

VARIATION IN FLOWERING PHENOLOGY OF *CASSIA FISTULA* LINN. POPULATION IN OTA, OGUN STATE. NIGERIA.

Okusanya, O. T.¹, Shonubi, O. O.² Bello, O. A.¹ and Bamidele, J. F.³

¹Department of Biological Science, Applied Biology and Biotechnology Unit, Covenant University, Ota, Ogun State. Nigeria.

²Department of Botany, University of Lagos, Yaba, Lagos State. Nigeria.

³Department of Plant Biology and Biotechnology, University of Benin, Benin City. Edo State. Nigeria.

Corresponding Author's email address: okusanya41@yahoo.com

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ABSTRACT

Flowering phenology in the population of *Cassia fistula* Linn. at Ota, Ogun State, Nigeria was investigated for three years to determine if there was variation in the phenology and the patterns were compared with some environmental factors to determine if there was any correlation. The number of plants flowering each month was monitored for three years. Data for mean monthly maximum and minimum temperatures, mean monthly rainfall and number of days with rain per month were obtained from Meteorological Institute, Oshodi, Lagos-Nigeria. In each year, there was synchronous flowering showing early and late flowering plants but the start and end of flowering vary between years. The peak months of flowering vary from year to year so also the period of flowering. Statistical analysis showed significant difference in flowering pattern between two of the years and from month to month. All these show clear variation in the flowering phenology of the species. Commencement of flowering was correlated with the rainfall and temperature in July and August while the end was correlated with the amount of rainfall and number of rainy days. With the overlap of flowering between the years, flowering is continuous in contrast to annual flowering in its country of origin; a phenomenon that has not been reported for the species before. The ecological implication was discussed.

Key words: Cassia, correlation, flowering, phenology, rainfall, temperature.

INTRODUCTION

Cassia fistula Linn. is an ornamental and medicinal deciduous or semi-deciduous tree commonly known as the 'golden shower tree', golden pipe tree, Indian Laburnum, Amaltas or purging Cassia. It is also referred to as "Aragvadha" meaning 'disease killer' because of its use in treating many diseases (Akinyede and Amoo, 2009; Orwa *et al.*, 2009). It is of the large genus Cassia and it belongs to the subfamily Caesalpiniaceae and the family Fabaceae (Satorelli *et al.*, 2009). Its origin is from the Indian subcontinent and it is distributed in various tropical and sub-tropical regions including Asia, Central and South America, Australia, West Indies, Africa, (Orwa *et al.*, 2009) and in Florida and Texas in the United States of America (Brown, 2001). It has recently been spotted in Brick Township, New Jersey, U. S. A. and in Israel by the first author in this publication.

The flowers are conspicuous and large, golden-yellow in colour and borne on raceme inflorescence on which there could be as many as 84 flowers (Shonubi *et al.*, 2016). The golden-

yellow petals remain on the flower for much longer after the senescence of the other floral parts, a process which helps the species maintain its ornamental property (Shonubi *et al.*, 2016). The fruits are long, usually straight indehiscent brownish-black pods. The seeds are glabrous and glossy-brown in colour and they do not readily germinate unless scarified (Babalola *et al.*, 2014; Karaboon *et al.*, 2005).

C. fistula is widely used in landscaping because of its golden-yellow flowers. It is also drought tolerant and has low maintenance requirements (Ghouse *et al.*, 1980). It was planted at Covenant University, Ota, Ogun State in 2002 at the inception of the University and it is the dominant landscaping species there. The plants started flowering about 10 years ago. The population consists of more than 200 trees planted along the major roads in the University.

Its ornamental property (flowering) is mainly responsible for its rapid spread into many areas outside of the tropics and subtropical regions (Bosch, 2007). Apart from its large yellow flowers,

a long flowering period would enhance its ornamental property. Murali (2000) reported flowering in South India between March and June, with rain falling between May and November; Brown (2001) reported flowering in South Florida between April and August with rainfall between June and September; Bosch (2007) reported flowering in Singapore between June and August with the monsoon season between November and January and Kauer *et al.*, (2013) reported flowering in North West Punjab, India between April and September with rainfall between July and September.

All flowering occurred during the high temperature (summer) months and during the dry periods going into the wet periods in these cases, a common situation with Neotropical species (Bentos *et al.*, 2008). Shonubi *et al.* (2016) summarized the periods of flowering of *C. fistula* from different parts of the tropics, compared the results with the flowering period of the species in Ota, Ogun State, Nigeria and concluded that environmental factors specifically temperature and rainfall may be the major factors affecting flowering in *C. fistula*. Brown (2011) also reported that the severity of cold temperature in winter and spring affects the onset of flowering and the number of Intense Blooming Days (IBD) in *C. fistula* in Florida.

As a result of the above and the profuse flowering of the species observed during the last research (Shonubi, *et al.*, 2016), it was decided to study the flowering phenology of *C. fistula* during three consecutive flowering periods to determine whether there would be variation in the phenology and if so, which environmental factors at the location in Ota, Ogun State may be responsible.

MATERIALS AND METHODS

Study site: The population studied in this work and their geographic locations were as reported in Shonubi *et al.* (2016).

Method: The population was observed for onset of flowering and number of trees flowering each month was monitored until there was no more flowering. This was done for three consecutive flowering seasons in 2013-2014, (Year 1); 2014-2015, (Year 2) and 2015-2016, (Year 3).

The meteorological data for (i) mean monthly maximum and minimum temperatures (ii) mean monthly rainfall and (iii) number of rainy days in each month for Abeokuta, the nearest town to Ota, for which the data was available in the 3 flowering periods, were obtained from the Meteorological Institute, Oshodi, Lagos.

The flowering patterns taken as number of plants flowering each month in the three years were compared with one another using the 2-way ANOVA to determine if there were any differences in the flowering phenology in the three years by month and by year. In addition, the flowering patterns also taken as number of plants flowering per month were compared with the meteorological data, temperature and rainfall, to determine if there was any correlation using the Spearman method (Krzanowski 2007).

RESULTS AND DISCUSSION

Figure 1 showed that there was synchronous flowering in the *C. fistula* population in each of the three flowering seasons. This was as reported by Murali (2000) and by Shonubi *et al.* (2016). Similarly, the flowering in the population follows a typical near normal distribution curve starting with few plants that are termed early flowering between August and November; then flowering increased rapidly till reaching a peak, the Intense Blooming Days, (IBD), (Brown, 2011) between November and May/June when the plants are termed late flowering. After this period, there was a decline in number of plants flowering probably due either to ageing of the flowers leading to senescence of the flowers or to pod (fruit) formation until there was no more flowering in July/August.

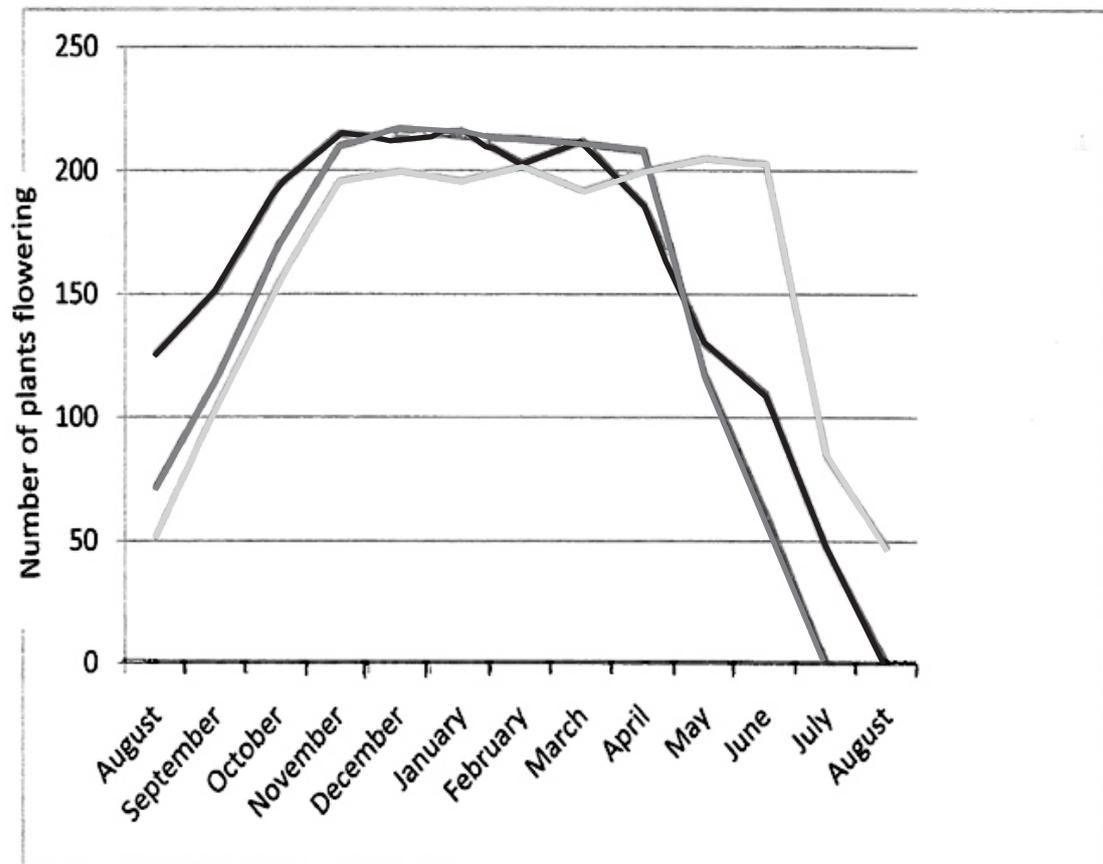


Figure 1. Comparative number of *C. fistula* plants flowering in each month during three years of flowering at Ota, Ogun State, Nigeria. Blue line 2013-2014; red line 2014-2015; green line 2015-2016

The non-uniform flowering of the population is not uncommon in many species. Its cause has not been well established. Possible reasons include genetic variation within the population or it may be due to edaphic factors since the population occupies a fairly large area. However, genetic variation may be limited since the individuals were from the same source and were planted at the same time (pers. comm.).

Flowering started in August in each year, probably in July by Year 2, indicating that the environmental conditions in July/August may have triggered flowering. Brown (2011) stated that the flowering

of most commonly-grown tropical flowering trees is controlled by temperature. Also, Korner and Basler (2010) reported that in extra humid tropical areas, temperature is one of the three most important factors controlling phenology in dominant forest tree species. In this area of Nigeria, July and August of each year had the lowest mean maximum and minimum temperatures (Table 1a and 1b). This implies that a drop in temperature at this period of the year acts as a stimulus to trigger flowering in this species. The high correlation between temperature and flowering ($r = 0.8986$ in Year 1; $r = 0.8647$ in Year 2 and $r = 0.7813$ in Year 3) supports this assertion.

Table 1. METEOROLOGICAL DATA FOR THE THREE FLOWERING YEARS OF *C. FISTULA* AT OTA, OGUN STATE, NIGERIA

	January	February	March	April	May	June	July	August	September	October	November	December
Table 1a. MEAN MAXIMUM TEMPERATURE °C												
2013	35.9	36.3	35.2	33.5	32.1	31.1	29.1	29.1	30.4	31.9	33.8	34.5
2014	35.1	36.4	34.8	34.1	32.8	31.6	29.7	29.1	30.1	31.7	33.2	35.1
2015	35.4	36.1	36.1	35.2	33.9	30.8	30.1	30.1	30.2	32.2	33.9	35.5
2016	36.2	36.6	36.9	35.8	33.7	32.8	32.5	32.9	N/A	N/A	N/A	N/A
Table 1b. MEAN MINIMUM TEMPERATURE °C												
2013	22.8	24.6	24.7	23.9	23.7	23.7	22.1	22.2	23.6	23.7	24.6	23.7
2014	25.1	25.1	25.2	24.7	24.5	24.1	23.8	22.9	23.4	23.4	24.1	23.6
2015	25.1	25.8	25.9	25.3	25.1	24.1	23.6	23.6	23.9	24.2	24.8	24.1
2016	23.2	25.9	26.8	26.1	26.2	25.6	25.1	25.5	N/A	N/A	N/A	N/A
Table 1c. MONTHLY RAINFALL (mm)												
2013	5.7	33.8	82.2	221.4	161.3	168.9	142	80.6	157.1	87.2	10.6	11.1
2014	16.1	19.4	187.3	179.2	144.2	206.1	163	96.5	274.8	222.5	37.7	TRACE
2015	TRACE	16.5	52.4	90.1	106.3	168.6	78.1	31.2	209.7	169.9	78.1	TRACE
2016	7.9	20.1	66.4	111.2	84.4	120.2	86.6	36.8	N/A	N/A	N/A	N/A
Table 1d. NUMBER OF DAYS WITH RAIN PER MONTH												
2013	1	2	8	14	13	12	13	10	10	12	1	2
2014	4	4	9	10	14	13	17	12	17	15	6	0
2015	0	3	6	7	10	12	15	5	16	16	3	0
2016	2	5	8	9	8	10	13	7	N/A	N/A	N/A	N/A

During the 'August break', there is usually a break in rainfall (Table 1c) with concomitant decrease in number of rainy days (Table 1d) and possibly of storm days. The significant difference in number of early flowering plants in August from year to year (Fig. 1) ($p < 0.05$) may be due to the severity of the August break (Table 1c). In Year 3, with the lowest number of early flowering plants in August, the drop in rainfall was from low 78 mm to 31 mm; in Year 2, with the highest number, the drop in rainfall was from high 163 mm to 97 mm while in Year 1 with medium number, it was from 142 mm to 81 mm (Table 1c). Thus for *C. fistula* at Ota, it appears that temperature and rainfall determine the start of flowering. A significant change in climate is expected to alter the flowering start dates for many tropical ornamental flowering trees (Brown, 2011). The negative correlation ($r = -0.5603$, Year 1; -0.6030 , Year 2 and -0.1744 Year 3) between rainfall and flowering supports this assertion.

All the individual plants did not commence flowering at the same time, neither did they end flowering at the same time in each of the three years (Fig. 1). Analysis of Variance (ANOVA)

showed that there is significant difference in the pattern of flowering between Year 1 and Year 2 only ($p < 0.05$). There was also significant difference from month to month ($p < 0.05$) especially in July and August ($p < 0.02$) in the declining period. Thus there was variation in flowering phenology between the months and between some years. There was also variation in flowering phenology within the locality (Bawa, 1983) and across the habitat (Primack, 1980). In addition, since the three curves in Figure 1 did not fully synchronise with each other, most especially at the start of flowering, July to September and towards the end of flowering from April to August, it is obvious that there is variation in the flowering phenology of *C. fistula* population in Ota. Variation in the weather mainly temperature and rainfall, in different years may be responsible for this.

Figure 2 showed that *C. fistula* has continuous flowering. This is similar to the report by Bentos *et al.* (2008) for five pioneer tree species from Central Amazon. The figure for *C. fistula* (Fig. 2) is similar to that for *Isertia hypoleuca* Benth., one of the five pioneer tree species reported by Bentos *et*

al. (2008). The continuous flowering indicates that resources are available to pollinators and dispersers all the year round. The ecological importance of this to *C. fistula* is that being an out crossed and self-incompatible species, the chances

of cross-pollination are enhanced. The continuous flowering also has competitive advantage of making nectar available throughout the year.

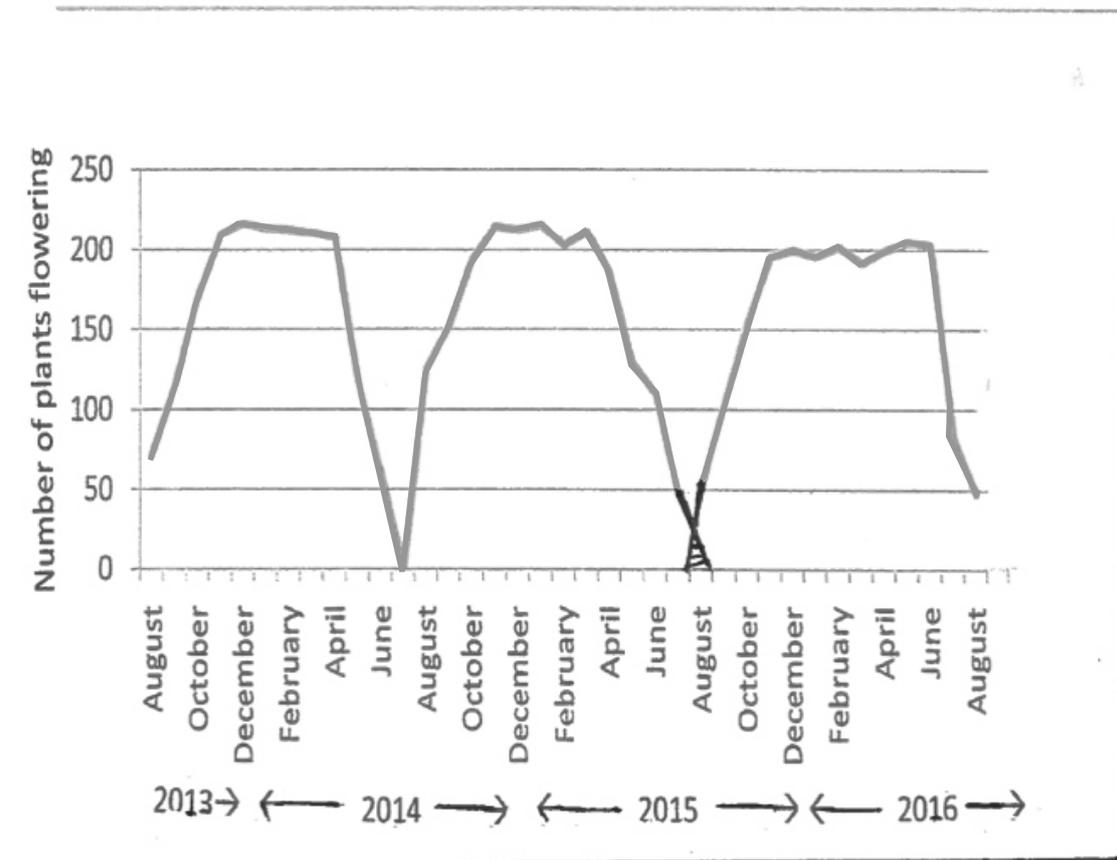


Figure 2. Number of *C. fistula* plants flowering in each month at Ota, Ogun State, Nigeria over three years. Hatched area shows overlap in flowering

The continuous flowering of *C. fistula* in Ota, Nigeria is contrary to the five-month annual flowering in its native country India (Murali, 2000). Obviously, the environmental conditions in Ota, Nigeria must be more conducive to its development than the conditions in India. Long period of flowering will not only increase the chances of cross-pollination in an outcrossed and self-incompatible species as well as increase (pod) fruit and seed production, but it may also result in better chances of dispersal and distribution. Benthos *et al.* (2008) reported that continuous flowering species tend to exhibit continuous fruiting. The dry pods (fruits) of *C. fistula* are present on the mother trees throughout the year making dispersal possible throughout the year;

consequently germination may be possible whenever the conditions are favourable. Whether this species can become a successful invasive species in South West Nigeria or even in the whole of Nigeria is yet to be seen. However this is highly unlikely in view of the extremely poor natural germination of the seeds. Scarification is required for good seed germination (Babalola *et al.*, 2014; Karaboon *et al.*, 2005).

In view of this result and because the climate at Ota is not representative of all the climatic zones in Nigeria, another experiment is being planned to determine the flowering phenology of *C. fistula* in the various climatic zones of Nigeria.

One of the ten new seedlings planted in Lagos at the University of Lagos Estate in 2013 first flowered in April 2016 just after three years and that was the only month it flowered. It is probably a late flowering type. Further investigation is being carried out concerning this plant and the others especially to determine whether their flowering would then commence in August like those in Ota and for how long they would flower.

It is abundantly clear that rainfall, especially number of days with rainfall affect the length of flowering (Fig. 1; Table 1c and 1d). With high number of rainfall days, 13 in May and 12 in June (Table 1d), and with concomitant high rainfall, 144 mm in May and 206 mm in June, (Table 1c), flowering stopped in June of Year 1 (Fig. 1). However, with few rainy days, eight days in May and 10 in June, and with subsequent low rainfall, 84 mm in May and 120 mm in June (Table 1c) and possibly few rain storms, flowering continued till August in Year 3. Many flowers were observed to fall down during rain storms (Shonubi *et al.*, 2016). Benthos *et al.* (2008) also indicated that heavy rainfall damage flowers. The negative correlation ($r = -0.5603$ in Year 1; -0.6030 in Year 2 and -0.1744 in Year 3) between rainfall and flowering supports this assertion. This is probably another reason why the species flowers during the dry season and early rainy season.

This is an interesting result in that it contrasts with reported peak flowering in rainy season by tropical rainforest species. This difference can be accounted for by the fact that when *C. fistula* flowers, it is virtually leafless thus there are no leaves to protect the flowers from the rains unlike the tropical evergreen trees in the rainforest. So the species may have evolved the mechanism for flowering during the dry season to early rainy season for effective reproduction. It may also be pertinent to state that while a drop in temperature as in July and August triggers flowering, high temperature during the dry season in November to April, enhances flowering (Table 1a and 1b).

The peak of flowering, the Intense Blooming Days (IBD) varies (Figs. 1 and 2). In year 1 it was from November to April, in Year 2, the peak was from November to March while in Year 3 it was between November and June; up to two and three

months wider than Years 1 and 2. The increase to June in Year 3 may be due to generally more favourable weather conditions, mainly higher temperature (Table 1a and 1b), less heavy rainfall and fewer rainy days during the period (Table 1c and 1d). The high positive correlation coefficient, ($r = 0.8986$ in Year 1; 0.8647 in Year 2 and 0.7813 in Year 3,) between temperature and flowering and the negative correlation between rainfall and flowering support this assertion.

In like manner, the last month for flowering was different. In Year 1, it was in June, in Year 2 it was in July and in Year 3 it was August (Fig. 1). What is remarkable about this extended flowering till July and August is that flowering started again in the early flowering plants in July (Fig. 2). So, it appears that this population of *C. fistula* might flower continuously from year to year making it a remarkable ornamental plant. This phenomenon has never been reported before for this species. Temperature has been reported as one of the important environmental factors that affect flowering (Cook, *et al.*, 2012; Nemani *et al.*, 2003). Other factors include photoperiod, (Evans, 1975); length of sunshine, (Ng, 1977) and rainfall (Opler *et al.*, 1976). A number of environmental factors may even interact to determine flowering onset (Rathcke and Lacey, 1985).

The implication of the above is that this species which flowers for only five months in its country of origin India flowered practically throughout the year in Ota, Ogun State, Nigeria. Thus, it is better suited as an ornamental plant in this part of Nigeria than its country of origin. *C. fistula*, an exotic species in Nigeria may have shifted flowering pattern in another climate showing flowering plasticity (Wolkovich *et al.*, 2013).

Flowering throughout a year may not be unique to this species. Aikpokpodion (2012) reported that *Theobroma cacao* introduced from Trinidad, West Indies to Ibadan, Nigeria flowered for 12 months. However, it was not reported how long it flowered in Trinidad.

The highest number of flowering plants in Year 3 (205) was slightly smaller than in Years 1 and 2 (217 and 216 respectively) (Fig. 2). This may indicate either that some plants which flowered in

Years 1 and 2 did not flower in Year 3 or that some plants may have died. A plausible explanation could be mast flowering where plants after using a lot of resources to produce many flowers in a year, produce fewer flowers in the following year while recouping the resources used earlier.

The high number of flowering plants in July in Year 3 (144) was further investigated to determine whether they were old flowers denoted by the senescence of the floral parts except the brightly coloured yellow petals (Shonubi, *et al.*, 2016) or new flowers denoted by the presence of many flower buds on the inflorescence and the presence of all or most floral parts on the flowers. The investigation showed that about 35% of the trees had new flowers, thus some plants started flowering in July as was possibly the case in Year 2.

Figure 2 showed clearly that there was the strong possibility of overlap between the flowering periods in Years 2 and 3 (hatched area). The population was recorded as starting flowering in August but could have possibly started in July consequently the overlap. Thus a remarkable discovery from this investigation is the ability of this population of *C. fistula* to flower continuously from year to year in contrast to five-month annual flowering in its country of origin. This flowering behaviour can potentially be exploited by the horticultural industry in Nigeria.

Except in one report was it made clear that the flowering period referred to a population rather than individual tree. It is hereby suggested that researchers should indicate which group flowering report refers to. In addition, it may be necessary to indicate the environmental conditions prevailing in the area at the time of observation.

In conclusion, environmental factors, mainly temperature and rainfall affect the flowering phenology of *C. fistula* in Ota, Ogun State even though it is a pan tropical ornamental plant.

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REFERENCES

- Aipokpodion, P. O. 2012. Phenology of flowering in cacao (*Theobroma cacao*) and its related species in Nigeria. *African Journal of Agricultural Research* 7(23): 3395-3401.
- Akinyede, A. I. and Amoo, I. A. 2009. Chemical and Functional Properties of Full Fat and Defatted *Cassia fistula* seed flours. *Pakistan Journal of Nutrition* 8 (6): 765-769.
- Babalola, S. E., Shonubi, O. O. and Okusanya, O. T. 2014. Seed dormancy in *Cassia fistula* Linn. population from Nigeria. *Journal of American Science* 10(10): 85-93.
- Bawa, K. S. 1983. Pattern of flowering in tropical plants. In: Handbook of Experimental Pollination Biology, Jones, C. E., Little, R. E. (eds.), 394-410. New York. USA.
- Bentos, T. V., Mesquita, R. C. G. and Williamson, G.B. 2008. Reproductive Phenology of Central Amazon Pioneer Trees. *Tropical Conservation Science* 1 (2): 186-203.
- Bosch, C.H. 2007. *Cassia fistula* L. Record from PROTA4U. Schmelzer, G. H. and Gurib-Fakim, A. (Editors). PROTA (Plant Resources of Tropical Africa/Resource l" Afrique tropicale), Wageningen, Netherlands <<http://www.prota4u.org/search.asp>>. Accessed September 1st, 2015 at 1.35pm.
- Brown, H. S. 2001. *Cassia fistula*: Golden Shower tree. UF/IFAS, Lee County Extension, Fort Meyers. Florida. <http://lee.ifas.ufl.edu/Hort/GardenPubsAZ/CassiafistulaGoldenShowerTree.pdf>. Accessed May 10th, 2015 at 2.05pm.
- Brown, H. S. 2011. Assumed Effects of Cold Weather on the Flowering of Five Ornamental Trees in Southwest Florida. <http://lee.ifas.ufl.edu/Hort/GardenPubsAZ/IBD-of-5-Flowering-Trees.pdf>. Accessed August 22nd 2016 at 2.30pm.
- Cook, B. I., Wolkowich, E. M., Davies, T. J., Ault, T. R., Betancourt, J. L., Alle, J. M. and

- Bolmgren, K. 2012. Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent data bases. *Ecosystem* 15: 1283-1294.
- Evans, L. T. 1975. *Daylength and Flowering of Plants*. Menlo Park, Calif: Benjamin. 122pp.
- Ghouse, A. K., Hasmi, M. S. and Jamal, A. 1980. Certain anatomical characteristics of the bark of some ornamental trees suitable for arid zone environment. *Annals of Arid Zone* 19(4): 425-426.
- Karaboon, S., Ripona, S., Thanapornpoonpong, S., Pawelzik, E. and Vearasilp, S. 2005. Breaking dormancy and optimum storage temperature of golden shower (*Cassia fistula*) seeds. *Conference on International Agriculture Research for Development*, Stuttgart-Hohenheim, Tropentag. 6pp.
- Kauer, G., Singh, B. P. and Nagpal, A. K. 2013. Phenology of some phanerogams (trees and shrubs) of Northwestern Punjab, India. *Journal of Botany*. 10pp. <http://dx.doi.org/10.1155/2013/712405>
- Korner, C. and Basler, D. 2010. Phenology under global warming. *Science* 327, 1461. DOI : 10.1126/Science.1186473.
- Krzanowski, W. J. 2007. *Statistical Principles in Scientific and Social Investigations*. Oxford University Press, Oxford. 256pp.
- Murali, K. S. 2000. Constraints on reproductive success due to timing of flowering in *Cassia fistula* L. *Journal of Palynology* 35-36: 129-140.
- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Turcker, C., Mymeni, R. B. and Running, S. W. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science* 300: 1560-1563.
- Ng, F. S. P. 1977. Gregarious flowering of dipterocarps at Kepong. 1976. *Malaysian Forester* 40: 126-137.
- Opler, P. A., Frankie, G. W. and Baker, H. G. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *J. Biogeography* 3: 231-236.
- Orwa, C., Mutua, A., Kindt, R., Jamnadass, R. and Simons, A. 2009. Agroforestry Database: a tree reference and selection guide. (<http://www.worldagroforestry.org/af/treedb/>). Accessed July 29, 2013 at 11:16 A.M
- Primark, R. 1980. Variation in phenology of natural populations of montane shrubs in New Zealand. *Journal of Ecology* 80: 849-862.
- Rathche, B. and Lacey, E. P. 1985. Phenological patterns of terrestrial plants. *Annual Review of Ecology, Evolution and Systematics* 16: 179-214.
- Satorelli, P., Carvalho, C. S., Reimao, J. Q., Fereirra, M. J. P. and Tempone, A. G. 2009. Antiparasitic activity of biochanin A, an isolated isoflavone from fruits of *Cassia fistula*. (Leguminosae). *Parasitology Research* 104: 311-314.
- Shonubi, O. O., Okusanya, O. T., Omolewa, K. and Babalola, S. E. 2016. Quantitative and qualitative investigations in the flowering and fruiting patterns of *Cassia fistula* Linn. from Ota, Ogun State, Nigeria. *Nigerian Journal of Botany* 29: (1) 59-72.
- Wolkowich, E. M., Davies, T. J., Schaefer, H., Cleland, E. E., Cook, B. I., Travers, S. E., Wills, C. G. and Davis, C. C. 2013. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. Special Invited paper—Global Biological Change. *American Journal of Botany* 100(7): 1407-1421.