

Flowering and fruiting phenology and floral visitation of four native tree species in the remnant moist Afromontane forest of Wondo Genet, south central Ethiopia

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Abstract: The flowering and fruiting timing of four native tree species-*Allophylus abyssinicus*, *Polyscias fulva*, *Syzygium guineense* subsp. *guineense* and *Millettia ferruginea* and their floral visitation by insects were investigated to understand their phenological pattern and the species richness and pattern of visitation. In the natural forest of Wondo Genet, Ethiopia, 25 mature individuals of four indigenous species were selected and monitored over two years. Flower visiting insects were trapped with sweep nets at an interval of every two hours between 8:00-18:00 for 20 days. Circular statistics were employed to test for seasonality in flowering and fruiting. The visitor community compositions of the four species were compared with permutational ANOVA. While the tree species expressed synchronous seasonal flowering that peaked during the dry period, fruiting was also seasonal. The mean monthly rainfall and temperature correlated significantly with the periods of the phenophases. Visitor communities of *M. ferruginea* differed significantly from visitor communities on *A. abyssinicus*, *P. fulva* and *S. guineense*.

Key words: Insect diversity, plant-animal interaction, reproductive phenology, seasonality, tropical trees.

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Introduction

According to Yadav & Yadav (2008) phenology is the study of relationships between climatic variables and periodic phenomena in organisms. Some of the periodic phenomena in plants include germination, leafing, flowering, fruiting and growth. Among the most important phenological events in flowering, for example, are the timing, duration and flowering frequency. Flowering phenologies vary in the tropics and trees can potentially flower at any time of the year (Bawa *et al.* 2003), which can affect the reproductive output of the plants. According to Gomez (1993) plants

belonging to the same population do not always have the same phenological pattern. The variation in the flowering phenological events range from a few days to the whole year (Opler *et al.* 1980). Some of the climatic variables that affect these periodic phenological phenomena include rainfall (Dutta & Devi 2015; Mouplea *et al.* 2014; Opler *et al.* 1976), temperature (Ashton *et al.* 1988), insolation (Stevenson *et al.* 2008; Van Schaik *et al.* 1993) and water stress (Borchert 1983). For example, in the seasonal tropics rainfall affects subsequent germination and thus trees should time flowering and fruiting during the sunniest time of the year so that seed maturation coincides

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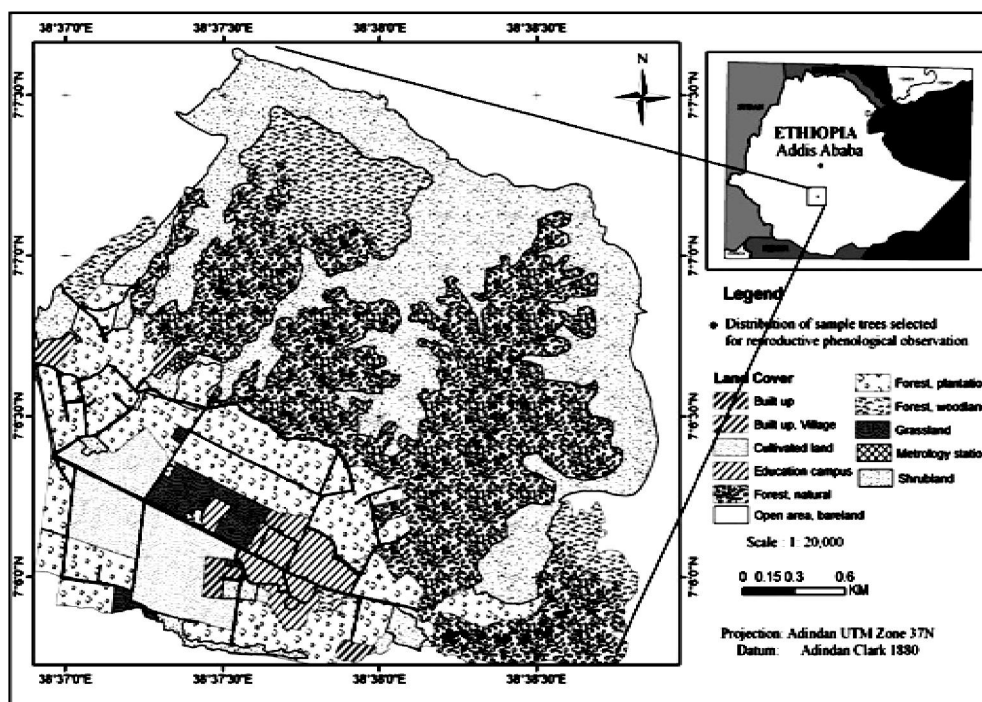


Fig. 1. Location map of study site and sample trees in Wondo Genet forest.

with the onset of the rainy season in seasonally dry forest (Anderson *et al.* 2005; Williams *et al.* 1999). Biotic factors that affect phenological patterns include differential preferences of pollinators (Lobo *et al.* 2003) and timing of animal seed dispersal agents (Biard 1980; Levy 1988) or florivorous insects (McCall & Irwin 2006). Likewise, seasonal variation in the availability of consumer resources such as flowers and fruits, has presumably led to adaptations in primary and secondary consumers (Van Schaik *et al.* 1993).

Tropical trees are mostly self-incompatible and rely on animals to transfer pollen (Bawa 1990). Therefore, tree species have evolved relationships with a variety of animals ranging from tiny thrips and midges to bees and large bats, and the relationships can be quite specific and specialized in tropical pollination systems (Johnson & Steiner 2000; Kay & Schemske 2003; Mishra *et al.* 2004). The degree of specialization in pollinator communities is poorly understood in the tropics. The few available studies, however, indicate that different assemblages of flower visitors can be associated with different forest tree species (Kato *et al.* 2008) and they are often attracted to a given plant species only after a certain threshold density of individuals or flowers are in bloom (Heithaus 1982).

Information on reproductive phenology is basic to the understanding of biological processes in trees, and of their interactions with other organisms and the dynamics and functioning of ecosystems (McLaren & McDonald 2005); for example, the timing of flowering and fruiting controls the activities of many herbivores, flower visitors (pollinators), and frugivores (Van Schaik *et al.* 1993). Thus, an understanding of reproductive phenology and pollination biology are basic elements that should be considered in the conservation, management and exploitation of plant species (Peba & Tabla 2007) and when predicting the reproductive potential of vegetation at a landscape level. Restoration and rehabilitation of degraded forest lands for their biodiversity conservation, watershed protection, carbon sequestration and other ecosystem services requires detailed knowledge of plant phenology (FORRU 2006). Healthy ecosystem functioning depends also on the interactions between organisms, including plants and animals, such as pollination or flower visitation.

Nevertheless, information on phenology and flower visitation is scanty in Ethiopia and other African forested regions. In the Afromontane forest of South central Ethiopia, we set out to: (i) assess

the timing, duration and frequency of flowering and fruiting of the four selected tree species at the study site and to test for their seasonality; (ii) determine the relationship between flowering, fruiting and environmental factors (rainfall and temperature); (iii) compare the flower visitor assemblages associated with the four tree species and (iv) with the different times of day, during their peak flowering. Since many pollinator species are known to temporally specialize their activity to certain flowering plants (Ollerton *et al.* 2009; Ramos & Santos 2008), or to certain times of day (McCall & Primack 1979; Ramos & Santos 2008; Stone *et al.* 1998) we hypothesize that the visitor communities will differ among species and among times of day.

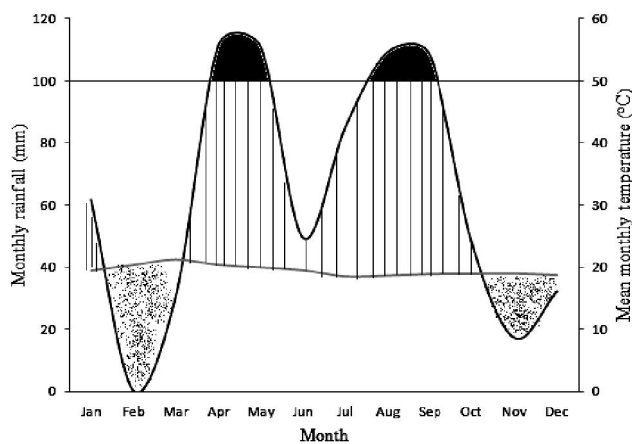


Fig. 2. Climate diagram of the study site for the period from January 2009 - 2011 (mean monthly rainfall and temperature was 764 mm and 19.4 °C, respectively).

Materials and methods

Site description

Wondo Genet is situated in the south-eastern central highlands of Ethiopia, about 263 km from Addis Ababa, at 7° 5' 30" N to 7° 7' 40" N latitude and 38° 36' 55" E to 38° 39' 00" E longitude on the eastern slope of the Rift Valley escarpment (Fig. 1). The large-scale physiographic setting is defined by a tectonic depression bounded by steep escarpments. The floor of the depression is covered by lakes, wetlands and alluvial plains, which together cover half the watershed. The remaining half consists of uplands and escarpments with slopes varying between 8 and 85 degrees. The altitude ranges from 1800 m to 2500 m. The mean annual

rainfall varies between 700 mm and 1200 mm in a bimodal pattern (Fig. 2). A short rainy season is expected from March to April and a long rainy season from June to August. The period from November to February is relatively dry. The mean annual temperature is 19 °C with daily fluctuations between 8 to 21 °C. The soils are young and of volcanic origin, characterized by well-drained loam or sandy loam, and it is shallow at steep convex slopes but deeper at lower altitudes (Eriksson & Stern 1987). The forest is characterized as moist Afromontane forest (Friis *et al.* 2010), it harbours important fauna and flora, and provides watershed, ecosystem, economic, research, and educational services.

Tree species examined

Four indigenous tree species having significant ecological and economic importance, namely *Allophylus abyssinicus* (Hochst.) Radlk., *Polyscias fulva* (Hiern) Harms, *Syzygium guineense* (Willd.) DC subsp. *guineense* and *Millettia ferruginea* (Hochst) were selected for study. These species are widely distributed in tropical Africa (Friis 1992). *P. fulva* and *M. ferruginea* are pioneer species whose seeds can germinate under canopy gaps soon after disturbance. *A. abyssinicus* and *S. guineense* are shade tolerant species whose seeds can germinate and establish in shaded understory forests (Teketay 1997; Tesfaye *et al.* 2002). *Millettia ferruginea* is an endemic, nitrogen-fixing leguminous tree species that is known to have a number of positive effects on soil chemical properties that make it a suitable multipurpose agroforestry tree (Hailu *et al.* 2000). In Ethiopia, the leaves of *Allophylus abyssinicus* are used as an anthelmintic (a natural or pharmaceutical substance that destroys or expels intestinal parasitic worms) and the fruits to cure venereal diseases; in Kenya roots are grated and eaten in small quantities to treat coughs and rheumatism (Bosch 2011).

Tree phenology

A total of 100 mature trees (25 individuals per species with their diameter at breast height (dbh) ranging from 25 - 100 cm) were selected based on their crown visibility and proximity to trail, road and foot paths for accessibility. Their position was recorded using GPS. The phenological events between January 2010 and December 2011 were recorded with binocular observations and by dropping of buds, flowers and fruits from each

selected tree. We estimated the proportion of the crown covered by inflorescences and fruits each month, and total flowering length. As a direct account of inflorescences or fruits was not possible, we implemented a technique that is called crown partition phenological accounting which divided each crown into, equal-sized sections which is easier to sample (Fernández *et al.* 2013). Each section of the crown is observed with binoculars to calculate the proportion covered by reproductive structures. The coverage by flowers and fruits in each section is then estimated separately and finally the proportional values of all sections are summed to obtain the full crown coverage. Intensity of flowering and fruiting 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 flowering and fruiting in the crown. Daily average temperature and rainfall data of the study site were acquired from the Wondo Genet College Meteorological station located in the forest.

Flower visitation

Collection of flower visiting insects from selected tree species was conducted in the natural forest from January - December 2010 when most of the four tree species were at their peak flowering. The insects visiting flowers of the trees under observation was assessed at 2 - hour intervals between 8:00 - 18:00 for 20 consecutive days (adapted from Soehartono & Newton 2001). The visiting insects were trapped with sweep nets and labelled according to the hour they were trapped. The climber climbed the neighbouring tree or the sample tree where possible. The sweep net was attached to an extendable handle. The sweep net was swept back and forth through the target tree crown quickly turning the opening from side to side. Sweeping continued for some distance and then the net is flipped over with the bag handling over the rim, trapping the insects until they can be removed. Once collected for about half an hour, a killing jar is used to kill the insects. The collected insects were then placed in a killing jar containing 75 % alcohol (and distilled water) and subsequently sent to Addis Ababa University for identification.

Data analysis

Flowering and fruiting events were analysed based on four parameters: onset (the first date of

flowering or fruiting), mean date, peak and duration (the period between the first flowering or fruiting and the last month when the event was observed) and mean date. We first calculated flowering date for each individual as the number of days between 1 January and the day that its first flower was produced. Similarly, flowering peak date was defined as the number of days between 1 January and the day that the maximum number of open flowers was reached. Flowering duration was estimated as the number of days the plant remained in bloom. Finally, for flowering synchrony, we estimated the number of days that the flowering of one individual overlapped with the flowering of the rest of the plants in the sample (Gómez 1993).

The proportion of individuals (of each 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 month, 360° by Dec 30) 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 flowering and fruiting and (2) r , which is a measure of the intensity of concentration around the mean. The 'circular' software package (*Circular Statistics* v. 0.4 - 3), which provides methods for the descriptive and inferential statistical analysis of directional data was used for the analysis of the phenological data. The hypotheses tested were: H_0 = phenophase is distributed uniformly across months around the year and consequently no seasonality present; H_A = phenophase is not distributed uniformly across the months around the year and consequently there is seasonality. If H_A is accepted, r can be considered as a measure of the 'degree' of seasonality.

An F-test was computed with the R-program (R Development Core Team 2010) to determine the significance of seasonality in the distribution of the phenophases. The circular - Linear regression analysis of fruiting and flowering with mean monthly temperature and rainfall was also computed. The Rayleigh test of uniformity was computed by using the 'circular' package in R-software (Agostinelli & Lund 2011) to determine the significance of seasonality in the distribution of the phenophases.

Differences in flower visitor communities were analysed with the program Primer-E (Clarke & Gorley 2006). First, we drew dominance curves of insect visitor communities for each tree species.

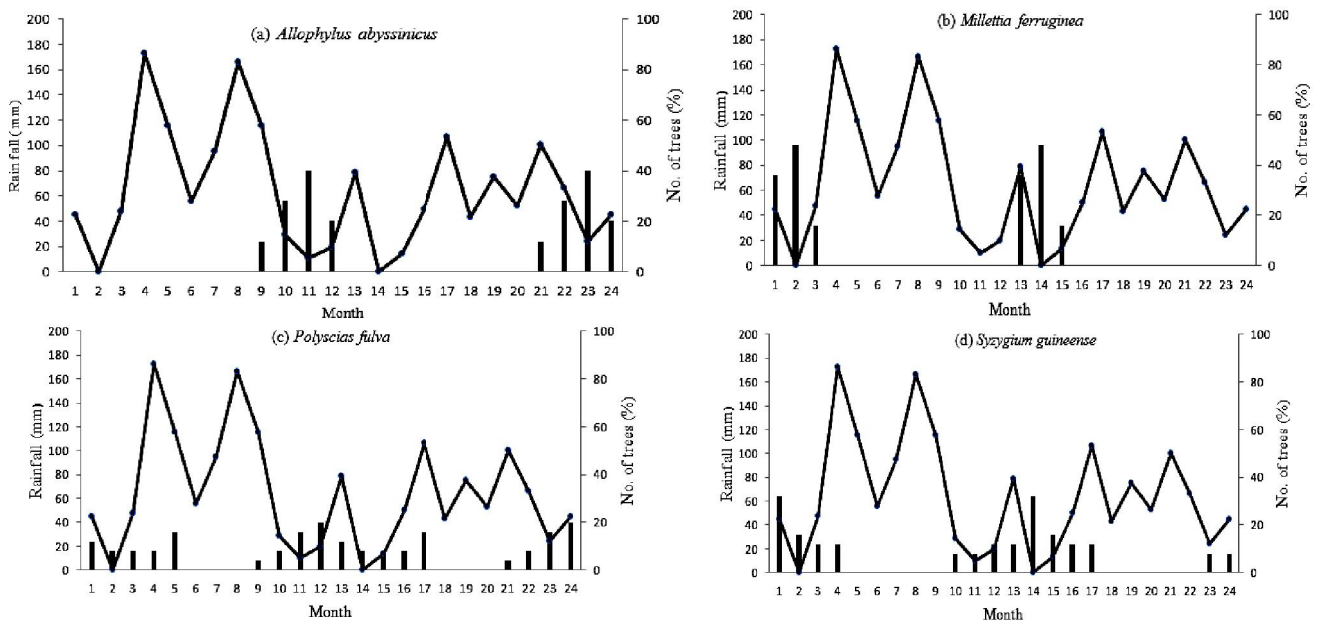


Fig. 3. Percentage of flowering individuals of the four tree species (a, b, c, and d) from January 2010 (month 1) to December 2011 (month 24) in the Wondo Genet Forest (bars refer to phenology while the line graph indicates monthly total rainfall).

Dufrene Legendre Indicator species values were calculated for each visitor species to identify the species characterizing each host tree (species with index value > 0.25 considered as indicator species; Dufrêne & Legendre 1997), with package 'labdsv' (Roberts 2012) in program R 2.12.0 (R Development Core Team 2010). The Permanova + routine of Primer-E (Anderson *et al.* 2008) was used to test if, and to what degree, the tree and sampling time explain the variation in flower visitor assemblages, on the basis of the Bray-Curtis similarity matrix. The differences in visitor communities are illustrated with non-metric dimensional scaling (MDS) ordination plots.

Results

Phenology of the study species

Flowering

Flowering phenology of the four studied species was seasonal (Fig. 3, Table 1). There was also significant variation in the mean dates of flowering between the tree species ($F_{3, 96} = 22.8$, $P < 0.001$). Although the seasonal pattern was clearly annual in *A. abyssinicus*, *M. ferruginea* and *S. guineense*, one of the species, *P. fulva*, follow a bi-annual flowering pattern (Fig. 3), although individual trees of this species flowered only once per year (data not shown).

Flowering period of all the species was negatively correlated with rainfall and positively correlated with temperature (Table 2). Duration of flowering periods ranged from 3 - 9 months among species. Each species has flowered annually in roughly the same month each year. Flowering in *A. abyssinicus* was unimodal and varied between 12 - 40 % of the population. Flowering lasted from August to December and did not vary between the years. While flowering started in August, the peak of flowering was in November. Flowering in *M. ferruginea* was also unimodal and varied between 16 - 48 % of the population. Flowering continued for three months from January to March. Flowering started as the leaf started to dehisce and the peak coincided with branches left without leaves right before the onset of the rainy season in April. Flowering in *P. fulva* was bimodal at species level but unimodal at the individual level. It is less concentrated with a brief break throughout the year and varied between 4 - 100 % of the population. Flowering extended for nine months, with peaks in May and November. Flowering in *S. guineense* was unimodal and varied between 8 - 100 % of the population. Flowering lasted for seven months from October to April with the peak of flowering in January.

Fruiting

Fruiting phenology of the four species takes

Table 1. Mean date of flowering (Julian calendar day followed by mean angular date \pm S.E.), concentration around the mean (r), and Rayleigh test of uniformity for testing seasonality in flowering patterns of the four tree species in Wondo Genet natural forest.

Species	Duration (months)	Mean angular date (a)	r	P -value
<i>Allophylus abyssinicus</i>	4	November 20, 320.6° \pm 0.48	0.88	< 0.001
<i>Millettia ferruginea</i>	3	February 23, 53.8° \pm 0.36	0.93	< 0.001
<i>Polyscias fulva</i>	9	January 26, 26.2° \pm 1.38	0.38	< 0.05
<i>Syzygium guineense</i>	7	February 8, 38.13° \pm 0.89	0.66	< 0.001

Table 2. Circular-linear regression results showing the association between flowering and rainfall or temperature.

Rainfall				
Species	Estimate	Std. Error	t value	P -value
<i>Allophylus abyssinicus</i>	-0.008	0.0003	26.50	< 0.001
<i>Millettia ferruginea</i>	-0.001	0.0007	2.23	< 0.05
<i>Polyscias fulva</i>	-0.016	0.005	2.68	< 0.01
<i>Syzygium guineense</i>	-0.009	0.002	3.97	< 0.001
Temperature				
Species	Estimate	Std. Error	t value	P -value
<i>Allophylus abyssinicus</i>	0.053	0.005	10.34	< 0.001
<i>Millettia ferruginea</i>	0.051	0.003	14.90	< 0.001
<i>Polyscias fulva</i>	0.050	0.016	3.02	< 0.01
<i>Syzygium guineense</i>	0.050	0.008	5.79	< 0.001

place annually in roughly the same month each year (Fig. 4). Seasonality of fruiting (Table 3) was observed for all studied species. *P. fulva* seemed to follow a bi-annual fruiting pattern, although individual trees of this species fruited only once per year (data not shown). There was significant variation ($P < 0.001$) in the mean dates of fruiting among the four tree species ($F_3 = 120.6$, $P < 0.001$). All species showed an extended fruiting period, lasting up to three months for *A. abyssinicus*, and *M. ferruginea*, four months for *S. guineense* and five months for *P. fulva*.

Table 3. Mean date of fruiting (Julian calendar day followed by mean angular date \pm S.E.), concentration around the mean (r), and Rayleigh test of uniformity for testing seasonality in fruiting patterns of four tree species in Wondo Genet natural forest.

Species	Mean angular date (a)	r	P -value
<i>Allophylus abyssinicus</i>	December 13, 343.6° \pm 0.36	0.93	< 0.001
<i>Millettia ferruginea</i>	August 2, 212° \pm 0.52	0.86	< 0.001
<i>Polyscias fulva</i>	January 24, 24.6° \pm 1.38	0.38	< 0.05
<i>Syzygium guineense</i>	March 11, 71.45° \pm 0.89	0.66	< 0.001

Table 4. Circular-linear regression of rainfall and temperature on fruiting.

Rainfall				
Species	Estimate	Std. Error	t value	P -value
<i>Allophylus abyssinicus</i>	-0.007	0.0001	52.57	< 0.001
<i>Millettia ferruginea</i>	-0.004	0.0006	7.08	< 0.001
<i>Polyscias fulva</i>	0.008	0.003	2.25	< 0.05
<i>Syzygium guineense</i>	-0.004	0.002	1.65	< 0.05
Temperature				
Species	Estimate	Std. Error	t value	P -value
<i>Allophylus abyssinicus</i>	0.052	0.003	13.72	< 0.001
<i>Millettia ferruginea</i>	-0.051	0.00	10.16	< 0.001
<i>Polyscias fulva</i>	0.050	0.016	3.00	< 0.01
<i>Syzygium guineense</i>	0.050	0.008	5.93	< 0.001

The mean monthly rainfall and the mean monthly temperature significantly correlated with the period of fruiting of all the tree species but the direction of the association (positive/negative) varied among the species (Table 4). Unlike other species, fruiting in *P. fulva* is sub-annual. Fruiting

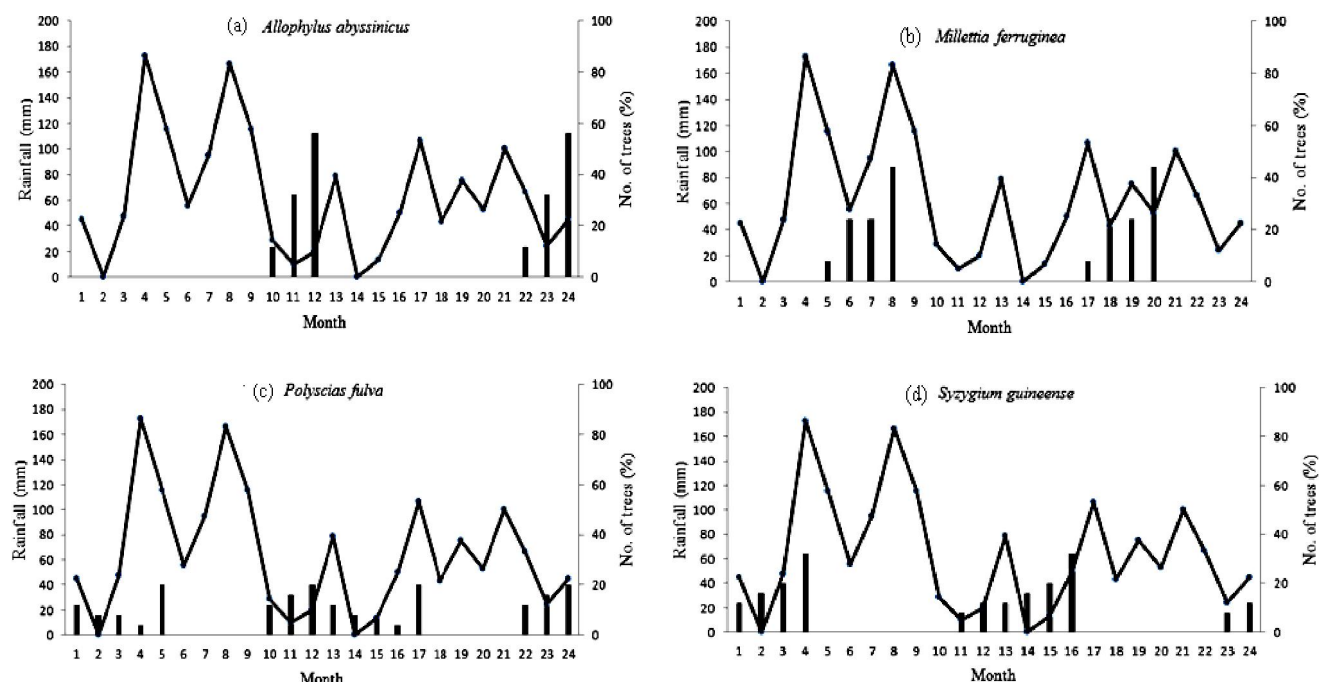


Fig. 4. Percentage of fruiting individuals of four tree species (a-d) from January 2010 (month 1) to December 2011 (month 24) in the Wondo Genet Forest (bars refer to phenology while the line graph indicates monthly total rainfall).

in *M. ferruginea* was non-seasonal, that is extended into the rainy season. Although it is extended to the rainy season, fruiting peaked during the dry season.

Flower visitation

A total of 40 insect taxa were identified from collections during peak flowering of each tree species under study (Supplementary Table S1). The insects belonged to the order Coleoptera, Diptera, Hemiptera and Hymenoptera. Within these four orders 13 families were identified. Altogether 18 taxa (345 individuals) were observed from *A. abyssinicus*, 17 taxa (374 individuals) were observed from *P. fulva*, 11 taxa (169 individuals) from *S. guineense* and 5 taxa (458 individuals) from *M. ferruginea*. The most common visitor accounted for almost 99 % of all individuals in *M. ferruginea*, for 76 % in *A. abyssinicus*, for 56 % in *S. guineense* and only for 29 % in *P. fulva* (Fig. 5). According to the Dufrene-Legendre Indicator species analysis, *Trichostetha facicularis* and *Pachnoda thoracia* were characteristic visitors of *A. abyssinicus*, *Musa domestica*, *Sceliphrona ementsrium*, *Ammo philatyde* and *Apis mellifera* characteristic of *P. fulva*, *Apis mellifera*, *Pachnoda* sp. and *Neodiprion lecontei* characteristic of *S. guineense* and *Xylocopa caerulea* characteristic of *M. ferruginea*.

The visitor communities of the three species differed from each other significantly (results of PERMANOVA; Table 6). According to the pair-wise tests, visitor communities of *M. ferruginea* differed significantly from visitor communities on *A. abyssinicus*, *P. fulva* and *S. guineense*. The MDS graph of visitor communities is given in Fig. 6.

Discussion

The flowering patterns of *A. abyssinicus*, *S. guineense*, and *M. ferruginea* species are annual, unimodal and seasonal while *P. fulva* exhibited bi-modal pattern although individuals within the species showed flowered only once per year. Such strong seasonality and annual flowering has been previously reported for several tropical tree species (Anderson *et al.* 2005; Adler & Kielpinski 2000; Berlin *et al.* 2000; McLaren & McDonald 2005; Stevenson *et al.* 2008; Tesfaye *et al.* 2011). Yadav & Yadav (2008) reported flowering throughout the year with two peaks in the Rajasthan tropical deciduous forest of India. Berlin *et al.* (2000) also recorded few species with continuous flowering pattern from forests in Hawaii. In western Amazonia forests, Stevenson *et al.* (2008) reported that continuous flowering was relatively rare (14 %)

Supplementary Table S1. Flower visiting insets and the tree species they visited.

Species	Family	Order	Common name	Visited a flower of			
				<i>A.</i> <i>abyssinicus</i>	<i>P. fulva</i>	<i>S.</i> <i>guineense</i>	<i>M.</i> <i>ferruginea</i>
<i>Ammophila procera</i>	Sphecidae	Hymenoptera	Thread-waisted wasp		X		
<i>Ammophila</i> sp.	Sphecidae	Hymenoptera	Thread-waisted wasp		X	X	
<i>Ammophila tydei</i>	Sphecidae	Hymenoptera	Thread-waisted wasp		X		
<i>Anomalina orientalis</i>	Scarabaeidae	Coleoptera	Flower beetle	X			
<i>Apis mellifera</i>	Apidae	Hymenoptera	Honey bee	X	X	X	X
<i>Ceratosolenca capensis</i>	Agaonidae	Hymenoptera	Fig wasp		X		
<i>Comsocephalus dmitriewi</i>	Scarabaeidae	Coleoptera	Flower beetle	X			
<i>Epicauta cinerea</i>	Meloideae	Coleoptera	Blister beetle	X			
<i>Epicauta</i> sp.	Meloideae	Coleoptera	Blister beetle		X		
<i>Eremnophila aureonotata</i>	Sphecidae	Hymenoptera	Thread-waisted wasp		X		
<i>Marmylida marginella</i>	Scarabaeidae	Coleoptera	Flower beetle	X			
<i>Melanostoma scalare</i>	Syrphidae	Diptera	Hover fly			X	
<i>Musa domestica</i>	Muscidae	Diptera	House fly		X		
<i>Neodiprion lecontei</i>	Diprionidae	Hymenoptera	Saw fly	X	X	X	
<i>Neodiprion</i> sp.	Diprionidae	Hymenoptera	Saw fly	X		X	
<i>Nezara</i> sp.	Pentatomidae	Hemiptera	Green stink bug	X			
<i>Nezara viridula</i>	Pentatomidae	Hemiptera	Green stink bug				X
<i>Pachnoda ephippiata</i>	Scarabaeidae	Coleoptera	Flower beetle	X			
<i>Pachnoda marginata</i>	Scarabaeidae	Coleoptera	Flower beetle	X			
<i>Pachnoda</i> sp. 1	Scarabaeidae	Coleoptera	Flower beetle		X		
<i>Pachnoda</i> sp. 2	Scarabaeidae	Coleoptera	Flower beetle			X	
<i>Pachnoda</i> sp. 3	Scarabaeidae	Coleoptera	Flower beetle	X			
<i>Pachnoda</i> sp. 4	Scarabaeidae	Coleoptera	Flower beetle	X		X	
<i>Pachnoda stehelini</i>	Scarabaeidae	Coleoptera	Scarab beetle	X		X	
<i>Pachnoda thoracia</i>	Scarabaeidae	Coleoptera	Flower beetle	X			
<i>Pachnoda marginata</i>	Scarabaeidae	Coleoptera	Flower beetle			X	
<i>Pachnoda sinuata</i>	Scarabaeidae	Coleoptera	Flower beetle			X	
<i>Polistes annularis</i>	Vespidae	Hymenoptera	Red wasp		X		
<i>Polistes carolinab</i>	Vespidae	Hymenoptera	Paper wasp		X		
<i>Polistes fuscatus</i>	Vespidae	Hymenoptera	Paper wasp	X	X		
<i>Polistes</i> sp.	Vespidae	Hymenoptera	Paper wasp		X		
<i>Rhagonycha fulva</i>	Cantharidae	Coleoptera	Red soldier beetle	X			

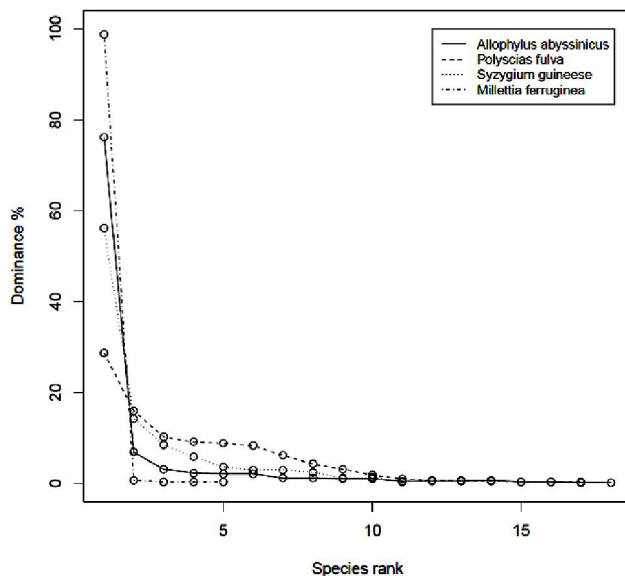
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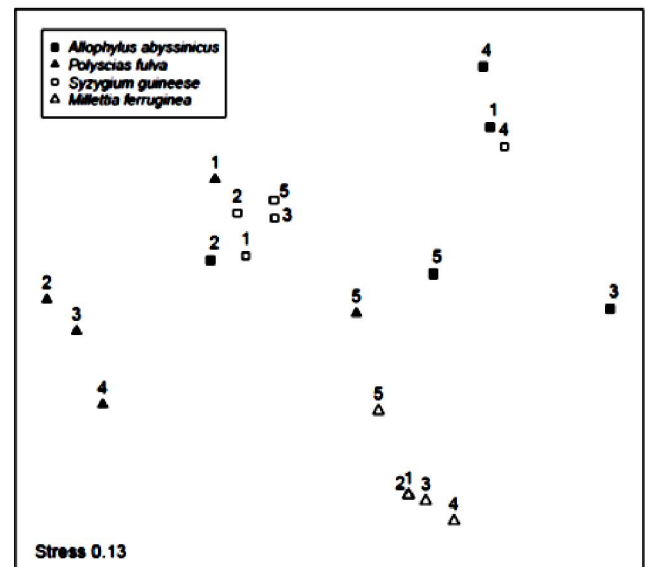
Species	Family	Order	Common name	Visited a flower of			
				A. <i>abyssinicus</i>	<i>P. fulva</i>	S. <i>guineense</i>	M. <i>ferruginea</i>
<i>Sceliphron caementsrium</i>	Sphecidae	Hymenoptera	Mud dauber		X		
<i>Trichopoda</i> sp. 1	Tachinidae	Diptera	Tachina fly		X		
<i>Trichopoda</i> sp. 2	Tachinidae	Diptera	Tachina fly			X	
<i>Trichopoda</i> sp. 3	Tachinidae	Diptera	Tachina fly		X		
<i>Trichostetha - facicularis</i>	Scarabaeidae	Coleoptera	Scarab beetle	X			X
<i>Trichostetha</i> sp.	Scarabaeidae	Coleoptera	Scarab beetle	X			
<i>Xylocopa caerulea</i>	Pentatomidae	Hemiptera	Carpenter bee				X
<i>Xylocopa olivacea</i>	Pentatomidae	Hemiptera	Carpenter bee				X

Table 6. Results of the PERMANOVA analysis showing the test for the two factors (tree species and study time).

Source	df	SS	MS	Pseudo-F	P (perm)	Unique perms
Tree	3	29674	9891.4	4.9046	0.001	999
Time	4	9727.9	2432	1.2059	0.249	997
Res	12	24201	2016.8			
Total	19	63603				

**Fig. 5.** Dominance curves of insect visitor communities at the four studied tree species.

and was common only with figs, palms and some terrestrial herbs.

**Fig. 6.** MDS ordination graph of visitor communities on the four tree species at the five different times of day (time of sampling indicated above symbol: 1 = 8:00 - 10:00, 2 = 10:00 - 12:00, 3 = 12:00 - 14:00, 4 = 14:00 - 16:00, 5 = 16:00 - 18:00).

The synchronous flowering among individuals of the same species is beneficial, because a plant that flowers asynchronously with other individuals is likely to fail in producing fruits and seeds due to pollen limitation to the pollinators or fruits to frugivore communities. Therefore, the plant would flower again in subsequent years and produce large fruit and seed set only when many others are flowering. This induces synchronized resource depletion and finally flowering cycles are completely synchronized among different indivi-

duals (Tachiki *et al.* 2010). Environmental cues and pollinator coupling can induce synchronized flowering in different plant species resulting in an enhanced species co-existence and persistence through reproductive facilitation (Tachiki *et al.* 2010). Chen & Hsu (2011) explained that synchronously flowering species increased pollen and nectar resources attracting an increased number of generalist pollinators, thereby leading to enhancement of pollination success. Synchronous flowering may also reduce the proportion of seeds attacked by seed predators due to predator satiation (Sakai 2001).

According Torres *et al.* (2002) and Morellato *et al.* (2000), flower production is influenced by temperature, day length, moisture availability, and internal physiological factors such as a specific balance of growth regulators. In the present study, the timing of flowering is concentrated around dry and hot periods. In tropical rain forest trees, Bawa *et al.* (2003) found that there was shorter flowering duration for species flowering in the dry season. Anderson *et al.* (2005) also found the percentage of flowering to be high throughout the short dry season where water stress may not have been high enough to inhibit flowering. Similar studies (Berlin *et al.* 2000; Morellato *et al.* 2000; Peba & Tabla 2007; Williams *et al.* 1999) have also reported the concentration of peak flowering around dry seasons.

Fruit production in *A. abyssinicus*, *S. guineense*, *M. ferruginea* and *P. fulva* experienced annual peaks, although *P. fulva* peaked twice per year. Each species fruited in roughly the same month each year. Fruiting peaked in the late drier period and extended to the onset of the rainy season except for *M. ferruginea* where fruiting has extended further throughout the rainy season. In the fruiting phenology of Atlantic forest trees, Morellato *et al.* (2000) found that fruiting was aseasonal. The availability of the fruit both in the drier and wetter period (asynchronously) will ensure resources to frugivore animals throughout the year (Berlin *et al.* 2000). The occurrence of fruit maturity and concomitant dispersal prior to the onset of the rainy season for most species will give a better chance for germination and seedling establishment as a response to the first rains (Williams *et al.* 1999). Some studies have reported late dry season peak in fruiting tropical dry forests of Australia (Williams *et al.* 1999) and Ethiopia (Tesfaye *et al.* 2011). In the present study fruiting was significantly correlated with mean monthly rainfall and mean monthly temperature and fruit

has also peaked during the dry period although *M. ferruginea* fruit extended to the rainy season.

The phenological pattern of plant species may be an important aspect of community organization. The flowering phenology of a plant may be an outcome of competition for pollinators or of facilitation processes in which various plant species together maintain a population of pollinators (Proctor *et al.* 1996). Pollination results in the production of dispersal units (fruits and seeds) which permits colonization of new sites. The large majority of tropical trees rely exclusively on animals to transfer their pollen (Mishra *et al.* 2004). In a study performed by Soehartono & Newton (2001), none of the covered flowers of *Aquilaria* species produced fruits while uncovered flowers did so. Twenty different species of insects were recorded visiting the flowers of these species. Non-viable seed set and abortions of immature fruits due to self-pollination among out-crossing populations have been reported in several tropical tree species reproductive studies (Sakai 2001). This might be due to the on-going fragmentation and selective exploitation of the mature tree species that brought an increased distance as to hamper an effective cross-pollination and occurrence of self-pollination.

Structurally complex vegetation types show more diverse spectra of pollinators than less complex vegetation types (Dulmen 2001). The Wondo Genet Afromontane forest in this study apparently has shown diverse visitor communities within the four study species. An increasing number of studies show that sympatric species may share pollinators and have overlapping flowering seasons (Stone *et al.* 1998). In the present study some of the visitors, during overlapping flowering periods, were shared by the tree species. For example *Apis mellifera* was shared by all four tree species. Conversely, there were visitors that were not shared among species. For example, *Xylocopa caerulea* and *Xylocopa olivacea* visited, among the four tree species, only *Millettia ferruginea*. According to Ramos & Santos (2008), the visits of *A. mellifera* and all native visitors (bees, wasps, dipterans, and lepidopterans) differed spatially and temporally in their visitation.

The results of this study suggest that failure of flowering is not likely to explain the previously documented failure of *P. fulva* and *A. abyssinicus* to reproduce in Wondo Genet forest (Kebede *et al.* 2012). All of the tree species flowered and produced fruits abundantly. Fruits of *S. guineense*, *A. abyssinicus* and *P. fulva* and *M. Ferruginea*

were observed to be consumed and dispersed by primates (monkeys and baboons) and birds; *M. ferruginea* fruits also crack upon drying and showed self-dispersal as well. (MamoKebede, personal observation). *M. ferruginea* seeds were also dispersed upon cracking and release of seeds (self-dispersal) and seeds were released. A significant number of immature fruits of *P. fulva* and *A. abyssinicus* were found under the crowns of the trees probably contributing to the low reproduction of this tree species in this forest. An increased understanding of the flowering and fruiting phenologies and associated pollinator communities of these species will hopefully contribute to their future successful cultivation in Wondo Genet forest.

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