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Generation mean analysis of yield components and yield in tomato (*Solanum lycopersicum* L.) under high temperature conditions

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Abstract

Generation mean analysis was studied among eighteen yield components and yield characters in the cross Arka Vikas x AVTO-9803 of tomato for five generations in Randomised Block Design replicated thrice during *summer*, 2017 at Vegetable Research Station, Agricultural Research Station, Rajendranagar, Hyderabad. The results revealed that The dominance (h) and dominance \times dominance (l) had opposite sign for the traits root to shoot ratio, fruit set per cent, days to first fruit harvest, number of fruits per cluster, number fruits per plant, fruit length, fruit width, average fruit weight and fruit yield indicating the presence of duplicate dominance epistasis. The predominance of complimentary epistasis was noticed from similar signs of (h) and (l) for the expression of plant height, root length, number of primary branches per plant, days to 50% flowering, number of flowers per cluster, stigma exertion per cent, days to last fruit harvest and number of seeds per fruit indicating the presence of additive, dominance, additive \times additive and dominance \times dominance interaction effects were present along with either duplicate dominant epistasis or complementary epistasis for fruit yield and most of its contributing traits under high temperature conditions for the cross Arka Vikas x AVTO-9803.

Keywords: Generation, tomat *Solanum lycopersicum* L

Introduction

Tomato (*Solanum lycopersicum* L.) is an important vegetable crop and particularly now a commercial crop widely grown all over tropical, sub-tropical and temperate regions of the world for both fresh and processing purpose. Popularity of this crop stems from its short life cycle, wider adaptability, high yielding potential, acceptable flavor, nutritive value and suitability for a variety of uses in culinary and processing industries (FAOSTAT, 2013) [2]; hence area under its cultivation is increasing day by day.

The optimum temperature for tomato growth and development is 20–24°C. Temperatures above 34°C are considered super-optimal thermal stress. The optimum range of night temperature for fruit set is 15-20 °C, however above 18°C is likely to inhibit pollen production and fruit set. With high day and night temperatures, the plant shows symptoms of irregular flower development, reduction in pollen production, pollen viability, fruit drop and ovule abortion, all of which ultimately leads to decreased yield. Flowering and fruit set are the most sensitive stages to heat stress and its productivity in warm summer areas is likely to be adversely effected by even slight increase in temperature. Furthermore, in tomato, high temperatures can lead to remarkable losses in its yield because of the diminished fruit set, small sized fruits with low quality (Stevens and Rudich, 1978) [11]. Hence, it is necessary to identify or develop tomato varieties that are resistant to high-temperature stress to enhance tomato production.

Generation mean analysis, a first degree statistics and a simple but useful technique for characterizing gene affects for a polygenic character (Hayman, 1958) [7] which, it determines the presence & absence of non-allelic interactions. The greatest merit of generation mean analysis is that it helps in the estimation of epistatic gene effects namely additive \times additive (i), additive \times dominance (j) and dominance \times dominance (l). The most commonly used design Line \times Tester analysis fails to detect the epistasis. The nature of gene action governing the inheritance of yield and its components of heat tolerance tomato cross combination was therefore studied using generation mean analysis. The generation mean analysis was carried out in selected cross obtained from the Line \times Tester testing programme. Any one or both the scaling tests were found to be significant in all the traits indicating the presence of epistasis. The type of epistasis was determined as complementary when dominance (h) and dominance \times dominance (l) gene effects have same sign and duplicate epistasis when the sign was different.

Keeping the above in view, five generations of tomato have been studied to estimate the genetics of yield components and yield characters in tomato under high temperature conditions.

Materials and methods

An field investigation was carried out with five generations namely, P₁, P₂, F₁, F₂ and F₃ of cross Arka Vikas x AVTO-9803. The material was raised in Randomised Block Design replicated thrice during *summer*, 2017 at Vegetable Research Station, Agricultural Research Station, Rajendranagar, and Hyderabad. A spacing of 60 cm between rows and 50 cm between plants was followed. Data from 50 plants in P₁, P₂ and F₁ generations, 600 plants in F₂ generations, 300 plants in F₃ generations were recorded for eighteen characters namely, plant height (cm), root length (cm), root to shoot ratio, number of primary branches per plant, days to fifty per cent flowering, number of flowers per cluster, number of clusters per plant, stigma exertion (%), fruit set (%), days to first fruit harvest, days to last fruit harvest, number of fruits per cluster, number of fruits per plant, fruit length (cm), fruit width (cm), average fruit weight (g), fruit yield per plant (kg) and number of seeds per fruit under high temperature conditions (Appendice).

The data were collected for three generations and five populations and were analysed according to Mather (1949)^[8], Hayman (1958)^[7] and Jinks and Jones (1958)^[9] to detect and estimate the additive (d), dominance (h) and genetic interactions *viz.*, additive × additive (i), dominance × dominance (l). The variation among the means of different generations in all the seven characters studied suggesting the usefulness of the estimation of additive, dominance and epistatic interaction.

Results and discussion

Plant height (cm)

This character recorded significant values for all the five components as revealed by the five parameter model. It recorded a mean height of 79.89 cm where dominant gene effects (25.52) were predominant over additive effects (8.27). Dominance x dominance component (35.15) had higher values over additive x additive component (20.61). Dominance and dominance x dominance gene effects have same sign indicating that the trait is governed by complementary epistasis.

Root length (cm)

Root length recorded significant values for all the five components as revealed by the five parameter model. It registered a mean root length of 31.59 cm, where dominant gene effects (7.61) were higher over additive gene effects (-1.64). Dominance x dominance component (37.21) had higher values over additive x additive component (-0.82). Dominance and dominance x dominance have same sign showing that the trait is governed by complementary epistasis.

Root to shoot ratio

Significant values for root to shoot ratio was observed for 'm', 'd', 'i' and 'l' components in the five parameter model except dominant component which was non-significant. The mean values for the trait was recorded as 0.39. Negatively significant additive gene effects (-0.06) were noticed. Dominance x dominance component (0.28) of epistasis had higher value than additive x additive (-0.20) epistasis. Dominant and dominance x dominance gene effects have opposite signs indicating the presence of duplicate epistasis.

Number of primary branches per plant

This character recorded significant values for four components i.e., mean performance, additive gene effect and dominance x dominance and additive x additive component of epistasis. A mean of 7.73 primary branches per plant with additive effects (1.20) was recorded. Dominance x dominance component (6.93) had higher values over additive x additive component (0.90). Dominant and dominance x dominance values with same sign indicating that the trait governed by complementary epistasis.

Days to 50% flowering

All the generations on an average took 33.67 days to 50% flowering with significance of remaining four components of generation mean. Dominant gene effects (-0.49) were lower than additive gene effects (4.00). Dominance x dominance component (-3.56) had lower values in comparison with the additive x additive component of epistasis (6.11). Days to 50% flowering falls under the category of complementary type of epistasis as revealed by negative signs for both dominant and dominance x dominance gene effects.

Number of flowers per cluster

Tomato genotypes with three generations under high temperature conditions when analysed for five parameter model of GMA registered significant values for this character. Mean performance was 5.33 flowers per cluster with negative significant additive gene effect (-0.30) and additive x additive (-0.68) component whereas, dominant effect (0.62) and dominance x dominance (2.49) components were positive and significant. On observation of the signs the character found to be governed by complementary type of epistasis for its phenotypic expression.

Number of clusters per plant

This character recorded significant values for four components i.e., mean performance, additive gene effect, dominant gene effect and additive x additive component of epistasis whereas, dominance x dominance was found non-significant. A mean of 35.26 number of clusters per plant with dominant effects (2.80) were higher than additive effects (-4.43) was recorded. Dominance x dominance component (2.66) had higher values over additive x additive component (-15.30). Dominance and dominance x dominance was found values with similar signs indicating that the trait is governed by complementary epistasis.

Stigma exertion (%)

All the generations on an average recorded 17.27 per cent stigma exertion with significance of remaining four components of generation mean. Dominant gene effects (-6.01) was lower than the additive gene effects (0.88). Dominance x dominance component (-13.08) had lower values in comparison with the additive x additive component of epistasis (-4.59). Stigma exertion per cent falls under the category of complementary type of epistasis as revealed by similar negative signs among dominant and dominance x dominance gene effects.

Fruit set (%)

Both the parents of the cross Arka Vikas x AVTO-9803, its first filial generation and two segregating generations (F₂ and F₃) mean values were subjected to generation mean analysis for unravelling gene actions. On an average 78.73 fruits were set with significance for three kinds of gene actions. Only

dominant gene effect (15.80) was significant whereas additive gene effect (-13.39) and 'l' x 'l' (-56.84) and 'i' x 'i' (-30.83) components of epistasis were negative and significant. The 'h' and 'l' x 'l' components were observed opposite in their signs claiming that the character falls under duplicate type of epistasis.

Days to first fruit harvest

This character recorded significant values for all the five components as revealed by the five parameter model. All the generations on an average took 65.66 days to first fruit harvest where, dominant gene effects (-17.11) were lower than additive effects (3.167). Dominance x dominance component (48.88) had higher values than additive x additive component (-24.94). Dominance and dominance x dominance gene effects have different sign indicating that the trait is governed by duplicate epistasis.

Days to last fruit harvest

Significant values for three components viz., m, d and i as revealed by the five parameter model whereas, h and l components were found negative and non-significant. All the generations on an average took 145.33 days to last fruit harvest where, dominant gene effects (-7.34) were lower than the additive effects (13.34). Dominance x dominance component (-24.00) had lower values than additive x additive component (16.00). Dominance and dominance x dominance gene effects have similar sign indicating that the trait is governed by complementary epistasis.

Number of fruits per cluster

This character recorded significant values for all five components i.e., mean performance, additive gene effect, dominant gene effect, dominance x dominance and additive x additive component of epistasis. A mean of 4.20 number of fruits per cluster with dominant effects (1.28) were higher than additive effects (-9.00) was recorded in the cross Arka Vikas x AVTO-9803. Dominance x dominance component (-1.24) was high over additive x additive component (-2.07). Dominance and dominance x dominance was found values with different signs indicating that the trait is governed by duplicate epistasis.

Number of fruits per plant

Significant values for five components i.e., m, d, h, dominance x dominance and additive x additive component of epistasis for this character has recorded. A mean of 67.08 number of fruits per plant with dominant effects (12.03) were higher than additive effects (-10.40) was recorded. Dominance x dominance component (-45.66) had lower values over additive x additive component (-27.40). Dominance and dominance x dominance was found values with opposite signs indicating that the trait is governed by duplicate epistasis.

Fruit length (cm)

Fruit length recorded significant values for all the five components as revealed by the five parameter model. It registered a mean fruit length of 4.17 cm, where dominant gene effects (-0.37) were lower than additive gene effects (0.21). Dominance x dominance component (1.55) had higher values over additive x additive component (-0.29). Dominance and dominance x dominance have opposite sign showing that the trait is governed by duplicate epistasis.

Fruit width (cm)

Fruit width recorded significant values for all the five components as revealed by the five parameter model. It registered a mean fruit width of 4.60 cm, where dominant gene effects (-0.36) were lower than additive gene effects (0.89). Dominance x dominance component (1.96) had higher values over additive x additive component (0.93). Dominance and dominance x dominance have opposite sign showing that the trait is governed by duplicate epistasis.

Average fruit weight (g)

All the generations on an average recorded 52.02 grams as average fruit weight with significance of remaining four components of generation mean. Dominant gene effects (-5.66) had lower values than additive gene effects (7.22). Dominance x dominance component (40.22) had highest values in comparison with the additive x additive component of epistasis (2.32). Average fruit weight falls under the category of duplicate type of epistasis as revealed by opposite signs recorded among dominant and dominance x dominance gene effects.

Fruit yield per plant

Tomato genotypes with three generations under high temperature conditions when analysed for five parameter model of GMA registered significant values for this character. Mean performance was 3.47 kilograms fruit yield per plant with negative significant additive gene effect (-0.24) and additive x additive (-1.66) component whereas, dominant effect (0.36) and dominance x dominance (1.11) components were positive and significant. On observation of the signs the character found to be governed by complementary type of epistasis for its phenotypic expression.

Number of seeds per fruit

Five parameters as analysed considering mean number of seeds per fruit (34) for three generations along with their two parents has positive sign. Its dominant (31.16) as well as additive (4.63) direct gene effects and 'd' x 'd' (6.22) and 'l' x 'l' (16.72) components of epistasis were positive and significant except for 'l' x 'l' which was non-significant. Seeds per fruit can be further improved as revealed by the signs of 'h' and 'l' hence, it governed by complementary epistasis.

The dominance (h) and dominance x dominance (l) had opposite sign for the traits root to shoot ratio, fruit set per cent, days to first fruit harvest, number of fruits per cluster, number fruits per plant, fruit length, fruit width, average fruit weight and fruit yield. It indicated the presence of duplicate dominance epistasis. The predominance of complimentary epistasis was noticed from similar signs of (h) and (l) for the expression of plant height, root length, number of primary branches per plant, days to 50% flowering, number of flowers per cluster, stigma exertion per cent, days to last fruit harvest and number of seeds per fruit. These results are corroborative with the findings of Jasmina *et al*, (2011) [10] in tomato. It could be noted that the presence of additive, dominance, additive x additive and dominance x dominance interaction effects were present along with either duplicate dominant epistasis or complementary epistasis for fruit yield and most of its contributing traits under high temperature conditions for the cross Arka Vikas x AVTO-9803. This could be due to contribution of heat tolerant genes present in the tester AVTO-9803. Hence, selection in the early segregating generations may not give desirable recombinants. Therefore,

selection may be delayed to later segregating generations when the dominance and epistasis disappear and resorting to inter-mating of segregants followed by recurrent selection. Simple selection procedures or pedigree breeding method is sufficient to harness additive gene action. But the presence of dominance gene action in most of the characters warrants postponement of selection to later generations after effecting crosses. Heterosis breeding procedures are effective in

harnessing and exploiting dominance gene action to the fullest extent. Both additive and dominance gene actions play major role in several characters. In such circumstances, bi-parental mating design or reciprocal recurrent selection can be followed for further recombination of alleles to produce desirable segregants. These methods can also be well adopted in order to harness the epistatic interactions by way of breaking the undesirable linkages.

Table 1: Mean \pm SE performance for five generations of generation mean analysis for yield components and yield for the cross Arka Vikas x AVTO-9803 in tomato

S. No	Character	P ₁	P ₂	F ₁	F ₂	F ₃
1	Plant height	88.26 \pm 1.84	71.71 \pm 0.91	101.44 \pm 1.76	79.89 \pm 0.54	75.71 \pm 0.38
2	Root length (cm)	30.46 \pm 0.26	33.75 \pm 0.25	44.70 \pm 0.60	31.59 \pm 0.24	32.02 \pm 0.64
3	Root to shoot ratio	0.35 \pm 0.00	0.47 \pm 0.01	0.44 \pm 0.00	0.39 \pm 0.00	0.42 \pm 0.01
4	No. of primary branches	9.60 \pm 0.04	9.27 \pm 0.17	10.07 \pm 0.07	7.73 \pm 0.04	7.87 \pm 0.07
5	Days to 50% flowering	37.33 \pm 0.25	29.33 \pm 0.13	30.33 \pm 0.25	33.67 \pm 0.07	34.67 \pm 0.13
6	No. of flowers per cluster	5.27 \pm 0.03	5.87 \pm 0.05	6.27 \pm 0.03	5.33 \pm 0.01	5.33 \pm 0.03
7	No. of clusters per plant	23.67 \pm 0.43	32.53 \pm 0.41	37.33 \pm 0.25	35.27 \pm 0.17	34.73 \pm 0.35
8	Stigma exertion (%)	11.53 \pm 0.26	9.76 \pm 0.39	11.00 \pm 0.39	17.28 \pm 0.42	17.96 \pm 0.76
9	Fruit set (%)	39.17 \pm 1.08	65.95 \pm 1.15	72.42 \pm 1.66	78.73 \pm 0.3	71.22 \pm 0.55
10	Days to first fruit harvest	58.33 \pm 0.55	52.00 \pm 0.22	69.33 \pm 0.33	65.67 \pm 0.19	73.00 \pm 0.79
11	Days to last fruit harvest	145.67 \pm 0.98	119.00 \pm 1.53	135.67 \pm 1.53	145.33 \pm 1.25	145.67 \pm 1.20
12	No. of fruits per cluster	2.07 \pm 0.07	3.87 \pm 0.07	4.53 \pm 0.09	4.20 \pm 0.02	3.80 \pm 0.04
13	No. of fruits per plant	32.65 \pm 1.12	53.45 \pm 1.20	61.68 \pm 1.82	67.08 \pm 0.98	61.22 \pm 1.23
14	Fruit length (cm)	4.24 \pm 0.09	3.80 \pm 0.07	4.38 \pm 0.02	4.18 \pm 0.00	4.37 \pm 0.01
15	Fruit width (cm)	5.32 \pm 0.09	3.53 \pm 0.04	4.91 \pm 0.05	4.60 \pm 0.03	4.81 \pm 0.06
16	Average fruit weight (g)	60.01 \pm 1.12	45.56 \pm 0.58	59.24 \pm 0.56	52.02 \pm 0.4	55.95 \pm 0.61
17	Fruit yield per plant (kg)	1.94 \pm 0.03	2.43 \pm 0.03	3.64 \pm 0.07	3.48 \pm 0.04	3.42 \pm 0.05
18	No. of seeds per fruit	32.07 \pm 0.26	22.80 \pm 0.12	51.13 \pm 0.76	34.00 \pm 0.28	26.60 \pm 0.42

P₁- Arka Vikas, P₂-AVTO-9803, F₁-first filial generation of Arka Vikas x AVTO-9803, F₂-Second filial generation of Arka Vikas x AVTO-9803 and F₃-Third filial generation of Arka Vikas x AVTO-9803

Table 3: Scaling test and gene effects for yield, yield components and heat tolerance for the cross Arka Vikas x AVTO-9803 in tomato

Character	Genetic parameters		Gene Effects					Type of Epistasis
	C	D	m	d	h	l	i	
Plant height	-43.28 \pm 4.61	-16.92 \pm 2.78	79.89 \pm 0.54	8.27 \pm 1.03	25.52 \pm 1.90	35.15 \pm 6.70	20.61 \pm 2.91	C
Root length (cm)	-27.25 \pm 1.59	0.66 \pm 2.64	31.59 \pm 0.24	-1.65 \pm 0.18	7.61 \pm 1.83	37.22 \pm 4.26	-8.27 \pm 1.46	C
Root to shoot ratio	-0.13 \pm 0.01	0.07 \pm 0.04	0.39 \pm 0.00	-0.06 \pm 0.00	-0.04 \pm 0.03	0.28 \pm 0.06	-0.20 \pm 0.02	D
No. of primary branches	-8.07 \pm 0.26	-2.87 \pm 0.33	7.73 \pm 0.04	0.17 \pm 0.09	1.20 \pm 2.00	6.93 \pm 0.50	0.90 \pm 0.19	C
Days to 50% flowering	7.33 \pm 0.64	4.67 \pm 0.59	33.67 \pm 0.07	4.00 \pm 0.14	-4.89 \pm 0.40	-3.56 \pm 1.11	6.11 \pm 0.45	C
No. of flowers per cluster	-2.33 \pm 0.09	-0.47 \pm 0.12	5.33 \pm 0.01	-0.30 \pm 0.03	0.62 \pm 0.07	2.49 \pm 0.19	-0.68 \pm 0.07	C
No. of clusters per plant	10.2 \pm 1.04	12.20 \pm 1.56	35.27 \pm 0.17	-4.43 \pm 0.30	2.80 \pm 1.01	2.67 \pm 2.42	-15.30 \pm 0.96	C
Stigma exertion (%)	25.82 \pm 1.90	16.01 \pm 3.20	17.28 \pm 0.42	0.89 \pm 0.23	-6.02 \pm 2.22	-13.08 \pm 5.37	-4.59 \pm 1.82	C
Fruit set (%)	64.95 \pm 3.87	22.31 \pm 2.78	78.73 \pm 0.30	-13.39 \pm 0.79	15.80 \pm 1.94	-56.84 \pm 5.83	-30.83 \pm 2.22	D
Days to first fruit harvest	13.67 \pm 1.17	50.33 \pm 3.22	65.67 \pm 0.19	3.17 \pm 0.30	-17.11 \pm 2.14	48.89 \pm 4.55	-24.94 \pm 1.69	D
Days to last fruit harvest	45.33 \pm 6.12	27.33 \pm 5.71	145.33 \pm 1.25	13.33 \pm 0.91	-7.33 \pm 4.19	-24.00 \pm 12.53	16.00 \pm 4.19	C
No. of fruits per cluster	1.80 \pm 0.23	0.87 \pm 0.20	4.20 \pm 0.02	-0.90 \pm 0.05	1.29 \pm 0.14	-1.24 \pm 0.39	-2.08 \pm 0.15	D
No. of fruits per plant	58.86 \pm 5.60	24.61 \pm 5.55	67.08 \pm 0.98	-10.40 \pm 0.82	12.04 \pm 4.01	-45.66 \pm 11.34	-27.43 \pm 3.87	D
Fruit length (cm)	-0.10 \pm 0.12	1.07 \pm 0.12	4.18 \pm 0.00	0.22 \pm 0.06	-0.37 \pm 0.04	1.56 \pm 0.09	-0.29 \pm 0.11	D
Fruit width (cm)	-0.27 \pm 0.19	1.20 \pm 0.25	4.60 \pm 0.03	0.89 \pm 0.05	-0.36 \pm 0.16	1.96 \pm 0.41	0.94 \pm 0.17	D
Average fruit weight (g)	-15.97 \pm 2.33	14.19 \pm 2.86	52.02 \pm 0.40	7.23 \pm 0.63	-5.66 \pm 1.85	40.22 \pm 4.80	2.33 \pm 2.03	D
Fruit yield per plant (kg)	2.26 \pm 0.21	2.34 \pm 0.21	3.48 \pm 0.04	-0.24 \pm 0.02	0.27 \pm 0.15	0.12 \pm 0.44	-1.67 \pm 0.14	C
No. of seeds per fruit	-21.13 \pm 1.92	-16.47 \pm 1.78	34.00 \pm 0.28	4.63 \pm 0.14	31.16 \pm 1.35	6.22 \pm 3.77	16.72 \pm 1.23	C

*, ** -significant at 5 and 1 per cent level of significance, respectively

C- Complementary, D-Dominance, m-mean, d-additive, h-dominance, l-dominance x dominance and i-additive x additive

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Appendix

Mean meteorological data recorded at Agricultural Research Institute, Rajendranagar, Hyderabad during the year 2017

Month and Year	Temperature (° C)		Relative Humidity (%)		Rainfall(mm)	Rainy days	Sunshine (hrs)
	Max.	Min.	8.00 hrs	14.00 hrs			
Feb, 2017	32.7	13.6	79.0	27.0	0.0	0	9.6
March, 2017	35.7	18.2	73.7	24.7	5.6	0	8.4
April, 2017	38.6	22.4	69.2	25.2	2.5	0	8.6
May, 2017	39.7	24.6	64.0	29.0	61.8	1	9.3
June, 2017	33.0	23.2	85.0	58.0	213.4	12	5.0
July, 2017	30.8	22.2	84.9	63.0	158.0	12	4.9