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Degree of biasedness in estimates of gene action in the presence of epistasis in *Capsicum annuum*

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Abstract

This experiment was conducted with an aim to know the effect of epistasis on the estimates of additive and dominance components of variation in hot pepper. Triple test cross analysis was applied to progenies produced from two hot pepper crosses (Arka Suphal × Gowribidanur and Susan Joy × PBC-483) to study the effect of epistasis on the estimates of gene action for plant height (PH), fruit length (FL), fruit width (FW), average green fruit weight (AFW), number of fruits per plant (NFP), fresh green fruit yield per plant (FY), reaction to thrips infestation (TI) and response to anthracnose infection (AI). The additive and dominance components manifested differences in the presence or absence of epistasis for traits like PH, FL, AFW, FY and AI. Additive genetic variation (D) was higher in magnitude than that of dominance genetic variation (H) for all the characters except FI where dominance component was pre-dominant.

Keywords: additive genetic variance, dominance genetic variance, epistasis

I. Introduction

An adequate knowledge of relative components of genetic variation provides useful guidelines for designing suitable strategies to develop high yielding stable hybrids. Various biometrical methods have been used in the past in different crops to estimate components of genetic variation. In most of the designs used, it is assumed that non-allelic interactions are absent. However, the fact is often contrary to the assumptions. Information regarding epistatic variation with respect to yield and its components in hot pepper is limited. Hence, triple test cross analysis (Jinks *et al*., 1969) which specifically tests the non-allelic interactions and also provides equally precise estimates of additive and dominance components of genetic variation in the absence of epistasis is used for genetic analysis of yield and its component traits in the present investigation. Triple test cross (TTC) analysis provides unambiguous test for the presence of epistasis regardless of gene frequencies, degree of inbreeding and linkage relationships.

Different kinds of gene effects generally exhibit different degree of sensitivity to environmental differences. Further, the estimates of additive and dominance components of genetic variation and their interactions with environment may not exhibit the same rate of change in the presence of epistasis. Triple test cross method not only detects different kinds of gene effects (additive, dominance and epistatic) and their interaction with environment, it also suggests whether a particular parent (for backcross plant or homozygous line) used in the crossing programme has contributed towards epistasis.

II. Material and Methods

An essential criteria for generation of triple test cross progenies is that the parents must be contrasting for a trait under study. To fulfill this requirement, two sets of triple test cross progenies involving four different parents were generated. Two of these i.e Arka Suphal (AS) and Gowribidanur (GB) (refer **Table 1**) which were contrasting for fresh green fruit yield plant^{-1}, plant height, response to anthracnose disease (lesion diameter in Arka suphal – 14 mm and Gouribidanur – 6 mm) and thrips

infestation (per cent leaf curling in Arka suphal - < 10% and Gouribidanur - >80 %) and Susan's Joy (SJ) and PBC 483 which were contrasting for fruit length, fruit width, average fruit weight and number of fruits plant^{-1} were used as parents to develop two different F_1's during 2009 *Kharif* and 2010 summer, respectively.

The two F_1 hybrids were raised and selfed to generate F_2 populations during 2010 summer and 2011 summer, respectively. The F_2 populations of size 100 of the two crosses were raised in *kharif* 2010 and *kharif*, 2011, respectively.

Arka Suphal × Gowribidanur

Twenty five randomly selected F_2 individuals of the cross AS × GB were crossed back to testers P_1 (L_1), P_2 (L_2) and F_1(L_3). Fruit setting was successful only in crosses involving 18 F_2 plants with three testers designated as L_{1i}, L_{2i} and L_{3i}. Fifty four (18 × 3) triple test cross progenies were evaluated during summer, 2011. Forty plants were raised in each of the fifty four triple test cross progenies. Forty days old seedlings of each TTC progeny was transplanted at the experimental plots of the Department of GPB, 'K'-block with row spacing of 0.6 m and 0.4 m between plants within a row. Data was recorded on all the forty plants of each TTC progenies except in cases where few seedling deaths occurred due to transplanting shock. In such cases observations were taken on all the survived plants. Observations were recorded on plant height and green fruit yield plant^{-1} for the entire triple test cross progenies. Data on responses to anthracnose infection and thrips infestation (under natural field condition) is detailed below.

Reaction to anthracnose:

Ten random fruits from each of the twenty randomly selected plants in each TTC progeny were picked at red ripe stage. The fruits were surface sterilized and inoculated with virulent strain of *Colletotrichum capsici* i.e., 'Cc 38' (Nanda, 2011). The Cc (*Colletotrichum capsici*.) 38 cultures maintained at the HPI unit, Department of GPB, CoA, UAS, GKVK, Bengaluru was used for microinjection method of screening for anthracnose reaction. Cc 38 culture of *Colletrotrichum* spp. was found to be most virulent strain among 72 *Colletotrichum* spp collected and screened for their virulence by Nanda (2011). The pathogen was isolated following standard tissue isolation method on Potato Dextrose Agar (PDA) media under aseptic conditions in a laminar airflow. The pathogen from such plates was purified using single spore isolation technique (Karuna-vishunavat and Kolte, 1998).

The pure culture obtained was sub cultured on PDA slants and allowed to grow at 27± 1^{o}C for 12 days. Such slants were kept at 5^{o} C for maintenance. Sub culturing was carried out once in a month and such cultures were used for the study. Virulence of the pathogen was maintained by inoculating the pathogen onto red ripe chilli fruits and re isolation from the host after every three months. The presence of *Colletotrichum* spp. pathogen was confirmed based on the morphological characters of mycelium and conidia shape.

The size (diameter) of the lesion was recorded nine days after by using a specialized scale and expressed in milli meters. The following scale based on lesion diameter was used to classify the accessions into different disease response categories (Modified from Hartman and Wang, 1995):

Lesion size (mm)	Reaction type
No lesion	Immune
1.0- 5.0	Highly resistant
5.1-10.0	Moderately resistance
10.1-20.0	Moderately susceptible
>20.0	Highly susceptible

Reaction to thrips infestation:

Upward leaf curling is typical symptom in response to thrips infestation. In Southern Karnataka the incidence of thrips infestation was found to be maximum during the months of April to May before the onset of monsoon. According to Morison (1957), rain caused reduction of the thrips by washing them off the plants. Borah (1987) observed that thrips population tended to increase during dry periods with lower minimum temperature and fewer rainy days having lower intensity of rainfall. Keisa *et al*. (1994) reported higher incidence of thrips during May and September which coincided maximum temperature. The correlation co-efficient between thrips population and maximum temperature was statistically significant and the regression equation fitted with maximum temperature showed that with a increase of one unit of maximum temperature would result in an increase of 3.77 thrips per leaf (Varadharajan and Veeravel, 1995). The summer season of 2011 was chosen as the ideal time for screening of the triple test cross progenies for thrips infestation. The experiment comprised of fifty four sets of TTC progenies which were raised in pots with twenty plants in each TTC progeny and grown in two replications. All agronomic practices were taken to raise the crop except application of insecticides. At the end of the season, the leaves of the plants were observed and number of leaves infected out of the total number of leaves in the plant was recorded as per cent leaf curling according to the following grading system.

Grade	Percent leaf curling	Category
Grade 1	> 0 and < 25	Resistant completely healthy
Grade 2	> 25 and < 50	Moderately resistant few top leaves showing curling (about 25 per cent of leaves)
Grade 3	>50 and < 75	Susceptible Moderate curling (about 50 per cent of leaves showing curling)
Grade 4	< 75	Highly susceptible Complete curling (more than 75 per cent showing curling)

Susan's Joy × PBC 483

Thirty randomly selected F_2 individuals of the cross SJ × PBC 483 were crossed back to P_1 (L_1), P_2 (L_2) and F_1(L_3). Fruit setting was successful only in crosses involving twenty five F_2 individuals with three testers. Seventy five (25×3) triple test cross progenies were evaluated during summer, 2012. Thirty plants were raised in each of the seventy five triple test cross progenies. Forty days old seedlings of each TTC progeny was transplanted at the experimental plots of the Department of GPB, 'K'-block with row spacing of 0.6 m and 0.4 m between plants within a row. Data on seventy five TTC progenies were recorded for fruit length, fruit width and average green fruit weight. Further, number of fruits per plant was recorded by counting the total number of fruits produced plant^{-1} across all the pickings.

Statistical Analysis

Triple test cross progenies generated by crossing ith randomly selected plant from F_2 generation to P_1, P_2 and F_1 respectively was subjected to scaling test $\overline{L_{1i}} + \overline{L_{2i}} - 2\overline{L_{3i}} = 0$ (Kearsey and Jink, 1968) where $\overline{L_{1i}}$, $\overline{L_{2i}}$ and $\overline{L_{3i}}$ are the means of progeny families produced by crossing ith randomly selected plant from F_2 to P_1, P_2 and F_1 respectively. Significance of deviation of $\overline{L_{1i}} + \overline{L_{2i}} - 2\overline{L_{3i}}$ from zero was regarded as evidence for the presence of epistasis.

ANOVA of components of epistasis:

Traits for which epistasis was detected, variance due to $\overline{L_{1i}}$, $\overline{L_{2i}}$ and $\overline{L_{3i}}$ was partitioned into components specifying 'i' type (i.e. additive × additive) and "j+l" type (i.e. additive × dominance and

dominance × dominance) of epistasis and tested for their significance. The structure of ANOVA for epistasis is as follows.

Source	df	MSS	F-ratio
Non-allelic interaction	n	MSS_E	MSS_E/Me
Overall $[i]^2$	1	MSS_i^2	MSS_i^2/Me
J+L	n-1	$MSS_{(j+l)}$	$MSS_{(j+l)}$/Me
Within progeny families	3n (m-1)	Me	Me

where,
'n' is the number of F_2 plants which were crossed to $L_1(P_1)$, $L_2(P_2)$ and $L_3(F_1)$
'm' is number of individuals in each of TTC progenies

Detection and estimation of components of additive and dominance components of genotypic variation

Traits for which epistasis was absent, significance of additive genetic variance (D) and dominance variance (H) components of genotypic variance were detected and estimated using ANOVA as under (Jinks and Perkins, 1970):

Source of variation	d.f	Expectation Mean Squares	Designation
Sums ($\overline{L_{1i}} + \overline{L_{2i}}$)	(n-1)	$\sigma^2 + 2m\,\sigma^2_s$	M_s
Differences ($\overline{L_{1i}} - \overline{L_{2i}}$)	(n-1)	$\sigma^2 + 2m\,\sigma^2_d$	M_d
Error	n(m-1)	σ^2	M_e

Significance of mean squares due to sums ($\overline{L_{1i}} + \overline{L_{2i}}$) and differences ($\overline{L_{1i}} - \overline{L_{2i}}$) indicate the presence of 'D' and 'H' components of genotypic variance.

D and H components were estimated using the following relationships:

Mean squares due to sums ($\overline{L_{1i}} + \overline{L_{2i}}$) ($\sigma_s^2$) = $\frac{1}{8}D$

Mean squares due to difference ($\overline{L_{1i}} - \overline{L_{2i}}$) values ($\sigma_d^2$) = $\frac{1}{8}H$

$$\sigma_s^2 = \frac{M_s - M_e}{2rm}$$

$$\sigma_d^2 = \frac{M_d - M_e}{2rm}$$

Where m = number of plants on which data are recorded

Hence, D = $8\sigma_s^2$

H = $8\sigma_d^2$

Bias caused by the epistasis in the estimates of additive and dominance components of genotypic variance:

The additive and dominance components of genotypic variance were estimated in the presence of epistatic variance. In all cases indicating epistasis, the scaling test $\overline{L_{1i}} + \overline{L_{2i}} - 2\overline{L_{3i}}$ was applied individually to the three kinds of families (L_{1i}, L_{2i} and L_{3i}) of each F_2 plant. The F_2 individuals exhibiting epistasis were excluded and data on the remaining plants were again subjected to the analysis.

After removing the data on the TTC progenies generated from the F_2 individuals contributing to epistasis, the additive and dominance components of genotypic variance were re-estimated. The difference in the estimates of genotypic variance in the presence and absence of epistasis was considered as the bias due to epistasis.

One further useful statistic that was used but not discussed by Kearsey and Jinks is the covariance of sum (L_{1i} +L_{2i}) on difference (L_{1i} —L_{2i}) for all values of i (Jinks and Perkins, 1970). In the absence of epistasis and correlated gene distributions, this covariance has the expectation.

Covariance of $(\overline{L_{1i}} + \overline{L_{2i}})/(\overline{L_{1i}} - \overline{L_{2i}})$ was estimated to understand the direction of dominance controlling the inheritance of traits as 'd' and 'h' are additive and dominance gene effects at loci controlling the inheritance of traits.

$$Cov\ of\ sum/difference = -\sum_{j} uvd_j h_j = -\frac{1}{4}F$$

Where,

$$F = \sum_{i=1}^{n} d_j\, h_j$$

F was calculated as $F = -8\ Cov\ (sum\ /dif)$

$$Cov\ (sum/dif) = \frac{1}{n-1}\left\{\sum (L_{1i} + L_{2i})(L_{1i} - L_{2i}) - \left(\frac{\Sigma(L_{1i} + L_{2i})\Sigma(L_{1i} - L_{2i})}{n}\right)\right\}$$

To test the significance of covariance (sums/differences), it was converted into correlation coefficients with (n-3) degrees of freedom

$$r\ (sum/diff) = \frac{cov\ (sum/dif)}{\sigma_{sums} \times \sigma_{diff}}$$

III. Results and discussions

Analysis of variance for dissecting components of epistasis

The analysis of variance for detection of epistasis revealed significant overall epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) for all traits except fruit width, number of fruits per plant and reaction to thrips infestation. Mean squares due to both additive and non-additive interaction i.e (i^2) type and ($j+l$) type epistasis was significant for all the traits. However, in all cases, additive × additive (i^2) type was relatively greater in magnitude as compared to corresponding ($j+l$) type of epistasis except for average green fruit weight for which ($j+l$) type of epistasis was higher. Pre-ponderance of additive component of genetic variance suggests effectiveness of selection. It should be possible to identify pure breeding line with desirable traits.

Scaling Test: Analysis of variance for detecting epistasis

The mean sum of square values for epistasis is given in Table . The analysis of variance for detection of epistasis revealed significant overall epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) for all traits except fruit width (PBC-483 × Susan's Joy), number of fruits per plant (PBC-483 × Susan's Joy) and reaction to attack of thrips (Arka suphal × Gouribidanur). After excluding the data of plants showing epistasis for a particular trait all the cases indicated adequacy of additive-dominance model.

Analysis of variance for detecting epistasis

The analysis of variance for detection of epistasis revealed significant overall epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) for all traits except fruit width, number of fruits per plants and reaction to attack of

thrips. Partitioning of the total epistatic effect revealed the presence of highly significant additive × additive (i) type of epistasis for all the traits where epistasis was present. Also, estimates of additive × dominance and dominance × dominance (J+L) epistatic types were highly significant for the traits showing significant epistasis. Additive × additive (i) type of epistasis was found to be much larger in magnitude than additive × dominance and dominance × dominance (J+L) epistatic types for plant height, fresh green fruit yield per plant, fruit length and response to anthracnose infection while additive × dominance and dominance × dominance (J+L) epistatic types was much larger in magnitude than additive × additive (i) epistatic type for average green fruit weight.

Estimates of additive and dominance components of genotypic variance, correlation and F-values

The estimation of genetic components of variance was based on analysis of sums and differences. Additive component and dominance component was significant for all traits except reaction to attack of thrips. In all cases, additive component was greater in magnitude compared to corresponding dominance component except for fruit length where dominance component was greater. The correlation coefficient of sums and differences and correspondingly F-value was significant for fruit width, average green fruit weight and number of fruits per plant while non-significant for plant height, fruit length, fresh green fruit yield per plant, reaction to attack of thrips and reaction to anthracnose. F-value was positive for plant height, number of fruits per plant, fresh green fruit yield per plant, reaction to attack of thrips and reaction to anthracnose.

Estimates of biasness caused in estimates of additive and dominance components of genetic variance:

Plant height (cm) (Arka Suphal × Gouribidanur)

In the presence of epistasis, additive genetic variance was observed to have a value of 8.654 while in its absence it was 8.083 giving a biasness of 0.571 units while for dominance genetic variance biasness was 0.122 units (in presence of epistasis – 2.380 units and in absence of epistasis – 2.258). Correlation coefficient of sums and differences and hence F value remained non-significant both in presence and absence of epistasis showing a biasness of 0.191 units and -19.86 units respectively. F value was positive for plant height, number fruits per plant, fresh green fruit yield per plant and reaction to attack of thrips but negative for remaining traits.

Fruit length (cm) (PBC-483 × Susan's Joy)

A biasness of -3.3768 units was observed for additive genetic variance, 2.836 units for dominance genetic variance, 0.025 units in correlation coefficient and -0.067 units for F-value due to the presence of epistasis.

Average fresh green fruit weight (g) (PBC-483 × Susan's Joy)

A large amount of biasness was caused in the estimate of additive genetic variance (63.26 units) in comparison to dominance genetic variance (5.16 units) for average fresh green fruit weight due to presence of epistasis. Correlation coefficient exhibited negligible amount of change due to presence of epistasis (-0.006) but the F-value reported a biasness of 14.64 units.

Fresh green fruit yield per plant (g) (Arka Suphal × Gouribidanur)

Biasness in dominance component of genetic variance (214.075) was much higher in comparison to additive component of genetic variance (94.299). Large amount of biasness was also recorded for correlation of sums and differences (0.3595) and F-value (16609.16).

Reaction to anthracnose disease (Arka Suphal × Gouribidanur)

Bias in the estimates of genetic components of variance was there to considerable extent but was more for dominance component compared to additive component. Bias in the values of correlation and F-value was relatively less.

Discussion

Estimates of additive (σ^2_A) and dominance (σ^2_D) components of genotypic variance

Considering that estimates of σ^2_A and σ^2_D in the presence of epistasis are biased, the bias was estimated as the difference in the estimate of σ^2_A and σ^2_D in the presence and absence of epistasis. The results indicated larger bias in the estimates of σ^2_A for fruit length, average green fruit weight and of both σ^2_A and σ^2_D for fresh green fruit yield per plant. However, for other traits, such as plant height, fruit length, fruit width and number of fruits per plant, bias in the estimates of σ^2_A and σ^2_D was negligible. These results suggest that epistasis driven bias in the estimates of σ^2_A and σ^2 vary with the trait. Despite the presence of bias, the additive and dominance components of genetic variance provide their relative importance.

From the results it was evident that both additive and dominance genotypic variation played an important role in the inheritance of all the quantitative traits except for reaction to thrips infestation as revealed from the highly significant mean squares due to sums ($\overline{L_{1i}} + \overline{L_{2i}}$) and differences ($\overline{L_{1i}} - \overline{L_{2i}}$).

The estimates revealed that the additive genetic variation (D) was higher in magnitude than that of dominance genetic variation (H) for all the characters except fruit length where dominance component was pre-dominant. It implied major contribution of additive gene action for the expression of plant height, fruit width, average green fruit weight, number of fruits per plant and fresh green fruit weight per plant. Pre-ponderance of additive genetic variance suggests effectiveness of selection in developing inbreds from an inbreeding programme for use in hybrid cultivar development or directly as a pureline cultivar. Considering that TTC is by far the most efficient design, the design estimate of σ^2A and σ^2D obtained from TTC are more reliable. In this context, it is important to note predominance of additive genetic variance augur well with expectation of the same in self pollinating crops such as hot pepper.

One further useful statistic could be estimated that was not discussed by Kearsey and Jinks (1968) but explained by Beddow *et al.* (1962) is the F value. F is the covariance of sums ($L_{1i} + L_{2i}$) and differences ($L_{1i} - L_{2i}$). F has the same coefficient as additive genetic variance and dominance genetic variance but it measures the sum of the products of the additive effects (d) and dominance effect (h) genetic effects at the loci controlling the inheritance of target traits. Both the magnitude and the sign of the covariance provide information about the magnitude and direction of dominance. To determine whether or not the covariance is significant it was converted into a correlation coefficient with (n-3) degrees of freedom.

The significant mean square due to σ^2_H and F-value suggested that there is dominance contribution and the dominance is predominantly in one direction for number of fruits per plant, fruit length and average green fruit weight. Further positive F value suggested the dominance of increasing alleles more often than decreasing alleles. Significant σ^2H but non-significant F-value suggest that there is a dominance contribution to the variation which is ambidirectional and decreasing alleles are more

often dominant than increasing alleles for plant height, fresh green fruit yield plant^{-1} and reaction to anthracnose.

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Table 1: Analysis of variance for detecting di-genic epistasis for fruit yield and its contributing traits in hot pepper

Contrast	PBC-483 × Susan's Joy				Arka Suphal × Gouribidanur			
	Fruit length (cm)	Fruit width (cm)	Average green fruit weight (g)	Number of fruits per plant (g)	Plant height (cm)	Fresh green fruit yield per plant (g)	Reaction to thrips infestation (%)	Response to anthracnose infection (lesion diameter in mm)
$\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$ Including all F_2 plants:	0.3386*	0.0079	2.701**	7.801	14.065**	2212.19**	91.544	21.67**
$\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$ Excluding plants contributing to epistasis	0.2775	--	0.180	--	6.66	1280.87	--	12.56

* Significance @ P = 0.01, ** Significance @ P = 0.05

Table 2a:ANOVA for components of digenic epistasis for plant height, fresh green yield per plant, reaction to thrips and response to anthracnose (Arka Suphal × Gouribidanur cross)

Source of variation	Plant height (cm)		Fresh green fruit yield per plant (g)		Reaction to thrips (% leaf infestation)		Response to anthracnose (lesion diameter in mm)	
	df	Mean Sum of Squares	df	Mean Sum of Squares	df	Mean Sum of Squares	df	Mean Sum of Squares
Epistasis	18	14.065212**	18	2212.19**	18	91.544	18	21.67**
Overall $(i)^2$	1	23.470599**	1	4390.907**	1	57.568	1	15.56**
(J+L)	17	13.511954**	17	2084.031**	17	93.543	17	9.78**
Within progenies	1014	4.745	1331	972.665	1080	120.001	1002	1.278

* Significance @ P = 0.01, ** Significance @ P = 0.05

Table 2b: ANOVA for components of digenic epistasis for fruit length, fruit width, average green fruit weight and number of fruits per plant (PBC-483 × Susan's Joy)

Source of variation	Fruit length (cm)		Fruit width (cm)		Average green fruit weight (g)		Number of fruits per plant	
	df	Mean sum of squares	df	Mean sum of squares	df	Mean sum of squares	df	Mean sum of squares
Epistasis	25	0.3386**	25	0.0079	25	2.701**	25	7.80
Overall (i)^2	1	1.522**	1	0.0188	1	1.64**	1	9.34
(J+L)	24	0.2894*	24	0.0075	24	2.75**	24	7.74
Within progenies	1565	0.1561	1565	0.0053	1741	0.1675	1741	8.36

* Significance @ P = 0.01, ** Significance @ P = 0.05

Table 3: Estimates of additive and dominance components of genotypic variance for eight metric traits in TTC progenies of hot pepper

	Components of genotypic variance	In the presence of epistasis	In the absence of epistasis	Bias caused due to epistasis
Plant height (cm)	Additive (σ^2_A)	8.654**	8.083**	0.571
	Dominance (σ^2_D)	2.380**	2.258**	0.122
	Correlation (sum/diff)	-0.0021	-0.1933	0.1912
	F (covariance of additive and dominance gene effects)	79.02	98.86	-19.86
Fruit length (cm)	Additive (σ^2_A)	0.6072**	3.984**	-3.3768
	Dominance (σ^2_D)	25.896**	23.060**	2.836
	Correlation (sum/diff)	-0.236	-0.261	0.025
	F (covariance of additive and dominance gene effects)	-5.107	-5.040	-0.067
Fruit width (cm)	Additive (σ^2_A)	--	0.0033**	--
	Dominance (σ^2_D)	--	0.00095**	--
	Correlation (sum/diff)	--	-0.702**	--
	F (covariance of additive and dominance gene effects)	--	-0.118**	--
Average green fruit weight (g)	Additive (σ^2_A)	85.37**	22.106**	63.264
	Dominance (σ^2_D)	14.43**	9.271**	5.159
	Correlation (sum/diff)	-0.764**	-0.758**	-0.006
	F (covariance of additive and dominance gene effects)	-10.07**	-24.71**	14.64
Number of fruits plant^{-1}	Additive (σ^2_A)	--	642.487**	--
	Dominance (σ^2_D)	--	120.323**	--
	Correlation (sum/diff)	--	0.817**	--
	F (covariance of additive and dominance gene effects)	--	570.56**	--
Fresh green fruit yield plant^{-1} (g)	Additive (σ^2_A)	351.593**	257.294**	94.299
	Dominance (σ^2_D)	375.368**	161.293**	214.075
	Correlation (sum/diff)	0.353	-0.0065	0.3595
	F (covariance of additive and dominance gene effects)	16837.60	228.44	16609.16
Reaction to thrips infestation (per cent leaf infestation)	Additive (σ^2_A)	--	29.665	--
	Dominance (σ^2_D)	--	30.634	--
	Correlation (sum/diff)	--	0.233	--
	F (covariance of additive and dominance gene effects)	--	1.787	--
Response to anthracnose (lesion diameter in mm)	Additive (σ^2_A)	234.79**	179.67**	55.12
	Dominance (σ^2_D)	167.67**	93.46**	74.21
	Correlation (sum/diff)	0.267	0.212	0.055
	F (covariance of additive and dominance gene effects)	12.36	16.78	-4.42

Significance @ P = 0.05, ** Significance @ P = 0.01

