Inbreeding depression in cocoa (*Theobroma cacao* L) over generations

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Abstract

Cocoa (*Theobroma cacao* L.) is the third important beverage from Amazon forest basin. The processed seeds are used for the production of chocolate, cocoa powder and cocoa butter. The cross pollinating nature coupled with existence of self/cross incompatibility poses much difficulty to the cocoa breeders. Variation within the population is the basis for the selection. The cocoa inbreds of various genotypes belonging to different generations, maintained at Cocoa Research Centre (CRC) were evaluated from 2016-2019. In the S₁, S₂, generation of M 18.7 genotype positive inbreeding depression was observed for 17 and 16 characters respectively, whereas, maximum inbreeding depression (10%) was observed for wet bean weight per pod.

In the S₁, S₂ and S₃ generation of G II 7.4 genotype, positive inbreeding depression was observed for 10, 15 and 7 characters respectively, whereas, highest negative inbreeding depression (-92.45 per cent) for ridge thickness *i.e.*, high ridge thickness was observed in S₄ generation.

In the S₁ and S₂ generation of G IV 35.7, positive inbreeding was observed in 16 and 15 characters respectively. The similar trend of inbreeding depression in various genotypes has shown both negative and positive inbreeding depression. The inbreeding depression in cocoa inbreds over generation was not stable. ridge thickness and bean thickness, yield per pod per tree, pod index and phenol content have shown negative inbreeding depression indicating that these characters are controlled by additive genes.

Introduction

Cocoa (*Theobroma cacao* L.) is the third important beverage from neo-tropical rain forest Amazon basin and Guyana Plateau of South America. The processed seeds of which are used for the production of chocolate, cocoa powder and cocoa butter. Cocoa butter is of great importance because of its use in the chocolate and cosmetic industry. It is native species of tropical humid forests on the lower eastern equatorial slopes between 10 to 20 degrees' latitude north and south of equator in the Andes, in South America. It is spread all over the tropical regions of the world in the 18th and 19th centuries.

The productivity of cocoa can be improved by following good management practices, inclusion of high yielding varieties and hybrids and by proper management of pests and diseases. Cocoa is predominantly out breeding with highly complex genetic structure. The cross pollinating nature coupled with existence of self/cross incompatibility poses much difficulty to the cocoa breeders. Though, synthesis of dynamic population of hybrids has become a reality, very high variability is exhibited by these hybrids. All the hybrids in a cross do not show the same level of superiority due to the use of heterozygous parents in the breeding programme

Genetic variation is a key factor in competition among individuals in ecological communities which provides an opportunity for plant breeder to develop new and improved cultivars with the desirable characteristics. The use of variability is the ultimate objective of the activities of breeding programme in selection as well as in crop improvement programme. Variation within the population is the basis for the selection and adaptation which makes it possible to continue and advance the adaptive process on which evolutionary success depends. The macro evolutionary concept of conversion was from out crossing to self-fertilization. The self-fertilization in out crossing plants would benefit about 50 percent of transmission because of the contribution of the pollens to their own ovules. As the crossing shift to selfing, the associated changes occur mainly in floral morphology and the reproductive investment and mating pattern (Loveless and Hamrick, 1984) which in turn changes the population size and their stability to survive. The possibility of shifting mating system may promote to speciation which can affect the inferences about speciation and extinction (Magnuson and Otto, 2012). While, the increased selfing will leads to inbreeding depression indicates the reduced fitness. As a result, becomes homozygous which may be unfavorable or favourable recessive genes. The unfavorable recessive genes will be eliminated whereas the favourable genes with no injurious effects will be utilized.

Inbreeding depression is the lowered fitness of inbred individuals compared to out crossed individual that can directly affect the intrinsic selective advantage of increased selfing. The magnitude of inbreeding depression in natural populations is expected to evolve with the mating system. Darwin (1876) reported that progeny obtained from self fertilization were weaker than those obtained from out crossing which published in his book *Cross and Self Fertilization in Vegetable Kingdom*. The genetic basis beyond the self fertilization will reveal how the increased homozygosity will lead to the inbreeding depression which is due to non-

additive gene action. The rate at which deleterious alleles are eliminated from population will depend on the genetic parameters. The effect of deleterious recessive allele or partially recessive allele will result in phenotype appearance.

As the cocoa is a perennial and cross-pollinated crop, limited availability of inbreds and self pollinated cocoa varieties is the basic reason for its insufficient exploitation in breeding at present. The hybrid developed now in cross pollinated crops doesn't give the hybrid vigour to the full potentials of the crop, because the selected type is cross-pollinated one and hence it's a hybrid by itself. These crosses with open pollinated ecotypes will yield segregation for different characters in first generation itself and give only weak hybrids. The cross between two diverse inbreds is only useful in developing hybrids to its full potential with high vigour, early flowering, high yield and other beneficial traits. This also segregates faster to lesser valued individuals. Hence inbreeding depression study was undertaken to evaluate inbreds in cocoa and then identify the diverse inbreds for developing good hybrids in cocoa. On inbreeding open pollinated cocoa, there will be possibility of obtaining variable forms by crossing two outcrossing cocoa plants. The variability will be useful for selection of parents for developing hybrid with low segregation and high vigour, high yield and beneficial economic and biochemical characters of commercial importance.

Materials And Method

The cocoa inbreds of various genotypes belonging to different generations, maintained at Cocoa Research Centre (CRC), College of Horticulture was used as base material for evaluation of inbreds and to study the different methods to overcome the self-incompatibility.

A total of 113 cocoa inbreds were evaluated and the details are given in appendix 1. The inbreds were selected on the basis of availability of preceding and succeeding generations in the field maintained at CRC

Inbreeding depression in various selfed generations was computed and the significance was tested as per the procedure

$$\text{Inbreeding depression (\%)} = \frac{S_0 - S_1}{S_1} \times 100$$

S_0 = Average Performance of the inbreds in the preceding generation

S_1 = Average performance of the inbreds in the succeeding generation

Result And Discussion

The present investigation on inbreeding depression was carried out for yield, pod, bean, economic and biochemical characters in 13 genotypes, of which, 2 genotypes belongs to S_1 generation, 8 genotypes to S_2 generations, two genotypes to S_4 generations and one genotype to S_5 generation.

Inbreeding depression in M 18.7 genotype over generations

The details of inbreeding depression for yield, pod, bean, economic and biochemical characters of M18.7 genotype are presented in table 1. In the S_1 generation of M 18.7 genotype positive inbreeding depression was observed for 17 characters out of 21 characters. The pod weight, ridge thickness, furrow thickness, pod length, pod breadth and number of beans per pod are interdependent and are directly associated with dry bean yield per plant (Veeresh, 2018). The husk furrow thickness and number of flat beans expressed negative inbreeding depression of -12% and -7.5 respectively. The increased husk thickness and number of flat beans per pod is negatively associated with dry bean yield per pod. The average yield per tree per year has shown a very meager inbreeding depression of 4.21 per cent over the preceding generation indicating the decrease in yield over the preceding generation of S_0 . There is no inbreeding depression for husk ridge thickness. Pod weight, pod length, number of beans per pod, weight of wet bean per pod, bean length, breadth, and thickness, fat and phenols content have expressed an inbreeding depression of less than 5 percent. Pod breadth, single bean weight, conversion index and dry matter recovery have shown an inbreeding depression of less than 10 percent. Negative inbreeding depression was expressed for pod index and efficiency index This clearly confirm that dry weight of beans per pod and pod weight required to produce one gram of dry bean is high. Similar results were

reported by Minimol *et al.*, (2015) in breeding cycle of GII 7.4 genotype of cocoa. Results of their study reveal an inbreeding depression of 40.44 for wet bean yield per pod, in contrast in the present study only 4.21 per cent inbreeding was observed.

Rubino and Wehner (1986) also reported some yield improvement during the inbreeding process of pickling cucumber population, which is also a cross pollinated crop. When average girth (cm) at three years after planting was compared among generations not much differences were observed between inbred populations and parental populations. Inbreeding depression was studied for S2 nut yield and its attributes in coconut. The family IIS₂-2 and VS2-1 expressed positive inbreeding depression for palm height and inter nodal length, but no inbreeding depression for stem girth. The leaf characteristics also exhibited positive inbreeding depression in S₂ (Chetana, 2016).

In the S₂ generation of M 18.7 genotype, positive inbreeding depression was observed for 16 characters. For all the 16 characters the inbreeding expression is to a tune of less than five per cent. Pod value, conversion index, dry matter recovery have shown an inbreeding depression between 5 to 10 percent. Negative inbreeding depression was observed for husk ridge thickness, number of flat bean per pod, pod index, efficiency index and fat content. The similar trend was observed for these traits in S₁ generation too. The magnitude of inbreeding depression is quite low compared to S₁ generation.

Chetana (2016) assessed the inbreeding depression in coconut, the germination percentage revealed positive inbreeding depression in all the selfed families of 12 families. High inbreeding depression was noticed in IAS3-2, IIS3-2, IVS3-2, VS3-1 and IVS3-1 and the lowest in family 1BS3-1 and 1AS3-1. Seedling height expressed high inbreeding depression in VS3-1. Collar girth didn't show inbreeding depression in S₃. The collar girth is an important trait correlated with yield. Both positive and negative inbreeding depression was recorded for total number of leaves produced by the seedlings in S₃ generation.

In the S₃ generation of M 18.7 genotype, maximum inbreeding depression (10 %) was observed for wet bean weight per pod followed by pod length (6.86 per cent), the main yield deciding factors. The negative inbreeding depression for number of flat bean per pod, pod value and efficiency index persist in S₃ generation. The conversion index, dry matter recovery and fat content have also shown negative inbreeding depression. The magnitude of inbreeding depression is less than 10 per cent for most of the characters. In the S₄ generation of M 18.7 genotype, over the generations, the maximum inbreeding depression is observed for majority of the characters in the study. Highest inbreeding depression of 43.58 per cent was observed for number of pods/tree/year. The negative inbreeding depression for number of flat bean pod, pod index, conversion index, dry matter recovery and fat estimation persisted and was more than in the preceding generation. The characters like number of flat bean per pod, has negative association with the final yield.

Inbreeding depression of G II 7.4 genotype over generation

The details of inbreeding depression for yield, pod, bean, economic and biochemical characters of G II 7.4 genotype are presented in table 1. In the S₁ generation of G II 7.4 genotype, positive inbreeding depression was observed for 10 characters out of 21 characters. The husk ridge and furrow thickness and number of flat beans expressed negative inbreeding depression of -64.52, -44.29 and -9.09 respectively. The negative inbreeding depression for these traits demonstrate the increase in these traits over preceding generation and these are all negatively correlated with the final dry bean yield per plant. Hence, increase in these parameters over the preceding generation is a disadvantage. The expression of negative inbreeding depression for characters like husk ridge thickness, furrow thickness, pod breadth, number of beans per pod, number of flat beans per pod, bean thickness, pod index and efficiency index is attributed to the additive gene control. The average yield per tree per year, single bean weight, pod value, conversion index, dry bean weight per pod, and dry matter recovery, have shown positive inbreeding depression. The reduction in the values for these parameters and increase in inbreeding depression over the past generation results in lower yield. The fat content has shown a negative inbreeding depression of -18.43 per cent over the preceding generation. Less inbreeding depression was observed for wet bean weight per pod, bean breadth and phenol content. A similar result of was reported by Minimol *et al.*, (2015) in breeding cycle of GII 7.4 genotype of cocoa. Results of their study reveal an inbreeding depression of 40.44 for wet bean yield per pod, in contrast in the present study only 4.21 per cent inbreeding was observed. The variation in inbreeding depression among the genotypes was reported by Mallika *et al.*, 2002. Further, the possibility of utilizing homozygous inbreds for production of commercial hybrids cannot be ruled out by analyzing inbreeding generation of only one genotype. The percentage of inbreeding depression in G II 7.4 varied significantly for different traits selected under study.

Although most cross pollinated species have higher or lower levels of inbreeding depression as a consequence of inbreeding, there are some in which self-pollination can happen in a continuous way with no vigor loss. Cucurbits, being cross-pollinated, are an example of a group of species in which certain lines seem to lose little vigor by inbreeding (Allard, 1971; Whitaker & Robinson, 1986; Robinson, 1999). In some aspects, research results are contradictory regarding loss of vigor in inbred or cross pollinated crops like cucurbits. The vigour and reproductive capacity did not affected in *Cucurbita maxima* after self-pollination for 10 generations (Cummings, 1928). Bushnell, (1922), while studying the effect of inbreeding in *C. pepo* opined that the vigor loss during self pollination did not necessarily occur.

In the S₂ generation of G II 7.4 genotype, positive inbreeding depression was observed for 15 characters. The maximum inbreeding depression was observed for bean thickness (31.80%) followed by fat content (26.46%), and efficiency index (23.17%). An inbreeding depression of 15.42 per cent and 18.49 per cent was registered for average pod yield per tree per year and wet bean weight per pod. Negative inbreeding depression was observed for conversion index, dry matter recovery, pod value, single dry bean weight, husk thickness and pod length. A contrary result was obtained for pod breadth, bean thickness, dry bean weight per pod, dry matter recovery and fat content in S₁ generation. In the S₃ generation of G II 7.4 genotype, only seven characters expressed positive inbreeding depression in S₃ generation of G II 7.4 genotype. When compared to the preceding generation, contrary results are observed for pod weight(g), husk furrow thickness (mm), pod breadth (mm), wet bean weight per pod (g), bean breadth, bean thickness, efficiency Index, fat content (%). Bushnell (1922) opined that inbreeding depression may necessarily occur in the succeeding generations in his studies on inbreeding in *Cucurbita maxima*. Maximum inbreeding depression of 30.55 per cent was observed for dry matter recovery (%), followed by conversion index (table 1). In the S₄ generation of G II 7.4 genotype, highest negative inbreeding depression (-92.45 per cent) was observed for ridge thickness *i.e.*, high ridge thickness, which has negative association with economic yield. A contrary result was obtained for average yield, pod weight, husk thickness, bean characters, pod value and phenol content. The expression of inbreeding depression over S₃ generations is unstable when compared to its earlier generation S₂. In the S₅ generation of G II 7.4 genotype, the maximum inbreeding depression (63.95 per cent) was observed for husk furrow thickness followed by husk ridge thickness (49.02), average yield (No. of pods per tree per year, pod weight (g) (39.11 per cent), efficiency index (33.39 per cent). Negative inbreeding depression was observed for number of beans per pod (-11.50), number of flat per pod (-11.11). bean length, Bean breadth, pod value, conversion index, dry bean weight per pod (g), dry Matter Recovery (%), fat content (%), phenol content (%) have also shown negative inbreeding depression (Table 1).

Inbreeding depression of H1 1.2 genotype over generation

The inbreeding depression of H1 1.2 is presented in table 1. In the S₁ generation, positive inbreeding was observed in 16 characters indicating the reduction in their values over the preceding generation. Chekania (1976) had already reported a reduction in fruit weight of different cultivars of *C. maxima* and *C. pepo*, two cross pollinated crops as a result of inbreeding after three generations of self pollination. Number of flat bean per pod recorded -33.33 percent inbreeding indicating more number of flat beans over preceding generation. Several scientists assumed the hypothesis of reduced inbreeding depression in *Cucurbita*, some researchers have shown inbreeding depression for several characters of *C. pepo* and *C. maxima* (Borghi *et al.*, 1973; Chekalina, 1976). In the S₂ generation of H1 1.2 genotype, the inbreeding depression was observed for 16 characters. Husk thickness increased in S₂ generation significantly.

Inbreeding depression of G IV 35.7 genotype over generation

The details of inbreeding depression in of G IV 35.7 genotype over generation is presented in table 2. In the S₁ generation, positive inbreeding depression was observed for 13 characters. Av. Yield (No. of pods per tree per year, pod weight (g), husk ridge thickness (mm), husk furrow thickness (mm), wet bean weight per pod (g), single bean weight(g), efficiency index have shown the inbreeding depression over S₀ generation. These characters lost some vigour due to inbreeding depression. Cucurbits, being cross pollinated, are the other examples in which certain lines loose little vigour by inbreeding (Allard, 1971; Whitaker & Robinson, 1986; Robinson, 1999). In the S₂ generations, the positive inbreeding depression was observed for fifteen characters out of 21. Maximum inbreeding was observed for pod weight (34.12), followed by efficiency index (31.79), furrow thickness (15.70), 20 bean weight (11.59) and average pod yield(10.46). In the S₃ generation, the maximum negative inbreeding depression was observed for wet bean weight per pod (-79.70) followed by average pod weight (-44.09) and efficiency index (-44.21). These observations point out

the increase in their values over the S_2 generation. Whereas, the average pod yield, conversion index (44.40) and dry matter recovery (44.40) have shown maximum inbreeding depression. The inbreeding depression in S_4 generation is almost similar to that of S_3 generation except the fat content and poly phenol content expressed negative inbreeding depression.

Inbreeding depression of G VI 135 genotype over generation

The details of inbreeding depression in of G VI 135 genotype over generations are presented in table 2. Positive inbreeding depression over the preceding generation was observed for majority of the characters except wet bean weight per pod (-5.44) and pod index (-2.33) in S_1 generation and number of flat beans per pod (-71.43), conversion index (-44.37) and dry matter recovery (-44.56) and pod index (-27.62) in S_2 generations. This trend in increase and decrease in the vigour was similar to that of results obtained by Allard, 1971; Whitaker & Robinson, 1986; Robinson, 1999 in their study of inbreeding depression in cucurbits

Inbreeding depression of G VI 141 genotype over generation

The details of inbreeding depression in of G VI 141 genotype over generations is presented in table 2. The positive inbreeding depression was observed in majority of characters in S_1 generations. Negative inbreeding depression was expressed for index (-18.83) followed by efficiency index (-13.70) and phenol content (-11.92). The negative inbreeding depression was observed for average yield per tree per year (-27.59) followed by dry matter recovery (-23.58), conversion index (-22.77) and number of beans per pod (-21.47). These characters were at par or even superior when compared to preceding generation indicating little inbreeding depression. This is supported by the study of Luiz *et al.*, (1997). The reason for non expression of inbreeding depression can be attributed to additive gene control for these traits.

Inbreeding depression of P II 13.12 genotype over generation

The details of inbreeding depression in of P II 13.12 genotype over generation is presented in table 2. The positive inbreeding depression was expressed for majority of the characters in S_1 generation over S_0 generation. In case of S_2 generation, positive inbreeding depression was expressed for 16 characters and negative inbreeding depression for five characters with a maximum negative inbreeding depression of -95.45 for husk thickness indicating the increased husk thickness over proceeding generation followed by efficiency index (-66.30) and pod index (-49.94).

Inbreeding depression of P II 4.8 genotype over generation

Significant inbreeding depression was observed for average yield per tree per year and phenol content. In S_2 generation the majority of the characters have shown little or no inbreeding depression. These kinds of results in cocoa are supported by Luiz *et al.*, (1997). Wet bean weight has shown positive inbreeding depression in S_2 generation.

Inbreeding depression of P II 13.8 genotype over generation

The details of inbreeding depression in P II 13.8 genotype over generations is presented in table 3. Significant inbreeding depression was observed for average yield per tree per year, single bean weight, bean length, bean breadth, dry bean weight per pod and dry matter recovery. Negative and less inbreeding depression was observed for conversion index (-13.82) and fat content (-15.21), the non expression of inbreeding depression for these characters are controlled by additive gene. In S_2 generation the majority of the characters have shown little or no inbreeding depression except number of flat beans per pod (-41.43), pod index (-33.63), conversion index (-87.83), dry matter recovery (-87.27) and phenol content (-26.79).

Inbreeding depression of PII 12.9 genotype over generation

Inbreeding depression of PII 12.9 over S_1 generation shown negative inbreeding depression (-39.14) for number of beans per pod indicating an improvement over the preceding generation S_0 . In the S_2 generation, negative inbreeding depression was observed for yield (-29.56), pod index (-38.43) and phenol content (-14.96).

Inbreeding depression of H 7.3 genotype over generation

The details of inbreeding depression in H 7.3 genotype over generations are presented in table 3. In the S₁ generation, the positive and significant inbreeding depression was observed for average yield per tree per year (21.74) husk thickness furrow thickness (10.99), pod value (13.12), conversion index (8.99), dry bean weight per pod (13.96) and dry matter recovery(9.56) whereas the negative inbreeding depression was observed for pod index (-30.59) and efficiency index(-11.59). In the S₂ generation, positive inbreeding depression was observed for 15 characters. Pod weight (-24.22), husk ridge thickness (-22), husk furrow thickness (-13.94), number of flat beans per pod (-28.21) pod index (-26.32), efficiency index (-66.48) have expressed negative inbreeding depression. The general tendency of cocoa population is exhibited in inbreeding population also (Nair, 2010). S₂ generation showed inferiority in maximum number of traits when compared to its preceding generation S₁. Generally most of the characters were at par or even superior when compared to preceding generation indicating little inbreeding depression. This is supported by the study of Luiz *et al.* (1997). Similar reports were also recorded in a highly cross pollinated family cucurbitaceous (Allard, 1990., Nurgul and Rana, 2003. and Oviedo *et al.*,2008). Non significant role played by dominance and dominance x dominance form of epistasis may be the reason for lack of inbreeding depression. It was reported in INGENIC (1994) that, most of the economic traits of cocoa is controlled by additive genes.

All the characters under study showed a positive inbreeding depression except pod index and efficiency index in G VI 256.5 genotype over generation (table 3)

Inbreeding depression of H 1.2 genotype over generation

The details of inbreeding depression in H 1.2 genotype over S₁ generation is presented in table 3. The husk ridge thickness (-16.35) and bean thickness (-12.23) have shown negative inbreeding depression indicating that these characters are controlled by additive genes. In the S₁ generation, the number of flat beans per pod (-39.14) expressed negative inbreeding depression indicating that these characters are controlled by additive genes in the S₁ generation. In the S₂ generation, majority of the characters expressed positive inbreeding depression expect average yield per pod per tree (-29.56), pod index (-38.43) and phenol content (-14.96) indicating these characters are controlled by additive gene action.

Conclusion

The inbreeding depression in cocoa inbreds over generation was not stable. ridge thickness and bean thickness, yield per pod per tree, pod index and phenol content have shown negative inbreeding depression indicating that these characters are controlled by additive genes. There was a step up in the characteristic performance for some traits and depression for some of the characteristics. Hence, the cocoa inbreds of advanced generations with high homozygosity can be utilized for production highly heterozygous hybrids. Generally most of the characters were at par or even superior when compared to preceding generation indicating little inbreeding depression.

Declarations

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Conflict of interest

We, the authors, contributed fairly and substantively to this study, and we state that we have no competing interests.

Ethical statement

The manuscript was not submitted elsewhere, and the findings were provided without any distortion, falsification, or data manipulation. There is no risk to public health or national security from research.

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Tables

Table 1. Inbreeding depression of M 18.7 genotype over generation												
S. No.	Character	M 18.7				G II 7.4					H1 1.2	
		S ₁	S ₂	S ₃	S ₄	S ₁	S ₂	S ₃	S ₄	S ₅	S ₁	S ₂
1	Av. Yield (No. of pods/tree/year)	4.21	3.93	5.70	43.58	21.92	15.42	21.14	-5.37	39.11	16.32	9.38
2	Pod weight (g)	2.50	2.24	2.58	19.06	9.61	5.71	-18.70	4.32	24.06	12.66	-10.91
3	Husk Ridge thickness (cm)	0.00	-1.23	1.95	25.68	-64.52	-9.8	5.36	-92.45	49.02	4.35	-95.45
4	Husk furrow thickness (cm)	-12.00	0.00	1.79	19.09	-44.29	-9.11	12.09	-1.15	63.95	4.31	-0.90
5	Pod length (mm)	0.08	0.15	6.86	-6.47	6.09	-6.01	-0.75	0.04	0.10	6.68	0.01
6	Pod breadth (mm)	5.80	0.12	3.92	13.57	-4.45	0.85	-13.47	10.30	10.90	5.69	-5.90
7	No. of beans per pod	2.78	4.38	3.32	-5.14	-3.74	5.67	-4.92	18.75	-11.50	7.02	22.10
8	No of flat per pod	-7.50	-4.65	-6.67	-14.58	-9.09	8.33	-100	18.18	-11.11	-33.33	0.00
9	Wet bean weight per pod (g)	4.59	2.40	10.00	28.17	-0.70	18.49	-54.64	-10.15	-5.30	8.99	21.67
10	Dry bean weight per pod (g)	12.31	7.50	4.75	11.81	16.02	-23.46	-7.39	34.89	-8.48	25.67	33.32
11	Single bean wt. (g)	9.80	3.26	1.48	16.12	19.05	-30.88	-2.36	19.87	2.74	20.05	14.34
12	Bean length (mm)	0.10	0.21	1.55	10.26	-7	0.12	-9.47	0.01	-7.64	0.70	8.31
13	Bean breadth (mm)	0.70	3.04	0.87	13.69	0.38	-1.81	-28.68	13.40	-7.33	0.21	25.41
14	Bean thickness (mm)	0.14	0.00	-0.01	1.15	-6.01	31.60	-56.40	1.85	14.08	1.63	1.67
15	Pod value	12.31	7.50	4.20	12.09	16.04	-22.93	-7.62	34.93	-14.00	25.57	33.31
16	Pod index	-14.04	-8.11	-4.39	-13.75	-19.11	18.66	7.08	-53.68	12.28	-34.36	-49.94
17	Efficiency Index	-11.19	-5.68	-1.69	7.92	-7.59	23.17	-10.17	-47.05	33.39	-17.36	-66.30
18	Conversion Index	8.09	5.22	-6.44	-22.38	16.62	-50.82	30.41	40.93	-8.27	18.22	14.85
19	Dry Matter Recovery (%)	8.09	5.22	-5.83	-22.78	16.6	-51.46	30.55	40.89	-3.02	18.33	14.87
20	Fat content (%)	1.77	-0.02	-3.77	-10.96	-18.43	26.56	-32.31	20.16	-9.6	2.66	4.50
21	Phenol content (%)	0.84	0.42	1.71	13.59	0.78	13.24	-4.5	17.36	-29.01	1.57	8.55

Table 2. Inbreeding depression of G IV 35.7 genotype over generation											
S. No.	Character	G IV 35.7				G VI 135		G VI 141		P II 13.12	
		S ₁	S ₂	S ₃	S ₄	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂
1	Av. Yield (No. of pods/tree/year)	18.12	10.46	25.14	16.19	23.95	45.81	32.78	-27.59	21.05	27.46
2	Pod wt (g)	15.22	34.12	-44.09	-51.94	3.02	37.10	4.32	32.20	6.75	15.05
3	Husk Ridge thickness (mm)	2.04	2.08	5.33	3.37	2.7	13.89	0.70	-1.25	1.47	10.82
4	Husk furrow thickness (mm)	1.63	15.70	0.00	0.00	2.75	25.00	2.78	0.90	6.52	13.37
5	Pod length (mm)	-28.05	0.16	-0.05	-0.88	2.88	0.19	0.33	0.14	1.04	0.03
6	Pod breadth (mm)	0.10	2.60	2.56	3.51	6.32	7.80	3.19	10.00	3.87	8.90
7	No. of beans per pod	-6.67	-6.25	-1.96	-5.77	2.57	15.20	13.9	-21.47	1.71	21.00
8	No of flat per pod	-20.79	-8.20	-9.09		0.94	-71.43	7.41	39.26	0.41	-19.79
9	Wet bean weight per pod (g)	82.20	6.17	-79.70	-8.93	-5.44	45.73	0.62	13.89	0.96	29.40
10	Dry bean weight per pod (g)	2.22	3.41	0.08	-2.10	6.50	21.54	16.77	-6.42	3.50	14.75
11	Single bean wt. (g)	8.33	9.09	2.00	3.47	4.03	7.46	3.33	12.39	1.82	-7.91
12	Bean length (mm)	-0.21	0.31	-0.10	0.01	1.34	3.24	3.42	9.22	2.18	-6.41
13	Bean breadth(mm)	0.24	1.26	0.32	0.24	0.83	4.92	0.09	8.23	1.53	6.99
14	Bean thickness(mm)	1.47	0.93	0.56	0.30	0.400	20.48	0.50	13.00	2.01	1.27
15	Pod value	2.22	3.41	0.08	-2.10	2.28	21.64	15.85	-5.72	0.00	15.43
16	Pod index	-2.27	-3.53	-0.08	2.06	-2.33	-27.62	-18.83	5.41	0	-18.24
17	Efficiency Index	13.29	31.79	-44.21	-48.81	0.76	19.73	-13.70	35.84	6.75	-0.45
18	Conversion Index	-39.72	-2.94	44.40		7.32	-44.37		-22.77		-19.79
19	Dry Matter Recovery (%)	-449.37	-2.94	44.40	6.27	11.32	-44.56	16.25	-23.58	2.56	-20.75
20	Fat content (%)	-59.25	1.99	0.04	-7.46	0.24	-1.42	1.60	0.19	1.30	0.79
21	Phenol content (%)	1.21	-0.40	1.63	-4.67	2.40	0.40	-11.92	6.17	2.02	25.27

Table 3. Inbreeding depression of G VI 256.5 genotype over generation											
S. No.	Character	P II 4.8		P II 13.8		PII 12.9		H 7.3		G VI 256.5	H 1.2
		S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₂	S ₁	S ₁
1	Av. Yield (No. of pods/tree/year)	17.82	-13.04	8.70	59.88	25.28	-29.56	21.74	-8.34	21.95	17.36
2	Pod wt (g)	3.51	-2.73	1.54	31.35	9.01	35.73	3.39	-24.65	3.92	13.62
3	Husk Ridge thickness (mm)	2.61	11.98	0.31	44.92	2.33	38.10	3.05	-22.00	4.46	-8.14
4	Husk furrow thickness (mm)	1.47	12.15	1.25	50.89	7.14	35.50	10.99	-13.94	9.35	-16.35
5	Pod length (mm)	8.60	-0.13	2.12	0.17	14.05	0.20	5.25	10.52	2.49	19.00
6	Pod breadth (mm)	0.78	1.85	0.80	13.2	12.48	85.50	0.31	2.73	0.78	13.07
7	No. of beans per pod	6.44	2.01	0.97	9.15	-39.14	5.01	10.02	15.72	6.44	6.25
8	No of flat per pod	1.59	1.32	2.78	-41.43	10.96	38.46	-3.17	-28.21	1.59	9.43
9	Wet bean weight per pod (g)	8.41	31.52	7.49	60.16	1.10	1.01	4.86	-5.26	1.64	24.00
10	Dry bean weight per pod (g)	4.40	13.15	20.39	25.39	-	23.54	13.96	24.32	19.41	30.81
11	Single bean wt. (g)	2.44	4.26	19.61	17.87	-	19.51	4.38	10.20	13.86	26.19
12	Bean length(mm)	1.08	-9.99	10.30	10.75	-	11.46	1.51	0.91	0.69	12.38
13	Bean breadth(mm)	.13	5.62	5.72	4.10	-	0.15	0.46	9.75	6.03	1.15
14	Bean thickness(mm)	0.74	-9.37	0.28	-0.03	-	-4.22	3.19	-1.68	1.44	-12.23
15	Pod value	5.17	13.62	-5.30	25.16	-	27.76	13.42	25.12	13.28	0.00
16	Pod index	-5.45	-15.77	5.03	-33.63	-	-38.43	-30.59	-26.32	-15.32	0.00
17	Efficiency Index	-1.75	-18.92	6.50	8.26	-	11.04	-11.59	-66.48	-10.80	13.62
18	Conversion Index	-3.54	-26.15	-13.82	-87.83	-	27.75	8.99	28.86	11.84	-
19	Dry Matter Recovery (%)	-4.37	-26.84	13.94	-87.27	-	23.53	9.56	28.10	18.07	8.95
20	Fat content (%)	1.55	-1.88	-15.21	23.30	1.18	11.07	-3.18	-4.39	0.81	2.14
21	Phenol content (%)	12.89	-4.26	34.76	-26.79	12.04	-14.96	0.75	23.15	7.08	8.16

Supplementary

Appendix 1 is not available with this version

Figures

Figure 1

Legend not included with this version