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SHORT COMMUNICATION

Short-term drought causes synchronous leaf shedding and flushing in a lowland mixed dipterocarp forest, Sarawak, Malaysia

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Tropical rain forests are evergreen and experience a climate suitable for plant growth year round (Whitmore 1998). However, most tropical rain-forest trees display periodic shoot growth (Borchert 1991) and show synchronous leaf flushing at the community level (Itioka & Yamauti in press, Medway 1972, Ng 1981). Synchronous leaf flushing may have a great impact on animal population such as herbivores, because young leaves are suitable food resources for many herbivores (Aide 1988, 1992; Coley 1983, Itioka & Yamauti 2004, Lowman 1985).

As to the triggering mechanism of leaf flushing, Larcher (2003) suggested that even tropical plants respond to small changes in climate. But there are still no clear answers about environmental triggers that induce leaf flushing in the tropical rain forest (Medway 1972, Ng 1981). In tropical dry forests, which have a severe dry season lasting several months, it is known that flushing of many evergreen and leaf-exchanging species is immediately preceded by, and presumably triggered by, leaf shedding after severe drought at the end of dry season and/or occasional abnormal drought even during the rainy season (Borchert *et al*. 2002, Williams *et al*. 1997). In the tropical rain forest of South-East Asia, after the unusually severe drought associated with the 1997/98 El Niño event (Kinnaird & O'Brien 1998, Nakagawa *et al*. 2000, Potts 2003, Williamson & Ickes 2002), an extreme burst of leaf shedding and subsequent leaf flush was observed in many species (Harrison 2001, Itioka & Yamauti in press, Nomura *et al*. 2003). Therefore, we can hypothesize that severe droughts induce leaf shedding and flushing in the tropical rain forest. However, there have been few studies on the environmental triggers of leaf flushing in tropical rain-forest trees under normal conditions of high rainfall.

The aim of this paper was to identify the threshold of drought-induced synchronous leaf shedding and flushing at the community level in a tropical rain forest in South-East Asia. We paid particularly close attention to the relation between the pattern of leaf shedding and flushing and rainfall fluctuations. Furthermore, we investigated the relationship between vegetative phenology and cambium growth.

Our study was conducted in the Canopy Biology Plot (CBP, 200 × 400 m) at Lambir Hills National Park, Sarawak, Malaysia (4°20′ N, 113°50′ E, 150–250 m asl; Inoue *et al*. 1995, Kato *et al*. 1995). The vegetation of the study site is typical lowland mixed dipterocarp forest (Ashton & Hall 1992), which is characterized by an extremely high tree species diversity; within the park 1174 tree species were identified in a 52-ha plot (Condit *et al*. 2000, Lee *et al*. 2002). The area has a perhumid tropical climate with a weak seasonal change in rainfall and temperature (Kato *et al*. 1995). Annual precipitation

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approximately 3 km north-west of the study site averaged 2751 mm from 1985 to 2001, and ranged from 2044 to 3827 mm. Monthly mean rainfall was over 150 mm in every month, although the area occasionally experiences reduced precipitation for brief periods of a few weeks and rare severe droughts are associated with unusual climatic events, such as El Niño (Harrison 2001, Nakagawa *et al.* 2000). The air temperature is high and fairly constant. The average annual temperature at the climate station at Miri Airport, located approximately 20 km north of the study site (average from 1968 to 2001), was 26.7 °C, with monthly means that ranged from 25.9 in January to 27.4 in May.

In this study, 48 trees from 39 species, comprising 21 families, were selected for leaf and shoot phenological and cambium growth measurements (Table 1). Observations were made twice a month at the beginning and middle of every month from June 1996 to December 1997. All individuals were mature or beyond the sapling stage (dbh > 10 cm) and were evergreen or leaf-exchanging species.

In 1995, all individuals were fitted with homemade stainless steel dendrometer bands which measured to the nearest 0.1 mm in diameter. The dendrometer bands were placed at breast height (1.30 m above ground level or above buttress roots, if present) on a smooth bark surface.

Access to tree crowns was obtained via a system of towers and walkways of approximately 360 m in length (Inoue *et al.* 1995, Yumoto *et al.* 1996). Nine shoots per individual were marked haphazardly in the outer portion of the crown prior to June 1996. We measured the shoot length from the marked scar to the base of the terminal bud, and the numbers of attached, new and fallen leaves were counted. We defined flushing or leaf shedding periods of each tree as when shoot elongation with leaf development or leaf shedding were observed in more than 30% of the marked shoots.

Rainfall data were available from the Bukit Lambir Station, *c.* 3 km north-west of the study site, 200 m asl, collected by the Department of Irrigation and Drainage, Malaysia (Nakagawa *et al.* 2000). Running total rainfall was summed over 30 d and 14 d up to and including the day in question.

Our results are summarized in Figure 1. The proportion of individuals shedding and flushing leaves approximately doubled from August to September 1996 and from April to May 1997 (Figure 1e). The total ratios of flushing individuals during those two periods were respectively 52.1% and 60.4%, well above the rest of the duration period, when the ratio was usually less than 15.0%. The two peaks of leaf fall and flushing activity related well with the running rainfall total in the preceding 14-d period (Figure 1c). After periods of short-term drought (defined as less than 5 mm of rainfall in 14-d running total), synchronous flushing occurred within 2 mo. The running 30-d total rainfall proved too insensitive (Figure 1b). In general, monthly rainfall with less than 100 mm was considered a dry period, but the timing of such droughts did not correspond with the two peaks of leaf flushing, since only one of the peaks was a match (Figure 1e).

As a mechanism to explain leaf shedding and flushing in dry tropical forests, Borchert (1991, 2000) proposed that severe water stress caused rapid abscission of older leaves with poor stomatal control, and then, the massive loss of leaves and consequent change in the root–shoot ratio induces flushing. Our results suggest that trees in tropical

Table 1. Species of trees studied in order of dbh at the beginning of the study.

Scientific name	Family	dbh (cm)
Xanthophyllum sp.	Polygalaceae	10.7
Canarium sp.	Burseraceae	12.1
Hopea griffithii	Dipterocarpaceae	13.9
Shorea pilosa	Dipterocarpaceae	14.5
Ganua pierrei	Sapotaceae	14.8
Mallotus penangensis	Euphorbiaceae	14.9
Shorea pilosa	Dipterocarpaceae	15.0
Eugenia sp.	Myrtaceae	15.4
Gonystylus micranthus	Thymelaeaceae	15.5
Shorea smithiana	Dipterocarpaceae	18.8
Knema latifolia	Myristicaceae	19.5
Monocarpia euneura	Annonaceae	20.4
Teijsmaniodendron simplicifolium	Verbenaceae	24.6
Memecylon paniculatum	Melastomataceae	24.8
Shorea macroptera ssp. *bailonii*	Dipterocarpaceae	25.2
Shorea bullata	Dipterocarpaceae	25.9
Archidendron microcarpum	Leguminosae	27.2
Crypteronia griffithii	Crypteroniaceae	27.6
Sloanea javanica	Elaeocarpaceae	29.1
Gironniera nervosa	Ulmaceae	29.4
Shorea macroptera ssp. *baillonii*	Dipterocarpaceae	30.7
Amyxa pluricornis	Thymelaeaceae	31.1
Trigonostemon capillipes	Euphorbiaceae	31.8
Chisocheton sarawakanus	Meliaceae	32.6
Vatica micrantha	Dipterocarpaceae	32.6
Gonystylus micranthus	Thymelaeaceae	32.8
Parkia singularis	Leguminosae	34.4
Gluta macroptera	Anacardiaceae	35.2
Gluta macroptera	Anacardiaceae	35.4
Atuna excelsa	Chrysobalanaceae	35.4
Santiria mollis	Burseraceae	35.8
Shorea macroptera ssp. *macropterifolia*	Dipterocarpaceae	38.4
Artocarpus integer	Moraceae	44.4
Dipterocarpus geniculatus	Dipterocarpaceae	61.1
Dryobalanops aromatica	Dipterocarpaceae	64.7
Quassia borneensis	Simaroubaceae	74.9
Quassia borneensis	Simaroubaceae	75.4
Eusideroxylon zwageri	Lauraceae	79.9
Shorea xanthophylla	Dipterocarpaceae	93.1
Shorea bullata	Dipterocarpaceae	95.4
Shorea ferruginea	Dipterocarpaceae	105.1
Shorea fallax	Dipterocarpaceae	106.5
Shorea bullata	Dipterocarpaceae	113.5
Shorea pilosa	Dipterocarpaceae	113.8
Shorea parvifolia	Dipterocarpaceae	130.5
Dipterocarpus pachyphyllus	Dipterocarpaceae	135.0
Shorea smithiana	Dipterocarpaceae	138.6
Dryobalanops lanceolata	Dipterocarpaceae	158.1

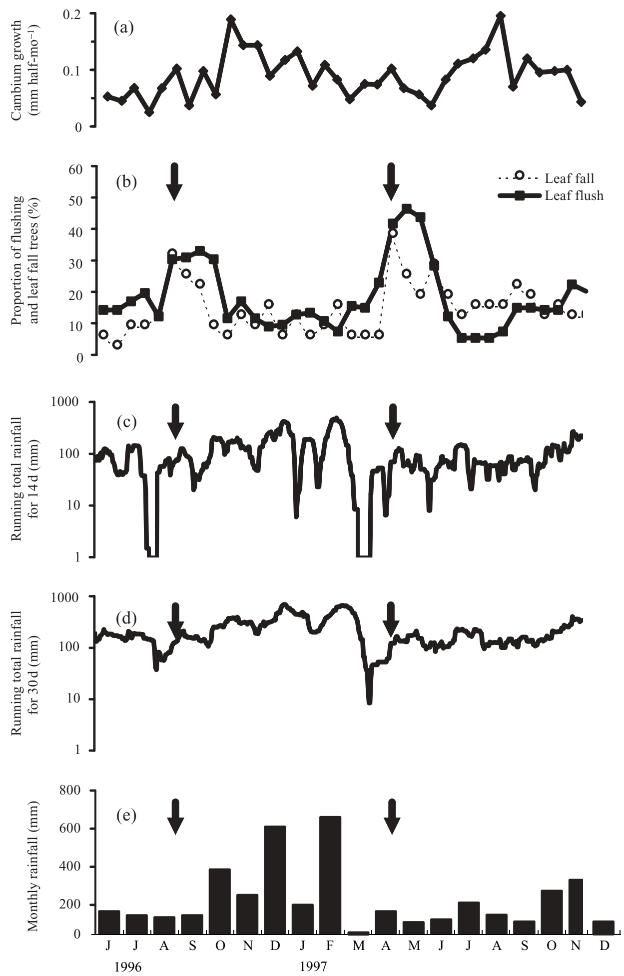

Figure 1. Relation between rainfall and leaf phenology and cambium growth during the study period at Lambir Hills National Park: (a) average cambium growth of the study trees per half month; (b) percentage of individuals undergoing leaf fall and flushing; (c) running total rainfall for 14 d; (d) running total rainfall for 30 d; (e) monthly rainfall. Arrows indicate the timing of a drastic increase in leaf shedding and flushing. Rainfall data are from the Bukit Lambir Station.

rain forests may also rapidly shed older leaves and start flushing when they experience severe water stress during brief dry spells. In fact, based on the long-term climate data at Bukit Lambir Station from 1985 to 2001, such short-term droughts (less than 5 mm of rainfall in 14-d running total) were detected 1.76 ± 1.03 (mean ± SD) times per year, though such droughts occurred fairly irregular throughout the year (data not shown, Harrison 2001). If short-term drought and/or subsequent rainfall is a trigger that induces synchronous leaf shedding and flushing, trees have several chances to change leaf every year even in the tropical rain forest.

The two peaks of cambium growth in November 1996 and August 1997 came after the two peaks of flushing from August to September 1996 and from April to May 1997, although we always observed positive cambium growth (> 0 mm) throughout this study (Figure 1f). In contrast, cambium growth had a tendency to temporarily decline during dry spells. It is known that cambium activity in trees is generally induced by flushing in tropical dry forests (see Borchert 1999). Moreover, Borchert (1999) also showed that rapid flushing induced a resumption of cambium growth just after an abnormal drought induced by the 1997 El Niño event in a tropical semi-deciduous forest. Similarly, our results suggest that flushing after brief droughts induces active cambium growth in tropical rain-forest trees, even though they are capable of year-round growth. Evidence for reduced growth during dry spells has important implications for the production of timber in tropical rain forests, if droughts become more common and more severe as predicted by models of global warming (Corlett & LaFrankie 1998).

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