

SHORT COMMUNICATION

Severe drought, leafing phenology, leaf damage and lepidopteran abundance in the canopy of a Bornean aseasonal tropical rain forest

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(Accepted 28 July 2003)

Key Words: Borneo, Dipterocarpaceae, El Niño, forest canopy, herbivory damage, insect herbivores, Lambir Hills National Park, leaf-chewing moth larvae, Sarawak, South-East Asia

Rainfall fluctuation influences the physiology and leaf production of the trees in tropical rain forests (Burslem *et al.* 1996, Condit *et al.* 1995, Reekie & Wayne 1992, Reich 1995), and consequently it may have an impact on the community of herbivores that depend on forest trees for their food resources (Aide 1988, 1992; Basset 1991, Coley 1998, Lowman 1985, van Schaik *et al.* 1993).

At the centre of the South-East Asian tropical region that includes the Malay Peninsula, Borneo, Sumatra and Java, temperature is constantly high, with no distinct dry season (Richards 1996), and supra-annual climatic change is relatively pronounced in the lowland rain-forest areas (Inoue *et al.* 1993). Although seasonal fluctuations in insect assemblages have been described in other tropical areas (Basset 1991, Lowman 1985, Wolda 1989), few studies exist on the seasonality of the insect assemblages in the lowland rain forests of South-East Asia. However, the seasonality of abundance of some insect species has been reported in relation to the supra-annual general flowering events characteristic of the region (Itioka *et al.* 2001, Kato *et al.* 2000).

Beginning in early 1998, a severe drought occurred over most of the tropical areas of South-East Asia (Harrison 2001, Nakagawa *et al.* 2000). The event was extraordinary in terms of length and degree of drought, and the extent of areas affected resulting in death or damage of many trees. During the drought, many trees shed their leaves. We found that, when the drought ended and rainfall came again, most trees flushed and the abundance of young leaves drastically increased. Because young leaves are suitable food resources for many

insect herbivores, especially leaf chewers (Aide 1988, 1992; Barone 1998, Coley 1983, Lowman 1985), such community-wide leaf-flushing (leafing) may enhance the survival and population growth of insect leaf chewers, including lepidopterans.

In a Bornean tropical rain forest, we monitored the temporal change of lepidopteran abundance in relation to the severe drought and the subsequent community-wide leafing in 1998. In parallel, we censused the abundance of young and mature leaves in the forest canopy, and the herbivory damage on leaves caused by leaf chewers.

The study site is the lowland mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia (4°2'N, 113°50', 150 m asl). The mean temperature and annual precipitation there are 26 °C and 2700 mm, respectively, with average monthly precipitation (1985–1998 at a Telecom station near the study site) ranging from 167.5 mm in July to 328.4 mm in November, and with no conspicuous dry season (Nakagawa *et al.* 2000). There is a canopy-access system consisting of a series of ladder, towers, platforms and aerial walkways in the forest canopy (Inoue *et al.* 1995). Using this canopy-access system, we investigated the leafing phenology, herbivory damage on leaves, and the abundance of lepidopteran larvae in the forest canopy.

Beginning early in 1998, a severe drought due to the intensive El Niño Southern Oscillation occurred in the study site (Harrison 2001, Nakagawa *et al.* 2000). Monthly rainfall during the first quarter of 1998 was consistently less than 100 mm, and the total rainfall in that quarter was 138.5 mm, which is 24% of the mean rainfall from January to March of the last 14 y (576.5 mm) (Figure 1). In the 3 mo (hereafter, called the 'drought period') analysed, many trees were observed

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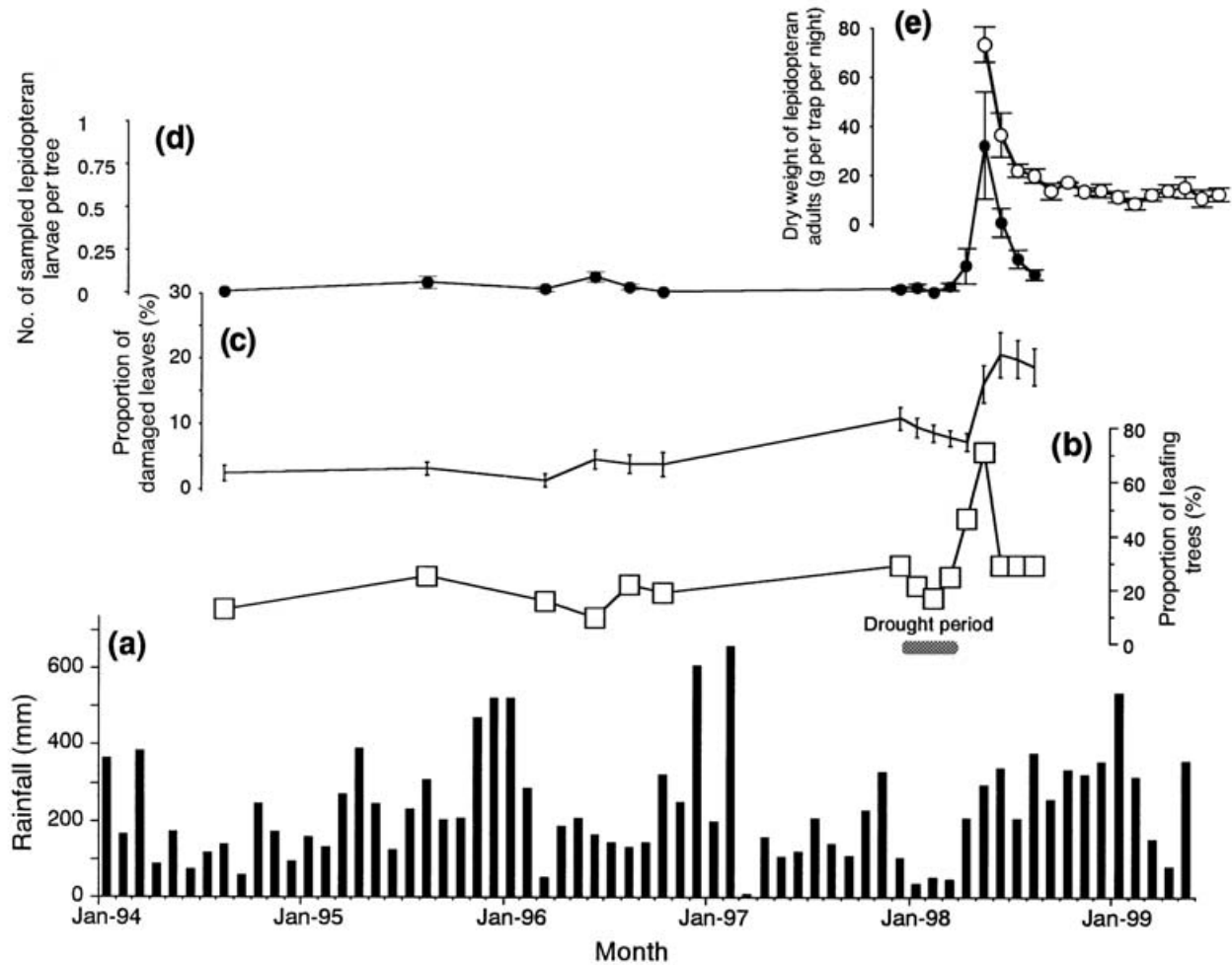


Figure 1. (Bottom to top) (a) Monthly rainfall (mm, bars) at Bukit Lambir (Site No. 4239001 of the meteorological observation by Jabatan Pengairan dan Saliran, Sarawak), 3 km north-west of the study plot of Lambir National Park, Sarawak. (b) Percentage of leafing trees (open squares). Leafing trees were defined as trees that bore newly flushed leaves at the time of each census. (c) Percentage of damaged leaves (middle points of vertical lines with SE) estimated from 51–200 leaves on each of the 32 trees (28 species) in 1994–1996 and of the 24 trees (16 species) in 1997 and 1998 (see Table 1). A damaged leaf was defined as a leaf with > 30% leaf surface area damaged by herbivores. (d) Average number of lepidopteran larvae per tree (closed circle) with SE (vertical line) in the canopy of the study trees (same as (c)). The larvae were sampled by net-beating for 470–530 leaves for each tree. (e) Dry weight of light-trapped adult lepidopterans per night per trap (open circle) with SE (vertical line). The lepidopterans were collected by three light-traps for four consecutive nights during the new-moon period of the month.

shedding leaves. The drought imposed high mortality on young and mature trees in the forest (Nakagawa *et al.* 2000). The drought ended with the heavy rain on 13 April 1998. Beginning in late April, most surviving trees began to flush shoots simultaneously and many young leaves flushed and developed.

In August 1994, August 1995, and March, May, July and October 1996, we censused herbivory damage on leaves of 32 individual trees of 28 species (12 families), including 22 trees of Dipterocarpaceae, in the forest canopy (Table 1). At each census event, we randomly selected 51–152 (77.9 on average) leaves of all ages per tree and measured the proportion of damaged area for each leaf, which was estimated from the inferred intact leafshape. We considered that the damaged area consisted

of the lost area and the area where the surface was mined, chewed, galled or decolourised by suckers.

From December 1997 to August 1998, we conducted a monthly census of leafing phenology and herbivory damage on leaves of dipterocarp canopy trees (24 individuals of 16 species, 5 genera, Table 1) in the forest canopy. At least 100 (maximum = 200) leaves per tree were randomly selected around the platforms and walkways and scrutinized at each census event. For each leaf, we estimated the damaged area in the same way as described above. Based on the leaf colour, the leaf size, the leaf location on the shoot, and the branching patterns of the shoot, we distinguished immature (flushing or developing) leaves from mature leaves on each tree. By checking the presence/absence of immature leaves at

Table 1. List of trees studied for leafing phenology, herbivory damage on leaves, and caterpillar density.

Species	No. of trees (1994–96, 1997–98)
Anacardiaceae	
<i>Gluta macrocarpa</i> (Engl.) Ding Hou	1, 0
<i>Parishia sericea</i> Ridley	1, 0
Annonaceae	
<i>Monocarpaea euneurum</i> Miq.	1, 0
Bombacaceae	
<i>Coelostegia griffithii</i> Benth.	1, 0
Burseraceae	
<i>Canarium denticulatum</i> Blume	1, 0
Chrysobalanaceae	
<i>Atuna excelsa</i> (Jack) Kosterm.	1, 0
Dipterocarpaceae	
<i>Dipterocarpus geniculatus</i> Vesque	0, 1
<i>Dipterocarpus pachyphyllus</i> Meijer	2, 1
<i>Dryobalanops aromatica</i> Gaertn. f.	0, 1
<i>Dryobalanops lanceolata</i> Burck	1, 1
<i>Hopea griffithii</i> Kurz	1, 2
<i>Shorea bullata</i> Ashton	2, 3
<i>Shorea exelliptica</i> Meijer	1, 1
<i>Shorea falciferoides</i> Foxw.	0, 1
<i>Shorea fallax</i> Meijer	1, 0
<i>Shorea ferruginea</i> Dyer ex Brandis	1, 1
<i>Shorea macrophylla</i> (D. Vr.) Ashton	1, 0
<i>Shorea macroptera</i> Dyer	2, 3
<i>Shorea parvifolia</i> Dyer	2, 3
<i>Shorea pilosa</i> Ashton	0, 2
<i>Shorea scaberrima</i> Burck	1, 1
<i>Shorea smithiana</i> Symington	1, 1
<i>Shorea xanthophylla</i> Symington	1, 1
<i>Vatica micrantha</i> Slooten	1, 1
Euphorbiaceae	
<i>Cleistanthus sumatranus</i> (Miq.) Muell. Arg.	1, 0
<i>Cleistanthus venosus</i> C.B. Rob.	1, 0
<i>Macaranga conifera</i> Muell. Arg.	1, 0
Fagaceae	
<i>Lithocarpus leptogyne</i> (Korth.) Soepadmo	1, 0
Lauraceae	
<i>Cinnamomum javanicum</i> Blume	1, 0
Leguminosae	
<i>Parkia singularis</i> Miq.	1, 0
Moraceae	
<i>Artocarpus integer</i> L.	1, 0
Verbenaceae	
<i>Teijsmanniodendron simplicifolium</i> Merr.	1, 0
32 species (12 families)	32, 24

each census event, we determined whether the tree was flushing leaves or not. In addition, we sampled herbivorous insects by net-beating. At each census, several branches were randomly selected so that the number of leaves on the branches ranged from 470–530 per tree, and beaten 10 times with a net of 30 cm in diameter.

Monthly light-trapping was conducted to assess the abundance of adult lepidopterans from May 1998 to May 1999. Light traps were set on a tree tower at different

heights, 1 m, 17 m and 35 m above ground, for four consecutive nights around the new moon of each month. The details of our light-trapping procedure were described by Itioka *et al.* (2001). Because adult lepidopterans that were attracted to the lights fell into ethyl alcohol in the buckets of the traps, we were unable to identify them correctly at species or family levels (but the specimens collected by hand-catch on the same dates at the same sites revealed that the number of species never fell below 200 species). Instead, we measured the total dry weight of each sample, using oven-drying. The number of lepidopteran catches (adult individuals) collected by light-trapping in each month always exceeded 1500 and sometimes reached 6000, which seemed to be sufficient for the estimation of abundance.

Our results are summarized in Figure 1. In 1994, 1995 and 1996, less than 25.0% of the 32 study trees had new leaves or shoots at any observation date. From December 1997 to August 1998, 16.7–29.2% of the 24 study trees were leafing during the drought period, and the proportion increased to 45.8% in April and to 70.8% in May. Almost all (95.8%) individuals developed new leaves at least once during the 3 mo after the drought broke, while 45.8% did so during the drought period.

We defined a 'damaged leaf' as a leaf with > 30% leaf surface area damaged by herbivores. The percentage of damaged leaves in 1994, 1995, and 1996 was always below 4.6%. From December 1997 to August 1998, the percentage of damaged leaves decreased gradually until April, drastically increased from April to June, and thereafter increased slightly and gradually. After the percentage peaked in June, it did not return to the level found before May. Most leaf damage was loss of leaf area.

Before March 1998, the number of all herbivorous insects sampled by net-beating remained below 0.125 individuals per tree, and the number of all sampled lepidopteran larvae never exceeded 0.06 individuals per tree. Thereafter, the number of sampled herbivorous insects increased remarkably and lepidopteran larvae became dominant; more than 80% of the herbivorous insects were lepidopteran larvae after February 1998. The number of sampled lepidopteran larvae was below 0.012 individuals per tree during the drought period (from January to March 1998), while it increased rapidly by 38-fold in the following 2 mo. After the peak in May, the sampled number decreased linearly until August 1998. The dry weight of the monthly catch of adult lepidopterans was the highest in May 1998. Thereafter, the dry weight decreased drastically until September 1998, and then did not show any clear change during the following 9 mo.

We postulate that the 3-mo-long severe drought and the subsequent drastic increase of rainfall that began with the breaking of the drought in mid-April 1998 triggered community-level leafing in the canopy trees. Although this study did not measure leaf production before the

drought period, Ichie *et al.* (unpubl. data) censused canopy trees and found that the average proportion of trees leafing pre-drought (from 1996 to 1997) ranged from 20–40%. Together with his data, we surmise that, about 3 mo after the end of the drought, the levels of leaf production went back to those before the drought.

The total abundances of larval and adult lepidopterans and the herbivory damage all increased rapidly and simultaneously in May 1998. Moreover, these coincident increases concurred with the community-level leafing. It has been argued that folivorous insects may prefer younger leaves as their food because younger leaves tend to contain more nutrients and to have less-effective antiherbivore defences, compared with mature leaves (Aide 1988, 1992; Coley 1983, Shure *et al.* 1998). This argument suggests the possible causality between the community-wide leafing and the drastic increase of lepidopteran abundance. Here we form the hypothesis that supra-annual drought might cause an interspecific synchronization of leafing phenology among canopy trees and consequently affect the abundance of lepidopteran leaf-chewers, and call the attention to impacts of supra-annual climatic events on abundances of various organisms in aseasonal tropical rain forests.

ACKNOWLEDGEMENTS

We are grateful to Hua-Seng Lee, Tamaiji Inoue and Tohru Nakashizuka for providing the opportunity to study in the study site, and to Shoko Sakai and Tomoaki Ichie for providing the data of precipitation and leafing phenology of canopy trees. We are obliged to Jabatan Pengairan dan Saliran, Sarawak for providing the meteorological observation data. We express our thanks to Abang Abdul Hamid, Lucy Chong, Sarkawi Mohamad Umar, Het Kaliang and Johan bin Rahman for support on our field study. This study was partly supported by Grants-in-Aid for Scientific Research (No. 09NP1501 and No. 14405004) from the Ministry of Education, Science, and Culture, Japan, and by CREST of JST (Japan Science and Technology Corporation).

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