London.

## APPENDIX 1: CORRECTION OF ANNUALIZED MORTALITY RATES FOR TIME INTERVAL DIFFERENCE WITH A. HÄMMERLI

### Introduction to the problem

In communities with a heterogeneous distribution of  $m_a$  at the group (e.g. species) level, annualized mortality rates will be lower for longer compared with shorter census intervals (Sheil & May 1996). Comparing values of  $m_a$  from two time intervals of unequal length with an extreme event occurring in the shorter one will bias the difference (make it larger) and hence overestimate the effect of the event. The largest problem in estimating group mortalities is that in highly diverse communities, such as the forest at Danum, most species are rare.



**App. Figure 1.** Overall mortality based on group mortalities,  $m_{all}$ , as a function of census interval ( $t$ ) for (a) period 2 (1996–99) and  $n_{min}=1, 2$  and 3, with the value for mean annual mortality rate at the subplot level  $\pm 1$  SE (open circle), the value of  $m_{all}$  at  $t =$  interval length of period 1 (1986–96) (filled circle), and  $m_d$  indicating the reduction applied to  $m_a$  after the correction; (b) periods 1 and 2 for  $n_{min}= 2$ , with the values for the uncorrected (open circles) and the corrected (filled circles) mortality rates ( $\pm 1$  SE). Following a line (period 1 or 2) from an open to filled circle indicates the shift in values due to the correction for time interval and group mortality differences:  $d_1$  (at  $t = 2.61$ ) and  $d_2$  (at  $t = 9.99$ ) indicate the differences in mortality rates (between periods 1 and 2) applying the correction from the longer to the shorter interval ( $d_1$ ) and from the shorter to the longer one ( $d_2$ ). Note that the points might not be exactly on the lines due to variation among subplots.

Sheil & May (1996) suggested the calculation of an overall average mortality as:

$$m_{all}(t^*) = 1 - \left( \frac{\left[ \sum_{i=1}^S (n_{i0}(1 - m_i)^{t^*}) \right]}{\sum_{i=1}^S n_{i0}} \right)^{\frac{1}{t^*}}$$

where  $S$  is the number of groups (species),  $n_{i0}$  is the number of individuals of group  $i$  at time 0,  $m_i$  is annual mortality of group  $i$  and  $t^*$  is the census interval. This formulation takes into account differences in mortality rates across all groups of trees in a certain area of forest. In a natural, species-rich forest, however, group mortality estimates for rare species are unreliable because their sample sizes are so small. From

the binomial distribution, standard errors are particularly large when  $n_{i0} = 1, 2$  or 3, so that  $m_{all}$  is sensitive to these ‘extreme’ mortality rates.

Species with only one individual make up a considerable percentage of the whole population and they account for a large majority of the mortality rate values of 0 and 1. Therefore, including all trees of all species would lead to large errors in a correction procedure for differences in census interval. The function of  $m_{all}$  on  $t^*$  can thus be made conditional on a new variable, the minimum number of individuals per species ( $n_{min}$ ).

### The correction procedure

For each subplot in a given period (1 or 2) the annualized mortality rates were found from the general equation for  $m_a$  given in the main

text (*Rate calculations; Mortality*) and using just those species in the subplot with  $n_{i0} \geq n_{min}$  (all trees  $\geq 10$  gbh). These S values of  $n_{i0}$  and  $m_i$  were then placed in the equation above and  $m_{all}$  was found for a range of  $t^*$  which covered the periods enumerated at Danum, viz. 1–15 y. At  $t^* = 1$  y,  $m_{all}$  decreased steeply as  $n_{min}$  changed from 1 to 4, and then decreased more gradually to  $n_{min} = 15$ . But at  $t^* = 10$  y,  $m_{all}$  increased slightly to a maximum at  $n_{min} = 5$  and then declined. This was a consequence of the much steeper fall in  $m_{all}$  with  $t^*$  at  $n_{min} = 1$  (strong heterogeneity in  $m_i$ ) compared with  $n_{min} = 5$  where the rare species are omitted (weaker heterogeneity). At  $n_{min} = 15$  the change in  $m_{all}$  was very small (due to the homogeneity in  $m_i$  among the fewer common species). Nevertheless, as  $n_{min}$  increased the SE of the subplot values rose almost linearly. This was because the higher the value of  $n_{min}$  the more different were the subplots in the common species that they retained. A simple optimization procedure was therefore sought that minimized the error of mean  $m_{all}$  at the subplot level but gave the most reliable estimates of  $m_i$  with which to find the function of  $m_{all}$  on  $t^*$  and hence the most acceptable correction factor.

For  $n_{min} = 1$ ,  $m_{all} = m_a$  at  $t = t^*$ , as shown for the period 2 in App. Figure 1a. The error bar shown in App. Figure 1b is the same as that in App. Figure 1a for these parameters. For  $t^* < t$ ,  $m_{all}$  is  $> m_a$  and for  $t^* > t$ ,  $m_{all}$  is  $< m_a$ . This effect was strongest at  $n_{min} = 1$ , but much less at  $n_{min} = 2$  and 3. Thus,  $m_{all}$  was calculated for  $n_{min} = 2$  because, with this value, (1) a large proportion of the 0- and 1-values of mortality rate was excluded (55.3% in period 1;  $n = 16$  subplots), (2) the subset still included a high percentage of trees (84.6%) and species (45.6%) averaged over the 16 subplots; and (3) the variability of  $m_{all}$  across the 16 subplots at  $n_{min} = 2$  was relatively low compared to that of  $m_{all}$  for  $n_{min} > 2$  (Hämmerli 1999). In App. Figure 1a,  $m_d$  indicates the difference between the observed period 2 mortality rate  $m_a$  and the corrected mortality rate  $m_{a-corr}$  that was calculated for  $m_{all}$  with  $t$  of the longer period 1 interval and  $n_{min} = 2$ .

The subset of trees and species with  $n_{min} = 2$  was then used to calculate  $m_{all}$  for all trees  $\geq 10$  cm gbh in each of the 16 subplots for period 2. This allowed a comparison of the two possible forms of correction and their corresponding differences in  $m_a$  between census intervals, viz. long-to-short ( $d_1$ ) and short-to-long ( $d_2$ ) (App. Figure 1b). The short-to-long approach was adopted because, for *this* data set, (1) on average there were more trees and species left in the subset for  $n_{min} = 2$ , and (2) a greater percentage of 0 and 1 mortality rates were excluded, compared with the long-to-short correction. Each subplot  $m_a$  was recalculated using the mean correction value (0.739).

With this correction procedure,  $m_a$  ( $\pm$  SE) at the subplot level for period 2 decreased by  $26.1 \pm 2.5\%$ , averaged over the 16 subplots. The procedure shown could be generally applied but the value of  $n_{min}$  and the direction of the correction will depend on the composition of the particular data set.

## Comments

The comparison of  $m_a$  for the two periods is determined by the value of the correction factor used. That the HDI period was the shorter of the two periods, any correction would lower its  $m_a$  and bring it closer to the LDI-period  $m_a$ . The analysis of Sheil & May (1996) considered one cohort with varying lengths of interval until remeasurement: in the present data set, the second period included recruits from the first one. A more important concern, however, is whether the species within the whole forest stand are homogeneous. If species can be subdivided into subspecies, or ecotypes, or size classes, then putting them further into truly homogeneous groups is required to strictly meet the assumptions of the equation of Sheil & May (1996). The method of finding  $m_a$  also relies on the idea that it is constant over time which would seem unrealistic in natural situations.