Separating the effects of severe drought and subsequent fire on tree survival in a lowland dipterocarp rain forest in East Kalimantan, Indonesia

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Abstract

Over the last decades, extreme droughts and fires damaged extensive areas of forest in Indonesia. Notwithstanding the environmental impact of such large-scale disturbances, their effect on tree mortality has not been investigated in much detail in Southeast Asia. Especially data on the performance of very large trees are generally lacking. This study provides data on the patterns of tree mortality in a lowland rainforest in East Kalimantan after the drought of 1997-1998, which is one of the most extreme droughts that has so far been recorded in tropical ecological literature. Second, it gives a detailed account of the effects of the fire that followed at the end of this drought.

Eighteen permanent sample plots (psp) were established after the drought and fire in nine pairs of one unburned and one burned psp. This layout enabled us to separate the effects of drought and fire, which are entangled in the burned forest. The 1.8 ha size of each psp made accurate estimates of mortality among large trees possible. The psp were monitored twice, 8 months and 21 months after the disturbances.

Tree mortality was high in the first eight months after the drought (19.1 ± 4.4% dead trees >10 cm dbh). We observed a high level of retarded mortality, resulting in 28.6 ± 4.2% dead trees after 21 months. Tree mortality after the drought was positively related to dbh. The burned forest showed an even much higher mortality (60.6 ± 10.4% dead trees after eight months, and 74.4 ± 8.7% after 21 months). By subtracting mortality after drought from mortality after drought x fire in each pair of adjacent psp, we estimated that the fire was responsible for roughly 2/3 of the mortality in the burned psp. Fire mortality was negatively related to dbh: Drought x fire resulted in nearly complete mortality for individuals <10 cm dbh, whereas fire did not cause a significant increase in tree mortality >70 cm dbh. For the community as a whole the relation between dbh and fire mortality could be explained in terms of average bark thickness per dbh class.

For trees >30 cm dbh, mortality after drought and drought x fire ranged widely between species. Trees with a high wood density had a higher drought survival. For the trees in this size class, species-specific bark thickness did not explain the observed patterns in mortality after fire.

We related the intensity of occasional droughts in different everwet tropical forest sites (measured as the cumulative water deficit) with the percentage of drought-induced mortality, and found that below a cwd of 100-200 the increase in mortality is low, whereas it rapidly increases when the cwd becomes larger. We argue that the soil water reserve acts as a buffer which delays the actual onset of water stress for trees after a rainfall deficit has started to develop.

We conclude that the combined effect of drought and fire causes great damage to the forest vegetation, partly because the two disturbances act on different strata of the vegetation. The high level of retarded mortality that we observed underscores the necessity of long-term observations in order to understand the effects of such severe disturbances.
Keywords: Drought, fire, large-scale disturbance, lowland dipterocarp rain forest, Southeast Asia, tree mortality.

Introduction

Extreme droughts and the repeated occurrence of fires have formed an increasing threat to the lowland rain forests of Indonesia over the past decades. On the island of Borneo, dry spells (defined as periods in which the monthly rainfall remains below 100 mm) of three to four months have occurred over the past 50 to 100 years in most locations (Walsh 1996b, Walsh & Newbery 1999). They are to some extent related to the El Niño-Southern Oscillation (ENSO) phenomenon. During the two extreme ENSO events in 1982–1983 and 1997–1998, these long droughts were accompanied by subsequent widespread forest fires. In the province of East Kalimantan, 2.6 million ha of forests burned during the drought of 1997-1998 (Hoffmann et al. 1999, Siegert et al. 2001). Despite these massive impacts few studies have documented the impact of drought and fire on the forest vegetation.

Increased tree mortality in tropical rain forest caused by an exceptional drought has been observed on several occasions (Leighton & Wirawan 1986, Condit et al. 1995, Nakagawa et al. 2000, Williamson et al. 2000). However, the severity of these “extreme” droughts is highly variable. With three dry months, followed by three wet (but less than average) months and a second dry period of another three months, this study reports the effects of the most severe drought in tropical rain forest modern ecological literature.

Fire can enter a tropical rain forest only after a dry period during which the soil litter layer dries out and becomes flammable (Uhl et al. 1988). Inside a forest with a closed canopy, a burn characteristically takes the form of a ‘surface fire’, which is largely confined to this dry litter layer. The low available fuel load, relatively high fuel humidity and low wind speed inside the forest limit the fire intensity and the speed at which it spreads (Uhl et al. 1988). Virtually all woody plants that are killed remain standing after the fire (Leighton & Wirawan 1986, Woods 1988). High levels of tree mortality have nonetheless been reported in primary forests after such fire events (Leighton & Wirawan 1986, Woods 1988, Kinnaird & O’Brien 1998).

Since forest fires are confined to long periods of drought, fire induced tree mortality cannot easily be separated from mortality resulting from the preceding drought. The separate effects of drought and fire on tree survival cannot readily be studied on the same location, because the mortality caused by the drought is not yet quantifiable by the time the subsequent fire burns the area. The comparison of a burned forest with a nearby unburned forest is therefore the best available solution. Separating the effect of fire from the effect of drought on tree mortality by making such a comparison between bordering areas is the main objective of this paper.

In the current study we investigated the impact of an extreme drought on the vegetation. We monitored the changes in the overall stand structure of the forest. We analysed the influence of tree size and tree species, on mortality. We expected to find a negative correlation between tree size and mortality rate because larger trees with a deeper root system have more prolonged access to soil water (Wright 1992). Second, we expected that heavy-wooded species would have a lower mortality rate, because wood density is correlated with prevention of xylem implosion during drought stress, especially for wood densities >0.7 g cm⁻³ (Hacke et al. 2001). We compared the effect of the drought on tree mortality with other available studies in everwet tropical forest, in order to explore the relationship...
between the severity of a drought and the resulting increase in tree mortality.

We investigated how fire-induced tree mortality in a primary forest is influenced by tree size and species. Mortality has been correlated with bark insulation properties, and especially bark thickness (Gill & Ashton 1968, Vines 1968, Uhl & Kauffman 1990, Pinard & Huffman 1997). We expected to find a positive correlation between tree size and bark thickness, as well as substantial species-specific differences in bark thickness. As a consequence, we hypothesised tree mortality after fire to be highest amongst small trees and amongst thin-barked species.

Because retarded mortality has been observed after large-scale disturbances (Burslem, Whitmore & Brown 2000, also see Pedersen 1998), we monitored the patterns of mortality over a period of nearly two years following the disturbance. Due to the large proportion of dead trees that remained upright after the drought and the fire we expected an increase in tree fall during this period. The patterns of tree fall in relation to dbh were studied in both unburned and burned forest.

### Study sites

The main research site is a water catchment reserve of circa 100 km², called Sungai Wain protection forest near to Balikpapan, East Kalimantan (1°16’ S and 116°54’ E) at 15 km from the Strait of Makasar (Figure 1.2). The largest part of this area was originally covered with lowland dipterocarp rain forest. A more detailed description of the vegetation is given in chapter 1. Some of the poorly drained valleys and lower parts of the area carry a shorter stature, infrequently flooded forest. The topography of the reserve consists of gentle to sometimes steep hills, and is intersected by several small rivers. The area varies in altitude from 40 to 140 m.a.s.l. Alisols, which are strongly weathered, very deep, infertile soils with a high fraction of loam and clay form the major soil type (FAO/Unesco/ISRIC 1988, van Bremen et al. 1990, MacKinnon et al. 1996).

Additional data on tree mortality were collected in the protected Wanariset Wartonokadri research forest (10 km Northeast of the Sungai Wain forest). This is a forest fragment of 50 ha surrounded on three sides by degraded forest and agricultural fields, and on the fourth
side is separated from another forest patch by a narrow road. The altitude, soil types, topography and rainfall are similar to the Sungai Wain forest. Although also this fragment is inevitably disturbed by small scale harvesting, the existing density of large trees is considered to be natural for the area.

Climate and fire regime

The average yearly rainfall is 2790 mm (Figure 1.3) (Vose et al. 1992). On average, the area does not experience less than 100 mm monthly rainfall. During the period 1948-1980, short dry periods (defined as having a monthly rainfall below 100 mm) were frequent (30 x one month, and 3 x two months), and most frequently occurred between September and November. Longer droughts were not recorded. After 1980, the pattern changed dramatically. Extensive droughts occurred in 1982-1983 and in 1997-1998, which were related to the occurrence of extreme ENSO events.

For a detailed characterisation of the drought in 1997-1998, we calculated the period during which the seven-day running average rainfall remained below 3.3 mm. This is equivalent to the commonly used limit of 100 mm rain per month when the dry period is prolonged. The drought consisted of two periods, which were similar in Balikpapan and Samarinda (Figure 1.3, Table 2.1). The first drought lasted for 12-13 weeks. During this period, precipitation was limited to a total of 16 to 48 mm. The following 13-14 weeks were wetter, and experienced a total of 388 to 482 mm rainfall. The wet intermission was interrupted by frequent short droughts: In Balikpapan 33 out of 99 days had a 7-day running average rainfall below 3.3 mm, and in Samarinda 51 out of 91 days. After this wet intermission a second drought of more than 14 weeks followed, with a cumulative precipitation of 3 to 13 mm. The drought ended around 20 April 1998.

To enable a comparison with other studies, for which only the relatively crude monthly rainfall patterns are available, we also analysed the monthly rainfall data. To estimate the intensity of the drought, the cumulative water deficit (cwd) was calculated. We developed the cwd as a refined version of the cumulative rainfall deficit (the sum of the amounts by which the rainfall of each month in a dry month sequence fell below 100 mm) (Walsh & Newbery 1999). In the cwd index, the rainfall deficit is gradually counterbalanced by any surplus precipitation above 100 mm per month, instead of returning to zero instantaneously, once the threshold of 100 mm monthly precipitation is reached.

The 1998 fire in the Sungai Wain primary forest was a typical surface fire, with an estimated average flame height of 0.5 m, an estimated depth of 20-30 cm, an estimated speed of 10-15 m/h (MvN pers. obs.), and a calculated fire intensity of circa 60 kW/m (Alexander 1982). A 0.5 m wide firebreak was enough to stop the fire, after which permanent control was necessary to prevent its escape. One third of the total area in the reserve burned during the 1982-1983 dry episode and burned again in 1997-1998 (Figure 1.2). Another third burned for the first time in March – April 1998, during the last part of the dry period. A core area of one third of the total area (3.5 x 8 km) was saved from the fire. The research was performed in the unburned area and the area that burned once.

Material and methods

In the Sungai Wain forest (SW forest), 18 permanent sample plots (psp) of 60 x 300 m (1.8 ha) each were laid out in unburned forest and in forest that burned once in 1998 (Figure 1.2). The psp were laid out in nine pairs, each pair of psp adjacent to each other over a man-made firebreak between burned and unburned forest. Thus, each pair of psp forms one contiguous transect of 60 x 600 m half in burned and half in unburned forest. The psp are spread over a total area of circa 20 km². In those areas where the psp are located, the firebreak does not correspond to any topographical feature.

Two surveys were done in the two years following the drought and fire. The
average date of measurement of the first survey was December 1998 (eight months after the drought and fire). During this survey, all dead and living stems larger than 28 cm dbh (diameter measured at 1.3 m height) were labelled and assessed. In each psp a subplot of 20 x 200 m was established, in which all trees between 8 cm and 28 cm dbh were assessed and labelled (Table 2.2). The lower limits of 8 cm dbh and 28 cm dbh were chosen in order to avoid the omission of trees with a dbh close to respectively 10 cm and 30 cm. In the analyses of the responses of trees, the lower limits of 10 cm and 30 cm dbh are used. Palmae above 8 cm dbh were labelled, but not included in the analysis unless specifically mentioned.

For trees which had protruberances at 1.30 m (buttresses or other irregularities), the diameter (Dx) was measured at 30 cm above the protruberances (Sheil 1995). The diameter was measured with a measurement tape up to a height of 2.5 m. Above this height, a ruler attached to a pole was rested against the stem and read from 10 m distance, following the method described in Alder and Synnott (1992).

If the diameters (Dx) collected above 1.30 m height were used as an uncorrected proxy for dbh, stem tapering would introduce a systematic underestimate of stem size in the dataset. To avoid such a systematic error, we estimated the relation between dbh and Dx to correct for stem tapering. For a set of 43 trees between 25 and 82 cm dbh with a straight stem, the diameter at 130 cm (dbh) was measured with a measuring tape, and the diameter (Dx) was estimated with the method described above (Alder & Synnott 1992) at 1.30 m, 2.50 m and 4.00 m height. We then calculated the ratio between dbh and Dx. We predicted that both the dbh of the tree and the height of measurement would influence the ratio (Dx /dbh). A multiple linear regression revealed that for a fixed height of measuring, the ratio (Dx /dbh) was independent of dbh (multiple regression anova, n= 43, F= 1.13, sign = 0.35). Therefore dbh was not introduced as an independent variable in the equation. Curve estimation showed that the relationship between the ratio (Dx /dbh) and height of measurement was best predicted by a power function with the form (Dx /dbh)= 1.1816 * h –0.1168 (R²= 0.40, df= 123, F= 80.6, p< 0.001). This function was subsequently used to estimate the dbh of stems which had been measured above 1.30 m high. We estimated that, if the correction was not applied, an underestimation of 9% and 16% in basal area would have been made for trees that were measured respectively at 2.0 m height and 4.0 m height.

In 16 unburned and 51 burned subplots of 100 m² each, which were evenly spread over the psp, all (dead and living) seedlings and saplings (stem length >50 cm and dbh <8 cm) were assessed and labelled (Table 2.2). Of these plants, the diameter was measured at 25 cm above ground level with a calliper, this is termed the diameter at ankle height (dah).

The position of each tree in the psp was determined, and the topography of each psp was mapped with a clinometer (Suunto) in steps of 10 m in the 20 x 200 m subplots and 20 m in the 60 x 300 m plots. Individuals with a leafless crown were considered dead in the sense that they had been killed aboveground. This included individuals that were re-sprouting from the roots or from the base.

Table 2.2. Psp in Sungai Wain and numbers of individuals per dbh category.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Psp</th>
<th>Dbh (cm) &lt; 8</th>
<th>Psp</th>
<th>Dbh (cm) 8 &gt; x &gt; 28</th>
<th>Psp</th>
<th>Dbh (cm) &gt; 28</th>
</tr>
</thead>
<tbody>
<tr>
<td>Drought</td>
<td>1, 7, 9, 11, 13, 15, 17</td>
<td>1284</td>
<td>1, 3, 5, 7, 9, 11, 13, 15, 17</td>
<td>2654</td>
<td>1560</td>
<td></td>
</tr>
<tr>
<td>Drought x fire</td>
<td>2, 4, 6, 8, 10, 12, 14, 16, 18</td>
<td>3589</td>
<td>2, 4, 6, 8, 10, 12, 14, 16, 18</td>
<td>2214</td>
<td>1497</td>
<td></td>
</tr>
</tbody>
</table>
of the stem. The resprouting of stems that are killed above ground is discussed in chapter 3.

Local experts trained at the herbarium of the nearby Wanariset Sambodja research station identified living trees, as well as dead trees larger than 28 cm dbh belonging to 10 common species (Table 2.3). Dead trees below 28 cm were not identified because the result was expected to be taxonomically difficult and unreliable. Because of this, species-specific mortality is analysed only for trees above 30 cm dbh. Specific wood densities of these species were obtained from the literature (Burgess 1966, Suzuki 1999). Nomenclature follows Sidiyasa et al. 1999.

The average date of measurement of the second survey was January 2000 (21 months after the drought and fire). In this survey, we re-assessed whether trees were living or dead. We did not assess dbh during this survey. We also observed resprouting of trees and tree fall. Tree fall included both uprooting and stem breakage, of which the latter was defined as a stem which lacked primary branches (a snapped stem cannot easily be discerned from a stem that has lost all its primary branches).

In the Wanariset Wartonokadri forest, measurements were taken in five parallel transects of 10 x 200 m spaced at distances of 100 m (Slik et al. 2001). 599 trees above 10 cm dbh were labelled and identified in September 1997, during the early phase of the drought. Tree mortality was re-measured four months after the end of the drought (August 1998) and again 22 months after the drought (February 2000). To ensure that the Wartonokadri forest and the Sungai Wain forest carried a similar vegetation type prior to the disturbances, which would justify the combined use of some of the data from the two sites, we tested for differences in the overall stand structure between the two sites.

The first survey in Wartonokadri provided us with an estimate of the average percentage of dead trees per transect before the onset of the drought. These results were used to estimate the number of living stems prior to the drought in the Sungai Wain forest, where plots were established only after the disturbance. We estimated the density of living stems before the drought in Sungai Wain, by subtracting the percentage of dead trees as observed in the earliest survey in the Wanariset forest from the total stem density (i.e. the sum of living and dead stems) in the Sungai Wain forest after the drought.

Fire occurs only in unison with an extended drought, and as a result the tree mortality that is recorded after fire is a combination of drought-induced mortality and truly fire-induced mortality. Our aim is not only to measure tree mortality as the result of the combined effect of drought and fire, but also to partition the effects of these two factors. By subtracting the former from the latter we propose that we can quantify the additional mortality due to the influence of fire on the drought impacted forest stand. Percentages mortality were measured per psp.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Abbreviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artocarpus anisophyllus Miq.</td>
<td>Moraceae</td>
<td>Arto anis</td>
</tr>
<tr>
<td>Dipterocarpus confertus Sloot.</td>
<td>Dipterocarpaceae</td>
<td>Dipt conf</td>
</tr>
<tr>
<td>Dipterocarpus cornutus Dyer</td>
<td>Dipterocarpaceae</td>
<td>Dipt corn</td>
</tr>
<tr>
<td>Drypetes kikir Airy Shaw</td>
<td>Euphorbiaceae</td>
<td>Dryp kiki</td>
</tr>
<tr>
<td>Eusideroxylon zwageri Teijsm. &amp; Binn.</td>
<td>Lauraceae</td>
<td>Eusi zwag</td>
</tr>
<tr>
<td>Gironniera nervosa Planch.</td>
<td>Ulmaceae</td>
<td>Giro nerv</td>
</tr>
<tr>
<td>Koompassia malaccensis Maing. Ex Benth.</td>
<td>Caesalpinioideae</td>
<td>Koom mala</td>
</tr>
<tr>
<td>Madhuca kingiana (Brace) H.J.Lam</td>
<td>Sapotaceae</td>
<td>Madh king</td>
</tr>
<tr>
<td>Shorea laevis Ridl.</td>
<td>Dipterocarpaceae</td>
<td>Shor laev</td>
</tr>
<tr>
<td>Shorea ovalis (Korth.) Blume</td>
<td>Dipterocarpaceae</td>
<td>Shor oval</td>
</tr>
</tbody>
</table>
The mortality due to fire was calculated by the pairwise subtraction of the mortality rate from burned and unburned forest in each pair of plots at any particular moment in time.

The effect of the drought on tree mortality was compared with data from other studies in everwet tropical rainforest. Census-periods differed between the studies in the comparison, and so did the background mortality (i.e. the annual mortality during a census period in which no major disturbance occurred). We calculated the drought-induced mortality by subtracting the site-specific background mortality from the mortality that was observed over the census period in which a drought occurred. In the case of Wartonokadri and Sungai Wain, the background mortality was estimated as the average background mortality from the other studies. Drought mortality and fire mortality are not presented in annualised rates, because the models used to calculate such rates assume a constant probability of mortality (e.g. Sheil et al. 1995). In the situation where a peak in mortality occurs in time, annualised mortality values are sensitive to small changes in the duration of the observation period and the exact dates of observation relative to the disturbance event.

To test whether the species-specific thickness of the bark is a good predictor of the mortality of a species after the fire, we sampled the bark from trees of known dbh of 14 species in the unburned forest, using 15 to 34 trees per species (10 for *Macaranga lowii*). Each sample consisted of a single square piece (4 x 4 cm) of bark, which was removed with a chisel at 1.3 m height, avoiding obvious anomalies in the bark caused by buttresses. Bark thickness was measured in the field on four sides of the hole, using a calliper. The best fitting curve to these data was sought, which appeared to be a linear regression on log-log transformed data for all species except *M. lowii*. In order to maintain uniformity in the analysis, the relationship for *M. lowii* was established using the same relationship on log-log transformed data.

Two approaches were followed to test the effect of bark thickness on species-specific tree survival. Firstly, the populations above 10 cm dbh of 14 species were tested, based on the difference in the density of living trees between unburned and burned forest. A backward stepwise regression was used, which included (1) the values for a and b that described the regression line on the log-log transformed relation between dbh and bark thickness, and (2) the dbh value which is the 95% size limit for each population (95% dbh

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Average date</th>
<th>Since last observation</th>
<th>Cumulative perc. dead trees</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Wanarise</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Samboja Wartonokadri forest (5 plots, 599 trees)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Sep-97</td>
<td>-</td>
<td>2.62</td>
</tr>
<tr>
<td>Aug-98</td>
<td>4</td>
<td>11</td>
<td>11.4</td>
</tr>
<tr>
<td>Feb-00</td>
<td>22</td>
<td>19</td>
<td>22.2</td>
</tr>
<tr>
<td><strong>Sungai Wain forest, unburned (9 plots, 3444 trees)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought</td>
<td>Dec-98</td>
<td>8</td>
<td>-</td>
</tr>
<tr>
<td>Jan-00</td>
<td>21</td>
<td>13</td>
<td>28.6</td>
</tr>
<tr>
<td><strong>Sungai Wain forest, burned (9 plots, 3104 trees)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Drought x fire</td>
<td>Dec-98</td>
<td>8</td>
<td>-</td>
</tr>
<tr>
<td>Jan-00</td>
<td>21</td>
<td>13</td>
<td>74.4</td>
</tr>
<tr>
<td><strong>Sungai Wain forest (9 paired plots)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exclusively fire</td>
<td>Dec-98</td>
<td>8</td>
<td>-</td>
</tr>
<tr>
<td>Jan-00</td>
<td>21</td>
<td>13</td>
<td>45.8</td>
</tr>
</tbody>
</table>

Table 2.4. Average percentages of dead trees above 10 cm dbh per permanent sample plot at various censuses in the Wanarise Wartonokadri forest and Sungai Wain research forest.
limit). Ninety-five percent of the trees (>10 cm dbh) in a population had a dbh smaller than this value.

The second test, performed on nine populations above 30 cm dbh (of species which could be identified even when they were dead), was different in the respect that it was based on the numbers of living and dead trees in the burned forest.

**Results**

Stand structure and mortality at the community level

At the first census in the Wartonokadri forest, taken during the beginning of the drought, the average stem density of all trees per plot (living and dead, >10 cm dbh) was 627 ± 105 trees ha⁻¹ (mean ± sd, n= 5), of which 610 ± 100 trees ha⁻¹ were alive (Figure 2.1 a), which can be translated into an average of 2.6% ± 1.7 dead standing trees per plot (Table 2.4). The basal area of all trees (living and dead, >10 cm dbh) was 32.4 ± 7.0 m² ha⁻¹ (mean ± sd, n=5) and the basal area of all living trees was 31.5 ± 6.4 m² ha⁻¹ (Figure 2.1 b). The overall stand structure in Wartonokadri was not significantly different from Sungai Wain (t-test comparison between plots in Wartonokadri forest (n= 5) and Sungai Wain forest (n= 18); Tree density of all trees: F= 0.37, p= 0.86, df= 21, and basal area of all trees: F= 2.37, p= 0.85, df= 21), which justified the use of the value of 2.6% as the percentage of standing dead trees present prior to the drought in the plots in Sungai Wain. Four months after the drought the percentage dead trees had increased to 11.4% ± 1.7 in the unburned Wartonokadri plots, which corresponds to a total mortality of 8.8% over this 11 month period (Table 2.4). There was a high level of retarded mortality: The percentage dead stems nearly doubled between August 1998 and February 2000, resulting in 22.2% ± 2.4 dead trees (19.6% mortality) 22 months after the drought.

At the first inventory of the unburned psp in Sungai Wain, eight months after the extreme drought, the stem density of all dead and living trees (>10 cm dbh)

![Figure 2.1](image_url). Stem density and basal area of the permanent sample plots (I) at the onset of the drought, (II) eight months after the end of the drought and fire and (III) 21 months after the end of the drought and fire. (a) Stem density per psp (stems ha⁻¹) of all living trees in Wanariset forest (WA) and Sungai Wain forest (SW). (b) Basal area per plot (m² ha⁻¹) of all living trees in Wanariset forest and Sungai Wain forest. All bars represent averages ± sd across psp. The data from Wanariset are based on 5 psp of 0.2 ha each. The data from Sungai Wain are based on 9 psp of 0.4 ha for trees <30 cm dbh and 9 psp of 1.8 ha for trees >30 cm dbh. The stem density and basal area of living trees in Sungai Wain at the onset of the drought are estimates, based on the observation that of all standing trees (both living and dead) at the first census after the drought, an estimated 2.6% was standing dead at the onset of the drought. Two burned psp were excluded from the calculation of the average basal area, because the presence of a few very large trees made them outliers in this respect.

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was 683 ± 94 stems ha⁻¹ (average ± sd, n=9), of which 545 ± 59 stems ha⁻¹ were alive (Figure 2.1 a). Considering that 2.6% of these trees where standing dead prior to the drought, we estimate that the density of living stems at the beginning of the drought was 626 ± 90 stems ha⁻¹. The basal area of all (living and dead) stems was 30.6 ± 1.7 m² ha⁻¹ (mean ± sd, n=9) per unburned psp, of which the basal area of all living stems was 22.1 ± 2.3 stems ha⁻¹ (Figure 2.1 b). This translates into an estimated basal area of living stems of 29.8 ± 1.6 m² ha⁻¹ at the beginning of the drought.

The stem density per diameter class and basal area per diameter class are presented in figure 2.2 a-d. It appeared that two burned psp (14 and 16) were outliers in terms of their basal area, because of the slightly higher frequency of very large trees. These two psp were excluded from the calculation of total basal area and the basal area per diameter.

![Figure 2.2](image)

Figure 2.2. Time series of the stand structure of Sungai Wain forest (a, b) in the dried out and burned psp. (a) and (c) show the average density of living stems per dbh class (stems ha⁻¹) (average + sd, n= 9) per psp, and (b) and (d) show the basal area per dbh class (m² ha⁻¹) (average + sd, n= 9) per psp. White bars: Stand structure at the onset of the drought, hatched bars: eight months after the end of the drought, and speckled bars: 22 months after the end of the drought. The stem density and basal area of living trees at the onset of the drought are estimates, based on the observation that of all standing trees (both living and dead) at the first census after the drought, an estimated 2.6% was standing dead at the onset of the drought. Two burned psp were excluded from the calculation of the average basal area, because the presence of a few very large trees made them outliers.
Tree density rapidly decreases with dbh. After the occurrence of the drought, this pattern is largely maintained, whereas in the burned forest the relationship is greatly flattened. We calculated an average density of living very large trees (>80 cm dbh) prior to the disturbances of respectively 11 ± 3 trees ha⁻¹ in the un-

![Figure 2.3. Average percentage tree mortality per dbh class per psp (average ± sd, n= 9) in the Sungai Wain forest. (a) Unburned psp, (b) burned psp, (c) exclusive fire mortality. White bars: eight months after the end of the drought. Shaded bars: 21 months after the end of the drought. The exclusive fire mortality is calculated by pairwise subtraction of the drought mortality from the drought x fire mortality for each pair of psp. Stems below 10 cm dbh were monitored only once. Where values were not available "na" is shown.](image-url)
burned plots and 8 ± 3 trees ha⁻¹ in the burned plots (Figure 2.2 a & c). From the
four figures (2.2 a-d) it can be inferred, that these uncommon very large trees
contribute largely to the basal area, and that most of the variation in basal area
between the psp is caused by the presence or absence of a few of these very large
trees.

Eight months after the extreme
drought, the mortality rates in the un-
burned Sungai Wain plots were in the
same order of magnitude as the Wartono-
kadri plots, leaving 19.1% ± 4.4% (mean ±
sd) trees dead per psp (Table 2.4). Also
here, mortality remained high during the
second year after the drought, resulting
in 28.6% ± 4.2% dead stems after 21
months.

In the burned psp in Sungai Wain,
the percentage of dead stems above 10 cm
dbh after eight months was 60.6% ±
10.4% per psp, and increased to 74.4% ±
8.7% after 21 months. This was equiva-
 lent to a mortality rate of 39 ± 8.1%
among the trees that were alive at the
first inventory. The exclusive fire induced
mortality was 41.5% ± 11.1% at the first
census and 45.8% ± 8.7% at the second
census.

In both the unburned forest and the
burned forest, mortality is related to dbh
(Figure 2.3 a & b). However, while the
percentage dead trees in the unburned
forest increases with increasing dbh, the
opposite is true in the burned forest. Be-
low 10 cm dbh, mortality in the burned
forest is above 85%. Above 40 cm dbh,
where drought induced mortality becomes
increasingly important, the percentage of
dead trees in the burned forest remains
approximately constant. For trees with a
dbh above 70 cm, we found no significant
difference between the percentages of

table 2.5. Paired samples t-test on the percent-
age dead trees per dbh-class in nine pairs of
unburned and burned psp in Sungai Wain forest
21 months after the end of the drought and fire.

<table>
<thead>
<tr>
<th>DBH class</th>
<th>df=</th>
<th>t</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>8-9</td>
<td>8</td>
<td>24.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>10-19</td>
<td>8</td>
<td>24.0</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>20-29</td>
<td>8</td>
<td>10.7</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>30-39</td>
<td>8</td>
<td>7.5</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>40-49</td>
<td>8</td>
<td>5.6</td>
<td>0.001</td>
</tr>
<tr>
<td>50-59</td>
<td>8</td>
<td>4.0</td>
<td>0.004</td>
</tr>
<tr>
<td>60-69</td>
<td>8</td>
<td>3.6</td>
<td>0.007</td>
</tr>
<tr>
<td>70-79</td>
<td>8</td>
<td>0.86</td>
<td>0.417</td>
</tr>
<tr>
<td>&gt;80</td>
<td>8</td>
<td>1.3</td>
<td>0.241</td>
</tr>
</tbody>
</table>

Figure 2.4. Percentage retarded mortality (average ± sd, n= 9) in
Sungai Wain forest in the period between eight and 21 months after
the end of the drought and fire in the unburned forest (white bars)
and burned forest (shaded bars).
dead trees in the unburned and burned plots after 21 months (Table 2.5).
The retarded mortality showed a similar pattern in relation to dbh class as the mortality during the first observation period. In the unburned forest, retarded mortality between 8 and 21 months was fairly constant over all dbh classes, whereas in the burned forest the retarded mortality was negatively related to dbh (Figure 2.4). The frequency of tree fall was high in the burned forest: 28% of the standing dead trees and 7.5% of the living trees fell during the second year after the fire (Figure 2.5 a & b). Living trees had nearly twice as much chance to fall in the burned forest as compared to the unburned forest (4.0%), a difference which was mainly due to the high rate of small trees falling in the burned forest (Figure 2.5 a). Tree fall of living and dead trees decreased with increasing dbh in both the unburned and the burned forest.

Species-specific mortality

Twenty-one months after the drought, the percentage of dead trees above 30 cm dbh ranged from 5% to 30%, while Koompassia malaccensis was an outlier with a mortality rate of 69% (Table 2.6). We assume that the high mortality of Koompassia was caused by another factor than the drought. Species-specific drought mortality of trees >30 cm dbh was negatively correlated to wood density (Figure 2.6, Pearson corr. = -0.84, p= 0.005, n=9). Especially Eusideroxylon zwageri appeared to be highly drought resistant.

In the burned forest, the percentage dead trees per species varied from 11% to 91%. For half the species, the exclusive fire mortality among trees above 30 cm dbh roughly equalled the drought mortality. In some species (Dipterocarpus confertus, Shorea ovalis) the trees above 30 cm dbh were unaffected altogether by the fire, while for most species the exclusive fire mortality was around 25%, with an extreme 75% mortality for Artocarpus anisophyllus. It should be noted that, obviously, the measured impact of the fire would have been manifold higher, had it been possible to include species-specific mortality amongst smaller size classes in the census. The percentage of dead Palmae above 10 cm dbh (mainly Borassodendron sp. and Oncosperma sp.) was 3% ± 4% after the drought and 10% ± 11% after the fire (not shown in table).

Fire mortality and bark thickness

Curve estimation revealed that for all species combined, the relation between dbh and bark thickness was best described by a linear regression on log-log transformed data (Figure 2.7 a). The percentage mortality per dbh class that was caused exclusively by fire (i.e. corrected for drought mortality) is linearly related to the average bark thickness of trees in...
that class (Figure 2.7 b). The same linear regression based on log-log transformed values provided the best predictive relationship for the 14 individual species (Figure 2.8).

To test the influence of bark thickness on species-specific tree survival, populations above 30 cm dbh of nine species (which could be identified even when they were dead) were tested based on the numbers of living and dead trees in the burned forest.

A backward stepwise regression revealed that for trees above 10 cm dbh, differences in population density in the unburned and the burned forest could not be explained by either the values a or b from the log-log transformed relation between dbh and bark, nor by the 95% dbh limit (n= 14, for all fitted models F< 2.52, p> 0.13).

Likewise, a backward stepwise regression on the percentage fire mortality of nine species above 30 cm dbh showed that neither the 95% dbh limit, nor the values a and b, explained a significant part of the variation of the species-specific fire mortality (n= 9, for all fitted models F< 0.52, p> 0.57). In other words, in neither case was bark thickness a good predictor of species-specific fire sensitivity.

### Table 2.6. Species-specific mortality after drought and fire of trees above 30 cm dbh 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 psp (n= 6). To calculate the mortality exclusively caused by fire, the mortality after drought per psp is subtracted pairwise from the mortality after “fire + drought” for each pair of adjacent psp.

<table>
<thead>
<tr>
<th>Species</th>
<th>Wood density (g cm⁻³)</th>
<th>Percentage dead trees</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Drought</td>
<td>Fire</td>
</tr>
<tr>
<td>Arto anis</td>
<td>0.718</td>
<td>20</td>
</tr>
<tr>
<td>Dipt conf</td>
<td>0.803</td>
<td>15</td>
</tr>
<tr>
<td>Dipt corn</td>
<td>0.843</td>
<td>14</td>
</tr>
<tr>
<td>Dryp kiki</td>
<td>0.999</td>
<td>13</td>
</tr>
<tr>
<td>Eusi zwag</td>
<td>1.066</td>
<td>5</td>
</tr>
<tr>
<td>Giro nerv</td>
<td>0.603</td>
<td>30</td>
</tr>
<tr>
<td>Koom mala</td>
<td>0.934</td>
<td>64</td>
</tr>
<tr>
<td>Madh king</td>
<td>0.794</td>
<td>17</td>
</tr>
<tr>
<td>Shor laev</td>
<td>0.933</td>
<td>23</td>
</tr>
<tr>
<td>Shor oval</td>
<td>0.537</td>
<td>28</td>
</tr>
</tbody>
</table>

Drought mortality

The current paper gives an account of tree mortality as a result of large-scale disturbance caused by an extreme drought and fire in the tropical lowland rainforest of East Kalimantan. Notwithstanding the severity of the drought event, similar droughts have been natural to tropical rain forest ecosystems in South East Asia and Latin America (Walsh &
This study shows to what extent an extreme drought may affect forest structure and species composition. Mortality soared to 20-26% amongst trees >10 cm dbh two years after the drought, and species-specific mortality amongst trees >30 cm dbh varied ten-fold. Thus, differences in species-specific mortality may cause significant changes in local species composition.

In several researches it has been observed that in mixed tropical rain forest, mortality rate is not related to dbh for trees above a certain minimum size limit (Gentry & Terborgh 1990, Lieberman & Lieberman 1987, Manokaran & Kochummen 1987), or shows a slightly decrease with dbh (Rankin-de-Merona et al. 1990, Clark & Clark 1996). The marked size-dependent increase in mortality that was found in our study strongly deviates from this general pattern. A similar, if less pronounced, pattern of dbh-dependent mortality was found after unusual drought in the Neotropics (Hubbell & Foster 1990). It was expected that large trees would be least affected by drought due to their deep root system (Condit et al. 1995). However, the large trees in the present study appeared most vulnerable to drought, as was found in various other studies (Leighton & Wirawan 1986, Hubbell & Foster 1995, Condit et al. 1995).

Xylem cavitation is the most frequent cause of death (Walsh & Newbery 1999). It seems that during a drought larger trees build up a water deficit more rapidly than smaller trees do. Probably, a smaller tree, which is more likely to grow in the shade, has a lower water evaporation rate per unit leaf area and thus depletes the available water in its root zone more slowly. The hypothesis that small individuals have an insufficient access to water supplies during drought may only apply to seedlings and saplings (Caven der-Bares & Bazzaz 2000), which were observed in some neotropical forests to suffer from high mortality during excessive drought (Hartshorn 1990), although this was not observed in the present study, nor in some other neotropical sites (Hubbell & Foster 1990, Condit et al. 1995). Differences in soil characteristics such as depth and drainage are probably responsible for this.

Species mortality after drought was negatively related with wood density. In a tropical dry forest, hardwood species grew on the driest sites, and could withstand a strongly negative xylem pressure (Borchert 1994). Hacke et al. (2001) argued that high wood density is primarily the

![Figure 2.7](image_url)
consequence of thick walls of xylem vessels, which prevent their implosion under high negative xylem pressure. The observed pattern of drought mortality suggests that the hypothesis of Hacke forms a highly meaningful alternative to the common view that high wood density is
produced to avoid damage by external forces (Niklas 1992).

The substantial level of retarded mortality found in this study indicates that a single measurement in time will in general not suffice to estimate the mortality caused by an extreme drought. Ideally, measurements should be repeated every year until the yearly mortality has returned to the annualised mortality rate prior to the disturbance event. The repeated measures on tree mortality in the study by Williamson et al. (2000) and in this study (Table 2.7) show that total retarded mortality increases as the drought event becomes more extreme.

In comparison with the other available studies on drought events in everwet tropical rain forest (Table 2.7), the drought in Sungai Wain caused a very...
high mortality. Whereas the cumulative water deficit in Sungai Wain was two to three times larger than in the other studies, the resulting tree mortality was on average six times higher. The relationship between the percentage drought induced mortality after 20-22 months and the cwd (Table 2.7) is described adequately by an exponential relationship \( y = 0.023e^{0.016x} \) (\( R^2 = 0.92 \)) as well as by a linear relationship \( y = 0.048x - 4.32 \) (\( R^2 = 0.80 \)). It is currently not possible to define the exact relationship between cwd and tree mortality. However, both models predict a negligible effect of drought as long as the cwd remains below 100 (linear model) to 200 (exponential model). Above that value the mortality rapidly increases with cwd. This pattern probably results from the fact that trees experience a delay in their actual water shortage after the onset of a rainfall deficit, resulting from the water reserve that is buffered in the soil (Poorter & Hayashida-Oliver 2000, van Dam 2001).

Fire mortality and its interaction with drought

The current paper presents the first study in a Southeast Asian rain forest comprising of a comparison between burned and unburned forest complete with replicates and a large set of trees >10 cm dbh as well as >30 cm dbh. For trees larger than 10 cm dbh the mortality in Sungai Wain was 74% 21 months after the fire, compared with 57% mortality 22 months after fire in Sabah (Woods 1988), 36% after four months in Kutai National Park, East Kalimantan (Leighton & Wirawan 1986) and 25% after six months in south-west Sumatra (Kinnaird & O’Brien 1998). Partly these differences result from methodology: the actual mortality in the study of Woods (1988) may have been higher, because trees that had fallen by the time of observation were not taken into consideration. The other two surveys were done shortly after the fire, and therefore have missed retarded mortality. Still, part of the variation is likely to be explained by differences in the intensity of the droughts preceding the fires. The comparison of unburned and burned plots in our study elucidated the additive effect of drought and fire on tree mortality. Out of the total mortality among trees >10 cm dbh 21 months after the fire, almost 40% was caused by the drought.

Like in the unburned forest, a substantial level of retarded mortality was observed in the burned forest. The retarded mortality in the burned forest was two-fold higher than in the unburned forest, and was caused by a much higher mortality rate amongst trees of 10-40 cm dbh. Tree fall among trees in these size classes that were still alive at the first census was much higher in the burned forest. This can partly be explained by the high density of falling dead trees in the burned forest (even if the frequency of dead trees falling was not increased), which took living trees with them in their fall. Because the open canopy in the burned forest forms little obstacle for gusts of wind, wind throw of living trees was higher as well.

Tree specific fire mortality rate

Several studies have aimed at predicting the species-specific and dbh-specific chance of mortality of tropical rain forest trees after fire by assessing bark insulation properties and experimentally heating the bark of living trees (Gill & Ashton 1968, Vines 1968, Uhl & Kauffman 1990, Pinard & Huffman 1997). In these studies bark insulation turned out to be mainly determined by bark thickness. Few studies looked at the actual species-specific mortality of tropical rain forest trees after fire to validate the predictions made by the above mentioned experiments.

We found that, over the entire range of dbh classes, mortality caused by fire was negatively related to dbh and to bark thickness. Above 70 cm dbh, we did not observe a significant effect of fire on tree mortality. Leighton & Wirawan (1986) found the same pattern of dbh-related mortality. However, bark thickness did not explain the species-specific survival rates of trees >30 cm dbh. This may be due to the rather small differences in bark thickness between species of that
size, but it may also indicate that other factors than merely bark thickness have a large influence on tree mortality, such as an increased risk of fire mortality for size classes and species which frequently have a damaged stem base (Yeaton 1988). At any rate, the results suggest that in order to predict the fire sensitivity of a species, it is more effective to assess the dbh structure of the population than the species-specific bark characteristics. Attaining a large dbh appears one effective means to increase the chance of fire survival.

Conclusion

Our study shows that fire as well as drought may cause high levels of tree mortality. The effect of both disturbances is for a large part on different strata of the vegetation: Drought causes high mortality among trees in the canopy, whereas fire destroys most of the understorey and midstorey. Since fires only occur in unison with extended drought, their effect is disastrous to the forest vegetation. The most vulnerable tree species seem to be those which are confined to the understorey and midstorey. Species that grow to a large stature are likely to survive as a population, although interspecific differences in sensitivity are considerable, and not well understood.

Because of the high levels of retarded mortality, the full extent of the damage resulting from drought and fire can only be determined if a forest is monitored for a considerable period of time after the disturbance. It seems likely that even our inventory 21 months after the event did not record the entire mortality caused by the disturbance events.

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