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Generation mean analysis of fruit quality traits in eggplant (*Solanum melongena* L.)

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Abstract

Very limited information is available on gene action for eggplant fruit quality parameters related to consumer market. Therefore, a detailed study on key quality traits of eggplant was carried out to examine the gene action to support the breeding approach. In the present study, six parents were inter-crossed to study gene action governing different fruit quality traits in eggplant. The parents were selected on the basis of phenotypic superiority and divergent fruit quality traits i.e size, shape, colour and bitterness. Four crosses were made among the six parents *viz.*, Doli-5 × GBL-1 (cross 1), Doli-5 × KS-331 (cross 2), Pusa Uttam × KS-331 (cross 3) and AB 07-02 × GOB 1 (cross 4) to generate six populations for study of ten fruit quality parameters. The generation mean analysis in six populations, namely P_1, P_2, F_1, F_2, B_1 and B_2 revealed significant digenic interactions for all the characters in majority of the crosses studied. Character and cross combination revealed the adequacy of simple additive dominance model for anthocyanin content (in crosses 2 and 3), glycolalkaloid content (in crosses 2, 3 and 4), dry matter content (in cross 4) and reducing sugars (in cross 2) indicating the absence of non-allelic interactions. Most of the crosses for all the quality traits showed low magnitude of dominance and environmental variances, revealing higher estimates of broad and narrow-sense heritabilities. Duplicate type of epistasis was observed in glycoalkaloid content (in cross 1), oil content in seeds (in cross 1), dry matter content (in cross 3), total phenol content (in cross 3) , total soluble sugars (in cross 3), reducing sugars (in cross 3), polyphenol oxidase activity (in cross 3) and 1000 seed weight (all crosses) suggesting that the selection intensity should be mild in the earlier and intense in the later generations because it marks the progress through selection. However, in few cases the average dominance ratio was more than unity which showed the importance of the dominance gene effects. These results indicated that for the improvement of eggplant, additive variation is of great importance and makes it possible to successfully select better individuals in segregating populations, since the selective gains will depend only on gametic variation. Therefore, backcross, pedigree, single-seed descent or gametic selection methods are recommended to advance the segregating populations.

Keywords: Eggplant; Epistasis; Gene effects; Quality traits; *Solanum melongena*.
Abbreviations: GMA: Generation Mean Analysis; PPO: Poly Phenol Oxidase.

Introduction

The link between food and health is long and well documented, but food access depends on income. Therefore, billions of people worldwide, especially in developing countries, suffer from the sinister form of hunger called malnutrition. A past focus on increasing production of staple crops has exacerbated the problem of imbalanced diets and malnutrition, and decreased diversity in cropping systems (Keatinge et al., 2011). Globally, India is the largest producer of vegetables and ranks second in production of eggplant (*Solanum melongena* L., 2n = 24). Eggplant, grown throughout the year, is a common and popular vegetable crop in the subtropics and tropics, therefore, can play a vital role in achieving the nutritional security (Sarker et al., 2006). However, the present production and productivity of eggplant is not enough to meet the nutritional security of increasing population. Additionally, there are also regional preferences for fruit shape, size, taste, color etc as these traits vary significantly with the type of eggplant cultivar. Being an important source of plant-derived nutrients, the identification of genotypes with higher nutrients and better consumer preference could be beneficial for society, particularly for poor consumers. This would be especially important in southern Asia, where annual per capita vegetable supply is 62.4 kg (FAO, 2011), far below the recommended level of 73 kg (Ali and Tsou, 1997). The fruits of eggplant are widely consumed in various culinary preparations and are rich source of protective nutrients (Hedges and Lister, 2007). The nutritional value per 100 g of eggplant fruit contains 92.70 per cent moisture, 0.1 g fat, 5.7 g carbohydrate and 1.0 g protein. In addition, numerous vitamins and minerals, such as B_1, B_6, folate, copper, manganese (0.25 mg), magnesium (14 mg), potassium (230 mg) and about 10 per cent of the daily value of fibre are also present (USDA Nutrient Database, 2005). Eggplant contains a higher content of free reducing sugars, anthocyanin, phenols, glycoalkaloids (solasodine) and amide proteins. Bitterness in eggplant is due to the presence of saponins and glycoalkaloids (Mariola et al., 2013). Eggplant is well known for its medicinal properties and has also been recommended as an excellent remedy for liver complaints and diabetic patients (Tiwari et al., 2011). The eggplant phytochemical that have received most research attention is the phenolics, a powerful antioxidants (Vinson et al., 1998). Polyphenols have shown to be beneficial for human health due to its many biological activities like free-radical scavenging, regulation of enzymatic activity and anti-cancer activities and regulator of cell signaling pathways

(Sato et al., 2011). Consequently, due to the multiple health benefits of eggplant, which include anti-oxidant, anti-diabetic, hypotensive, cardioprotective, and hepatoprotective effects, the demand for eggplant has been on a rapid and steady rise in the recent years (Ojiewo et al., 2007).

But the development of cultivars with improved fruit quality and good phytochemical properties, a pressing need for better market value, through breeding has received relatively little attention in vegetables especially in eggplant. However, genetic control of different yield related as well as agronomic traits has been studied extensively (Patil and Shinde, 1984; Sidhu and Chadha, 1985; Chadha et al., 1990) in eggplant. Heterosis for yield and/or its associated components has also been reported in eggplant (Mishra, 1966; Dahiya et al., 1984; Singh et al., 1983). Direct selection for quality traits in eggplant, same as in all other crops, will not be successful due to interaction of many genes with environment. Knowledge of the genetic controlling system of the character to be selected and genetic variation are the pre-requisite for viable breeding strategy. Therefore, the present study comprises genotypes contrasting for fruit quality traits to study the components of genetic variation using generation mean analysis (GMA) (Cavalli, 1952; Mather, 1949). GMA, in generations P_1, P_2, F_1, F_2, B_1 and B_2 , is an efficient tool to understand the nature of gene effects involved in the expression of a character in interacting and non-interacting crosses. Though GMA has been extensively used to understand the gene effects in different crops, but no report is available on the use of this technique for understanding the gene effects in eggplant for quality traits. An assessment of these genetic parameters will allow for the development of efficient breeding strategies for egg plant cultivar improvement.

Results and discussion

The result of analysis of variance revealed significant differences among generations for all the characters investigated indicating the presence of sufficient genetic variability and depicting the possibility of selection for desirable fruit quality traits in eggplant.

Gene action

Anthocyanin content

Mean comparison (Table I) among the six generations of crosses 1 and 2 showed higher levels of anthocyanin content in fruit peel. The F_1 from crosses 1, 2 and 3 exhibited higher magnitude of mean for anthocyanin content. The additive-dominance model was adequate in crosses 2 and 3 for anthocyanin content (Table 2). The results obtained from 3-parameter model revealed that the additive gene effect (d) was significant for anthocyanin content in cross 2 while dominance gene effect (h) was significant in crosses 2 and 3. The role of dominance gene action in anthocyanin content was also noticed by Deep et al. (2006) with different set of breeding material. In contrast, Gulam-ud-din et al. (1997) revealed both additive and dominance types of gene effects for anthocyanin content. In case of 6-parameter model, positive and significant dominance gene effect was observed in cross 1 for anthocyanin content. Additive × dominance (j) gene effect was significant in crosses 1 and 4 but additive × additive (i) was found significant only in cross 1.

Glycoalkaloid content

Pertaining to glycoalkaloid content, the mean performance of all the six generations of cross 2 was better fruits having less bitterness. According to individual scaling and joint χ^2 tests, dominance gene effect was found significant for glycoalkaloid content in three crosses (cross 2, 3 and 4) as 3-parameter model was adequate. Non-additive type of allelic interaction was also reported for glycoalkaloid content by Chadha et al. (1990). Significant individual scaling and joint χ^2 tests in cross 1 revealed the existence of additive × additive (i) and dominance × dominance (l) gene effects (digenic interactions). A comparison between signs of dominance (h) and dominance × dominance (l) gene effects revealed the existence of duplicate gene interaction (opposite h and l signs) in cross 1 for glycoalkaloid content.

Dry matter content

Maximum dry matter content was observed in the segregating generations of cross 1. The additive-dominance model fitted well in cross 4 for dry matter content revealing the existence of significant additive gene effect (d). The importance of additive gene effects for dry matter content was previously reported by Devi and Sankar (1990) and Patel (1994) for dry matter content. On the other hand, non-additive gene actions were reported by many researchers (Kapadia, 1995; Ingale et al., 1997; Kaur, 1998; Patil, 1998; Gulam et al., 1999; Jha, 2003; Ajjappalavara, 2006; Tha et al., 2006 and Suneetha et al., 2008) for dry matter content. In six-parameter model, positive and significant dominance gene effect was observed in cross 3. Additive × additive (i) gene effect was observed significant in crosses 1 and 3, additive × dominance (j) gene effect was significant in cross 2 and dominance × dominance (l) gene effect was found significant in cross 3. Duplicate type of gene interaction was present in cross 3. These findings were in agreement with the results of Jha (2003) for dry matter content where duplicate and complimentary type of epistasis was observed.

Total phenol content and polyphenol oxidase activity (PPO)

Crosses 1 and 2 showed minimum total phenol content and polyphenol oxidase enzyme activity respectively, which is of immense importance in controlling the degree of browning of fruit pulp. In case of phenol content, individual scaling and joint χ^2 tests confirmed the effect of digenic interactions for all the four crosses. In six-parameter model, significant positive dominance gene effect was observed in cross 3. Additive × additive (i) gene effect for cross 2, additive × dominance (j) gene effect for all crosses except cross 1, dominance × dominance (l) gene effect for crosses 3 and 4 were observed significant. Therefore model confirmed the duplicate epistasis in cross 3. For polyphenol oxidase activity, significance of scaling tests and joint χ^2 tests inferred the presence of digenic interactions for all the four crosses. In six-parameter model, only additive gene effect (d) in cross 4, additive × additive (i) gene effect in crosses 1 and 3, additive × dominance (j) gene effect in crosses 1 and 2, dominance × dominance (l) gene effect in cross 3 were found significant revealing duplicate type of gene interaction in cross 3.

Total soluble sugars

The mean total soluble sugar was higher in F_1 of all the four crosses.

Table 1. Comparison of means (±SE) for various characters in four crosses of eggplant.

Character	Populations						
	P_1	P_2	F_1	F_2	B_1	B_2	CD (0.05%)
Anthocyanin content (mg/100g)							
C-I	118.38 ± 6.99	226.96± 12.09*	182.53± 22.81*	140.50± 16.53*	180.92 ± 21.07*	160.27 ±17.95*	6.99
C-II	101.20± 7.06	135.50± 17.73*	177.83± 19.76*	169.50± 19.51*	164.55 ± 28.94*	151.72 ± 17.84*	10.91
C-III	100.49± 2.14	102.15± 2.93	151.06±14.96*	118.89± 8.34*	127.79± 10.89*	121.22 ± 9.41*	7.47
C-IV	119.68± 14.50	159.20±15.60*	117.35±14.72*	145.63±13.58*	145.08± 17.18*	121.09 ±15.84*	13.56
Glycoalkaloid content (mg/100g)							
C-I	0.214± 0.016	0.195± 0.021*	0.171± 0.027*	0.168± 0.009	0.164± 0.014	0.140± 0.01	0.02
C-II	0.144± 0.007	0.147± 0.006	0.162± 0.008	0.147± 0.006	0.141± 0.006	0.149± 0.008	0.01
C-III	0.235± 0.05*	0.240± 0.035*	0.332± 0.011	0.326± 0.033*	0.283± 0.038*	0.314± 0.03	0.03
C-IV	0.174± 0.01	0.175± 0.014*	0.157± 0.012*	0.180±0.012*	0.165± 0.013*	0.154±0.013*	0.01
Dry matter content (%)							
C-I	8.47± 0.070	8.31± 0.169	8.37± 0.163	9.57± 0.281*	8.80± 0.235	8.98±0.412*	0.28
C-II	9.36± 0.295*	7.78± 0.281*	8.70± 0.123	8.08± 0.149	8.45± 0.154	8.19±0.170	0.22
C-III	8.08±0.308*	7.88± 0.363*	8.64± 0.137	7.11± 0.258	8.29± 0.335*	8.07±0.348*	0.29
C-IV	8.39± 0.267	8.16± 0.397	8.57± 0.506*	8.19± 0.282	8.73± 0.253	7.85±0.327	0.42
Total phenol content (%)							
C-I	0.37± 0.087*	0.34± 0.0124	0.29± 0.012	0.42± 0.037	0.41± 0.054*	0.40± 0.025	0.05
C-II	0.81± 0.1	0.86± 0.091	0.88± 0.107*	0.59± 0.069	0.91± 0.122*	0.55± 0.063	0.1
C-III	0.58± 0.023	0.53± 0.024	0.51± 0.022	0.54± 0.022	0.50± 0.027	0.66± 0.034	0.05
C-IV	0.55± 0.107*	0.60± 0.087*	0.79± 0.151*	0.50± 0.050*	0.61± 0.095*	0.30± 0.028	0.04
Total soluble sugars (%)							
C-I	2.36± 0.219*	2.39± 0.243*	2.53± 0.085	1.01± 0.063	2.31± 0.096	1.15± 0.051	0.11
C-II	2.59± 0.242*	2.31± 0.233*	2.93± 0.320*	2.34± 0.165	2.41± 0.189	2.74± 0.168	0.2
C-III	2.46± 0.032	2.48± 0.176	2.78± 0.279*	2.06± 0.167	1.98± 0.21*	2.29± 0.111	0.19
C-IV	3.42± 0.237*	3.11± 0.424*	3.22± 0.293*	2.36± 0.257*	3.25± 0.331*	2.45± 0.310*	0.15
Reducing sugars (%)							
C-I	1.72± 0.145*	1.73± 0.153*	1.95± 0.22*	1.46± 0.341*	2.05± 0.137*	1.01± 0.202*	0.1
C-II	0.46± 0.047	0.48± 0.059	0.69± 0.030	0.61± 0.063	0.62± 0.101*	0.59± 0.042	0.07
C-III	1.53± 0.078	1.51± 0.086	1.60± 0.189*	1.65± 0.153*	1.86± 0.129	1.88± 0.190*	0.13
C-IV	1.74± 0.152*	1.81± 0.281*	1.75± 0.116	1.59± 0.1	1.68± 0.106	1.47± 0.113	0.14
Ascorbic acid content (mg/100g)							
C-I	28.18± 1.879	29.48± 1.038	31.44± 1.392	26.62± 2.02*	23.98± 1.62	30.01± 2.463*	1.96
C-II	44.37± 2.568*	34.88± 2.622*	38.20± 4.162*	34.22± 1.757*	32.70± 1.733*	35.80± 2.176*	1.02
C-III	30.58± 0.448	34.68± 0.861	36.13± 0.769	42.78± 1.654	39.58± 2.631*	41.82± 1.788	2.05
C-IV	30.43± 2.116*	39.31± 1.448	37.86± 1.531	29.23± 1.491	32.75± 2.273*	31.78± 1.357	1.97
Polyphenol oxidase activity (Change in O.D/min)							
C-I	4.53± 0.659*	4.35± 0.55*	4.32± 0.906*	5.19± 0.413*	3.86± 0.633*	4.84± 0.424*	0.4
C-II	1.15± 0.160*	1.49± 0.442*	1.97± 0.322*	1.94± 0.184*	2.06± 0.220*	1.77± 0.235*	0.06
C-III	6.74± 0.516*	6.92± 0.489*	6.62± 0.506*	6.83± 0.451*	5.98± 0.510*	5.70± 0.498*	0.22
C-IV	6.66± 0.271	5.67± 0.314	6.59± 0.267	5.31± 0.442*	5.75± 0.493*	5.49± 0.701*	0.39
1000 seed weight (gm)							
C-I	3.44± 0.016	3.60± 0.022	4.01± 0.007	4.49± 0.042	3.88± 0.025	4.10± 0.058	0.17
C-II	3.63± 0.005	4.62± 0.002	4.29± 0.014	3.52± 0.013	4.43± 0.011	4.34± 0.022	0.21
C-III	4.27± 0.069	3.63± 0.106	4.28± 0.076	4.59± 0.050	4.55± 0.076	3.83± 0.058	0.23
C-IV	3.94± 0.099	3.99± 0.078	4.25± 0.015	3.46± 0.025	4.28± 0.020	3.82± 0.032	0.15
Oil content in seeds (%)							
C-I	7.58± 0.036	7.25± 0.084	8.18± 0.06	7.71± 0.043	8.20± 0.564*	8.08± 0.191	0.55
C-II	9.53± 0.221	8.59± 0.103	8.48± 0.018	8.40± 0.112	8.62± 0.472*	8.15± 0.404*	0.38
C-III	10.03± 0.195	9.86± 0.134	10.16± 0.096	8.47± 0.133	9.65± 0.377	9.42± 0.482*	0.48
C-IV	10.98± 0.228	8.65± 0.038	9.04± 0.009	11.60± 0.204	8.39± 0.063	11.80± 0.905*	0.35

C-I = Doli-5 × GBL-1 C-II = Doli-5 × KS-331 C-III = Pusa Uttam × KS-331 C-IV = AB 07-02 × GOB 1.

Genic interactions for total soluble sugars showed a positive and significant dominance gene effect in cross 1 and while interaction was significantly negative in cross 3. On the other hand, additive × additive (i) and additive × dominance (j) gene effects were significant in all crosses. All the three epistatic gene effects *viz.,* (i), (j) and (l) were significant for total soluble sugars in cross 3 and showed the duplicate type of epistasis. Non-additive gene actions were reported by Patil (1998), Ajjappalavara (2006), Tha et al. (2006) and Suneetha et al. (2008) for total soluble sugars.

Reducing sugars

Similarly, F_{1s} of all crosses except cross 3 had higher magnitudes for reducing sugars. The dominance gene effect (h) was found significant for reducing sugar content in cross 2 under additive-dominance model. Estimation of gene effects using 6-parameter model revealed positive and significant dominance gene effect in cross 3. Further, additive × additive (i), dominance × dominance (l) gene effects as well as duplicate type of epistasis were detected in cross 3.

However, in cross 1 only additive × additive (i) gene effect was observed significant for the inheritance of this trait.

Ascorbic acid content

However, the segregating generations of cross 3 showed highest magnitudes of ascorbic acid content. A simple additive-dominance model could not satisfactorily account for the variation observed in any of the families for ascorbic acid-an anti-browning agent in fruit (Macheix et al., 1990). The 6-parameter model indicated the significance of additive gene effect (d) only for ascorbic acid content in cross 3. Additive × additive (i) gene effect in cross 4, additive × dominance (j) gene effect in all crosses except cross 3 and dominance × dominance (l) gene effect in cross 2 were found significant.

1000 seed weight

For 1000 seed weight, higher magnitudes were observed in the F_1 of crosses 1 and 4. The additive-dominance model was rejected for 1000 seed weight as more than two scales were significant in scaling tests. In six-parameter model, 1000 seed weight was controlled by dominant gene effect in crosses 4 and 2 with all three types of epistatis *viz.*, (i), (j) and (l). Non-additive gene actions were reported by Patil et al. (1989) and Suneetha et al. (2008) for 1000 seed weight. However, both additive × additive (i) and additive × dominance (j) gene effects were also observed significant for controlling the inheritance of 1000 seed weight in cross 1. The negative sign of dominance effect indicates that alleles from males of crosses 1 and 3 are recessive to alleles for 1000 seed weight from females.

Oil content in seeds

The F_1 of crosses 1 and 3 exhibited higher magnitudes of mean for oil content in seeds. Estimation of gene effects using 6-parameter model revealed the interaction components to be significant in cross 2 for oil content in seeds. The dominance gene effect for oil content in crosses 1 and 3 were significant and positive; and their magnitude was also higher than that of additive effects, suggesting greater importance of dominance effects in the expression of trait. However, dominance effect was significantly negative in the remaining crosses. Additive × additive (i) interaction in all crosses except cross 2, additive × dominance (j) interaction in cross 4 and dominance × dominance (l) interaction in cross 1 were observed significant for inheritance of oil content in seeds. Duplicate type of gene interaction was observed in cross 1 with prevalence of dominance effect for this trait.

Duplicate epistasis

The signs of dominance (h) and dominance × dominance (l) gene effects were opposite in the case of glycoalkaloid content and oil content in seeds (cross 1); dry matter content, total phenol content, total soluble sugars, reducing sugars and polyphenol oxidase activity (cross 3) and for all crosses in case of 1000 seed weight suggesting duplicate type of interaction in these traits. This kind of epistasis generally hinders the improvement through selection and hence, a higher magnitude of dominance and (l) type of interaction effects would not be expected. Since none of signs of (h) were similar to the (l) type of epistasis, it was concluded that no complementary type of interaction was present in the genetic control of the studied traits. Positive or negative sign of additive × additive (i) interaction show association and dispersion of alleles in parents, respectively. Therefore, negatively significant values of (aa) in this study showed alleles dispersion in parents for anthocyanin content (cross 4), glycoalkaloid content (cross 1), dry matter content (cross 1), polyphenol oxidase activity (crosses 1 and 3), 1000 seed weight (crosses 1 & 3) and oil content in seeds (cross 4).

Variance components and heritability estimates

Variance component estimates are presented in Table 3 and varied considerably across crosses. Large variations were observed for both components with σ^2_A ranging from 0.0001 to 3278.18 and σ^2_D from -0.00012 to 2512.03. The additive genetic variance estimates for glycoalkaloid content was positive, while its dominance variance estimates was negative. The additive and dominance variance differed greatly from cross to cross. Conversely, the magnitude of dominant variance is less than the additive variance for all reviewed traits so breeding methods based on backcross/SSD/pedigree selection should be used for the above traits. The results of the estimates for the variance model, broad and narrow sense heritability values and the degree of dominance ratio are presented in Table 3. The average dominance ratio was more than unity for dry matter and ascorbic acid content (cross 3), for total phenol content (crosses 2, 3 and 4), for glycoalkaloid content and total soluble sugars (cross 1), for polyphenol oxidase activity (cross 4) and for 1000 seed weight (crosses 2 and 4), which showed the importance of the dominance gene effects that is in agreement with low narrow sense heritability for these traits (Table 3). During present study, most of the crosses for all the quality traits showed low magnitude of dominance and environmental variances, revealing higher estimates of broad and narrow-sense heritabilities. Considerable differences were observed between broad-sense and narrow-sense heritabilities in all crosses. Broad-sense heritabilities were relatively high for all traits and ranged from 2.67 to 99.38 depending on the trait and crossing combination. Oil content exhibited high broad as well as narrow sense heritability (more than 85%) in all crosses. The additive component contributed a large proportion of the variation for anthocyanin content, reducing sugar and oil content. The narrow sense heritability in cross 1 for three traits i.e. anthocyanin, dry matter content and total soluble sugars ranged from 52-59%. The results of high heritability are in congruence with Doshi (1996) for anthocyanin content; Kapadia (1995), Doshi (1996), Gulam-ud-din et al. (1997) and Gangani (2006) for dry matter content; Kapadia (1995) and Doshi (1996) for total soluble sugars. Moderate heritability for anthocyanin content in crosses 3 & 4 is in accordance with the results of Gulam-ud-din et al. (1997); and for reducing sugars in cross 2 was also intermediate. However, high heritability has also been reported by Doshi (1996) for reducing sugars. On the other hand, narrow sense heritability for total soluble sugars was spanned a narrow range (3.29-15.46%) in all crosses except cross 1.

The heritability for polyphenol oxidase activity was low to high in all crosses, similar to the findings of Doshi (1996). Similarly, same trend was observed for ascorbic acid content in all crosses except cross 1. The low narrow sense heritability in present study might be due to large epistatic

Table 2. Estimates of gene effects (±SE of mean) for various quality traits in four crosses using Mather and Jinks (1982) six-parameter model.

Character	Gene effects							
	m	d	h	i	j	l	χ^2	Epistasis
Anthocyanin content								
C-I	52.277 ± 45.273	-54.289 ± 3.464**	222.62 ± 112.598*	120.39 ± 45.140**	149.87 ± 30.037**	92.37 ± 72.399	36.45**	No epistasis
C-II	118.64 ± 4.199**	-16.620 ± 4.204**	67.092 ± 10.036**				5.76 ns	No epistasis
C-III	10.117 ± 1.727**	-0.553 ± 1.713	44.924 ± 5.761**				2.10 ns	No epistasis
C-IV	189.64 ± 40.159**	-19.763 ± 5.146**	-103.74 ± 99.658	-50.204 ± 39.828	87.512 ± 27.653**	31.451 ± 62.332	13.69**	No epistasis
Glycoalkaloid content								
C-I	0.269 ± 0.0302**	0.009 ± 0.0083	-0.308 ± 0.0799**	-0.064 ± 0.029*	0.029 ± 0.026	0.209 ± 0.0567**	15.34**	Duplicate
C-II	0.143 ± 0.002**	-0.0023 ± 0.0025	0.013 ± 0.0049**				4.94 ns	No epistasis
C-III	0.251 ± 0.012**	-0.007 ± 0.012	0.084 ± 0.0153**				5.91 ns	No epistasis
C-IV	0.174 ± 0.0046**	0.0018 ±0.0045	-0.0177 ±0.0079*				6.52 ns	No epistasis
Dry matter content								
C-I	11.116 ± 0.821**	0.0803 ± 0.114	-3.439 ± 2.0091	-2.728 ± 0.8138**	-0.530 ± 0.5518	0.694 ± 1.2278	50.11**	No epistasis
C-II	7.624 ± 0.4897**	0.792 ± 0.0974**	0.756 ± 1.264	0.948 ± 0.479	-1.059 ± 0.393*	0.317 ± 0.804	36.90**	No epistasis
C-III	3.720 ± 0.841**	0.100 ± 0.102	8.650 ± 2.141**	4.260 ± 0.834**	0.249 ± 0.617	-3.726 ± 1.339**	53.50**	Duplicate
C-IV	8.220 ± 0.135**	0.312 ± 0.130*	0.271 ± 0.252				7.39 ns	No epistasis
Total phenol content								
C-I	0.422 ± 0.105**	0.014 ± 0.021	0.135 ± 0.259	-0.071 ± 0.103	-0.002 ± 0.077	-0.267 ± 0.161	28.97**	No epistasis
C-II	0.285 ± 0.233	-0.023 ± 0.030	0.648 ± 0.609	0.546 ± 0.231*	0.761 ± 0.179**	-0.057 ± 0.412	36.35**	No epistasis
C-III	0.394 ± 0.085**	0.026 ± 0.011*	0.463 ± 0.223*	0.163 ± 0.085	-0.355 ± 0.065**	-0.347 ± 0.145*	30.31**	Duplicate
C-IV	0.729 ± 0.170**	-0.024 ± 0.029	-0.772 ± 0.438	-0.150 ± 0.168	0.638 ± 0.129**	0.635 ± 0.298*	51.46**	No epistasis
Total soluble sugars								
C-I	-0.487 ± 0.204*	-0.015 ± 0.071	2.979 ± 0.526**	2.865 ± 0.191**	2.341 ± 0.189**	0.040 ± 0.362	639.90**	No epistasis
C-II	1.492 ± 0.444**	0.140 ± 0.091	1.935 ± 1.086	0.956 ± 0.435*	-0.953 ± 0.313**	-0.494 ± 0.715	18.74**	No epistasis
C-III	2.175 ± 0.447**	-0.010 ± 0.044	-1.055 ± 1.081**	0.294 ± 0.445*	-0.597 ± 0.276*	0.166 ± 0.689*	38.97**	Duplicate
C-IV	1.292 ± 0.758	0.153 ± 0.126	2.335 ± 1.897	1.971 ± 0.747**	1.287 ± 0.549*	-0.404 ± 1.210	28.83**	No epistasis
Reducing sugars								
C-I	1.436 ± 0.823	-0.005 ± 0.052	-0.427 ± 1.763	0.291 ± 0.821	2.075 ± 0.291**	0.937 ± 0.978	55.39**	No epistasis
C-II	0.478 ± 0.015**	-0.009 ± 0.016	0.212 ± 0.021**				1.29 ns	No epistasis
C-III	0.622 ± 0.417	0.011 ± 0.027	3.125 ± 0.971**	0.898 ± 0.416*	-0.066 ± 0.222	-2.145 ± 0.596**	18.01**	Duplicate
C-IV	1.850 ± 0.358**	-0.034 ± 0.074	-0.929 ± 0.926	-0.077 ± 0.350	0.499 ± 0.289	0.830 ± 0.602	8.84**	No epistasis
Ascorbic acid content								
C-I	27.334 ± 5.741**	-0.646 ± 0.640**	-6.963 ± 13.99	1.496 ± 5.706	-10.765 ± 3.730**	11.066 ± 8.588	28.08**	No epistasis
C-II	39.505 ± 5.342**	4.744 ± 1.045**	-19.823 ± 13.133	0.116 ± 5.239	-15.680 ± 3.754**	18.521 ± 8.831*	32.65**	No epistasis
C-III	40.948 ± 6.022**	-2.049 ± 0.496**	12.154 ± 15.356	-8.322 ± 6.001	-0.361 ± 4.333	-16.976 ± 9.621	73.94**	No epistasis
C-IV	22.725 ± 5.336**	-4.437 ± 0.885**	10.873 ± 13.368	12.145 ± 5.262*	10.812 ± 3.888**	4.263 ± 8.410	50.95**	No epistasis
Polyphenol oxidase activity								
C-I	7.774 ± 1.300**	0.092 ± 0.153	-6.897 ± 3.188*	-3.377 ± 1.290**	-2.139 ± 0.858*	3.445 ± 2.001	14.01**	No epistasis
C-II	1.423 ± 0.572*	-0.171 ± 0.116	1.511 ± 1.454	-0.101 ± 0.560	0.913 ± 0.441*	-0.964 ± 0.957	11.14*	No epistasis
C-III	10.778 ± 1.270**	-0.093 ± 0.180	-11.644 ± 3.057**	-3.949 ± 1.258**	0.748 ± 0.816	7.484 ± 1.864**	17.64**	Duplicate
C-IV	4.944 ± 1.383**	0.496 ± 0.123**	-0.162 ± 3.500	1.220 ± 1.377	-0.471 ± 0.981	1.803 ± 2.170	26.46**	No epistasis
1000 seed weight								
C-I	5.517 ± 0.220**	-0.081 ± 0.034*	-2.590 ± 0.558**	-2.000 ± 0.217**	-0.270 ± 0.163	1.079 ± 0.355**	221.99**	Duplicate
C-II	0.659 ± 0.152**	-0.493 ± 0.026**	7.801 ± 0.384**	3.465 ± 0.150**	1.165 ± 0.111**	-4.174 ± 0.259**	745.44*	Duplicate
C-III	5.528 ± 0.238**	0.318 ± 0.041**	-2.526 ± 0.646**	-1.576 ± 0.235**	0.798 ± 0.203**	1.279 ± 0.442**	95.65**	Duplicate
C-IV	1.605 ± 0.158**	-0.027 ± 0.041	4.785 ± 0.396**	2.358 ± 0.153**	0.976 ± 0.125**	-2.144 ± 0.265**	336.98**	Duplicate
Oil content in seeds								
C-I	5.678 ± 0.747**	0.162 ± 0.071*	5.598 ± 2.160**	1.733 ± 0.744*	-0.087 ± 0.707	-3.095 ± 1.430*	8.61**	Duplicate
C-II	9.119 ± 0.830**	0.473 ± 0.080**	-2.240 ± 2.329	-0.058 ± 0.826	-0.021 ± 0.742	1.598 ± 1.522	12.70**	No epistasis
C-III	5.665 ± 0.827**	0.087 ± 0.114	6.702 ± 2.321**	4.277 ± 0.819**	0.302 ± 0.752	-2.206 ± 1.522	152.67**	No epistasis
C-IV	15.833 ± 1.140**	1.164 ± 0.130**	-10.135 ± 3.182**	-6.022 ± 1.132**	-9.144 ± 1.017**	3.341 ± 2.068	511.93**	No epistasis

C-I = Doli-5 × GBL-1, C-II = Doli-5 × KS-331, C-III = Pusa Uttam × KS-331, C-IV = AB 07-02 × GOB 1.

Table 3. Different components of genetic variances, degree of dominance and heritability estimates of various traits studied in four crosses.

Character	Additive variance(D)	Dominance Variance(H)	Environmental Variance (E)	Degree of Dominance (√H/√D)	Broad sense heritability (h^2b)	Narrow sense heritability (h^2n)
Anthocyanin content						
C-I	3278.18	647.19	1545.42	0.440	71.75	59.92
C-II	3675.29	2512.03	1432.10	0.826	81.20	48.24
C-III	711.75	104.87	576.13	0.383	58.63	51.10
C-IV	1923.83	659.96	1109.90	0.585	69.95	52.08
Glycoalkaloid content						
C-I	0.0001	-0.0011	0.0028	3.316	-61.33	4.12
C-II	0.00076	-0.00016	0.00035	0.458	62.98	80.09
C-III	0.0208	-0.0021	0.0040	0.317	82.55	92.00
C-IV	0.00235	-0.00012	0.00074	0.225	75.04	78.91
Dry matter content						
C-I	0.91	0.56	0.11	0.784	93.13	57.73
C-II	0.36	-0.16	0.25	0.666	45.02	80.87
C-III	0.33	0.67	0.33	1.424	75.20	24.92
C-IV	1.47	-0.80	0.93	0.737	41.95	92.38
Total phenol content						
C-I	0.0190	-0.0004	0.0093	0.145	66.70	68.14
C-II	0.003	0.044	0.050	3.829	48.40	3.29
C-III	0.0016	0.0061	0.0028	1.952	73.47	15.46
C-IV	0.0038	-0.0285	0.0765	2.738	-47.69	7.25
Total soluble sugars						
C-I	0.04	-0.11	0.15	1.658	-87.46	52.82
C-II	0.46	-0.26	0.36	0.751	35.00	82.88
C-III	0.55	-0.22	0.23	0.632	57.98	98.06
C-IV	0.59	0.27	0.47	0.676	64.28	44.21
Reducing sugars						
C-I	1.69	0.46	0.18	0.521	92.41	72.74
C-II	0.042	0.029	0.009	0.830	88.32	52.44
C-III	0.42	-0.050	0.11	0.345	77.39	88.03
C-IV	0.16	-0.12	0.16	0.866	19.38	79.51
Ascorbic acid content						
C-I	76.42	-5.36	10.61	0.264	87.01	93.57
C-II	46.25	-44.60	60.18	0.982	2.67	74.81
C-III	8.29	43.83	2.66	2.299	95.14	15.13
C-IV	18.87	11.52	14.08	0.781	68.33	42.43
Polyphenol oxidase activity						
C-I	1.02	-0.58	2.98	0.754	12.86	29.73
C-II	0.32	-0.18	0.54	0.750	20.87	46.99
C-III	3.05	-0.26	1.28	0.291	68.63	74.92
C-IV	0.49	3.04	0.39	2.490	89.94	12.39
1000 seed weight						
C-I	0.032	0.0028	0.0012	0.295	96.77	88.91
C-II	0.0007	0.0022	0.0005	1.772	85.25	19.78
C-III	0.0091	0.0069	0.0351	0.870	31.25	17.81
C-IV	0.0125	-0.0194	0.0204	1.245	-51.37	92.93
Oil content in seeds						
C-I	2.84	0.34	0.020	0.346	99.38	88.86
C-II	3.53	0.09	0.08	0.159	97.94	95.46
C-III	2.89	0.34	0.093	0.342	97.19	87.00
C-IV	7.88	0.11	0.07	0.118	99.16	97.78

C-I = Doli-5 × GBL-1, C-II = Doli-5 × KS-331, C-III = Pusa Uttam × KS-331, C-IV = AB 07-02 × GOB 1

Table 4. Salient features of parental lines used in the study.

S. No.	Parents	Height (cm)	Fruit bearing habit	Fruit weight (g) (H=>400, M=200-400, L=<200)	Fruit shape	Fruit colour	Taste
1.	Doli 5	Tall	Solitary	High	Oblong	Black	Medium bitter
2.	GBL 1	Tall	Solitary	High	Round	Purple	Low bitter
3.	KS 331	Medium	Cluster	Medium	Round	Dark purple	Bitter
4.	Pusa Uttam	Tall	Solitary	Medium	Round	Light purple	Low bitter
5.	AB-07-02	Medium	Solitary	Medium	Oblong	Green with purple lines	Medium bitter
6.	GOB 1	Dwarf	Cluster	Low	Oblong	Black	Medium bitter

effects which has also supported by Hakizimana et al. (2004). Estimates of narrow sense heritability indicated that additive effects were primarily responsible for the genetic variation in these hybrids. In the improvement of self-pollinated plants like eggplant, additive variation (fixable) is of great importance and makes it possible to successfully select better individuals in segregating populations, since the selective gains will depend only on gametic variation (Warner, 1952). For this reason, backcross, pedigree, single-seed descent or gametic selection methods are recommended for advances the segregating populations (Bernado, 2003).

Materials and Methods

Plant materials

Crosses *viz*., Doli-5 × GBL-1 (cross 1), Doli-5 × KS-331 (cross 2), Pusa Uttam × KS-331 (cross 3) and AB 07-02 × GOB 1 (cross 4) were made between six parents by manual

emasculation and pollen transfer. Phenotypically divergent parents with superior fruit quality characteristics i.e. size, shape, colour and taste were selected (Table 4). F_1 plants were selfed to obtain seed for the F_2 generation and backcrossed with their respective parents to create the B_1 and B_2 generations using a total of 20 pollinations per backcross. Thus, a total of 6 generations were obtained, corresponding to the 2 parents and the F_1, F_2, B_1 and B_2 generations.

Field trials

The six generations (P_1, P_2, F_1, F_2, B_1 and B_2) for each population were planted during July 2011 at Main vegetable research station, AAU, Anand (latitude/longitude 22°-35' North latitude and 72°-55' East longitude, elevation 45.1m a.s.l., yearly rainfall 877.6 mm, average yearly temperature 24°C). This location has inceptisol soils of sandy loam texture and pH of 7.2. Four populations were planted in separate experimental plots each in a compact family block design with three replications. All agronomic practices and preventive measures were taken to raise a healthy crop. Each plot had one row each of two parents (P_1 & P_2) and F_1, two rows of each backcross (B_1 & B_2) and four rows of F_2. Each row consisted of 15 plants and inter and intra-row spacing was 90 and 60 cm, respectively. The number of plants evaluated varied depending on the treatment and was larger for the segregation generations such as the F_2 (with 60 plants per repetition) and the B_1 and B_2 (with 30 plants per repetition each) than for treatments with non-segregating generations such as the P_1 and P_2 parents and the F_1 generation (with 15 plants per repetition each). Plantlets were thinned to one plant per planting hole when the seedlings reached a height of 10 cm.

Traits evaluated

Fresh and marketable fruits were collected from ten selected plants which are phenotypically superior for evaluation of ten quality traits. The traits assessed were anthocyanin, glycoalkaloid, dry matter, total phenol, total soluble sugars, reducing sugars, ascorbic acid, polyphenol oxidase (PPO) activity, 1000 seed weight and oil content in seeds. In the evaluations, plants at the end of each row were not considered to avoid border effects. Anthocyanin was extracted with ethanolic-hydrochloride and colour intensity was measured colorimetrically at a wavelength of 535 nm as suggested by Ranganna (1986). The glycoalkaloid content and PPO content were determined using ultravoilet-visible spectrophotometry (Elicon Ltd, India) according to Currier and Kuc (1975) and Malik and Singh (1980), respectively. The dry matter content, total soluble sugars and total phenols were estimated using the procedure given by Awasthi and Dixit (1986), Dubois et al. (1956) and Malik and Singh (1980), respectively. Reducing sugars content was estimated by the method suggested by Somogyi (1952). Ascorbic acid was estimated by 2, 6-dichlorophenol indophenol dye method as described by Sadasivam and Manickam (2008). For thousand seed weight, three to five ripened fruits from tagged plants were crushed and washed in tap water to remove the seeds from pulp. The sun dried seeds were used for seed weight. For seed weight, 100 seeds were counted and weighed in thrice and average value was extrapolated to get weight of 1000 seeds and expressed in grams. Total oil from the seeds was extracted by Soxhlet method using hexane (AOAC, 1990).

Statistical analysis

The generation mean analysis of the six populations (P_1, P_2, F_1, F_2, B_1 and B_2) and scaling tests (Cavalli 1952; Mather 1949) were performed based on the assumption that populations have non-homogenous variances (Mather and Jinks, 1971). The three-parameter model of Jinks and Jones, (1958) was used to test the adequacy of the additive-dominance model in the absence of non-allelic gene interaction. The six-parameter model of Hayman (1958) was used to estimate various gene effects including the non-allelic interaction. Variance components (additive, dominance and environment) were estimated as described by Mather and Jinks (1971). Broad and narrow-sense heritability was estimated using method proposed by Warner (1952). The degree of dominance ratio was measured using $[H/D]^{1/2}$, where H is the dominance variance and D is additive variance.

Conclusion

Eventually, it can be concluded that the nature and magnitude of gene effects vary with different cross/character-wise. Hence, specific breeding strategy has to be adopted for a particular cross to get improvement in fruit quality traits. The results showed that as a consequence of higher magnitude of interactions, the non-fixable gene effects were higher than the fixable. Further, duplicate type of epistasis was also found in majority of traits in one or the other cross combinations. In such crosses, the selection intensity should be mild in the earlier and intense in the later generations because it marks the progress through selection. Therefore, methods which exploits non-additive gene effect and take care of non-allelic interactions like restricted recurrent selection by way of intermating among desirable segregates, followed by selection or diallel selective mating or multiple crosses or biparental mating in early segregating generations could be promising for genetic improvement of fruit quality traits. In addition, few cycles of recurrent selection, followed by pedigree method may also be useful for the effective utilization of all three types of gene effects simultaneously. It will lead towards an increased variability in later generations for effective selection by maintaining considerable heterozygosity through mating of selected plants in early segregating generations.

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