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Genetic control of fruit yield and quality characters in tomato genotypes possessing *hp-1*, *og^c*, *dg*, *Aft* and *rin* genes

P. Biswas, A. Chattopadhyay[1] and P. Hazra[1]*

PFDC, Agricultural and Food Engineering Department, Indian Institute of Technology Kharagpur 721302; [1]Department of Vegetable crops, Faculty of Horticulture, Bidhan Chandra Krishi Viswavidyalaya, Nadia 741252, West Bengal

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Abstract

Five inbred lines of tomato possessing one each of the specific genes *viz*., *hp-1*, *og^c*, *dg*, *Aft* and *rin* were crossed in a half diallel fashion to determine the combining ability and gene action of fruit yield/plant, fruit weight and eight important fruit quality characters. Additive genetic component was predominant for TSS, ascorbic acid and anthocyanin contents; both additive and non-additive components was important for fruit yield/plant, fruit weight and lycopene content, and non-additive gene action was overwhelmingly important for pericarp thickness and total sugar content while estimates of both the genetic components was zero for titrable acidity and β-carotene content of fruit. General combining ability effects of the parents corresponded well to their *per se* performance. Homozygous recessive condition of the genes, *hp-1*, *og^c*, *dg* governed enhanced lycopene content in the fruits. Homozygous *Aft/Aft* plant had higher anthocyanin content in the fruit than the heterozygous plant indicating additivity of the *Aft* gene in expressing the character. The hybrid of two widely divergent parent BCT-115 *dg/ dg* x Alisa Craig *Aft/Aft* emerged as outstanding for both fruit yield and quality which also opened up the possibility of developing tomato hybrid rich in both lycopene and anthocyanin contents. The hybrid BCT-115 *dg/ dg* x BCT-111 *rin/ rin* was also promising for commercial utilization.

Key words: Combining ability, gene action, single gene, lycopene, anthocyanin, tomato

Introduction

Tomato (*Solanum lycopersicum* L.) fruits are valuable source of several carotenoid pigments particularly, lycopene, βcarotene, phytoene etc. which are very important in human diet. Different mutant genes *viz*., *hp-1*, *og^c*, *dg* primarily enhance lycopene however, some other genes like, *tangerine* (*t*), *yellow flesh* (*r*), *sherry* (*sh*) and minor genes also influence the carotenoid contents in fruit (Sacks and Francis, 2001). Tomato fruits do not usually produce anthocyanins unlike the fruits of other Solanaceae due to lack of expression of the *chalcone isomerase* (*CH1*) gene in the flavonoid biosynthetic pathway in the peel of the tomato fruit (Mes et al. 2008). *Anthocyanin fruit* (*Aft*) gene introgressed from *Solanum chilense* cause anthocyanin expression in tomato fruit (Jones et al. 2003). The ripening inhibitor gene *rin* inhibit fruit ripening process through negative and pleiotropic effects on the ripening process, carotenoid biosynthesis, fruit softening and ethylene production (Giovannoni et al. 1995). All these five monogenically inherited genes are located in different chromosomes *viz*., *hp-1* in chromosome 2 (Yen et al. 1997), *og^c* in chromosome 6 (Yang et al. 2004), *dg* in chromosome 1 (Levin et al. 2003), *Aft* in chromosome 10 (Sapir et al. 2008) and *rin* in chromosome 5 (Giovannoni et al. 1995).

The present study was undertaken to evaluate five promising genotypes possessing one specific gene each (*hp-1*, *og^c*, *dg*, *Aft* and *rin*) and their hybrids to determine the combining ability and nature of gene action of fruit yield and quality to outline the breeding strategy for genetic improvement of tomato for these characters.

Materials and methods

Of the five parental lines, three near isogenic lines *viz*., Alisa Craig *hp-1/hp-1*, Alisa Craig *og^c/og^c* and Alisa Craig *Aft/ Aft* were received from the Institute of Genetics and Physiology, Bulgarian Academy of

*Corresponding author's e-mail: hazra.pranab05@gmail.com
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Science, Sofia, Bulgaria. The genotype BCT 115 *dg* possessing *dg/dg* gene was received from United States Department of Agriculture and the other BCT 111 *rin* possessing *rin/rin* gene from Chaudhary Charan Singh Haryana Agricultural University, Hisar, India. The investigations were carried out during 2009-2014 period. A set of 10 hybrids were developed by crossing these five parental lines in diallel mating design. The parental lines and hybrids were evaluated at Central Research Farm, Gayeshpur, Bidhan Chandra Krishi Viswavidyalaya, Location situated at 22^{o}57'N latitude and 88^{o}20' E longitude with average altitude of 9.75 m above the mean sea level following randomized block design with three replications in open field condition during autumn-winter season (October to March) for three consecutive years under the average day temperature range of 22.5^{o} to 31.9^{o}C and night temperature range of 8.4^{o} to 22.4^{o}C, the average day/night being 27.6^{o}/15.1^{o}C. Each plot comprised of 20 plants which were maintained without pruning.

Total fruit weight in the periodical harvest at advanced turning stage from five selected plants in each genotype (parental lines and hybrids) per replication was averaged to depict fruit yield/plant (kg). Five such fruits sampled periodically were kept in the room temperature condition till they riped completely for estimation of different quality characters. Fruits of the *rin*/*rin* genotype did not turn red and somewhat soft, bright yellow fruits were used for fruit quality analysis. The tomato fruit is composed of different tissues: the pericarp (flesh), which is subdivided into the exocarp, mesocarp, and endocarp, the placenta, septum, and the locules filled with jelly and seeds (pulp). After taking the fruit weight (g), the fruits were cut into two halves and pericarp thickness was measured with the help of digital slide calipers. The cut fruits were used to make replication-wise composite sample to estimate different fruit quality characters on fresh weight basis *viz*., total soluble solids (^{o}Brix) by hand refractometer, ascorbic acid content (mg/100g) by titration with 2.6-dichlorophenolindophenol sodium salt solution (AOAC, 1990), lycopene and βcarotene contents (mg/100g fresh) spectrophotometrically (Davies, 1976) and anthocyanin content (mg/100g fresh) spectrophotometrically (Sadasivam S. and Manickam, 1996). Anthocyanins present in the skin and pericarp tissues of *Aft*/*Aft* fruit were petunidin, malvidin and delphinidin 3-(p-coumaryl-rutinoside)-5-glucoside (Jones et al. 2003). However, purple skin colour was not uniform throughout the fruit surface hence, areas of skin and pericarp tissue expressing high anthocyanin was sampled to estimate the anthocyanin content of the fruits of *Aft* genotypes. The average data of all the characters were statistically analyzed. Combining ability analysis was carried out based on Griffing's fixed effect model (Griffing, 1956). Heritability in narrow sense (h^2_{ns} %) for each character was calculated by using the formula of Gibrel et al. (1982).

Results and discussion

Performance of the parents and hybrids

Among the parents, heaviest fruit of 103.42 gram was produced in BCT 115 *dg/dg* and the lightest fruit of 39.87 g in Alisa Craig *hp-1/hp-1*. BCT 111 *rin/rin* had the fruits with thickest pericarp of 6.84 mm which was statistically *at par* to that of BCT 115 *dg/dg* (6.47 mm). BCT 111 *rin/rin* was the highest yielder (4.07 kg/plant) followed by BCT 115 dg (3.60 kg/plant). Average fruit yield of the hybrids (3.82 kg fruits/plant) was slightly higher than that of the parental lines (3.43 kg fruits/plant) although specific hybrid combinations registered high fruit yield. Average enhancement of lycopene content in the ripe fruits of the genotypes possessing the lycopene enhancing mutant genes (*hp-1*/*hp-1*, *dg/dg*, og^c/og^c) was 37.07% compared to Alisa Craig *Aft*/*Aft* which did not possess such gene (Table 1). Lycopene content in the fruits (mg/100 g fresh weight) was highest in *hp-1*/*hp-1* (7.18 mg) followed by *dg/dg* (6.42 mg) and og^c/og^c (5.91 mg) genotypes (Table 1). Fruits of the ripening inhibitor *rin*/*rin* genotype did not ripe and remained bright yellow till the end and had very low lycopene content (0.38 mg/100g fresh weight). On an average, β-carotene content constituted 11.86 % of the total carotenoids (lycopene + β-carotene content) in the fruits however, it was the lowest (0.43 mg/100 g fresh) in the og^c/og^c genotypes. Fruit carotenoid content particularly lycopene is primarily enhanced by different fruit carotenoid content enhancing mutant genes *viz*., *high pigment* (*hp-1*), *old gold crimson* (og^c) and *dark green* (*dg*) however, og^c gene enhance lycopene content in the fruits with concomitant decrease in â-carotene content (Ronen et al. 2000). This might be the reason why fruits of the og^c/og^c genotype had the lowest â carotene content in the ripe fruits. Ripe fruits of the genotypes possessing photo- responsive mutant genes *viz*., *hp-1*/*hp-1, dg/dg* and og^c/og^c had higher ascorbic acid content (average 39.47 mg/100 g fresh) than the fruits of the genotypes possessing other genes *viz*., *Aft/Aft* and *rin*/*rin* (average 25.22 mg/100 g fresh). Fruits of the *Aft*/*Aft* genotype had high anthocyanin content in

Table 1. Mean fruit yield and quality characters of the parental lines and hybrids

Genotypes	Fruit yield/ plant (kg)	Fruit weight (g)	Pericarp thickness (mm)	TSS (° Brix)	Total sugar (%)	Acidity (%)	Ascorbic acid (mg/100g)	Lycopene (mg/100g)	β-carotene (mg/100g)	Anthocyanin (mg/100g)
dg/dg	3.60	103.42	6.47	4.58	2.74	0.60	37.30	6.42	0.61	0.00
Aft/Aft	3.46	85.25	6.22	4.14	2.28	0.47	24.78	4.09	0.59	14.29
og^c/ og^c	3.27	53.13	5.36	5.16	3.19	0.68	33.36	5.91	0.43	0.00
hp-1/ hp-1	2.75	39.87	4.77	4.95	2.64	0.54	47.75	7.18	0.60	0.00
rin/ rin	4.07	97.50	6.84	3.95	1.61	0.36	25.66	0.38	0.24	0.00
dg x Aft	4.48	101.90	7.69	4.34	2.05	0.44	32.82	4.12	0.62	11.62
dg x og^c	3.44	65.75	5.66	4.32	2.31	0.59	32.07	3.93	0.66	0.00
dg x hp-1	3.40	70.22	6.28	4.76	2.18	0.57	37.02	4.16	0.74	0.00
dg x rin	4.72	83.70	6.78	4.28	2.07	0.53	26.98	3.45	0.64	0.00
Aft x og^c	4.23	63.33	6.12	4.71	2.02	0.61	26.22	3.72	0.61	10.85
Aft x hp-1	3.97	62.99	5.83	4.35	1.95	0.53	27.72	3.55	0.66	11.15
Aft x rin	3.88	83.92	7.56	3.92	2.01	0.42	25.17	3.39	0.67	8.66
og^c *x hp-1*	3.51	65.07	6.16	4.90	2.55	0.53	32.32	4.28	0.71	0.00
og^c *x rin*	3.35	64.09	6.74	4.08	1.98	0.56	28.27	3.55	0.67	0.00
hp-1 x rin	3.17	49.44	6.01	4.09	2.44	0.65	25.57	3.62	0.55	0.00
S.E.	0.28	2.27	0.18	0.11	0.11	0.02	1.53	0.13	0.04	0.32
C.D.(P=0.05)	0.83	6.58	0.54	0.32	0.33	0.07	4.44	0.39	0.12	0.96

fruit pericarp (14.29 mg/ 100g fresh). Tomato fruits do not usually produce anthocyanins unlike the fruit of other Solanaceae (Mes et al. 2008). A major constraint found in the flavonoid biosynthetic pathway is the lack of expression of the *chalcone isomerase* (*CH1*) gene in the peel of the tomato fruit, which is probably caused by a mutation in a fruit-specific element of the promoter (Willits et al. 2005). *Chalcone synthase* (*CHS*) is the first committed enzyme in flavonoid biosynthesis (Tohge et al. 2007). *CHS* interacts with *chalcone isomerase* (*CHI*), a consecutive step enzyme, as well as other non-consecutive step enzymes *flavanone 3-hydroxylase* (*F3H*), *dihydroflavonol 4-reductase* (*DFR*), and *flavonol synthase*I*n* flavonoid biosynthesis (*Crosby* et al. 2011). The gene *Aft* is more likely a regulatory gene or promoter region of a structural gene (Aust et al. 2003) and it reintroduce the expression of *CH1* gene resulting higher levels of flavonoids including anthocyanins in the fruits of cultivated tomato (Willits et al. 2005). Average of 3.50 mg lycopene content/100g fresh fruits of the 4 *rin/Rin* - - hybrids (*Aft*/ *aft rin/Rin*, *dg*/*Dg rin/Rin*, og^c/Og^c *rin/Rin* and *hp-1/Hp-1 rin/Rin*) was lesser than Alisa Craig *Aft*/*Aft* (4.09 mg/100g fresh). The *dg*/*Dg rin/Rin* hybrid was medium-big fruited (83.70 g fruit weight) and highest yielding (4.72 kg fruit yield/ plant) with medium lycopene content (3.45 mg/100g fresh) in the fruit. All the hybrids of *Aft* genotype expressed anthocyanin in the fruits however, the fruits of the homozygous *Aft*/*Aft* plant had greater anthocyanin content (14.29mg/100g fresh weight) than the heterozygous plants for *Aft* gene (average 10.57 mg/100 g fresh weight) indicating additive response of the *Aft* gene which was also proposed earlier (Rick et al. 1968, Mes et al. 2008). Expressivity of the *Aft* gene varied with the genotypes because different genotypes acquired this gene in different way which caused variation in anthocyanin content in the fruits of different *Aft* hybrids. The *dg*/*Dg Aft*/*aft* hybrid was big fruited (101.90 g fruit weight) and second highest yielding (4.48 kg fruit yield/plant) with the highest anthocyanin (11.62 mg/100g fresh) and appreciable lycopene (4.12 mg/100 g fresh) contents in the fruits.

Fruits with over-production of chlorophyll in the three photo-responsive genotypes (*hp-1/hp-1*, *dg/dg* and og^c/og^c) contained comparatively more sugar in the ripe fruits because sugar content is influenced by plastid numbers and photosynthetic activity in unripe fruit and later by starch and sugar catabolism during ripening (Nguyen et al. 2014). Highly significant

increase in chloroplast size and number in pericarp cells of mature-green fruits of these photo-responsive mutants provide molecular trigger which might have exaggerated phytochrome response (Peters, 1998) for over production of carotenoids and other phyto-nutrients (Kolotilin et al. 2007). It was also recorded earlier that the high pigment tomato fruits have high level of carotenoids, flavonoids and ascorbic acid due to a mutation that exaggerates phytochrome response (Sapir et al. 2008). Significantly lower lycopene content in the fruits of *Aft*/*Aft* genotype clearly indicated that it was unlikely that the *Aft*/*Aft* gene conditioning anthocyanin expression in the fruits could markedly alter carotenoid quantity in the fruits. The ripening inhibitor mutant gene, *rin*/*rin* had marked depressive effect on the TSS and sugar contents in the fruits because carbohydrate metabolism, ethylene biosynthesis and signal transduction are inhibited which highly down regulated carotenoid biosynthesis (Giovannoni, 2001). Earlier reports that *rin* mutant decreased lycopene content even in the heterozygous form (Giovannoni et al. 2004; Leseberg et al. 2008) has found support from the present result however, the decrease was too little to their use in commercial hybrid breeding programme. Appreciable ascorbic acid content in the fruits of *rin*/*rin* genotype suggested that inhibition to trigger climacteric respiration and ripening related ethylene biosynthesis due to mutated allele *rin*/*rin* could not hinder ascorbic acid synthesis in the fruits. All the hybrids of *Aft* genotype expressed anthocyanin in the fruit which supported the hypothesis of a single dominant gene conditioning anthocyanin content in the fruits.

Genetic control and heritability for the characters

The estimates general combining ability variances (σ^2_{GCA}) exhibited higher values than those of the specific combining ability variances (σ^2_{SCA}) for TSS and anthocyanin content of fruit, while σ^2_{SCA} was higher than σ^2_{GCA} for fruit yield/plant, fruit weight, pericarp thickness, total sugar, lycopene, β-carotene and ascorbic acid contents of fruit (Table 2). A general trend of the genetic control of the characters could be ascertained from the estimate of additive and non-additive genetic components (Table 2). Additive genetic component was predominant in the inheritance of TSS, ascorbic acid and anthocyanin contents of fruit and both additive and non-additive genetic components was important for the conditioning of fruit yield/plant, fruit weight and lycopene contents of fruit. Pericarp thickness and total sugar content was conditioned overwhelmingly under non-additive gene action. Variation for titrable acidity and â-carotene contents among the parents and hybrids was inconspicuous which resulted zero estimates for both additive and non-additive variance. Narrow sense heritability estimates were relatively high for TSS and anthocyanin contents of fruit (70.5-87.9%); medium to medium-low for fruit weight, ascorbic acid and lycopene content (46.9-55.9%); relatively low for fruit yield/ plant, pericarp thickness, titrable acidity, and â-carotene contents (20.0-33.3%) and very low for total sugar content (2.35%). Predominance of additive genetic component in the inheritance of TSS, ascorbic acid and anthocyanin contents of fruit commensurate with high narrow sense heritability estimates suggested that selection of these traits in conventional breeding

Table 2. Estimates of different components variance and heritability for different characters

Characters	GCA variance (σ^2_{GCA})	SCA variance (σ^2_{SCA})	Environmental variance (σ^2_e)	Additive variance (V_A)	Non-additive variance (V_D)	Heritability in narrow sense (h^2_{ns}) (%)
Fruit yield per plant (Kg)	0.06	0.18	0.08	0.12	0.10	31.58
Fruit weight (g)	98.93	150.79	5.17	197.86	145.62	55.92
Pericarp thickness (mm)	0.08	0.38	0.03	0.17	0.35	28.07
TSS (° Brix)	0.06	0.04	0.01	0.13	0.03	70.58
Total sugar (%)	0.02	0.12	0.01	0.01	0.11	2.35
Acidity (%)	0.01	0.02	0.06	0.00	–0.01	20.00
Ascorbic Acid (mg/100g fresh)	11.77	13.83	2.35	23.53	11.48	59.26
Lycopene (mg/100g fresh)	0.43	0.95	0.02	0.80	0.93	46.99
β-carotene (mg/100g fresh)	0.02	0.07	0.01	0.00	–0.01	33.32
Anthocyanin (mg/100g fresh)	570.42	152.83	3.32	1140.85	149.51	87.96

methods from highly heterotic crosses would be effective. Transgressive segregants obtained by crossing the parents with higher value of the traits can be used as potential parents in the hybrid development. Some earlier reports of lycopene and â carotene contents of the fruit under the control of both fixable and non-fixable gene effects, non-fixable gene effect being more important (Droka et al. 2012; Akhtar and Hazra, 2013) supported the present findings. Larger proportion of non-additive gene effects in self-pollinated crops seems to be due to additive x additive epistatic effect (Singh et al. 1992). However, possibility of improving the characters *viz*., fruit yield/plant, fruit weight and lycopene content of fruit by hybridization and selection breeding method is somewhat limited due to medium-low to low narrow sense heritability estimates for these characters.

General and specific combining ability effects

Choice of parents either for the development of a hybrid or line bred variety is one of the most important consideration in plant breeding programme (Borém and Miranda, 2005). General combining ability effects of the parental lines corresponded well to their

Table 3. Estimates of general combining ability (GCA) effects for different characters of the parents

Characters	Parentalgenotypes					CD(Gi–Gj)
	dg/dg	*Aft/Aft*	*og^c/ og^c*	*hp-1/ hp-1*	*rin/ rin*	
Fruit yield/plant	0.09	0.12	–0.19	–0.41	0.40	0.12
Fruit weight	13.51	5.55	–8.48	–13.77	3.19	0.99
Pericarp thickness	0.12	0.32	–0.29	–0.51	0.36	0.08
TSS	–0.01	–0.11	0.28	0.23	–0.38	0.05
Total sugar	–0.20	–0.04	0.20	0.00	0.04	0.05
Acidity	0.01	–0.04	0.06	0.02	–0.04	0.01
Ascorbic Acid	2.61	–3.39	0.06	4.70	–3.99	0.66
Lycopene	0.34	–0.20	0.49	0.57	–1.20	0.06
β-carotene	0.02	0.00	0.05	0.02	–0.10	0.02
Anthocyanin	–9.51	43.51	–10.46	–11.03	–12.50	1.29

(Gi-Gj)=Differences between GCA estimates of parental lines

Table 4. Estimates of specific combining ability (SCA) effects for different characters in the hybrids

Hybrids	Fruit yield/ plant	Fruit weight	Pericarp thickness	TSS	Total sugar	Acidity	Ascorbic acid	Lycopene	β-carotene	Antho-cyanin
dg x Aft	0.33	12.20	0.89	0.06	–0.01	–0.07	2.73	–0.38	–0.03	20.42
dg x og^c	–0.19	–9.92	–0.41	–0.35	0.00	–0.02	–1.46	–0.95	–0.04	–4.91
dg x hp-1	–0.01	–0.16	0.44	0.14	0.08	0.00	–1.17	–0.88	0.07	–4.34
dg x rin	0.50	–13.64	–0.93	–0.25	–0.07	0.02	–2.52	0.45	0.10	–2.87
Aft X og^c	0.56	–4.37	–0.15	0.15	–0.44	0.05	–1.32	–0.43	–0.07	15.12
Aft x hp-1	0.52	0.58	–0.21	–0.16	–0.31	0.02	–4.47	–0.68	0.01	10.66
Aft x rin	–0.38	–15.44	0.78	0.01	–0.29	–0.03	1.68	0.93	0.15	5.91
og^c x hp-1	0.38	16.67	0.73	0.00	–0.53	–0.09	–3.31	–1.16	0.02	–3.40
og^c x rin	–0.60	–1.26	0.44	–0.21	0.01	0.01	1.34	0.40	0.09	–1.92
hp-1 x rin	–0.56	–10.62	–0.07	–0.16	0.10	0.14	–6.02	0.38	0.01	–1.36
CD (Sij – Sik)	0.22	1.71	0.14	0.08	0.09	0.02	1.16	0.10	0.03	1.37
CD (Sij – Skl)	0.20	1.56	0.13	0.08	0.08	0.02	1.05	0.09	0.03	1.25

P=0.05

Sij – Sik = Difference between SCA of two hybrids, with a common parent
Sij – Skl = Difference between SCA of two hybrids, with a non-common parent

performance. Alisa Craig *hp-1/hp-1* registered the highest and positive GCA effects for lycopene and ascorbic acid content of fruit; BCT-111 *rin/rin* for fruit yield per plant; BCT-115 *dg/dg* for fruit weight; Alisa Craig og^c/og^c for TSS, total sugar, titratable acidity and β-carotene content of fruit. All the three parental lines possessing lycopene enhancing mutant genes (BCT-115 *dg/dg*, Alisa Craig *hp-1/hp-1*, Alisa Craig og^c/og^c) registered high and positive GCA effects for lycopene content of fruit similarly, Alisa Craig *Aft/ Aft* possessing anthocyanin fruit gene showed the highest GCA effects for anthocyanin content of fruit (Table 3).

Combination of divergent genomes can result in profound changes in both genome and transcriptome within a hybrid and many of these changes to gene expressions are non-additive in nature (Hegarty et al. 2008) which was amply evident in BCT-115 *dg/dg* x Alisa Craig *Aft/Aft* hybrid which registered highest SCA effects for most of the characters (Table 4). All the hybrids of the parental lines possessing the lycopene enhancing mutant genes (*hp-1/hp-1*, og^c/og^c and *dg/dg*) showed negative SCA effects for lycopene content of fruit. Mean lycopene content in the 3 hybrids (*dg/dg* x *hp-1/hp-1*, *dg/dg* x og^c/og^c and og^c/og^c x *hp-1/hp-1*) was 35.53 % lower than the average in the genotypes possessing these genes in homozygous condition which amply suggested that homozygous recessive condition of these genes govern enhanced lycopene content in the fruits.

The present investigation suggested the utilization of the genotypes having these five specific genes in hybrid breeding programmes of tomato. The hybrid BCT115 *dg*/*dg* x Alisa Craig *Aft*/*Aft* emerged as outstanding for both fruit yield and quality which also supported the proposition of developing hybrids rich in both lycopene and anthocyanin contents in fruits. The medium-big fruited and highest yielding hybrid BCT-115 *dg/dg* x BCT-111 *rin/rin* with medium lycopene content in the fruit also appeared to be promising for commercial utilization.

Authors' contribution

Conceptualization of research (PB); Designing of the experiments (PH); Contribution of experimental materials (PH); Execution of field/lab experiments and data collection (PB, PH, AC); Analysis of data and interpretation (PB, PH, AC); Preparation of the manuscript (PB, PH, AC).

Declaration

The authors declare no conflict of interest.

References

Akhtar S. and Hazra P. 2013. Nature of gene action for fruit quality characters of tomato (Solanum lycopersicum). African J. Biotech., **12**: 2869-2875.

AOAC 1990. Official methods of analysis of the association of official analytical chemists, 15th edition, (Ed. Helrich K.), Association of Official Analytical Chemists, Inc., Arlington, Virginia, USA.

Aust O. A. A. N., Zhang L., Wollersen H., Sies H. and Stahl W. 2003. Lycopene Oxidation Product Enhances Gap Junctional Communication. Food and Chem. Toxicol., **41**: 1399-1407.

Borém A. and Miranda G. V. 2005. Melhoramento de plantas. 4th edition. Viçosa: Editora UFV, Imprensa Universitária.

Crosby K. C., Pietraszewska-Bogiel A., Gadella T. W. and Winkel B. S. 2011. Förster resonance energy transfer demonstrates a flavonoid metabolon in living plant cells that displays competitive interactions between enzymes. FEBS Lett., **585**: 2193-2198.

Davies B. H. 1976. Carotenoids. In: Chemistry and biochemistry of plant pigments. (Ed. Goodwin T.W.). Academic Press, London, UK.

Droka D., Kumar R., Joshi S. and Yadav R. K. 2012. Genetic studies of quality traits in tomato (*Solanum lycopersicum* L.) under low temperature. Veg. Sci., **39**: 189-191.

Gibrel G. A. A., Simpson W. R. and Everson D. O. 1982. Evaluation of F_1 hybrid tomato cultivars for earliness, fruit size and yield using diallel analysis. J. Amer. Soc. Hort. Sci., **107**: 243-247.

Giovannoni J. 2001. Molecular biology of fruit maturation and ripening. Annu. Rev. Plant Physiol. Plant Mol. Biol., **52:** 725-749.

Giovannoni J., Noensie E. N., Ruezinsky D. M., Lu X., Tracy S. L., Ganal M. W., Martin G. B., Pillen K., Alpert K. and Tanksley S. D. 1995. Molecular genetic analysis of the ripening-inhibitor and non-ripening loci of tomato: a first step in genetic map-based cloning of fruit ripening genes. Mol. Gen. Genet., **248**: 195-206.

Giovannoni J., Tanksley S. D., Padmanabhan V., Ruezinsky D., Vrebalov J. and White R. 2004. Rin gene compositions and methods for use thereof. US Patent No. 6787687 issued 07 September 2004.

Griffing B. 1956. Concept of general and specific combining ability in relation to diallel system. Aust. J. Biol. Sci., **9**: 463-493.

Hegarty M. J., Barker G. L., Brennan A. C., Edwards K. J., Abbott R. J. and Hiscock S. J. 2008. Changes to gene expression associated with hybrid speciation in plants: further insights from transcriptomic studies in Senecio. Phil. Trans. R. Soc. B, **363**: 3055-3069.

Jones C. M., Mes P. and Myers J. R. 2003. Characterization and inheritance of the anthocyanin fruit (*Aft*) tomato. J. Hered., **94**: 449-456.

Kolotilin I., Koltai H., Tadmor Y., Bar-Or C., Reuveni M., Meir A., Nahon S., Shlomo H., Chen L. and Levin I. 2007. Transcriptional profiling of high pigment-2^{dg} tomato mutant links early fruit plastid biogenesis with its over-production of phytonutrients. Plant Physiol., **145**: 389-401.

Leseberg C. H., Eissler C. L., Wang X., Johns M. A., Duvall M. R. and Mao L. 2008. Interaction study of MADS-domain proteins in tomato. J. Expt. Bot., **59**: 2253-65.

Levin I., Frankel P., Gilboa N., Tanny S. and Lalazar A. 2003. The tomato dark green mutation is a novel allele of the tomato homolog of the DEETIOLATED1 gene. Theor. Appl. Genet., **106**: 454-460.

Mes P. J., Boches P. and Myers J. R. 2008. Characterization of tomatoes expressing anthocyanin in the fruit. J. Amer. Soc. Hort. Sci., **133**: 262-269.

Nguyen C. V., Vrebalov J. T., Nigel E., Gapper N. E., Zheng Y., Zhong S., Fei Z., James J. and Giovannoni J. J. 2014. Tomato GOLDEN2-LIKE transcription factors reveal molecular gradients that function during fruit development and ripening. Plant Cell, **26**: 585-601.

Peters J. L., Széll M. and Kendrick R. E. 1998. The expression of light-regulated genes in the high-pigment-1 mutant of tomato. Plant Physiol., **117**: 797-807.

Rick C. M., Reeves A. F. and Zobel R. W. 1968. Inheritance and linkage relations of four new mutants. Rep. Tomato Genet. Coop., **18**: 34-35.

Ronen G., Carmel-Goren L., Zamir D. and Hirschberg J. 2000. An alternative pathway to beta-carotene formation in plant chromoplasts discovered by map-based cloning of beta and old-gold color mutations in tomato. Proc. Nat. Acad. Sci., USA, **97**: 11102-11107.

Sacks E. J. and Francis D. M. 2001. Genetic and environmental variation for tomato flesh colour in a population of modern breeding lines. J. Amer. Soc. Hort. Sci., **126**: 226-226.

Sadasivam S. and Manickam A. 1996. Biochemical Methods. New Age International Publisher, New Delhi.

Sapir M., Oren-Shamir M., Ovadia R., Reuveni M., Evenor D., Tadmor Y., Shlomo N., Chen L., Meir A. and Levin I. 2008. Molecular Aspects of Anthocyanin fruit Tomato in Relation to high pigment-1. J. Hered., **99**: 292-303.

Singh O., Gowda C. L. L., Sethi S. C., Dasgupta T. and Smithson J. B. 1992. Genetic analysis of agronomic characters in chick pea I. Estimates of genetic variances from diallel mating design. Theor. Appl. Genet., **83**: 956-962.

Tohge T., Yonekura-Sakakibara K., Niida R., Wantanabe-Takahasi A. and Saito K. 2007. Phytochemical genomics in Arabidopsis thaliana: A case study for functional identification of flavonoid biosynthesis genes. Pure Appl. Chem., **79**: 811-23.

Willits M. G., Kramer C. M., Prata R. T., De Luca V., Potter B. G., Steffens J. C. and Graser G. 2005. Utilization of the genetic resources of wild species to create a non-transgenic high flavonoid tomato. J. Agril. Food Chem., **53**: 1231-1236.

Yang W., Bai X., Kabelka E., Eaton C., Kamoun S., van der Knaap E. and Francis D. 2004. Discovery of single nucleotide polymorphisms in Lycopersicon esculentum by computer aided analysis of expressed sequence tags. Mol. Breed., **14**: 21-34.

Yen H., Shelton A., Howard L., Vrebalov J. and Giovanonni J. J. 1997. The tomato high-pigment (hp) locus maps to chromosome 2 and influences plastome copy number and fruit quality. Theor. Appl. Genet., **95**: 1069-1070.