**Exploiting the Cocoa genetic variation for flowering time and pod development period for climate adaptation: relationship to selected yield components.**

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ABSTRACT

Cocoa beans from the tropical tree crop, cacao (Theobroma cacao L.) is the main ingredient in chocolates, cocoa-based confectionaries, beverages, alcohol, cosmetics and nutraceuticals. There is considerable genetic diversity within the species that falls into 10 genetic clades. The diversity is centred in the Amazonian tropics with the greatest diversity observed in populations from Peru, Bolivia, Brazil, Ecuador and Colombia. Climate change poses an important challenge to agriculture, globally, characterised by increased carbon dioxide, elevated temperature and scarcity of rainfall or changes in the rainfall pattern resulting in severe drought. Flowering time and pod development period are important physiological traits associated with geographical adaptation. Although these traits are genetically determined, very little is known regarding the genetic variation for those traits in cocoa and its populations. The presence of representative accessions from the 10 genetic groups as well asvarious geographical populations of cocoa at a single location (International Cocoa Gene Bank, Centeno, Trinidad (ICGT)), allows for a comprehensive study of genetic diversity for flowering time and pod development period without the complication of environmental influences. The study was conducted during the period April to March over two consecutive years (2016-2017 and 2017-2018) with a minimum of 10 accessions from each genetic group and from three hybrid populations. Three trees were selected and labelled and the flowering times noted. From each accession 20 flowers were tagged, and successful pod sets determined after 7 days. At least 10 pods from each accession were followed to maturity with pod length and width measurements taken at fortnightly intervals. At pod maturity the pod dimensions, the number of beans and bean size, bean weight (10 beans-fresh and dry) were determined. This study will help to understand the genetic variation for flowering time and pod development period among the geographical populations of cocoa. It will also help to understand the relationships among the various traits studied. Together this information along with geographical information could provide interesting insights into the evolutionary mechanisms that govern flowering time and pod development period, which in the future will be useful in developing accessions for climate change adaptation.

**KEY WORDS**: climate resilience, genetic variation, pod maturity, average pod growth rate, pod index.

# Introduction

Cocoa (Theobroma cacao L.) is a diploid (2n=2x =20), allogamous, understory tropical tree species, belonging to the family Malvaceae (Alverson et al. 1999), with a relatively small genome size of 411-494 Mb. From Amazonia to the Guianas, South America has been shown to be both its geographical origin and its centre of diversity (Cheesman 1944; Motamayor et al. 2003), although historically cacao had reached Central America (Wood and Lass, 1985). The Olmecs, Incas, and other prehistoric peoples of Central and South America used the cocoa beans harvested from cocoa pods. The beans were used by the Mayans and Aztecs to make a ritual beverage that was shared on rare occasions (McNeil, 2006). Christopher Columbus' discovery of the New World led to the development of a US$9.94 billion worldwide cocoa industry, which is centred on cocoa beans ([www.fortunebusinessinsights.com](http://www.fortunebusinessinsights.com)).

Despite having its roots in the Americas, the production of cocoa has now spread to many tropical nations in Africa, South and South-East Asia, and the Pacific (Wood and Lass, 1985). Afoakwa (2014) claims that West African nations including Côte d'Ivoire, Ghana, Nigeria, and Cameroon account for more than 70% of the world's 4 million metric tons of annual cocoa production. Worldwide, cocoa is farmed as a cash crop on millions of modest, family-run farms. More than 4.5 million families' livelihoods depend on it globally. Cocoa is frequently produced on mixed farms or as an agroforestry crop (Somarriba and Beer, 2011).

A significant amount of the world's cocoa is grown in tropical regions with a clear alternation between wet and dry seasons since cocoa is a drought-sensitive crop. More recently, it has been demonstrated that the predicted effects of climate change on cocoa output will be negative, especially in West Africa, which produces more than 70% of the world's supply of cocoa beans (Hirron et al., 2018; Bunn et al., 2019; Wongnaa and Babu, 2020). Severe droughts have already been caused by insufficient rainfall and changes in rainfall patterns (Masroor et al., 2020; Wichitarapongsakun et al., 2016), so climate-wise agriculture strategies have to be developed for production in such locations (Zakaria et al., 2020; Mazhar et al.,2020).

Understanding the physiology of high temperature and drought stresses on cocoa growth and production, as well as developing climate smart agricultural practices to mitigate the negative effects of these stresses on cocoa production, have been the main areas of focus of previous work on developing climate change resilience in the cocoa industry Check for error in citation. Recent research into the genetic and metabolic mechanisms underlying drought tolerance has begun (Baily et al., 2006; Bae et al., 2008). Bioversity International in its review of research on the impact of climate change on cocoa (Medina, V. and Laliberte B. 2017.) concluded that the development of breeding programmes aimed at mitigation have been hampered by the lack of knowledge of the genetic diversity of traits contributing to climate change resilience. Like other qualities influencing tolerance, drought tolerance is probably a polygenic trait controlled by a variety of mechanisms, some of which may be able to successfully prevent drought stress while others may help to avoid such stresses.

Cocoa populations adapt to the surroundings by using available genetic variation. Larger the variation greater the likelihood that certain members of a group will have allele variants that are appropriate for the environment. Those individuals have a higher chance of survival than those that do not carry that allele. In the past, the "Criollo" and "Forestero" genetic groups were distinguished from one another based on physical variations, particularly those of the fruit (pod) and seed (bean), and their respective geographic origins (the former was found in Central America and the latter in South America). A third group known as "Trinitario," a cross between "Criollo" and "Forestero," was later recognized (Cheesman 1944; Wood and Lass 1985; Lachenaud 1997; Lachenaud et al,.1997). Amelonado, Contamana, Criollo, Curaray, Guiana, Iquitos, Maranon, Nacional, Nanay, and Purus are 10 genetic groups that have been identified in more recent studies by Motomayor et al. (2008) based on analysis of SSR-based DNA fingerprints of cocoa accessions collected from across the centre of diversity. Additionally, two hybrid populations have been identified: Refractario (Motamayor et al., 2003), which originated through the hybridization of Nacional with other Upper Amazon Forastero or Trinitario, and Trinitario, which originated from the hybridization of Criollo with Amelonado type.

Two international cocoa gene banks—International Cocoa Genebank, Trinidad (ICGT) and International Cacao Collection, Costa Rica (IC3)—hold a large portion of the genetic diversity of cacao (Johnson et al., 2009). The ICGT is thought to be the largest and most diverse public cocoa collection, with 2400 accessions representing the 10 genetic groups (Bekele, 2012). The IC3 is more robust in the Criollo germplasm than the ICGT since it was developed based on a collection of Criollo and Trinitario varieties grown in Central America. In addition to maintaining primary populations ICGT also has developed two genetically enhanced populations for black pod and witches' broom resistance. These populations have been used to support breeding programmes run by the Ministry of Agriculture, Land, and Fisheries of the Government of Trinidad and Tobago. Through an intermediary quarantine facility at the University of Reading in the United Kingdom, the material in these two international collections is made freely available to legitimate breeding programme around the world.

A survey of the literature reveals that there is a dearth of knowledge regarding the genetic variation for phenotypic traits such as flowering time, pod development period, and their interactions with pod size, bean number, bean size, and bean weight. The overall goal of the study is to identify the genetic diversity that exists within a representative subset of the germplasm held at the International Cocoa Genebank (core collection) for the above traits and to determine the interrelationships between them. Understanding the genetic diversity for drought avoidance traits such as flowering time and pod development period and understanding their relationship to yield components would give breeders a way to supplement and support efforts to make cocoa more reliant to climate change.

# Materials and Methods

2.1 Location and season

The study was conducted at the University Cocoa Research Station, Centeno, Trinidad (UTM 685617E, 1,169,849N). and Tobago, where the ICGT is located. The ICGT is a 34-ha field site where each genotype is planted in 8-16 clonal trees per plot. The soil type at ICGT is Aquic Eutropets with a mean pH of 4.94. The location experiences a mean annual temperature between 22o C(minimum)and 33o C(maximum) and a mean annual rainfall of 2000 mm. The study was conducted during the main crop season between April – March during the years 2016/2017 and 2017/2018.

2.2 Genotypes and sampling

One hundred accessions were selected for the study representing the 8 genetic groups of Motomayor et al (2008) as well as two hybrid populations, Trinitario (Johnson et al, 2009) and Refractario (Zhang et al, 2007). Table-1 provides a summary of the accessions selected and the genetic groups to which they belong. The accessions are present in a single location with replicate trees. The sampled trees of the various accessions varied in age between 30 to 35 years.

Table 1: The accessions of Theobroma cacao L selected from the various genetic groups for this study.

2.3 Experimentation

A minimum of 3 replicate trees were selected for each of the 100 accessions. Each of selected trees had been previously subjected to DNA fingerprinting and had been identified as true-to-type for the respective accessions. Among those 100 accessions from the core collection, 60 accessions were selected and complete results had been obtained for 48 accessions of the parameters studied in the year 2016/2017. Similarly, for the year 2017/2018, 100 accessions were selected and complete results had been found for 81 accessions of the parameters studied. Among those two sets of accessions, 32 accessions were common. These 32 accessions were studied in the following season 2018/2019. The selected accessions and the representative trees were labelled using flagging tape. The trees were subjected to light sanitation pruning, moss cleaned from the trunks to expose the active cushions to support flowering. If excessive shade was present from the shade trees these trees were also pruned to allow light into the tree canopies.

Following the onset of rains in April in 2016 and 2017 the trees of each of the selected accessions were monitored on a weekly basis for evidence of flowering. The flowering time for each tree per accession was recorded. Ten flowers were tagged with the date of flower opening per tree and were allowed to set pods spontaneously. To reduce errors flowers were tagged on the main trunk of each tree. The cacao accessions are mostly self-incompatible and require pollination by cacao midges (*Forcipomiya* spp.) belonging to the family *Ceratopogonidae* (Wood and Lass, 1985). Small plastic tags were pinned to the tree trunk. Successful pod sets are determined after 7 days. Most drop due to insufficient pollination or as cherelle wilt (the wilting and dropping of immature pods) and hence flowers had to be repeatedly tagged to obtain sufficient number of pods per tree.

Following pod set, each pod was separately caged with wire mesh cages to prevent rodent attack and were sprayed routinely with a copper fungicide (OXI-CUP 87 WG, active ingredient- Copper oxychloride, distributed by Carlsen chemical ltd. Trinidad and Tobago) to prevent black pod and witches’ broom diseases. Upon maturity indicated by 50% change in pod colour (green to yellow or purple to orange) the pods were individually harvested with the maturity date noted and placed into separate labelled plastic bags and were transported to the laboratory.

At the laboratory, the perpendicular length and width of each harvested pod was measured using slide calliper and recorded. Each pod was then separately cracked using a mallet and beans separated carefully from the placenta, counted and recorded. Fifteen beans from each pod were randomly selected, the pulp removed manually and the bean size and weight recorded. Bean size determined as length and width of beans was measured using a metric ruler. The beans were then dried to constant weight in a laboratory oven set at 80oC and the weight of 15 beans determined using an electronic balance (ae ADAM, Adam equipment USA) to two decimal points. The average bean weight was determined for each pod and recorded.

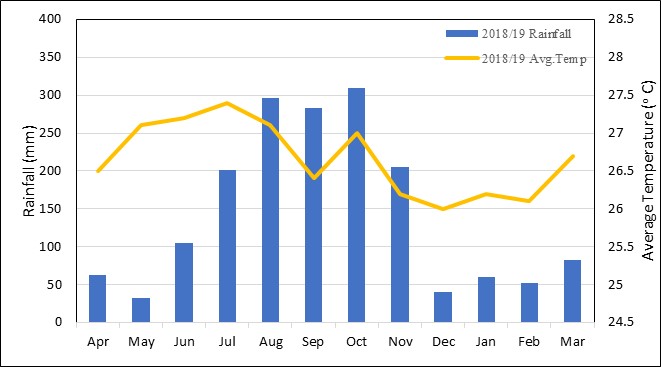
2.4 Data Analysis

Analysis of variance (ANOVA) of data collected was performed using the NCSS software (NCSS, LLC, 2007) to determine significant differences among groups and between accessions. The means were separated using Tukey Multiple Range Test. Data from 2016/2017 and 2017/2018 were analysed separately as well as combined.

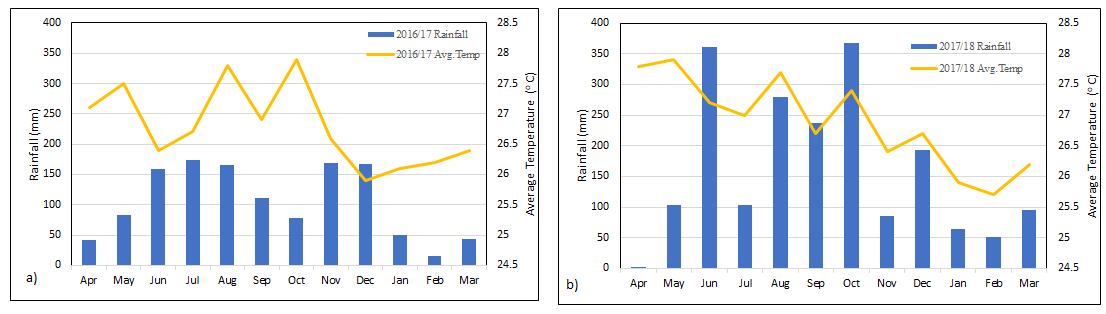
# Results and Discussions

The experimental site at Centeno experiences a bimodal rainfall pattern typical of the tropics with a distinctive dry season between January to April-May, followed by a wet season (Figure 1 a, b, c). Over the three-year period of the study (Table 1, and Figure 1), although the first rains were experienced during the latter part of April, flushing and flowering did not occur in any of the cacao accessions investigated until after more regular rainfall was experienced during middle to late May. Flowers from the first flowering abscised in the cacao accessions and only subsequently formed flowers formed pods. Hence pod settingoccurred in a staggered fashion resulting in successful pod set during the July to September period with maturation between December to March.

Figure 1:  Monthly average rainfall (mm) and temperature (oC) for the seasons a) 2016/17 b) 2017/18 and c) 2018/19 in Trinidad and Tobago (Data obtained from University Field Station, Valsayn, Trinidad and Tobago)



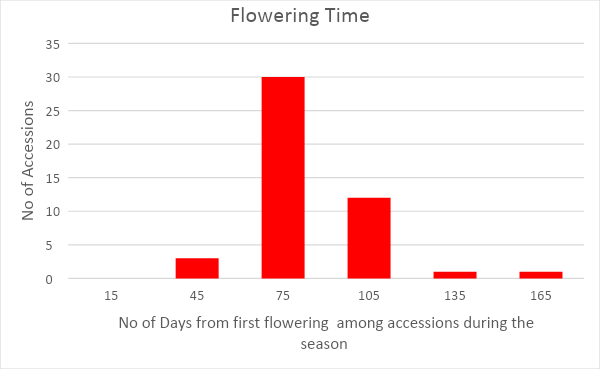
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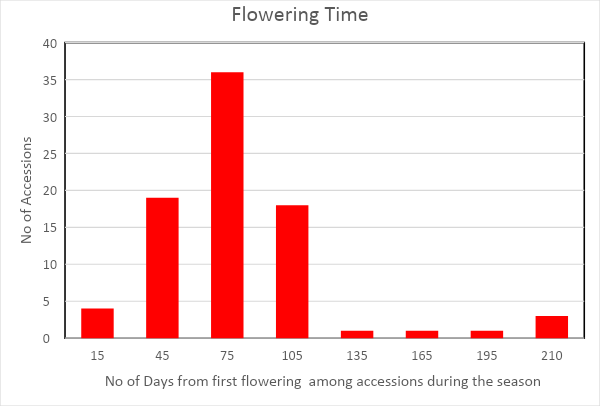
3.1 Flowering time

Analysis of variance of flowering time in 2016/2017, determined as the number of days from the 15th of April, showed significant differences between accessions, varying between 45 to 165 days with a mean of 80 days and mode of 75 days (Figure 2a). Similarly, in 2017/2018, again there were significant differences (P <0.05) in flowering time among accessions studied with a mean of 81 days and mode 75 days (Figure 2b). In general, accessions belonging with prefixes SIC, MO, CL and ICS flowered within 45 days of the first showers in April, while accessions belonging to the groups ICA and AGU were late flowering taking more than 135 days to flower. Flowering time among 81 accessions under 9 genetic groups and 3 hybrid populations were accomplished. The others (GU, AMELONADO, SIAL, NA, PA, JA, SIC, LC TEEN, EET and LV) fell in between.

Figure 2: Frequency distribution for flowering time evaluated in – accessions in Theobroma cacao in 2016/17 and – accessions evaluated in 2017/18 a single site at Centeno, Trinidad.

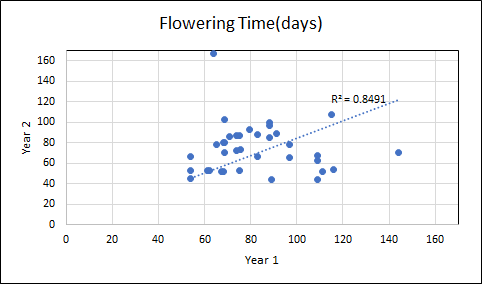


a)

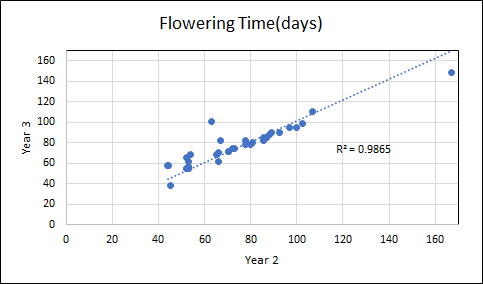


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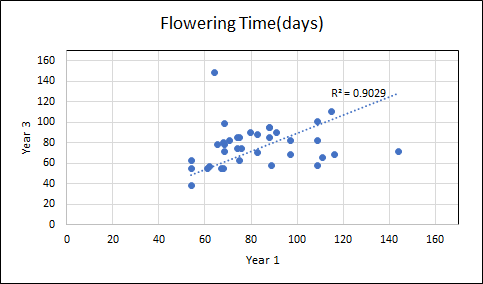
A combined analysis of variance of 32 accessions that were common between the two years showed significant differences (P <0.05) between years, accessions and a year x accession interaction. The F value for year x accession interaction was however 10-fold smaller than those for year and accession effects. The flowering time on average was 15 days later in 2016/2017 than in 2017/2018. There was however a strong correlation (Figure 3) found for flowering time among 32 common accessions in year-1 and year-2, year-2 and year-3 as well as year-1 and year-3.



a)



b)



c)

Figure 3: Correlation for flowering time (days after commencement of wet season) among 32 cacao accessions evaluated over three years (a, b and c) at Centeno, Trinidad.

This study shows wide variations in flowering time following a dry spell among cocoa accessions selected across different genetic groups and has identified accessions with varying flowering time. Although the environment has a role to play in the inheritance of the trait the moderately strong correlation of accessions across three years indicates a genetic component. Understanding the genetic basis of this trait would allow for it be better manipulated in breeding programmes so that cocoa varieties resilient to climate change can be developed.

3.2 Pod development period

Analysis of variance of pod development period defined as number of days to pod maturity showed significant differences (P <0.05) between accessions for both years 2016/2017 and 2017 and 2018. The pod development period among accessions varied between 90 to 210 days with a mean of 146 days and mode of 140 days in 2016/2017 (Figure 4a) and between 120 to 210 days in 2017/2018 with a mean of 149 days and a mode of 150 days (Figure 4b). The coefficient of variation was 0.002 to 0.116 for 2016/2017 and 2017/2018, respectively.

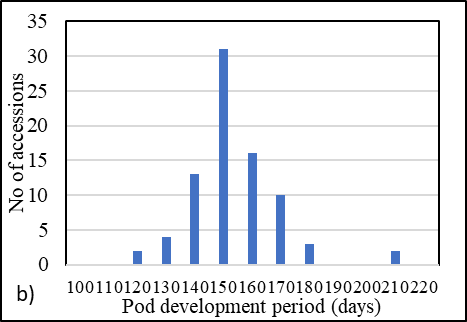
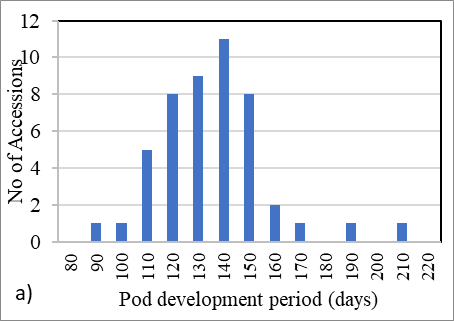
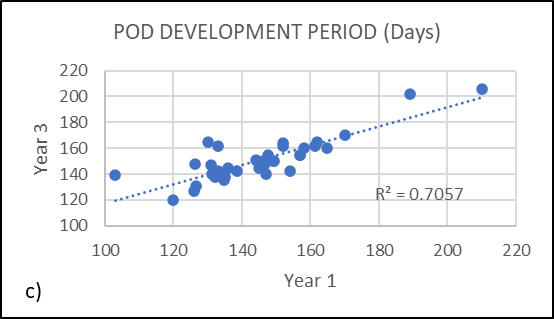
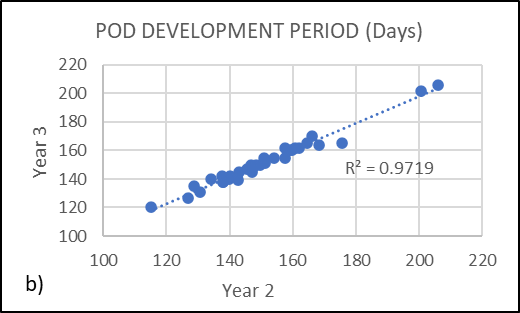
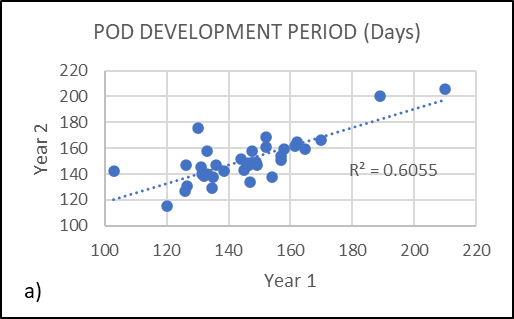


Figure 4: Pod development period for Theobroma cacao accessions in (a) 2016/2017 (n = 48) and (b) 2017/2018 (n = 81) held at the International Cocoa Gene bank, Trinidad.

A combined analysis of variance of 32 common accessions for the two years under study showed significant differences between years, accessions and a year x accession interaction. The F value for year x accession interaction was however smaller than those for year and accession effects. The pod development period for 2017/2018 was on average 25 days longer than for 2016/2017. The longest pod development period (over 200 days) was observed for LV 20 and PA 120 and the shortest pod development period was observed for MO 121 (117 days). The year-to-year variation in accessions shows that accessions varied between -16 to +25 days depending on the year. Consequently, there was a strong and significant correlation for pod development period among 32 accessions over three years (Figure 5 a, b, c).

Figure 5: Correlation between pod development period of 32 cacao accessions evaluated over three years (a) 2016/2017, b) 2017/2018 and c) 2018/2019) at Centeno, Trinidad.

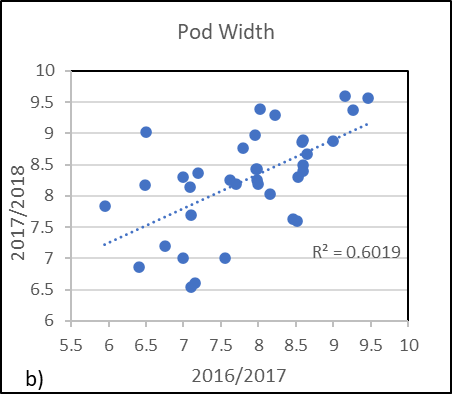
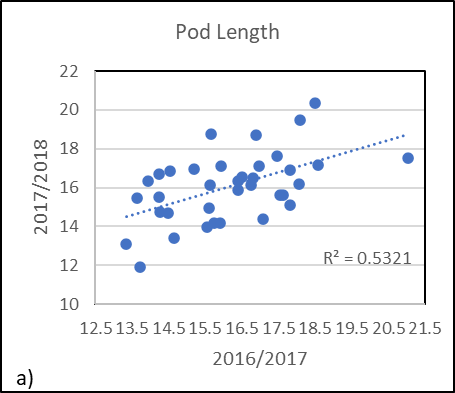


The pod development period was generally slightly longer in 2017/2018 compared to 2016/2017.The variation in temperature (higher in 2017/18 than 2016/17) and total monthly rainfall (more in 2017/18 than 2016/17) during the season, were the possible cause for the difference ( Figure 1). Researchers have shown that high temperatures can hasten pod growth (Daymond and Hadley,2008). Despite this a strong correlation between selected accessions evaluated in 2016/2017 and 2017/2018 suggested that pod development period was consistent over the years and hence can be considered to have a strong genetic component. Pod development period was moderately negatively but significantly correlated to both L/W ratio and average pod growth rate, suggesting in addition to those with a long pod development period or slow growers they tend to have a more spherical pod morphology.

3.3 Pod length and width

A combined analysis of variance for final pod length and width of 32 common accessions in two years showed significant differences between years, accessions and a year x accession interaction. The F value for year x accession interaction was however smaller than those for year and accession effects. Therefore, a strong correlation is evident among the common accessions between 2016/2017 and 2017/2018 for pod length (Figure 6a and b).

Figure 6 Correlation between (a) pod length and (b) pod width of mature pods of 32 cacao accessions evaluated over two years at Centeno, Trinidad.

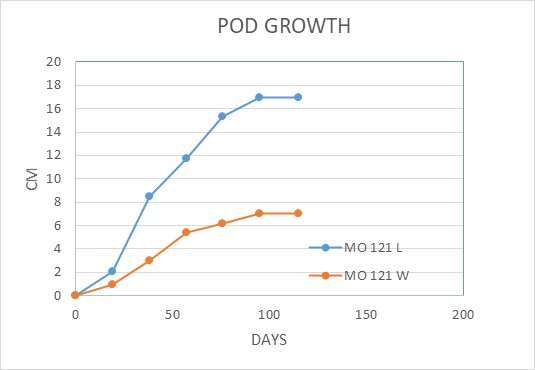


* 1. Pod growth

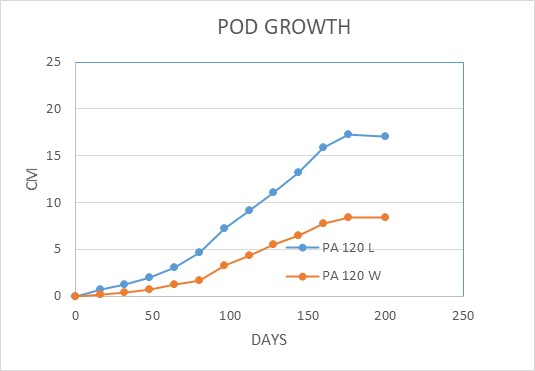
Pod size was measured as pod length and pod width over the pod development period and pod growth curves were generated for each accession over the two years. The pod growth curves are shown for six selected cacao accessions (2017-2018) in Figure 7. A few observations could be noted from the pod growth curves as follows:

1. There were differences in the shape of the curve with respect to the various accessions. Shapes varied from being linear to showing an exponential or cubic growth curve. All accessions had a linear growth period, however, the start and end of that period as well as the length of the linear growth phase varied. As a consequence, there were almost a four-fold difference in final pod size or volume.
2. the growth rate for pod length was much greater than for pod width. As a consequence, the pod shape became increasingly oblong as pod maturation occurred, albeit differences existed between accessions.
3. Variation in pod width of cacao accessions at full pod maturity was much smaller than the variation observed for pod length.
4. The pod growth slowed down and stopped during the last fortnight or last two fortnights during pod maturity. This cessation of growth was observed for both pod length and for pod width.
5. Figure 7a) represents a genotype with shorter pod development period where as Figure 7b) represents the genotype with longer pod development period than the others shown in Figure 7c) and d). The pod growth rates for accessions (eg. PA 120) with a longer pod development period had a longer lag phase (as much as 75 days) compared to those (eg Amelonado and IMC 105) with a shorter pod development period (less than 25 days).
6. SCA 6 (Figure 7 e) that represents one of the smallest pods amongst all the cocoa accessions studies however did not show a significant lag phase as the pod development period was relatively short.

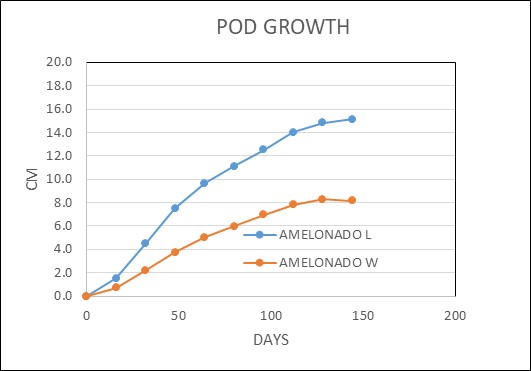
Figure 7: Pattern of pod growth measured as increase in pod length (cm) and pod width (cm) over time (days) in 4 accessions of Theobroma cacao L in 2017-2018 (a) MO 121 (b) PA 120 (c) Amelonado (d) IMC 105 (e) NA 342 and (f) SCA 6



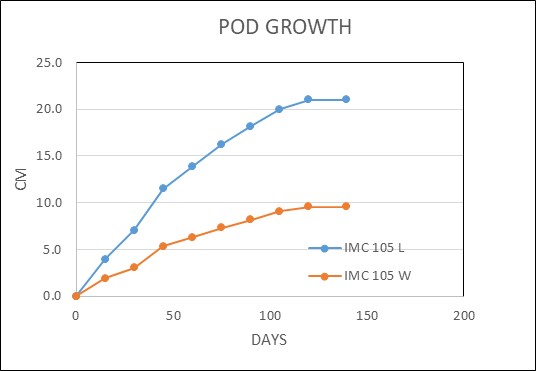
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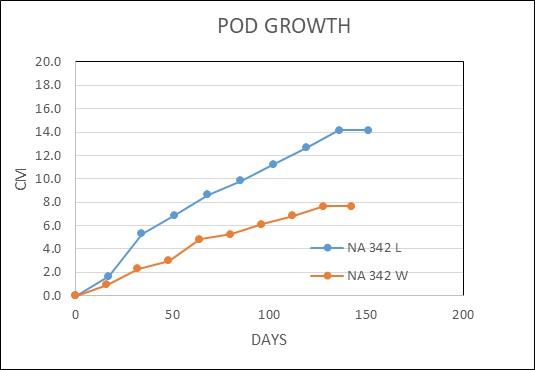
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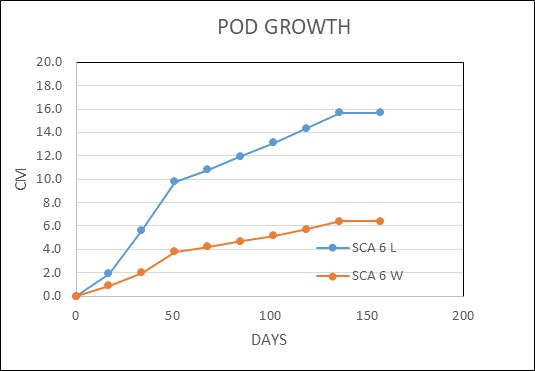
c)



d)



e)



f)

3.5 Correlation between phenotypic traits

Flowering time did not show a significant correlation between most traits studied (Table 2) except a moderate but significant (P <0.05) positive correlation with bean size and average bean weight. Pod development period had a moderate significant (P <0.05) negative correlation with APGR and L/W ratio, suggesting that accessions with a longer pod development period tended to have a slower average pod growth rate. Pod length and pod width were moderately correlated (r= 0.49; P <0.05) but as expected were strongly correlated (r = 0.83-8.88) with pod size. Consequently, average pod growth rate showed strong positive correlations with pod length, pod width and pod size (r = 0.1- 0.95; P <0.05). Pod length was strongly positively correlated (r= 0.74; P <0.05) with length to width ratio while pod width showed a moderate negative correlation (r = -0.23; P <0.05). Pod length, pod width and pod size showed moderate correlations with both average bean weight and bean number. Bean size and average bean weight showed near perfect correlation.

Table 2: Pearson Product Moment Correlations between 10 agronomic traits investigated in 81 cocoa accessions at the International Cocoa Genebank at Centeno, during the 2017/2018 period.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | FT | PDP | Pod Len | Pod Wid | Pod Size | L/W | APGR | Bean # | Bean Siz | ABW |
| FT | 1 | 0.15 | 0.22 | 0.11 | 0.17 | 0.16 | 0.11 | 0.01 | 0.32\* | 0.32\* |
| PDP |  | 1 | -0.17 | 0.07 | -0.06 | -0.25\* | -0.35\* | -0.07 | 0.13 | 0.13 |
| Pod Len |  |  | 1 | 0.49\* | 0.83\* | 0.74\* | 0.82\* | 0.34\* | 0.39\* | 0.39\* |
| Pod Wid |  |  |  | 1 | 0.88\* | -0.23\* | 0.81\* | 0.40\* | 0.50\* | 0.50\* |
| Pod Size |  |  |  |  | 1 | 0.24\* | 0.95\* | 0.42\* | 0.53\* | 0.53\* |
| L/W |  |  |  |  |  | 1 | 0.29\* | 0.08 | 0.05 | 0.05 |
| APGR |  |  |  |  |  |  | 1 | 0.42\* | 0.45\* | 0.45\* |
| Bean# |  |  |  |  |  |  |  | 1 | -0.05 | -0.05 |
| BeanSiz |  |  |  |  |  |  |  |  | 1 | 0.99\* |
| ABW |  |  |  |  |  |  |  |  |  | 1 |

Table 3 The genetic variation for 8 mopho-physiological characteristics of 48 accessions (2016/2017) and 81 accessions (2017/2018) of Theobroma cacao evaluated at the International Cocoa Genebank, Trinidad situated in Centeno, Trinidad.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Character | 2016/2017 (n =48) | | | 2017/2018(n=81) | | |
|  |
| Mean | Range | cv | Mean | Range | cv |  |
| FT (days) | 80 | 16 - 144 | 0.28 | 79 | 11 - 208 | 0.49 |  |
| PDP (days) | 143 | 97 - 210 | 0.15 | 149 | 115 - 206 | 0.1 |  |
| PL (cm) | 16.3 | 13.1 - 21.0 | 0.11 | 16.1 | 10.4 - 22.9 | 0.15 |  |
| PW (cm) | 7.7 | 5.7 - 9.8 | 0.13 | 8.5 | 6.3 - 11.1 | 0.1 |  |
| PS (dm3) | 4.17 | 2.00 -7.45 | 0.33 | 5.02 | 2.0 – 11.0 | 0.31 |  |
| BN (No.) | -\* | - | - | 36 | 22.1 – 49.0 | 0.16 |  |
| BS (cm3) | - | - | - | 7.27 | 2.43-18.70 | 0.38 |  |
| ABW (gm) | - | - | - | 1.25 | 0.94 – 1.96 | 0.14 |  |

FT = Flowering time; PDP = pod development period; PL = pod length; PW = pod width; PS = pod size; BN = bean number; BS = bean size and ABW = average bean weight

\* data was not collected for BN, BS and ABW during 2016/2017

# Conclusion

In conclusion, the study showed considerable genetic variation for flowering time following dry spell and pod development period over three years involving 97 accessions (Table 3). There were climatic differences between the two years that on average resulted in a delay in flowering following the dry spell in 2017/2018 compared to 2016/2017 and a longer pod development period in 2017/2018 compared to 2016/2017, indicating a role for environment on the inheritance of these traits. Significant differences with respect to flowering time and pod development period were observed. Despite large year-to-year variation in climatic conditions PDP and FT showed remarkable consistency across accessions over the three years of study, suggesting a strong genetic influence. There was evidence of genetic differences in PDP and FT across genetic groups from different geographical origins indicating that this variation could be an evolutionary adaptive response. No correlation was seen between pod development period and yield components; bean number, bean size and bean weight whereas no/weak correlation was seen between FT and yield components, indicating that these traits can be selected , independent of yield. Both traits were not correlated to pod size or bean number. Although PDP had no correlation with average bean weight, FT had a small but significant positive correlation with average bean weight. In summary the study showed that both flowering time and pod development period where traits can play an important role in drought avoidance in cocoa and can be improved through breeding without compromising pod size, bean number or bean weight, important yield components in cocoa.

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