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## Drought and the consequences of El Niño in Borneo: a case study of figs

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**Abstract** Borneo has a perhumid climate but occasional severe droughts have an important impact. Droughts may affect the composition and size structure of plant communities through differential mortality or, via their impact on the availability of plant resources, affect plant–animal interactions. From January to April 1998, northern Borneo suffered a very severe drought linked to the El Niño Southern Oscillation event of 1997–1998. In this article, the impacts of this drought on the rain forest at Lambir Hills National Park, Sarawak, are considered with special reference to a keystone plant group, the figs. Small fires entered the edge of the forest from the roadside, killing saplings, climbers, and understory trees. Community-wide mortality for adult trees was 0–7 times higher than in nondrought years, with larger trees showing a greater proportional increase. In figs, mortality was significantly higher in pioneers, but hemiepiphytes and roadside species were unaffected. Phenology was substantially affected. Leaf and flower/fruit production decreased or ceased during the drought and increased suddenly following renewed rain. Pollinators of dioecious figs became locally extinct during the drought, and other plant–animal interactions may also have been disrupted. The frequency and severity of droughts has increased substantially in the past three decades, and climate models suggest this may be the result of global warming. The impacts of the 1998 drought at Lambir Hills National Park suggest that, should this trend continue, a substantial alteration of habitats and overall loss of biodiversity can be expected in Borneo.

**Key words** Aseasonal climate · Rain forest · Conservation of biodiversity · Fig wasp · Local extinction · Mortality · Phenology

### Introduction

The tropical rain forests of Southeast Asia are the most diverse terrestrial ecosystem on Earth and have existed since at least the Tertiary (Whitmore 1984). Their antiquity and the favourableness of a perhumid equatorial climate was formerly implicated in the evolution of such extraordinarily high biodiversity. Nowadays, however, it is recognized that major climatic and sea-level fluctuations during and since the Pleistocene glaciations led to corresponding advances and retreats of the forests (Whitmore 1981; Flenley 1998), and over ecological time scales catastrophic disturbances such as drought, fire, typhoon, and landslides have been recorded (Whitmore 1984; Ashton 1993). Such rare but severe disturbances are clearly important in the ecology of these forests. Yet our knowledge of the impacts of severe disturbances remains fragmentary. Moreover, in recent decades the forest has been reduced to smaller and more isolated patches through the expansion of human populations, the intensification of agriculture, and logging. The survival of a large part of the biodiversity of tropical regions will thus depend on the extent to which these small reserves are able to withstand occasional catastrophic disturbances (Whitmore 1984; Ashton 1993; Turner et al. 1994; Bawa and Dayanandan 1998; Whitmore 1998; Nepstad et al. 1999).

In this article, it is my intention to review briefly the current knowledge of one type of major disturbance in Borneo, that of drought. Drought affects the ecology of forests in several ways: through fire (only associated with a severe drought) and plant mortality, and via plant phenology, the abundance of resources available to herbivores, pollinators, and seed dispersers. I consider the impacts of each of these in turn, with particular reference to a keystone group, the figs (*Ficus*; Moraceae), on the forest at Lambir Hills National Park (LHNP), Sarawak (4°20' N, 113°50' E, 150–250m above sea level; Fig. 1). Finally, I draw from these observations some implications for the maintenance of biodiversity in the region.

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**Fig. 1.** Location of Lambir Hills National Park (LHNP)

### Natural history of figs

Figs (*Ficus* spp.; Moraceae) have a unique pollination system that permits a detailed examination of how environmental factors can affect their reproductive success (Herre 1996; Nefdt and Compton 1996). There are approximately 750 species of figs in the world (Berg 1989), and in LHNP figs are the most speciose genus with at least 80 species (LaFrankie et al. 1995; Harrison, unpublished data). Monoecious figs are all hemiepiphytes, often called stranglers, in Borneo and are generally rare. Dioecious figs, generally understory shrubs, small pioneer trees, and climbers, are particularly common and can make up to 50% of the individuals in secondary forests (Corner 1965, 1988; Harrison, unpublished data).

All figs have a closed, urn-shaped inflorescence, or syconium, lined with tiny uniovulate flowers. Species-specific pollinating wasps (Agaonidae, Chalcidoidea, Hymenoptera) enter the syconium through the bracts of the narrow entrance, pollinate the flowers, and attempt to oviposit on the ovules (Galil and Eisikowitch 1968, 1969; Galil 1973). Ovules that receive an egg form a gall on which the wasp larva feeds, while those missed by the wasp, if pollinated, develop into seed normally. Several weeks later, the new adult wasps emerge and mate within the syconia. The female wasps then collect pollen and depart in search of a receptive syconium. A few days later the syconium ripens and vertebrates feed on the fruit. Monoecious figs produce pollinators and seed in the same syconium, while in dioecious figs there are two types of trees bearing different syconia: female trees produce only seeds, and male trees only pollinators and pollen (Galil 1973). A suite of species-specific nonpollinating wasps (gallers, gall parasites, and parasitoids) (Compton and van Noort 1992; West and Herre 1994; Kerdelhue and Rasplus 1996) are also dependent on fig syconia.

Adult female pollinators have extremely short life spans (Kjellberg et al. 1988; Harrison, unpublished data); most live less than a day. At the population level, therefore, figs must fruit almost continuously to enable the pollinator population to cycle from one cohort of syconia to the next, either on the same tree or on neighbouring trees (Bronstein et al. 1990; Kameyama et al. 1999). The continuous availability of fig fruit, especially when other more seasonal fruits are not to be found, makes figs valuable for vertebrate seed dispersers (Terborgh 1986; Lambert 1989; Lambert and Marshall 1991; Shanahan 1997; Tan et al. 1998).

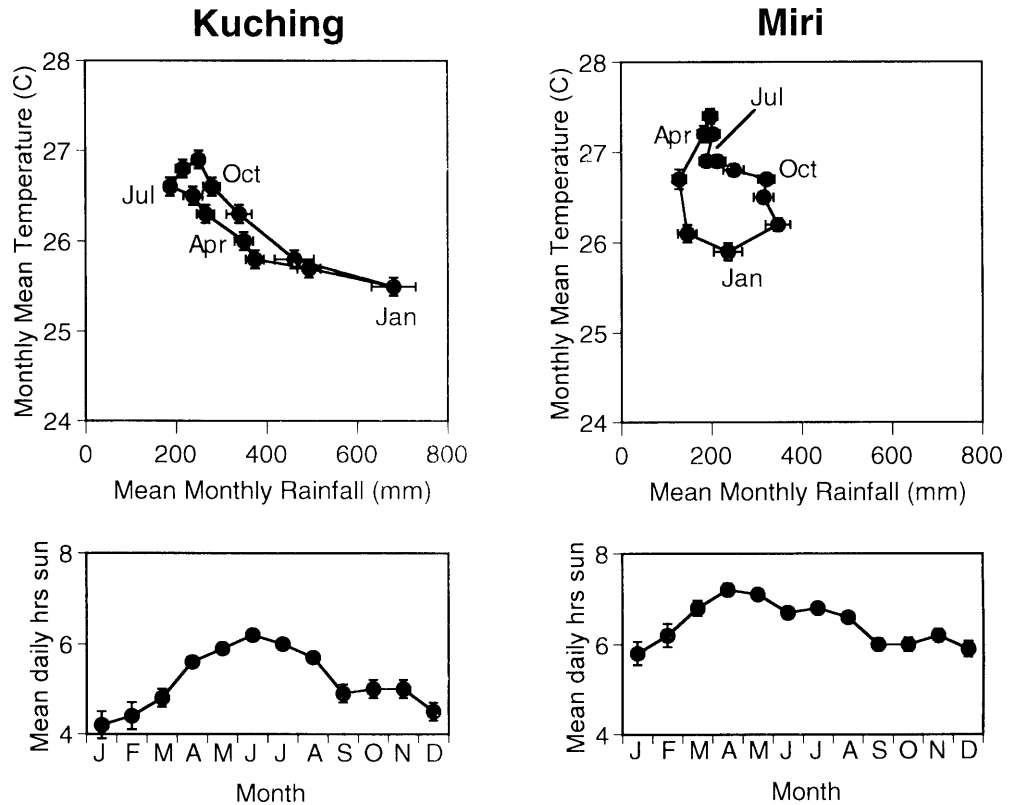
The diversity of species and habits among figs, their dominance in secondary forests (Corner 1988) and importance in succession (Thornton 1994, 1996), and the value of figs for maintaining seed disperser communities have led to figs being regarded as a keystone component of tropical forests in Southeast Asia (Corner 1988; Lambert and Marshall 1991).

### Incidence of drought in Borneo

In Borneo occasional, severe droughts, often associated with the El Niño Southern Oscillation (ENSO), are perhaps the most significant type of natural catastrophic disturbance visited upon the rain forest. Borneo and the rest of the central Southeast Asia region experience a tropical maritime climate with monsoon rains from the Pacific Ocean in winter and from the Indian Ocean in summer. It is thus one of the wettest and most aseasonal climates of any tropical region (Fig. 2; Whitmore 1984). Nevertheless, occasional dry periods may occur between the end of one monsoon and the start of the next, depending on the variable movements of the intertropical convergence zone (Brunig 1969; Baillie 1976; Whitmore 1984; Cranbrook and Edwards 1994).

Recently, irregular supraannual climatic oscillations such as the ENSO have received a great deal of attention in the popular and scientific press (Webster and Palmer 1997; Hughen et al. 1999; Pearce 1999; Toma 1999). El Niño conditions follow when the pool of warm surface water normally located in the western Pacific region flows eastward, shutting off the cold upwelling off the Pacific Coast of South America (Gill and Ramusson 1983; Webster and Palmer 1997; Guilderson and Schrag 1998). The warmer surface waters lead to the now familiar flooding along the eastern Pacific Coast, while in the western Pacific cooler conditions, and hence lower evaporation, cause drought over much of the Southeast Asian and Australian region (Barber and Chavez 1983). Despite the fact that the ENSO phenomenon is probably at least 100 000 years old (Hughen et al. 1999), there is considerable evidence that the intensity and frequency of ENSO events have suddenly increased in recent decades (Guilderson and Schrag 1998; Huppert and Stone 1998; Salafsky 1998; Hughen et al. 1999), which follows predictions from climate models that this will be a consequence of global warming (Meehl 1997; Timmermann et al. 1999). Hence, not only does the more and more frag-

**Fig. 2.** Comparison of the climate (1970–1999) at Miri Airport (*right*) (04°02' N, 113°47' E), 30 km north of LHNP, and Kuching Airport (*left*) (01°29' N, 110°20' E), Sarawak, by hythergraphs and monthly mean daily hours of sunshine. The climate is more seasonal in Kuching, but annual rainfall is higher than in Miri



mented rain forest have to contend with occasional catastrophic droughts, but these droughts also appear to be becoming more frequent and more severe.

Within Borneo there is considerable variation in the rainfall patterns both in terms of the total amount and in its seasonal distribution. Comparing daily records over the 30-year period from 1970 to 1999 from Miri Airport (04°02' N, 113°47' E), just 30 km north of LHNP, and Kuching Airport (01°29' N, 110°20' E), in the south of Sarawak (see Fig. 2), it is clear that Kuching is much more seasonal but also has a higher total annual rainfall (Kuching,  $4048 \pm 57$  mm; Miri,  $2923 \pm 56$  mm). This difference means that the incidence of droughts (30-day rainfall total  $<100$  mm; Brunig 1969; Whitmore 1984) is actually higher in Miri (Fig. 3). In fact, in Miri brief droughts occurred in almost every 12-month period over the 30-year record (Fig. 4). In LHNP minor droughts are, therefore, not rare and occur most often in February–March, before the onset of the southern monsoon, or sometimes in August–September, before the monsoon off the Pacific (Fig. 3) (Seal 1957; Brunig 1969; Baillie 1976). Even droughts that lasted for two or more months occurred seven times and more intense droughts, in which the 30-day total dropped below 10 mm, occurred eight times. However, most droughts are slight.

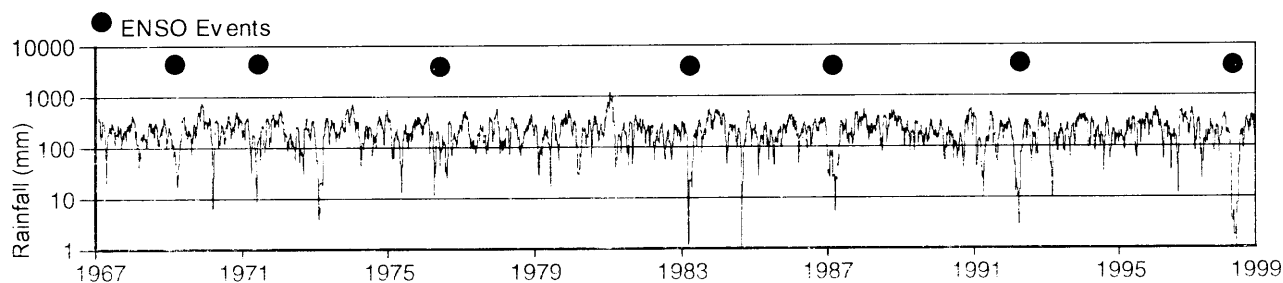
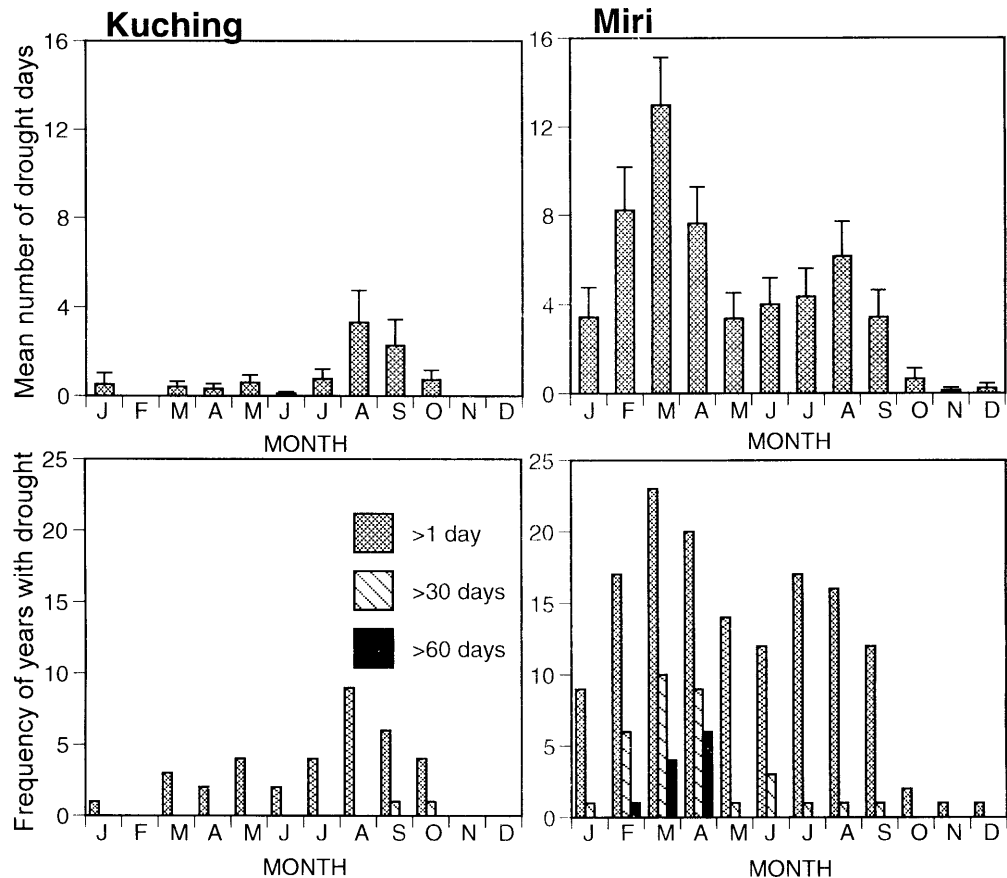
Severe droughts are rare (Fig. 4). A parameter often used to assess the occurrence of severe droughts in a perhumid climate is the 3-month shifting-average rainfall, as minor droughts rarely exceed one month's duration and it also enables one to use long-term monthly rainfall records. Using this parameter, it can be seen that in both Miri and Kuching severe droughts are usually associated

with ENSO events (Fig. 5). In Kuching the 3-month shifting-average rainfall was less than 100 mm on only 3 occasions, and all were ENSO events. In Miri there were 15 such droughts, and 10 of these were ENSO events. Since about 1966 an increase in the severity of ENSO events has led to a corresponding increase in the severity of the droughts associated with them in Miri (Fig. 5), and the same pattern has been reported from Pontianak in southern Borneo (Salafsky 1998). However, it is also evident that there is no such trend in Kuching (Fig. 5).

Walsh (1996) has suggested that the latest spate of droughts simply reflected long-term periodic changes in frequency, with an earlier episode of severe droughts evident between about 1877 and 1915 in Sandakan, northeast Borneo. The same tendency can be seen in the data from Kuching (Fig. 5). However, although rainfall data were not collected from the Miri area before 1912, the droughts of the past two decades do appear extraordinary (Fig. 5). Clearly, different areas are being affected to different extents. However, the evidence that droughts are becoming worse in at least two widely separated locations suggests the predictions of climate models (Timmermann et al. 1999) may yet be borne out. Certainly, when the recent fires over much of Kalimantan and in northern Borneo are considered (Bertault 1991; Toma 1999), the impacts of recent droughts have been much more severe if only because of human disturbance.

By far the strongest drought in Miri was that associated with the recent 1997–1998 ENSO event, when the 30-day rolling rainfall total remained below 10 mm for more than two months (see Figs. 4, 5). Comparing the annual

**Fig. 3.** Incidence of drought (1970–1999) at Miri Airport (right) (04°02' N, 113°47' E), 30 km north of LHNP, and Kuching Airport (left) (01°29' N, 110°20' E), Sarawak. Mean monthly evapotranspiration is approximately 100 mm (Baillie 1976; Whitmore 1984); hence, droughts were defined as 30-day rolling rainfall total <100 mm. *Upper graphs*, mean number of drought days per month; *lower graphs*, frequency of droughts >1 day, >30 days, and >60 days duration per month (the same drought may be recorded in consecutive months). The graphs also show the tendency for southern Borneo to be affected by droughts in August–October before the winter monsoon, whereas in northern Borneo droughts usually occur in January–March, before the summer monsoon

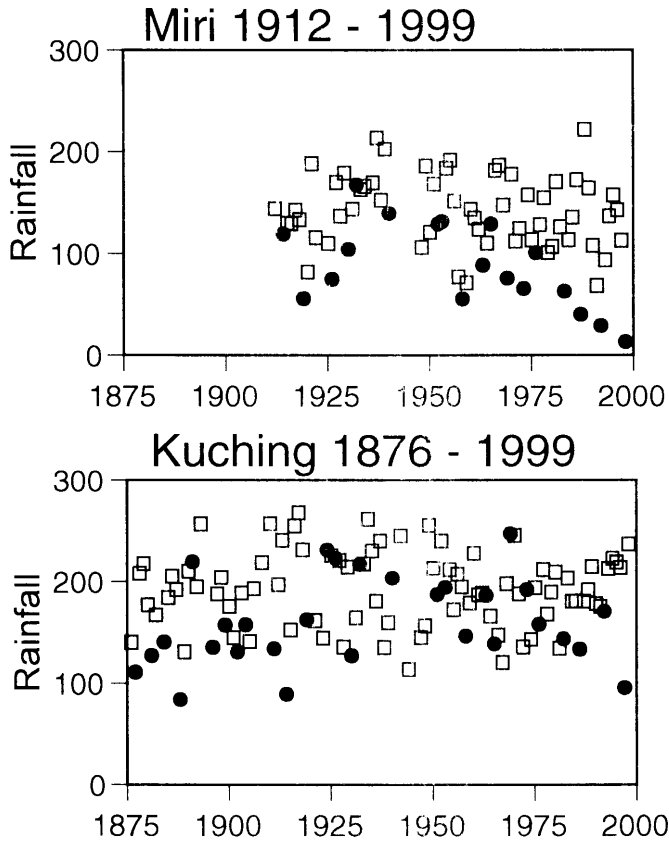


**Fig. 4.** Thirty-day rolling rainfall totals from Miri Airport (04°02' N, 113°47' E), 30 km north of LHNP (1967–1998). El Niño Southern Oscillation (ENSO) events are indicated (solid circles). Mean monthly evapotranspiration is approximately 100 mm (Baillie 1976; Whitmore 1984). Minor droughts are clearly very common, but severe droughts are rare and usually associated with ENSO events

minimum 3-month shifting-average rainfall figures since 1912 (Fig. 5) against a normal distribution, from which the data did not differ significantly, suggests droughts of such severity would normally be expected at intervals of substantially more than once per century.

The 1997–1998 drought was also very widespread, affecting the entire northern region of Borneo (Fig. 6) (Toma 1999). The fact that severe droughts affect very wide areas, as compared to other disturbances such as landslides or fires (Ashton 1993), has major implications for the conservation of biodiversity given the high levels of endemism in many taxa and the aforementioned fragmentation of remaining forest reserves. Significantly, however, some areas with high annual rainfall such as Kuching and especially Belalong in

Brunei were less affected (Fig. 6). Belalong is surrounded by a large area of undisturbed forest (>100 000 ha). Other inland sites with high annual rainfall that are surrounded by cultivated land and logged forest were, however, severely affected (e.g., Mt. Kinabalu; Kudo and Kitayama 1999; or Kelabit Highlands, personal observation). This difference is perhaps surprising as the contribution of evapotranspiration to total precipitation is not generally thought to be very significant compared to that of monsoon rain in Borneo. However, even if the total contribution is small it may be especially important in periods of drought. Areas that escape the worst of a drought should act as refugia for drought-sensitive species and hence will be particularly important for the conservation of biodiversity.



**Fig. 5.** Severity of droughts in Miri (1912–1998) (*top*) and in Kuching (1876–1999) (*bottom*). The rainfall value given is the yearly minimum 3-month shifting-average rainfall. Data are given for the total period for which records are available, and ENSO events are indicated by *filled circles*, normal years by *open squares*. Three-month shifting-average rainfall is often used as an indicator of droughts in perhumid climates where dry seasons rarely exceed 1 month. This figure, therefore, indicates the severity of the driest period of each year. The frequency and severity of droughts has very clearly increased in recent decades in Miri

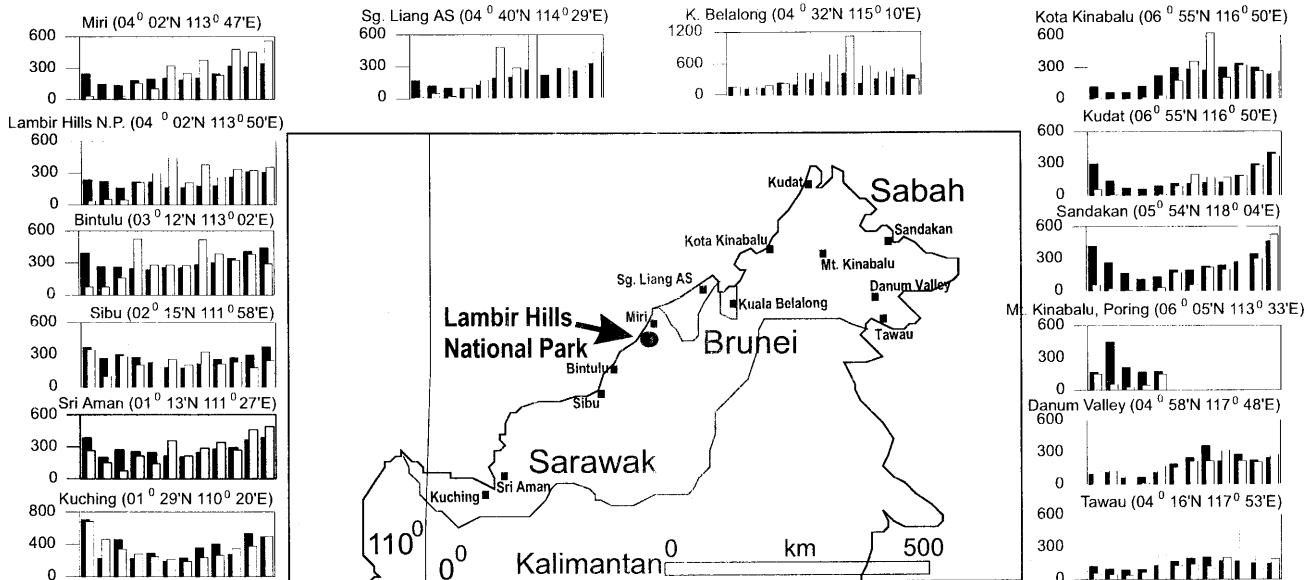
We can conclude, then, that minor droughts are common in LHNP but that very severe droughts are rare and usually associated with ENSO events. In recent decades, ENSO events have become more frequent and the droughts associated with them more severe. Such droughts have an impact over very large areas, but inland sites with large areas of primary forest may be less susceptible.

## Impacts of drought on the rain forest in Borneo

### Drought and fire

When drought is accompanied by fire, usually deliberately started to clear land and then burning out of control, the destruction of habitat is much more severe (Leighton and Wirawan 1986; Woods 1989; Bertault 1991; Nykvist 1996; Toma 1999). A large area of impoverished *Imperata cylindrica* and *Baeckea frutescens* grassland known as the Sook Plain in Sabah was created during the 1915 drought when approximately 100000ha of forest over peat burnt (Cockburn 1974). Other similar large areas of grassland in central Borneo were quite likely created by fire.

Fire burning in forests over mineral soils is only slightly less destructive. During a fire in East Kalimantan associated with the 1982–1983 ENSO event, 80% of lianas and 80% of stems less than 5 cm dbh (diameter at breast height) died. For the latter, this was four times the figure for mortality caused by drought alone. Larger trees (>30 cm, dbh) were less affected and mortality was lower than in unburnt plots (Table 1; Leighton and Wirawan 1986). During the same drought in Sabah, Woods (1989) showed that logged forest was much more prone to fire and that the mortality of trees (>10 cm dbh) much higher than in unlogged forest. Forest succession in logged forest was reversed and *Imperata*



**Fig. 6.** Rainfall in northern Borneo during the 1998 drought period. *Solid bars* indicate long-term monthly mean rainfall; *open bars* indicate monthly rainfall during 1998. Southern Borneo was not affected by the drought in 1998, but there were droughts in September–October 1997. Kuala Belalong, in Brunei, also escaped the worst effects of the drought even though nearby sites suffered severe droughts

**Table 1.** Mortality in burnt and unburnt areas in Kalimantan after the 1982–1983 drought

	Lianas	<4 cm dbh	4–10 cm dbh	11–30 cm dbh	>30 cm dbh
Burnt	83.2% (357)	82.4% (922)	66.0% (465)	37.0% (786)	21.8% (353)
Unburnt	–	14.5%***	18%***	21%***	35%***

dbh, breast height diameter

G-test probability, \*\*\*  $P < 0.001$

From Leighton and Wirawan (1986)

*cylindrica* and creepers invaded, whereas in primary forest the forest structure was not greatly altered. Nykvist (1996) also reported that 8 years after the drought the above-ground biomass was still only 24% of the prefire level in a logged forest.

During the 1998 drought at LHNP, several small fires entered the edge of the forest. The fires burnt slowly, eating their way through the leaf litter, and hence heat in the surface soil layer must have been intense. Leaf litter and surface soil humus was completely reduced to ash, and personal observations indicated mortality among seedlings and saplings was 100% although most large trees escaped. Among the figs under observation, the single climber, 13 of 14 hemiepiphytes, and 100% of pioneers (29 individuals, 10–30 cm dbh) died in the burnt areas. This observation compares to 83% for hemiepiphytes and 100% for climbers in the Leighton and Wirawan (1986) study.

There is also evidence that fires exacerbated the 1998 drought. At one point, more than 300 ha of cleared peat land and peat forest were burning around Miri in March 1998. Fires were also widespread in Brunei, Sabah, and East Kalimantan over the entire area affected by the drought (Toma 1999). Smoke from these fires formed a pall over much of the northern area of Borneo. The smoke particles in this haze caused water to condense as tiny droplets too small to allow cloud formation, thus reducing rainfall even further (Rosenfeld 1999).

#### Plant mortality caused by drought

Rare severe droughts in Borneo cause high plant mortality in primary lowland rain forest (Leighton and Wirawan 1986; Becker et al. 1998; Nakagawa et al. 2000), in heath forest (Becker and Wong 1993), and in mountain vegetation (Kudo and Kitayama 1999). Severe drought may also alter the composition and structure of a habitat through differential mortality among species and size classes. It has been suggested that the lower diversity of forests in eastern Borneo compared to Sarawak and Brunei is the result of a higher frequency of severe droughts (Davies and Becker 1996). In lowland rain forest in Sabah and Kalimantan during the 1982–1983 drought, mortality rates varied from 0% to 71% for individuals greater than 60 cm dbh, but there was little differential mortality between timber types (Dipterocarpaceae) or size classes (Leighton and Wirawan 1986; Becker et al. 1998).

During the 1998 drought in LHNP, overall tree (>10 cm dbh) mortality was 0–7 times higher than the during the

**Table 2.** Plant mortality at Lambir Hills National Park during a severe drought (1998) and in nondrought periods

	<i>n</i>	Nondrought (1995–1997) mortality (% yr <sup>-1</sup> )	<i>n</i>	Drought (1998) mortality (% yr <sup>-1</sup> )
Community:				
Trees (>10 cm dbh)	771 <sup>a</sup>	0.9	816	6.4***
Figs:				
Total	317	6.26	267	15.73***
Hemiepiphytes	24	8.30	18	00.00 (ns)
Climber	18	5.56	15	26.67 (ns)
Understory pioneers	222	8.45	183	17.98**
Roadside	53	3.77	51	09.80 (ns)

<sup>a</sup>From Nakagawa et al. (2000)

G-test probability: ns  $P > 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$

previous non(severe) drought period (Table 2) (Nakagawa et al. 2000; M. Potts, unpublished data), although these are probably underestimates because many individuals under phenological census did not die until slightly later (Canopy Biology Program Sarawak; unpublished data held by author). A higher proportion of larger individuals died compared to the nondrought period, indicating a change sustained to the size structure of the forest. A similar pattern of mortality during droughts was found in Panamanian forests (Condit et al. 1995). In LHNP there was also considerable differential mortality among plant families, with the highest mortality among dipterocarps, 15 to 30 times the nondrought level (Nakagawa et al. 2000) and among soil types (M. Potts, unpublished data). Thus this drought altered not only the size structure of forest toward smaller individuals but also the species composition, with timber species suffering most. Seedlings also showed significantly higher mortality during the drought but only marginally, and mortality was still within the range of nondrought mortality rates (L. Delissio, unpublished data). Interestingly, there were also no species differences in drought-induced mortality rates.

Among figs at those sites not burnt, mortality rate was two to four times higher during the severe drought in 1998 than during the previous 3 years, except for hemiepiphytic figs, which had zero mortality during the drought (see Table 2). The normal mortality rate of figs is generally high compared to other groups: hemiepiphytes and climbers are prone to tree falls as they often colonize old trees, and free-standing trees are pioneers, which are often killed by disturbances or when they are overtopped by late successional

species (Harrison, unpublished data). Hemiepiphytes may be preadapted to drought conditions. During the epiphytic phase, they are often acutely stressed by a shortage of water (Holbrook and Putz 1996a, b). Mortality of adult fruit trees will clearly have repercussions for the seed-disperser populations dependent on them and possibly also for the stability of the pollinator populations.

Minor droughts may also cause mortality, but distinguishing this effect from background mortality levels is difficult. Indirect effects through competition may be especially important in segregating species according to the soil type and topographical preferences described for many species (Whitmore 1984; Ashton 1988; Becker and Wong 1993; Itoh et al. 1995; Newbery et al. 1996; Davies et al. 1998).

### Plant phenology

Generally, in tropical regions, where daily temperature range often exceeds the yearly variation in mean temperature, it is the amount of rainfall and especially the length of the dry season that dictates forest seasonality (Whitmore 1984; Reich 1995; Corlett and Lafrankie 1998). However, even the short dry periods that occur in aseasonal tropical forests are an important influence on phenology (van Schaik 1986).

The tropical rain forests of Southeast Asia engage in general flowering (Wood 1956; Burgess 1972; Medway 1972; Ng 1977; Appanah 1985; Ashton et al. 1988; Momose et al. 1998; Sakai et al. 1999); this is a community flowering and fruiting event in which a large proportion of the individuals (>50%), covering varied taxonomic groups and flowering syndromes (Momose et al. 1998), participate usually after several years of little or no reproductive activity (<5% of individuals; Sakai et al. 1999). The flowering trigger is thought to be a drop in nighttime temperature about a month before flowering (Ashton et al. 1988) or a sharp increase in the amount of sunlight (Ng 1977; van Schaik 1986), but most researchers have found a poor correlation with rainfall or drought (Burgess 1972; Ashton et al. 1988). Leaf production is thought to correlate with the two annual peaks of rainfall (Medway 1972; Ng 1981).

At LHNP, a phenology census of 424 individuals in 253 species from tree towers and a canopy walkway system clearly demonstrated the general flowering characteristic of these forests (Fig. 7) (Sakai et al. 1999). Nevertheless, rainfall and especially drought have a strong influence on phenology. Leaf production and flowering generally increase following droughts. The pattern was much stronger in general flowering years, but there was a tendency to renew leaves and flower following periods of lower rainfall in all years. This trend resulted in a biannual periodicity for leaf production, but flowering was dominated by the general flowering phenomenon (Fig. 7; Harrison, unpublished data). Drought is unlikely to be the trigger for flowering in most species (Burgess 1972; Ashton et al. 1988), but it can still affect the physiology of plants during the development of a flowering period. Heavy tropical rain may damage

flowers and disrupt pollination, while drought through its effect on seedling mortality (Whitmore 1984; Turner 1990) may open up germination sites and will on average indicate a longer period until the next drought.

Trees in LHNP rarely lose a substantial part of their leaves; however, during the severe drought in 1998 there was a sudden increase in the deciduousness of the forest. There was then a major flush of new leaves shortly after the drought (see Fig. 7). However, the impact of this drought on flowering was less clear and does not appear significant at the community level.

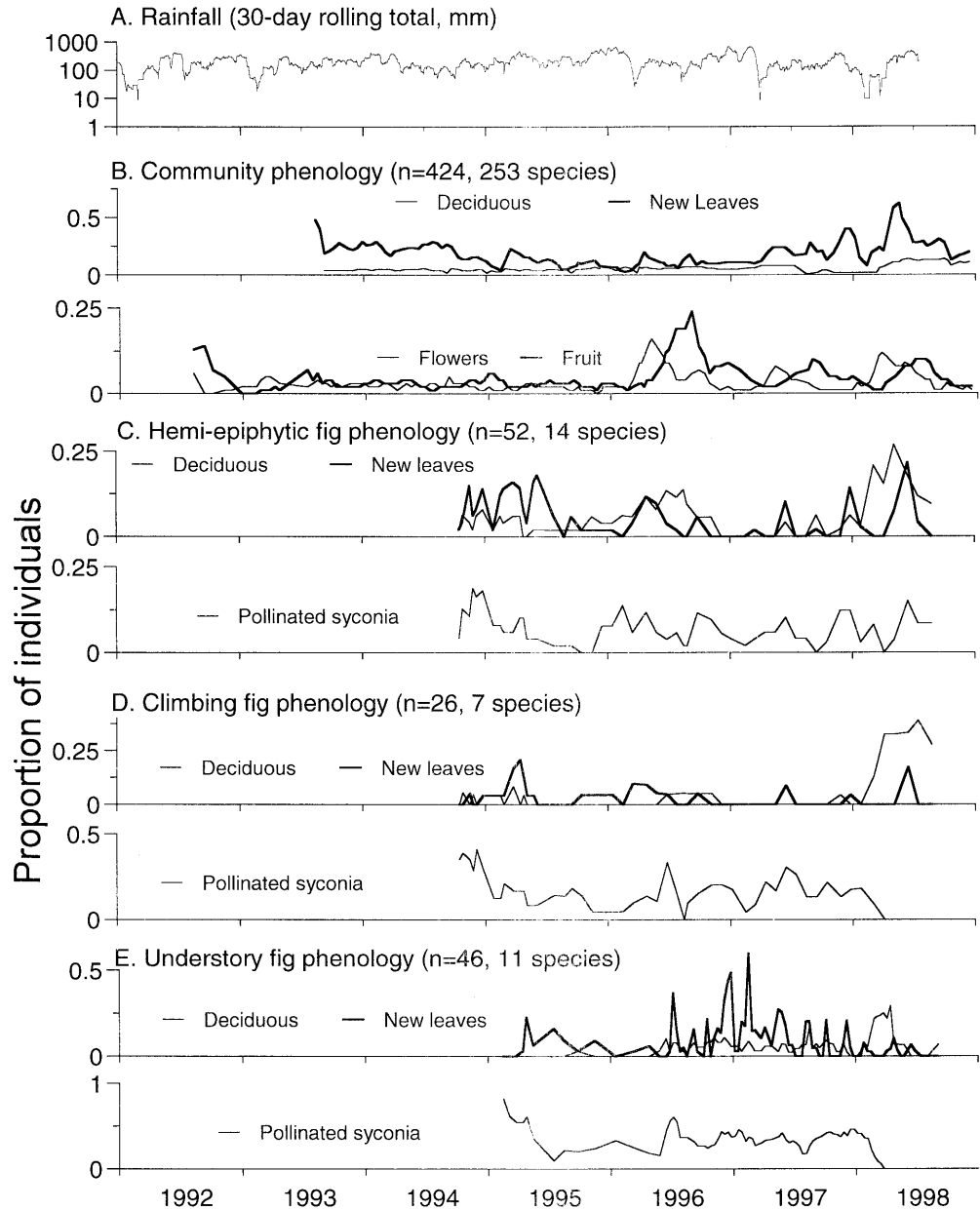
The phenology of figs is constrained by their need to produce syconia continuously. Hence, we might expect fig phenology to be less influenced by environmental factors such as drought and more under the control of endogenous rhythms. Leaf production and to some extent syconia production were quite variable (Fig. 7). There was a slight biannual rhythm of leaf production similar to other trees in the forest, which was also disrupted by the severe drought in 1998, but syconia production did not show any distinct periodicity.

Most tropical phenology studies have been conducted at the community level; however, at the population level different species, even those in the same genus, often respond in different ways (Corlett and Lafrankie 1998). *F. cereicarpa* (Corner) and *F. schwarzii* (Koord) are both pioneer figs but their phenology is clearly quite different (Fig. 8). Syconia production in *F. schwarzii* was more susceptible to disruption by minor droughts. Individual trees have a highly synchronous phenology and even short dry periods tended to cue individuals in the population. *F. cereicarpa* individuals stagger the initiation of syconia, so the population was not synchronized by dry spells (Harrison 2000a). However, the phenology of both species was totally disrupted by the severe drought in 1998. *Ficus fulva* Reinw. ex. Bl. is a common roadside species in Sarawak and exhibits a third type of phenology. It has synchronous crops, but these are produced at longer intervals than those of *F. schwarzii*. In this case, the staggered initiation of entire crops appeared to mitigate against minor droughts, although the period of observation was shorter (Fig. 8; Harrison et al. 2000). In all three species there was a tendency to produce new leaves following minor droughts. During the severe drought in 1998, most individuals lost their leaves, and the initiation of immature syconia temporarily ceased (Fig. 8) (Harrison 2000b; Harrison et al. 2000). Following the drought a high proportion of those plants that did not actually die suffered canopy dieback and renewed leaves from the trunk.

### Herbivores, pollinators, and seed dispersers

Plant phenology affects the availability of plant resources for pollinators, seed predators, and herbivores and hence influences the ecology of forests. Given that for most plant species the duration of a drought is short in relation to their total life span, the impact of drought on phenology will likely have only a marginal effect on plant fitness. However, the impact on plant resources for herbivores, pollinators,

**Fig. 7.** Comparison of rainfall data from LHNP and community phenology. **A** Thirty-day rolling rainfall totals (mm) from the Telecom tower in LHNP. **B** Proportion of individuals with *deciduous* crowns (defined as when 25% of leaves had fallen), with *new leaves* (>10% of crown consists of new leaf), and with *flowers* and *fruit* by census from 1992 to 1998 (figs not included). **C–E** The proportion of individuals of hemiepiphytic figs, climbing figs, and understory figs, respectively, with *deciduous* crowns, with *new leaves*, and with *pollinated syconia*



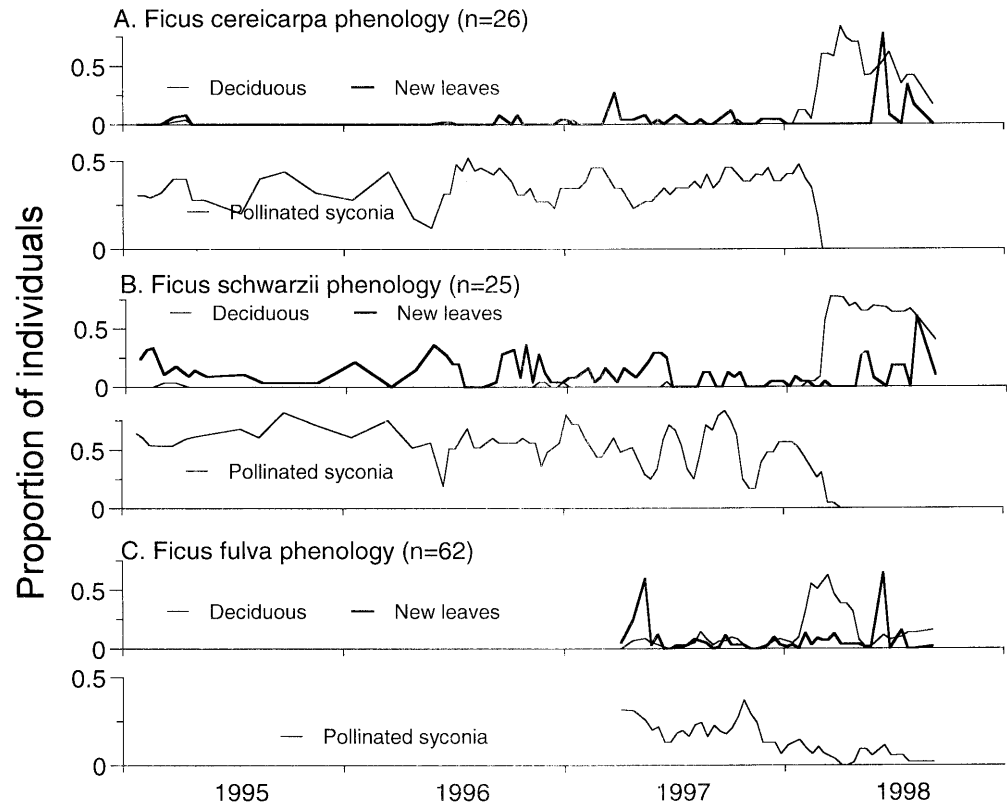
and seed dispersers can often be expected to have a substantial influence on the populations of these animals (Wolda 1978; Aiello 1992; Inoue et al. 1993; Coley 1998; Wright et al. 1999).

Rates of herbivory are higher in tropical forests, despite the fact that leaves are better protected, which must reflect greater herbivore pressure (Coley 1998). Furthermore, most herbivory in the tropics is on young leaves, which are an ephemeral resource (Aide 1993). Herbivores also tend to be more specialized (Janzen 1988; Marquis 1992). Hence, reduced leaf production and higher direct mortality of larval stages likely cause reductions in herbivore populations during droughts (Aiello 1992). However, often the most noticeable effect of a drought is an explosion of herbivore populations following the renewal of rains (Aiello 1992; Coley 1998). This event has been recorded in Sarawak on at

least two occasions when unidentified lepidopteran species defoliated species of Sapotaceae, especially *Palaquium walsurifolium*, in 1953 and of *Dactylocladus stenostachys* (Crypteroniaceae) in 1958 (Anderson 1961 quoted in Coley 1998). The most likely explanation for herbivore outbreaks such as these is that the populations of their natural enemies, especially parasitoids, are severely reduced by the drought (Aiello 1992; Coley 1998). Following the typical pattern, captures of all insects, including herbivores, at light traps set in the canopy in LHNP decreased to record low levels during the severe drought in 1998. The populations of some herbivores, especially Lepidoptera, then exploded following the drought coinciding with the leaf flushing peak (Takao Itoika, unpublished data). In the roadside fig species *F. fulva*, a large proportion of individuals were partially, and in some cases completely, defoliated by an



**Fig. 8.** Phenology of three fig populations by census, January 1995–September 1998 (data from these species were omitted from Fig. 7), showing proportion of individuals with deciduous crowns, with new leaves, and with pollinated syconia. **A** *Ficus cereicarpa* Corner. **B** *Ficus schwarzii* Koord. **C** *Ficus fulva* Reiw. ex. Bl



unidentified lepidopteran approximately 1 month after the drought (Harrison et al. 2000).

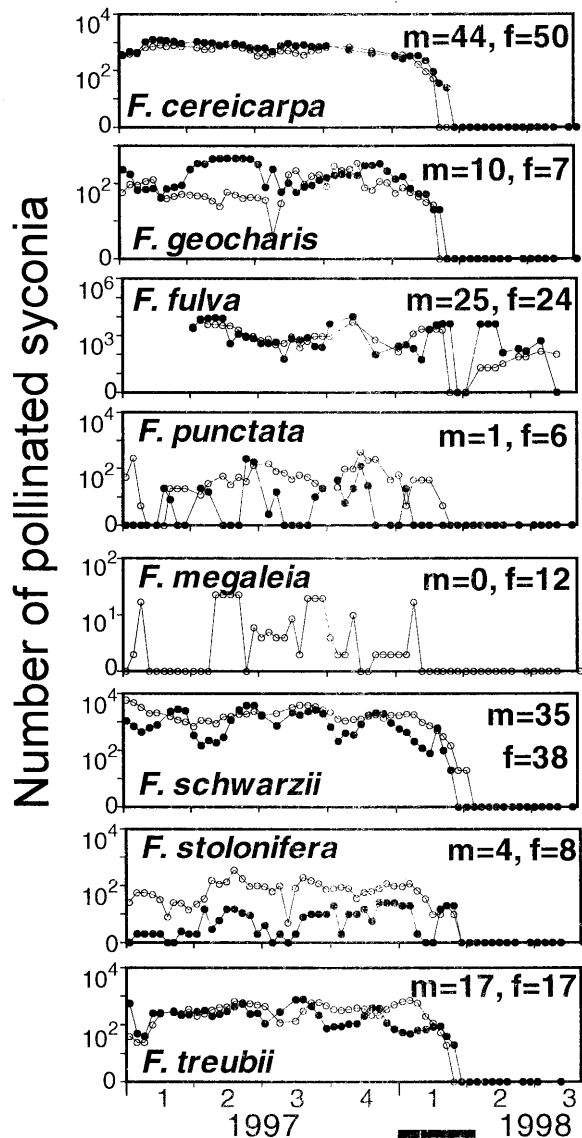
The impacts of drought on tropical pollinators is even less well understood. It stands to reason that species that can hoard resources should be better able to withstand food shortages caused by a drought. More than a decade's data from Panama showed no correlation with rainfall and bee abundance, even when ENSO and rainy years were included (Roubik and Wolda 2001), but euglossine bee populations tend to increase following the annual flowering peak and also showed a positive correlation between big ENSO flowering years and peak bee populations (Roubik 2001). The impact of the 1998 drought on the pollinating and nonpollinating wasps of figs in LHNP was very significant: the fig wasp populations of all dioecious figs under observation in LHNP became locally extinct (Harrison 2000b) (Fig. 9). Trees failed to initiate syconia for a period of approximately 2 months or roughly twice the total life span of the wasps, preventing emerging wasps from finding any receptive syconia.

The density of many of these fig species is very high in the secondary forest around LHNP, but because all trees in the population were similarly affected, fig population size was irrelevant. In all but one species, *F. fulva*, the wasp populations had still not reinvaded by October 1998. Southern Borneo was unaffected by the drought, and some species may also have survived in places such as Belalong, Brunei, which escaped the worst effects of the drought. Nevertheless, 1 year after the drought the pollinators of only two more species had recovered. Two years after the

drought, another three species had recolonized. However, the pollinator of *F. cereicarpa*, which is thought to be endemic to northern Borneo, still had not returned (Table 3). One cannot say yet whether the pollinator of *F. cereicarpa* is extinct or if it simply has an extremely limited dispersal ability, but the 1998 drought clearly had a very severe impact on all the pollinators of dioecious figs and especially this species.

Interestingly, the pollinators of monoecious figs were less affected by the drought (Harrison 2000b). In one species, *F. benjamina*, there were low rates of pollination among the first crops after the drought but at least 10% of a crop was always pollinated. One possible explanation is that the monoecious figs were less susceptible to the drought, allowing a small number of individuals to maintain the pollinator population. All monoecious figs in LHNP are hemiepiphytes and, as explained earlier, these may be pre-adapted to drought conditions because of the water stress they suffer during the epiphytic stage (Holbrook and Putz 1996b). Another possibility is that the pollinators are capable of long-distance dispersal and arrived from trees outside the area affected by the drought. Paternity studies have shown that the pollinators of similar species in Panama can disperse long distances (Nason et al. 1996, 1998), and following Hurricane Andrew in Florida the pollinators returned almost immediately (Bronstein and Hossaert McKey 1995), presumably from outside the path of the storm.

The absence of pollinating wasps on figs prevents any fruit production because all unpollinated syconia are



**Fig. 9.** Extinction of pollinating wasps of dioecious figs during the 1998 drought at LHNP. The number of pollinated syconia on male ( $m$ ) trees indicate the population of wasp larvae developing in the observed population and, for both sexes ( $m, f$ ), the presence of pollinating wasps at the time of receptivity. Pollinators live 1 day; hence, a period of longer than 1 day without any pollinated syconia on male trees indicates local extinction of the population (From Harrison 2000b)

aborted. Therefore, the impact of the 1998 drought on the seed dispersers of dioecious figs in LHNP was probably also significant. Anecdotal evidence of fruit bats feeding on *F. schwarzii* suggests they disappeared from the site following the drought, having either migrated or starved. These bats are very important seed dispersers (Boon and Corlett 1989; Tan et al. 1998) and hence there will likely be a local impact on the tree species dependent on their services, at least until their populations recover (Harrison 2000b). Surveys of the vertebrate fauna in LHNP have revealed that 14 bird and 9 mammal species recorded in 1984 (Watson 1985) have not been seen recently. Moreover, there has been a significant increase in the proportion of open-space and montane bird

**Table 3.** Recolonization of dioecious fig pollinators at Lambir Hills National Park following the severe drought in January–March 1998

Fig species	$n$	Pollinators recorded			
		April 1998	October 1998	April 1999	May 2000
<i>F. cereicarpa</i>	77				
<i>F. fulva</i>	49	*	*	*	*
<i>F. geocharis</i>	12				*
<i>F. megaleia</i>	12				?
<i>F. punctata</i>	7				*
<i>F. schwarzii</i>	52			*	*
<i>F. stolonifera</i>	12				*
<i>F. treubii</i>	34			*	*

*F.*, *Ficus*

\*indicates presence

species (Shanahan and Debski, in press). Several factors, such as increased disturbance around LHNP and hunting within the park, must be contributing to these changes, but severe droughts are likely to exacerbate the effects.

## Conclusions

Drought demonstrably influences the ecology of forests in Borneo. Even minor droughts, which are clearly not infrequent, may influence the outcome of competitive interactions between plant species (Whitmore 1984; Ashton 1988; Becker and Wong 1993) and through the impact on plant phenology affect the availability of resources for herbivores, pollinators, and seed dispersers (Aiello 1992; Inoue et al. 1993). This may then in turn have consequences for the reproductive fitness of certain plant species (Augsburger 1981; Brody 1997). For example, in *F. schwarzii* at LHNP synchronization of phenology at the population level, caused by brief dry spells, led to peaks and crashes in pollinator production and reduced pollination success (Harrison 2000a).

Droughts as severe as that in 1998 can reasonably be described as catastrophic. The rarity of such severe droughts, which occur at intervals of several generations or more for all but the longest-lived plants, means species are ill adapted to adjust to such an event. Fire is particularly destructive, especially over peat or in secondary forests, but even in the primary forest the understory layer is generally destroyed. Plant mortality during severe droughts is considerably higher than at normal times, and the differential mortality among species and tree size classes, with an increased proportion of big trees succumbing, alters the community composition and population structure of the forest.

The disruption to plant phenology, while it may have only a temporary impact for most plant species, has more dire consequences for the herbivores, pollinators, and seed dispersers dependent on the regular availability of plant resources. This will be especially true for short-lived species, and for highly specific interactions, as was evidenced

by the local extinction of all pollinating and nonpollinating wasps on dioecious figs at LHNP. It is not unreasonable to expect that some other short-lived insects also became either locally extinct or very rare at this time. The explosion of Lepidoptera populations following the renewal of rains suggests a case of ecological release resulting from an adverse affect of the drought on their natural enemies, most likely parasitoids (Aiello 1992; Coley 1998). The consequences for vertebrate seed dispersers, such as the hornbills and primates, are also likely to be serious (Wright et al. 1999). These species require large home ranges (Bennett et al. 1997). Therefore, when resources become scarce during a severe drought, compounded by the small size and isolation of many reserves, the prospects for such far-ranging animals are not good. Moreover, if plant–pollinator interactions are also disrupted, such as occurred in the dioecious figs, then fruit production for a considerable period after the drought may be affected.

One question that arises from these observations is why have these forests remained so diverse given severe droughts have occurred numerous times over evolutionary time scales? The answer can be guessed at if we examine again the case of the pollinators of dioecious figs. These wasps all became locally extinct during the drought but most had recolonized 2 years later. The stability of this interaction, despite the calamity of losing one of the partners, is impressive. It arises because the fig trees are capable of waiting many pollinator generations, albeit without any reproductive success, for the arrival of their short-lived pollinators. Also, most of these dioecious figs are very common in the secondary forests that cover most of the land area in Sarawak, which probably assisted the gradual migration of pollinators from surviving populations. In the past, large areas of contiguous forest would have mitigated against severe droughts by preserving intact communities next to the affected areas. Large forests probably also reduced the severity of droughts by maintaining small-scale hydrological cycles. The small size and isolation of forest patches today casts some doubt over whether these will be able to recover fully following a severe drought.

The rarity of droughts in the past would also have allowed forests the time to recover before the next drought. The climate data presented here and by other researchers (Guilderson and Schrag 1998; Huppert and Stone 1998; Salafsky 1998) indicate that ENSO events and the droughts associated with them in Borneo have become more frequent and more severe in recent decades. It thus becomes all the more urgent that reserves are made bigger and the matrix surrounding them managed so far as possible to provide corridors and secondary habitat (Bawa and Dayanandan 1998).

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