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RESEARCH ARTICLE

Genetic control of reproductive and fruit quality traits in crosses involving cultivars and induced mutants of tomato (*Solanum lycopersicum* L.)

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Abstract. Development of mutants and their effective utilization to incorporate desirable traits in tomato would be a sound improvement strategy to develop so called 'smart' tomato variety of the coming century. Initially we developed three induced mutants from two varieties, 'Patharkuchi', a local adapted cultivar and an introduced variety 'Berika', and then three crosses (Berika × P Mut-5, Berika × P Mut-11, Patharkuchi × B Mut-1) were made to involve in these two varieties and their respective mutants. Six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of three crosses were utilized to study the genetic control of yield and quality traits, and to study the genetic basis of formation of dark green fruit. The nature and magnitude of gene action controlling the inheritance of 27 quantitative traits differed from one cross to another and from one trait to another, mostly conditioned by nonadditive gene action and duplicate epistasis. The prevalence of duplicate epistasis in three crosses for most of the traits revealed that the pace of progress through conventional selection process would be hindered as this kind of epistasis might result in decreased variation in F_2 and subsequent generations. Recurrent selection in biparental progenies would be helpful for exploiting this type of nonallelic interaction through generation of high frequency of desirable recombination and concentration of genes having cumulative effects in the population. We also observed complex genetic behaviour of some of the traits revealing significant epistatic components. Inheritance study of 'dark green fruit' (*dg1*) of Berika × P Mut-5 cross revealed a single recessive gene governing the trait and expressed when the mutant gene was in homozygous recessive condition (designated as *dg-1/dg-1*).

Keywords. dark green fruit; fruit quality; gene action; induced mutant; segregation pattern; Tomato; yield.

Introduction

Tomato ranks second after potato in terms of consumption and agro-based industries worldwide (Sikder *et al*. 2013). The most critical challenge for tomato production is the attainment of enhanced productivity in farmers' fields, especially in developing countries. Increased incorporation of traits from nonadapted genetic resources including landraces, mutants and crop wild relatives would be a sound strategy in tomato improvement programme to develop 'smart' crop varieties of the 21st century (Mba *et al*. 2012). Spontaneous and induced mutations facilitate plant breeding programmes through enhancing the genetic resources. Either spontaneous or induced mutated phenotype with clear changes in particular traits has been a key material for gene discovery, mapping and definition of its function in foreword genetics. Bridging the phenotype gap is especially important for the post-genomic era of plant genome investigation whose main objective was to merge DNA sequence with its function. Even several years after sequencing the *Arabidopsis* genome, the definitive functions have been established for less than 10% of 26,828 of individual genes (Ostergaard and Yanofsky 2004). To narrow this phenotype gap, it is necessary to increase both the breadth and depth of the mutant resources. Mutation-assisted improvement of crops, especially local varieties, has been continued and

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currently strengthened by the application of other methods such as doubled haploids and molecular markers.

The collection, description, propagation and distribution of genetic materials are of utmost importance in tomato breeding. In addition to preservation of wild species accessions, a comprehensive mutant population has been developed and maintained in the Tomato Genetics Resource Centre in Davis, California and the Botanical and Experimental Garden, The Netherlands. The isogenic tomato 'mutation library' contains a total of 13,000 M_2 families of both spontaneous and induced mutants serve as basic resources for exploring gene function to discover the 'genes that make tomatoes' (Menda *et al*. 2004).

The generalized scheme for induced crop mutagenesis, as a crop improvement strategy, is straightforward and involves the sequential steps of the exposure of plant propagules to predetermined doses of a mutagen, the identification of stable mutants among the progeny, and the incorporation of desirable mutants into breeding programmes or the use of mutant stocks for identification of genes and the elucidation of their functions. To be successful, the researcher would have to make informed decisions that range from the choice of mutagen through the doses to be administered to the handling of putative mutants.

Among various approaches, mutational analysis of plant traits appears to be one of the simplest routes linking the function with the sequence of a gene. Mutation techniques have been used for many years in basic plant research. Induced mutations in *Arabidopsis*, pea, tobacco, tomato, barley, maize and rice have made possible to identify many genes involved in metabolic pathways as well as various biotic and abiotic stresses.

Tomato acts as a powerhouse of nutrients and contains intermediate levels of vitamin C, carotenoids, provitamin A, but because of the volume of fresh tomato and tomato products which are consumed, tomatoes make important contribution to the dietary intake (Stommel 2007; Causse *et al*. 2007; Atanossova *et al*. 2010). Lycopene, the red pigment in tomato fruit is the predominant carotenes, comprising up to 90% of the total carotenoids, while the amount of provitamin A carotenoid, β-carotene is 2 to 15% (Stommel 2007). 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 (Wu *et al*. 2004; Stacewicz-Sapuntzakis and Bowen 2005) and breast cancer (Sesso *et al*. 2005).

Despite the interest of mutations in tomato for basic and applied research, only a few dozen mutants have so far been characterized (http://tgrc.ucdavis.edu/), whereas the number of genes in the tomato genome is estimated to be around 35,000 (Van der Hoeven *et al*. 2002). Large-scale development of mutants and their subsequent characterization have been done in recent past to start filling this gap (Menda *et al*. 2004; Giovannoni 2007; Jáquez-Gutiérrez *et al*. 2019).

The information on genetics of different traits is of paramount important for devising any breeding methodology for the improvement of various traits. The knowledge of genetic structure and mode of inheritance of different characters help breeders to employ suitable breeding methodology for their improvement (Kiani *et al*. 2007; Akhtar and Hazra 2013; Dutta *et al*. 2013; Somraj *et al*. 2017; Somraj *et al*. 2018; Rajan *et al*. 2018). Generation mean analysis is an efficient tool to understand the nature of gene effects involved in the expression of the character. The presence and absence of epistasis can 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.

Keeping in view, the availability of three induced mutant genotypes (P Mut-5, P Mut-11 and B Mut-1) developed by the Department of Vegetable Science, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, India (Sikder *et al*. 2013), and exploring the possibility of their utilization in further breeding programme of tomato, the present investigation was undertaken to determine the gene action of important fruit and fruit quality characters through analysis of mean of six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of three selected crosses involving induced mutant genotypes, and to study the inheritance pattern of 'dark green fruit' in cross having contrasting green colour fruit.

Material and methods

Plant material

The following three induced mutants, two of 'Patharkuchi' and the other of 'Berika' could be isolated by gamma radiation in the Department of Vegetable Science, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur, India, during 2009–2013. (i) P Mut-5: dark green fruit mutant of Patharkuchi, a local adapted cultivar, by 150 Gy gamma radiation. (ii) P Mut-11: dwarf plant having pyriform fruit mutant of Patharkuchi by 200 Gy gamma radiation. (iii) B Mut-1: branched cyme inflorescence mutant of Berika by 50 Gy gamma radiation. The following three crosses were developed during autumn–winter season, 2013–2014. Cross-I: Berika × P Mut-5; cross-II: Berika × P Mut-11; cross-III: Patharkuchi × B Mut-1.

During the 2014–2015, seedlings of three hybrids were transplanted in the main field, selfed their seeds to obtain F_2 families and then backcrossed with their respective parents. The final experiment consisted of three parental lines, F_1's, F_2's and back cross generations of above three crosses to study the gene action of flower, fruit and fruit quality characters. These genetic populations (60 plants each of P_1, P_2 and F_1; 180 F_2 and 90 each of BC_1 and BC_2) were field grown in autumn–winter season (October 2015 to March 2016) in three replications keeping 20 plants each of P_1, P_2

Table 1. Scaling test for different quantitative characters of three cross combinations.

Characters	Patharkuchi × B Mut-1				Berika × Pmut-5			
	A	B	C	D	A	B	C	D
Plant height	− 15.67** ± 3.93	20.00** ± 3.08	44.33** ± 11.24	20.00** ± 5.93	− 26.33** ± 5.40	− 4.00 ± 4.54	3.67 ± 6.03	17.00** ± 4.31
Primary branches/plant	0.67* ± 0.25	− 2.00** ± 0.35	1.33* ± 0.58	1.33** ± 0.30	− 1.00 ± 0.53	− 2.67** ± 0.58	− 2.33** ± 0.55	0.67 ± 0.36
Days to first flowering	− 8.00** ± 1.79	− 16.33** ± 1.44	− 4.33 ± 3.62	10.00** ± 1.78	7.00** ± 1.43	− 5.33** ± 0.99	− 39.67** ± 2.43	− 20.67** ± 1.37
Span of flowering	1.67 ± 1.23	− 16.67** ± 1.35	9.00** ± 2.19	12.00** ± 1.29	− 22.33** ± 1.52	− 11.33** ± 2.12	− 15.00** ± 3.36	9.33** ± 1.89
Flower clusters/plant	13.00** ± 1.05	2.33* ± 1.04	12.00** ± 1.94	− 1.67 ± 1.11	3.33** ± 0.90	5.00** ± 0.87	13.00** ± 2.33	2.33* ± 1.08
Flowers/cluster	2.33 ± 1.41	5.67** ± 1.50	6.67* ± 3.32	− 0.67 ± 1.85	− 1.00** ± 0.31	− 1.67** ± 0.47	0.67 ± 0.58	1.67** ± 0.24
Fruits/plant	27.00** ± 3.26	21.00** ± 1.93	45.33** ± 5.83	− 1.33 ± 3.42	4.67 ± 2.40	− 3.67 ± 2.35	3.67 ± 3.73	1.33 ± 2.06
Fruit weight	18.40** ± 2.64	33.10** ± 5.24	69.43** ± 4.84	8.97* ± 3.50	21.83** ± 3.13	41.80** ± 5.19	26.10** ± 3.66	− 18.77** ± 3.42
Equatorial diameter	5.39** ± 1.12	2.59 ± 1.89	− 1.87 ± 2.18	− 4.93** ± 1.42	− 8.00** ± 1.48	− 8.81** ± 2.27	7.15** ± 2.34	11.98** ± 1.51
Polar diameter	− 5.53** ± 1.35	1.41 ± 1.39	− 2.36 ± 1.86	0.88 ± 1.03	11.11** ± 0.88	− 4.29** ± 0.95	− 13.60** ± 1.39	− 10.21** ± 0.85
Locules per fruit	− 0.33 ± 0.25	− 0.67* ± 0.25	0.33 ± 0.42	0.67** ± 0.19	− 1.33** ± 0.25	− 2.00** ± 0.35	− 2.00** ± 0.42	0.67** ± 0.23
Pericarp thickness	1.73** ± 0.09	1.16** ± 0.06	− 2.47** ± 0.14	− 2.68** ± 0.05	− 0.58** ± 0.08	1.54** ± 0.06	− 3.16** ± 0.28	− 2.06** ± 0.14
Seeds/fruit	18.00** ± 2.32	− 13.00** ± 1.80	− 6.33 ± 3.43	− 5.67** ± 2.01	− 9.67** ± 2.74	− 2.33 ± 2.88	− 6.00 ± 4.16	3.00 ± 2.60
Fruit yield/plant	3.73** ± 0.44	3.41** ± 0.10	9.77** ± 0.76	1.31** ± 0.43	2.13** ± 0.21	2.03** ± 0.17	3.83** ± 0.35	− 0.17 ± 0.21
Total soluble solids	0.06 ± 0.09	− 1.00** ± 0.07	− 0.37** ± 0.11	0.29** ± 0.05	− 1.46** ± 0.09	− 0.96** ± 0.08	− 1.79** ± 0.15	0.31** ± 0.07
Total sugar content	− 0.39** ± 0.08	0.53** ± 0.13	− 2.20** ± 0.17	− 1.17** ± 0.10	0.77** ± 0.07	0.04 ± 0.06	0.04 ± 0.23	− 0.38** ± 0.11
Reducing sugar	0.09** ± 0.02	− 0.36** ± 0.05	1.37** ± 0.04	0.82** ± 0.01	0.49** ± 0.02	0.51** ± 0.02	0.42** ± 0.04	− 0.29** ± 0.01
Titratable acidity	− 0.11** ± 0.02	0.12* ± 0.05	− 0.21** ± 0.05	− 0.11** ± 0.03	− 0.07 ± 0.04	− 0.05 ± 0.04	0.27** ± 0.04	0.19** ± 0.03
Lycopene	0.01 ± 0.05	1.19** ± 0.07	0.20** ± 0.07	− 0.50** ± 0.03	1.96** ± 0.12	0.23** ± 0.07	0.05 ± 0.13	− 1.07** ± 0.06
B-carotene	0.00 ± 0.04	0.15** ± 0.03	0.09 ± 0.05	− 0.03 ± 0.02	− 0.05* ± 0.02	0.09** ± 0.03	− 0.02 ± 0.03	− 0.03 ± 0.02
Ascorbic acid	− 4.62** ± 1.31	13.96** ± 1.25	− 4.41** ± 1.52	− 6.87** ± 0.96	− 2.21** ± 0.78	− 6.39** ± 0.90	− 0.15 ± 1.31	4.22** ± 0.59
Chlorophyll a content of leaf	23.84** ± 3.60	11.96** ± 2.76	49.33** ± 5.07	6.77* ± 3.27	33.25** ± 2.07	13.39** ± 2.52	23.30** ± 3.90	− 11.67** ± 2.10
Chlorophyll b content of leaf	− 3.99 ± 5.06	− 31.02** ± 4.45	− 22.32** ± 7.29	6.35 ± 4.76	29.03** ± 2.60	− 26.60** ± 4.46	17.95* ± 6.98	7.76* ± 3.61
Total chlorophyll content of leaf	− 3.00 ± 3.54	24.83** ± 4.34	74.52** ± 5.83	26.35** ± 3.18	35.37** ± 5.42	15.65** ± 4.85	− 28.22** ± 5.09	− 39.62** ± 3.91
Chlorophyll a content of immature fruits	0.12 ± 0.16	− 0.39 ± 0.29	− 0.34 ± 0.51	− 0.04 ± 0.27	1.71** ± 0.41	− 2.35** ± 0.26	− 5.03** ± 0.89	− 2.19** ± 0.41
Chlorophyll b content of immature fruits	0.94** ± 0.26	2.34** ± 0.27	2.73** ± 0.61	− 0.28 ± 0.33	1.90** ± 0.35	− 2.06** ± 0.34	− 4.92** ± 0.53	− 2.38** ± 0.33
Total chlorophyll content of immature fruits	− 1.31** ± 0.31	− 0.79* ± 0.31	0.90* ± 0.36	1.50** ± 0.23	28.18** ± 0.57	1.96* ± 0.91	19.83** ± 2.50	− 5.15** ± 1.32

Characters	Berika × P Mut-11			
	A	B	C	D
Plant height	− 73.33** ± 7.01	17.33** ± 4.60	− 47.33** ± 11.18	4.33 ± 6.25
Primary branches/plant	− 0.67 ± 0.35	− 2.00** ± 0.31	− 1.33 ± 0.70	0.67* ± 0.28
Days to first flowering	14.00** ± 1.52	− 1.67 ± 0.91	− 0.33 ± 1.33	− 6.33** ± 0.94
Span of flowering	− 6.33** ± 1.69	7.67** ± 1.62	− 14.67** ± 3.26	− 8.00** ± 1.80
Flower clusters/plant	− 10.67** ± 1.38	4.67** ± 0.97	− 1.33 ± 2.09	2.33* ± 1.13

Table 1 (*contd*)

Characters	Berika × P Mut-11			
	A	B	C	D
Flowers/cluster	− 1.33** ± 0.31	− 0.67* ± 0.31	− 0.67 ± 0.55	0.67** ± 0.19
Fruits/plant	8.33** ± 2.16	22.67** ± 2.14	33.00** ± 3.91	1.00 ± 2.29
Fruit weight	37.40** ± 4.12	35.27** ± 8.29	18.07** ± 5.13	− 27.30** ± 4.91
Equatorial diameter	− 11.12** ± 1.59	− 19.66** ± 1.13	− 18.30** ± 1.84	6.24** ± 1.00
Polar diameter	0.00 ± 1.09	− 8.50** ± 1.14	− 7.80** ± 1.61	0.35 ± 0.92
Locules per fruit	− 0.33 ± 0.25	− 0.33 ± 0.35	0.00 ± 0.42	0.33 ± 0.23
Pericarp thickness	1.41** ± 0.09	0.02 ± 0.15	− 2.74** ± 0.48	− 2.08** ± 0.23
Seeds/fruit	− 1.33 ± 4.42	29.33** ± 2.32	− 12.67** ± 2.77	− 20.33** ± 2.55
Fruit yield/plant	2.70** ± 0.13	5.19** ± 0.19	4.22** ± 0.32	− 1.83** ± 0.16
Total soluble solids	− 0.30** ± 0.08	− 1.73** ± 0.06	− 0.20 ± 0.16	0.92** ± 0.08
Total sugar content	0.22** ± 0.04	0.12** ± 0.03	− 0.62** ± 0.09	− 0.48** ± 0.03
Reducing sugar	− 0.32** ± 0.02	0.79** ± 0.02	0.65** ± 0.05	0.09** ± 0.03
Titratable acidity	− 0.03 ± 0.03	0.16** ± 0.04	0.60** ± 0.06	0.23** ± 0.03
Lycopene	2.24** ± 0.09	1.78** ± 0.17	2.64** ± 0.44	− 0.69** ± 0.19
B-carotene	− 0.14** ± 0.03	0.12** ± 0.04	0.09 ± 0.07	0.05 ± 0.03
Ascorbic acid	− 2.18 ± 1.10	1.57 ± 0.97	13.35** ± 1.92	6.98** ± 0.89
Chlorophyll a content of leaf	− 7.90 ± 1.51	− 3.20 ± 2.15	3.28 ± 2.71	7.19** ± 1.46
Chlorophyll b content of leaf	− 4.82 ± 4.38	− 19.66** ± 4.24	17.46** ± 4.67	20.97** ± 3.01
Total chlorophyll content of leaf	− 46.34 ± 4.74	16.56** ± 3.58	20.14** ± 5.91	24.96** ± 3.20
Chlorophyll a content of immature fruits	− 0.15 ± 0.40	− 0.39 ± 0.32	1.36** ± 0.45	0.95** ± 0.28
Chlorophyll b content of immature fruits	1.32** ± 0.35	− 1.18** ± 0.27	1.27 ± 0.68	0.57 ± 0.39
Total chlorophyll content of immature fruits	− 1.26** ± 0.43	− 0.09 ± 0.23	1.81* ± 0.86	1.58** ± 0.43

*, **Significant at 0.05 and 0.01 level of probability, respectively.

Table 2. Gene effects based on six-parameter model for different characters of three crosses.

Character	Cross	m	d	h	i	j	l	Epistatic gene action
Plant height (cm)	C I	119.17** ± 11.90	8.50** ± 0.98	− 53.50* ± 25.92	− 40.00** ± 11.86	− 17.83 ± 2.45	35.67* ± 14.38	Duplicate
	C II	169.50** ± 8.69	27.50** ± 1.06	− 139.17** ± 23.01	− 34.00** ± 8.62	− 11.17 ± 3.49	64.33** ± 14.61	Duplicate
	C III	122.00** ± 12.52	49.67** ± 0.91	− 84.33** ± 30.29	− 8.67 ± 12.49	− 45.33 ± 3.85	64.67** ± 18.69	Duplicate
Primary branches per plant	C I	9.67** ± 0.61	− 0.67** ± 0.09	− 7.33** ± 1.47	− 2.67** ± 0.60	1.33 ± 0.20	4.00** ± 0.91	Duplicate
	C II	10.17** ± 0.74	− 0.83** ± 0.20	− 7.50** ± 2.14	− 1.33 ± 0.71	0.83 ± 0.38	5.00** ± 1.42	Duplicate
	C III	10.00** ± 0.57	− 0.67** ± 0.13	− 6.00** ± 1.31	− 1.33* ± 0.55	0.67 ± 0.18	4.00** ± 0.86	Duplicate
Days to first flowering	C I	59.83** ± 3.58	− 2.83** ± 0.30	− 67.83** ± 8.30	− 20.00** ± 3.57	4.17 ± 0.95	44.33** ± 5.12	Duplicate
	C II	0.17 ± 2.76	− 5.50** ± 0.31	83.17** ± 6.57	41.33** ± 2.74	6.17 ± 0.84	− 43.00** ± 3.95	Duplicate
	C III	26.83** ± 1.92	− 3.50** ± 0.36	32.17** ± 5.30	12.67** ± 1.89	7.83 ± 0.87	− 25.00** ± 3.44	Duplicate
Span of flowering	C I	80.17** ± 2.60	1.50** ± 0.32	− 62.50** ± 6.42	− 24.00** ± 2.58	9.17 ± 0.88	39.00** ± 3.95	Duplicate
	C II	76.83** ± 3.81	3.50** ± 0.48	− 71.17** ± 9.25	− 18.67** ± 3.78	− 5.50 ± 1.24	52.33** ± 5.67	Duplicate
	C III	37.33** ± 3.63	8.33** ± 0.37	28.00** ± 8.66	16.00** ± 3.61	− 7.00 ± 1.10	− 17.33** ± 5.27	Duplicate
Flower clusters per plant	C I	13.00** ± 2.24	− 2.33** ± 0.20	19.33** ± 5.42	3.33 ± 2.23	5.33 ± 0.70	− 18.67** ± 3.31	Duplicate
	C II	20.50** ± 2.18	1.83** ± 0.20	0.17 ± 4.81	− 4.67* ± 2.17	− 0.83 ± 0.47	− 3.67 ± 2.90	–
	C III	19.00** ± 2.26	3.33** ± 0.20	− 8.00 ± 5.60	− 4.67* ± 2.25	− 7.67 ± 0.75	10.67** ± 3.56	–
Flowers per cluster	C I	7.00 ± 3.71	− 2.33** ± 0.20	14.00 ± 8.59	1.33 ± 3.70	− 1.67 ± 0.98	− 9.33 ± 5.07	–
	C II	8.67** ± 0.50	− 0.67** ± 0.13	− 9.67** ± 1.38	− 3.33** ± 0.48	0.33 ± 0.23	6.00** ± 0.97	Duplicate
	C III	6.33** ± 0.39	− 0.33** ± 0.09	− 3.67** ± 1.00	− 1.33** ± 0.38	− 0.33 ± 0.15	3.33** ± 0.74	Duplicate
Fruits per plant	C I	61.33** ± 6.84	− 8.33** ± 0.36	74.00** ± 16.01	2.67 ± 6.83	3.00 ± 1.88	− 50.67** ± 9.41	Duplicate
	C II	48.50** ± 4.14	2.50** ± 0.48	6.17 ± 10.58	− 2.67 ± 4.12	4.17 ± 1.51	1.67 ± 6.84	–
	C III	− 42.17** ± 4.60	8.17** ± 0.44	38.83** ± 11.17	− 2.00 ± 4.58	− 7.17 ± 1.46	− 29.00** ± 6.81	Duplicate
Fruit weight (g)	C I	91.28** ± 7.00	3.58** ± 0.45	18.48 ± 18.82	− 17.93* ± 6.99	− 7.35 ± 2.82	− 33.57** ± 12.16	Duplicate
	C II	45.48** ± 6.85	− 4.38** ± 0.37	128.68** ± 19.14	37.53** ± 6.84	− 9.98 ± 3.00	− 101.17** ± 12.46	Duplicate
	C III	20.87* ± 9.84	3.17** ± 0.47	180.17** ± 28.14	54.60** ± 9.83	1.07 ± 4.51	− 127.27** ± 18.64	Duplicate
Equatorial diameter (cm)	C I	33.56** ± 2.86	1.69** ± 0.30	29.69** ± 7.37	9.85** ± 2.84	1.40 ± 1.07	− 17.84** ± 4.64	Duplicate
	C II	77.98** ± 3.05	1.95** ± 0.50	− 62.65** ± 8.22	− 23.97** ± 3.01	0.40 ± 1.30	40.78** ± 5.33	Duplicate
	C III	64.54** ± 2.05	3.91** ± 0.47	− 54.91** ± 5.51	− 12.48** ± 1.99	4.27 ± 0.91	43.26** ± 3.63	Duplicate
Polar diameter (cm)	C I	58.29** ± 2.08	1.70** ± 0.29	− 3.96 ± 5.61	− 1.76 ± 2.06	− 3.47 ± 0.87	5.88 ± 3.76	–
	C II	29.58** ± 1.72	− 5.60** ± 0.30	44.04** ± 4.34	20.42** ± 1.69	7.70 ± 0.64	− 27.24** ± 2.68	Duplicate
	C III	50.70** ± 1.87	− 5.60** ± 0.30	− 8.19 ± 4.86	− 0.70 ± 1.85	4.25 ± 0.74	9.20** ± 3.14	–
Locules per fruit	C I	3.83** ± 0.39	− 0.17 ± 0.09	− 3.50** ± 0.98	− 1.33** ± 0.38	0.17 ± 0.15	2.33** ± 0.65	Duplicate
	C II	5.33** ± 0.46	0.33** ± 0.09	− 5.67** ± 1.23	− 1.33** ± 0.45	0.33 ± 0.20	4.67** ± 0.82	Duplicate
	C III	4.67** ± 0.46	0.33** ± 0.09	− 1.33 ± 1.23	− 0.67 ± 0.45	0.00 ± 0.00	1.33 ± 0.82	–
Pericarp thickness (mm)	C I	2.28** ± 0.11	0.03 ± 0.04	13.37** ± 0.28	5.36** ± 0.11	0.29 ± 0.05	− 8.25** ± 0.18	Duplicate
	C II	2.23** ± 0.27	0.10** ± 0.02	9.12** ± 0.57	4.12** ± 0.27	− 1.06 ± 0.04	− 5.08** ± 0.31	Duplicate
	C III	0.90 ± 0.46	1.40** ± 0.07	11.00** ± 0.94	4.17** ± 0.45	0.69 ± 0.07	− 5.59** ± 0.50	Duplicate
Seeds per fruit	C I	67.50** ± 4.03	− 5.17** ± 0.25	27.83** ± 10.07	11.33** ± 4.02	15.50 ± 1.36	− 16.33* ± 6.34	Duplicate
	C II	91.33** ± 5.23	2.67** ± 0.55	− 24.33** ± 13.36	− 6.00 ± 5.20	− 3.67 ± 1.91	18.00* ± 8.42	Duplicate
	C III	37.00** ± 5.14	10.33** ± 0.68	114.33** ± 14.81	40.67** ± 5.10	− 15.33 ± 2.45	− 68.67** ± 9.81	Duplicate
Fruit yield per plant (kg)	C I	7.47** ± 0.86	− 0.18** ± 0.06	6.66** ± 1.98	− 2.62** ± 0.86	0.16 ± 0.22	− 4.53** ± 1.15	Duplicate
	C II	4.32** ± 0.41	0.18** ± 0.04	6.08** ± 1.00	0.33 ± 0.41	0.05 ± 0.13	− 4.50** ± 0.61	Duplicate
	C III	0.29 ± 0.33	0.88** ± 0.05	17.60** ± 0.78	3.67** ± 0.33	− 1.24 ± 0.10	− 11.56** ± 0.48	Duplicate

Table 2 (*contd*)

Character	Cross	m	d	h	i	j	l	Epistatic gene action
Total soluble solids (%)	C I	5.56** ± 0.10	− 0.16** ± 0.03	− 2.58** ± 0.27	− 0.57** ± 0.09	0.53 ± 0.05	1.51** ± 0.19	Duplicate
	C II	6.15** ± 0.14	− 0.24** ± 0.04	− 4.24** ± 0.34	− 0.63** ± 0.13	− 0.25 ± 0.06	3.04** ± 0.21	Duplicate
	C III	7.50** ± 0.16	− 0.38** ± 0.04	− 6.33** ± 0.35	− 1.83** ± 0.15	0.72 ± 0.05	3.87** ± 0.20	Duplicate
Total sugar content (%)	C I	1.16** ± 0.21	0.11** ± 0.03	4.77** ± 0.52	2.34** ± 0.20	− 0.46 ± 0.07	− 2.48** ± 0.32	Duplicate
	C II	2.88** ± 0.22	− 0.16** ± 0.02	2.35** ± 0.46	0.77** ± 0.22	0.36 ± 0.03	− 1.58** ± 0.26	Duplicate
	C III	2.49** ± 0.06	0.04** ± 0.01	2.50** ± 0.12	0.95** ± 0.05	0.05 ± 0.01	− 1.29** ± 0.09	Duplicate
Reducing sugar (%)	C I	3.43** ± 0.03	− 0.14** ± 0.02	− 3.20** ± 0.10	− 1.65** ± 0.03	0.23 ± 0.03	1.92** ± 0.07	Duplicate
	C II	1.12** ± 0.03	0.08** ± 0.01	2.48** ± 0.07	0.59** ± 0.03	− 0.01 ± 0.01	− 1.59** ± 0.05	Duplicate
	C III	1.86** ± 0.05	0.10** ± 0.01	0.22* ± 0.11	− 0.18** ± 0.05	− 0.55 ± 0.01	− 0.29** ± 0.06	Duplicate
Titratable acidity (%)	C I	0.27** ± 0.07	0.01 ± 0.01	0.40* ± 0.18	0.21** ± 0.07	− 0.11 ± 0.03	− 0.22 ± 0.11	–
	C II	1.01** ± 0.07	− 0.03** ± 0.00	− 0.85** ± 0.19	− 0.38** ± 0.07	− 0.01 ± 0.03	0.49** ± 0.12	Duplicate
	C III	1.07** ± 0.06	− 0.01 ± 0.00	− 0.86** ± 0.15	− 0.47** ± 0.06	− 0.09 ± 0.02	0.34** ± 0.10	Duplicate
Lycopene content (mg 100 g)	C I	3.55** ± 0.07	0.35** ± 0.01	3.50** ± 0.20	1.00** ± 0.07	− 0.59 ± 0.04	− 2.20** ± 0.15	Duplicate
	C II	4.14** ± 0.12	− 1.39** ± 0.02	5.29** ± 0.34	2.14** ± 0.12	0.86 ± 0.06	− 4.33** ± 0.24	Duplicate
	C III	3.90** ± 0.39	− 0.39** ± 0.08	6.29** ± 0.81	1.38** ± 0.38	0.23 ± 0.08	− 5.40** ± 0.44	Duplicate
β-carotene (mg per 100 g fresh pulp)	C I	0.43** ± 0.05	0.06** ± 0.01	0.34** ± 0.13	0.06 ± 0.05	− 0.07 ± 0.02	− 0.21* ± 0.08	
	C II	0.48** ± 0.04	− 0.02** ± 0.01	0.05 ± 0.11	0.06 ± 0.04	− 0.07 ± 0.02	− 0.10 ± 0.07	–
	C III	0.60** ± 0.06	0.03** ± 0.01	− 0.20 ± 0.15	− 0.11 ± 0.06	− 0.13 ± 0.02	0.12 ± 0.10	–
Ascorbic acid content (mg per 100 g)	C I	15.58** ± 1.97	6.16** ± 0.42	36.20** ± 5.34	13.75** ± 1.92	− 9.29 ± 0.88	− 23.08** ± 3.46	Duplicate
	C II	45.85** ± 1.24	− 2.15** ± 0.39	− 25.67** ± 3.18	− 8.44** ± 1.18	2.09 ± 0.55	17.03** ± 2.06	Duplicate
	C III	45.51** ± 1.82	3.71** ± 0.40	− 29.20** ± 4.41	− 13.96** ± 1.77	− 1.88 ± 0.65	14.57** ± 2.81	Duplicate
Chlorophyll a content of leaf	C I	66.50** ± 6.55	− 2.04** ± 0.38	12.19 ± 16.38	− 13.53* ± 6.53	5.94 ± 2.22	− 22.27* ± 10.12	–
	C II	43.35** ± 4.24	− 9.08** ± 0.54	85.82** ± 10.57	23.33** ± 4.20	9.93 ± 1.47	− 69.97** ± 6.72	Duplicate
	C III	67.50** ± 2.99	4.48** ± 0.63	− 30.78** ± 7.80	− 14.38** ± 2.93	− 2.35 ± 1.23	25.48** ± 5.04	Duplicate
Chlorophyll b content of leaf	C I	135.33** ± 9.54	− 13.33** ± 0.38	− 65.06** ± 24.05	− 12.70 ± 9.53	13.52 ± 3.29	47.72** ± 14.95	Duplicate
	C II	150.63** ± 7.30	− 9.14** ± 1.13	− 23.63 ± 17.53	− 15.52* ± 7.21	27.82 ± 2.36	13.09 ± 10.83	–
	C III	162.32** ± 6.24	5.59** ± 1.62	− 110.37** ± 17.31	− 41.94** ± 6.02	7.42 ± 3.02	66.42** ± 11.24	Duplicate
Total chlorophyll content of leaf	C I	209.05** ± 6.50	0.57 ± 1.34	− 83.83** ± 16.83	− 52.69** ± 6.36	− 13.91 ± 2.64	30.87** ± 10.80	Duplicate
	C II	120.12** ± 7.91	− 26.11** ± 1.27	189.52** ± 21.99	79.25** ± 7.81	9.86 ± 3.58	− 130.27** ± 14.32	Duplicate
	C III	210.22** ± 6.57	12.96** ± 1.49	− 127.31** ± 17.27	− 49.93** ± 6.40	− 31.45 ± 2.80	79.71** ± 11.18	Duplicate
Chlorophyll a content of immature fruits	C I	3.69** ± 0.54	0.11 ± 0.07	0.23 ± 1.26	0.07 ± 0.54	0.25 ± 0.16	0.19 ± 0.75	–
	C II	3.40** ± 0.82	− 1.96** ± 0.06	10.82** ± 1.83	4.39** ± 0.82	2.03 ± 0.18	− 3.74** ± 1.12	Duplicate
	C III	7.61** ± 0.57	0.11* ± 0.05	− 3.62* ± 1.54	− 1.90** ± 0.56	0.12 ± 0.23	2.44* ± 1.02	Duplicate
Chlorophyll b content of immature fruits	C I	3.97** ± 0.66	0.57** ± 0.06	5.28** ± 1.52	0.55 ± 0.66	− 0.70 ± 0.18	− 3.84** ± 0.90	Duplicate
	C II	4.45** ± 0.67	− 1.89** ± 0.08	8.67** ± 1.70	4.76** ± 0.67	1.98 ± 0.24	− 4.60** ± 1.05	Duplicate
	C III	9.11** ± 0.79	− 0.67** ± 0.06	− 2.23 ± 1.85	− 1.13 ± 0.79	1.25 ± 0.22	0.99 ± 1.08	–
Total chlorophyll content of immature fruits	C I	9.51** ± 0.46	1.02** ± 0.03	− 7.74** ± 1.28	− 3.00** ± 0.45	− 0.26 ± 0.20	5.10** ± 0.87	Duplicate
	C II	8.53** ± 2.64	− 9.28** ± 0.24	41.64** ± 5.73	10.31** ± 2.63	13.11 ± 0.54	− 40.44** ± 3.15	Duplicate
	C III	12.42** ± 0.87	0.28** ± 0.10	− 7.69** ± 1.95	− 3.16** ± 0.86	− 0.58 ± 0.22	4.51** ± 1.15	Duplicate

M, mean; d, additive effect; h, dominance effect; I, additive × additive type gene interaction; j, additive × dominance type gene interaction; l, dominance × dominance type gene interaction; CI, Patharkuchi × B Mut-1; C II, Berika × P Mut-5; C III, Berika × P Mut-11.
*,**Significant at 0.05 and 0.01 level of probability, respectively.

and F_1; 60 plants of F_2 and 30 plants each of BC_1 and BC_2 per replication.

Data recording

Five randomly selected plants per replication of each of six genetic populations were sampled for taking the observations on plant height (cm), primary branches per plant, days to first flowering, span of flowering (span between first and last flower in the plants), flower clusters per plant, flowers per cluster, fruits per plant, fruit weight (g), equatorial diameter (mm), polar diameter (mm), locules per fruit, pericarp thickness (mm), fruit yield per plant (kg) and seeds per fruits. After taking the morphological characters of fruit, the fruits were cut into two halves to record pericarp thickness (mm) and locules per fruit. The cut fruits were used to make replication-wise composite sample to estimate fruit quality characters on total soluble solids (°brix), determined by hand refractometer; total and reducing sugar contents (%), estimated by anthrone method (Dubois *et al.* 1951); titratable acidity (expressed as % anhydrous citric acid), estimated as per Sadasivam and Manickam (1996); ascorbic acid content (mg/100 g fresh weight), estimated by titration with 2,6-dichlorolindophenol sodium salt solution (AOAC 1990); lycopene content (mg/100 g fresh weight), β-carotene content (mg/100 g fresh weight), determined by spectrophotometrically (Davies 1976), chlorophyll a content (mg/100 g fresh weight), chlorophyll b content (mg/100 g fresh weight) and total chlorophyll content (mg/100 g fresh weight) of leaf and immature fruit, estimated as per Sadasivam and Manickam (1996). First three leaflets of the third compound leaf from the top of the plant was sampled from all the five selected plants 30 days after transplanting and five fruits were sampled from the selected plants 20 days after setting of the fruit to determine chlorophyll contents.

Statistical analyses

In the experiment with six generations (P_1, P_2, F_1, F_2, B_1 and B_2), the mean and variance of each generation for each character were calculated separately considering each plant data for the generations. The scaling test was performed following Mather (1949) and Hayman and Mather (1955). The interaction components based on the 6-parameter model were estimated from progeny means as per method suggested by Mather and Jinks (1971) and Jinks and Jones (1958). The significance of the scales and gene effects were tested by using the '*t*' test (Singh and Chaudhary 1985). Segregation pattern of the dark green fruit (*dg1*) at the immature stage in F_2 segregating population of contrasting cross Berika (light green fruit) × P Mut-5 (dark green fruit) was also determined by χ^2-test.

Results and discussion

Determination of gene action through analysis of generation means

The present experiment was conducted to obtain the information on the nature of gene action for 27 reproductive and fruit quality characters involving six generations (P_1 and P_2, F_1, F_2, BC_1 and BC_2) of three cross combinations, namely Berika × P Mut-5, Berika × P Mut-11 and Patharkuchi × B Mut-1.

The mean values, standard errors and variances of different generations calculated over all the plants in each generation were used. The 'A' and 'B' scaling tests provided the evidence for the presence of additive × additive (i), additive × dominance (j) and dominance × 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. The type of epistasis was determined only when dominance (h) and dominance × dominance (l) effects were significant; when these effects had the same sign, the effects were complementary while different signs indicated duplicate epistasis (Kearsey and Pooni 1996).

The 'A', 'B', 'C' and 'D' scaling tests were carried out for all characters indicating the presence of nonallelic interactions except chlorophyll, a content of immature fruit in Patharkuchi × B Mut-1, number of fruits per plant in Berika × P Mut-5, and number of locules per fruit in Berika × P Mut-11 (table 1). A simple additive/dominance model was not adequate to explain the gene effects of most of the characters under study because of the significance of the scales in all three crosses. Most of the epistatic components were significant in these crosses suggesting very complex nature of inheritance for most studied characters. Duplicate epistasis was predominant in most of the characters under study in all three crosses.

The scaling test and gene effects of studied characters are presented in tables 1–2. In crosses Patharkuchi × B Mut-1 and Berika × P Mut-5, additive (d), dominance (h), additive × additive (i) and dominance × dominance (l) gene actions controlled plant height, while additive (d), dominance (h) and dominance × dominance (l) gene actions were predominant for this character in cross Berika × P Mut-11. Primary branches per plant was controlled by additive, dominance, additive × additive and dominance × dominance gene actions in crosses Patharkuchi × B Mut-1 and Berika × P Mut-11, while by additive, dominance and dominance × dominance genetic effects in cross Berika × P Mut-5. Three scales ('A', 'B', 'D') were significant in cross Patharkuchi × B Mut-1 for days to first flowering which was controlled by additive, dominance, additive × additive and dominance × dominance gene actions. In crosses Berika × P Mut-5 and Berika × P Mut-11, additive, dominance, additive × additive and dominance × dominance gene actions were predominant for this character. Additive,

dominance, additive × additive and dominance × dominance gene actions controlled span of flowering in three crosses. Dominance × dominance interaction effect was larger than additive × additive effect in three crosses. Flower clusters per plant was controlled by additive, dominance, and dominance × dominance gene actions in cross Patharkuchi × B Mut-1, while additive (d), additive × additive and dominance × dominance gene effects were predominant in crosses Berika × P Mut-5 and Berika × P Mut-11. Only additive gene action was predominant for flowers per cluster in cross Patharkuchi × B Mut-1, while additive, dominance, additive × additive and dominance × dominance gene actions were predominant in crosses Berika × P Mut-5 and Berika × P Mut-11. A simple additive/dominance model was adequate to explain the gene effects because no scales were significant in cross Berika × P Mut-5 for fruits per plant. However, the model was not adequate in crosses Patharkuchi × B Mut-1 and Berika × P Mut-11, where additive, dominance and dominance × dominance gene effects were predominant for this character. Fruit weight was controlled by additive, additive × additive and dominance × dominance gene actions in cross Patharkuchi × B Mut-1. Dominance effect was not significant for this character hence the type of epistasis could not be determined. While in crosses Berika × P Mut-5 and Berika × P Mut-11, additive, dominance, additive × additive and dominance × dominance gene actions were predominant for this character. Dominance × dominance interaction effect was larger than additive × additive effect in all the crosses. Additive, dominance, additive × additive and dominance × dominance type epistatic gene actions were predominant for equatorial diameter of fruit in all three crosses. Dominance × dominance interaction effect was larger than additive × additive effect in all the crosses for this character. In cross Patharkuchi × B Mut-1, only additive gene action was predominant for polar diameter of fruit. Hence the type of epistasis could not be determined in this cross. Whereas, in cross Berika × P Mut-5, additive, dominance, additive × additive and dominance × dominance gene actions were predominant for this character which showed very complex nature of inheritance for this character. In cross Berika × P Mut-11, additive, and dominance × dominance gene actions controlled this character. Type of epistasis could not be determined in this cross. A simple additive/dominance model was adequate to explain the gene effects because no scales were significant in cross Berika × P Mut-11 for locules per fruit. In cross Patharkuchi × B Mut-1, dominance, additive × additive and dominance × dominance gene actions were predominant for this character. While in cross Berika × P Mut-5, additive, dominance, additive × additive and dominance × dominance type epistatic gene actions were predominant for this character. In cross Patharkuchi × B Mut-1, dominance, additive × additive and dominance × dominance gene actions were predominant for pericarp thickness. While in crosses Berika × P Mut-5 and Berika × P Mut-11, additive, dominance, additive × additive and dominance × dominance gene actions controlled this character. Dominance × dominance interaction effect was larger than additive × additive effect in all the crosses. In crosses Patharkuchi × B Mut-1 and Berika × P Mut-11, additive, dominance, additive × additive and dominance × dominance gene actions were predominant for seeds per fruit, while in cross Berika × P Mut-5, additive and dominance × dominance effects were significant, hence the type of epistasis could not be determined. Additive, dominance, additive × additive and dominance × dominance gene actions controlled fruit yield per plant in crosses Patharkuchi × B Mut-1 and Berika × P Mut-11. Dominance × dominance interaction effect was larger than additive × additive effect in these two crosses. While gene actions controlled this character in cross Berika × P Mut-5 were additive, dominance and dominance × dominance. Additive, dominance, additive × additive and dominance × dominance gene actions were predominant for TSS, total sugar, reducing sugar, lycopene and ascorbic acid contents in all three crosses. Dominance × dominance interaction effect was larger than additive × additive effect for these characters in all three crosses. In cross Patharkuchi × B Mut-1, dominance and additive × additive epistatic gene actions were predominant for titratable acidity content, hence type of epistasis could not be determined for this cross. In cross Berika × P Mut-5, additive, dominance, additive × additive and dominance × dominance gene actions were predominant for this character, whereas, in cross Berika × P Mut-11, dominance, additive × additive and dominance × dominance gene actions were predominant for this character. In cross Patharkuchi × B Mut-1, additive, dominance, and dominance × dominance type epistatic gene actions were predominant for β-carotene content. Only additive gene action was predominant for this character for other two crosses. In cross Patharkuchi × B Mut-1, additive, additive × additive, and dominance × dominance gene actions were predominant for chlorophyll, a content of leaf. Additive, dominance, additive × additive and dominance × dominance gene actions controlled this character in other two crosses. Dominance × dominance interaction effect was larger than additive × additive effect. In cross Patharkuchi × B Mut-1, additive, dominance, and dominance × dominance gene actions were predominant for chlorophyll b content of leaf. Additive and additive × additive gene actions were predominant for this character in cross Berika × P Mut-5, hence type of epistasis could not be determined. In cross Berika × P Mut-11, additive, dominance, additive × additive and dominance × dominanc epistatic gene actions were predominant for this character. Dominance × dominance interaction effect was larger than additive × additive effect. Type of epistasis for this character was 'Duplicate' in this cross. In cross Patharkuchi × B Mut-1, dominance, additive × additive and dominance × dominance gene actions were predominant for total chlorophyll content of leaf. Additive, dominance, additive × additive and dominance × dominance epistatic gene actions were predominant for this

Table 3. χ^2 analysis for F_2 segregation for dark green fruit character of cross Berika × P Mut-5.

χ^2 analysis for 160 F_2 segregating population					
Expected ratio for the plant having dark green fruit	Observed (O)	Expected (E)	O–E	d^2	$\chi^2 = d^2/E$
1/4	42	40	2	4	0.026

d.f. = (n − 1)=1; χ^2 = 0.026.

character in other two crosses. A simple additive/dominance model was adequate to explain the gene effects because no scales were significant in cross Patharkuchi × B Mut-1 for chlorophyll, a content of immature fruits. The model was not adequate to explain the gene effects because of the significance of the scales in other two crosses. Additive, dominance, additive × additive and dominance × dominance actions were predominant for this character in other two crosses. Dominance × dominance interaction effect was larger than additive × additive effect. In cross Patharkuchi × B Mut-1, additive, dominance, and dominance × dominance gene actions were predominant for chlorophyll b content of immature fruits. In cross Berika × P Mut-5, additive, dominance, additive × additive and dominance × dominance gene actions were predominant for this character. Only additive gene action was predominant for this character in cross Berika × P Mut-11, hence type of epistasis could not be determined. Additive, dominance, additive × additive and dominance × dominance type epistatic gene actions were predominant for total chlorophyll content of immature fruits in all three crosses. Dominance × dominance interaction effect was larger than additive × additive effect in all three crosses.

The use of variance-component analysis to study the quantitative traits began early in the 20th century. Fisher (1918) described a partition of the total variance (Vt) of a quantitative trait in an outbred population into variance due to environment (Ve), additive genetic effects (Va), dominance (Vd), and epistasis (VI). The sum of all those components, apart from environmental variance, is generally called the 'genetic variance' (Vg).

Gene action determined from the six genetic populations of three cross combinations somewhat agreed well that additive–dominance–epistasis of polygenes dominated the inheritance of most studied traits. It appeared that yield components, fruit yield, and quality traits were under the control of both fixable and nonfixable gene effects which corroborated the findings of Zdravkovic *et al.* (2011) and Akhtar and Hazra (2013) because of the revelation of significance of 'd', 'h', 'i' and 'l' type gene interactions which indicated that to have a positive shift in the expression of the phenotypic mean it would be essential to harness both additive and nonadditive gene effects prevalent in the characters.

The results of gene action study revealed that the nature and magnitude of gene action controlling the inheritance of studied traits deferred from one cross to another and from one trait to another. Presence of duplicate epistasis for most characters will decrease variation in F_2 and subsequent generations, and will hinder the pace of progress through selection which agreed well with the findings of previous workers (Dhankar *et al.* 2003; Dixit *et al*. 2006; Zdravkovic *et al*. 2011; Somraj *et al*. 2017; Somraj *et al*. 2018; Rajan *et al*. 2018). However, positive additive × additive type gene action and duplicate epistasis recorded in some traits like days to first flowering and fruit weight in crosses Berika × P Mut-5 and Berika × P Mut-11, chlorophyll a content of leaf, chlorophyll a content of immature fruits, chlorophyll b content of immature fruits and total chlorophyll content of immature fruits in cross Berika × P Mut-5, span of flowering and fruit yield per plant in cross Berika × P Mut-11, equatorial diameter and pericarp thickness in cross Patharkuchi × B Mut-1 suggested the possibility of obtaining transgressive segregates in later generations for these characters from these crosses which supported well by Sharmila *et al*. (2007). Additive × additive type nonallelic interaction was found significant for most characters but with negative sign which indicated little scope of improvement through simple selection which agreed well with the findings of Akhtar and Hazra (2013), Somraj *et al*. (2017) and Somraj *et al*. (2018).

Presence of significant amount of all types of gene action, additive, dominance and epistasis for most of the important characters indicated that methods designed to utilize all of them such as recurrent selection (Comstock *et al.* 1949), multiple cross or diallel selective mating system of Jensen (1970) need to be adopted in breeding programme. Presence of dominance gene effect and additive × additive components suggested that the selection for yield would be delayed till dominance and epistatic components are reduced through selfing. Postponement of selection in later generations or intermating among the selected segregates followed by one or two generation(s) of selfing to break the undesirable linkage and allow the accumulation of favourable alleles for improvement of these traits. Such result corroborated the findings of Devi *et al*. (2005), Somraj *et al.* (2017, 2018) and Rajan *et al*. (2018) in tomato and Hasanuzzaman and Golam (2011) in chilli. Heterosis breeding in tomato appeared to be the most important breeding strategy because of the prevalence of high magnitude of nonadditive gene effects for most fruit and fruit quality characters studied. Similar findings were observed by previous workers (Kumar *et al.* 1997;

Roopa *et al*. 2001; Biswas *et al*. 2011; Rajan *et al*. 2018; Das *et al*. 2019).

Segregation pattern of the dark green fruit (dg1)

A study was conducted to know the segregation pattern of 'dark green fruit' in Berika × P Mut-5 cross having contrasting green fruit colour. Among 160 F_2 segregating population of cross Berika × P Mut-5, 42 : 118 ratio of plants with characteristic dark green fruits all over with exaggerated chlorophyll content: normal dull green fruit with or without green shoulder (table 3) confirmed the expected 1 : 3 ratio for single recessive gene governing the 'dark green fruit' character (χ^2 value = 0.026). The segregation pattern of this cross clearly indicated that high chlorophyll containing dark green fruits were only produced when the mutant gene governing this character was present in homozygous recessive condition (designated as *dg-1/dg-1*) and such characteristic fruit was not produced when the gene was present either in homozygous dominant or heterozygous condition. The χ^2 statistic value for $P = 0.05$ (95% confidence level) with 1 degrees of freedom was 3.84. The calculated χ^2 value (0.026) was much lesser than the table value, hence, the hypothesis for segregation of single recessive gene for the designated gene (*dg-1*) was statistically significant (table 3).

The segregation pattern of Berika × P Mut-5 cross clearly indicated that high chlorophyll containing dark green fruits were only produced when the mutant gene governing this character was present in homozygous recessive condition (designated as *dg-1/dg-1*) and such characteristic fruit was not produced when the gene was present either in homozygous dominant or heterozygous condition. Dark green fruit character has been found associated with highest lycopene (7.47 mg/100 g) and ascorbic acid (46.51 mg/100 g) contents and this character was conditioned by single recessive gene (Das 2019). Hence, the designated *dg-1* gene needs to be introgressed in two parental lines by conventional breeding approach with the view of developing hybrid with enhanced lycopene and ascorbic acid contents. It was earlier reported that the spontaneous mutant gene '*dg*' was present in chromosome 1 (Levin *et al*. 2003). In some induced mutants of tomato, the same 'dark green' fruit character was manifested (El-Sayed *et al*. 1994; Kendrick *et al*. 1997; Asmahan and Al-Twaty 2006) which amply suggested that the same character may be expressed in both spontaneous and induced mutants.

The results on generation mean analysis illustrated that individual crosses significantly differed for the genetic control of studied traits. Some of the traits examined in the present study have shown complex genetic behavior. The simple selection procedure in the early segregating generation may not worthy for the improvement of these traits. The complex genetic behaviour particularly additive and dominance components could successfully be exploited in later generation (F_4 or F_5) of segregating population in tomato. Nonadditive gene action and duplicate epistasis were the most predominant types of gene effects controlling yield and quality traits. Therefore, selection should be practiced in later segregating generations and intermating among the selected segregates followed by one or two generations of selfing could be advised to break the undesirable linkage and allow the accumulation of favourable alleles. The pattern of segregation of dark green fruit (*dg1*) in cross between cultivar and mutant genotype stated that a single recessive gene governing the 'dark green fruit' character and such fruits were formed when the mutant gene governing this character was in homozygous recessive condition.

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