Reproductive phenology over a 10-year period in a lowland evergreen rain forest of central Borneo

FRANCIS Q. BREARLEY, JOHN PROCTOR†, SURIANTATA†, LASZLO NAGY*‡, GEMMA DALRYMPLE* and BENEDICT C. VOYSEY†

*Department of Botany, Trinity College, University of Dublin, Dublin 2, Ireland, *Department of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK, and ‡EcoScience Scotland, 2/1, 27 Glencairn Drive, Glasgow G41 4QP, Scotland, UK*

Summary

1 The aim of this study was to document patterns in tree reproductive phenology in a rain forest of central Borneo and examine relationships between phenology and climatic patterns.

2 A 10-year data set (1990–2000) of monthly observations of flowering and fruit production of 171 trees (including 39 members of the Dipterocarpaceae) at Barito Ulu, Central Kalimantan, Indonesia, showed that most trees (73%) underwent reproductive activity on a supra-annual timescale.

3 There were three general flowering (GF) events, in 1991, 1994 and 1997, which were preceded by major drought periods (30-day sliding total rainfall of less than 100 mm for more than 10 days) in which at least 40% of dipterocarps and at least 18% of all other trees underwent synchronized reproductive activity; there was also a minor event in 1990. Around 1.3% of trees flowered and 3.8% produced fruit in months outside of these four events.

4 At the community level, the strongest negative correlation was found between the percentage of flowering individuals and total rainfall in the preceding 150 days.

5 Within three genera of dipterocarps examined in more detail (*Dipterocarpus*, *Shorea* and *Vatica*) there were clear and consistent patterns of sequential flowering with certain species flowering early in the GF events and others towards the end of these events.

6 Our results confirm the importance of large-scale climatic fluctuations (El Niño-Southern Oscillation) on plant reproductive phenology in South-east Asian tropical forests and indicate that drought may be a more important cue than low night-time temperatures.

Key-words: Borneo, Dipterocarpaceae, drought, El Niño-Southern Oscillation, general flowering, Indonesia, mast-fruiting, phenology, synchronized reproductive activity, tropical lowland evergreen rain forest

Introduction

'Phenology is the study of the timing of recurrent biological events, the causes of the timing with regard

Correspondence and present address: F. Q. Brearley, Department of Environmental and Geographical Sciences, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, UK (e-mail f.q.brearley@mmu.ac.uk).
†Deceased.
This paper is dedicated to the memory of John Proctor who passed away during the final stages of completing this manuscript. He inspired us, and many others, to carry out research in tropical forest ecology.

to biotic and abiotic forces, and the interrelation among phases of the same or different species' (Lieth 1974, p. 4). For plants, recurrent biological events include vegetative processes such as leaf flushing and shedding as well as reproductive events such as bud formation, flowering and production of fruit. The timing of many of these events is likely to represent trade-offs between resource availability, pollinator availability and competition, abundance of herbivores, suitable conditions for seed germination and establishment, and phylogenetic constraints (e.g. Mosquin 1971; Johnson 1992; van Schaik *et al.* 1993; Murali & Sukumar 1994; Wright & Calderón 1995). The abiotic factors most likely to affect

phenological patterns are temperature and photoperiod (Ratheke & Lacey 1985; Badeck *et al.* 2004; Molau *et al.* 2005) which, in temperate regions, are clearly seasonal. In tropical regions, there is less seasonality with regard to temperature and day length; indeed, there is often greater diurnal than seasonal temperature variation. However, many tropical regions experience seasonality of rainfall, and phenological patterns are often related to this seasonality with peaks in fruit production occurring at the beginning of the rainy season (e.g. Murali & Sukumar 1994; Justiniano & Fredericksen 2000; Bollen & Donati 2005). It has been hypothesized that this allows the greatest chance for seedling survival as seeds are dispersed when soil moisture conditions are most favourable for seed germination and rapid seedling growth (van Schaik *et al.* 1993).

In much of the South-east Asian tropical rain forest region there is relatively little seasonality, and a spectacular population-level phenomenon known as mast-fruiting, and the associated community-level general flowering (GF), has evolved. Approximately every 3–8 years, trees undergo a reproductive event (Medway 1972; Appanah 1985, 1993; Ashton *et al.* 1988; Curran *et al.* 1999; Sakai *et al.* 1999, 2006). The most popular hypothesis for the evolution of mast-fruiting is that it causes seed-predator satiation by swamping them with an abundance of seeds (Janzen 1974; Ashton *et al.* 1988; Kelly 1994; Numata *et al.* 1999; Curran & Leighton 2000; Curran & Webb 2000). A more recent hypothesis, proposed by Sakai *et al.* (1999, 2004), is that pollination is more likely to occur successfully when there are large numbers of individuals flowering in synchrony. It appears that during a GF event nearly all the dipterocarp species flower, along with a number of other species from other families. Cues for this irregular event have been suggested as prolonged droughts (Burgess 1972; Medway 1972; Janzen 1974; Whitmore 1984, p. 69; Sakai *et al.* 2006), a drop in night-time temperature (Ashton *et al.* 1988; Yasuda *et al.* 1999), or an increase in sunshine hours (Wycherley 1973; Ng 1977; Wright & van Schaik 1994). However, all of these events are highly likely to be correlated in time and all are likely to occur with close temporal synchrony during an El Niño-Southern Oscillation (ENSO) event, which makes determining the precise flowering cue highly problematic. ENSO events lead to drought (most spectacularly during 1982–83 and 1997–98 in South-east Asia), increased sunshine hours due to fewer clouds, and an associated increase in radiative cooling during the night.

In this paper we present a 10-year phenological record from a lowland evergreen rain forest in Borneo, examining a range of tree families, including the dominant Dipterocarpaceae. We aim to document the phenological patterns occurring over this period, examine relationships between phenology and climatic factors, and evaluate hypotheses that have been presented above (namely the drought and low night-time temperature hypotheses) to account for these relationships.

Study site

The Project Barito Ulu (PBU) research area is situated in Central Kalimantan, Indonesia, at 114°0′ E, 0°06′ S, in the centre of the island of Borneo. The research area covers 430 ha and contains a range of forest types, most of them having high species richness (α-diversity). These include several types of tropical lowland evergreen rain forest and heath forest (*kerangas*) as well as areas of shifting cultivation fallows of various ages (Prajadinata 1996; Nagy & Proctor 1999; Brearley *et al.* 2004; J. Proctor *et al.* unpublished data). The main research area is bounded by the rivers Busang and Rekut with a main ridge running in an approximately north–south direction dividing the two watersheds; the PBU Rekut base-camp is situated at the confluence of these two rivers. The geology is based on a Tertiary sedimentary formation which has given rise to sandy ultisols that are acidic and low in nutrients (Mirmanto *et al.* 1999; Brearley *et al.* 2004). The base-camp is around 150 m a.s.l. and the topography is rugged with ridges up to 100 m high and slopes often in excess of 30°.

Materials and methods

The sample comprised 171 trees (39 of which were dipterocarps) in 34 families, drawn from 90 non-dipterocarp species and 22 dipterocarp species (see Table 1 for full species list). Each family was represented in approximate proportion to its stem abundance in tree plots set up in the research area (Mirmanto 1996; Brearley *et al.* 2004; J. Proctor *et al.* unpublished data). There were up to six individuals of each species under observation. All trees were marked along a trail that traversed around half of the research area (in a figure-of-eight fashion). The majority were found in undisturbed lowland evergreen rain forest with the exception of 16 that were found in secondary rain forest (around 15–45 years old at the start of the study). The trees chosen were those that appeared to be reproductively mature, whose crowns were not obscured by other trees, and were easily observable from the trail. Trees ranged in height from 10 m to 42 m [diameters at breast height (1.3 m) were < 10 cm to > 100 cm]. Their reproductive systems were recorded as hermaphrodite, monoecious, andromonoecious, dioecious or polygamous by reference to standard works. Voucher specimens from all trees were identified at the Herbarium Bogoriense (BO) with duplicates kept at the PBU Rekut base-camp herbarium and additional specimens for some at the Royal Botanic Gardens Edinburgh (E).

Between 1990 and 2000, eight dipterocarp trees died, leaving 31 at the end of the study period. The number of non-dipterocarps under observation increased during the first 18 months of the study until there were 132 trees, 27 of which died during the study, leaving 105 in 2000. A considerable proportion of the mortalities were from November 1997 onwards following a severe storm at Barito Ulu (Proctor *et al.* 2001). Trees whose records

Table 1 Number of trees of each species included in the phenology study at Barito Ulu, Central Kalimantan, from 1990 to 2000 (also includes their reproductive system by reference to standard works)

Family	Species	Number	Flowering type	Reproductive system
Anacardiaceae	*Gluta* cf. *aptera*	1	GF only	Hermaphrodite
	Gluta curtissii	1	Supra-annual	Hermaphrodite
	Gluta malayana	1	Supra-annual	Hermaphrodite
	Koordersiodendron sp.	1	Non-flowering	Hermaphrodite
	Mangifera pajang	1	Supra-annual	Andromonoecious
	Parishia maingayi	2	GF only	Dioecious
	Swintonia floribunda	1	GF only	Hermaphrodite or andromonoecious
	Swintonia glauca	1	GF only	Hermaphrodite or andromonoecious
Annonaceae	*Mezzettia* sp.	1	Supra-annual	Hermaphrodite
	Polyalthia sumatrana	3	Supra-annual	Hermaphrodite
	Xylopia stenopetala	1	Non-flowering	Hermaphrodite
Bombacaceae	*Durio* sp.	1	Non-flowering	Hermaphrodite
Burseraceae	*Dacryodes rostrata*	1	Non-flowering	Dioecious
	Santiria apiculata	1	GF only	Dioecious
	Santiria rubiginosa	1	Supra-annual	Dioecious
	Burseraceae sp.	1	GF only	Dioecious
Clusiaceae	*Calophyllum austocoriaceum*	1	Non-flowering	Hermaphrodite
	Calophyllum sp.	3	Supra-annual (2) or non-flowering (1)	Hermaphrodite
	Garcinia cornea	1	GF only	Usually dioecious
	Garcinia dulcis	1	Supra-annual	Andromonoecious
	Garcinia eugeniaefolia	1	Supra-annual	Usually Dioecious
	Garcinia hombroniana	1	Supra-annual	Usually Dioecious
	Garcinia sp.	1	Non-flowering	Usually Dioecious
	Mesua borneensis	1	Non-flowering	Hermaphrodite
	Mesua conoidea	2	GF only	Hermaphrodite
Ctenolophonaceae	*Ctenolophon parvifolium*	1	Non-flowering	Hermaphrodite
Dilleniaceae	*Dillenia excelsa*	1	Supra-annual	Hermaphrodite
Dipterocarpaceae	*Cotylelobium melanoxylon*	2	Supra-annual	Hermaphrodite
	Dipterocarpus acutangulus	1	GF only	Hermaphrodite
	Dipterocarpus crinitus	1	GF only	Hermaphrodite
	Dipterocarpus rigidus	4	Supra-annual	Hermaphrodite
	Dryobalanops oblongifolia	1	Non-flowering	Hermaphrodite
	Shorea atrinervosa	1	GF only	Hermaphrodite
	Shorea bracteolata	1	GF only	Hermaphrodite
	Shorea crassa	1	GF only	Hermaphrodite
	Shorea fallax	1	GF only	Hermaphrodite
	Shorea cf. *foxworthyii*	1	GF only	Hermaphrodite
	Shorea kunstleri	2	GF only	Hermaphrodite
	Shorea laevis	2	GF only	Hermaphrodite
	Shorea macroptera	2	GF only	Hermaphrodite
	Shorea cf. *multiflora*	4	GF only	Hermaphrodite
	Shorea parvifolia	3	GF only	Hermaphrodite
	Shorea pauciflora	1	GF only	Hermaphrodite
	Shorea rugosa	1	Non-flowering	Hermaphrodite
	Shorea scorbiculata	1	GF only	Hermaphrodite
	Shorea sp.	1	Non-flowering	Hermaphrodite
	Vatica micrantha	3	GF only	Hermaphrodite
	Vatica sarawakensis	3	Supra-annual (2) or GF only (1)	Hermaphrodite
	Vatica sumatrana	2	GF only	Hermaphrodite
Ebenaceae	*Diospyros confertiflora*	5	Supra-annual	Usually dioecious
Euphorbiaceae	*Aporosa lunata*	2	Supra-annual	Dioecious
	Baccaurea cf. *minor*	1	Supra-annual	Dioecious
	Baccaurea stipulata	2	Supra-annual	Dioecious
	Blumeodendron tokbrai	2	Supra-annual	Dioecious
	Drypetes sp.	2	Supra-annual (1) or GF only (1)	Monoecious or dioecious
	Macaranga hypoleuca	1	Non-flowering	Dioecious
	Neoscortechinia kingii	1	GF only	Dioecious
	Euphorbiaceae sp. 1	1	Supra-annual	Monoecious or Dioecious
	Euphorbiaceae sp. 2	1	Supra-annual	Monoecious or Dioecious
	Euphorbiaceae sp. 3	1	Supra-annual	Monoecious or Dioecious

Table 1 *Continued*

Family	Species	Number	Flowering type	Reproductive system
Fabaceae	*Dialium indum*	6	GF only (4) or non-flowering (2)	Hermaphrodite
	Koompassia malaccensis	2	Non-flowering	Hermaphrodite
	Sindora beccariana	2	Supra-annual	Hermaphrodite
Fagaceae	*Lithocarpus* sp.	2	GF only (1) or non-flowering (1)	Monoecious
Flacourtiaceae	*Casearia* sp.	1	Non-flowering	Hermaphrodite
	Hydnocarpus kunstleri	1	Supra-annual	Usually dioecious
Hypericaceae	*Cratoxlyon* cf. *arborescens*	1	Supra-annual	Hermaphrodite
Lauraceae	*Cryptocarya* sp.	2	Non-flowering	Hermaphrodite
	Dehaasia incrassata	1	Non-flowering	Hermaphrodite
	Lauraceae sp.	1	Supra-annual	Hermaphrodite or dioecious
Lecythidaceae	*Barringtonia lanceolata*	2	Supra-annual (1) or non-flowering (1)	Hermaphrodite
Melastomataceae	*Pternandra* sp.	2	Supra-annual	Hermaphrodite
Meliaceae	*Chisocheton divergens*	1	Supra-annual	Dioecious or polygamous
Moraceae	*Artocarpus nitidus*	2	Non-flowering	Monoecious
	Artocarpus odoratissima	1	Non-flowering	Monoecious
	Ficus kirchovemi	1	Non-flowering	Monoecious
	Ficus stupender	1	Non-flowering	Monoecious
	Ficus sp.	1	Supra-annual	Monoecious or dioecious
Myristicaceae	*Gymnacranthera contracta*	1	Supra-annual	Dioecious
	Knema latericia	1	Non-flowering	Dioecious
	Knema latifolia	1	Supra-annual	Dioecious
	Myristica cinnamomea	1	Non-flowering	Dioecious
	Myristicaceae sp.	1	Supra-annual	Dioecious
Myrtaceae	*Eugenia* sp.	3	Supra-annual (2) or non-flowering (1)	Hermaphrodite
	Eugenia sp. 16	1	Supra-annual	Hermaphrodite
	Syzgium lineatum	4	Supra-annual (2) or non-flowering (2)	Hermaphrodite
	Tristaniopsis whitiana	1	GF only	Hermaphrodite
Polygalaceae	*Xanthophyllum affine*	3	Supra-annual (1) or non-flowering (2)	Hermaphrodite
	Xanthophyllum amoneum	1	Non-flowering	Hermaphrodite
	Xanthophyllum stipitatum	2	GF only (1) or non-flowering (1)	Hermaphrodite
Proteaceae	*Helicia* sp.	1	Non-flowering	Hermaphrodite
Rhamnaceae	*Ziziphus angustifolius*	1	Supra-annual	Hermaphrodite
Rubiaceae	*Wendlandia* sp.	1	Supra-annual	Hermaphrodite
Sapindaceae	*Pometia pinnata*	1	Supra-annual	Monoecious
	Xerospermum norohianum	1	GF only	Dioecious
Sapotaceae	*Ganua kingiana*	1	GF only	Nearly always hermaphrodite
	Ganua motleyana	2	Supra-annual (1) or GF only (1)	Nearly always hermaphrodite
	Palaquium quercifolium	1	Supra-annual	Nearly always hermaphrodite
	Palaquium sp.	6	Supra-annual (2), GF only (2) or non-flowering (2)	Nearly always hermaphrodite
	Planchonella sp.	1	Non-flowering	Nearly always hermaphrodite
Sterculiaceae	*Heritiera simplicifolia*	1	Non-flowering	Monoecious
	Scaphium macropodum	1	Supra-annual	Monoecious
	Sterculiaceae sp.	1	Supra-annual	Hermaphrodite or monoecious
Theaceae	*Adinandra collina*	1	Continual	Hermaphrodite
	Ternstroemia sp.	1	Supra-annual	Hermaphrodite
Thymelaeaceae	*Gonystylus affinis*	1	GF only	Hermaphrodite
	Gonystylus borneensis	2	Supra-annual (1) or GF only (1)	Hermaphrodite
Tiliaceae	*Brownlowia ferruginea*	2	GF only (1) or non-flowering (1)	Hermaphrodite
	Pentace excelsa	1	Non-flowering	Hermaphrodite
Ulmaceae	*Gironniera nervosa*	1	Supra-annual	Monoecious
Verbenaceae	*Vitex quinata*	1	Supra-annual	Hermaphrodite
Violaceae	*Rinorea lanceolata*	1	Non-flowering	Hermaphrodite (rarely dioecious)

© 2007 The Authors
Journal compilation
© 2007 British
Ecological Society,
Journal of Ecology,
95, 828–839

were less than the full 10 years were included in all analyses.

The phenological status of each tree was recorded on the first day of every month, by the third author, from 1 March 1990 to 1 June 2000 using binoculars from the ground (no observations were made in October 1990, September 1993 or October 1999). The following were recorded (presence or absence only): (i) leaf flushing, (ii) leaf senescence, (iii) flowering (i.e. with flower buds or flowers at anthesis) and (iv) fruit production (encompassing all ripeness stages). At least one-eighth of the tree crown had to show the presence of the phenological state for it to be recorded as such. In this paper we are concerned only with the flowering and fruit production events. Where percentages of flowering or fruit production are given in the results, these are percentages of the number of trees remaining in the study at that time.

Rainfall and minimum and maximum temperatures were recorded daily at the PBU Rekut base-camp. Rainfall was recorded throughout the study period and temperature recording started on 1 October 1993. The rain gauge was situated in a small clearing and the thermometer was placed in the shade on the side of a hut with negligible heat retention. Thirty-day sliding total rainfalls were calculated by summing the rainfall in a given day with the rainfall on the preceding 29 days; this allows identification of dry periods to be made without artificially dissecting the year into months. On the few occasions (< 2% of days) when rainfall was not measured on a given day(s), the next day on which it was recorded was the sum of all the missing days. In these cases, to calculate the 30-day sliding total, it was assumed that the rainfall was equally partitioned among all the missing days.

We determined whether tree height or reproductive system had an effect on reproductive phenology using a *t*-test or χ^2 test, respectively. Sequential flowering patterns were analysed using Spearman's rank correlations or sign tests depending upon the sample size. Spearman's rank correlations were calculated between percentages of flowering trees in each month and sliding rainfall totals over the preceding 365 days, in 5-day increments.

Results

CLIMATIC SUMMARY

Mean annual rainfall between 1990 and 2000 was around 3800 mm and no month had a mean of less than 200 mm rainfall; the climate is therefore considered to be perhumid aseasonal. However, there were consistent annual fluctuations in rainfall with the wettest months being November–April (with the exception of February) and the driest months being June–September (Fig. 1). Since climate records began in 1989, there have been three severe droughts (30-day sliding total rainfall of less than 60 mm for more than 10 days) in 1991, 1994 and the strong El Niño year of 1997 (Fig. 2a).
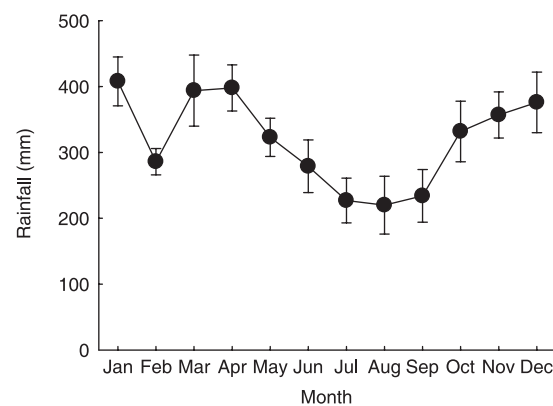
Fig. 1 Mean (± SE) monthly rainfall at Barito Ulu, Central Kalimantan, Indonesia, over a 10-year period (1990–2000). Mean annual rainfall over the same period was 3834 ± 161 mm.

REGULARITY OF FLOWERING AND FRUIT PRODUCTION ACTIVITY

Dipterocarps underwent reproductive activity on a supra-annual time scale and most of them only flowered during one or more of the GF events (Table 1, Fig. 3). Of those that only flowered in the GF events, most of them flowered in two or three of these events (Fig. 3, inset) Non-dipterocarps also mostly underwent reproductive activity on a supra-annual time scale; of these, around one-third only flowered during one or more of the GF events (Table 1, Fig. 3). Only one species (*Adinandra collina*, Theaceae) exhibited continuous flowering from 1992 onwards (Table 1, Fig. 3).

In total, 7.7% of dipterocarps and 31.8% of non-dipterocarps were not observed to flower. However, all three non-flowering dipterocarp individuals were recorded as producing fruit and half of the non-flowering non-dipterocarps were recorded as producing fruit. There was no difference in height between the trees that did and did not flower (*t* = 1.47, *P* = 0.14), indicating that those that did not flower were not all immature trees. Of the trees that were not observed to flower but did produce fruits, a higher than expected proportion were monoecious (Table 2; χ^2 = 63.9, *P* < 0.001).

Outside GF events, mean background levels of flowering were 0.54% per month for dipterocarps and 2.01% for non-dipterocarps; background levels of fruit production were 1.75% for dipterocarps and 5.91% for non-dipterocarps (or 4.71% if the other fruit production peaks are excluded; see below).

GENERAL FLOWERING

General flowering events for dipterocarps occurred between September and December 1991 (68% of all trees flowered; 47% in the peak month), November 1994 and January 1995 (46% of all trees flowered; 35% in the peak month), and August and November 1997 (65% of all trees flowered; 43% in the peak month). There was also a minor event in November–December 1990 (26%
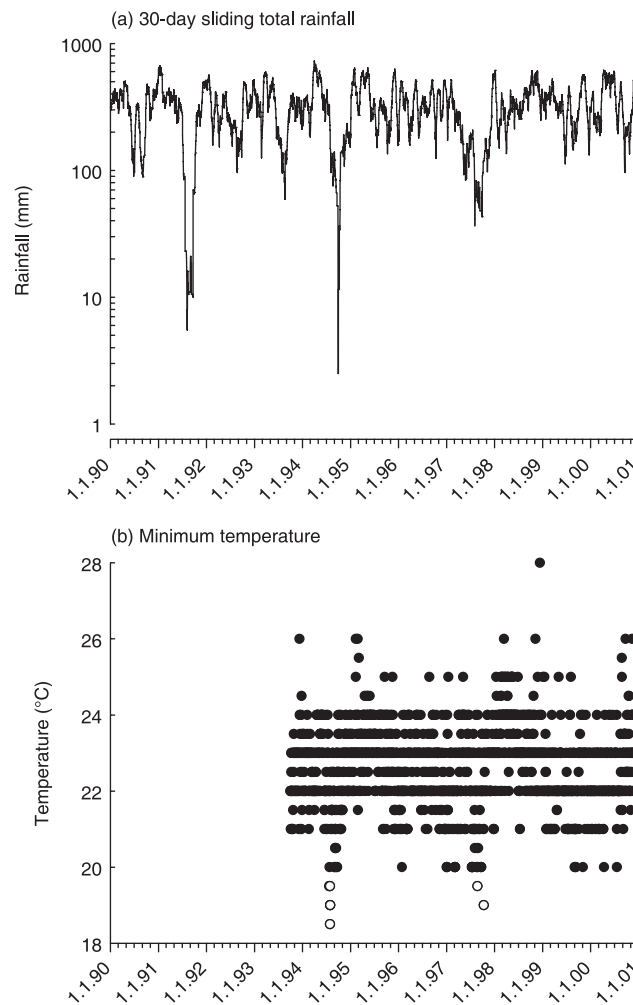
(a) 30-day sliding total rainfall

(b) Minimum temperature

Fig. 2 Thirty-day sliding total rainfall and minimum night-time temperature at Barito Ulu, Central Kalimantan, Indonesia, over a 10-year period (1990–2000) (October 1993–2000 for temperature). Open circles in (b) indicate periods of low night-time temperature (i.e. less than 20 °C).
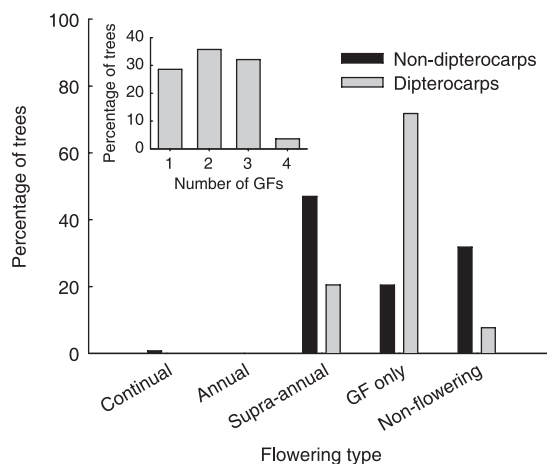
Fig. 3 Numbers of continual flowering, supra-annual flowering, general flowering (GF) only and non-flowering trees within dipterocarps and non-dipterocarps at Barito Ulu, Central Kalimantan, Indonesia, over a 10-year period (1990–2000). The inset shows the number of general flowerings in which dipterocarps that were reproductively active in general flowering events participated.

Table 2 Number of trees in three reproductive system classifications and their observed production of flowers and fruit at Barito Ulu, Central Kalimantan, Indonesia, over a 10-year period (1990–2000)

	Flowers and fruits	No flowers but fruits	No flowers and no fruits
Hermaphrodite	83	14	18
Monoecious	4	6	1
Dioecious	26	3	2
Not classified	13	0	0

of all trees flowered; 19% in the peak month) (Fig. 4a). In addition to activity in the GF events, all four individuals of *Dipterocarpus rigidus* also flowered in January 2000 when no other dipterocarps flowered. *Cotylelobium melanoxylon* showed unusual patterns of flowering, being later than other dipterocarps in the 1991 GF event, when it flowered in February–March 1992, but earlier in the 1994 event, when it flowered in July–August 1994; flowering was not recorded in the 1997 event. In
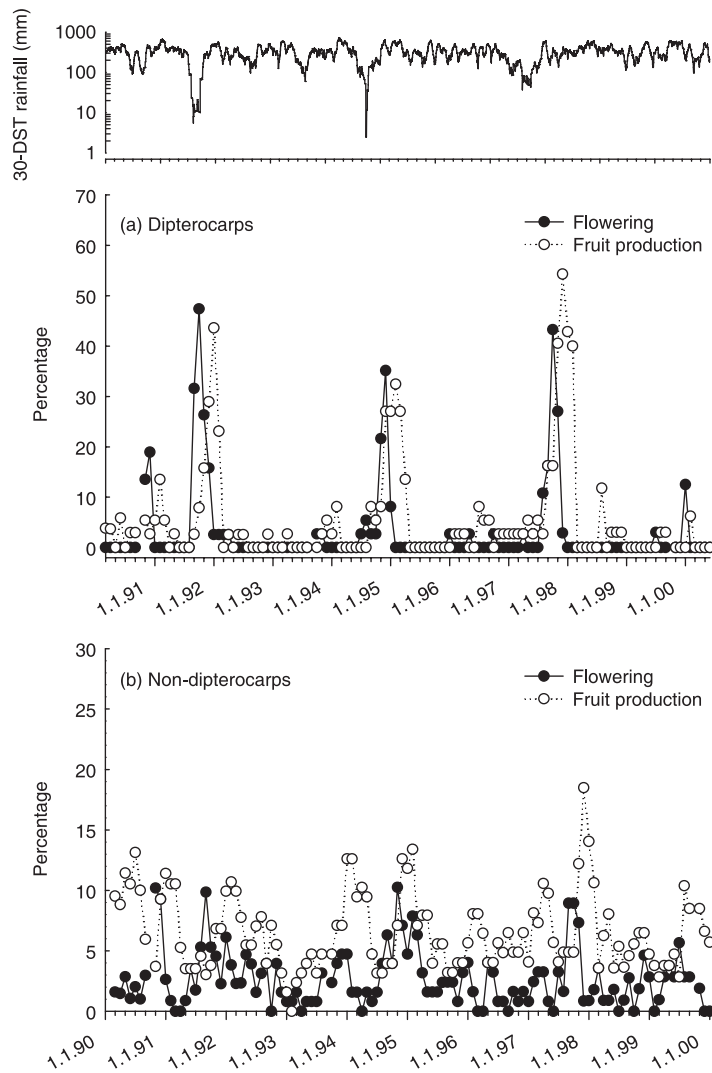
Fig. 4 Percentage of flowering and fruiting (a) dipterocarps and (b) non-dipterocarps at Barito Ulu, Central Kalimantan, Indonesia, over a 10-year period (1990–2000). Also shown is the 30-day sliding total rainfall amended from Fig. 2.

all GF events, fruit production followed flowering by 1–2 months and continued for 2–3 months after completion of flowering; it was of similar magnitude to the number of trees observed to flower (Fig. 4a).

Flowering in non-dipterocarps showed a similar pattern. The GF events for non-dipterocarp trees were centred on those for the dipterocarps but were generally extended, i.e. November to December 1990, August 1991 to January 1992, September 1994 to March 1995, and September to November 1997 (Fig. 4b). During the GF events noted above, up to 29.1% of non-dipterocarp trees flowered and up to 26.0% produced fruit (with up to 10.2% of non-dipterocarps flowering and up to 18.5% producing fruit in the peak month). Fruit production followed flowering by 1–3 months and continued for up to 3 months after the completion of flowering (Fig. 4b). Non-dipterocarps also showed fruit production peaks on a number of other occasions (March to August 1990, November 1993 to May 1994, March to August 1997, August 1999 to May 2000). Interestingly, these were not preceded by any increase in flowering activity.

Table 3 Percentage of trees in the commonest families* at Barito Ulu, Central Kalimantan, Indonesia, flowering in three GF events over a 10-year period (1990–2000)

	n (trees)	1991–92	1994–95	1997–98
Anacardiaceae	9	67	56	67
Clusiaceae	11	42	36	10
Dipterocarpaceae	39	68	46	65
Euphorbiaceae	14	36	31	42
Fabaceae	10	20	40	0
Myristicaceae	5	0	40	20
Myrtaceae	9	33	11	0
Sapotaceae	11	36	36	45

*More than 5% of stems or basal area in this study, Mirmanto (1996), Brearley *et al.* (2004) or L. Nagy *et al.* (unpublished data).

During the GF events, the Dipterocarpaceae were the major family to undergo reproductive activity with 46–68% of individuals flowering in each event (Table 3). The Anacardiaceae were also notably active during GF

Table 4 Sequential flowering pattern in 10 dipterocarp species during three GF events over a 10-year period (1990–2000) at Barito Ulu, Central Kalimantan, Indonesia (all values are percentages of flowering trees)

1991–92	n (trees)	Sep. 1991	Oct. 1991	Nov. 1991	Dec. 1991	Jan. 1992
Dipterocarpus						
D. rigidus	4	100	100			
D. acutangulus	1		100			
Shorea						
S. bracteolata	1	100				
S. macroptera	2	100	50			
S. cf. multiflora	4	25	75	50		
S. parvifolia	3		33		33	33
S. atrinervosa	1		100			
S. kunstlerii	2		100	100	100	
Vatica						
V. sumatrana	2	100	100	50		
V. sarawakensis	3			67		

1994–95	n (trees)	Sep. 1994	Oct. 1994	Nov. 1994	Dec. 1994	Jan. 1995
Dipterocarpus						
D. rigidus	4			75	75	
D. acutangulus	1			100		
Shorea						
S. bracteolata	1		100			100
S. macroptera	2			50		
S. cf. multiflora	4			50	75	
S. parvifolia	3				33	
S. atrinervosa	1				100	
S. kunstlerii	2				50	50
Vatica						
V. sumatrana	2	50				
V. sarawakensis	3				67	

1997	n (trees)	Aug. 1997	Sep. 1997	Oct. 1997	Nov. 1997	Dec. 1997
Dipterocarpus						
D. rigidus	4	75			75	
D. acutangulus	1		100	100		
Shorea						
S. bracteolata	1		100	100		
S. macroptera	2			100	50	
S. cf. multiflora	4			50	25	
S. parvifolia	3			67	33	
S. atrinervosa	1				100	
S. kunstlerii	2					50
Vatica						
V. sumatrana	2		100	100		
V. sarawakensis	3			67	33	

events (56–67% of individuals flowering). Other families had 10–45% of individuals flowering in GF events. In the Fabaceae, Myristicaceae and Myrtaceae the percentage of flowering trees was lower (0–40%; Table 3).

SEQUENTIAL FLOWERING PATTERNS

Ten dipterocarp species had at least one individual flowering in each of the three GF events (Table 4). In the genus *Dipterocarpus*, *D. rigidus* usually flowered before *D. acutangulus* although this was not statistically significant (Sign test, $P = 0.50$) due to a low sample size. In the genus *Shorea*, *S. bracteolata* was always one of the first species to flower followed by *S. macroptera* and *S.* cf. *multiflora*. In the middle of the sequence were *S. atrinervosa* and *S. parvifolia*, with *S. kunstlerii* the last species to flower. When analysed at the species level, there were positive rank correlations between years ($r_s > 0.70$ in all cases), but only statistically significant between 1991 and 1994: $r_s = 0.80$, $P = 0.016$). In the genus *Vatica*, *V. sumatrana* flowered before *V. sarawakensis* in all three GF events (Sign test, $P = 0.25$).

The 30-day sliding total rainfall dropped below 60 mm on four occasions, in 1991 (60 days), 1993 (2 days), 1994 (23 days) and 1997 (2 days, 4 days, 3 days, 3 days, 13 days and 3 days within a 2-month period) although 1993 was only marginally below the threshold at 59.5 mm. The sliding total dropped below 10 mm on two of these occasions in 1991 and 1994 (both 4 days) (Fig. 2a). These three severe droughts preceded the three main GF events. Prior to the 1994 GF event there was a low night-time temperature (LNTT) of less than 20 °C (Fig. 2b); however, in 1997, the flowering in dipterocarps had already started by the time of the LNTT. Unfortunately, temperature records did not start until 1993 so we cannot determine if there was an LNTT, or not, prior to the 1991 GF event.

Spearman's rank correlations were calculated between the percentage of trees flowering and the total rainfall over the preceding 365 days, in 5-day increments. The strongest negative correlation was found between the percentage of trees flowering and total rainfall over the preceding 150 days ($r_s = -0.638$, $P < 0.001$); if this was separated into dipterocarps and non-dipterocarps, the correlation was stronger for dipterocarps ($r_s = -0.625$, $P < 0.001$) than for non-dipterocarps ($r_s = -0.511$, $P < 0.001$).

Discussion

We present here phenological data for 171 tropical trees over a 10-year period. This is the longest study in South-east Asia that has included quantitative data on both dipterocarps and non-dipterocarps over a period including more than one GF event.

REGULARITY OF FLOWERING AND FRUIT PRODUCTION ACTIVITY

The majority of trees in our study (67.4%) underwent reproductive activity on a supra-annual time-scale with around one-third of these (20.5%) only active during the three GF events. We found almost no trees with annual (0%) or subannual (0.8%) patterns of reproductive activity. At Lambir Hills in Sarawak, Sakai *et al.* (1999) found that a similar proportion of plants were reproductively active on a supra-annual basis (54%) but that around two-thirds of these were only active in GF events; 13% reproduced annually and 5% reproduced subannually. Differences in these figures will be due to the different species chosen for observation as well as the shorter study of Sakai *et al.* (just under 4$^{1}/_{2}$ years) and the fact that their analysis was on a species, rather than individual, basis.

GENERAL FLOWERING

Over our 10-year and 4-month recording period there were three GF events and one minor flowering event,

giving a probability of a GF event occurring within a year of 0.29. Our value is at the higher end of the range for other areas in the region where the probabilities range between 0.16 and 0.39 (Medway 1972; Ashton *et al.* 1988; Curran *et al.* 1999; Wich & van Schaik 2000; Sakai *et al.* 2006) but our high figure will be partly due to the different lengths and low temporal overlap of the noted studies.

Of the three GF events occurring at Barito Ulu, the largest (i.e. greatest total number of reproductive individuals) were in 1991 and 1997 for dipterocarps and in 1994 for non-dipterocarps. Our finding of up to 31.1% of all individuals and 38.7% of species undergoing reproductive activity can be compared with other studies that have shown similar patterns. A number of these studies examined dipterocarp reproductive activity only, e.g. two-thirds of the dipterocarp species underwent reproductive activity in Sabah in 1955 (Wood 1956), 'about 50% of the individuals' of dipterocarps in Sabah during 'good years' (Cockburn 1975), and 80–93% of dipterocarp individuals in West Kalimantan in 1987 and 1991 (Curran *et al.* 1999). Other studies examined reproductive activity for a number of tree species including non-dipterocarps as well as dipterocarps, e.g. 57% and 58% of the trees in 1963 and 1968, respectively, at Ulu Gombak, peninsular Malaysia (Medway 1972), 46% of the trees at Pasoh, peninsular Malaysia, in 1981 (Appanah 1985), and 17% of the trees and 21% of the species during a GF in Sarawak in 1996 (Sakai *et al.* 1999).

However, the proportions of the non-dipterocarps flowering in GF events at Barito Ulu (19–29%) may be lower than in other studies. For example, Medway (1972) found that 55–60% of non-dipterocarps flowered in GF events and Appanah (1985) found that 43% of non-dipterocarps flowered in 1981 at Pasoh. Another interesting result from our study is that there appears to be a slightly lower proportion of 'background' flowering trees (1.25%) during non-GF periods when compared with other Malaysian sites, e.g. < 3% in Sarawak (Sakai *et al.* 1999) and 5.4% in peninsular Malaysia (data calculated from Medway 1972), although the value for 'background' fruit production was 3.8% so it may simply be that flowers were missed during non-GF events.

SEQUENTIAL FLOWERING

In all three of the GF events we found that there were consistent patterns of sequential flowering with the species sequence approximately maintained in each of the three events. *S. macroptera* was one of the first *Shorea* species to start flowering, in agreement with Appanah (1985), Ashton *et al.* (1988) and LaFrankie & Chan (1991), with *S. parvifolia* in the middle of the sequence, also in agreement with data from the above studies. We extend their data from *Shorea* species to show also that consistent sequential flowering occurs within *Dipterocarpus* and *Vatica* as well. It has been

suggested that sequential flowering may be a way to avoid competition for pollinators (Mosquin 1971; Stiles 1977; Appanah 1985). However, pollination biology needs to be studied in much greater detail in the forests of South-east Asia for us to evaluate this hypothesis properly.

CORRELATIONS WITH CLIMATE AND CUES FOR FLOWERING

Determining the cue for GF in the forests of South-east Asia is a problem that has intrigued and puzzled researchers since the phenomenon was first recorded. Early work focused on evaluating the importance of prolonged drought as the potential cue (Foxworthy 1932, p. 27; Boswell 1940; Wood 1956; Burgess 1972; Medway 1972). Ashton *et al.* (1988) then considered the importance of LNTTs and later work found flowering to follow LNTTs even when there was no prolonged drought (Yasuda *et al.* 1999; Sakai *et al.* 1999). Numata *et al.* (2003) considered both LNTTs and drought to be important. The most recent analysis by Sakai *et al.* (2006) has shown that drought appears to be the cue for GF as it was the only climatic factor that was consistent in preceding four GF events in Sarawak between 1993 and 2003.

An LNTT of 5–8 days around 2 months before a flowering event is considered to induce the development of floral buds of dipterocarps (Ashton *et al.* 1988). We found LNTTs (including nights of 20 °C or less) of two nights followed by four nights in July 1994 and four nights in August 1997 with one night in October 1997. Flowering started about 1 month after the LNTT in 1994 but had already started by the time of the LNTT in 1997. Our minimum temperatures were recorded in a small clearing at *c.* 1.5 m above the ground and are likely to be higher than those at the top of the exposed canopy where the reproductive parts of mature trees are found. Nevertheless, we suggest that LNTTs do not always lead to GF, as has also been reported by Brown and Corlett (cited in Whitmore 1998, p. 241) and Curran (cited in Corlett & LaFrankie 1998) in eastern and western Borneo as well as Singapore. As temperature records at Barito Ulu did not start until 1993 we cannot distinguish between an LNTT or drought as the flowering trigger for the first flowering event. However, for the 1994 event, both a drought of less than a 30-day sliding total of 60 mm for over 10 days and an LNTT of less than 20 °C were found. In 1997, only a drought was observed showing that LNTTs are not always found before a GF event.

Following the analysis of Wich & van Schaik (2000), at Barito Ulu, the probability of a GF event following an ENSO year was 0.5 and the probability of a GF event following a non-ENSO year was 0.0. This is a statistically significant difference ($\chi^2 = 66.7$, $P < 0.001$) and consistent with other results that have shown strong relationships between ENSO events and mast-fruiting in Borneo and the eastern Malay peninsula (Ashton *et al.* 1988; Curran *et al.* 1999; Wich & van Schaik 2000).

However, there is often spatial variation in the occurrence of GF events and Ashton *et al.* (1988) suggested that the effects of ENSO conditions would be strongest on the eastern sides of the Malesian land masses. This was confirmed by Yasuda *et al.* (1999) and Wich & van Schaik (2000) who suggested that there are other more localized factors that will affect the onset of GF events. Indeed, there is no reason to suggest that all families, or even species, will have the same cues for flower induction and there are a number of examples that suggest that different species respond to different cues for flowering. For example, the only dipterocarp species to flower in 1993 and 2000 was *Dipterocarpus rigidus*, when no other dipterocarps flowered. An interesting pattern of flowering was also shown by *Cotylelobium melanoxylon* that flowered later than other dipterocarps in the 1991 GF event but earlier in the 1994 GF event. This unusual activity was also recorded by Kiyono & Hastianah (2000) who showed that *C. melanoxylon* flowered earlier than other dipterocarps in 1994; they suggested that flowering was induced by a dry spell 10 months earlier. It is also not clear what the cues for minor flowering are and how these differ from those for the larger GF events.

Correlations between the percentage of flowering trees and total rainfall in the preceding number of days was strongest for total rainfall over the preceding 150 days (about 21 weeks). This long period of time is composed of two parts, the period over which soil water is depleted sufficiently to act as a cue to flowering and then the 9–16 weeks between the flowering cue and flower anthesis (Ashton *et al.* 1988). In contrast, Putz (1979) found the strongest correlations between the number of flowering species and rainfall in the last two ($r_s = -0.37$) and three ($r_s = -0.36$) months but these correlations were less strong than ours ($r_s > -0.50$). It is noteworthy that most previous correlation analyses between numbers of flowering trees and rainfall have been done on monthly rainfall totals rather than sliding rainfall totals which are more informative as they do not dissect the rainfall values artificially. Re-analysis of some of the previous data using sliding totals may show that droughts are actually a more important cue than has been considered previously.

CONSTRAINTS TO OUR ANALYSIS

Often, trees were recorded as flowering but did not produce fruit. Failure to produce fruit may have been due to a number of reasons including a lack of pollinators, poor climatic conditions or insufficient carbohydrate reserves. In addition, our monthly records may not have noted fruit if they matured and were removed or dropped rapidly after flowering; it is also conceivable that trees flowered in one year but produced fruit in the next year and thus did not produce fruit immediately after flowering. Conversely, it is also possible that, with our monthly recording, we missed flowering in some species but recorded fruit production. Other reasons

for recording fruit production but not flowering may be: (i) flowers opened at night (as in some Sapotaceae; Corner 1952, p. 597; Ng 1972), (ii) flowers were inconspicuous (as in some *Artocarpus* species; Corner 1952, p. 649), (iii) *Ficus* species producing synconia would not have been recorded as flowering, or (iv) cleistogamy occurred, when flowers do not fully open and are self-fertilized.

Minimal replication for some species makes generalizations difficult, but the long-term nature of our observations increases their value considerably. The number of species in our study overlapping with studies mentioned previously was low, making comparisons within species difficult. However, family overlap was high and the majority of our analyses were at family level or above. For example, whilst only 14% of the species observed in our study were recorded by Sakai *et al.* (1999) in Sarawak, 82% of the families were common to the two studies.

Conclusions

We have shown that during a 10-year period at Barito Ulu, Kalimantan, Indonesia, there were three general flowering events and one minor flowering event during which a large number of dipterocarps and many of the other families flowered in close synchrony, the occurrence of which was strongly correlated with ENSO conditions. Our data indicate that drought periods are a more important cue to these general flowering events than low night-time temperatures, in agreement with recent results from northern Borneo (Sakai *et al.* 2006).

Acknowledgements

References

Appanah, S. (1985) General flowering in the climax rain forests of South-east Asia. *Journal of Tropical Ecology*, **1**, 225–240.

Appanah, S. (1993) Mass flowering of dipterocarp forests in the aseasonal tropics. *Journal of Biosciences*, **18**, 457–474.

Ashton, P.S., Givnish, T.J. & Appanah, S. (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist*, **132**, 44–66.

Badeck, F.-W., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J. & Sitch, S. (2004) Responses of spring phenology to climate change. *New Phytologist*, **162**, 295–311.

Bollen, A. & Donati, G. (2005) Phenology of the littoral forest of Sainte Luce, southeastern Madagascar. *Biotropica*, **37**, 32–43.

Boswell, A.B.S. (1940) Rainfall and the flowering of Shorea. *Malay Forester*, **9**, 175–177.

Brearley, F.Q., Prajadinata, S., Kidd, P.S., Proctor, J. & Suriantata. (2004) Structure and floristics of an old secondary rain forest in Central Kalimantan, Indonesia, and a comparison with adjacent primary forest. *Forest Ecology and Management*, **195**, 385–397.

Burgess, P.F. (1972) Studies on the regeneration of the hill forests of the Malay peninsula: the phenology of dipterocarps. *Malayan Forester*, **35**, 103–123.

Cockburn, P.F. (1975) Phenology of dipterocarps in Sabah. *Malaysian Forester*, **38**, 160–170.

Corlett, R.T. & LaFrankie, J.V. Jr (1998) Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climatic Change*, **39**, 439–453.

Corner, E.J.H. (1952) *Wayside Trees of Malaya*, 2nd edn. Government Printing Office, Singapore.

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

Curran, L.M. & Leighton, M. (2000) Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**, 101–128.

Curran, L.M. & Webb, C.O. (2000) Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecological Monographs*, **70**, 129–148.

Foxworthy, F.W. (1932) *Dipterocarpaceae of the Malay Peninsula*, Malayan Forest Records 10. Forest Department, Kepong, Malaysia.

Janzen, D.H. (1974) Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica*, **6**, 69–103.

Johnson, S.D. (1992) Climate and phylogenetic determinants of flowering seasonality in the Cape flora. *Journal of Ecology*, **81**, 567–572.

Justiniano, M.J. & Fredericksen, T.S. (2000) Phenology of tree species in Bolivian dry forests. *Biotropica*, **32**, 276–281.

Kelly, D. (1994) The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution*, **9**, 465–470.

Kiyono, Y. & Hastianah (2000) Flowering and fruiting phenologies of dipterocarps in a rainforest in Bukit Soeharto, East Kalimantan. *Rainforest Ecosystems of East Kalimantan: El Niño, Drought, Fire and Human Impacts*, Ecological Studies 140 (eds E. Guhardja, M. Fatawi, M. Sutisna, T. Mori & S. Ohta), pp. 121–128. Springer, Tokyo.

LaFrankie, J.V. Jr & Chan, H.T. (1991) Confirmation of sequential flowering in *Shorea* (Dipterocarpaceae). *Biotropica*, **23**, 200–203.

Lieth, H. (1974) *Phenology and Seasonality Modeling*, Ecological Studies 8. Springer, New York.

Medway, Lord (1972) Phenology of a tropical rain forest in Malaya. *Biological Journal of the Linnean Society*, **4**, 117–146.

Mirmanto, E. (1996) *A lowland rain forest fertilization experiment in central Kalimantan, Indonesia*. MSc thesis, University of Stirling.

Mirmanto, E., Proctor, J., Green, J.J., Nagy, L. & Suriantata. (1999) Effects of nitrogen and phosphorus fertilisation in a lowland evergreen rain forest. *Philosophical Transactions of the Royal Society Series B – Biological Sciences*, **354**, 1825–1829.

Molau, U., Nordenhall, U. & Eriksen, B. (2005) Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *American Journal of Botany*, **92**, 422–431.

Mosquin, T. (1971) Competition for pollinators as a stimulus for the evolution of flowering times. *Oikos*, **22**, 398–402.

Murali, K.S. & Sukumar, R. (1994) Reproductive phenology of a tropical dry forest in Mudumalai, southern India. *Journal of Ecology*, **82**, 759–767.

© 2007 The Authors
Journal compilation
© 2007 British
Ecological Society,
Journal of Ecology,
95, 828–839

Nagy, L. & Proctor, J. (1999) Early secondary forest growth after shifting cultivation. *Management of Secondary and Logged-Over Forest in Indonesia* (eds P. Sist, C. Sabogal & Y. Byron), pp. 1–12. Centre for International Forestry Research, Bogor, Indonesia.

Ng, F.S.P. (1972) Sapotaceae. *Tree Flora of Malaya*, Vol. 1 (ed. T.C. Whitmore), pp. 388–439. Longman Malaya, Kuala Lumpur, Malaysia.

Ng, F.S.P. (1977) Gregarious flowering of dipterocarps in Kepong, 1976. *Malaysian Forester*, **40**, 126–137.

Numata, S., Kachi, N., Okuda, T. & Manokaran, N. (1999) Chemical defences of fruits and mast-fruiting of dipterocarps. *Journal of Tropical Ecology*, **15**, 695–700.

Numata, S., Yasuda, M., Okuda, T., Kachi, N. & Nur Supardi, M.N. (2003) Temporal and spatial patterns of mass flowerings on the Malay peninsula. *American Journal of Botany*, **90**, 1025–1031.

Prajadinata, S. (1996) *Studies on tree regrowth on shifting cultivation sites near Muara Joloi, Central Kalimantan, Indonesia.* MSc thesis, University of Stirling.

Proctor, J., Brearley, F.Q., Dunlop, H., Proctor, K., Supramono & Taylor, D. (2001) Local wind damage in Barito Ulu, Central Kalimantan: a rare but essential event in a lowland dipterocarp forest? *Journal of Tropical Ecology*, **17**, 473–475.

Putz, F.E. (1979) Aseasonality in Malaysian tree phenology. *Malaysian Forester*, **42**, 1–24.

Ratheke, B. & Lacey, E.P. (1985) Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics*, **16**, 179–214.

Sakai, S., Harrison, R.D., Momose, K., Kuraji, K., Nagamasu, H., Yasunari, T., Chong, L. & Nakashizuka, T. (2006) Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany*, **93**, 1134–1139.

Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid Karim, A.A., Nakashizuka, T. & Inoue, T. (2004) Plant reproductive phenology and general flowering in a mixed dipterocarp forest. *Pollination Ecology and the Rain Forest: Sarawak Studies*, Ecological Studies 174 (eds D.W. Roubik, S. Sakai & A.A. Hamid Karim), pp. 35–50. Springer, New York.

Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A.A. & Nakashizuka, T. (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *American Journal of Botany*, **86**, 1414–1436.

van Schaik, C.P., Terborgh, J.W. & Wright, S.J. (1993) The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, **24**, 353–377.

Stiles, F.G. (1977) Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science*, **198**, 1177–1178.

Whitmore, T.C. (1984) *Tropical Rain Forests of the Far East*, 2nd edn. Oxford University Press, Oxford.

Whitmore, T.C. (1998) *An Introduction to Tropical Rain Forests*, 2nd edn. Oxford University Press, Oxford.

Wich, S.A. & van Schaik, C.P. (2000) The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology*, **16**, 563–577.

Wood, G.H.S. (1956) The dipterocarp flowering season in North Borneo, 1955. *Malay Forester*, **19**, 193–201.

Wright, S.J. & Calderón, O. (1995) Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology*, **83**, 937–948.

Wright, S.J. & van Schaik, C.P. (1994) Light and the phenology of tropical trees. *American Naturalist*, **143**, 192–199.

Wycherley, P.R. (1973) The phenology of plants in the humid tropics. *Micronesica*, **9**, 75–96.

Yasuda, M., Matsumoto, J., Osada, N., Ichikawa, S., Kachi, N., Tani, M., Okuda, T., Furukawa, A., Rahim Nik, A. & Manokaran, N. (1999) The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology*, **15**, 437–449.