

Phenological study on a tropical secondary forest in West Sumatra, Indonesia

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ABSTRACT We made litter fall observations in a West Sumatran tropical rain forest every 2 weeks through 3 years (including the drought year, 1997). Seasonal changes in long-term average rainfall were bimodal, but even in the two dry seasons average monthly precipitation was > 200 mm. Leaf-fall rates in a year with normal rainfall peaked in the first dry season; leaves made up one-third of mean annual litter fall. Larger trees had highly synchronized leaf fall during the peak shedding period. Smaller trees shed simultaneously during severe drought. Twigs < 0.5 cm diameter tended to fall in proportion to the 3/2 power of leaf-fall rates; therefore, we considered autonomous twig fall in relation to the pipe model theory. Variances in reproductive organ shedding rates (seasonal and annual) were larger than those of leaves and branches, possibly because of the higher susceptibility of reproductive parts to drought. Reproductive fall rates in the year with normal weather peaked in May (flowers) and August (fruits). Seasonal patterns of flowering and fruiting were classified into three groups. Understory species had an "extended flowering" pattern. We discuss phenological patterns found in this very high humidity climate and the impacts of increasingly frequent droughts.

Key words: Indian Ocean Dipole Mode, Sumatra, defoliation, drought weather, litter-fall, phenology, pipe model theory, seasonal changes, a tropical secondary forest

Abbreviation

dbh : stem diameter at breast height

R^2 : coefficient of determination

P : significance probability

N : number of samples

INTRODUCTION

Plant phenology in aseasonal climates is a topic of considerable ecological interest. Attempts have been made to determine the factors regulating observed patterns of plant development (Koriba, 1947, 1958; Frankie et al. 1974; Whitmore, 1988; Richards, 1996). The high species diversity in tropical rain forests that occurs in aseasonal climates leads to complexity in the community-level phenological patterns expressed in processes of growth (Ng and Tang, 1974; Hatta and Darbaedu, 2005), regeneration (Medway, 1972; Sakai et al. 1999), and food-chain structure (Jansen, 1974; Schaik et al. 1993). Recent climate changes and increasing anthropogenic activities are risk factors in rain forests because they can disturb endogenous rhythms and discontinuities in phenological sequences (Corlet and Lafrankie, 1998; Turner, 1996).

Endogenous traits of wet tropical species are acquired characteristics that develop over the long term as populations expand and contract in response to unstable climate periodicity; the outcomes of these processes are successful regeneration mechanisms. Some species in a given community may have plastic responses to temporal shifts in climate (Valladares et al. 2000; Osada et al. 2002), whereas others do not (Williams, 1997), which often obscures the relationships between phenology and climatic factors.

Drought is widely recognized as a trigger for seasonal behaviors such as defoliation, new leaf flush, flowering, and fruiting (Medway, 1972; Frankie et al. 1974; Schaik, 1986; Yamada, 1997; Osada et al. 2001); drought may also be correlated with supra-annual events such as mast flowering in Asia (Burgess, 1972; Medway, 1972; Apanah, 1985). Abnormally low temperatures may

have similar effects (Ashton et al. 1988; Yasuda et al. 1999; Sakai et al. 1999; Numata et al. 2003). Forest tree condition (e.g., size and preceding growth rate) is associated with susceptibility to drought (Yoneda et al. 2000, 2006; Nakagawa et al. 2000). However, drivers of the overall drought–phenology relationship are still unresolved. Field experiments manipulating soil water conditions would certainly help to identify the cues for defoliation (Wright & Cornejo, 1990, Wright, 1991).

The equatorial region of west Sumatra facing the Indian Ocean has a highly humid climate with average monthly rainfall >200 mm through the year (Hardjono, 1971; Laumonier, 1997). However, regional meteorological data for Padang, West Sumatra, demonstrate an increased frequency of severe drought (< 50 mm cumulative rainfall in the preceding 30 days) over the last 15 years. These changes must have some impacts on plant phenology. Accordingly, we studied litter-fall rates in a tropical West Sumatran secondary forest at 2-week intervals through 3 years from the beginning of December 1994 (Yoneda et al. 2000). This forest suffered severe drought during this period. We (1) tracked seasonal changes in defoliation, branch fall, flowering, and fruiting, and (2) evaluated impacts of drought on phenological behaviors at the levels of individuals, species, and community.

MATERIALS AND METHODS

Study site

The study was conducted within the School of Biology Forest, Andalas University, located 17 km east of Padang City (00° 53' S, 100° 21' E), West Sumatra, Indonesia (Yoneda et al. 2000). Annual rain fall in long-term average rainfall between 1971 and 1997 at Tabing Airport, Padang, was 4162 mm with two dry seasons (January-February and June-August) and two rainy seasons, and average monthly fall still exceeded 200 mm in these dry seasons (Fig. 8). The secondary forest tract studied was on a sloping ridge at an altitude of 400 m, and covered a ground area of 0.234 ha. The dimensions of the stand structure in 1996 were 161 t ha⁻¹ in aboveground biomass, 22 m² ha⁻¹ in basal area, and 20–25 m in canopy height. There were 25 families, 41 genera, and 54 species of trees with a diameter at breast height (*dbh*) > 5 cm. Dominant families (expressed as relative dominance: basal area + abundance) were Euphorbiaceae, Lauraceae, Melastomataceae, and Myrtaceae, and dominant genera were *Ptenandra*, *Litsea*, *Bridelia*, *Macaranga*, and *Eurya*. The stand suffered severe drought in 1994, the year preceding observations, and in 1996 and 1997. The

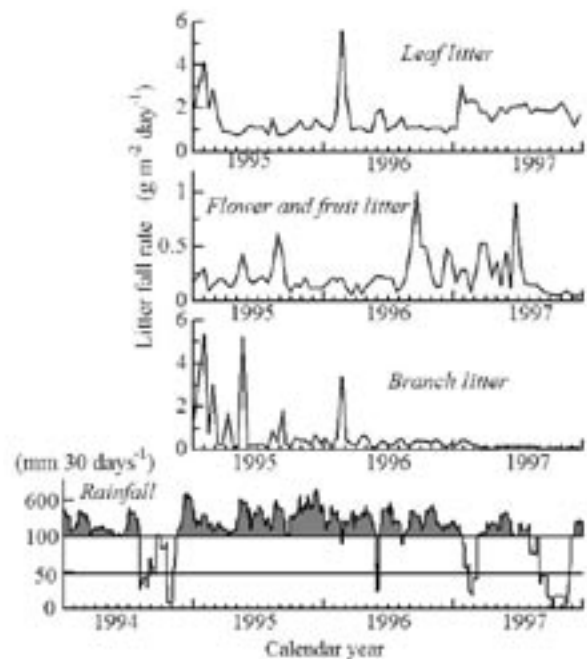


Fig. 1. Trends in cumulative rainfall in the preceding 30 days and litter-fall rates of leaves, flowers, fruits, and branches. Rainfall over 100 mm (black scale) is reduced to 1/10. Modified from Figure 3 of Yoneda et al. (2000).

drought event in 1997 was the most severe (Fig. 1).

Litter fall measurement

Litter samples were collected 78 times from a forest stand of 50 m × 50 m at 2-week intervals through 3 years from the beginning of December 1994; there were 25 litter traps, and trap contents were sorted into four categories, viz. leaves, branches, flowers–fruits, and miscellaneous components. Their oven-dry weights were measured. Seasonal and yearly changes in total weight in each category have been presented elsewhere (see Fig. 1 of Yoneda et al. 2000).

Trapped leaves of 45 trees (cf. Fig. 2) directly above the traps were sorted by tree individual, and their oven-dry weights were measured. Trees belonged to 18 families, 24 genera, and 29 species. The total litter weight from these trees on each collection occasion was directly proportional to total litter mass in the 25 traps deployed ($N = 78$, $R^2 = 0.971$).

Litter samples in the 1995 “flowers–fruits” category were further sorted into two groups of flowers and fruits for the nine major species immediately above 20 traps. Their total weights were in direct proportion to the weights in the 25 traps deployed ($N = 28$, $R^2 = 0.843$); we

Table 1. Tree species for which we estimated shedding rates of flowers and fruits. There were 33 individuals belonging to nine species.

Family	Species	Number of trees		
		Flowers	Fruits	Total
Euphorbiaceae	<i>Macaranga javanica</i> M.A.	0	3	3
Lauraceae	<i>Persea</i> sp.	1	1	1
Lauraceae.	<i>Litsea</i> spp.	6	6	6
Myrtaceae	<i>Eugenia cf. filiformis</i> Wall.	1	0	1
Melastomataceae	<i>Ptenandra cordata</i> (Korth.) Baill.	0	5	5
Malvaceae	<i>Commersonia bartramia</i> (L.) Merr.	2	2	2
Theaceae	<i>Eurya acuminata</i> DC.	7	3	7
Unidentified	Sp.1	5	0	5
Unidentified	Sp.2	3	3	3
Total		25	23	33

recorded either the numbers of these organs in traps or their oven-dry weights. These nine species belonged to six families and seven genera; there were two unidentified species (Table 1). Litter samples collected in 1997 in two fixed traps were sorted into flowers and fruits regardless of species, and we measured weights of these two categories. The total weight in these two traps was in direct proportion to the weights in the 25 traps deployed ($N = 21$, $R^2 = 0.784$).

Litter samples in the "branches" category were further sorted into three groups by their diameters (small, medium, and large branches of < 0.5 cm, 0.5–1.0 cm, and > 1.0 cm diameter, respectively) and their weights were measured.

Classification of seasonal patterns of leaf-fall rates by cluster analysis

Mass defoliations of 45 trees were identified by rates of leaf fall exceeding an average value plus one standard deviation for individuals over the whole 3-year study period. We assigned a score of 1 or 0 to each collection date on which mass defoliation occurred or not, and the 45 trees under observation were classified by cluster analysis using Ward's method (SPSS Ver. 15); the clustering procedure was based on the similarity of seasonal patterns in these scores because of serious consideration of the period without intensity of mass defoliation.

RESULTS

Synchrony of mass defoliation

Three clusters (A, B, C) were recognized at a value of 7

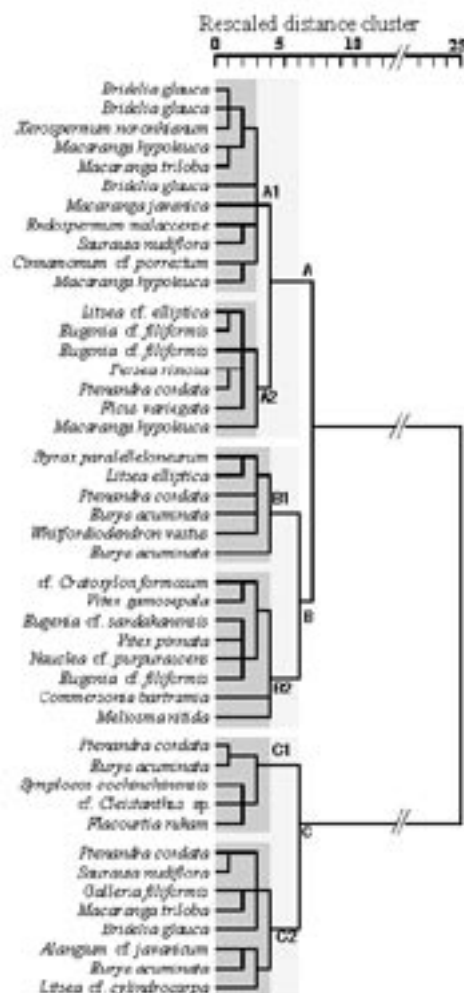


Fig. 2. Cluster analysis based on similarities in temporal mass defoliation among 45 trees. Phenological analysis was conducted on three clusters (A, B, C) that separated at a value of 7 on the coordinate scale and six clusters separating at values of 4–5.

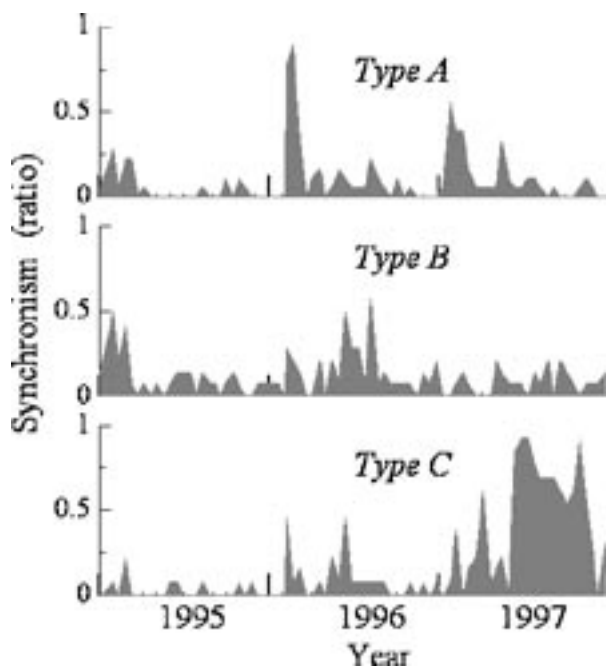


Fig. 3. Synchrony trends in mass defoliation of trees within three clusters (A, B, and C). Synchrony was measured for the ratio of the number of mass flowering trees to the total number of trees on each observation date.

on the coordinate scale of similarity; these three clusters were further classified into two clusters with values of 4–5 on the coordinate scale of similarity (Fig. 2). The clusters did not reflect taxonomy or ecological similarity. Figure 3 plots time trends in the synchrony of mass defoliation in three clusters, A, B, and C. Synchrony was measured for the ratio of the number of mass defoliating

trees to the total number of trees on each observation date. Cluster A was characterized by high synchrony, particularly in the first quarters of 1996 and 1997. Cluster C had high synchrony ratios in the latter half of 1997 under severe drought conditions. Two high ratios for cluster C (0.46 in June 1996 and 0.61 in March 1997) occurred at the ends of the droughts in each year (Fig. 1). Cluster B had no marked synchronies except for high ratios (each 0.5) in early 1995 and mid-1996. These synchronies corresponded in time with those of Cluster A in the first quarter of 1995 and that in Cluster C in June 1996.

We compared synchronies at lower levels in the cluster hierarchy with those at higher levels (Fig. 2). Clusters A2 and C1 had synchronies (which were characteristic of clusters A and C) that were more pronounced than those of A1 and C2. There were no clear differences between B1 and B2, however.

The *dbh* varied significantly ($P < 0.05$) among three clusters, but growth rates and stem hardness were not significantly different among these groups (Table 2). Lower in the cluster hierarchy (Fig. 2), *dbh* varied more among groups ($P = 0.093$ – 0.135 , *t*-test), than the other two parameters ($P = 0.273$ – 0.948). *dbh* values of clusters A2 and C1 were the largest and smallest among the six clusters, respectively. Hence, tree size could be a major correlate of seasonal patterns of mass defoliation at the community level.

Seasonal changes in fall rates of flowers and fruits

Fall rates of total reproductive organs followed no

Table 2. General traits of groups extracted by cluster analysis (Fig.2). Symbols Dbh_{94} , ΔD_{94-97} , and Hd are average *dbh* in 1994, *dbh* increment through 3 years, and stem hardness, respectively (Yoneda et al., 2009). Bold numerals indicate significant differences (*t*-test: $P < 0.05$) between values with the same superscript letters.

Cluster	Number of trees	Dbh_{94} (cm)	ΔD_{94-97} (cm period ⁻¹)	Hd (kg f cm ⁻¹)
A	18	23 ± 13^{**ab}	2.9 ± 3.1	33 ± 12
B	14	15 ± 10^{ab}	1.6 ± 1.9	43 ± 16
C	13	11 ± 10^{**a}	1.6 ± 1.9	38 ± 7.0
A1	11	19 ± 7.9	2.8 ± 3.8	30 ± 7.9
A2	7	28 ± 17	3.0 ± 1.9	38 ± 17
B1	6	20 ± 12	2.1 ± 2.9	40 ± 9.3
B2	8	11 ± 6.6	1.2 ± 0.8	45 ± 21
C1	5	5.1 ± 1.1	1.0 ± 0.8	40 ± 4.2
C2	8	14 ± 11	2.2 ± 2.5	38 ± 8.6

* : $P < 0.05$, ** : $P < 0.01$

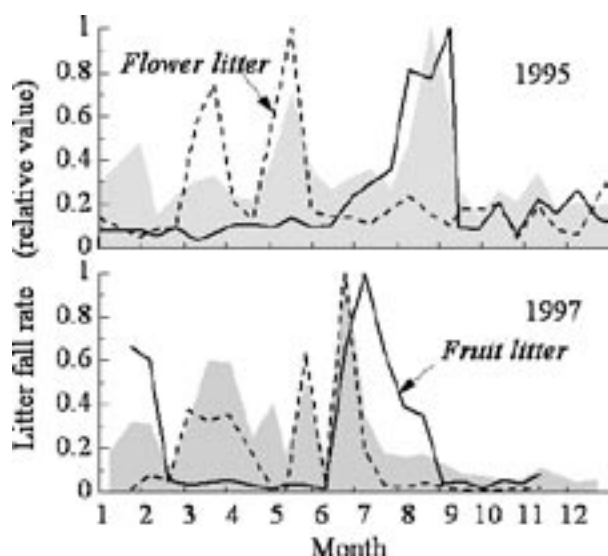


Fig. 4. Seasonal trends in the fall rates for flowers (broken lines) and fruits (solid lines). Rates in 1995 were computed across nine species. Rates in 1997 were for two fixed traps. Filled gray line plots show time trends for all reproductive organ litter collected in 25 traps.

particular seasonal trends through the 3-year study period (Fig. 1). However, there were high rates in the 11 months following August 1996, and increased shedding correlated with severe dry weather in mid-1996 and early 1997 (Yoneda et al. 2000).

When we examined seasonal changes in flower and fruit falls separately in sorted samples of nine species in 1995, we found two peaks in flower-fall rates and a single autumn peak in fruit fall (Fig. 4). The highest flower-fall peak occurred in May, when the absolute rate was more than six-fold higher than that for fruit fall. The fruit-fall rate peaked in August when it was double the flower-fall rate. These results suggest that flower fall was largely responsible for the first peak in the community rate of total reproductive organ shedding in May 1995 (Fig. 1), whereas fruits were responsible for the second peak in August.

Flower shedding rates were high during the first 6 months of 1997, reaching a maximum in June, and were double the rate of fruit fall during a period of mast fruiting (Fig. 4). Because of the high levels of seasonal synchrony in flower shedding among nine species and in total reproductive organ falls in the 25 traps, large variances in total reproductive organ data in 1997 can be attributed to flower falls (except for a small spike in January, which corresponded well with high rates of fruit fall; Fig. 4).

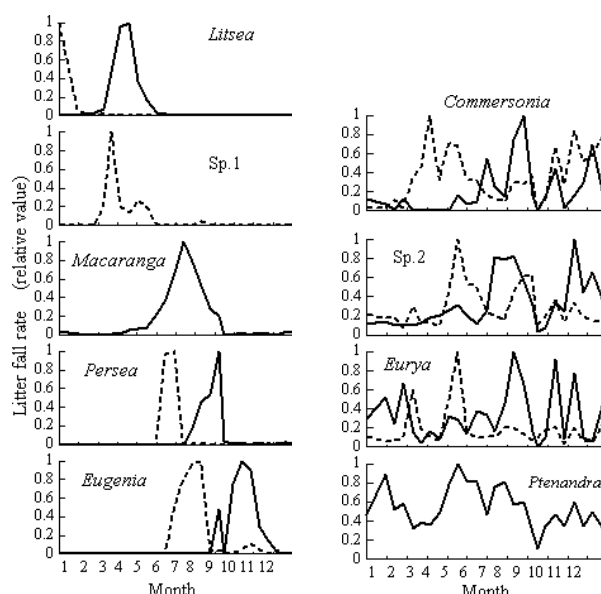


Fig. 5. Seasonal trends in the fall rates of flowers (broken lines) and fruits (solid lines) for nine species in 1995. Rates are relative values.

Based on the frequencies of mass flowering and fruiting in 1995, the nine species under observation may be classified into three groups. Five (*Litsea* sp., unidentified Sp. 1, *Macaranga javanica*, *Persea* sp., and *Eugenia cf. filiformis*) peaked once annually, and their flowering periods were different from one another (Fig. 5). Two species of *Commersonia bartramia* and unidentified Sp. 2 tended to peak twice a year, although they produced reproductive organs to a certain extent throughout the year. Two undergrowth species, *Eurya acuminata* and *Ptenandra cordata*, had constant fall rates throughout the year.

Seasonal changes in branch-fall rates.

Branch-fall rates were high in January and February during the first 2 years, and greatly decreased in 1997, in clear contrast to the concurrent increase in defoliation rates (Fig. 1). The proportions of small, medium, and large branches in total branch litter-fall rates were 54%, 16%, and 30%, respectively. High rates in the initial 2 months of 1995 were attributable to large and small branches, and a high rate in May 1995 resulted from a localized large branch fall into two neighboring traps. High fall rates in February of 1995 and 1996 occurred when storm winds exceeded 13 m s^{-1} .

We examined spatial and temporal variances of these fall rates using data for 25 traps in a $50 \text{ m} \times 50 \text{ m}$ area; 53 biweekly samples were collected during the first 2 years

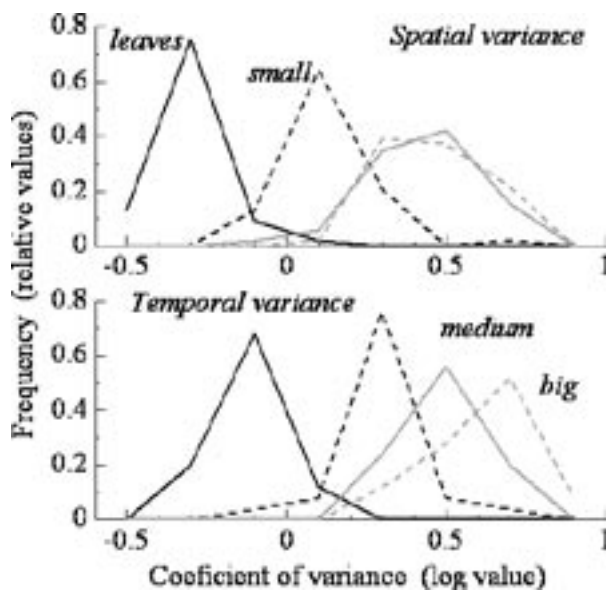


Fig. 6. Frequency distributions of coefficients of variance for leaf litter and branch-fall rates in space (50 m × 50 m) and time (3 years at 2-week intervals).

before the drought year of 1997. Coefficients of variance tended toward log-normal distribution patterns, and this was also the case for leaf litter CVs (Fig. 6). The ratios for their geometric means were 1.0 : 2.6 : 4.0 : 6.9 (leaf : small branch : medium branch : large branch) for temporal variances, and 1.0 : 2.7 : 5.4 : 5.6 for spatial variances, respectively.

Average fall rates of branch litter (y) into 25 traps at each collection time were positively correlated with those of leaf litter (x) over space and time; during the initial 2

years, the data fit an approximately straight line on log-log coordinates (Table 3). Branch-fall rates in 1997 were clearly lower than in the two preceding years in consideration of the correlation (Fig. 7). When we adopted the logarithmic regression model (i.e. $\log y = a \log x + b$) for the small branch-leaf relationship, the parameter a (slope of the regression line) was 1.439. Average fall rates in each trap and leaf-fall rates during the initial 2 years displayed similar relationships in their spatial correlations. The regression parameters a and b of the logarithmic regression models for small and medium branch litters were almost identical for both temporal and spatial correlations (Table 3)

DISCUSSION

Seasonal changes in long-term average rainfall between 1971 and 1997 were bimodal in the Padang region, with two dry seasons (January-February and June-August) and two rainy seasons; average monthly fall still exceeded 200 mm in these dry seasons (Fig. 8). The first dry season resulted from a dry monsoon from the Asian mainland; it was short but more severe (Gong and Ong, 1983; Schaik, 1986; Wakatsuki, 1986) than the second dry season, which resulted from an Australian desert monsoon (Hardjono, 1971). Strong winds $> 13 \text{ m s}^{-1}$ were frequent throughout these two dry seasons (Fig. 8), and storms in the first dry period often inflicted extensive damage in the Padang forest (Hardjono, 1971; Yoneda et al. 1998). The inter-annual event driven by the Indian Ocean Dipole Mode (IODM) caused severe dry weather,

Table 3. Correlations between leaf-fall rates and branch-fall rates over time and space. Symbols x , y , a , b , N , R^2 , and P are the fall rates of leaves (x , $\text{g m}^{-2} \text{ day}^{-1}$) and branches (y , $\text{g m}^{-2} \text{ day}^{-1}$), regression constants (a , b), the number of samples, the coefficient of determination, and significance probability, respectively.

Category of branch litter	$y = a x + b$					$\log y = a \log x + b$				
	N	a	b	R^2	P	N	a	b	R^2	P
temporal correlation										
total	53	0.805	-0.382	0.357	0.000	53	1.324	-0.523	0.301	0.000
small	53	0.435	-0.301	0.802	0.000	53	1.439	-0.844	0.535	0.000
medium	53	0.247	-0.193	0.776	0.000	52	1.879	-1.305	0.423	0.000
big	53	0.123	0.112	0.017	0.349	51	1.273	-1.281	0.105	0.020
spatial correlation										
total	25	0.657	-0.180	0.207	0.022	25	1.700	-0.467	0.399	0.000
small	25	0.276	-0.084	0.408	0.001	25	1.413	-0.765	0.548	0.000
medium	25	0.150	-0.060	0.261	0.009	25	1.821	-1.202	0.326	0.002
big	25	0.232	-0.037	0.038	0.349	25	2.922	-1.382	0.241	0.013

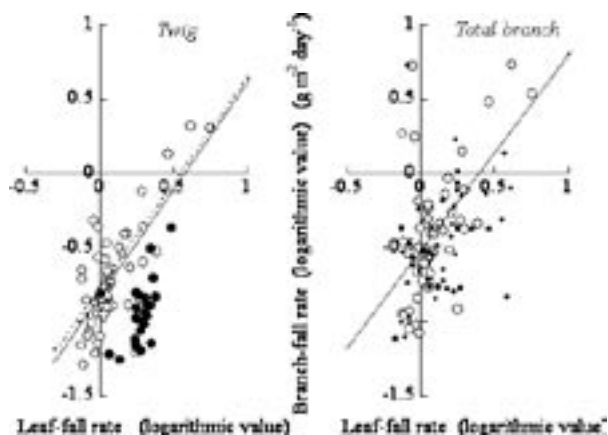


Fig. 7. Correlations between logarithmic values of leaf-fall and branch-fall rates ($\text{g m}^{-2} \text{day}^{-1}$) over time. Left panel: relationship between twig and leaf rates. Open and closed circles are values before and during 1997, respectively. Two straight lines with positive slopes are regressions from temporal (solid line) and spatial (broken line) correlations, respectively (Table 3). Right panel: relationship between total branch and leaf rates. Open and closed circles refer to our study site and Pasoh Forest Reserve in peninsular Malaysia (Ogawa, 1978), respectively. The straight line in the right panel is a regression plot of data collected in this study (temporal correlation, Table 3).

e.g., in 1994 and 1997 (Hamada et al. 2008); the effects of the El Niño-Southern Oscillation were reduced in this west coast region in the lee of the Barisan mountains (Wick and Schaik, 2000). These severe drought weather conditions have tended to increase in frequency since the middle of the 1990s (Yoneda et al. 2006). Such large-scale climatic phenomena very likely affected the phenological behavior of individual trees and the communities of which they are part.

Major community-level leaf fall occurred in the first dry season, followed by a minor fall in the second. Similar phenomena have been observed in the Asian aseasonal tropics (Corlett and Lafrankie, 1998) and also in the neotropics (Frankie et al. 1974). The forest we studied is characterized by relatively high fall rates with low variances across seasons, except during the initial 2 months of the year when leaf fall accounted for one-third of the annual total (1995 and 1996 under normal weather conditions).

Cluster analysis suggested that the initial high rates of leaf fall were attributable to larger trees, irrespective of their growth rates and stem hardnesses (a parameter of the tree guild; Yoneda et al. (2009)). The high synchrony among larger trees likely resulted from their elevated

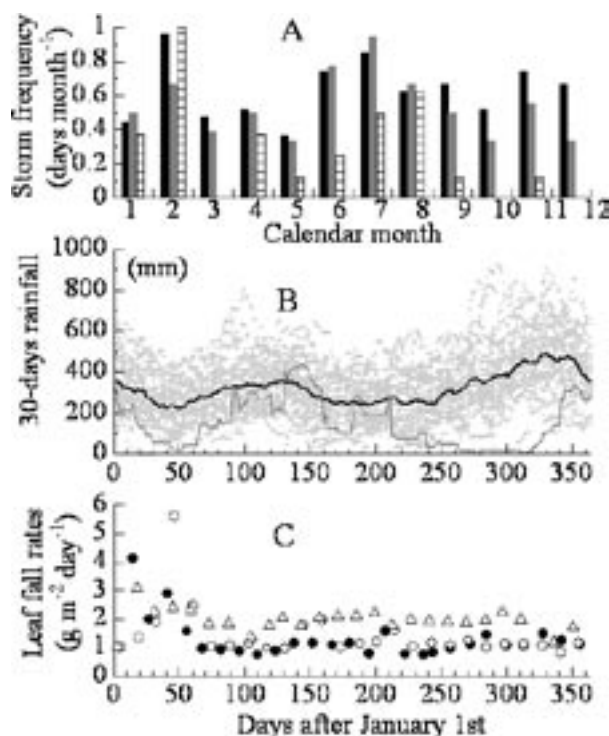


Fig. 8. A: seasonal changes in frequency of storms with winds $> 13 \text{ m s}^{-1}$ in Padang, West Sumatra. Black, gray, and horizontally striped bars show the average frequencies in the periods 1971–1997, 1980–1997, and 1990–1997, respectively. B: seasonal changes of cumulative rainfall in the preceding 30 days over 28 years (1971–1997). Thick and fine lines are averages of the entire period and 1997, respectively. C: trends in leaf-fall rates in 1995 (open circles), 1996 (closed circles), and 1997 (triangles).

susceptibility to drought, due to an active metabolism required to support a large leaf biomass (Yoneda et al. 2000) and high leaf turnover (Osada et al. 2001); however, Williams (1997) stressed an endogenous explanation rather than physiological responses to external triggers. New leaf flush in the overstory occurred almost concurrently with leaf fall, as in other wet tropical forests (Frankie et al. 1974; Schaik, 1986; Osada et al. 2001). In 1997, trees continued defoliating at high rates in the latter half of the year with no new leaf flushing, and many large trees were extensively defoliated by the end of drought in November 1997 (Yoneda et al. 2000).

Understory trees may have endogenous control of their phenologies (Wong, 1983) because of their low drought susceptibility; high synchronized leaf fall occurred only under the most severe dry conditions, such as the second dry seasons in 1996 and 1997. The diverse phenological behaviors of understory trees may

explain low variances in community-level seasonal leaf-fall patterns during normal weather.

Fall rates of small branch litter (< 0.5 cm diameter) mass and leaf litter mass had linear relationships (temporally and spatially) on log–log coordinate plots (Fig. 7). The slope of the regression line was close to 1.5 (3/2). If branch weight is proportional to the third power of its diameter, the relationship shows that the leaf-fall rate is proportional to the second power of the maximum diameter of a fallen branch. This relationship fits the pipe-model theory (Shinozaki et al. 1964a, 1964b), which shows that forest trees drop their small branches in proportion to the amount of fallen leaves. The average turnover time of small branches (estimated from the ratio of the frequency distributions of diameters of newly fallen branches to living branches) is 5 years (Yoneda et al. 1982). When the canopy structure is under dynamic equilibrium conditions, 20% ($1/5 \times 100$) of small branches fall each year. Branch-fall rates in the drought year were apparently low in relation to leaf-fall rates. The difference suggests influences other than drought stress. Strong wind in the dry seasons might be one of the proximate factors (Fig. 8-A). When we examined a relationship between fall rates of leaves and one of total branches in a lowland tropical forest within the Pasoh Forest Reserve (peninsular Malaysia) (Ogawa, 1978), we found no significant difference from that of the present study site (Fig. 7, ANOVA, $P = 0.392$). This suggests that a similar turnover mechanism operates in Pasoh.

Variances in the fall rates of large branches were larger than those of small branches, both temporally and spatially. Large branches were responsible for high rates in the initial few months in 1995. Protracted severe dry weather in the preceding year (1994) may have been a major influence. If this were the case, high fall rates would be predicted for 1998, following severe dry weather in 1997. Tree mortality in this region has increased since the mid-1990s (Yoneda et al. 2006), and we expect these internal changes in stand structure to have large effects on the multi-species forest community.

Variances in the community-level fall rates of reproductive organs were larger than those for leaves, both seasonally and annually (Fig. 1). In 1995, there was one peak in May (flowers) and another in August (fruits). The following year had one conspicuous peak in September following a short spell of severe dry weather in May. The major reproductive component in 1996 could be estimated to be flowers, followed by a peak of fruit fall in the following December–January (Fig. 4). In the dry year of 1997, there was a type of mast flowering from

March to July, but there was no subsequent mast fruiting under the severe dry weather that lasted until November. These phenomena suggest the high susceptibility of reproductive organs to drought.

The seasonal patterns observed in 1995 under normal weather conditions are typical of Asian aseasonal tropics, with a single peak in flowering after the initial dry season and a single peak in fruiting 3–6 months later (Medway, 1972; van Schaik, 1986; Corlett and Lanfrankii, 1998). Flowering patterns in 1996 and 1997 indicate that drought was probably a reproductive cue. Why does the first dry season in a normal-weather year (rather than the second) trigger the sequence of defoliation triggering the flushing of new leaves, which leads to flowering? Van Schaik's (1986) hypothesis considers, and suggests that (1) elevated pollination efficiency through the synchrony of flowering and pollinator activities, and (2) survival ratios of seedlings through successive seasonal changes, are of greatest importance in the expression of plant phenology in the wet tropics.

Frankie et al. (1974) classified flowering into two patterns, viz. "seasonal flowering" with blooms in one season and "extended flowering" over two or more consecutive seasons. Five species of our study bloomed once a year and are "seasonal flowering" species (*sensu* Frankie et al. 1974), and two species with flowers throughout the year are "extended flowering" species. Many species in secondary forests or forest fringe habitats are in the continuous-flowering group (Whitmore, 1988). *Eurya acuminata* and *Ptenandra cordata* were dominant understory species in the stand we studied. Their continuous seed production and high sprouting ability would be advantageous in sites suffering frequent disturbance. *Commersonia bartramia* is an early successional species that bloomed twice a year, as did Sp. 2, although it was classified as a continuous bloomer by Whitmore (1988). Further observations are necessary to determine the flowering types of these two species, and, indeed, to determine flowering traits of the forest as a whole.

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