

Phenology of seven indigenous tree species in a dry Afromontane forest, southern Ethiopia

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Abstract: The phenology of seven indigenous tree species was investigated in a dry Afromontane forest of Ethiopia over two years. About 210 mature trees were monitored for leaf fall, leaf flush, flowering and fruiting. The different phenophase events were correlated with climate variables and circular statistics was employed to test for seasonality. Leaf fall and leaf flush peaked during the long dry season. Leaf fall significantly correlated with mean monthly temperatures. Flowering was predominantly annual and seasonal. Most species flowered during the dry season between November and May. Flowering was temporally discordant among the species, which is interpreted as a kind of adaptation avoiding interspecific overlap and thus competition for pollinators. Unlike flowering, fruiting was less seasonal and trees bore fruits over extended periods of the year. Following flowering, fruiting peaked later in the dry season or the beginning of the rainy season. Both flowering and fruiting phenology of the study species were strongly influenced by temperature and rainfall. However, leaf phenology was influenced by temperature.

Resumen: A lo largo de dos años se investigó la fenología de siete especies arbóreas nativas en un bosque seco afromontano de Etiopía. La caída y la producción de hojas, la floración y la fructificación fueron monitoreadas en alrededor de 210 árboles maduros. Los diferentes eventos de las fenofases fueron correlacionadas con variables climáticas y se utilizó estadística circular para poner a prueba la estacionalidad. Los picos de caída y producción de hojas se presentaron durante la larga estación seca. La caída de las hojas se correlacionó significativamente con las temperaturas mensuales promedio. La floración fue predominantemente anual y estacional. La mayoría de las especies florecieron durante la temporada seca, entre noviembre y mayo. La floración fue discordante en el tiempo entre las especies, lo cual se interpreta como un tipo de adaptación que evita el solapamiento interespecífico y por lo tanto la competencia por polinizadores. A diferencia de la floración, la fructificación fue menos estacional y los árboles tuvieron frutos durante periodos extensos del año. Después de la floración, la fructificación tuvo un pico más tarde, en la época seca o al principio de la temporada de lluvias. Tanto la fenología floral como la fructificación de las especies de estudio estuvieron influenciadas fuertemente por la temperatura y la precipitación. Sin embargo, la fenología foliar estuvo influenciada por la temperatura.

Resumo: Durante dois anos investigou-se a fenologia de sete espécies arbóreas indígenas numa floresta seca afromontana da Etiópia. Foram monitorizadas cerca de 210 árvores maduras

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quanto à queda de folhagem, rebentação da folha, floração e frutificação. As diferentes fenofases foram correlacionadas com as variáveis climáticas e empregou-se estatística circular para testar a sazonalidade. Os picos de queda de folhagem e de rebentação das folhas verificaram-se durante a longa estação seca. A queda de folhagem encontrou-se significativamente correlacionada com as temperaturas médias mensais. A floração era predominantemente anual e sazonal. A maioria das espécies floresceu durante a estação seca entre Novembro e Maio. Verificou-se, no entanto, que a floração foi temporalmente discordante entre espécies, o que foi interpretado como uma espécie de adaptação que evita a sobreposição interespecífica e, assim, a competição pelos polinizadores. Contrariamente à floração, a frutificação foi menos sazonal e as árvores tiveram frutos durante longos períodos do ano. No seguimento da floração, a frutificação apresentou um pico no fim da estação seca ou início da estação das chuvas. Tanto a floração como a frutificação das espécies estudadas apresentaram-se fortemente influenciadas pela temperatura e a precipitação. Contudo, a fenologia foliar foi influenciada pela temperatura.

Key words: Flowering, fruiting, leaf fall and flush, seasonality, tree phenology, tropical dry forest.

Introduction

Plant phenologies are the results of interactions of biotic and abiotic factors. Over evolutionary time and through natural selection, the biotic and abiotic factors have entrained rhythmicity in plant life that results in an appropriate timing of flowering, fruiting and leaf flushing and efficient growth and reproduction (Grime 1979; van Schaik *et al.* 1993). Knowledge of phenological patterns is basic to the understanding of biological processes of tropical trees, of the interactions with other organisms and of the functioning of the ecosystems.

Tropical trees exhibit substantial seasonality in flowering and fruiting events (van Schaik *et al.* 1993). They often show temporal variations in phenological patterns that are associated with seasonality in climate or abundance or pressure of biotic factors (Frankie *et al.* 1974; Rathcke & Lacey 1985; Sakai 2001). According to Lobo *et al.* (2003) phenological events are affected by proximate or ultimate causes. Climatic variables such as seasonal variations in rainfall (Opler *et al.* 1976), temperature (Ashton *et al.* 1988), and irradiance (van Schaik *et al.* 1993) have been identified as proximate causes triggering phenological events in tropical plants.

In forests with a marked dry season, flowering and leaf flushing may be more sensitive to seasonal rainfall, changes in water availability and soil moisture (Borchert 1984; van Schaik *et al.* 1993). High water availability may also enhance

fleshy fruit production (Rathcke & Lacey 1985) and seed germination (Justiniano & Fredericksen 2000; van Schaik *et al.* 1993). In strongly seasonal dry forests leaf flushing peaks during late dry season and ends in the rainy season (Anderson *et al.* 2005; Justiniano & Fredericksen 2000; McLaren & McDonald 2005). Apparently, the majority of tropical plants flower regularly during peaks in temperature and their fruits ripen towards the end of the dry season or yet in the rainy season. These features may result in a better survival of the seedlings (Frankie *et al.* 1974; van Schaik *et al.* 1993).

Although scientific knowledge on the phenology of tropical trees and factors influencing them has been accumulating globally, such information from the montane forests in Ethiopia is critically lacking. Such information is basic to the understanding of biological processes and functioning of the forest ecosystem. The timing and duration of flowering and fruiting for instance, is crucial in understanding forest regeneration dynamics as the pronounced seasonality affects the reproductive output and performances such as seed production, germination, survival, and seedling growth (Augspurger 1981). This paper presents the first detailed studies on phenology of leaf, flowering and fruiting of seven indigenous tree species of a dry tropical montane forest in Ethiopia. The specific questions addressed in this study include (1) what are the timing, duration and frequency of leafing, flowering and fruiting of selected tree species at the study site and

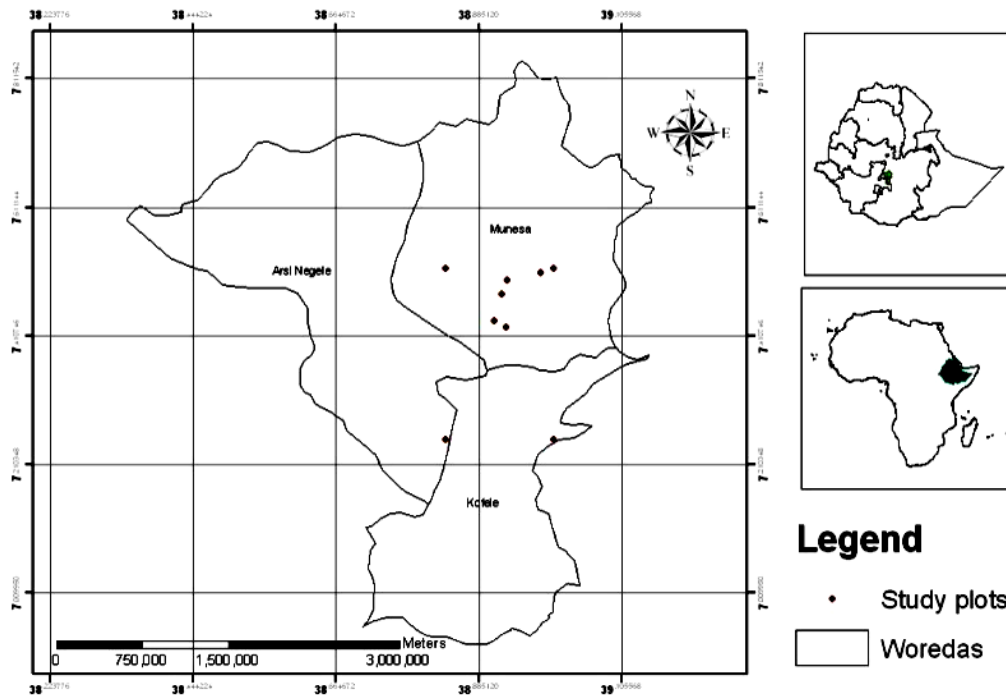


Fig. 1. Map of Ethiopia showing the study site, Munessa-Shashemene Forest.

(2) which environmental factors (temperature and rainfall) have the greatest influence for triggering these phenological events. Since climatic variables are highly correlated, the influence of these variables on plant phenology was carefully examined and the interplay between the climate effect and plant response are discussed.

Materials and methods

Study site

The study was conducted in Munessa-Shashemene Forest (MSF), southern Ethiopia, located at 7°13' N and 38° 37' E (Fig. 1). It is a dry montane forest with a total area of 21,000 hectares and covers an altitudinal range between 2100 and 2700 m. The mean annual temperature is 15 °C with daily fluctuations between 8 °C to 24 °C (Fig. 2). The annual rainfall varies between 900 and 1500 mm in a bimodal pattern where the short rainy season is from March to May and the long rainy season from July to September. The major dry season spans from October - February and the small dry season from May - June. However, the short rainy season is very unreliable. The soils are Mollic Nitisols developed from volcanic lavas, ashes, and pumices (FAO 1986).

Study species

Seven indigenous tree species, namely, *Celtis africana* Burm.f., *Croton macrostachyus* Hochst., *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb., *Polyscias fulva* (Hiern) Harms, *Pouteria adolfi-friederici* (Engl.) A. Meeuse (synonym: *Aningeria adolfi-friederici* (Engl.) Robyns & Gilbert), *Prunus africana* (Hook.f.) Kalkman, and *Syzygium guineense* (Willd.) DC. having significant ecological and economic importance were selected for the study. These species are widely distributed in tropical Africa and their ecology and biogeography has been discussed elsewhere (Getachew Tesfaye *et al.* 2002). *C. macrostachyus*, *C. africana* and *P. fulva* are pioneer species whose seeds germinate and establish under canopy gaps soon after disturbance (Demel Teketay 1997; Getachew Tesfaye *et al.* 2002). *P. falcatus*, *P. africana*, *P. adolfi-friederici* and *S. guineense* are shade tolerant species whose seeds germinate and establish in shaded understorey of forests (Demel Teketay 1997; Getachew Tesfaye *et al.* 2002). These seven species constitute 95 % of the total tree basal cover and 77 % of the Importance Value Index of trees at the study site (Getachew Tesfaye *et al.* 2010).

There is limited information on the biology of

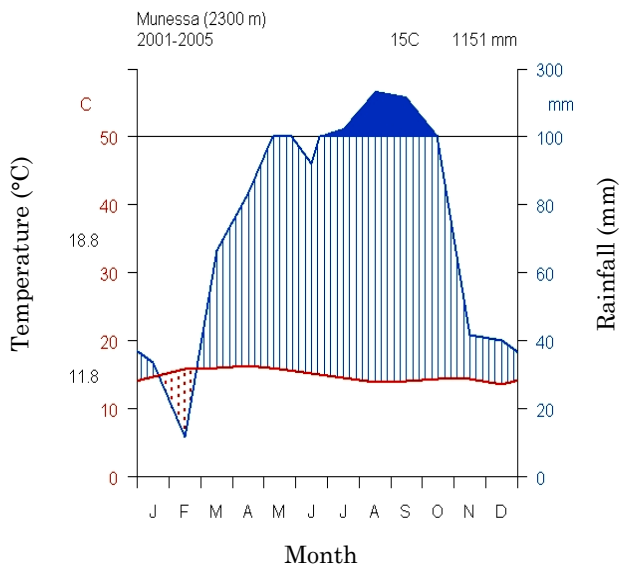


Fig. 2. Climate diagram of the Munessa-Shashemene Forest for the period from May 2001 to May 2007.

these tree species in particular on fruit/seed dispersal agents and pollinators. A study on the seed dispersal agents at the Munessa-Shashemene Forest had shown that at least more than 30 species of dispersal animals were identified in 2005 and 2006 (Getachew Tesfaye 2008). The animals were seen picking and feeding on the fruits/seeds of the above mentioned tree species. These include both birds and mammals. Some of the major animal dispersers recorded includes, among others, Abyssinian Black Colobus and White Colobus, Common Babbon, Vervet Monkey, Olive Thrush, White-cheeked Turaco, Red-winged Starling, White thighed Hornbill and Yellow-fronted Parrot (Getachew Tesfaye 2008). Studies from other tropical forests have shown that the major pollinators in such ecosystems may include beetles, wasps, butterflies, moths, humming birds, bats, and bees (Momose *et al.* 1998).

Tree phenology

A total of 210 mature trees (30 individuals per species with their DBH ranging between 30 - 105 cm) were selected, their diameter at breast height measured, marked and their position recorded using GPS at three different sites within the forest. Distances between the sites ranged from 2 - 11 km and 10 individuals of a species were represented in each site. Phenology of the trees, i.e. leaf flushing (only for *C. africana* and *C.*

macrostachyus), flowering and fruiting, was recorded every month from June 2005 to May 2007. In each census, reproductive events in each tree crown was observed using binoculars. Dropping flowers and fruits from the trees were additionally used as indicators. Intensity of flowering (amount of flower buds and open flowers) and fruiting (amount of unripe and ripe fruits) in each tree crown was assigned to four different classes: 0 (0 %), 1 (1 - 25 %), 2 (26 - 50 %), 3 (51 - 75 %), and 4 (> 75 %), with the percentage values referring to the proportions of each phenophase in the crown. For leaf phenology, only the two deciduous species, namely *C. africana* and *C. macrostachyus*, were investigated and recorded as leaf flush, senescent or leafless with similar classes as above. Temperature and rainfall of the study site were recorded throughout the study period (see also Fritzsche *et al.* 2006).

Data analyses

Phenological event analyses were based on the following four parameters: onset, mean date, peak and duration of leaf flushing, flowering and fruiting. Circular statistics was used to calculate the mean date of flowering, fruiting, leaflessness and leaf flushing (Zar 1996). The proportion of individuals (of a species) in each phenophase across the months of the year was treated as a circular frequency distribution with data grouped at 30° intervals (30° = 1 month) with January 1st as the starting point and December 1st (330° = 12 months) as the month closing the circle. The two circular statistics computed were (1) the mean angle (α) which is translated into days representing the mean date of the phenophase and (2) r , which is a measure of the intensity of concentration around the mean. Kolmogorov-Smirnov Z -test was used to determine the significance of seasonality in the distribution of the phenophases. The temporal variations in flowering and fruiting patterns were analyzed with one-way ANOVA using the general linear model (GLM) procedure. Post hoc test for significance between mean dates were calculated using paired samples t -test.

Since phenological data are time-dependent, time series analyses was employed to evaluate autocorrelation within phenophases and cross-correlations of climate factors and phenophases and correlation between different phenophases. To determine whether flowering patterns among species were overlapping in time or not, Pearson's correlation coefficients were used. For each pair of

Table 1. Mean date of leaf fall and leaf flush (Julian calendar followed by angular mean date), and peak leaf fall and leaf flush of *Croton macrostachyus* and *Celtis africana* in the Munessa-Shashemene Forest.

Period	<i>Celtis africana</i>	<i>Croton macrostachyus</i>
Mean date of leaf fall	February 6, 36.47°	February 9, 40.05°
Mean date of leaf flush	March 21, 81°	March 24, 84°
Date of peak leaf fall	1 March	1 March
Date of peak leaf flush	1 April	15 April

species the correlation coefficient between the numbers of flowering events in each month over the two-years period was calculated. High coefficient would indicate similarity in the timing of flowering between the species, low coefficient indices no association and negative correlation mean no overlapping flowering pattern.

Linear and multiple regression analyses were used to explore the potential association between the flowering and fruiting events for each species and the climatic variables (temperature and rainfall) with time lags up to 12 months. The time lag giving the greatest and significant correlation coefficient indicated the approximate interval (months) between climate effect and plant response. Cross correlation coefficient between temperature and rainfall at the study site was negative and non significant. Flowering and fruiting patterns were classified following Newstrom *et al.* (1994). All statistical tests were carried out using MINITAB 15.0 and STATISTICA 6.0. for Windows.

Results

Phenology of foliage

Individuals of the two deciduous species *C. africana* and *C. macrostachyus* may shed their

leaves annually. Both leaf flush and leaf fall were significantly seasonal ($P < 0.001$, $N = 12$ for both species). Leaf fall ranges between 26 and 86 % for *Celtis* and, 23 and 70 % for *Croton*. Mean leaf fall dates of *C. macrostachyus* and *C. africana* were non-significantly ($P = 0.19$) different, which also holds for leaf flush ($P = 0.72$) (Table 1). Moreover, leaflessness between *C. africana* and *C. macrostachyus* were significantly correlated ($r = 0.94$; $P < 0.001$).

Leaf fall of both *C. africana* and *C. macrostachyus* began in January/February and continued until March/April. Peak leaf fall was in March towards the end of the long dry season (Table 1). The period of leaflessness was generally three to four months. Leaf fall and mean monthly temperature were significantly correlated for both species (*C. macrostachyus*: $R^2 = 0.31$, $P = 0.004$; *C. africana*: $R^2 = 0.25$, $P = 0.01$). Leaf flushing commenced in March except for *C. africana* where it started in April. Leaf flushing peaked in April (Table 1) coinciding with the end of the long dry season when the temperature was still high and the small rains started. Leaf flushing was not significantly correlated with monthly rainfall ($R^2 = 0.007$, $P = 0.69$ for *C. africana*; and $R^2 = 0.19$, $P = 0.85$ for *C. macrostachyus*). Leaf flushing generally lasted for less than three months.

Flowering

Most species flowered twice while *P. fulva* exhibited four flowering peaks during the two-years study period. They exhibited annual flowering except *P. fulva* that showed continuous flowering (Fig. 3). In most species flowering varied significantly between months of the year (Table 2). Significant variations in mean dates of flowering were also observed for most species (Table 3). Thus seasonality in flowering pattern was exhibited by five species *C. macrostachyus*,

Table 2. Results of one-way ANOVA in which month ($n = 12$) was the fixed factor, year ($n = 2$) as random factor and tree flowering or fruiting as the dependent variable. F values and P values are shown.

Species	Flowering		Fruiting	
	F value	P value	F value	P value
<i>Podocarpus falcatus</i>	17.90	0.000	1.61	0.22
<i>Celtis africana</i>	1.18	0.39	1.92	0.14
<i>Croton macrostachyus</i>	4.77	0.008	2.67	0.05
<i>Pouteria adolfi-friederici</i>	5.42	0.005	0.80	0.63
<i>Polyscias fulva</i>	0.50	0.86	0.33	0.96
<i>Prunus africana</i>	6.87	0.002	3.08	0.03
<i>Syzygium guineense</i>	3.35	0.028	14.68	0.00

Table 3. Mean date of flowering and fruiting (Julian calendar followed by mean angular date \pm S.E.), concentration around the mean (r), and Z test for seasonality, in flowering and fruiting patterns of seven tree species in the Munessa-Shashemene Forest.

Species	Mean date of flowering		Mean date of fruiting	
	Mean angular date(a)	Z test P value and r	Mean angular date (a)	Z test P value and r
<i>P. falcatus</i>	December 26, 356.6 ⁰ \pm 2.2 F	$P < 0.001$, $r = 0.9$	May 3, 155.36 ⁰ \pm 5.5 E	$P = 0.329$
<i>C. africana</i>	August 1, 245.0 ⁰ \pm 4.0 B	$P = 0.001$, $r = 0.94$	February 6, 36.62 ⁰ \pm 2.9 B	$P = 0.393$
<i>C. macrostachyus</i>	May 27, 178.14 ⁰ \pm 3.9 C	$P = 0.002$, $r = 0.48$	February 9, 39.63 ⁰ \pm 3.7 BC	$P = 0.053$
<i>P. adolfi-friederici</i>	May 12, 162.51 ⁰ \pm 2.2 A	$P < 0.001$, $r = 0.75$	October 1, 301.4 ⁰ \pm 3.8 A	$P = 0.718$
<i>P. africana</i>	October 6, 306.29 ⁰ \pm 1.9 E	$P < 0.001$, $r = 0.9$	February 7, 67.71 ⁰ \pm 5.9 D	$P = 0.005$, $r = 0.22$
<i>S. guineense</i>	February 6, 66.0 ⁰ \pm 2.9D	$P = 0.139$, $r = 0.45$	April 15, 137.5 ⁰ \pm 3.1 F	$P = 0.002$, $r = 0.001$
<i>P. fulva</i>	May 18, 168.7 ⁰ \pm 6.8 AC	$P = 0.893$	May 12, 162.3 ⁰ \pm 7.1 EG	$P = 0.203$
(population level)				
individual cycle 2			March 2, 92.53 ⁰ \pm 4.9	
individual cycle 1			October 3, 303.65 ⁰ \pm 3.3	

Different letters across a column show significant mean variation ($P < 0.001$).

P. falcatus, *P. africana*, *P. adolfi-friederici* and *S. guineense*.

In most species flowering lasted for three to four months with unimodal pattern except *P. fulva* that exhibited bimodal and continuous flowering with a brief break throughout the year (Fig. 3). The onset and peak of flowering periods coincided with the long dry season for most species. However, for *C. africana*, the onset and peak of flowering coincided with the rainy season (Fig. 3).

Flowering periods between the years were significantly correlated for *P. adolfi-friederici* ($r = 0.73$, $P = 0.002$), *P. africana* ($r = 0.75$, $P = 0.005$) and *C. macrostachyus* ($r = 0.72$, $P = 0.007$), marginally significant for *S. guineense* ($r = 0.54$, $P = 0.05$) and non-significant for *C. africana* and *P. fulva*. Duration of the flowering periods varied among the species ranging from two to seven months. Relatively shorter flowering period was observed for *C. africana*, *P. adolfi-friederici* and *P. africana*.

The timing of flowering among species was not significantly correlated for most species and thus no overlapping in flowering period (Table 4). However, significant positive correlation and thus overlapping in flowering time was observed between *P. falcatus* and *P. africana*; and *C. macrostachyus* and *P. adolfi-friederici* (Table 4).

Flowering significantly preceded fruiting by four months for *P. adolfi-friederici* ($r = 0.45$, $P = 0.04$), *P. fulva* ($r = 0.57$, $P = 0.004$) and *C. africana* ($r = 0.47$, $P = 0.01$), by three months for *P. africana*

($r = 0.52$, $P < 0.01$) and *S. guineense* ($r = 0.40$, $P = 0.03$) and by two months for *C. macrostachyus* ($r = 0.69$, $P < 0.01$). These time-spans were apparently caused by species-specific traits that, however, are influenced by climate. All species showed significant coefficients of determination in regression analysis trying to predict the number of flowering event from the abiotic factors. Flowering period was significantly correlated with mean monthly temperature with different time lag for *P. falcatus*, *C. africana*, *C. macrostachyus*, and *P. adolfi-friederici* (Table 5). Moreover, flowering was significantly correlated with monthly rainfall at different time lag for *P. fulva*, *P. africana* and *S. guineense* (Table 5). The percent explained coefficients of variations were 19.9 - 39.8 for temperature and 31.8 - 52.8 for rainfall (Table 5).

Fruiting

One explicit fruiting period per year was recorded for *P. africana* and *S. guineense*, while fruits were seen year round or extended over several months in the case of *P. adolfi-friederici*, *C. macrostachyus*, *C. africana*, and *P. falcatus*. *P. fulva* was an exception again which exhibited two fruiting events per year (Fig. 4).

In most species fruiting did not significantly vary between the months of the year. Thus fruiting was non-seasonal in *C. africana*, *C. macrostachyus*, *P. falcatus*, *P. adolfi-friederici* and *P. fulva* but, seasonal in *P. africana* and *S. guineense*.

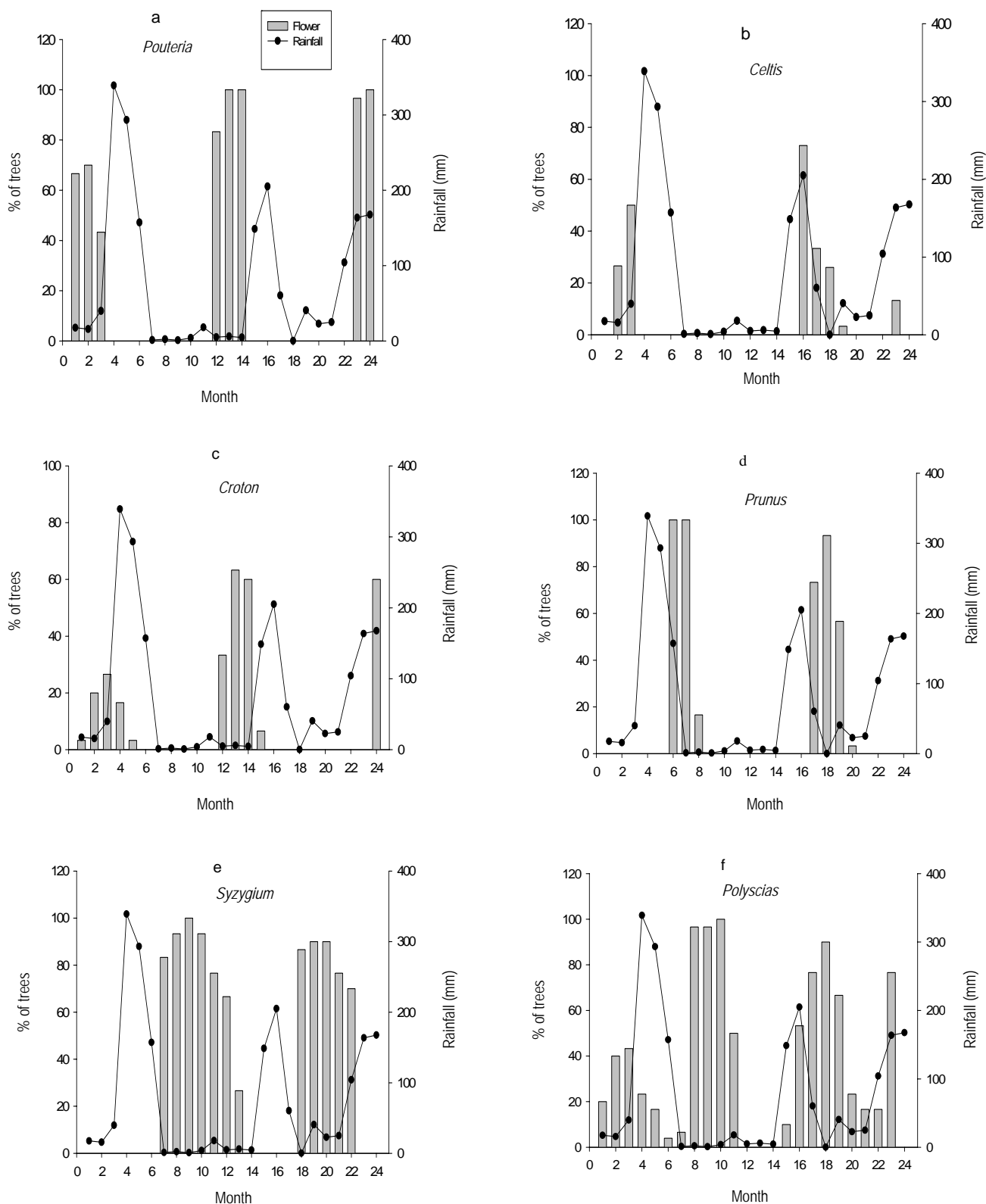


Fig. 3. a-f. Percentage of flowering individuals of six tree species from June 2005 (month 1) to May 2007 (month 24) in the Munessa-Shashemene Forest (bars refer to phenology while the line graph indicates monthly total rainfall).

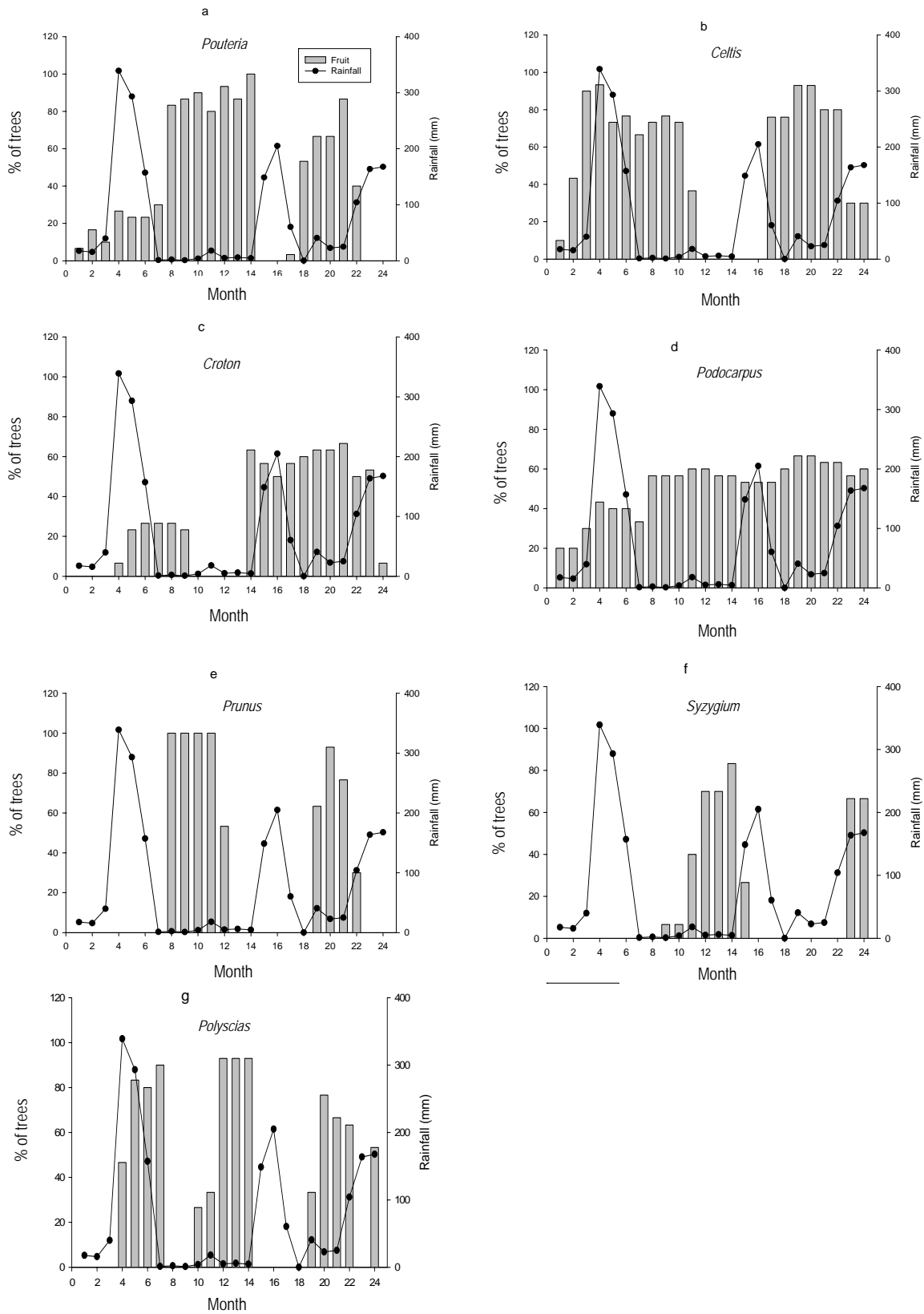


Fig. 4. a-g. Percentage of fruiting individuals of seven tree species from June 2005 (month 1) to May 2007 (month 24) in the Munessa-Shashemene Forest (bars refer to phenology while the line graph indicates monthly total rainfall).

Table 4. Results of correlation analysis of flowering pattern between the seven tree species at Munessa-Shashemene forest. Correlation coefficient (*R*) and the *P* value are shown. Significant correlations are highlighted.

Species	<i>C. africana</i>		<i>C. macrostachyus</i>		<i>P. adolfi-friederici</i>		<i>P. fulva</i>		<i>P. africana</i>		<i>S. guineense</i>	
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>
	<i>P. falcatus</i>	-0.05	0.78	-0.17	0.42	-0.19	0.35	-0.11	0.58	0.66	0.00	0.25
<i>C. africana</i>			-0.09	0.65	-0.04	0.82	0.29	0.16	0.05	0.79	-0.34	0.10
<i>C. macrostachyus</i>					0.79	0.00	-0.51	0.01	-0.31	0.13	-0.37	0.07
<i>P. adolfi-friederici</i>							-0.36	0.08	-0.35	0.08	-0.44	0.03
<i>P. fulva</i>									0.11	0.58	0.40	0.05
<i>P. africana</i>											0.16	0.44

Table 5. Results of linear and multiple regression analysis between the phenophase events (flowering and fruiting) of each species and the climatic variables (temperature and rainfall). The regression equation, explained variation (% *R*²), *P* value and lag time (month) are shown.

Species	Flowering				Fruiting			
	Regression equation with the predictor variable	% <i>R</i> ²	<i>P</i>	Time lag	Regression equation with the predictor variable	% <i>R</i> ²	<i>P</i>	
<i>P. falcatus</i>	Y = 53.3 - 3.35 (Temperature)	19.9	0.029	0	Y = 61.1 - 0.028 (Rainfall)	60.0	0.001	
<i>C. africana</i>	Y = 111 - 6.77 (Temperature)	35.4	0.03	1	Y = -271 + 21.2 (Temperature)	47.0	0.003	
<i>C. macrostachyus</i>	Y = 3379 - 22.4 (Temperature)	39.5	0.003	2	Y = 14.4 + 0.204 (Rainfall)	46.7	0.005	
<i>P. adolfi-friederici</i>	Y = -301 + 21.8 (Temperature)	39.8	0.02	2	Y = 61.1 - 0.214 (Rainfall)	36.7	0.003	
<i>P. fulva</i>	Y = 25.6 + 0.0209 (Rainfall)	31.8	0.01	6	Y = 2.18 + 0.15 (Rainfall)	59.7	0.001	
<i>P. africana</i>	Y = -0.59 + 0.59 (Rainfall)	52.8	0.00	2	Y = -355 + 26.0 (Temperature)	60.0	0.001	
<i>S. guineense</i>	Y = 58.8 - 0.24 (Rainfall)	40.5	0.003	0	Y = 15.1 + 0.316 (Rainfall)	56.8	0.000	

Most species exhibited extended fruiting periods lasting up to six months of the year. However, in *P. falcatus* cone production occurred year round with at least 20 % of the population with cones at a given time. In most species, peak fruiting period was towards the end of the dry season and/or the beginning of the long rainy season.

Fruiting was significantly correlated with mean monthly temperature for *C. africana* and *P. africana* (Table 5). On the other hand, fruiting also correlated significantly with monthly rainfall for *P. falcatus*, *C. macrostachyus*, *P. adolfi-friederici*, *P. fulva* and *S. guineense* (Table 5). For all species, the regression analyses model explained > 36.7 % of the variation in the number of fruiting events (Table 5).

Discussion

Leaf phenology of deciduous species

Trees of the Munessa-Shashemene Forest belong to two life-forms: evergreen and deciduous. Such a mix of evergreen and deciduous species is

also known from other tropical forests, for example, the Malagasy littoral forest. The latter though dominated by evergreen tree species, had few deciduous species with annual patterns and marked seasonality in their leaf phenology (Bollen & Giuseppe 2005). In Munessa-Shashemene Forest leaf fall and leaf flush of (facultative) deciduous species are annual and strictly seasonal, and leaf fall peaks during the long dry season when the temperature is high. Annual pattern and strong seasonality in leaf fall accords with leaf fall phenology of deciduous trees from tropical forests in Bolivia (Justiniano & Frederickson 2000) and Hawaii (Berlin *et al.* 2000). Leaf fall of deciduous species in a Bolivian dry forest begins at the beginning of the dry season and continues until the beginning of the rainy season. The significant correlation between leaf fall and mean monthly temperature at the Munessa-Shashemene Forest suggests that leaf fall is an adaptation to reduce the effect of water shortage stress in the dry season. According to Borchert (1984) and Reich & Borchert (1984) the timing of leaf fall in tropical trees is controlled by the water status of the plant.

Leaf flush peaked in April towards the end of the long dry season and the beginning of the small rains. A similar leaf flush pattern was observed in a forest from Tai National Park, Côte d'Ivoire (Anderson *et al.* 2005). Leaf flush during the end of dry season, when water stress is still high, is interpreted as a strategy to minimize herbivory of young vulnerable leaves (Aide 1993; Anderson *et al.* 2005). During the long rainy season of 2007, a massive attack of mature leaves in trees of *C. africana* by herbivore insects and subsequent complete shedding of all leaves by the infested plants was noted in the study forest.

Flowering

Flowering patterns at the Munessa-Shashemene Forest were predominately annual, unimodal and seasonal in all examined species except *P. fulva*, which showed continuous, bimodal and non-seasonal flowering. Such strong seasonality and annual flowering pattern was reported for trees in other dry tropical forests (Bendix *et al.* 2006; Berlin *et al.* 2000; Frankie *et al.* 1974; Justiniano & Fredericksen 2000).

Continuous flowering is very rare in tropical forests and constituted less than 12 % of the species (Berlin *et al.* 2000; Frankie *et al.* 1974). In the Malayan forest, sub-canopy species displayed continuous flowering (Appanah 1990), which also increased seed production and distribution year round. *P. fulva*, which contributes to the sub-canopy stratum in the Munessa-Shashemene Forest, showed continuous flowering (at the population level) with two major peaks in one year. Each peak was recognized as one complete flowering cycle at the individual tree level, thus, making *P. fulva* a sub-annual type. One species can, therefore, behave differentially in its flowering pattern as continual flowering at the population/species level and sub-annual flowering at the individual/tree level.

Several studies in other semi-arid tropical forests have reported that flower peaks were concentrated in the dry season (Berlin *et al.* 2000; Frankie *et al.* 1974; Justiniano & Fredericksen 2000). Most of the study species had flower peaks during the long dry season. Dry season flowering in tropical forests may be enhanced by the higher radiation as there was a significant positive correlation with mean monthly temperatures. Flowering in most species examined was significantly correlated to mean monthly temperature. In the present study, a significant positive

relationship between flowering and the increase in air temperature during the dry season was noted for *P. adolfi-friederici* allowing for a time lag of two months, between flower induction and onset of flowering. On the other hand, flowering phenology of tropical tree species can also be triggered by the humidity (Anderson *et al.* 2005; Augspurger 1981; Sakai 2001; van Schaik *et al.* 1993), which has also been noticed for *P. africana* and *P. fulva* in the Munessa-Shashemene Forest. For example, there was significant negative correlation between rainfall and flowering with lag time of two months for *P. africana*, which corresponded with the end of the long rainy season. The significant decrease in rainfall at the end of the rainy season was followed by a significant increase in the proportion of individuals flowering two months later. On the other hand, there was a significant positive correlation between rainfall and flowering for *S. guineense*. The significant increase in rainfall in the rainy season was followed by significant increase in the proportion of individuals flowering in *S. guineense*. Such strong correlations show the importance of climate factors in regulating flowering of trees in Munessa-Shashemene Forest.

According to Frankie *et al.* (1974), wet season flowering in tropical dry forests is rather low. As an exception in the present study, *C. africana* flowered profusely during the rainy season after the development of new foliage. Several tree species in tropical forests that share pollinators exhibit sequential flowering (Appanah 1985; Ashton *et al.* 1988). Such temporal segregation in flowering is an adaptation of plant species that share common pollinators to minimize interspecific overlapping in flowering times and, thus, ineffective pollination or competition for pollinators (Appanah 1985; Ashton *et al.* 1988; Sakai 2001; Stiles 1977). In most species, flowering significantly varied between the months of the year and also no significant correlation in flowering time among species. These differences segregated flowering temporally among the species.

Fruiting

Fruit production at the Munessa-Shashemene Forest is predominantly annual except for *P. fulva* that exhibited sub-annual fruiting. Most annual fruiting species exhibited non-seasonal fruiting, i.e. extended fruiting over several months of the year. Extended fruiting, which is caused by individuals within a population maturing fruits

asynchronously (Bawa & Ng 1990), ensures the availability of fruit resources for frugivore animals for most parts of the year (Berlin *et al.* 2000; Justiniano & Fredericksen 2000). Nevertheless, in tropical dry forests, fruit production remains low during the major rainy season (Justiniano & Fredericksen 2000). Similarly, few tree species fruited during the rainy season at the Munessa-Shashemene Forest.

Although fruiting period is extended over several months, fruiting peaked during the mid to late dry season for most species. Such pronounced dry season fruiting peaks have been reported from dry tropical forest in Costa Rica (Frankie *et al.* 1974), and Cote d'Ivoire (Anderson *et al.* 2005). Fruiting towards the end of the dry season or during the rainy season in tropical forests may have evolved to ensure dispersal of seeds when soil moisture conditions are favorable for seed germination, seedling growth and survival (Janzen 1969; van Schaik *et al.* 1993). Seedling recruitment (in *C. africana*, *C. macrostachyus*, *P. adolfi-friederici*, *P. africana* and *S. guineense*) in Munessa-Shashemene Forest during the major rainy season in 2005 and 2006 was 21 fold higher than in the dry season of the respective years (Getachew Tesfaye *et al.* 2010). Moreover, the survival and growth of tree seedlings at the study site were largely affected by drought and animal herbivory during the long dry season (87 % seedling mortality rates) of the year (Getachew Tesfaye *et al.* 2010). These observations strongly support the idea that the time of fruiting in tropical dry forests have evolved in relation to rainfall seasonality, the timing of favorable conditions for seed germination and survival and, hence, reproductive success of the plant.

Pioneer species in tropical forests start reproduction early in life, fruit abundantly and frequently, and have small seeds that can be effectively dispersed by wind (Croat 1978). *P. fulva* is one of the three pioneer species that displayed sub-annual fruiting pattern. Although *P. fulva* flowered and fruited frequently and abundantly, it showed hampered regeneration. It had no seedlings and also exhibited the lowest tree density at the Munessa-Shashemene Forest (Getachew Tesfaye *et al.* 2010). The other two pioneer species, *C. africana* and *C. macrostachyus* displayed a similar fruiting phenology with that of the climax species.

In the Munessa-Shashemene Forest, the female *P. falcatus* trees produced reproductive cones (56 % of the population) between November and December 2005 and the same individuals required a

period of 12 months to complete the cone maturation period. For *P. falcatus*, the complete reproductive cycle, i.e. from female reproductive cone production to the development of ripe cones and, then, dispersal took about 18 months, which is similar to what was reported by Wilson & Owens (1999). *P. falcatus* produced mature cones all year round and serves as the only available food source at times of food scarcity to frugivore animals in the forest.

All the studied species at the Munessa-Shashemene Forest flowered and produced fruits abundantly. Nevertheless, in *P. adolfi-friederici* significant numbers of immature fruits were observed on most branches of the trees and/or on the ground under the tree crowns, which indicates reproductive problems of the species during fruit development. *P. fulva* exhibited also similar reproductive problems. This may be partially attributed to the fragmentation of the reproductive trees within the forest, i.e. the average distance between two reproductively mature trees of *P. adolfi-friederici* and *P. fulva* in the forest was 61 and 64 m, respectively. Such fragmentation could limit out-crossing (at the time of pollination) among the different individuals of the same species. Abortions of immature fruits or non-viable seed set due to self-pollination among out-crossing populations have been reported in several tropical tree species (Sakai 2001).

In conclusion, the timing of leaf fall, flowering and fruiting of the studied species were concentrated in the long dry season although few species flowered or fruited during the long rainy season or continuously year round. For most species flowering was seasonal and segregated temporally. Patterns of fruiting phenology can be categorized as: (i) annual, where most species produce fruits during the long dry season and still few species produce fruits in the rainy season; (ii) continuous, where few species produce fruits year round; and (iii) sub-annual, where few species produce fruits two times a year. The fact that in most species both flowering and fruiting were significantly correlated with temperature and rainfall shows that multiple factors could influence the reproductive phenology of trees sometimes concurrently or at different times of the year. However, leaf phenology was influenced by temperature.

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References

- Aide, M. 1993. Patterns of leaf development and herbivory in a tropical understory community. *Ecology* **74**: 455-466.
- Anderson, D., V. E. Nordheim, C. T. Moermond, B. Z. Gone Bl & C. Boesch. 2005. Factors influencing tree phenology in Tai National Park, Cote d'Ivoire. *Biotropica* **37**: 631-641.
- Appanah, S. 1985. General flowering in the climax rainforests of Southeast Asia. *Journal of Tropical Ecology* **1**: 225-240.
- Appanah, S. 1990. Plant-pollinator interactions in Malaysian rain forests. pp. 85-102. In: K. S. Bawa & M. Hadley (eds.) *Reproductive Ecology of Tropical Forest Plants*. Unesco, Paris.
- Ashton, P. S., J. T. Givnish & S. Appanah. 1988. Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the seasonal tropics. *American Naturalist* **132**: 44-66.
- Augsburger, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinator and seed predators on *Hybanthus prunifolius* (Violaceae). *Ecology* **62**: 775-788.
- Bawa, K. S. & S. F. Ng. 1990. Phenology- commentary. pp. 17-20. In: K. S. Bawa & M. Hadley (eds.) *Reproductive Ecology of Tropical Forest Plants*. Unesco, Paris.
- Bendix, J., J. Homeier, C. Ortiz, P. Emick, S. Breckle & E. Beck. 2006. Seasonality of weather and tree phenology in a tropical evergreen mountain rainforest. *International Journal of Biometeorology* **50**: 370-384.
- Berlin, E. K., K. T. Pratt, C. J. Simon & J. Kowalsky. 2000. Plant phenology in a Cloud Forest on the Island of Maui, Hawaii. *Biotropica* **32**: 90-99.
- Bollen, A. & D. Giuseppe. 2005. Phenology of littoral forest of Sainte Luce, Southeastern Madagascar. *Biotropica* **37**: 32-43.
- Borchert, R. 1984. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* **75**: 1437-1449.
- Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford.
- Demel Teketay. 1997. Seedling population and regeneration of woody species in dry Afromontane forests of Ethiopia. *Forest Ecology and Management* **98**: 149-165.
- FAO. 1986. *World Reference Base for Soil Resources*. World soil resources reports 84. Food and Agricultural Organization of the United Nations, Rome, Italy.
- Frankie, W. G., G. H. Baker & A. P. Opler. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* **62**: 881- 919.
- Fritzsche, F., A. Abate, M. Fetene, E. Beck, S. Weise & G. Guggenberger. 2006. Soil-plant hydrology of indigenous and exotic trees in an Ethiopian montane forest. *Tree Physiology* **26**: 1043 -1054.
- Getachew Tesfaye, Demel Teketay & Masresha Fetene. 2002. Regeneration of fourteen tree species in Harenna forest, southeastern Ethiopia. *Flora* **197**: 174-181.
- Getachew Tesfaye, Demel Teketay, Masresha Fetene & Erwin Beck. 2010. Regeneration of seven indigenous tree species in a dry afromontane forest, southern Ethiopia. *Flora* **205**: 135-143.
- Getachew Tesfaye. 2008. *Ecology of Regeneration and Phenology of Seven Indigenous Tree Species in a Dry Tropical Montane Forest of Ethiopia*. Ph.D. Thesis. Addis Ababa University, Addis Ababa, Ethiopia.
- Grime, J. 1979. *Plant Strategies and Vegetation Processes*. Wiley, Chichester.
- Janzen, D. H. 1969. Seed-eaters vs. seed size, number, toxicity and dispersal. *Evolution* **23**: 1-27.
- Justiniano, M. & T. Fredericksen. 2000. Phenology of tree species in Bolivian dry forests. *Biotropica* **32**: 276-280.
- Lobo, J., M. Quesada, K. Stoner, E. Fuchs, Y. Herrerias-Diego, J. Rojas & G. Saborio. 2003. Factors affecting phenological patterns of Bombaceae trees in seasonal forests in Costa Rica and Mexico. *American Journal of Botany* **90**: 1054-1063.
- McLaren, K. & M. McDonald. 2005. Seasonal patterns of flowering and fruiting of a dry tropical forest in Jamaica. *Biotropica* **37**: 584-590.
- Newstrom, L. E., G. W. Frankie & H. G. Baker. 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.
- Momose, K., T. Yumoto, T. Nagamitsu, M. Kato, N. Nagamasu, S. Sakai, R. D. Harrison, T. Itioka, T. Hamida & I. Inoue. 1998. Pollination biology in a

- lowland dipterocarp forest in Sarawak, Malaysia. Characteristics of the plant pollination community in a lowland dipterocarp forest. *American Journal of Botany* **10**:1477-1501.
- Opler, A., G. Frankie & H. Baker. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *Journal of Biogeography* **3**: 231-236.
- Rathcke, B. & P. E. Lacey. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology and Systematics* **16**: 179-214.
- Reich, P. B. & R. Borchert. 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *Journal of Ecology* **72**: 61-74.
- Sakai, S. 2001. Phenological diversity in tropical forests. *Population Ecology* **43**: 77-86.
- Stiles, F. G. 1977. Coadapted competitors: the flowering seasons of hummingbird-pollinated plants in a tropical forest. *Science* **198**: 1170-1178.
- van Schaik, C., W. J. Terborgh & J. S. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* **24**: 353-377.
- Wilson, V. & J. Owens. 1999. The reproductive biology of totara (*Podocarpus totara*) (Podocarpaceae). *Annals of Botany* **83**: 401-411.
- Zar, J. H. 1996. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.

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