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Full Length Research Paper

Phenology of flowering in cacao (*Theobroma cacao*) and its related species in Nigeria

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Adequate utilization of genetic variability in both cultivated and wild relatives of any crop species is a major objective in genetic improvement and crop breeding programs. The timing of onset of flowering is also crucial to reproductive success of flowering plant. Flowering pattern in five species in the genus *Theobroma* and one *Herrania* spp. was studied over a 10 year period in Nigeria. Results showed that although at different intensities, flowering incidence was observed in *Theobroma cacao* in all the months of the year. In *Theobroma microcarpum* and *Theobroma bicolor*, flowering commenced at the onset of dry season in November / December and ceased at the end of the second module of rainfall. In *Theobroma speciosum* and *Theobroma grandiflorum*, flowering was mainly confined to the dry period between December and April. However, in *Herrania* spp., flowering occurred mainly during rainy season. Flowering incidence in *Herrania* spp. was significantly negatively (r = –0.906, P < 0.0001) correlated with duration of sunshine hours but significantly positively (r = 0.743, P < 0.004) correlated with rainfall. On the other hand, flowering in *T. speciosum* was significantly positively (r = 0.655, P = 0.015) correlated with duration of sunshine hours but negatively (r = – 0.743, P = 0.003) correlated with rainfall. Flowering in *T. grandiflorum* was in direct antithesis of the bimodal rainfall pattern observed annually.

Key words: *Theobroma*, inter-specific hybridization, flowering time, pollination.

INTRODUCTION

The cacao tree, *Theobroma cacao* L., which produces cocoa beans, the main source of butter and solids used in chocolate and confectioneries industry worldwide, is the most economically important species of the genus *Theobroma*. The genus *Theobroma* is also the most important genus in the plant family Sterculiaceae (Purseglove, 1968), now reclassified into Malvaceae (Alverson et al., 1999; Whitlock et al., 2001). *Theobroma* has 22 species (Cuatrecasas, 1964) which have great importance as gene reservoir for cacao improvement besides having an immense potential to be exploited as new crops (Silva and Figuera, 2005). Apart from *T. cacao*, other cultivated species include *Theobroma bicolor* and *Theobroma grandiflorum* ("Capuassu"). *T. grandiflorum* is cultivated widely in the Amazonia and used in juice, ice cream, and sweets that are now gaining global attention. *T. grandiflorum* is considered shade tolerant and produces large fruits. Other members of the *Theobroma* genus include *Theobroma speciosum*, *Theobroma microcarpum*, *Theobroma mammosum,* and *Theobroma angustifolium* amongst others which occur naturally in Brazilian Amazon. The genus *Herrania* Goudet is morphologically similar and closely related to *Theobroma* but distinguished by the unbranched trunk, compound palmate leaves, long petal-lamina, and exceeding the length of petal-hood (Cuatrecasas, 1964). Before the revision of Schultes (1958), *Herrania* was considered a sub-genus of *Theobroma* (Silva and Figuera, 2005).

The cross compatibility and viability of seeds produced by crosses of *Herrania* and *Theobroma* species including *T. cacao* (Addison and Tavares, 1951; Williams, 1975) and lack of separation between both genera based on phylogenetic analysis of rDNA polymorphism (Figuera et al., 1994) showed close relationship between these two genera. Whitlock and Baum (1999) based on parsimony analysis of the vicilin gene considered *Herrania* and *Theobroma* sister genera. Silva and Figuera (2005) also considered close relationship among *Theobroma* species and *Herrania* and concluded same ancestral population which divided into two genera. They supported the hypothesis of *Theobroma* species evolution including *T. cacao* in South America due to geographical restriction imposed by the Andes and Panama isthmus.

Although cultivated cocoa, *T. cacao*, is the widely known species for its use in the production of chocolate and cocoa butter, other species have some desirable qualities which can be introgressed into the cultivated cocoa genome through inter-specific hybridization. The potentials of inter-specific crosses with related species of cultivated *T. cacao* include the possibility of introgressing the very thick pod trait of *T. bicolor*, *T. microcarpum* and *T*. *grandiflorum,* high oil content of *Herrania*, the large beans of *T. bicolor,* and phytoalexin contents in related species especially *T. grandiflorum* (Williams, 1975; Dagunet, 1982; Kebe et al., 1996).

The transition from vegetative to reproductive development is one of the major phase changes during the life cycle of a plant. This transition referred to as flowering time is both controlled by endogenous and environmental factors (Koornneef et al., 2004; Salazar et al., 2009; Wilczek et al., 2010). Several quantitative genetic studies have shown that most of phenological traits have heritable genetic bases (Howe et al., 2003; Aikpokpodion, 2003) and plant response in terms of floral/seasonal trait network genes may differ by species (Nemoto et al., 2003; Wilczek, 2010). The timing of onset of flowering is crucial for reproductive success of flowering plant (Molau et al., 2005), and thus the endogenous and environmental factors interact to maximize the reproductive success of a plant by ensuring that flowering occurs only under conditions and time favourable for fertilization and seed formation (Coupland, 1995). Timing of flowering is also an important determinant of fitness of a plant (Ratchcke and Lacey, 1985; Pilson, 2000; Sandring et al., 2007) during the growing season. It is important that the plants flowering period must coincide with favourable climatic conditions, flowering con-specifics and availability of abiotic resources, and mutualistic partners (Forrest and Thomson, 2010).

Although, long term studies on phenological events such as onset of flowering has been documented in arctic and alpine landscape (Molau et al., 2005) and several temperate plant species (Fitter and Fitter, 2002; Miller-Rushing and Inouye, 2009), it is rarely reported for warm tropical climate in West Africa. This study was therefore conducted to determine the pattern of flowering in *T. cacao* and its relatives in response to climatic variables under tropical West African conditions.

MATERIALS AND METHODS

Study species and location

The five *Theobroma* species (*T. bicolor, T. grandiflorum, T. speciosum, T. microcarpum,* and *T. cacao*) and one *Herrania* species used in this study were introduced from the International Cocoa Genebank Collection, Trinidad into the Nigerian Genebank that is conserved at the Cocoa Research Institute of Nigeria headquarters in Ibadan, Nigeria (Lat. 07° 10´ N Long. 03° 52´ E; 122 m asl). They were planted in the germplasm conservation plot of cocoa relatives species located at N5/3A experimental block of the institute. Each of the species was represented by some 15 and 20 trees depending on number successfully established and species growth habit. Large trees like *T. bicolor and T. grandiflorum* were planted at a spacing of 3.6 × 3.6 m, while smaller trees like *T. microcarpum, T. speciosum*, *T. cacao, and Herrania* spp*.* were planted at a spacing of 3.0 × 3.0 m. These species were planted under the shade of *Gliricidia* spp.

Data collection on flowering incidence

Flowering incidence was monitored weekly and the data was recorded from the flowering trunk and branches. Since these species were cauliflorous, producing flowers on trunks and branches, it was quite easy to observe presence or absence of flowers. Flowering was scored as (1 = mature bud or flowers available) and (0 = no buds or flowers available). The minimum number of flowers required to score as 1 was never less than five flowers. Data collected was then summarized on a monthly basis. Monthly record of flowering incidence was done over a 10 year period (1989 to 1998).

Weather data collection

During the same period, record of climatic variables including rainfall amount (mm), minimum temperature (°C), maximum temperature (°C), temperature at 13.00 h, relative humidity (%) at 9.00 h and 13.00 h and sunshine hours was also taken. The weather station was located within 500 meters distance from the plot. Monthly trend in the climatic variables over the 10 years of study is shown in Table 3. The monthly distribution of annual rainfall amount followed the known bi-modal pattern with a break in August. Rainfall distribution ranged from 2.7 mm in January to 54.2 mm in March during the dry season that lasts from November to March; and 106.9 mm in April to 207.9 mm in July during the rainy season from April to October. Relative humidity at 09.00 h was usually high ranging from 70.5% in January to 88.9% in July. However, at 13.00 h, the relative humidity ranged from 41.7% in February to 82.1% in July. During the dry season in November to March, relative humidity at 13.00 h ranges from 41.7 to 64.7%. This however increased from 63.9 to 82.1% during the rainy period. The sunshine hours ranged from 2.2 h in August to 6.2 h in November and December. The minimum temperature ranged from 17.2°C in January to 20.9°C in May, while the maximum temperature ranged from 25.3°C in August to 29.2°C in May. The temperature at 13.00 h varied during the season from 27.3°C in August to 31.7°C in April.

Data analysis

Analysis of data was done using the SAS package v.9.2 (SAS Institute). The data on monthly flowering was summarized with the descriptive statistics option. The means obtained was used to plot a curve of annual pattern of flowering in the *Theobroma* and *Herrania* species. Analysis of variance was performed on the raw data of flowering incidence scores. The Student Newman-Keuls method was used to separate significant means of main effects on flowering incidence. Correlation analysis was carried out to determine the response of monthly flowering incidence in the species to climatic variables. In an attempt to understand the annual flowering pattern,

Table 1. Mean and standard error of flowering incidence in six *Theobroma* and *Herrania* species over a 10-year period (1989 to 1998) in Ibadan, Nigeria.

Month	*T. bicolor*	*T. speciosum*	*T. cacao*	*T. microcarpum*	*T. grandiflorum*	*Herrania* spp.
January	0.9 ± 0.10	0.9 ± 0.10	1.0	1.0	1.0	0.5 ± 0.17
February	1.0	1.0	1.0	1.0	1.0	0.4 ± 0.16
March	1.0	0.9 ± 0.11	1.0	0.7 ± 0.17	1.0	0.3 ± 0.17
April	0.8 ± 0.13	0.7 ± 0.15	1.0	0.9 ± 0.10	0.4 ± 016	0.6 ± 0.16
May	0.9 ± 0.10	0.3 ± 0.15	0.9 ± 0.10	0.9 ± 0.10	0.3 ± 0.15	0.6 ± 0.17
June	0.9 ± 0.10	0.3 ± 0.15	1.0	1.0	0.6 ± 0.16	0.9 ± 0.10
July	0.9 ± 0.10	0.0	1.0	1.0	0.5 ± 0.17	0.9 ± 0.10
August	0.7 ± 0.15	0.0	1.0	1.0	0.4 ± 0.16	1.0
September	0.5 ± 0.17	0.1 ± 0.10	1.0	0.6 ± 0.16	0.2 ± 0.13	0.8 ± 0.13
October	0.3 ± 0.15	0.2 ± 0.13	1.0	0.2 ± 0.13	0.4 ± 0.16	0.3 ± 0.15
November	0.6 ± 0.16	0.3 ± 0.15	1.0	0.1 ± 0.10	0.5 ± 0.17	0.3 ± 0.15
December	0.9 ± 0.10	0.5 ± 0.17	0.9 ± 0.10	0.5 ± 0.17	0.8 ± 0.13	0.2 ± 0.13

Table 2. Analysis of variance on flowering pattern in six *Theobroma* and *Herrania* species.

Source	df	Raw - values	
		MS	F-value
Species (S)	5	4.55	37.25***
Month (M)	11	1.57	12.5***
S × M	55	0.57	4.83***
Error	648	0.13	
Total	719		

***: Significant at *P*-level of 0.001.

flowering cycle was divided into three stages: a, non-flowering (*nf*) period (score of 0.0 to 0.3), when there was generally no flowering (floral dormancy); b, lean flowering (*lf*) period (score of 0.4 to 0.6), during which floral transition takes place and flowering occur in response to environmental factors, which could either trigger or de-activate flowering processes.

This period occur in either of two sub-phases; the none to lean (*nl*) flowering phase, from dormancy to floral evocation; or, peak to lean (*pl*) flowering phase, when flowering drops from its peak to lean flowering before cessation and floral dormancy; c, full bloom period (score of 0.7 to 1.0), when flowering is in abundance and its peak in the cycle.

RESULTS

Pattern of flowering incidence among species

The mean and standard error of monthly flowering incidence in all six species is presented in Table 1. Analysis of variance shown in Table 2 indicated that among the species and months of the year. From the analysis of variance, the species × month interaction effect was also significant ($p < 0.001$) on flowering incidence among the species. Flowering follows the pattern in each species as follows:

T. bicolor

Flowering transition begins at the onset of dry season in November and incidence continues to its first peak in March (Figure 1). A second peak of flowering is achieved in May to July before tailing off in August. Generally, *T. bicolor* rarely flowers between the months of September and October. There appear to be two phases of flowering in *T. bicolor*, that is, the November to March phase with abundant flowering followed by the May to July phase with lean flowering. This indicated two major cycles of flowering in *T. bicolor* during the flowering season.

T. speciosum

Events leading to floral transition in *T. speciosum* begin at the onset of dry season in November/December. Flowering incidence therefore occurred during the dry season from December to April with its peak in January to March. Flowering in *T. speciosum* follows an alternating cycle between incidence during the dry season and near total absence of flowering during the rainy season. Only one peak of flowering in *T. speciosum*

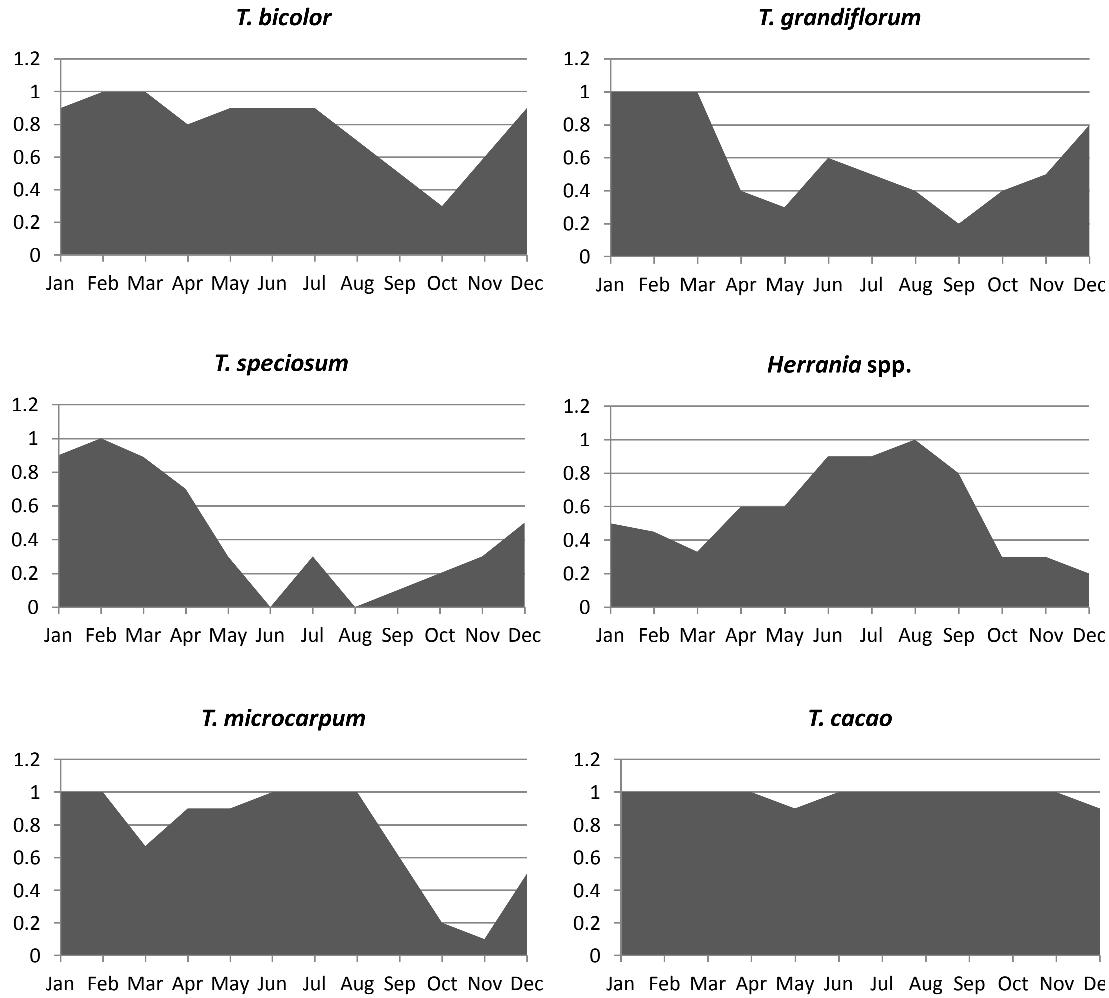

Figure 1. Mean annual flowering pattern in six *theobroma* and *Herrania* species observed over a 10 year period in Nigeria flowering score ranges from none flowering (0.0 to 3.0), lean flowering (4.0 to 6.0) to full flowering (0.7 to 1.0).

occurs in February to March.

T. microcarpum

Flowering transition begins with lean flowering around December leading to full flowering period extending from January to August. There appear to be three cycles of flowering bloom during the flowering period. The first bloom occur around January to February, the second in April to May and the third, June to August. Flowering in *T. microcarpum* appeared highly favoured during the wet season during high rainfall amounts and relative humidity.

T. grandiflorum

Flowering in *T. grandiflorum* presents a unique pattern of extended period of shy flowering (0.4 to 0.6) for about six to seven months alternating with a short full flowering (0.7 to 1.0) period of only four months. Floral transition which begins in November leads to full flowering that lasts till March. This is followed by a sharp drop to a lean flowering mode extending from April till November. Generally, flowering incidence is favoured during the dry season and drops significantly during the wet period in *T. grandiflorum*.

Herrania spp.

Flowering in *Herrania* spp. follows a pattern antithesis to that in *T*. *grandiflorum*. A long lean flowering from January to May is followed by a full flowering period from June to September, which sharply drops to non-flowering (0.0 to 0.3) period from October to December. *Herrania* flowers intensely during the rainy period between May and September. There is rarely any flowering between

October and March. Reliable flowering begins around April and May, and peaks between June and August. Flowering tails off in September.

Flowering pattern variation and response to environmental variables

Analysis showed that flowering incidence in *T*. *speciosum* had a significant positive correlation (r = 0.655, P = 0.015) with the duration of sunshine hours. However, flowering in *Herrania* spp. had a high negative correlation (r = – 0.906, P < 0.0001) with the duration of sunshine hours. Flowering in *T. speciosum* (r = – 0.743, P = 0.003) and *T. grandiflorum* (r = – 0.716, P = 0.006) was highly negatively correlated with rainfall. However, flowering incidence in *Herrania* spp. has a significantly positively correlated (r = 0.743, P = 0.004) with rainfall. Flowering incidence in *T. cacao, T. bicolor* and *T. microcarpum* appeared not to respond significantly to changes in climatic variables studied. Rainfall was strongly negatively correlated with sunshine hours (r = – 0.813, P = 0.001) while strongly positively correlated with relative humidity at 09.00 h (r = 0.836, P < 0.001), 13.00 h (r = 0.878, P < 0.001), and minimum temperature (r = 0.734, P < 0.001).

DISCUSSION

Understanding the pattern of flowering in *T. cacao* and its crop, wild relatives provides baseline information that is required in the inter-specific hybridization scheme in the cocoa breeding program. This provides a guide to the best period when inter-specific hybridization program involving these species could be carried out and synchronization of pollination among the species. Results obtained in this study showed that the intrinsic rhythms of physiological processes influencing flowering differ amongst the *Theobroma* and *Herrania* species under the Nigerian conditions. The pattern of flowering in *Herrania* spp. differs completely from its related species, *Theobroma*. *Herrania* spp. blooms mainly during the rainy season (April to September) in this environment and ceases flowering immediately at the onset of the dry season. However, spontaneous flowering occurs in January, perhaps as a trigger response to off-season rainfall or drop in temperature. Consequently, inter-specific hybridization involving *Herrania*, particularly as a female parent should be done during the rainy season.

A chart of flowering incidence pattern (Figure 2) provides a guide to effective planning of inter-specific hybridization program among the species. In planning pollination for an inter-specific hybridization scheme, the best period to get flowers in all the six species is between January and April. This period coincides with the peak of dry season and onset of rainy season and takes particular advantage of the abundant flowering in *T. bicolor, T. speciosum, T. microcarpum, and T. grandiflorum*. There is also lean flowering in *Herrania* spp. at this time that may provide pollens for pollination. From this study, it is shown that any inter-specific hybridization program involving all these species can best be carried out between January and April. During this period, all the *Theobroma* species are in good bloom and flowering would have begun in *Herrania* species, *T. cacao* on the other hand, flowers throughout the year. The period between June and August at the height of rainy season also provides another opportunity for inter-specific hybridization among all species except crosses involving *T. speciosum*. Hybridization scheme involving *T. speciosum* should not exceed April and crossing involving *Herrania* spp. should be targeted between April and September. However, in the case of *T. cacao*, inter-specific hybridization with any of the relatives can take place anytime of the year depending on availability of flower on the crop wild relative.

Generally, plant population show positively skewed flowering distributions, perhaps because most individuals begin flowering in response to a discrete environmental cue, while end of flowering is not similarly truncated (Ratchcke and Lacey, 1985; Forrest and Thomson, 2010). In this study, apart from *T. cacao*, all other *Theobroma* species begin flowering at the onset of dry season in October to December, most likely in response to increased temperature and longer day length. *Herrania* species on the other hand, appeared to be undergoing gradual adaptation in this environment with shy flowering observed in December/January. Flowering in *Herrania* appeared specifically adapted to high rainfall amounts and short sunshine hours in this environment and perhaps, this is its unique adaptation qualities as in the Amazon forests where it evolved (Cuatrecasas, 1964). This poor response of *Herrania* spp. may be in consonance with Fitter and Fitter (2002) who reported that species far away from their center of distribution were less likely to respond to a rise in temperature.

The significant effects of the months, the interaction of species, and month on flowering indicated that environmental factors, other than genetic differences among the species, which vary monthly greatly influence flowering. From this study, flowering in *T. speciosum* was most favoured during the dry season when the maximum temperature was high and rainfall and relative humidity at noon was low. In *T. speciosum*, seasonal flowering was restricted to the dry period before rainfall becomes steady in the year. Flowering in *T. grandiflorum* gave a particularly interesting picture as a direct antithesis to the bimodal rainfall distribution pattern in Southern Nigeria. It was at the peaks of the two modules that flowering incidence was lowest. Flowering in *Herrania* spp. appeared dependent mainly on the availability of high amount of rainfall and high relative humidity. However, flowering in *Herrania* spp. is not favoured during the

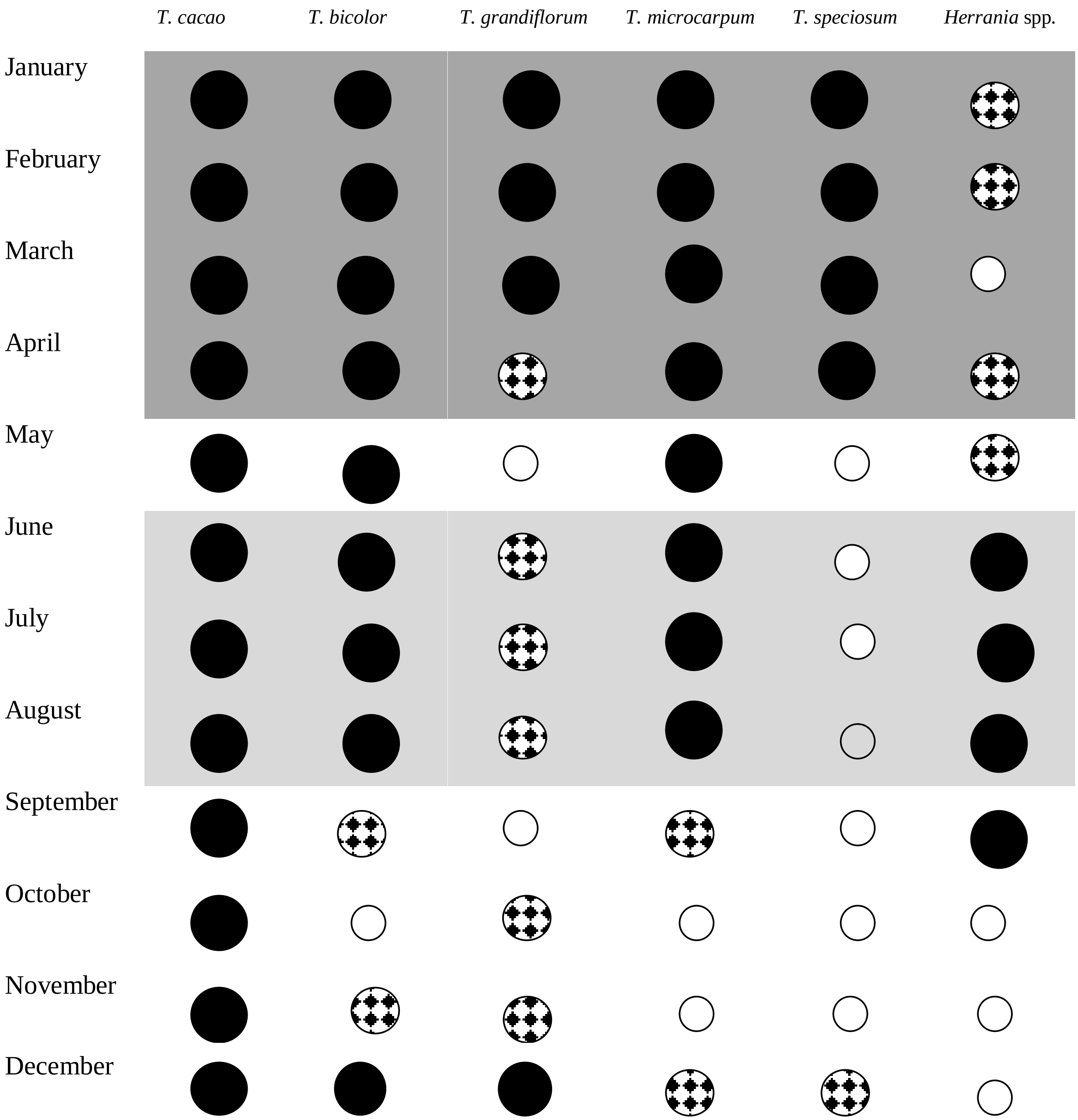

Figure 2. A chart of flowering incidence pattern in six *Theobroma* and *Herrania* species obtained over a 10-year period indicating full bloom (solid circle), lean-flowering (perforated solid circle) and non-flowering period (transparent circle).

period of high temperature. The sharp drop in sunshine hours by almost one hour to a mean of 4.4 h daily in May and further down to just 2.2 h in August from a duration of 5.0 to 6.2 h daily between November and April could have triggered flower evocation in *Herrania* spp.

In *T. speciosum* and *T. grandiflorum,* flower buds remain dormant during periods of continuous water supply and flower only after exposure to a 'dry shock'. This is similar to the 'dry shock' leading to flower bud burst in coffee, *Coffea* spp. (Alvim and Alvim, 1975). In *Herrania* spp. on the other hand, flowering exhibited strong 'hydrophilic' phenomenon. Flowering in this species appeared dependent mainly on continuous supply of water and humid conditions while its flower buds get dormant during dry periods. A period of 'moisture presence' is required to break dormancy of

Table 3. Mean and standard error of climatic variables observed over a 10-year period (1989 to 1998) of flowering incidence in six *Theobroma and Herrania* species in Ibadan, Nigeria.

Month	Rainfall (mm)	RH at 0900 h (%)	RH at 1300 h	Maximum temperature (°C)	Minimum temperature(°C)	Temperature at 1300 h (°C)	Sunshine hours
January	2.7 ± 1.81	70.5 ± 3.22	44.9 ± 3.22	26.1 ± 0.40	17.2 ± 0.76	28.8 ± 0.57	5.0 ± 0.76
February	28.9 ± 8.87	71.7 ± 2.61	41.7 ± 3.04	28.3 ± 0.30	19.6 ± 0.79	30.1 ± 0.69	5.1 ± 0.81
March	54.2 ± 12.89	76.1 ± 1.37	50.7 ± 2.71	29.2 ± 0.27	20.0 ± 0.73	31.0 ± 0.72	5.4 ± 0.61
April	106.9 ± 16.12	80.5 ± 0.93	63.9 ± 1.55	28.5 ± 0.19	20.3 ± 1.01	31.7 ± 1.37	5.0 ± 0.26
May	165.9 ± 12.46	83.5 ± 0.56	71.1 ± 1.34	28.2 ± 0.28	20.9 ± 0.63	30.2 ± 0.55	4.4 ± 0.49
June	199.8 ± 18.40	85.2 ± 0.82	75.3 ± 0.67	27.0 ± 0.17	20.6 ± 0.50	28.8 ± 0.28	3.7 ± 0.29
July	207.9 ± 32.97	88.9 ± 0.37	82.1 ± 0.77	25.5 ± 0.21	20.7 ± 0.33	27.7 ± 0.23	2.7 ± 0.54
August	150.9 ± 20.08	88.8 ± 0.56	80.8 ± 0.59	25.3 ± 0.13	20.5 ± 0.58	27.3 ± 0.20	2.2 ± 0.43
September	181.1 ± 20.93	87.9 ± 0.51	78.4 ± 0.95	25.8 ± 0.16	20.5 ± 0.58	27.8 ± 0.18	2.8 ± 0.69
October	154.5 ± 11.50	86.4 ± 0.81	73.9 ± 1.21	27.0 ± 0.15	20.0 ± 0.65	28.0 ± 0.18	4.4 ± 0.45
November	16.6 ± 5.28	82.5 ± 0.89	64.7 ± 2.58	27.9 ± 0.29	20.0 ± 0.65	29.0 ± 0.42	6.2 ± 0.45
December	20.0 ± 14.36	78.7 ± 1.79	55.7 ± 2.51	27.0 ± 0.26	19.5 ± 1.02	29.2 ± 0.66	6.2 ± 0.38

flower buds in *Herrania* spp. It appears that flowering in *T. cacao*, which takes place throughout the year, although with varying intensities somewhat independent of variation in environmental conditions, has evolved great resilience and adaptation to the local tropical weather.

T. bicolor and *T. microcarpum* also appear to follow *T. cacao* in the same pattern of flowering from 10 to 11 months of the year, and showed greater adaptability than *T. speciosum* adapted to flowering only during the dry months, and *Herrania* spp. adapted to flowering only during the wet months. *T. grandiflorum* on the other hand flowers profusely during the dry season but shyly during the rainy season. The plasticity in flowering among these species especially *T. cacao, T. bicolor,* and *T. microcarpum* may prevent large fluctuation in reproductive success despite climatic variation as also observed by Forrest and Thomson (2010).

In conclusion, a long-term observation in flowering has helped to establish the pattern of flowering incidence among the six *Theobroma* and *Herrania* species used in this study. This information has also been used to provide a guide to the appropriate time of pollination for an inter-specific hybridization scheme to exploit important variation in these crop wild relatives for genetic improvement of the cultivated cocoa and other species of importance. This scheme will be of great utility to cocoa improvement programs in cocoa producing countries especially in tropical West and Central African humid forest areas which accounted for more than 70% of the world's cocoa production.

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