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Nature of gene action for fruit quality characters of tomato (*Solanum lycopersicum*)

Shirin Akhtar and P. Hazra*

Department of Vegetable Crops, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur 741252, West Bengal, India.

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Nature of gene action for three important fruit quality characters of tomato viz., total soluble solids (TSS), β-carotene and lycopene contents were determined by analyzing one 7 x 7 half diallel population and six genetic populations (P_1, P_2, F_1, F_2 , BC_1 and BC_2) of two cross combinations. The nature of gene action determined from two biometrical methods matched well and it appeared that the fruit quality characters were under the control of both fixable and non-fixable gene effects, with the non-fixable gene effects with gene interactions being more important. Diallel analysis revealed moderate narrow sense heritability estimates and 6-parameter model suggested duplicate epistasis as well as significant additive x additive type non-allelic interaction with negative sign for the characters, which will hinder the pace of progress through simple selection. Single seed descent method with progeny row testing and deferred selection will be the best breeding method to develop line bred varieties with good fruit quality character.

Key words: Gene action, diallel, generation mean, fruit quality, tomato.

INTRODUCTION

Tomato (*Solanum lycopersicum*) belongs to the nightshade family Solanaceae which is believed to consist of 96 genera and over 2800 species distributed in three subfamilies, Solanoideae (to which *Solanum* belongs), Cestroideae and Solanineae (Knapp et al., 2004). The cultivated tomato is widely grown around the world and constitutes a major agricultural industry and it is the second most consumed vegetable after potato. Genetic determinants of nutritional quality have long been studied. However, it is only recently that these studies have largely focused on single, or at most, a handful of metabolites, such as carotenoid content in tomato (Liu et al., 2003). Hence, there has been much renewed interest in the possibility of breeding not only higher yielding but also better quality crops. The compositional fruit quality of tomato is receiving increasing interest, particularly given the results of recent studies highlighting the nutritional importance of lycopene, flavonoids, and chlorogenic acid in the human diet (Devaux et al., 2005; Dixon, 2005; Niggeweg et al., 2006; Rein et al., 2006). Today, fruit quality is a major focus of most tomato breeding programs, the major fruit quality traits of interest to both fresh market and processing tomato industries being fruit size, shape, total solids, lycopene, β-carotene, firmness, nutritional quality and flavour and other important fruit quality characteristics including pH, titratable acidity and vitamin contents (Foolad, 2007). Lycopene makes up approximately 80 to 90% of the total carotenoids in common cultivars of tomatoes (Shi and Le Maguer, 2000), the pigment that gives tomato its red color. There is considerable interest in the dietary role of lycopene in inhibition of heart disease (Rissanen et al., 2003) and reducing the risk of certain cancers, including prostate cancer (Clinton, 1998; Ansari and Gupta, 2003; Giovannucci, 2002; Wu et al., 2004; Stacewicz-Sapuntzakis and Bowen, 2005) and breast cancer (Sesso

*Corresponding author. E-mail: hazra.pranab05@gmail.com.

Table 1. Genotypes of tomato employed in the investigation.

Genotype (variety/line)	Specific character or gene in it	Source
Berika	High lycopene containing variety	Institute of Physiology and Genetics, Bulgarian academy of Science, Sofia, Bulgaria
FEB-2	Early blight resistant variety	I.A.R.I., New Delhi
BCT-115	Dark green and high pigmented line containing *dg* gene	United States Department of Agriculture, USA.
BCT-119	high pigmented line containing *hp* gene	United States Department of Agriculture, USA
CLN B	Heat tolerant line low in carotenoid pigments	AVRDC, Taiwan
BCT-53	High yielding line developed by selection from a material collected from Assam	Department of Vegetable Crops, B.C.K.V., Mohanpur, West Bengal
Patharkutchi	Highly adapted local cultivar	Department of Vegetable Crops, B.C.K.V., Mohanpur, West Bengal

et al., 2005). Other carotenoids present in ripe tomato fruits include β carotene and small amounts of phytoene, phytofluene, dcarotene, z-carotene, neorosporene and lutein (Khachik et al., 2002). β-Carotene is the carotenoid recognized as a nutrient in tomato fruit due to its pro-vitamin A activity. Each year, 750 million people suffer from vitamin A deficiency and a single serving of tomato products can supply in excess of 30% of recommended daily allowances. It has been amply justified that total soluble solids content which contain 50% carbohydrates (Helyes et al., 2006) is the most important indicator of the taste of tomato and the fruits containing soluble solids above 4.5 °Brix could be placed in the most desirable rank (Clement et al., 2008).

The proposition of candidate genes as well as QTLs has been put forward for different fruit quality traits like carotenoids (Liu et al., 2003), sugars, acid contents (Causse et al., 2004), antioxidant compounds (Rousseaux et al., 2005) and volatiles aromas (Tadmor et al., 2002). Because tomatoes represent a major contribution to dietary nutrition worldwide, there is a growing interest in the potential of genetic improvement for tomato antioxidant levels either by traditional breeding methods (Ronen et al., 2000; Zhang and Stommel, 2000) or by transgene incorporation (Giuliano et al., 2000; Romer et al., 2000). Improvement in tomato nutritional traits also offers the opportunity to determine basic information about the regulation of antioxidants in fruit crops. In this back drop, the present investigation has been outlined to determine the nature of gene action for the control of three most important fruit quality traits viz., total soluble solids, lycopene and β-carotene contents of the fruits by analyzing one 7 × 7 half diallel and two 6-genetic populations.

MATERIALS AND METHODS

The field experiments were conducted in three consecutive years (2008 to 2009 to 2010 to 2011) at the Central Research Farm, Gayeshpur, Bidhan Chandra Krishi Viswavidyalaya, West Bengal, India situated at 22°57′N lat and 88°20′E long with an average altitude of 9.75 m above the mean sea level. Seven homozygous line varieties and breeding lines viz., Berika, FEB-2, BCT-115, CLN B, Patharkutchi, BCT-53 and BCT-119 were utilized to develop two different genetic populations for the study of gene action (Table 1).

Diallel population

The seven parental lines were crossed in 7 × 7 half-diallel mating design during autumn-winter season (October to March, 2008-09) to produce 21 hybrids. These hybrids along with their parental lines were grown during autumn-winter season (October to March, 2009-10) under the day temperature range of 22.5 to 31.9°C and night temperature range of 8.4 to 22.4°C, the average day/night being 27.6/15.1°C in randomized block design with three replications keeping 20 plants per plot at 60 x 60 cm spacing. Three ripe fruits from 5 randomly selected plants per plot were harvested to make composite sample per replication for estimation of three fruit quality traits viz., TSS (°Brix), β-carotene (mg/100 g fresh weight), lycopene (mg/100 g fresh weight). Genetic components of variance for these characters were determined as per Hayman (1954).

Six-genetic population

The experiments involved the six basic generations (P_1 and P_2 parent lines, the F_1 and F_2, and the BC_1 and BC_2) of two crosses, Berika × BCT-115, Berika x FEB-2. The genetic populations (50 each of P_1, P_2 and F_1; 80 F_2 and 60 each of BC_1 and BC_2 of these three crosses were grown in two separate blocks without replication during autumn-winter season of 2010 to 2011 and data were recorded from all the plants of the six genetic populations. Composite fruit samples per plant were made taking three random ripe fruits per plant from all the genetic populations to estimate 3 fruit quality traits viz., TSS (°Brix), β-carotene (mg/100 g fresh weight) and lycopene (mg/100 g fresh weight) contents following standard spectrophotometric method as described by Sadasivam and Manickam (1996) in the Department of Vegetable Crops, Bidhan Chandra Krishi Viswavidyalaya, India. The mean values, standard errors and variances of the different generations calculated for all the plants in each generation were used for scaling test. The genetic effects were estimated from progeny means as per method suggested by Mather and Jinks (1971) and the significance of the scales and gene effects were tested by using the 't' test. The A, B C and D scaling tests were done as per

Table 2. Analysis of variance from the half diallel cross.

Sources of variation	Mean sum of squares			
	Degrees of freedom	TSS content	Lycopene content	β-carotene content
Replication	2	0.197	0.243	0.059
Diallel progenies	27	0.877**	3.215**	0.395**
Error	54	0.05	0.06	0.09

Table 3. Estimates of genetic components from diallel analysis.

Genetic component	TSS	Lycopene	β-carotene
Genetic components of variation			
$\hat{D}$	0.48 ± 0.11**	1.49 ± 0.14**	0.28 ± 0.02**
$\hat{H}_1$	0.59 ± 0.16*	1.75 ± 0.35**	0.30 ± 0.05**
$\hat{H}_2$	0.43 ± 0.13*	0.29 ± 0.08**	0.23 ± 0.05**
$\hat{h}^2$	0.15 ± 0.08*	0.75 ± 0.21*	0.58 ± 0.03**
$\hat{F}$	0.24 ± 0.26	1.60 ± 0.35**	0.25 ± 0.05**
$\hat{E}$	0.00 ± 0.04	0.00 ± 0.05	0.00 ± 0.01
Allied genetic parameters			
$(\hat{H}_1/D)^{1/2}$	1.11	0.84	1.05
$(\hat{H}_2 / 4\hat{H}_1)$	0.18	0.18	0.19
$(\hat{h}^2 / \hat{H}_2)$	0.19	2.58	2.52
KD/KR	1.58	2.24	2.52
Heritability in narrow sense (%)	57.43	50.12	53.28
Test of epistasis			
t^2 value	3.31	1.06	1.10

* and ** Significant at 5 and 1% level of significance, respectively.

Hayman and Mather (1955). The 'A' and 'B' scaling tests provided the evidence for the presence of additive x additive (i), additive x dominance (j) and dominance x dominance (l) types of gene interactions. The 'C' scaling test provided a test for 'l' type epistasis, whereas 'D' scaling test gave information about 'i' type of gene interaction.

RESULTS AND DISCUSSION

Diallel analysis

The diallel analysis has been hailed by plant breeders as a long over-due biometrical technique for rationalizing the genetic study of continuous variation. Analysis of variance for the half diallel cross depicted highly significant differences among the diallel progenies and the parents for all the characters (Table 2) indicating the divergence of the parents and the progenies which served the basic prerequisite for diallel analysis.

Total soluble solids (TSS)

Both additive ($\hat{D}$) and dominance ($\hat{H}_1$ and $\hat{H}_2$) components were highly significant suggesting the importance of both additive and dominance gene action for conditioning of this character (Table 3). The dominance was reflected due to significant dominance effect ($\hat{h}^2$). The $\hat{F}$ was positive (0.24) but low in magnitude suggesting somewhat majority of dominant alleles and minority of recessive alleles in the parents. The $(\hat{H}_1/D)^{½}$ exhibited somewhat complete dominance. The proportion of KD/KR (1.58) suggested majority of dominant alleles and minority of recessive alleles in the parents. The $\hat{H}_2$ /4 $\hat{H}_1$ (0.18) suggested comparatively less symmetrical distribution of positive and negative dominant genes in the parents. The $\hat{h}^2/\hat{H}_2$ (0.19) suggested that number of group of dominant genes for the control of this character appeared to be one. The

narrow sense heritability was moderate (57.43%).

Lycopene content

The additive ($\hat{D}$) and dominance ($\hat{H}_1$ and $\hat{H}_2$) components were highly significant suggesting the importance of both additive and non-additive gene action for this character (Table 3). However, the magnitude of $\hat{H}_1$ and $\hat{H}_2$ were somewhat higher than $\hat{D}$ suggesting importance of non-additive gene action for conditioning of this trait. The dominance was reflected due to significant dominance effect ($\hat{h}^2$) which amply suggests the importance of non-additive gene action for conditioning of this character. The $\hat{F}$ was positive (1.60) suggesting that dominant alleles are more frequent than recessive alleles in the parents. The $(\hat{H}_1/D)^{½}$ exhibited partial dominance (0.84). The proportion of KD/KR (2.24) suggested majority of the dominant alleles and minority of recessive alleles in the parents. The $\hat{H}_2$ /4 $\hat{H}_1$ (0.18) suggested comparatively less symmetrical distribution of positive and negative dominant genes in the parents. The $\hat{h}^2/\hat{H}_2$ (2.58) suggested that number of group of dominant genes appeared to be three. The narrow sense heritability was moderate (50.12%).

β-Carotene content

The additive ($\hat{D}$) and dominance ($\hat{H}_1$ and $\hat{H}_2$) components were highly significant suggesting the importance of both additive and non-additive gene action for this character (Table 3); however, the magnitude of $\hat{H}_1$ and $\hat{H}_2$ were almost double of $\hat{D}$ suggesting importance of non-additive gene action for conditioning of this trait. The dominance was reflected due to significant dominance effect ($\hat{h}^2$) which amply suggests the importance of non-additive gene action for conditioning of this character. The $\hat{F}$ was positive (0.25) but low in magnitude suggesting balanced distribution of dominant and recessive alleles in the parents. The $(\hat{H}_1/D)^{½}$ exhibited almost complete dominance (1.05). The proportion of KD/KR (2.52) suggested majority of dominant alleles and minority of recessive alleles in the parents. The $\hat{H}_2$ /4 $\hat{H}_1$ (0.19) suggested comparatively less symmetrical distribution of positive and negative dominant genes in the parents. The $\hat{h}^2/\hat{H}_2$ (2.52) suggested that number of group of dominant genes appeared to be three. The narrow sense heritability was moderate (53.28%).

Perusal of data emanated from the expression of the characters in the diallel population clearly suggesting the involvement of polygenes in the control of three fruit quality characters of tomato. It has been suggested earlier that in addition to the nine classically defined major genes (with a total 15 alleles) viz., old gold crimson and it's allele Beta-carotene; apricot; Delta, diospyros, green flesh; Green ripe; high pigment-1; high pigment-2; dark green; Intense pigment; modifier Beta-carotene; red colour in yellow fruit; sherry, tangerine; and yellow flesh (Stommel and Haynes, 1993; Tigchelaar, 1986), other genes that affect fruit pigmentation and colour probably exist and can be defined using quantitative methods (Sacks and Francis, 2001). Nature of gene action apparent from the present analysis for three fruit quality characters agreed well with the earlier observations of Potaczek and Michalik (1989) for carotenoid content; Li et al. (2006) for lycopene content; Garg et al. (2008) for total soluble solids (TSS), titratable acidity, TSS: acid ratio, pH and ascorbic acid content; Kumar et al. (1997) for TSS, ascorbic acid, lycopene and acidity and Mandal et al. (2009) for TSS and lycopene contents of the fruit.

The magnitude of dominance component ($\hat{H}_1$ and $\hat{H}_2$) and degree of dominance $(\hat{H}_1/D)^{½}$ amply suggested the importance of non-additive genetic system for the expression of the fruit quality characters. Proportion of dominant and recessive alleles pooled over all parents (KD/KR) indicated dominant alleles in the parents. However, dominant genes having increasing and decreasing effects were asymmetrically distributed in the parents for these characters which are not helpful in selecting the desirable traits without losing other traits of interest. Knowledge of number of gene groups which exhibit dominance and are responsible for particular trait is important for genetic progress for selection. One gene group controlled the inheritance of TSS content and three gene groups controlled lycopene and β-carotene content of fruit juice indicating complex inheritance of carotenoid pigments in tomato. Findings of some earlier works that five loci with a positive effect on fruit colour were identified in *Lycopersicon hirsutum* Dunal accession LA 1777 (Bernacchi et al., 1998) and three in *Lycopersicon pimpinellifolium* (B. Juss.) Miller accession LA 1589 (Tanksley et al., 1996) supported the present findings.

Moderate narrow sense heritability estimates for these characters agreed well with several earlier reports (da Silveira and Maluf, 2002; Hanson et al., 2002; Rodriguez et al., 2004; Mohamed and Badr, 2004). Single plant selection is not effective unless heritability for the particular trait is high (Nyquist, 1991). Hence, single plant selection in the F_2 generation will not be effective in improving these fruit quality characters. In order to develop line bred varieties with good fruit quality character, single seed descent with progeny row testing and selection method will be the best since backcrosses are not suitable for fixing such traits (Frimpong and Safo, 2006).

Generation mean analysis

It has already been established through diallel analysis

Table 4. Scaling test and generation mean analysis.

Model and effects	TSS content	Lycopene content	β-Carotene content
Berika × FEB-2			
Scaling test (Hayman and Mather, 1955)			
A	0.550 ± 0.247*	-0.562 ± 0.293	-0.003 ± 0.095
B	-0.560 ± 0.216*	0.960 ± 0.365**	0.554 ± 0.103**
C	0.198 ± 0.373	3.635 ± 0.672**	1.446 ± 0.203**
D	0.104 ± 0.160	1.619 ± 0.310**	0.447 ± 0.100**
Six parameter model (Mather and Jinks, 1971)			
m	4.763 ± 0.060**	5.161 ± 0.131**	1.612 ± 0.043**
d	0.535 ± 0.106**	-0.221 ± 0.165	-0.110 ± 0.051*
h	-1.602 ± 0.351**	-3.523 ± 0.654**	-1.194 ± 0.207**
i	-0.208 ± 0.321	-3.237 ± 0.620**	-0.894 ± 0.200**
j	0.555 ± 0.149**	-0.761 ± 0.195**	-0.279 ± 0.065**
l	0.217 ± 0.565	2.840 ± 0.943**	0.343 ± 0.108**
Non-allelic interaction	Could not be determined	Duplicate	Duplicate
Berika × BCT-115			
Scaling test (Hayman and Mather, 1955)			
A	0.867 ± 0.253**	-1.414 ± 0.337**	-0.529 ± 1.347**
B	0.359 ± 0.247	-0.450 ± 0.415	-0.351 ± 0.370
C	0.634 ± 0.430	-1.051 ± 0.700	-0.912 ± 0.702
D	-0.296 ± 0.169	0.407 ± 0.324	-0.016 ± 0.106
Six parameter model (Mather and Jinks, 1971)			
m	4.865 ± 0.067**	4.649 ± 0.135**	1.440 ± 0.044**
d	0.509 ± 0.104**	-0.622 ± 0.180**	-0.235 ± 0.058**
h	-0.765 ± 0.378*	-1.140 ± 0.386**	0.400± 0.063**
i	0.592 ± 0.338	-0.813 ± 0.648	0.031 ± 0.212
j	0.254 ± 0.153	-0.482 ± 0.247	-0.089 ± 0.098
l	-1.819 ± 0.598**	2.677 ± 1.003**	0.849 ± 0.140**
Non-allelic interaction	Complementary	Duplicate	Duplicate

* and **Significant at 5 and 1% level of significance, respectively.

that fruit quality characters were governed, at least in combination by the polygenes. Results of the diallel analysis supported the importance of both additive and dominance genetic effects in conditioning of the characters; however, dominance gene effects were more important. The presence and absence of epistasis could be detected by the analysis of generation means using the scaling test, which measures epistasis accurately whether complementary (additive × additive) or duplicate (additive × dominance and dominance × dominance) at digenic level.

Total soluble solids

A simple additive/dominance model was inadequate to explain the gene effects because of the significance of A and B scales in Berika × FEB-2 and only A scale in Berika × BCT-115 (Table 4). Additive and dominance components of genetic variance were significant but dominance variance was more important in both crosses. Only additive × dominance epistatic interaction effect was significant in Berika × FEB-2 and dominance x dominance interaction was significant for Berika × BCT-115, suggesting different epistatic interactions in two crosses. Dominance × dominance (l) interaction effect and additive x additive effect was of almost equal magnitude in Berika × FEB-2 while it was larger than additive × additive effect in Berika × BCT-115. The type of epistasis was ‘complementary’ for Berika × BCT-115 while it could not be determined in Berika × FEB-2, and dominance × dominance epistatic effect was non-significant in this cross.

Lycopene content

A simple additive/dominance model was inadequate to explain the gene effects because of the significance of B, C and D scales in Berika × FEB-2 and only A scale in Berika × BCT-115. In Berika × FEB-2, only dominance genetic variance was significant, while in Berika × BCT-115, both additive and dominance components of genetic variation were significant and it was higher in magnitude than additive genetic variance (Table 4). In Berika × FEB-2, all the epistatic variances were significant while only dominance × dominance epistatic interaction effect was significant in Berika × BCT-115. Dominance × dominance (l) interaction effect was higher than additive × additive effect in Berika × BCT-115, while it was lower in magnitude than additive × additive effect in Berika × FEB-2. Type of epistasis was 'duplicate' for both crosses.

β-Carotene content

A simple additive/dominance model was inadequate to explain the gene effects because of the significance of B, C and D scales in Berika × FEB-2 and only A scale in Berika × BCT-115. In both crosses, both additive and dominance components of genetic variation were significant and it was higher in magnitude than additive genetic variance. In Berika × FEB-2, all the epistatic variances were significant while only dominance × dominance epistatic interaction effect was significant in Berika × BCT-115 (Table 4). It amply indicated that inheritance pattern of both lycopene and β carotene content was almost similar which was established from diallel analysis also. Dominance × dominance (l) interaction effect was higher than additive × additive effect in Berika × BCT-115, while it was lower in magnitude than additive × additive effect in Berika × FEB-2. Type of epistasis was 'duplicate' for both crosses.

Li et al. (2006) through the combination analysis of six generations suggested that a major gene plus additive-dominance-epistasis polygenes dominated the inheritance of lycopene content in tomato. Presence of duplicate epistasis for lycopene and β-carotene content will decrease variation in the F_2 and subsequent generations and will hinder the pace of progress through selection as suggested by Dhankar et al. (2003) and Dixit et al. (2006). Additive × additive type non-allelic interaction was significant but with negative sign indicating little scope of improvement through simple selection. Such proposition was also put forward analyzing the diallel population because of low to moderate narrow sense heritability estimates for the characters.

In conclusion, the nature of gene action determined from two biometrical methods matched well and it appeared that fruit quality traits were under the control of both fixable and non-fixable gene effects, with the non-fixable gene effects with gene interactions being more important. Single seed descent method with progeny row testing and deferred selection will be the best breeding method to develop line bred varieties with good fruit quality character.

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