Flowering and fruiting phenology of a Philippine submontane rain forest: climatic factors as proximate and ultimate causes

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Summary

1 Phenological patterns of flowering and fruiting are presented for 5800 trees of a Philippine submontane forest community during a 4-year period. Circular vector algebra allowed species to be grouped into annual (34 species), supra-annual (3), irregular (7), and continuous (13) reproducers.

2 Wind- and gravity-dispersed species had extended fruiting periods coinciding with the typhoon season (July to November), whereas fleshy fruited trees showed peaks matching those of solar irradiance. Most species flowered at the beginning and fruited at the end of the first peak (April), or they flowered during the first peak and fruited during the second peak (September), indicating that solar irradiance may be a strong selective factor in shaping community-wide phenology patterns.

3 An El Niño and a La Niña climate anomaly occurred during the study period. Principal component analysis showed that 95% of intraspecific variation of flowering and fruiting dates could be explained by delayed or advanced flowering and fruiting of a limited number of species. Mast-fruiting of dipterocarp species could not be correlated with El Niño and La Niña events.

4 Large climate-induced variation in phenology was demonstrated for the percentage of trees that reproduce, while the timing of phenology remained unaffected for most species, suggesting that climatic factors are not directly responsible for triggering and synchronization of phenological events.

Key-words: abiotic factors, dispersal syndromes, reproductive phenology

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Introduction

In seasonal environments the timing of fruiting and flowering is usually correlated with climatic conditions that will be best for offspring survival. In tropical regions with a pronounced dry season reproductive synchrony may therefore simply be the consequence of selection for the same favourable time for reproduction in relation to climate. Fruiting often occurs at the beginning of the rainy season, which presumably minimizes the exposure of seeds to seed predators and provides maximum time for seedlings to develop the root systems needed to survive drought during their first dry season (van Schaik *et al*. 1993). A pronounced clustering of reproduction remains quite common, however, in tropical regions that lack a predictable dry season.

Predator swamping is the oldest, and probably the most popular, alternative explanation for reproductive synchrony, but biotic factors can also account for asynchronous patterns (Ims 1990). Although it is now widely acknowledged that biological interactions and phylogenetic relations can shape phenological patterns (Wheelwright 1985; Ollerton & Lack 1992; Poulin *et al*. 1992; van Schaik *et al*. 1993; Wright & Calderon 1995; Davies & Ashton 1999; Poulin *et al*. 1999), environmental factors are usually thought to function as external cues for organisms to time their reproduction.

Phenology in the south-east Asian lowland dipterocarp forests is relatively well researched, not least because of the unusual mast-fruiting of dipterocarps and the associated general flowering phenomenon (Ashton *et al*. 1988; Appanah 1993; Curran *et al*. 1999). No records, however, exist for the Philippines, and few attempts have been made to evaluate reproductive phenology at the community level over an extended period of

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time and with sufficient sample size to reliably analyse year-to-year variation in the reproductive phenology of tropical trees. I attempted to identify proximate factors that trigger phenological events, and ultimate factors that may have selected for particular patterns of phenology, concentrating on climatic variables that correlate with phenology at the community and species level. A subsequent paper will focus on the role of biotic factors based on an individual tree level analysis.

Methods

STUDY SITE AND DATA COLLECTION

The study was conducted in a submontane tropical rain forest in the North Negros Forest Reserve on the island of Negros, Philippines (10°41′ N, 123°11′ E). The study area lies on the north-west slope of Mt Mandalagan on volcanic soils at an elevation of 1000 m. The forest community belongs to the transition zone between the lowland evergreen rain forest and the lower montane forests and has floristic elements of both forest formations. Dominant families include Dipterocarpaceae, Lauraceae, Burseraceae, Sapotaceae, Moraceae, Euphorbiaceae and Icacinaceae. For more details refer to the botanical inventory by Hamann *et al.* (1999), which enumerates all species included in this study with references to voucher specimens at the Philippine National Museum, Manila, and the Rijksherbarium, Leiden.

Three adjacent forest plots of different successional stages (a 1.7-ha plot in 25-year-old forest, 1.9 ha in 50-year-old forest, and 4.4 ha in old-growth forest, approximate ages at start of study) were chosen to represent a wide range of tree species with sufficient sample size. Early and mid-successional stands had average canopy heights of 17 and 22 m, with basal areas of 16 m^2 ha^{-1} and 28 m^2 ha^{-1}, respectively, while the values for the old-growth community were 30 m and 56 m^2 ha^{-1}. All trees with at least 10 cm diameter at breast height were marked with aluminium tags and monitored by the same local field assistant, using binoculars, during the 13th to 17th calendar day of each month from January 1996 to December 1999 (n = 1368, 1366 and 3096 trees, respectively, for plots of increasing age). Flower buds, blooming, unripe and ripe fruits were recorded but only observations of blooming flowers and ripe fruits were used for this analysis.

Climatic conditions at the study site were relatively aseasonal. A summer monsoon from the Pacific and a winter monsoon from the South China Sea bring rain throughout the year, and although there is a period of less precipitation around March and April, this is not enough to create any deciduousness in the forest. Monthly rainfall at the study site is highly correlated with that of the 25-km distant coastal city of Silay (Fig. 1) but about twice as high. Daily maximum and minimum temperatures remain relatively constant year round, with slightly higher temperatures around May when the sun is in the zenith (Fig. 1). Day length
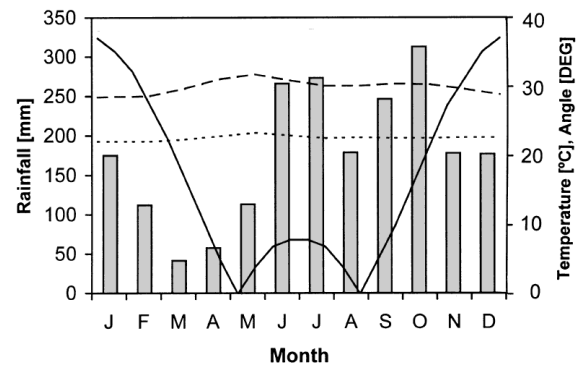
Fig. 1 Average monthly rainfall (□), average maximum (···) and minimum (– – –) temperatures, and sun angle from the zenith at noon (—) for the coastal city of Silay (24-year average 1974–98). Data from World Climate Database (2000) and Exell (1986).

changes by approximately 1 hour over the course of the year. Typhoons are frequent during the winter monsoon from July to November The study included a major El Niño event that peaked in November 1997 and a subsequent La Niña event that developed throughout the summer of 1998 with a peak in September These ocean surface temperature anomalies influence the Philippine weather patterns with several months delay. Weather data were collected at a research station 1.4 km distant from the study site. Minimum and maximum temperatures were read daily to the nearest 0.5 °C with a white-case shielded liquid-in-glass thermometer, mounted approximately 1.5 m above the ground. Rainfall measurements were taken using a manual rain gauge with a 0.5-mm resolution.

DATA ANALYSIS AND STATISTICS

Circular vector algebra was used to calculate statistics representing date, length and regularity of phenological events. Circular vector statistics provide an elegant method for numerical summary of events of a cyclical nature (Batschelet 1981), and have been used in phenological studies by Davies & Ashton (1999) and Wright & Calderon (1995), who also provide the required vector equations. The angle of a vector on a 360° circle indicates the mean date of fruiting or flowering events on a circular scale with 0° representing the 1 January. The length of the vector is zero when an equal number of phenology records occur in each month, and its maximal value of one is reached when all records occur in a single calendar month. As the vector lengths confound duration and regularity of flowering events, I first calculated mean vectors for each species in each year (each flowering event for species that reproduced multiple times per year). An average of the length of these first vectors represents the duration of an event. As this vector representation of the duration of an event had a high linear correlation with the length of phenological events (number of consecutive months with flowering or fruiting observations) obtained from
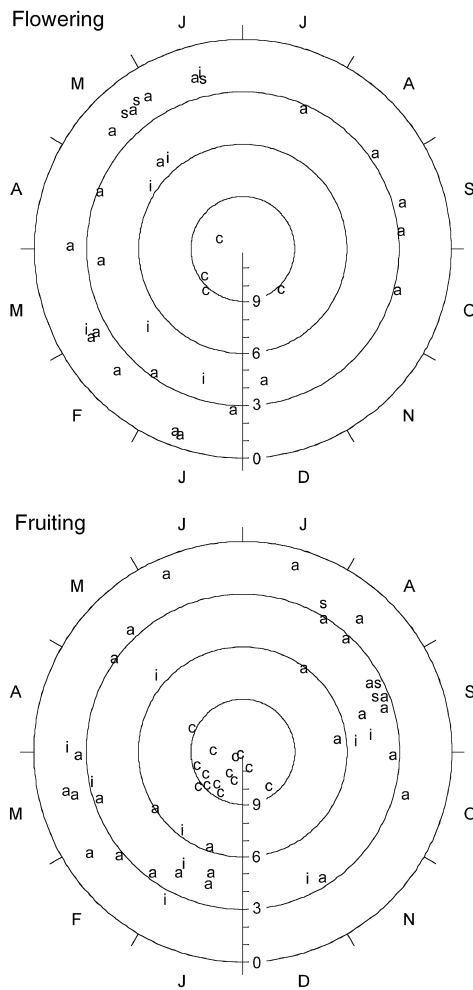
Fig. 2 Date and duration of flowering and fruiting events as indicated by the position of the symbols for regular annual (a), irregular (i), supra-annual (s), and continuous patterns (c). Months of the year are denoted by capital letters, the concentric circles represent duration of the event in months.

graphical representations ($y = -14.218x + 15.55$, $r^2 = 0.91$) results are reported in units of months (scale conversion for Fig. 2). I then calculated a second mean vector using the angles of the first vectors as input data. The length of the second vector represents the regularity of phenological events.

I grouped flowering patterns based on vector statistics similar to the graphical representations of Newstrom *et al*. (1994). However, only a small subset of their classes (continual, subannual, annual and supra-annual, with subclassifications into regular and irregular intervals, and short, intermediate and extended length of flowering) was observed. Irregular intervals were defined by a vector length less than 0.7 for regularity. Extended flowering was defined by a vector length less than 0.7 for duration. Newstrom *et al*. (1994) pointed out that numerical summaries often obscure temporal sequences in phenology, and I have therefore included graphs for unusual phenology patterns.

For analysing dependencies of phenological patterns on climatic events, no attempt was made to use time

series statistics because data were only available for 4 years. Instead, principal component analysis of annual deviations of flowering dates from the 4-year average was applied. Orthogonal variates, which are linear combinations of the original variables that best account for the total variance in the data set were extracted from the covariance matrix, which preserves the magnitude of deviations. Only principal components with Eigenvalues greater than one were retained. The first two variates were plotted against each other to identify species with common patterns of deviations. Only species with annual fruiting patterns and at least 20 observations were included in this analysis. All calculations were performed with the PRINCOMP procedure of the SAS statistical software package (SAS Institute Inc. 2000).

Results

COMMUNITY PATTERNS

Circular vector algebra allowed species to be grouped into annual (34 species), supra-annual (3), irregular (7) and continuous (13) reproducers. If all species are considered together, a number of general patterns emerge regarding length and timing of phenological events. Many species had regular annual patterns of flowering and fruiting, which typically lasted 3 months (Fig. 2). A discontinuity was observed for flowering and fruiting duration with values for most species being less than 6 months or more than 9 months. The latter group consisted mostly of understorey trees, which developed fruits and flowers continuously with peaks of fruiting activity between December and May. Note that more species were observed fruiting than flowering because some flowers were inconspicuous or difficult to observe (e.g. figs).

More species flowered during the first half of the year than in the second half, with clusters at the beginning and the end of the dryer period between February and May. Fruiting had two pronounced aggregations during February and March, and during August and September (Fig. 2). A plot of the time it requires for development of ripe fruits from the date of flowering reveals that species flowering between December and April have short development times, allowing fruiting between January and May (Fig. 3). Species that flower between May and June need approximately 3 months for the development of fruits, accounting for the peak around September. Species that flower in September have the longest development time, with the exception of the wind-dispersed composite *Vernonia arborea* Buch.-Ham., which fruits immediately (shown as an outlyer in Fig. 3).

INFLUENCE OF CLIMATIC FACTORS

Climatic data collected at the study site indicate that during 1996 and 1997, rainfall and temperature closely
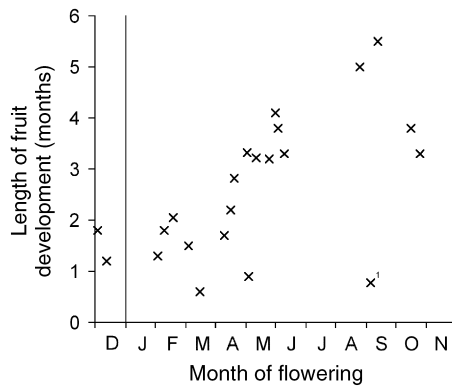
Fig. 3 Time required for development of ripe fruits as a function of the date of flowering. The outlier (1) is *Vernonia arborea*.

tracked the long-term average measured at the coastal city of Silay (Figs 1 and 4). There was a severe dry season in 1998, which extended from February through May, followed by very high rainfall, which extended from October through the first months of 1999, but temperature records remained relatively stable.

The total number of trees observed flowering fluctuated throughout the year, with approximately 2.5 times more activity around April and May than in November (Fig. 5), except in 1998 (the El Niño year) when flowering occurred only later in the year. Overall fruiting activity fluctuated about twice as much as flowering.

The proportion of zoochorous trees fruiting increased considerably around February and September, and fruiting was lower during 1998 and 1999. Bat-dispersed species fruited throughout the year during 1996 and 1997, but showed more seasonal patterns in 1998 and 1999, with lows at the same time as other zoochorous species. Fruiting of wind- and gravity-dispersed species was restricted to July to October and did not appear to be influenced by climatic abnormalities.

While there were changes in the magnitude of flowering and fruiting events in almost every species among years, the date of phenological events remained relatively constant for most tree species. Principal component analysis of the annual deviation in flowering and fruiting date from the 4-year average showed that the first two principal components explained 57% and 36% of the variation in the flowering deviations, having eigenvalues of 2.1 and 1.3, respectively. For deviations in fruiting date the eigenvalues of the first two components were 2.2 and 1.1 and the explained variation was 63% and 28%, respectively. The eigenvectors of principal components reveal that variance in the data set in both fruiting and flowering corresponds to orthogonal (independent) deviations of phenology patterns in 1998 and 1999 (Table 1). A plot of the first two principal components shows that eight species are mainly responsible for these deviations in the date of fruiting or flowering (Fig. 6). In this graph, positive scores in PC1 indicate a delayed event in 1998, negative scores in
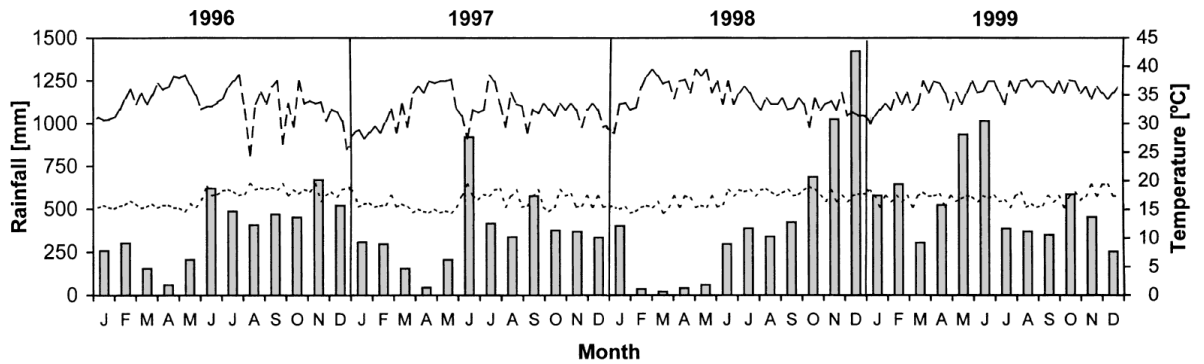
Fig. 4 Average monthly rainfall (▢), and daily maximum (⋯) and minimum (– – –) temperatures at the study site.
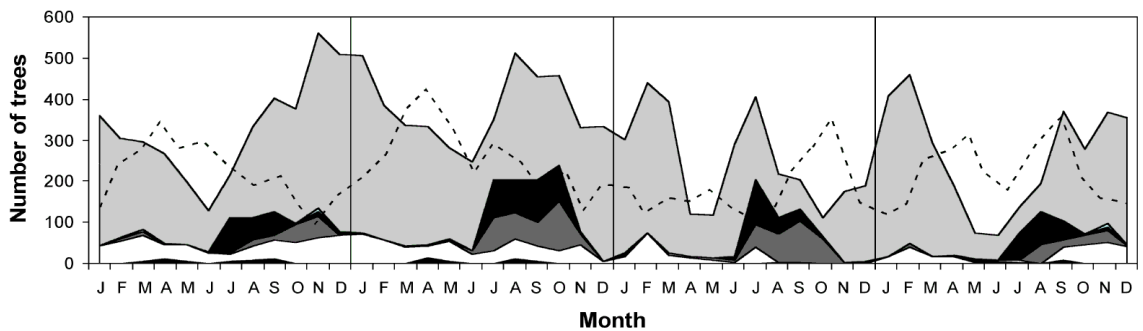
Fig. 5 Number of trees flowering (– – –) and fruiting, partitioned by seed dispersal syndrome as defined in Hamann & Curio (1999). From top to bottom: bird dispersed (▢), dispersed by gravity or unknown vector (■), wind dispersed (▣), fruit bat dispersed (▢), dispersed by other mammals (■).

Table 1 Principal component analysis of the annual deviation in flowering and fruiting date from the 4-year average

	Eigenvectors	
Variable	PC1	PC2
Flowering		
1996	−0.35	0.01
1997	−0.31	0.36
1998	0.87	0.27
1999	0.08	−0.77
Fruiting		
1996	−0.22	0.21
1997	−0.23	0.34
1998	0.88	−0.09
1999	−0.35	−0.78
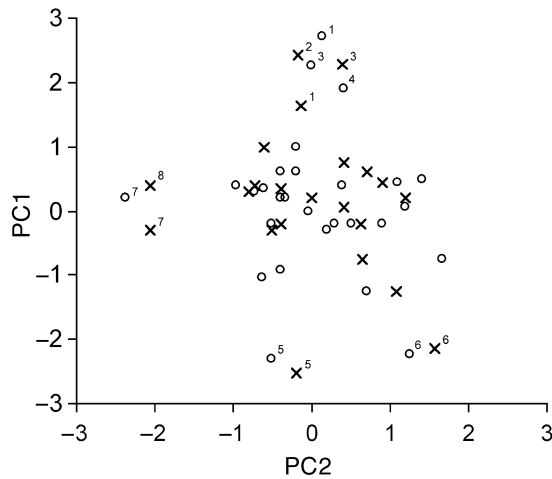
Fig. 6 Plot of the first two principal components for annual deviation in the date of flowering (×) and fruiting (○). Numbers identify the tree species mainly responsible for the effect and discussed in the text.

PC2 indicate a delayed event in 1999 (Table 1). Note that only species with regular annual flowering patterns and observations in every year could be included in this analysis.

SPECIES PATTERNS

Delayed flowering and fruiting, sometimes associated with a reduced number of trees in flower, was observed during the 1998 El Niño year, as in *Prunus fragrans* (Fig. 6 species 1, also Fig. 7a), *Litsea quercoides* Elm. (species 2), *Grewia multiflora* Juss. (species 3), and *Streblus glaber* (Merr.) Corner (species 4). However, there are also examples of the opposite (an advance in the date of flowering and fruiting and an excess number of trees in flower), such as in *Vernonia arborea* Buch.-Ham. (species 5), and *Alphitonia excelsa* (Fenzl) Reiss. ex End. (species 6, also Fig. 7b). An extra flowering event during this time was observed in the understorey species *Memecylon lanceolatum* Blco. (Fig. 7c) and two major canopy species failed to fruit: *Palaquium luzoniensis* Vid. (Fig. 7e), which normally fruits twice a

year, and *Elaeocarpus cumingii* Turcz. (Details of all species are given in Appendix S1, see Supplementary material.)

The weather patterns following the La Niña anomaly in 1999 generally had a smaller effect on the date of flowering and fruiting. *Weinmania camiguinensis* Elm. (Fig. 6 species 7, also Fig. 7d) and *Symplocus ophirensis* (Lour.) Moore (species 8) were the only species that had pronounced delays in phenology. *Elaeocarpus cumingii* did not flower, *Palaquium luzoniensis* (Fig. 7e) lacked the April fruiting peak, and many understorey trees that had continuous flowering patterns generally showed reduced activity during the La Niña event (data not shown).

The three dipterocarps *Parashorea malaanoan* (Blco.) Merr. (Fig. 7f), *Shorea polysperma* (Blco.) Merr. (Fig. 7g) and *Shorea almon* Foxw. were the only species with supra-annual patterns. In all cases one minor fruiting event was followed by a mast-fruiting during the subsequent year.

Discussion

ULTIMATE CAUSES

The observed tree species exhibited a wide variety of phenological behaviour. This is not surprising as phenological patterns potentially integrate a large number of selective forces caused by climatic factors as well as biotic factors such as escape from pests or optimization of pollination and seed dispersal. Nonetheless, the data indicate that seasonality in climatic factors plays a major role in shaping broad community-wide phenology patterns. There is, for example, an obvious selective advantage for wind-dispersed species to fruit during the windiest time of the year, and all wind-dispersed trees fruited during the typhoon season between July and November. In addition, dehiscent fruits without wings or other structures, which I classified as dispersed by gravity, were also exclusively produced during this period, indicating that they might be effectively dispersed by typhoons when wind speeds frequently reach 120 km h^{-1}.

All except one wind-dispersed species flowered around May and required approximately 3 to 4 months for the development of fruits. This pattern was shared by a large number of species with other dispersal syndromes, and coincides with peak solar irradiance. Temporal variation in solar irradiance is mainly a function of cloud cover and sun angle, with cloud cover becoming the more important factor close to the equator (Exell 1986; Wright & Schaik 1994). Long-term weather data suggest a major peak of solar irradiance in April and May when the amount of precipitation is lowest and the sun passes through the zenith for the first time. A second peak may occur in August, when precipitation is relatively low and the sun is in the zenith for the second time (Fig. 1). Almost all canopy tree species had phenology patterns that synchronized fruiting and flowering with these peaks. About half of the species
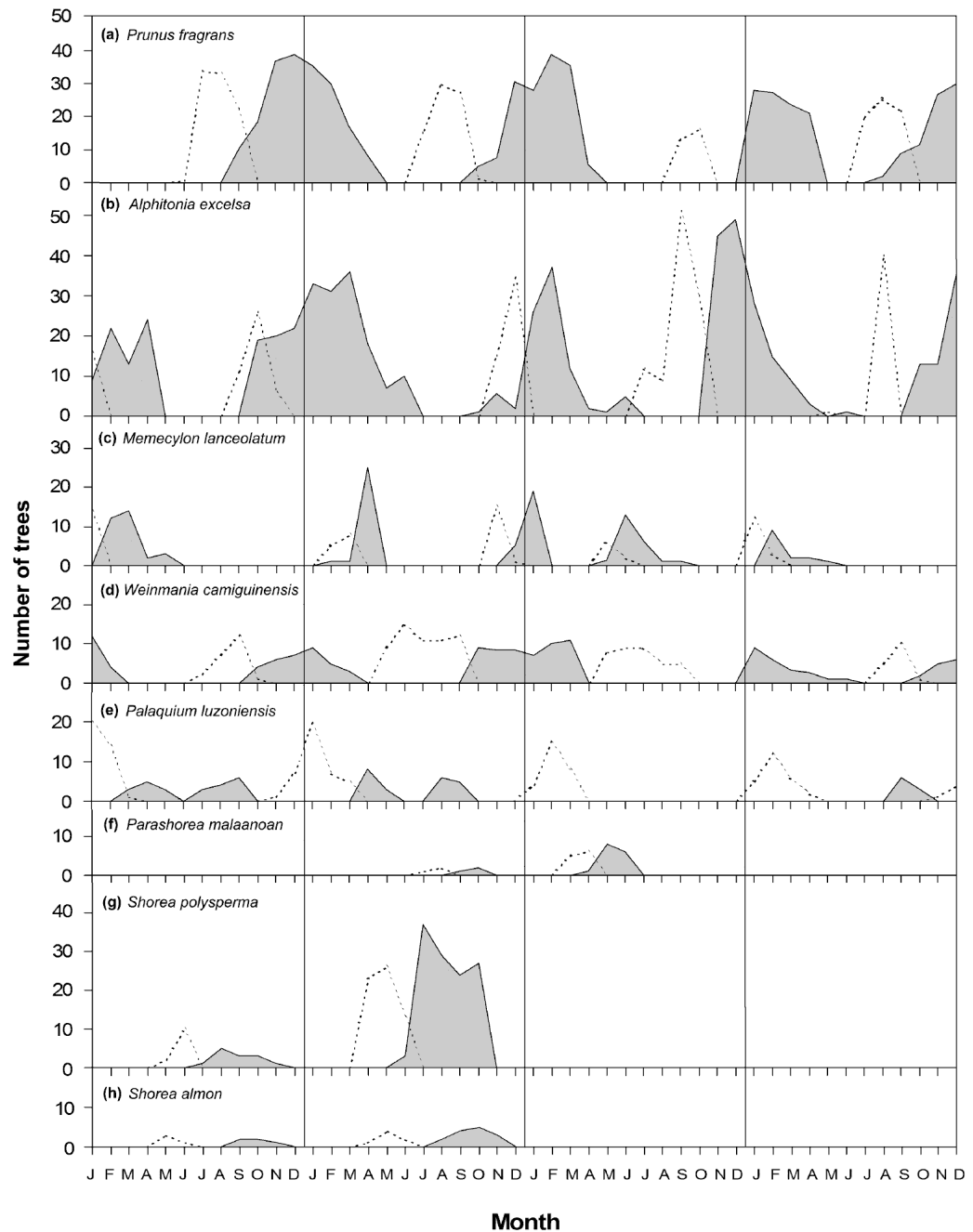
Fig. 7 Number of trees flowering (⋯) and fruiting (▨) during the 4-year observation period 1996–99.

flowered at the beginning and fruited near the end of the first major peak, needing only a short time for the development of fruits. Most other species flowered during the first peak and fruited during the second peak, with a moderate amount of time required for fruit development. The most striking example of both patterns in one species is *Palaquium luzoniensis*, with fruits ripening during both the first and second peak of irradiance. One wind-dispersed species with very small fruits fruited and flowered during the second peak, and two species flowered during the second peak and fruited in the subsequent dry season, with an extended amount of time required for fruit development.

Selection for synchronizing phenological patterns with peak irradiance requires light to be a limiting environmental factor for the production of fruits and flowers. This may frequently be the case in tropical rain forests, as indicated by recent experimental evidence (Graham *et al*. 2003) and by variation of net primary production that is tightly linked to seasonal changes in irradiance (Reich *et al*. 1991). Light limitation as a selective factor seems most obvious for understorey species. Their activity was severely reduced during unseasonal rains in 1999 (e.g. *Ficus congesta*) and an additional flowering event was even triggered during the drought period in 1998 (*Memecylon lanceolatum*).

However, canopy trees that produce flowers and fruits at peak irradiance also have a selective advantage. It is more efficient to transfer assimilates directly into growing organs rather than having to store them and mobilize and translocate them later (Wright & Schaik 1994). Two major canopy trees failed to develop fruits in 1998, suggesting that there may nevertheless be a trade-off between additional light and associated drought for some species. While light limitation appears to be a strong selective factor shaping phenology patterns in this forest community, it is possible that covarying factors are the actual selective forces. It has been reported that minimal pest pressure (Aide 1988) and maximal activity of pollinating insects (Foster 1993) may co-occur with peak irradiance during dry seasons. Also, fruit production at the end of a dry season ensures that seedlings are not immediately exposed to water stress.

PROXIMATE CAUSES

By responding to a reliable trigger mechanism, a plant can initiate development in advance of seasonal changes of the environment and so optimize phenological timing. Trigger mechanisms may be revealed by changes in phenology associated with unusual weather patterns. In order to differentiate between proximate and ultimate effects of environmental factors, it is enlightening to distinguish between effects on the timing and effects on the magnitude of phenological events. Effects on the number of trees flowering and fruiting (or the amount of flowers and fruits produced) point towards limiting factors that might be selected for, while effects on timing of an event identify trigger mechanisms regardless of the subsequent success of flower and fruit development.

It has repeatedly been observed that the onset of the dry season or rainy season precipitates flowering in many species (Frankie *et al*. 1974; Croat 1975). The delayed onset of both the rainy season and flowering in 1998 might indicate such a trigger mechanism for *Prunus fragrans*, *Litsea quercoides*, *Grewia multiflora* and *Streblus glaber*, but the majority of species were unaffected. Nor did a premature onset of the dry season cause advanced dates for species flowering earlier in the year. Therefore, precipitation and associated parameters such as water stress or humidity do not appear to be likely trigger mechanisms for phenological events in this forest community. Solar irradiation has been suggested as a more regular proximate cause of phenological patterns (Wright & Schaik 1994). The advanced date of flowering (and increased number of trees flowering) of *Vernonia arborea* and *Alphitonia excelsa* in 1998 may have been initiated by an increase in solar irradiance in the dry July of that year. The same mechanism is likely to account for an unseasonal flowering event in *Memecylon lanceolatum*. A presumed increase in solar radiation at the beginning of 1998, however, did not affect the timing in any species flowering or fruiting during the dry season. The data rather suggest that most species have rather dominant internal seasonal rhythms that are only slightly affected by annual variations in climate. This finding is not incompatible with results from Wright *et al*. (1999), who showed that climatic conditions associated with El Niño and La Niña events clearly influence the amount of fruits produced. I showed that the percentage of trees that fruit is also affected, and flower or fruit development may fail completely in some species. However, the timing of flowering and fruiting remains unchanged for most species, suggesting that climatic factors are not directly responsible for triggering and synchronization of phenological events.

Proximate factors that precipitate mast fruiting in dipterocarps have been subject to considerable investigation and debate. In Peninsular Malaysia and in Borneo, dipterocarp phenology shows similar periodicity among species and is correlated with El Niño anomalies (Ashton *et al*. 1988; Curran *et al*. 1999; Sakai *et al*. 1999; Curran & Leighton 2000) and floral induction may be triggered by a drop of 2 °C or more in minimum night-time temperature due to radiative cooling during dry spells (Ashton *et al*. 1988; Appanah 1993; Yasuda *et al*. 1999). Correlations of mass flowering with El Niño anomalies, however, weaken towards western Malesia (Yasuda *et al*. 1999; Wich & Schaik 2000), where interspecific synchrony is less common and the timing of mast-flowering can vary on a small geographical scale (Wich & Schaik 2000). Also in this study, climatic data collected at the site revealed that none of the events was associated with a drop in minimum temperature, or associated with an El Niño event. This suggests that factors other than those associated with El Niño anomalies may play a role in determining dipterocarp mast flowering in the Philippines.

Community-wide patterns of reproductive phenology suggest that climatic factors are important ultimate causes for tree phenology even under relatively aseasonal conditions. The typhoon season clearly determined fruiting season for wind-dispersed species, and for zoochorous species the observations are consistent with the hypothesis that flower and fruit production have generally been selected to coincide with peak solar irradiance. These apparently internal seasonal rhythms appear to be only slightly affected by annual variation in climate such as El Niño events.

Supplementary material

The following material is available from
http://www.blackwellpublishing.com/products/
journals/suppmat/JEC/JEC845/JEC845sm.htm

Appendix S1 Phenology statistics for study tree species.

References

Aide, T.M. (1988) Herbivory as selective agent on the timing of leaf production in a tropical understorey community. *Nature*, **336**, 574–575.

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.

Batschelet, E. (1981) *Circular Statistics in Biology*. Academic Press, London.

Croat, T. (1975) Phenological behavior of habitat and habitat classes on Barro Colorado Island (Panama Canal Zone). *Biotropica*, **7**, 270–277.

Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M. *et al.* (1999) Impact of El Nino 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.

Davies, S.J. & Ashton, P.S. (1999) Phenology and fecundity in 11 sympatric pioneer species of Macaranga (Euphorbiaceae) in Borneo. *American Journal of Botany*, **86**, 1786–1795.

Exell, R.H.B. (1986) A program in BASIC for calculating solar radiation in tropical climates on small computers. *Renewable Energy Review Journal*, **8**, 3–35.

Foster, R.B. (1993) Famine on Barro Colorado Island. *The Ecology of a Neotropical Forest: Seasonal Rhythms and Long-Term Changes* (ed. D.M. Windsor), pp. 201–212. Smithonian Institute, Washington DC.

Frankie, G.W., Baker, H.G. & Opler, P.A. (1974) Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, **62**, 881–919.

Graham, E.A., Mulkey, S.S., Kitajima, K., Phillips, N.G. & Wright, S.J. (2003) Cloud cover limits net CO_2 uptake and growth of a rain forest tree during tropical rainy seasons *Proceedings of the National Academy of Science*, **100**, 572–576.

Hamann, A., Barbon, E.B., Curio, E. & Madulid, D.A. (1999) A botanical inventory of a submontane tropical rain forest on Negros Island, Philippines. *Biodiversity and Conservation*, **8**, 1017–1031.

Hamann, A. & Curio, E. (1999) Interactions among frugivores and fleshy fruit trees in a Philippine submontane rain forest. *Conservation Biology*, **13**, 766–773.

Ims, R.A. (1990) The ecology and evolution of reproductive synchrony. *Trends in Evolution and Ecology*, **5**, 135–140.

Newstrom, L.E., Frankie, G.W. & Baker, H.G. (1994) A new classification for plant phenology based on flowering patterns in lowland tropical rain forest trees at La Selva, Costa Rica. *Biotropica*, **26**, 141–159.

Ollerton, J. & Lack, A.J. (1992) Flowering phenology: an example of relaxation of natural selection. *Trends in Ecology and Evolution*, **8**, 274–276.

Poulin, B., Lefebvre, G. & McNeil, R. (1992) Tropical avian phenology in relation to abundance and exploitation of food resources. *Ecology*, **73**, 2295–2309.

Poulin, B.S., Wright, S.J., Lefebvre, G. & Calderon, O. (1999) Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *Journal of Tropical Ecology*, **15**, 213–227.

Reich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Peterson, B.J., Grace, A.L. *et al.* (1991) Potential net primary production in South America. *Ecological Applications*, **1**, 399–429.

Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A.A. *et al.* (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.

SAS Institute Inc. (2000) *SAS/STAT User's Guide, Release 8·0*. SAS Institute Inc, Cary, North Carolina.

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 Ecological Systematics*, **24**, 353–377.

Wheelwright, N.T. (1985) Competition for dispersers, and the timing of flowering and fruiting in a guild of tropical trees. *Oikos*, **44**, 465–477.

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

World Climate Database (2000) http://www.worldclimate.com/. 12 December 2000.

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

Wright, S.J., Carrasco, C., Calderon, O. & Paton, S. (1999) The El Nino southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology*, **80**, 1632–1647.

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

Yasuda, M., Matsumoto, J., Osada, N., Ichikawa, S., Kachi, N., Tani, M. *et al.* (1999) The mechanism of general flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical Ecology*, **15**, 437–449.

Appendix 1. Phenology statistics for tree species of this study.

Species	N_{Trees}[1]	Event	$N_{Obs.}$[2]	Date of maximum[3] 1996	1997	1998	1999	Average Date[4]	Length[5]
Acer niveum Bl.	73	Flowering	30	1.3	1.1	1.2	1.0	1.1	1.6
		Fruiting	25	2.6	2.4	2.8	2.0	2.4	1.6
Agathis philippinensis Warb.	70	Fruiting	23	11.7	7.4	8.0	11.0	c	
Alphitonia excelsa (Fenzl)	146	Flowering	252	10.6	11.7	9.0	8.0	9.8	2.9
Reiss. ex. End		Fruiting	568	13.9	13.2	12.1	13.0	13.1	6.2
Astronia stapfii Kord.	32	Flowering	46	11.7	5.8	4.2	12.2	c	
Bischhofia javanica Bl.	38	Fruiting	23		11.8	8.6	1.0	i	4.5
Canarium asperum Bth.	296	Fruiting	240	8.4	7.3	2.9	11.6	c	
Clerodendron brachyanthum	10	Flowering	36	5.9	11.2	8.8	10.6	c	
Schauer		Fruiting	16	10.5	9.3	2.7	1.9	c	
Dendrocine stimulans (L.f.)	57	Flowering	59	8.5	$^{2.1}/_{12}$	12.1		i	2.3
Chew		Fruiting	28	12.4	7.6	3.0	2.3	i	3.4
Dillenia reifferscheidia Elm.	15	Flowering	7	11.5	2.2	1.0	2.3	i	2.6
		Fruiting	16	12.7	2.5	3.3	4.5	i	3.8
Dillenia philippinensis Rolfe	8	Fruiting	14	12.0	8.0	1.2	12.0	i	
Elaeocarpus cumingii Turcz.	67	Flowering	65	3.4	3.6			3.5	1.9
		Fruiting	34	5.0	5.7			5.6	1.5
Ficus benjamina L.	14	Fruiting	63	8.2	1.2	1.9	1.7	c	
Ficus chrysolepis Miq	9	Fruiting	10	10.8	9.0	5.5	8.0	i	2.3
Ficus congesta Roxb.	178	Fruiting	457	11.9	0.8	2.8	11.4	c	
Ficus heteropleura Bl.	55	Fruiting	472	4.0	11.7	2.2	6.8	c	
Ficus heteropoda Miq.	48	Fruiting	102	2.2	1.6	3.4	1.9	c	
Ficus irisana Elm.	8	Fruiting	77	10.0	3.0	3.0	12.1	c	
Ficus septica Burm. f.	7	Fruiting	21	2.0	3.5	2.4	2.3	2.5	3.7
Ficus ulmifolia Lam.	69	Fruiting	134	12.3	4.4	4.1	12.4	c	
Ficus variegata Bl.	13	Fruiting	12	2.3	1.7	2.0	10.0	c	
Ficus spec. 18	23	Fruiting	41	9.6	5.5	4.9	1.9	c	
Ficus spec. 19	56	Fruiting	54	1.3	3.1	2.5	2.4	c	
Garcinia binucao Merr.	6	Fruiting	17		11.0	10.7	4.0	i	3.8
Garcinia brevirostris Merr.	68	Flowering	37	4.1	3.6	8.7	4.3	4.5	5.8
Grewia multiflora Juss.	63	Flowering	112	10.9	0.6	12.3	11.1	12.0	4.6
		Fruiting	114	0.6	2.6	2.5	0.6	1.6	4.2
Guioa pleuropteris (Bl.) Radlk.	27	Flowering	30	2.0	1.7	0.6	1.0	1.3	1.7
		Fruiting	28	3.6	4.0	3.0	2.4	3.3	1.7
Homalanthus alpinus Elm.	7	Flowering	11		4.2	3.0		3.6	2.1
Homalanthus rotundifolius	109	Flowering	54	12.2	1.2	0.6	10.0	0.1	2.4
Merr.		Fruiting	74	3.3	3.1	3.9	1.0	2.9	3.4
Leucosyke capitellana (Poir.)	15	Fruiting	39	12.3	5.2	3.3	1.3	c	
Wedd.									
Lithocarpus sp. 17	98	Flowering	227	4.7	5.0	5.2	4.5	4.8	2.0

[1] Number of trees >10 cm DBH. Note that this may include a large number of immature individuals.

[2] Number of monthly fruiting or flowering records over a four year period

[3] Vector angle converted into month (1 = January 15th, 2 = February 15th, etc.)

[4] c = continuous pattern, i = irregular pattern

[5] Vector length converted into months (length of community level event, 1 = 30 days)

Species	N_{Trees}[1]	Event	$N_{Obs.}$[2]	Date of maximum[3]				Average	
				1996	1997	1998	1999	Date[4]	Length[5]
Lithocarpus sp. 17	98	Fruiting	464	8.0	8.5	7.5	8.0	8.0	3.5
Litsea luzonica F.-Vill.	339	Flowering	67	6.3	7.3	5.0	5.6	6.0	2.0
		Fruiting	186	9.3	9.1	7.8	9.3	8.9	4.1
Litsea quercoides Elm.	133	Flowering	86	9.2	9.1	10.8	8.5	9.4	2.9
Macaranga bicolor Muell.-Arg.	25	Fruiting	21	5.6	6.0	5.3	5.7	5.7	1.9
Macaranga tanarius (L.) M. A.	12	Fruiting	13	5.3	5.6	4.1	6.2	5.3	2.1
Mallotus rhizinoides Muell.-Arg.	114	Fruiting	199	11.7	10.5	9.6	10.9	10.7	5.9
Mallotus sp. 01	166	Flowering	316	3.9	3.4	3.5	3.5	3.6	2.9
		Fruiting	105	4.4	5.1	5.9	4.8	5.1	5.5
Mallotus sp. 02	67	Flowering	108	3.8	2.7	3.0	3.5	3.3	4.0
		Fruiting	278	5.1	5.3	5.1	4.6	5.0	4.0
Memecylon brachybotris Merr.	61	Fruiting	67	1.9	2.0	1.8	1.0	1.7	3.3
Memecylon cumingii Naud.	34	Flowering	102	8.3	8.6	8.9	9.0	8.7	2.5
Memecylon lanceolatum Blco.	77	Flowering	45	1.0	$2.8/_{11}$	5.3	1.2	i	2.8
		Fruiting	57	2.3	4.1	$1.1/_{6.2}$	2.6	i	4.2
Memecylon sp. 09	59	Flowering	47	0.9	1.6	2.2	2.1	0.9	3.1
		Fruiting	108	2.8	3.2	3.9	2.3	3.1	4.1
Myristica ceylanica A. DC.	15	Fruiting	93	1.0	7.2	2.5	1.3	c	
Nauclea philippinensis Hav.	55	Fruiting	22	9.0	10.0	8.9	10.0	9.5	2.4
Palaquium luzoniensis Vid.	152	Flowering	116	1.2	1.6	1.9	1.5	1.6	3.0
		Fruiting	63	$4.0/_{8.4}$	$4.1/_{8.4}$		9.2	i	3.6
Parashorea malaanoan (Blco.) Merr.	132	Flowering	7		7.8	3.8		s	2.6
		Fruiting	9		9.7	5.3		s	2.9
Platea excelsa (Heine) Sleum.	315	Flowering	367	5.3	4.9	4.7	5.3	5.0	5.6
		Fruiting	850	9.8	9.5	8.9	9.6	9.5	6.9
Pometia pinnata J. R. & G. Forst	27	Fruiting	14	7.1		8.0	7.6	7.6	1.9
Prunus fragrans (Elm.) Kalkm.	146	Flowering	414	7.9	8.2	9.6	8.0	8.4	2.8
		Fruiting	830	11.9	13.2	14.2	12.0	12.8	5.8
Saurauria polysperma (Blco.) Merr.	40	Flowering	26	11.6	4.0	7.2	10.4	c	
Shorea almon Foxw.	24	Flowering	5	5.2	5.0			s	2.3
		Fruiting	16	9.8	9.7			s	3.6
Shorea polysperma (Blco.) Merr.	132	Flowering	74	5.8	4.8			s	2.0
		Fruiting	133	8.8	8.3			s	2.8
Strebus glaber (Merr.) Corner	101	Fruiting	164	3.4	3.1	5.3	2.2	3.5	2.5
Symplocus ophirensis Clarke	148	Flowering	96	3.6	3.4	3.8	5.6	4.1	5.0
		Fruiting	65	8.7	7.9	8.4	9.1	8.5	5.6
Syzygium garciae (Merr.) Merr. & Perr.	40	Flowering	14	6.0		8.3		i	1.3
Ternstroemia megacarpa Merr.	44	Fruiting	7	8.3		8.0	8.2	5.6	1.8
Turpinia sphaerocarpa Hassk.	154	Fruiting	123	5.2	6.4	5.7	8.1	c	
Vernonia arborea Ham.	142	Flowering	234	9.2	9.5	8.6	8.4	8.9	1.9
		Fruiting	269	10.3	10.4	9.5	9.2	9.8	2.8
Weinmania camiguinensis Ham.	45	Flowering	132	8.4	7.0	6.7	8.9	7.8	4.4
		Fruiting	140	12.6	12.7	13.6	12.5	12.9	5.7
Meliaceae sp. 04	25	Fruiting	88		8.0	2.6	3.0	i	5.6