Gene Action of Shelf-Life and other Fruit Quality Traits in a Cross Between a Regular Cultivar and *Alc* Mutant of Tomato

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Abstract

Prolonged shelf-life and good quality fruit are crucial attributes for the marketing of tomato (Solanum lycopersicum L) and thus a major focus for breeding. This study was carried out to explore gene effects, heritability, heterosis and inbreeding depression for shelf-life, fruit quality and some quantitative traits of tomato using six generations derived from a cross between CSIR/CRI-P002 (P1) an adapted variety with good yield and short shelf-life, and Alc-LA3134 (P2), a ripening mutant tomato with long shelf-life but low yield. The P_1, P_2, F_1, F_2, $BC_{1.1}$, $BC_{1.2}$ generations were subjected to generation mean analysis. Mean performance of the F_1 was higher than the mid-parent for all traits except total soluble solids (TSS). Additive and dominance variances were higher than environmental variance for all traits. Apart from shelf-life, the simple additive-dominance (three-parameter) model was inadequate for explaining the gene action for the traits. Using the six parameter model, additive, dominance and epistatic gene effects were found to be significant for most of the studied traits. Duplicate epistasis was detected for all the traits except shelf life. The fixable and non-fixable gene effects exhibited by the traits can be improved through pure line breeding and heterosis, respectively.

Keyword: Additive, Non-additive, Genetic variability, Heritability, Inbreeding depression

Action Génique de la Durée de Conservation et d'autres Caractères de Qualité du Fruit dans un Croisement Entre un Cultivar Régulier et un Mutant Alc de Tomate

Résumé

La longue durée de conservation et les fruits de bonne qualité sont des attributs cruciaux pour la commercialisation de la tomate (Solanum lycopersicum L) et constituent donc une priorité majeure pour la reproduction. Cette étude a été réalisée pour explorer les effets des gènes, l'héritabilité, l'hétérosis et la dépression consanguine pour la durée de conservation, la qualité des fruits et certains caractères quantitatifs de la tomate en utilisant six générations dérivées d'un croisement entre CSIR/CRI-P002 (P1) une variété adaptée avec un bon rendement et une courte durée de conservation, et Alc-LA3134 (P2), une tomate mutante mûre avec une longue durée de

conservation mais un faible rendement. Les générations P1, P2, F1, F2, BC1.1 et BC1.2 ont fait l'objet d'une analyse des moyennes de production. Le rendement moyen du F1 était supérieur à celui du parent médian pour tous les caractères, sauf les solides solubles totaux (TSS). Les variances de l'additif et de la dominance étaient supérieures à la variance environnementale pour tous les caractères. Outre la durée de conservation, le modèle simple de dominance additive (trois paramètres) était inadéquat pour expliquer l'action des gènes sur les caractères. En utilisant le modèle à six paramètres, les effets additifs, dominants et épistatiques des gènes se sont révélés significatifs pour la plupart des caractères étudiés. Une double épistase a été détectée pour tous les caractères, sauf la durée de conservation. Les effets des gènes fixables et non fixables exposés par les caractères peuvent être améliorés par la sélection pure et l'hétérose, respectivement.

Mot-clé: Additif, Non-additif, Variabilité génétique, Héritabilité, Dépression consanguine

Introduction

Tomato (*Solanum lycopersicum* L) is vulnerable to rapid post-harvest softening and poor shelf-life leading to pronounced post-harvest loss. Firmness and shelf-life are high priority characters in purchase of fresh market produce (Osei *et al*., 2018a; Snels *et al*., 2018). These traits are however, not commonly found in tomato varieties in Ghana.

Calcium has been used to increase shelf-life of fresh fruit by maintaining cell wall integrity and reducing action of cell wall degrading enzymes and subsequent fruit softening (Kittemann *et al*., 2010). A genetically modified tomato variety, Flavr Savr, was developed using antisense RNA technology. The introduction of this gene in the reverse form, also called antisense, resulted in low production of the polygalactonurase enzyme. Consequently, the transformed ripe tomato fruit do not lose firmness because cell walls, which is made of cellulose, does not degrade as rapidly as in normal tomatoes. 'Flavr Savr' was commercialized in 1996 but was taken off the market by 1999 due to consumer concerns on the safety of the product. And there has not been any commercial tomato variety with long shelf-life to replace it. To avoid the 'Flavr Savr' fiasco, conventional breeding for tomato is recommended to meet consumer needs (Osei *et al.,* 2018b). Tomato fruit quality including firmness and long shelf-life is a major focus for breeders around the world (Foolad, 2007). The choice of selection and breeding procedures for genetic improvement of crops depends on the knowledge of the type of gene action for the traits of interest.

Generation mean analysis is a biometrical design which involves the generations P_1, P_2, F_1, F_2, B_1 and B_2 for estimation of genetic components of variation (Jinks *et al.,* 1969). This method provides information about presence or absence of epistasis and estimation of additive and dominance variances and effects. In this study, generation means analysis was used to determine the gene action of shelf-life and some other fruit quality traits in *S. lycopersicum*.

Materials and Methods

Two tomato varieties with diverse traits were used for the study. This included CSIR/CRI-P002 (P_1), an adapted variety with good yield, short shelf-life (SSL); and Alc-LA3134 (P_2), a ripening mutant tomato, with long shelf-life (LSL) and low yield. Seeds of the CSIR/CRI-P002 and Alc-LA3134 were obtained from the Council for Scientific and Industrial Research - Crops Research Institute (CSIR-CRI) and the Tomato Genetic Resource Center at University of California, respectively. Crosses were made between the parents to obtain F_1 individuals. The F_1 lines

were grown and backcrossed to both parents to produce $BC_{1.1}$ ($F_1 \times P_1$) and $BC_{1.2}$ ($F_1 \times P_2$) (Zdravkovic *et al*., 2011). Some F_1 plants were selfed to produce the F_2 generation. The parents, F_1, F_2, $BC_{1.1}$ and $BC_{1.2}$ generations were transplanted into a field at the CSIR-CRI, Kwadaso (latitude 6°40'35.6" N and longitude 1°40'04.6" W) in 2018. A randomized complete block design with 3 replications was used. There were 30 plants per replication for the parents and F_1, 120 F_2, 60 $BC_{1.1}$ and 60 $BC_{1.2}$ seedlings. A spacing of 100 cm and 50 cm between- and within-row, respectively, was used. Production practices followed that of Kanneh et al. (2016).

Data were collected on 30 non-segregated plants (P_1, P_2 and F_1), 60 BC_1, BC_2 and 120 individual F_2 plants from each replicate. Fifteen tomato fruits at breaker stage were harvested from each plant to assess the fruit shelf-life, total soluble solids (TSS), number of locules and pericarp thickness. Other data collected included days to 50% flowering, plant height, number of fruits per plant, and fruit yield per plant. Shelf-life was measured as number of days from harvest until first symptoms of deterioration and excessive softening appeared (Rodriguez et al., 2010). To detect this trait fruits were stored at room temperature in the range of 26.7-29.1°C and examined every day to discard spoiled or excessive softening fruit (Schuelter *et al.,* 2002; Garg *et al.,* 2007; Rodriguez *et al.,* 2010). The process of discarding fruit continued till the last fruit became unmarketable. To identify tomato lines with long shelf-life, the number of days taken for fruit breaker stage to get tomato fruits spoilt was determined. Total Soluble Solids (TSS) was estimated on samples and determined with a digital refractometer (model-H1 96801, Hanna Instruments Inc., Woonsocket, RI). The refractometer was cleaned with distilled water each time after use and dried with blotting paper. A hand-held electronic penetrometer (model-Omega HFH81, OMEGA Engineering, Inc, Taiwan) was used to measure fruit firmness. Five fruits from each replicate were sliced transversely to count numbers of locules. After slicing the equatorial plane of each fruit, pericarp thickness was measured at 2 places per fruit with a digital Vernier caliper (Sonic equipment Company Limited, Hong Kong, China) and averaged over 5 fruit.

The data were subjected to analysis of variance using PROC GLM in Statistical Analysis Software (SAS) (ver. 9.1, SAS Institute, Cary, NC), and means separated using LSD. Prior to analysis of variance, data were tested for normality using Shapiro–Wilk test (Shapiro and Wilk, 1965). Generation mean analyses were conducted by fitting the generation means for each trait to a 3-parameter model following a Joint Scaling test (Cavalli, 1952; Mather and Jinks, 1982; Kearsey and Pooni, 1998), in which generations means were subjected to a weighted least squares regression. Estimates of additive effect and dominance effect were used to estimate expected generation means, and tested for goodness of fit using chi square with 3 degrees of freedom. A model was declared adequate when the chi-square test was non-significant. The significance of chi square test for a three-parameter model provided evidence of presence of epistasis in moderating expression of traits. An extended genetic model was performed to estimate the non-allelic interaction using least square regression based on a six-parameter model. The expected generation means for the six-parameter model was estimated from genetic effects by substituting parameter estimates in the expected generation means equation. Observed, and expected, generation means were tested for goodness of fit of the six-parameter model using Chi-square test according to (Mather and Jinks, 1982) with modification to notations. A sequential step-

wise multiple regression analysis was used to identify the best model with significant parameter estimates. Non-significant parameters were deleted from the model one at a time during the fitting process until a best-fit model was found. The adequacy of the best-fit model was tested using chi square with degrees of freedom equal to the number of generations minus the number of parameters in the model (Checca *et al.,* 2006).

Estimates of additive variance (VA), dominance variance (VD), environment variance (VE), additive x dominance variance (VAD), narrow sense heritability (h2N), and broad-sense heritability (h2B), were calculated using the equations of Lynch and Walsh (1998) and Kearsey and Pooni (1998). Heterosis was calculated using the formulae of Kanneh et al. (2016). Inbreeding Depression (ID) was calculated by using the formula of Dagade et al. (2015).

Results

There were differences among generations for all the measured traits (Table 1). Mean performance for the tested characters in the generations of tomato varied (Table 2). Number of fruits per plant was lowest for the P_2 generation and highest for the F_1 and BC_1 generation. Fruit yield per plant was lowest for the P_2 generation and highest for the F_1 generation. Pericarp thickness ranged from 3.77 mm for P_1 to 5.37 mm for P_2 with a mean of 4.72 mm. The number of locules ranged from 4.16 for P_1 to 6.83 for BC_2 generation with a mean of 5.78. TSS ranged from 4.89 for F_1 to 5.09 for P_2 with a mean of 4.98. The maximum fruit firmness was recorded on P_2 (56.03) while P_1 (55.26) recorded the minimum with a mean of 55.68. Shelf-life was maximum in P_2 (57.11 days) and minimum for P_1 (26.32 days).

Variance component estimates varied considerably across the traits (Table 3). Large variations were observed for the genetic, additive and dominance variances with genetic variance ranging from 0.11 for TSS to 5525.95 for fruit yield per plant; additive variance from 0.00 for TSS to 1456.15 for fruit yield per plant and dominance variance from 0.00 for fruit firmness to 4069.80 for fruit yield per plant. The additive genetic variance estimates for all the traits were positive except TSS which was zero but positive for dominance variance estimates. Likewise, all the traits had positive dominance variance estimates except fruit firmness which was zero. The additive and dominance variances differed greatly from trait to trait. On the contrary, the magnitude of dominance variance was less than the additive variance for all the studied traits except for TSS, pericarp thickness, fruit yield per plant and number of fruits per plant. The V_{AD} was zero for plant height, fruit yield per plant, pericarp thickness, number of locules per fruit and shelf- life.

Table 1: Analysis of variance for fruit yield and fruit quality traits in tomato

Source	df	Plant height	Number fruit per plant (+)[a]	Fruit yield per plant (+)	Pericarp thickness	Number locules	TSS	Fruit firmness	Shelf-life
Rep	2	2112.89**	0.30*(9.81*)	0.09* (11002.18)	6.84**	1.27	0.22	0.38	11.93
Genotype	5	8165.29**	4.85** (112.70**)	2.89** (426804.01**)	33.52**	107.98**	0.49**	6.80**	4089.29**

**, ** = Significant at p = 0.05 or 0.01 probability levels, respectively.*
[a](+) = data transformed; data in the parenthesis not transformed.
TSS= Total soluble solids

Table 2: Mean performance of fruit yield, fruit quality and shelf-life in populations of tomato

Genotype	Plant height (cm)	Number fruit per plant (+)[a]	Fruit yield per plant (+)	Pericarp thickness (mm)	Number locules per fruit	TSS (%)	Fruit firmness ($N \cdot cm^{-2}$)	Shelf-life (days)
P_1	50.16	1.71 (5.56)	2.10 (126.75)	3.77	4.16	4.96	55.26	26.32
P_2	50.27	1.25 (3.51)	1.95(89.00)	5.37	6.27	5.09	56.03	57.11
F_1	71.43	1.85(6.40)	2.42 (264.62)	5.01	6.20	4.89	55.74	50.57
F_2	63.92	1.75(5.94)	2.27 (203.70)	4.81	5.73	4.95	55.74	49.11
BC_1	60.66	1.83(6.31)	2.33 (230.16)	4.32	5.18	5.02	55.52	53.29
BC_2	67.88	1.73(5.85)	2.28 (206.00)	4.95	6.83	5.00	55.73	55.22
Mean	62.24	1.72(5.78)	2.25 (197.04)	4.72	5.78	4.98	55.68	48.6
Lsd	2.30	0.06(0.30)	0.04 (15.19)	0.14	0.24	0.10	0.10	1.29

[a] *(+) = data transformed; data in parenthesis not transformed*
TSS= Total soluble solids

Table 3: Components of variance and heritability estimate for yield, fruit quality and shelf-life traits in six population of tomato

Trait	V_E[a]	V_G	V_A	V_D	V_{AD}	h^2_B (%)	h^2_N (%)
Plant height (cm)	4.70	149.77	122.12	27.65	0.00	97	79
Number fruit per plant	0.27	1.84	0.74	1.10	0.54	69	28
Fruit yield per plant (g)	60.31	5525.95	1456.15	4069.80	0.00	99	26
Pericarp thickness (mm)	0.11	0.35	0.07	0.28	0.00	76	15
Number locules per fruit	0.47	0.85	00.58	0.27	0.00	64	44
Total soluble solids (%)	0.07	0.11	0.00	0.11	0.15	33	0
Fruit firmness ($N \cdot cm^{-2}$)	0.11	0.18	0.14	0.00	0.04	62	48
Shelf-life (days)	2.14	43.2	32.98	10.22	0.00	95	73

[a] *V_E = Environmental variance, V_G = Genetic variance, V_A = Additive variance, V_D = Dominance variance, V_{AD} = Additive-Dominance Interaction, $h2_B$ = Broad base heritability, h^2_N = Narrow based heritability.*

Considerable differences were observed between broad-sense heritability and narrow sense heritability in the studied traits (Table 3). For all traits, broad-sense heritability (33 to 99 %) were greater than narrow-sense heritability (0 to 79 %). The high broad-sense heritability for yield per plant (99%) did not translate into high narrow sense heritability estimates (26%) (Table 3). Low narrow sense heritability was recorded for the number of fruits per plant, fruit yield per plant, pericarp thickness and TSS. The results of heterosis

Table 4: Estimate of mid-parent and better parent heterosis and inbreeding depression

Trait	Mid-parent heterosis	Better parent heterosis	Inbreeding depression
Plant height (cm)	42.23	42.09	10.51
Number fruit per plant	40.97	15.11	7.19
Fruit yield per plant (g)	146.43	108.77	23.02
Pericarp thickness (mm)	9.63	-6.70	3.99
Number locules per fruit	18.77	-1.12	7.58
Total soluble solids (%)	-2.78	-3.93	-1.22
Fruit firmness ($N \cdot cm^{-2}$)	0.16	-0.52	0.01
Shelf-life (days)	8.33	-17.62	4.78

and inbreeding depression indicated that mean performance of F_1 was higher than mid-parental value for all the traits except TSS (Table 4). The relative heterosis ranged from -2.78% to 146.43% while heterobeltiosis was from -0.52% to 108.77%. All the estimated mid-parent heterosis were positive except for TSS. For the better parent heterosis, all the estimates were negative with the exception of plant height, number of fruits per plant and fruit yield per plant. Values of inbreeding depression were positive for all studied traits except for TSS. The inbreeding depression estimates ranged from -1.22 for TSS to 23.02 for fruit yield per plant.

Apart from shelf-life, significant differences were observed for all the traits under the three-parameter model (Table 5a). The mean effects were highly significant for all the studied traits. Using the six-parameter model, additive effects [a] were significant for all traits except plant height. Apart from the number of fruits per plant and fruit yield per plant, all the additive effects were negative. The dominance gene effect was higher than additive gene effect for all the studied traits. Among the non-allelic interactions, additive x additive [aa] was significant for all the traits except number of fruits per plant and TSS. Similarly, additive x dominance [ad] interaction was significant for all the traits except yield per plant and TSS. Apart from TSS, all the traits showed significant differences for dominance x dominance [dd] interaction (Table traits (Table 5 b & c).

Discussions

The significant differences observed among the various generations as revealed by the analysis of variance indicated the existence of substantial amount of genetic variability for all the studied traits. Genetic variability for fruit yield, fruit quality and shelf-life in different populations of tomato were also found by Rodriguez *et al.* (2010), Ahmed *et al.* (2011), Rajasekhar *et al.* (2013), and Kumar and Paliwal (2016). The existence of significant differences among the generations for the studied traits necessitated the use of generation mean and variance analyses to explore the gene action controlling the inheritance of these traits. The results showed that the means of the F_1s for plant height, number of fruits per plant and fruit yield per plant were higher than the better parent and indicating over or partial dominance for those traits. These findings supported the observa-

Table 5a: Gene effects of shelf-life and other quantitative characters of tomato using three-parameter model

Para-meter	Plant height	Number fruit per plant (tf)	Yield per plant (tf)	Pericarp thickness	Number locules per fruit	TSS	Firmness	Shelf-life
m	50.44±0.15**	1.51±0.04**	10.37±0.14**	4.49±0.02**	5.37±0.18**	5.02±0.01**	55.47±0.15**	28.2±0.07**
[a]	-0.22±0.15ns	0.22±0.04**	0.93±0.14*	-0.72±0.02*	-1.23±0.18*	-0.06±0.01ns	-0.19±0.15ns	-8.88±0.07**
[d]	21.71±0.29*	0.38±0.07*	5.93±0.22**	0.48±0.04*	0.91±0.31ns	-0.11±0.03ns	0.29±0.03ns	2.24±0.22*
$\chi 2$ (df=3)	137.60***	75.43***	99.98***	39.48***	45.10***	8.72*	189.50***	3.37ns

tf = transformed data
, **, * = Significant at p = 0.05, 0.01, 0.001 probability levels, respectively*
ns = not significant
TSS= Total soluble solids

Table 5b: Gene effects of some quantitative characters of tomato using the six-parameter model

Para-meter	Plant height	Number fruit per plant (tf)	Yield per plant (tf)	Pericarp thickness	Number locules per fruit	TSS	Firmness
m	48.80±3.32**	1.36±0.08**	8.17±0.81**	5.276±0.20**	4.09±0.14**	4.79±0.14**	56.09±0.13**
[a]	-0.06±0.15ns	0.23±0.01**	0.91±0.03**	-0.80±0.03**	-1.06±0.01**	-0.06±0.01**	-0.39±0.03**
[d]	37.84±8.07**	1.05±0.19**	15.20±2.02**	-1.59±0.51*	4.43±0.82**	0.55±0.38ns	-1.06±0.32*
[aa]	1.42±3.32**	0.12±0.08ns	2.17±0.81*	-0.71±0.20*	1.21±0.32*	0.23±0.14ns	-0.44±0.12*
[ad]	-14.32±2.06**	-0.26±0.05**	-0.17±0.55ns	0.33±0.15*	-1.2±0.24**	0.17±0.12ns	1.21±0.10**
[dd]	-15.205±4.88*	-0.56±0.12**	-7.10±1.24**	1.33±0.32**	-2.32±0.52**	-0.45±0.26ns	0.71±0.20*

tf = transformed data
, **, * = Significant at p = 0.05, 0.01, 0.001 probability levels, respectively*
ns = not significant
TSS= Total soluble solids

tions made by Lakshmi and Mani (2004) and Singh et al. (2007). In general, plant height in many crops is positively correlated with yield. In tomato, plant height influences yield positively by having more bearing nodes and more leaves (Mahto 1996). Our results suggested the possibility of developing high yielding hybrids using the two parents used for this study.

The high mean performance recorded for pericarp thickness, total solid soluble, fruit firmness and shelf-life for Alc-LA3134 (P_2) implied that this parent was ideal for the transfer of traits associated with prolonged shelf-life and good taste. Several authors also found Alc-LA3134 to be a good donor for long shelf-life in tomato (Kopeliovitch *et al.,* 1981; Mutschler *et al.,* 1992; Dias *et al.,* 2003;

Table 5c: Gene effects of some quantitative characters of tomato using the sequential parameter model

Para-meter	Plant height	Number fruit per plant (tf)	Yield per plant (tf)	Pericarp thickness	Number locules per fruit	TSS	Firmness
m	50.47 ±0.87**	1.47±0.01**	10.34±0.04**	4.55±0.06*	5.78±0.19**	4.99±0.19**	55.72±0.11**
[a]	-	0.19±0.06ns	0.91±0.04**	-0.76±0.06*	-0.15±0.26*	-0.04±0.03ns	-
[d]	21.67±1.71**	0.71±0.07ns	10.34±0.04**	-	-	-	-
[aa]	-	-	-	-	-	-	-0.44±0.14**
[ad]	-	-	-	-	-	-	-
[dd]	-	-0.37±0.36ns	-3.94±0.78**	0.47±0.11**	-	-	-
$\chi 2$	139.69**	3.69ns	0.52ns	29.22**	12.69*	5.99ns	10.73*
Type of epistasis	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate	Duplicate

tf = transformed data
, **, * = Significant at p = 0.05, 0.01, 0.001 probability levels, respectively*
ns = not significant
TSS= Total soluble solids

Kopeliovitch et al., 2006; Rodriguez *et al.*, 2010; Pawar *et al.*, 2016).

The additive and dominance variances composed the largest portion of variability for all the traits studied signifying less environmental influence and feasibility of the improving the traits studied. The results showed that additive variance played the greatest role for inheritance in plant height, fruit firmness and shelf-life traits whereas dominance variance played key role in fruit yield per plant and TSS implying both fixable and non-fixable gene effects are involved respectively. Early selection can be done for the traits with high additive gene effects whereas recurrent selection methods can be used to improve for the non-fixable gene effects. The V_{AD} which is an indicator of association between V_A and V_D over all loci was zero for the number of fruits per plant, TSS and fruit firmness suggesting that the parent with high performance have dominant genes. Traits with dominant gene effect can be improved by heterosis breeding. These outcomes revealed that, genetic effect had a vital role in the expression of these characters.

A better indicator of genetic proportion of variation in any population is the heritability estimates (Holland *et al.,* 2013). Heritability in broad-sense reveals all potential genetic contributions to a population's phenotypic variance (Vengadessan, 2008). In this study, high broad sense heritability estimates was reported for almost traits (Haydar *et al.,* 2007). High values of broad-sense heritability for the traits explained that the expression of the traits was least affected by environmental influences and selection based on phenotypic performance would be reliable. According to Swarup and Chougule (1962), an effective selection based on the phenotype can be done on a particular plant character with high heritability. However, the high broad-sense heritability estimates reported in this present

study for yield, pericarp thickness and total solid soluble (TSS) did not translate into high narrow sense heritability. This suggests the predominance of non-additive gene effect for those traits. This might be due to large epistatic effects. Hakizimana *et al.* (2004) had similar results. Falconer and Mackay (1996) reported that low narrow sense heritability was caused by low additive and high dominance gene effects.

Narrow sense heritability was nonetheless high for shelf-life, fruit firmness and plant height. This result agrees with Reddy *et al.* (2013) who studied heritability on yield and quality traits in tomato.According to Robinson *et al.* (1949), narrow sense heritability is the best estimate of breeding value as it represents the portion of phenotypic variation due to additive effects. This suggests that selection for high for shelf-life, fruit firmness and plant height can be effective in early generations.

Varied range of heterosis for all the characters studied was revealed. The traits with positive heterosis showed the prominence of hybrid vigour. Nonetheless negative heterosis indicate that dominance was in the direction of the parents with lower values. For the traits that had positive heterosis for both mid and better parent, it suggested that dominance direction was toward the best parent. These findings generally agreed with results of Choudhary and Mishra (1988), Singh and Kumar (1978) and Singh *et al.* (1989) for plant height; Kalloo *et al.* (1989) and Kapadia (1995) for fruit per plant; Singh *et al.* (1998) and Jha (2003) for fruit yield per plant; Ahmed *et al.* (2011) and Chattopadhyay and Paul (2012) for pericarp thickness; Sekhar et al. (2010), Ahmed *et al.* (2011) and Chattopadhyay and Paul (2012) for number of locules per fruit; Zhou and Xu (1990) and Joshi *et al.* (2005) for total soluble solids (brix); Garg *et al.* (2008, 2013), for fruit firmness and Garg *et al.* (2013), and Kumar and Gowda (2016) for shelf-life.

The hybrid vigor expressed in F_1 generally breaks down in F_2 and in advanced generations. This is due to segregation of the favourable genes that direct the expression of the vigour. When this happens, there is a general decrease in the expression of traits. In this study, the decline in hybrid performance at F_2 generation was estimated and the degree of inbreeding depression was noted for the various traits. Inbreeding depression was positive for all studied traits except total solid soluble (brix). This was anticipated, as the manifestation of heterosis in the F_1 generation was followed by a decline in performance in F_2 due to an increase in homozygosity. The total solid soluble which had negative inbreeding depression may be attributed to the occurrence of transgressive segregation in the F_2 generation. It can be established from the results that traits showing higher estimate of heterosis displayed high inbreeding depression. This can be attributed to presence of non-additive gene action for those characters under study. These results were in conformity with the findings of Singh *et al.* (1996), Dagade *et al.* (2015) and Kumar *et al.* (2009).

The simple additive-dominance model was adequate for explaining the expression of shelf-life in the cross thus indicating the absence of non-allelic interactions in the inheritance of this trait. This result agreed with Rodriguez et al. (2010) who studied gene effects of tomato and reported the adequacy of three parameter model to explain the genetic control of shelf-life. Similar results were found by Adeniji and Kehinde (2003) for okra; Azizi et al. (2006) for maize; Abd-El *et al.* (2010) for cotton and Behmaram *et al.* (2014) for kenaf.

Using the six parameter model, additive,

dominance and epistatic gene effects were significant for most of the traits, indicating that both additive and non-additive effects were important for the inheritance of most of the studied traits. Similar result was described by Behmaram *et al.* (2014) on two Kenaf populations. Additive effect (-8.88 ± 0.07) was the most important factor contributing to the genetic control of shelf-life in the crosses. Dominance effects were positive, and estimated value was 2.24±0.22. Positive or negative sign of additive x additive interaction indicated association and dispersion of alleles in parents, respectively. Therefore, negatively significant values of additive x additive interaction for pericarp thickness and firmness in this study showed alleles dispersion in the parents.

The dominance gene effects were higher than the additive gene effects for most of the traits. This showed the preponderance of dominance gene effects in controlling the inheritance of these traits. For traits such as pericarp thickness and yield per plant that displayed dominance x dominance type of gene interaction, heterosis breeding can be used for improving of them. This agreed with findings of Ghosh and Syamal (1995) who reported that dominance effects govern the pericarp thickness. Significance of additive gene effect alone on the number of locules per fruit and fruit number per plant in the sequential best fitting parameter indicated that simple or direct selection on the character can be done.

Most of the traits examined exhibited opposite signs of dominance, and dominance x dominance effects thus indicating duplicate type of epistasis. To make progress in breeding mild and intense selection intensity in the earlier and later generations respectively is recommended.

Conclusions

The study established that genetic effects played a predominant role in the control of the studied traits thus breeding was feasible. The gene action for shelf life fitted into the additive-dominance model. Additive, dominance and epistatic gene effects were found to be significant for most of the studied traits. Duplicate epistasis was detected for all the traits. The fixable and non-fixable gene effects exhibited by the traits can be improved through pure line breeding and heterosis, respectively.

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