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Drought, fire and tree survival in a Borneo rain forest, East Kalimantan, Indonesia

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Summary

1 Droughts and fires are increasingly recognized as a significant component of tropical rain forest dynamics but detailed large-scale assessments of such events are scarce. Here we examine tree mortality in a lowland rainforest in East Kalimantan after an extreme drought (the most severe ever reported in a tropical forest study), and a subsequent fire. Eighteen 1.8-ha paired permanent plots that crossed a firebreak allowed us to examine the separate effects of the two events.

2 Eight months after the drought, stem mortality in unburned forests reached 18.5 ± 5.6% (average ± SD ≥ 10 cm diameter breast height, d.b.h.). After 21 months, this increased to 26.3 ± 5.0%. Mortality was higher in larger stems, being 46.6 ± 18.7% in stems > 80 cm d.b.h., but falling to 23.9 ± 3.7% in stems 10–20 cm d.b.h. (after 21 months). The burned forest showed an overall mortality of 64.2 ± 12.2%. This increased to 79.0 ± 10.2% after 21 months.

3 By subtracting mortality after drought alone from mortality with fire in each plot pair, we can estimate the distinct influence of drought and subsequent fire. Fire caused near complete mortality for individuals < 10 cm d.b.h., but did not increase tree mortality for individuals > 70 cm d.b.h.

4 Drought contributes approximately 30% of the stem death observed in the burned forest after 21 months but the estimated contributions to dead basal area and biomass are higher at 52% and 63%, respectively. The forest contained around 7.3 tonnes ha^{-1} (± 2.2, 95% confidence) of above-ground biomass as dead trees (≥ 10 cm d.b.h) prior to the drought, rising to 133 ± 30 tonnes ha^{-1} 21 months after drought alone, and 207 ± 50 tonnes ha^{-1} in burned forest.

5 *Eusideroxylon zwageri* survived the drought with only 5% mortality after 21 months. Overall per-species mortality appears negatively correlated to wood density, though *Koompassia malaccensis*, with 64% mortality, is an outlier.

6 Though species-specific mortality varied from 11 to 91% in burned forest, overall stem survival after fire was significantly correlated with greater bark thickness at larger sizes. Consequently, species well represented at large sizes, mainly Dipterocarpaceae, increase in relative dominance compared with smaller taxa. Palm mortality was low, reaching only 3% after drought and 10% in burned forest.

7 The stem mortalities recorded in this study are amongst the most severe ever observed in rainforest. Such droughts, though rare, are potent determinants of forest structure and composition. Drought and fire are an especially destructive combination as they act on larger and smaller stems, respectively.

Key-words: bark, biomass dynamics, diversity, forest fire, delayed mortality, large-scale disturbance, tree height, wood density.

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Introduction

Severe disturbances appear to be a significant component of tropical rain forest dynamics but detailed assessments of such rare events are scarce (Whitmore & Burslem 1998; Cochrane 2003). Historical records and palynological analyses imply that Borneo suffers occasional droughts, sometimes associated with fires (Brünig 1969; Goldammer & Seibert 1989; Brookfield *et al.* 1995; Dam *et al.* 2001). Droughts continue to occur on a supra-annual basis (Walsh & Newbery 1999). Here we report and distinguish the forest-stand-level impact of an unusually severe drought, and a subsequent fire.

Fire-induced tree mortality cannot usually be distinguished from mortality due to drought alone because fires strike only during droughts while drought mortality remains ongoing. Comparison of burned and nearby unburned forest provides the solution adopted here. We examine tree mortality caused by drought and by fire, and consider the influences of stem-size, species and bark thickness.

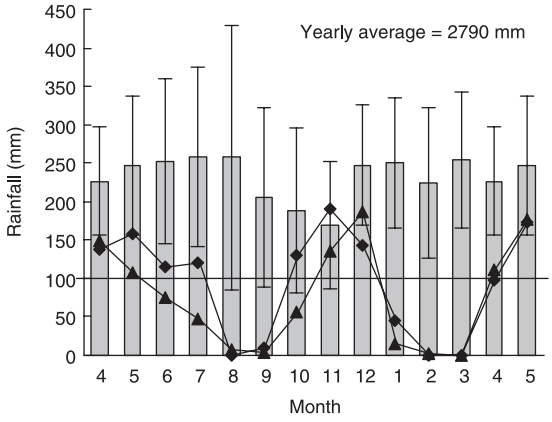


Fig. 2 Annual pattern of rainfall in Balikpapan airport from April to May over the period 1948–80 (bars; average ± SD, Vose *et al.* 1992). The lines represent the monthly rainfall in Samarinda (triangles) and Balikpapan airports (diamonds) during the 1997–98 season (collected by BMG Meteorological Service). In Balikpapan the two dry periods occurred from 12 July to 5 October 1997 and from 13 January to 24 April 1998. The cumulative rainfall in these periods was 48 and 13 mm, with 482 mm in the 99-day intermission. The number of days with a 7-day average below 3.3 mm was 86 and 99 (and 33 in the intermission). Similar values were recorded at Samarinda.

Materials and methods

SITES, RAINFALL AND FIRE

Sungai Wain is a 100-km^2 reserve including primary forest near Balikpapan, East Kalimantan, Indonesia (116.54° E, 1.16° S), 15 km from the sea (Fig. 1). Topography is gentle and varies from 40 to 140 m a.s.l. Soils are deep and infertile, with a high fraction of loam and clay (van Bremen *et al.* 1990). Wartonokadri is a similar forest sited 10 km to the north-east. Rainfall averages 2790 mm year^{-1} (Vose *et al.* 1992; Fig. 2). During the period 1948–80, short dry periods (rainfall < 100 mm month^{-1} over 1–2 months) occurred 33 times (Vose *et al.* 1992). Longer droughts (> over 3 months) occurred in 1982–83 and in 1997–98. This later drought consisted of two dry periods with a wetter intermission. The drought ended on 20 April 1998. We devised a refined version of the cumulative rainfall deficit (cf. Walsh & Newbery 1999) to consider monthly cumulative water deficits (cwd) in which deficits are gradually counterbalanced by cumulative precipitation above 100 mm month^{-1}, instead of returning to zero instantaneously, once the threshold of 100 mm monthly precipitation is reached.

The 1998 Sungai Wain fire occurred at the end of the drought (March to April). It was a surface fire (flame height 0.5 m, depth (width of burning front) 20–30 cm, speed 10–15 m h^{-1}, Mark van Nieuwstadt, personal observation) with an estimated intensity of 60 kW m^{-1} (cf. Alexander 1982). A 1 to 2 m wide firebreak helped stop the fire. Approximately one-third of the reserve

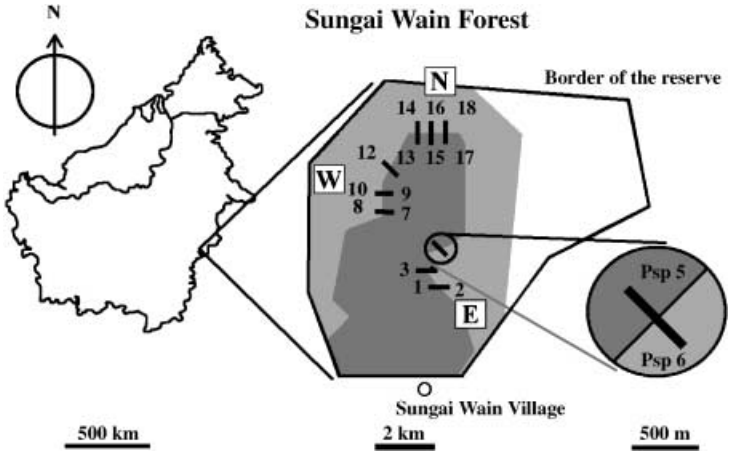


Fig. 1 The study location, Sungai Wain, in relation to Borneo. Enlargements show the forest (unburned area = dark grey, burned once = light grey, burned twice = white) and the paired-plot layout.

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burned for the first time in 1998. Additional information about these fires is given by Guhardja *et al.* (2000), Siegert *et al.* (2001), Slik (2001) and van Nieuwstadt (2002).

PLOT ALLOCATION, ASSESSMENT AND DATA

Five 10 × 200 m transects spaced by 100 m in Wartonokadri provided our estimate of dead tree densities before the drought (September 1997, Slik 2001). Here, mortality was assessed 4 months after the end of the drought (August 1998) and again after 22 months (February 2000).

In Sungai Wain forest, 18 permanent plots of 60 × 300 m (1.8 ha) were laid out in unburned forest and once-burned forest (Fig. 1). The plots were located in pairs across the firebreak that did not follow any topographical feature. The plots are nested in three groups spread over a total area of about 20 km^2. A narrower plot of 20 × 200 m (0.4 ha) was laid out within the larger plot. Topography was recorded at a scale of 20 × 20 m for the 1.8-ha plots and 10 × 10 m for the 0.4-ha plots (though these data pose analytical complications of spatial-dependence).

Two surveys were completed. The first was centred on December 1998 (8 months after the drought and fire) and the second on January 2000 (21 months after fire). In the first survey, all stems ≥ 28 cm d.b.h. (1.3 m) were labelled and assessed. All additional trees ≥ 8 cm d.b.h. were assessed in the 20 × 200 m subplot. In the analyses, lower limits of 10 cm and 30 cm d.b.h. are used. Palms were recorded but are not included in the general stem analyses.

For trees with buttresses or other irregularities at 1.30 m, the diameter was measured at a reference height 'x' of 30 cm above the deformity (Sheil 1995). A measuring tape was used to a height of 2.5 m. Above this, a ruler attached to a pole was rested against the stem and read from 10 m distance (Alder & Synnott 1992). To correct for the systematic deviation that stem tapering introduced into these measurements, we examined d.b.h. vs. $d.r.h._x$ (diameter at a reference height x). For a set of 43 trees of between 25 and 82 cm d.b.h. with straight stems, the d.b.h. was measured by tape, and diameters were estimated as described above at 2.5 m and 4.0 m height. We calculated the ratio ($d.r.h._x$/d.b.h.) anticipating that both diameter and height of measurement would be influential. A multiple linear regression indicated that the ratio was independent of d.b.h. ($F = 1.13$, $n = 43$). The best predictor was a power function ($d.r.h._x/d.b.h.) = 1.1816x^{-0.1168}$ ($R^2 = 0.40$, d.f. = 123, $F = 80.6$, $P < 0.001$), which was then used to estimate the 'd.b.h. equivalent' of stems measured above 1.30 m. Without this correction, basal-area estimates would be about 9% and 16% lower for trees measured at 2.0 m height and 4.0 m height, respectively. More specific analyses and larger samples would be needed to minimize biases with respect to each stand parameter of interest (Furnival 1961).

In subplots of 100 m^2 each, all dead and living seedlings and saplings (stem length > 50 cm and d.b.h. < 8 cm) were assessed and labelled. Sixteen unburned subplots and 51 burned subplots were recorded. The selected subplots were spread over four unburned and six burned plots. Diameter for these smaller stems was measured with callipers at 25 cm above ground level.

Individuals with a consistently leafless crown were considered 'dead' (at least above ground). We did not slash stems to seek live cambium. Trees long dead were excluded (these lacked all but primary branches and/or large portions of their bark). However, there were complications: trees killed above ground sometimes produced sprouts from below ground, and some trees with leafless crowns had resprouts along the main stem, although the bark below the point of sprouting was sometimes damaged around the entire stem circumference suggesting no viable connections to the root system. As these different determinations influence our estimates, we considered them separately in many analyses. However, unless specifically noted our summaries assign ambiguous stems as 'dead'. Fallen and snapped stems were noted.

We identified living and dead trees larger than 28 cm d.b.h. for 10 common and readily distinguished species. Wood densities follow Burgess (1966) and Suzuki (1999). Nomenclature follows Sidiyasa *et al.* (1999). The second survey only assessed mortality, resprouting and tree-falls.

Post-drought fire-dependent mortality (hereafter 'fire mortality') was estimated by subtracting the unburned forest mortality from that of the burned forest in each plot pair. These analyses assume that edge effects (i.e. the effect of the burned on the nearby unburned area) are negligible, and our exploratory analyses support this.

Above-ground biomass estimates employed equation 2 of Ketterings *et al.* (2001). Error is based on sample variance alone (without model bias and fit, Furnival 1961). Exploratory evaluations using other approaches (e.g. volume $\propto drh^{8/3}$) suggest similar patterns irrespective of the chosen volume or biomass estimator.

To test whether species-specific fire survival is related to bark thickness, we sampled 14 species in the unburned forest. A single 4 × 4 cm square bark sample was removed with a chisel at 1.3 m height, avoiding obvious anomalies. Callipers measured bark thickness on four sides of each hole.

The densities of living trees (14 species ≥ 10 cm d.b.h.) were compared between burned and unburned forest. These differences were examined against (i) coefficients of the log-log transformed relation between d.b.h. and bark thickness, and (ii) the upper 95% d.b.h. size limit for each population. Similar analyses addressed relative survival of nine species (identifiable when dead ≥ 30 cm d.b.h.) in the burned forest. Phylogenetic approaches proved unsuitable due to this limited sample of species (cf. Westoby *et al.* 1995).

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Table 1 Average percentages of dead trees above 10 cm d.b.h. per permanent sample plot at various assessments in the Wanariset Wartonokadri forest and Sungai Wain research forest. Two estimates are given based on the varying confidence with which stem death was indicated (see methods)

		Time (months)		Cumulative percentage dead trees	
Treatment	Average date	Since end of drought and fire	Since last observation	Total (Average ± SD)	Unambiguous (Average ± SD)
Wanariset Samboja Wartonokadri (5 plots, 599 trees)					
Drought	September 1997		–	2.6 ± 1.7	
	August 1998	4	11	11.4 ± 1.7	
	February 2000	22	19	22.2 ± 2.4	
Sungai Wain forest, unburned (9 p.s.p., 3221 trees)					
Drought	December 1998	8	–	18.5 ± 5.6	16.4 ± 5.7
	January 2000	21	13	26.3 ± 5.0	23.6 ± 5.4
Sungai Wain forest, burned (9 p.s.p., 2985 trees)					
Drought x fire	December 1998	8	–	64.2 ± 12.2	60.3 ± 12.0
	January 2000	21	13	79.0 ± 10.2	75.7 ± 11.0
Sungai Wain forest (9 paired p.s.p.)					
Exclusively fire	December 1998	8	–	47.8 ± 14.5	41.8 ± 14.6
	January 2000	21	13	55.4 ± 11.7	49.3 ± 12.4

Results

STAND STRUCTURE AND MORTALITY AT THE COMMUNITY LEVEL

At Wartonokadri, early in the drought, mean stem density (living and dead, ≥ 10 cm d.b.h.) was 627 ± 105 trees ha^{-1} (mean ± SD, $n = 5$), of which 610 ± 100 trees ha^{-1} were alive, i.e. standing dead trees were 2.6% ± 1.7 (Table 1). The basal area of all living and dead stems was 32.4 ± 7.0 m^2 ha^{-1} and of living stems alone was 31.5 ± 6.4 m^2 ha^{-1}. Wartonokadri was not significantly different from Sungai Wain in either stem density (*t*-test, $F = 0.37$, $P = 0.86$, d.f. = 21) or basal area ($F = 2.37$, $P = 0.85$, d.f. = 21). In the Wartonokadri plots 4 months after the drought, the percentage of dead trees rose to 11.4 ± 1.7%, corresponding with an 8.8% mortality over an 11-month period (Table 1). By 22 months after the drought dead stems had nearly doubled, resulting in 22.2 ± 2.4% dead trees (19.6% mortality).

At Sungai Wain, 8 months after the drought, the stem density (dead and living trees ≥ 10 cm d.b.h.) was 599 ± 82 ha^{-1} (average ± SD, $n = 9$), of which 487 ± 62 ha^{-1} remained alive. Assuming that about 2.6% were dead prior to the drought (cf. Wartonokadri), we estimate pre-drought densities of 584 ± 79 ha^{-1}. Eight months after the drought, mortality in the unburned Sungai Wain plots was similar to Wartonokadri, with 18.5 ± 5.6% dead trees. Mortality remained high, resulting in 26.3 ± 5.0% dead stems after 21 months, a mortality of 9.4 ± 3.6% among trees alive during the first census. By then total basal area was 29.6 ± 1.9 m^2 ha^{-1}, of which living stems contributed 21.9 ± 2.4 m^2 ha^{-1}. We estimated the live basal area to be 28.8 ± 1.9 m^2 ha^{-1} before the drought.

Unburned patches occurred in four 'burned' plots and amounted to 2.1% of the total area in the 0.4-ha plots and to 4.4% in the 1.8-ha plots. One plot provided half the area that escaped the fire. Such areas appear positively associated with valleys and low slopes (ignoring spatial non-independence: χ^2 test on 10×10 m, $n = 356$, and on 20×20 m, $n = 297$, subplots give $P < 0.001$ and $P = 0.008$, respectively). However, all site types had a high probability of burning. These patches are not excluded in our main analyses.

In Sungai Wain mean post-burn mortality was over three times unburned levels, and resulted in 192 ± 69 (≥ 10 cm d.b.h.) living stems ha^{-1} after 8 months and 113 ± 57 ha^{-1} after 21 months. Of surviving stems in the burned forest, 6 ± 11% grew on unburned ground. Trees alive at the first census had a mortality of 38.5 ± 8.7% in the following 13 months. Paired plot comparisons indicate a relatively consistent fire-dependent mortality of 47.8 ± 14.5% at the first census and 55.4 ± 11.7% at the second.

Stem density decreases with d.b.h. After drought, this pattern is accentuated, after fire the distribution becomes flatter (Fig. 3). Variation in basal area between the plots is influenced by the scattered presence of larger trees (> 80 cm d.b.h.). Two burned plots (14 and 16) were outliers in terms of basal area, because large stems locally occurred at a high density. The total basal area for stems > 80 cm d.b.h. was, respectively, 21.7 and 18.1 m^2 ha^{-1} in these plots, but averaged only 7.6 m^2 ha^{-1} for the other seven (as in Fig. 3d). Plot-by-plot summaries are provided in Appendices S1 and S2 (see Supplementary material).

While the percentage of dead trees increases with d.b.h. in the unburned forest, the opposite holds in burned forest (Fig. 4). Below 10 cm d.b.h., burned forest

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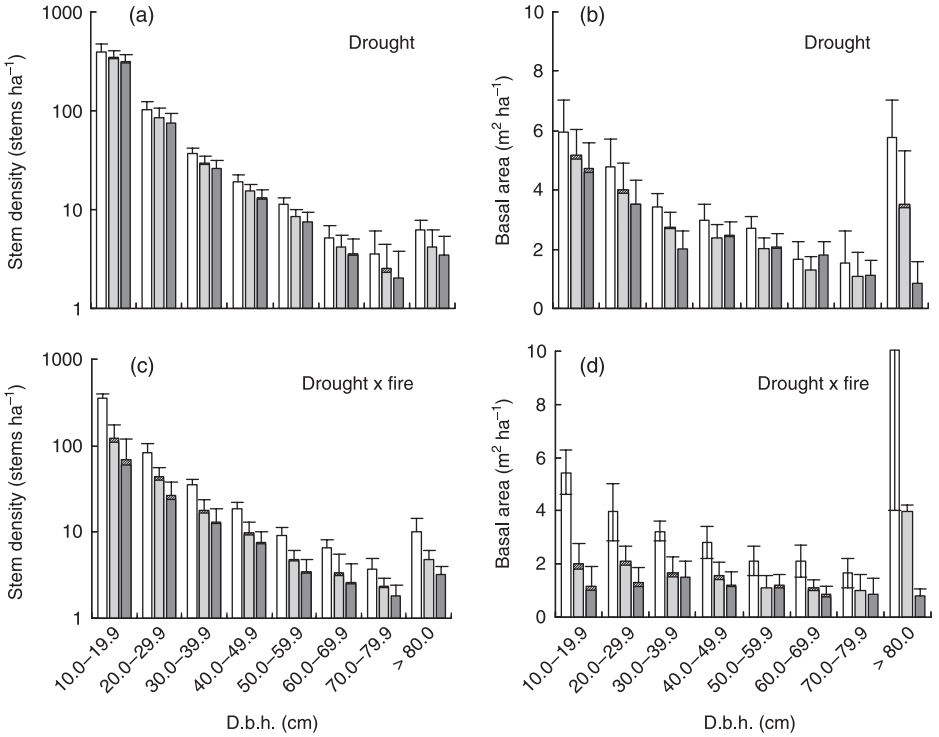


Fig. 3 Stand structure in unburned (a, b) and burned (c, d) plots. (a) and (c) show mean per-plot density of living stems per d.b.h. class (stems ha^{-1}) (average + SD, $n = 9$), and (b) and (d) show the basal area per d.b.h. class (m^2 ha^{-1}) (average + SD, $n = 9$). White bars = stand structure at the onset of the drought; light grey bars = 8 months after the end of the drought; dark grey bars = 21 months after the end of the drought. Hatched sections indicate stems for which survival is ambiguous. Two burned plots were excluded from the basal area calculations (see Methods).

mortality was above 80%. Below 5 cm d.b.h., it approached 100%. All *t*-tests between the percentages of dead trees in the unburned and burned plots after 21 months by 10-cm d.b.h. intervals up to 60–69.9 cm were significant at $P < 0.005$. At a larger diameter no significant difference were detected (pooling all stems over 70 cm gives $P = 0.3$).

In the unburned forest, delayed mortality between 8 and 21 months was similar across size classes. In the burned forest, mortality remained negatively related to d.b.h. Tree-falls were dominated by dead stems everywhere. Tree-fall frequency in the burned forest was 28% of the standing dead stems and 7.4% of living trees by the second year. Living tree-falls were lower in unburned forest (3.6%). Tree-falls (living and dead) decreased with size only in the burned forest.

Size-dependent mortality means that stem density, basal area and biomass summarize stand differences in distinctive ways. When all dead stems ≥ 10 cm d.b.h. were considered the unburned forest had 32% of the density compared with burned forest, but 54% of the basal area and 64% of the biomass, while for larger stems (≥ 40 cm d.b.h.) the respective estimates are both higher and more similar (68, 74 and 78%, respectively; see Fig. 5; note that we excluded plots to the north of the site as large stems are unevenly clumped in these samples). Our estimates suggest that before the drought the (Wartonokadri) forest contained around 7.3 ± 2.2 tonnes ha^{-1} (95% confidence) of above-ground biomass as dead standing trees, after 21 months the drought-stricken (Sungai Wain) forest held 133 ± 30 tonnes ha^{-1} of dead stems, while the equivalent number for burned forest was 207 ± 50 tonnes ha^{-1}.

SPECIES-SPECIFIC MORTALITY

Twenty-one months after the drought, dead stems species^{-1} (≥ 30 cm d.b.h.) ranged from 5% to 64% (Table 2). Dense timbered *Eusideroxylon zwageri* was especially resistant, while the emergent *Koompassia malaccensis* suffered considerable mortality. Variation was not significantly correlated with wood density when analysing across these species (Fig. 6, Pearson correlation coefficient = −0.16, $P = 0.65$, $n = 10$) but *K. malaccensis* mortality appears to be an outlier; such selective drought dieback of this species is neither previously reported nor consistent with the relative abundance of large stems despite previous droughts. Excluding *K. malaccensis* yields a significant negative correlation.

The percentage of dead trees per species varied from 11 to 91% in burned forest. In *Dipterocarpus confertus* and *Shorea ovalis* stems over 30 cm d.b.h. seemed unaffected by the fire. For most species, the fire mortality component was around 25%, though *Artocarpus anisophyllus* reached 67% (Table 2). When assessed by basal area (≥ 10 cm d.b.h.), the five most dominant families in unburned forest are, in order, Dipterocarpaceae, Lauraceae, Sapotaceae, Euphorbiaceae and

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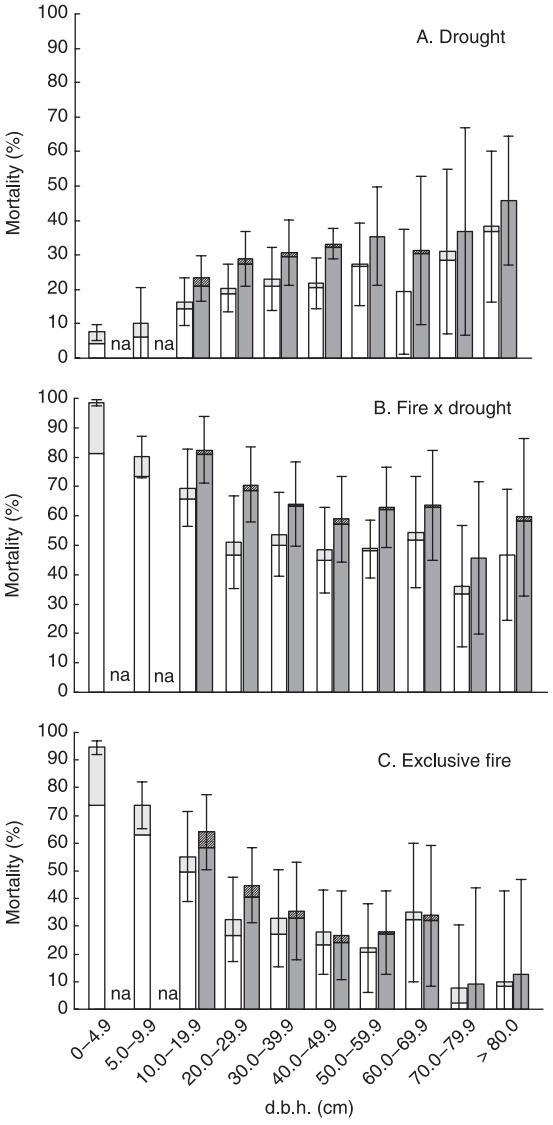


Fig. 4 Average percentage tree mortality per d.b.h. class (average ± SD, $n = 9$) in the Sungai Wain forest. (a) Unburned, (b) burned, and (c) 'fire mortality'. White bars = 8 months after the end of the drought; shaded bars = 21 months after the end of the drought. Hatched sections indicate stems for which survival is ambiguous. 'Fire mortality' is calculated by pairwise subtraction of the unburned from the burned mortality for each plot pair. Stems below 10 cm d.b.h. were monitored only once. Where values were not available 'na' is shown.

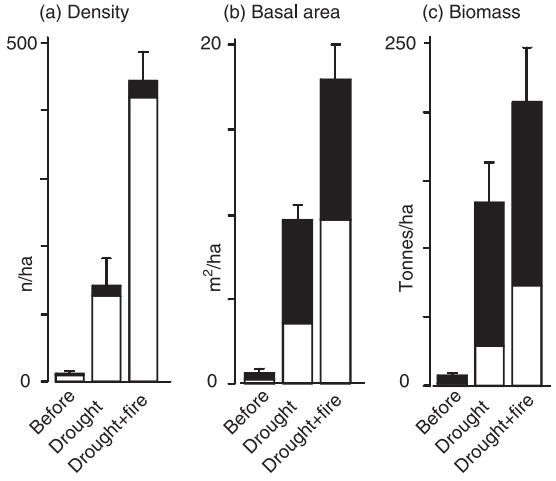


Fig. 5 Comparison of estimated standing dead stems density (a), basal area (b), and above-ground biomass (c) (equation 2 of Ketterings *et al*. 2001) in the six southerly plot pairs before (estimated using Wartonokadri observations, see Methods) and 21 months after drought and drought and fire. The contribution of stems between 10 and 40 cm d.b.h. are white, and those larger than 40 cm are black. Error bars are 95% confidence intervals based on per-plot sample variance treating each plot as independent.

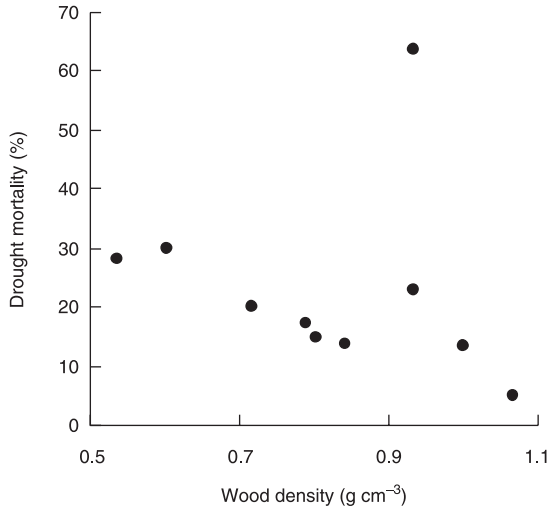


Fig. 6 Species-specific mortality of trees > 28 cm d.b.h. vs. specific wood density. The apparent high mortality outlier is *Koompassia malaccensis*.

Myrtaceae. After fire (second census) Euphorbiaceae moved ahead of Sapotaceae. However, relative density (stems ha^{-1}) showed that after the fire Dipterocarpaceae moved from third to first place while the other top six families maintained their rank (Euphorbiaceae, Sapotaceae, Myrtaceae, Myristicaceae, Lauraceae, Burseraceae). Palms (≥ 10 cm d.b.h.) were only 3 ± 4% dead after the drought and 10 ± 11% dead after the fire.

FIRE MORTALITY AND BARK THICKNESS

Log(d.b.h.) and log(bark thickness) (all species combined) fitted a linear regression (Fig. 7a). The percentage mortality per d.b.h. class attributed to fire (i.e. corrected for drought mortality) declined linearly with average bark thickness of trees in that class (Fig. 7b). A log-log regression again provided a good fit to all 14 species (mean R^2 ranging from 0.70 to 0.96%). Differences in tree densities over 10 cm d.b.h. in the unburned and the burned forest were examined using backwards-stepwise regression. Explanatory variables included the per-species intersect and gradients from the d.b.h. vs. bark thickness log-log regressions and the 95% d.b.h. limit ($n = 14$, for all fitted models $F < 2.52$, $P > 0.13$, NS). Also, a similar regression, using the same

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Table 2 Species specific mortality after drought and fire of trees above 30 cm d.b.h. in Sungai Wain forest 21 months after the end of the fire and drought. The percentage dead trees after 'drought' and 'drought + fire' are given as the average percentage dead trees per plot ($n = 6$). To calculate the additional mortality caused by fire, the mortality after drought per plot is subtracted pairwise from the mortality after 'drought + fire' for each pair of adjacent plot. Negative values in this second last column occur as an artefact caused by sample noise

			Percentage dead					
Species	Family	Wood density (g cm^{-3})	Drought	SD	Drought + fire	SD	Fire	SD
Artocarpus anisophyllus Miq.	Moraceae	0.72	20	27	92	17	67	24
Dipterocarpus confertus Sloot	Dipterocarpaceae	0.80	15	18	8	10	–14	19
Dipterocarpus cornutus Dyer	Dipterocarpaceae	0.84	14	13	29	6	15	18
Drypetes kikir Airy Shaw	Euphorbiaceae	1.00	13	14	31	30	27	18
Eusideroxylon zwageri Teijm. & Binn	Lauraceae	1.07	5	6	39	5	30	10
Gironniera nervosa Planch.	Ulmaceae	0.60	30	23	59	39	29	39
Koompasia malacensis Maing. Ex Benth	Caesalpiniodae	0.93	64	24	92	12	29	24
Madhuca kingiana (Brace) H.J. Lam	Sapotaceae	0.79	17	19	59	38	42	38
Shorea laevis Ridl.	Dipterocarpaceae	0.93	23	18	44	14	29	21
Shorea ovalis (Korth.) Blume	Dipterocarpaceae	0.54	28	22	20	27	–5	33

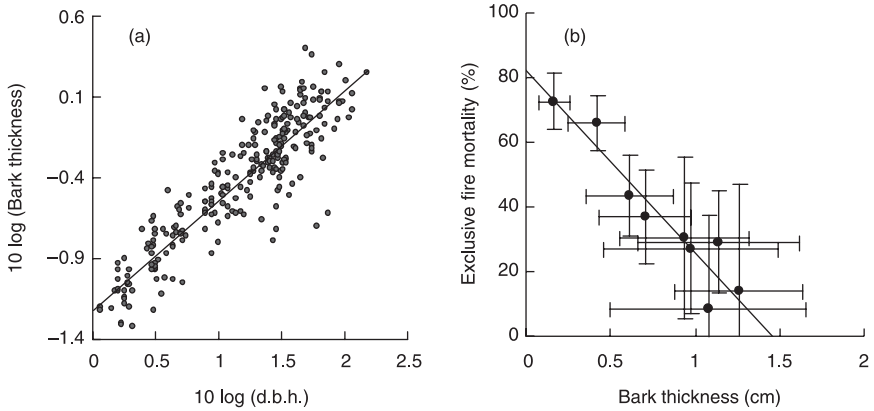


Fig. 7 The relationship between d.b.h., bark thickness and exclusive fire mortality. (a) The relationship between log d.b.h and log bark thickness (cm) for 16 species combined. Regression line: $y = 0.669x - 1.21$ ($R^2 = 0.788$). (b) Average bark thickness (± sd) per 10 cm d.b.h. class (of 16 species combined, as in Figure 5a) and the percentage mortality per d.b.h. class (mean ± sd) caused exclusively by fire. Regression line: $y = -56.3x + 82.1$ ($R^2 = 0.892$).

explanatory variables, against the percentage fire mortality of nine species above 30 cm d.b.h. showed no significant relationship ($F < 0.52$, $P = 0.57$, NS).

Discussion

DROUGHT MORTALITY

Our study describes one of the most severe drought effects ever reported in a tropical forest. Yet, it is not wholly without precedent. An explorer who visited Kutai, East Kalimantan, in 1879 reported a drought that lasted over 8 months, leaving a third of forest trees dead (Bock 1881 quoted in Brookfield *et al*. 1995). Our study shows how such events affect forest structure and composition. Mortality rose to 20–26% amongst trees > 10 cm d.b.h. 2 years after the drought, and species-specific mortality amongst trees > 30 cm d.b.h. varied tenfold, thus altering composition.

The estimated cumulative water deficit at Sungai Wain was more than twice that seen elsewhere, and tree mortality averaged six times higher (Table 3). The relationship between percentage drought-mortality after 20–22 months and the cwd is summarized adequately by a linear relationship ($y = 0.048x - 4.32$, $R^2 = 0.80$) or an exponential relationship ($y = 0.023e^{0.016x}$, $R^2 = 0.92$). Both models predict negligible influences while cwd remains below 100 mm (linear model) to 300 mm (exponential model). Above that, mortality increases rapidly. This lag probably results from soil water reserves (Poorter & Hayashida-Oliver 2000; van Dam 2001). Brünig (cited in Tyree *et al*. 1998) estimated that soil water depletion takes around 100 days in a northern Borneo forest (i.e. a cwd of approximately 330 mm).

Stomatal closure or leaf loss may slow or prevent embolism-inducing xylem tensions during drought (Tyree *et al*. 1998). Plants may die either because decreased photosynthesis leads to exhaustion of the

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Table 3 Mortality of trees above 10 cm d.b.h. resulting from drought events in tropical rain forests in tropical Asia and Latin America (for sites experiencing an average monthly rainfall over 100 mm)

	Site				
	Sarawak, Lambir (core and periphery)	Central Amazon, Manaus (site 1501)	Central Amazon, Manaus (site 1301)	East Kalimantan, Wartonokadri	East Kalimantan, Sungai Wain
Average					
Yearly rainfall (mm)	2700	> 2000	> 2000	2790	2790
Number of dry months	0	0	0	0	0
Drought event (< 100 mm rain per month)					
Year	1997–98	1997	1997	1997–98	1997–98
Duration rainfall deficit (months)	3	4	4	2 + 4*	2 + 4*
Total rain fall (mm)	139	195	195	10 + 142 (152)	10 + 142 (152)
Duration cwd (months)	3	5	5	3 + 5	3 + 5
Total rain fall during cwd period (mm)	139	295	295	140 + 316 (456)	140 + 316 (456)
cwd	162	205	205	190 + 258 (448)	190 + 258 (448)
Severe drought event (< 50 mm rain per month)					
Duration (months)	1 + 1	2	2	2 + 3	2 + 3
Total rain fall (mm)	37 + 49 (86)	55	55	10 + 45 (55)	10 + 45 (55)
Tree mortality					
Background annual mortality (% per year)	0.89	0.94	1.19	1.69†	1.69†
Time between observations (months)	12	19 – 13	14 – 13	11 – 19	15 – 13
Mortality since pre-drought observation (%) and (time since end of drought)	6.4 (4)–4.3 (4)	3.0 (8) – 4.8 (21)	2.2 (7) – 3.4 (20)	8.8 (4) – 19.6 (22)	16.5 [8] – 26.0 (21)
Drought induced mortality (%)‡	5.5 – 3.4	1.5 – 2.2	0.85 – 0.75§	7.3 – 15.4	14.4 – 22.1
Reference	Nakagawa *et al.* (2000)	Williamson *et al.* (2000)	Williamson *et al.* (2000)	This study	This study

*Balikpapan weather station: two dry spells, intervened by a 3-month wet period with a total 482 mm rainfall.
†Annual background mortality calculated from data from 1976 to 1982 in 6.5 ha of plots in primary forest in the ITCI concession, East Kalimantan (van Eijk-Bos & de Kock 1996).
‡The percentage drought-induced mortality is calculated as the observed mortality minus the expected background mortality during the observation period.
§The measure for the drought-induced mortality decreases because in the second year after the drought the post-mortality is below the average mortality before the drought.
cwd (mm), cumulative water deficit.

energy reserves, or because of failure to recover following hydraulic failure. In Sungai Wain, many tree species dropped most of their leaves. In such a state, the cost and risks of continued drought are uncertain. The drought's midway respite may have compounded plant stress and energy exhaustion. The brief rains initiated new leaf development, only for drought to strike again.

Background rates for forest tree mortality often appear relatively independent of stem diameter for larger trees (Lieberman & Lieberman 1987; Manokaran & Kochummen 1987; Gentry & Terborgh 1990), or show some decrease with size (Rankin de Merona *et al*. 1990; Clark & Clark 1996; Nakagawa *et al*. 2000; Sheil *et al*. 2000). An increase in survival with size is also typical for smaller seedling populations (e.g. Delissio & Primack 2003). The size-dependent increase in mortality in our study deviates from this typical background pattern. A similar, if less pronounced, pattern was found after drought in the Neotropics (Condit *et al*. 1995). As observed in this study (also Leighton & Wirawan 1986), drought has the greatest impact on the largest stems in East Kalimantan's lowland forests. Similar patterns are recorded following drought in seasonal dipterocarp forests in India (Seth *et al*. 1960) and in ridge top sites in peninsular Malaysia (Tang & Chang 1979) but not Lambir Hills, Sarawak (Nakagawa *et al*. 2000), where smaller stems suffered higher impacts. These size-related differences, and interspecific variation, are likely to be related to many factors, and may include root depth, mycorrhizal status (Becker *et al*. 1998), crown exposure, water use and susceptibility to xylem failure.

The drought survival of dense timbered *E. zwageri* is notable. Borchert (1994) found that in a tropical dry forest, the species on the driest sites had the densest timber, and could withstand higher negative xylem pressures. Vessel diameter is negatively correlated with wood density, so dense timbers usually have higher cavitation thresholds (Tyree *et al*. 1998), and Hacke *et al*. (2001) showed that high wood density results also from thicker-walled xylem vessels, which can withstand higher pressures. This drought tolerance may contribute to the relative dominance of *E. zwageri* in the region.

The hydraulic limitation hypothesis (HLH) predicts that, all else being held constant, water stress rises with tree height, thus increasing cavitation risks (as in temperate conifers, McDowell *et al*. 2002). If larger trees have better access to deeper soil water, they may be less affected by a moderate drought, but if this progresses to a point where all stems experience shortages, the HLH predicts that large stems are more vulnerable. In addition,

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smaller trees generally deplete their root zones more slowly than do larger, better-exposed individuals. Taller plants are exposed to greater desiccation loads while shaded plants stay cooler and can respire longer in dry conditions (Schwinning & Weiner 1998). As natural selection operates most forcefully where adaptations can most effectively extend viability, we should not be surprised to find multiple critical factors acting simultaneously (Westoby *et al*. 2002).

DROUGHT AS DISTURBANCE

The specific impacts of the drought were overshadowed by the subsequent fires, but in some important respects the effect of the drought was not only more extensive, but more severe. Drought mainly kills larger diameter stems and fire kills smaller stems. We estimate that even in burnt areas, around two-thirds of killed above-ground biomass is attributable to drought. Considerably more biomass may have died in the greater region from the drought (e.g. Nakagawa *et al*. 2000) than subsequently from the more localized fires. However, as stems can take years to decay, the implications for biomass and carbon remain uncertain. Larger stems contribute much of the ecological integrity of the forest. Smaller stems can be replenished in years, but canopy trees may take decades or centuries.

Droughts have numerous implications for forest ecosystems (e.g. Wright 1992; Corlett & Lafrankie 1998; Curran *et al*. 1999; Harrison 2000). Direct studies of rare events will never be simple, but recognizing their significance carries implications for larger questions such as tree species evolution and differentiation, and patterns of local and regional species richness (Whitmore & Burslem 1998; Loehle 2000; Sheil & Burslem 2003), and for details of the global carbon cycle (Malhi *et al*. 1999).

FIRE MORTALITY AND ITS INTERACTION WITH DROUGHT

Our study provides the first comprehensive tropical Asian account of a designed comparison between burned and unburned rainforest. Mortality (stems, d.b.h. ≥ 10 cm) reached 74% 21 months after the fire. In comparison, studies revealed 57% mortality 22 months after fire in Sabah (Woods 1989), 36% mortality 4 months after fire in Kutai National Park, East Kalimantan (Leighton & Wirawan 1986), and 25% mortality 6 months after fire in south-west Sumatra (Kinnaird & O'Brien 1998). Results are influenced by methods: Woods (1989) did not include trees that had fallen by the time of observation, while Leighton & Wirawan (1986) and Kinnaird & O'Brien (1998) were completed shortly after the fire. Studies also differ in preceding drought intensities. Our study implies that almost 40% of total mortality (≥ 10 cm d.b.h.) 21 months after burning would have happened after drought alone.

Impacts varied across the landscape. Lower moister areas more often escaped burning. Analysing topographic patterns 3 years after fire in the same area, Slik & Eichhorn (2003) found higher densities of living stems in low sites. However, incomplete burning is not the only explanation as their analyses included small stems, many of which are resprouts of stems that had died above ground (van Nieuwstadt 2002).

The delayed mortality in the burned forest was twice as high, in absolute terms, as in the unburned forest, and was mainly due to a high mortality for trees of 10–40 cm d.b.h. Tree-falls of stems alive in the first census were high in the burned forest and may reflect increased wind effects and the secondary impacts of other falling trees. A contrasting pattern in which larger trees show a higher delayed mortality than small trees has recently been noted in Amazonia and attributed to the greater endurance of larger trees (Barlow *et al*. 2003). The greater drought severity and physiological depletion to which larger trees had already been subjected in our study might reduce such influences.

Proximity to burned forest may influence mortality in unburned forest (via temperature, desiccation and wind) but no distance dependent effects were detected in our data. However, some small plots in the same general area (but >1 km from burned forest) show lower mortality (around 13–14% over the first 3 years, over 1 ha, G.M. Fredriksson, unpubl. data). The difference with our estimates may reflect landscape location effects, sample noise, or that edge effects are taking place but penetrate with near-uniform intensity over the first 300 m.

TREE-SPECIFIC FIRE MORTALITY

Mortality caused by fire was negatively related to both d.b.h. and to bark thickness, which are far from being independent variables. We did not observe significant fire mortality above 70 cm d.b.h. Leighton & Wirawan (1986) previously noted a similar pattern. Bark thickness did not explain variation in species survival > 30 cm d.b.h. As drought influences species differently, we suspect that, even amongst stems that did not die, their ability to survive and recover from further damage (i.e. fire) was affected. In any case, our results suggest that the fire sensitivity of a species may be more effectively estimated by the diameter structure of the population than by the bark characteristics.

There are marked community changes following fire. Several species of Dipterocarpaceae have an abundance of large individuals combined with a typically rapid increase in bark thickness with size which helps explain why the relative dominance of this family is higher in the burned than in the unburned forest. Palm mortality was low, reaching only 10% even in burnt forests, probably reflecting their less vulnerable vascular structure.

Drought and fire cause distinct tree mortality. Drought causes high mortality among larger trees, whereas fire kills most of the under- and mid-storey, but not larger, stems. The joint impact is especially severe. While most species, especially those that grow to

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a large stature, do survive, interspecific differences in sensitivity are considerable, and remain poorly understood. Because of delayed mortality, the full impact of drought and fire can only be determined over many years.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC954/JEC954sm.htm

Appendix S1 Stem density per size class per plot at the first census.

Appendix S2 Basal area per size class per plot.

References

Alder, D. & Synnott, T.J. (1992) *Permanent Sample Plot Techniques for Mixed Tropical Forest*. Tropical Forestry Paper 25. Oxford Forestry Institute, University of Oxford, Oxford.

Alexander, M.E. (1982) Calculating and interpreting forest fire intensities. *Canadian Journal of Botany*, **60**, 349–357.

Barlow, J., Lagan, B.O. & Peres, C.S. (2003) Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *Journal of Tropical Ecology*, **19**, 291–299.

Becker, P., Ong, C.L. & Goh, F. (1998) Selective drought mortality of dipterocarp trees: no correlation with timber group distributions in Borneo. *Biotropica*, **30**, 666–671.

Borchert, R. (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, **75**, 1437–1449.

van Bremen, H., Iriansyah, M. & Andriesse, W. (1990) *Detailed Soil Survey and Physical Land Evaluation in a Tropical Rain Forest, Indonesia*. Tropenbos Technical Series 6. Stichting Tropenbos, Wageningen, The Netherlands.

Brookfield, H., Potter, L. & Byron, Y. (1995) *In Place of the Forest – Environmental and Socio-economic Transformations in Borneo and the Eastern Malay Peninsula*. United Nations University Press, Tokyo, Japan.

Brünig, E.F. (1969) On the seasonality of droughts in the lowlands of Sarawak (Borneo). *Erdkunde*, **23**, 127–133.

Burgess, P.F. (1966) *Timber Trees of Sabah*. Sabah Forest Record No. 6. Forest Department, Sabah.

Clark, D.B. & Clark, D.A. (1996) Abundance, growth and mortality of very large trees in neotropical lowland rain forest. *Forest Ecology and Management*, **80**, 1–3.

Cochrane, M.A. (2003) Fire science for rainforests. *Nature*, **421**, 913–917.

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 climate change on tropical Asian forests through an influence on phenology. *Climatic Change*, **39**, 439–453.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M. *et al.* (1999) Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science*, **286**, 2184–2188.

van Dam, O. (2001) *Forest Filled with Gaps. Effects of Gap Size on Water and Nutrient Cycling in Tropical Rain Forest. A Study in Guyana*. Tropenbos-Guyana Series 10. Tropenbos-Guyana Programme, Georgetown, Guyana.

Dam, R.A.C., van der Kaars, S. & Kershaw, A.P. (2001) Quaternary environmental change in the Indonesian region. *Mammology, Palaeoclimatology, Palaeoecology*, **171**, 91–95.

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.

van Eijk-Bos, C. & de Kock, R.B. (1996) *Tree Species Composition and Increment of Dipterocarp Forest in Permanent Plots in East Kalimantan*. Wanariset technical report 1996–1. International MOF Tropenbos-Kalimantan Project, Balikpapan, Indonesia.

Furnival, G.M. (1961) An index for comparing equations used in constructing volume tables. *Forest Science*, **7**, 337–341.

Gentry, A.H. & Terborgh, J. (1990) Composition and dynamics of the Cocha Cashu 'mature' floodplain forest. *Four Neotropical Rainforests* (ed. A.H. Gentry), pp. 542–572. Yale University Press, New Haven, Connecticut.

Goldammer, J.G. & Seibert, B. (1989) Natural rain forest fires in eastern Borneo during the Pleistocene and Holocene. *Naturwissenschaften*, **76**, 518–520.

Guhardja, E., Fatawi, M., Sutisna, M., Mori, T. & Ohta, S. (2000) *Rainforest Ecosystems of East Kalimantan – El Nino, Drought, Fire and Human Impacts*. Ecological Studies 140. Springer-Verlag, Tokyo.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D. & McCulloh, K.A. (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia*, **126**, 457–461.

Harrison, R.D. (2000) Repercussions of El Niño: drought causes extinction of and the breakdown of mutualism in Borneo. *Proceedings of the Royal Society of London: Biology Sciences Series B*, **267**, 911–915.

Ketterings, Q.M., Coe, R., van Noordwijk, M., Ambagau, Y. & Oalm, C.A. (2001) Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests. *Forest Ecology and Management*, **46**, 199–209.

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Kinnaird, M.F. & O'Brien, T.G. (1998) Ecological effects of wildfire on lowland rainforest in Sumatra. *Conservation Biology*, **12**, 954–956.

Leighton, M. & Wirawan, N. (1986) Catastrophic drought and fire in Borneo tropical rain forest associated with the 1982–83 El Niño Southern Oscillation event. *Tropical Rain Forest and the World Atmosphere, AAAS Selected Symposium 101* (ed. G.T. Prance), pp. 75–102. American Association for the Advancement of Science, Washington DC.

Lieberman, D. & Lieberman, M. (1987) Forest tree growth and dynamics at La Selva, Costa Rica (1969–82). *Journal of Tropical Ecology*, **3**, 347–358.

Loehle, C. (2000) Strategy space and the disturbance spectrum: a life history model for tree species coexistence. *American Naturalist*, **156**, 14–33.

Malhi, Y., Baldocchi, D.D. & Jarvis, P.G. (1999) The carbon balance of tropical, temperate and boreal forests. *Plant, Cell and Environment*, **22**, 715–740.

Manokaran, N. & Kochummen, K.M. (1987) Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. *Journal of Tropical Ecology*, **3**, 315–330.

McDowell, N., Barnard, H., Bond, B.J., Hinckley, T., Hubbard, R.M., Ishii, H. *et al.* (2002) The relationship between tree height and leaf area/sapwood area ratio. *Oecologia*, **132**, 12–20.

Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubo, T., Kato, T., Maeda, T. *et al.* (2000) Impact of severe drought associated with the 1997–98 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology*, **16**, 355–367.

van Nieuwstadt (2002) *Trial by fire: postfire development of a tropical dipterocarp forest*. Published thesis, University of Utrecht, Print Partners Ipskam B.V., Enschede, the Netherlands.

Poorter, L. & Hayashida-Oliver, Y. (2000) Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology*, **16**, 481–498.

Rankin de Merona, J.M., Hutchins, R.W. & Lovejoy, T.E. (1990) Tree mortality and recruitment over a five-year period in undisturbed upland rain forest of the Central Amazon. *Four Neotropical Rainforests* (ed. A.H. Gentry), pp. 573–584. Yale University Press, New Haven, Connecticut.

Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, **113**, 447–455.

Seth, S.K., Waheed Khan, M.A. & Yadav, J.S.P. (1960) Sal mortality in Bihar. *Indian Forester*, **86**, 645.

Sheil, D. (1995) A critique of permanent plot methods and analysis with examples from Budongo forest, Uganda. *Forest Ecology and Management*, **77**, 11–34.

Sheil, D. & Burslem, D.F.R.P. (2003) Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution*, **18**, 18–26.

Sheil, D., Jennings, S.B. & Savill, P. (2000) Long-term permanent plot observations in Budongo, a Ugandan rain-forest. *Journal of Tropical Ecology*, **16**, 865–882.

Sidiyasa, K., Arbainsyah & Kessler, P.J.A. (1999) *List of Collections Stored at the Wanariset Herbarium, East Kalimantan, Indonesia*. The International MOFEC-Tropenbos Kalimantan Project, Samboja, Indonesia.

Siegert, F., Ruecker, G., Hinrichs, A. & Hoffmann, A.A. (2001) Increased damage from fires in logged forests during droughts caused by el Niño. *Nature*, **414**, 437–440.

Slik, J. (2001) *Macaranga & Mallotus (Euphorbiaceae) as Indicators for Disturbance in the Lowland Dipterocarp Forests of East Kalimantan, Indonesia.* Tropenbos-Kalimantan Series 4. Tropenbos International, Wageningen, Netherlands.

Slik, J.W.F. & Eichhorn, K.A.O. (2003) Fire survival of lowland tropical rain forest trees in relation to stem diameter and topographic position. *Oecologia*, **137**, 446–455.

Suzuki, E. (1999) Diversity in specific gravity & water content of wood among Bornean tropical rainforest trees. *Ecological Research*, **14**, 211–224.

Tang, H.T. & Chang, P.F. (1979) Sudden mortality in a regenerated stand of *Shorea curtissii*. Senaling Inas Forest Reserve, Negri Sembilan. *Malay Forester*, **42**, 240–254.

Tyree, M.T., Velez, V. & Dalling, J.W. (1998) Growth dynamics of root and shoot hydraulic conductance in seedlings of five neotropical tree species: scaling to show possible adaptation to differing light regimes. *Oecologia*, **114**, 293–298.

Vose, R.S., Schmoyer, R.L., Steurer, P.M., Peterson, T.C., Heim, R., Karl, T.R. *et al.* (1992) *The Global Historical Climatology Network: Long-term Monthly Temperature, Precipitation, Sea Level Pressure and Station Pressure Data*. Carbon Dioxide Information Analysis Center, Oak Ridge, Tennessee. Available from ftp://cdiac.esd.ornl.gov/pub/ndp041/ (accessed 8 November 2000).

Walsh, R.P.D. & Newbery, D.M. (1999) The ecoclimatology of Danum, Sabah, in the context of the world's rainforest regions, with particular reference to dry periods and their impact. *Philosophical Transactions of the Royal Society of London B*, **354**, 1869–1883.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

Westoby, M., Leishman, M.R. & Lord, J. (1995) On misinterpreting the 'phylogenetic correction'. *Journal of Ecology*, **83**, 531–534.

Whitmore, T.C. & Burslem, D.F.R.P. (1998) Major disturbances in tropical rainforests. *Dynamics of Tropical Communities. 37th Symposium of the British Ecological Society* (eds D.M. Newbery, H.H.T. Prins & N. Brown), pp. 549–566. Blackwell Science, Oxford.

Williamson, G.B., Laurance, W.F., Oliveira, A.A., Delamônica, P., Gascon, C., Lovejoy, T.E. *et al.* (2000) Amazonian tree mortality during the 1997 El Niño drought. *Conservation Biology*, **14**, 1538–1542.

Woods, P. (1989) Effects of logging drought and fire on structure and composition of tropical forests in Sabah Malaysia. *Biotropica*, **21**, 290–298.

Wright, S.J. (1992) Seasonal drought, soil fertility and the species diversity of tropical forest plant communities. *Trends in Ecology and Evolution*, **7**, 260–263.

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