Seth et al., Vegetos 2016, 29:3
DOI: 10.4172/2229-4473.1000137

Vegetos- An International Journal of Plant Research

Research Article

A SCITECHNOL JOURNAL

Evidence of Economic Heterosis and Genetic Control of Fruit Yield and Yellow Vein Mosaic Virus Disease Severity Traits of Okra

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Abstract

Ten diverse genotypes of cultivated and wild species were crossed in half diallel fashion to produce 45 F_1 hybrids to determine mode of gene action, extent of economic heterosis and dominance effect, and to estimate combining ability for eight quantitative traits. Predictability ratio revealed overwhelming response of non-additive gene action for controlling fruit length, number of fruits per plant, and fruit yield per plant; additive gene effects for days to 50% flowering, while both additive and non-additive genetic control for node number at first flowering, fruit weight, fruit girth, and PDI of YVMV disease. Appropriate breeding strategies for improvement of studied traits are highlighted here. Significant standard heterosis over two commercial hybrids, Shakti and Abantika was comparatively lower in magnitude for fruit yield per plant (4.62 % and 17.59 %, respectively) and higher in magnitude for PDI of YVMV disease (-71.28 % and -72.28 %, respectively). Partial- to over-dominance effects were involved in the inheritance of the studied traits. BCO-1 and 11/RES-6 were identified as potential donors for future use. The study could able to identify an outstanding hybrid (BCO-1 × Arka Anamika) having high tolerance both under field and artificial conditions. This hybrid would definitely make a room in okra growing zones of the tropics after critical testing.

Keywords

Combining ability; Dominance effect; Gene action; Heterosis; Okra; YVMV disease

Introduction

Being the leading producer of okra, India got major setback in recent times to attain the optimum productivity of this crop as compared to other leading countries like Ghana, Egypt etc. in spite of its well acceptability among growers and consumers and the maximum range of available genetic resources [1]. One of the major bottlenecks to get optimum productivity is high incidence of yellow vein mosaic virus (YVMV) disease that infects crop at all growth stages [2], and plants of 20, 50 and 65 days old reported to be suffered a yield loss of 94 %, 84 % and 49 %, respectively [3,4]. The hybrids so far developed show variable YVMV tolerance level in the hot spots of the tropics and sometimes having unacceptable fruit quality. Usually, the resistance mechanism of these hybrids has been broken within 2-3 years of cultivation which might be due to pathogenic variability, use of parents which are supposed to be symptomless carrier and emergence of B biotype of whiteflies having wide host range. Number of wild species (*Abelmoschus manihot ssp. manihot, A. tetraphyllus, Abelmoschus caillei, A. tuberculatus, A. pungens, A. crinitus, A. panduraeformis, and A. vitifolius*) has been reported to be of resistant to YVMV disease [5,6,7,8]. Attempts made in the past to study the inheritance pattern of resistance to YVMV disease is rather variable, complex and confusing [9,10,11]. Therefore, development of okra hybrids having high, consistent and durable tolerance against this menace is badly needed in the okra growing zone of the country.

Hybrid breeding offers an immense scope to increase in yield, reproductive ability, adaptability, disease resistance, and fruit quality of okra [12,13]. There seems to be an optimal level of genetic diversity beyond which heterosis does not increase or may even decrease due to unfavourable interaction of co-adopted gene complexes or physiological incompatibility [14]. The mean (*per se*) performance of genotype is not always a reliable indicator for their superior combining ability. Genetic analysis provides a guide line for the assessment of relative breeding potential of the parents or identifies best combiners in crops [15], which could be utilized either to exploit heterosis in F_1 or to accumulate fixable genes to evolve variety. The information about the relative contribution of components of variation *viz*., additive and non-additive, is essential for effective crop improvement programme [16]. The analysis of diallel cross by the method proposed by Griffing [17] which partition the total genetic variation into general combining ability (GCA) of the parents and specific combining ability (SCA) of the crosses have been widely used. Such studies also simultaneously demonstrate the nature and magnitude of gene action involved in the expression of desirable traits and to predict the performance of the progenies.

Thus, the main aim of the present study was to determine the magnitude of economic heterosis and to estimate the dominance effect for fruit yield and its components, and YVMV disease severity, and to assess the nature of gene action for these traits in order to identify good combiners, as well as to formulate the breeding strategy for the genetic improvement of such traits.

Materials and Methods

Breeding material and procedure

Eight optimally diverse genotypes viz. BCO-1, VNR Green, VRO-6, 11/RES-6, 10/RES-6, 10/RES-4, Pusa Sawani, Arka Anamika belonging to *Abelmoschus esculentus* and two wild genotypes of *Abelmoschus manihot* (IC-140950) and *Abelmoschus caillei* (IC-433483) were selected on the basis of fruit characters, yield potentiality and YVMV disease severity as per our previous study [18]. Two standard private bred commercial okra hybrids (Shakti and Abantika) showing high tolerance against YVMV disease for the last couple of years under the Gangetic plains of eastern India were also taken to study the standard heterosis.

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Received: July 27, 2016 **Accepted:** August 23, 2016 **Published:** August 29, 2016

Homozygous seeds of ten parents were sown in well-prepared plot having sandy loam soil (pH 6.5) during the third week of February, 2013 to raise 45 cross combinations in 10 × 10 half diallel mating design as per our previous study [12]. Seeds of 10 parents, 45 hybrids and 2 standard checks (Shakti and Abantika) were sown at a spacing of 60 cm (row to row) x 30 cm (plant to plant) in 3.6 m × 2.7 m plot during third week of July, 2014 following randomized complete block design with 3 replications in the research plots of All India Coordinated Research Project on Vegetable Crops, Bidhan Chandra Krishi Viswavidyalaya, West Bengal, India, situated at 23.5°N latitude and 89°E longitude at a mean sea level of 9.75 m. The period from July to September has been selected for screening of parents/hybrids against YVMV disease because of high population of viruliferous whiteflies which spread the maximum virus disease. Standard cultural practices were followed as per Chattopadhyay et al. [19,20]. No plant protection measures against sucking insect pests of okra were done in and around the experimental area to build up a reasonable amount of whitefly population. At the same time, one row of infected plants of local susceptible variety was sown after every plot of parents and hybrids to ensure sufficient virus inoculums.

Data recording

Data on days to 50% flowering, node number at first flowering, fruit length (cm), fruit diameter (cm), fruit weight (g), number of fruits per plant, and fruit yield per plant (g) were recorded from 20 randomly selected plants of each plot in each replication. Fifteen randomly selected fruits of marketable maturity (7 days after anthesis) were sampled from the selected plants per replication to record the observations on the following fruit characters. All harvested fruits of each plant were counted and weighed to determine average number of fruits per plant and total weight of fruits per plant which was recorded as fresh fruit yield per plant (g).

Monitoring of white fly population

The incidence of YVMV disease depends on the population build up of the vector (*Bemisia tabaci)* and the presence of virus source. Whitefly populations were monitored from July to September and were recorded on five leaves, two each from lower, middle and one from upper canopy of the plants between 5.30 a.m. and 6 a.m. from 5 randomly selected tagged plants of each plot at 10-days interval starting from 20 days after sowing.

Estimation of yellow vein mosaic virus disease severity

Ten parents, forty hybrids and two standard checks were grown without any protective cover of insecticides to take data on percent disease index (PDI). PDI was recorded replication wise at five stages at an interval of 15 days starting from 30 days after sowing (DAS) to 90 DAS. Vein clearing symptom of any form in the plant was treated as disease incidence. The PDI was expressed as percentage taken from all the 54 plants in a replication by using self-made disease severity scale (0-4) for single plant through visual evaluation. The rating of disease severity scale is mentioned below.

Scale	Description of symptom
0	No disease
1	Up to 20% leaf area affected of a plant
2	21 - 40% leaf area affected of a plant
3	41 - 60% leaf area affected of a plant
4	> 60% leaf area affected of a plant

Numbers of plants infected in each parent and hybrid was recorded and PDI (%) was calculated at 90 DAS

Physiological basis of YVMV resistance

Tolerance to YVMV was confirmed by feeding of viruliferous whitefly as suggested by Nariani and Seth [18] in related species of okra. Artificial inoculation by viruliferous whitefly for screening of virus free germplasm and confirmation of presence and/or absence of the virus was done under poly house condition. A wooden frame measuring 45 x 45 x 30 cm was fixed with glass and muslin cloth and the frame was fit on a wooden rectangular base of 45.5 x 45.5 x 10 cm. Twenty whiteflies were released on the twenty okra plants of two most field tolerant hybrids and one most susceptible hybrid grown inside the insect proof rearing cages and subsequently maintained by introducing the young plants into rearing cage. Whiteflies were collected from YVMV infected plants by sucking with the help of the aspirator by slowly turning the leaves slightly upwards. Whiteflies were starved for 1-2 hours and then they were subjected to artificial inoculation feeding for 4-5 hours using YVMV infected leaves. After the acquisition period, the flies were released on the seedlings inside the cages and the feeding of vector on the plants was ensured since they were protecting inside the cages.

Statistical analysis and estimation of genetic parameters

Data of all the eight characters were analyzed statistically using the standard methods of the randomized complete blocks design [21]. The magnitude of heterosis was estimated in relation to standard hybrids and was calculated as percentage increase or decrease of F_1s over standard hybrids (SH) values as per the formula suggested by Wynne et al. [22]. The dominance estimate (D.E.) usually referred to as "potence ratio" was computed using the following formula as suggested by Smith [23].

$$D.E.=F_1 - MP/0.5 \times P_2 - P_1$$

Where, F_1=mean of the hybrid; MP=mid-parent; P_2=mean of the highest parent; P_1=mean of the lowest parent. Over dominance is considered when D.E. exceeds ± 1; Complete dominance is realized when D.E.=+1; while partial dominance is indicated when D.E. is between −1 and +1; D.E.=0 suggests absence of dominance. The '+' and '–' signs indicate the direction of dominance of either parent.

Combining ability variances and effects were worked out according to Griffing's [17] Model 1 and Method 2 as parents and one set of non-reciprocal F'$_1$s were included. Statistical analyses were done using software SPSS Professional Statistics version 7.5 (SPSS Inc., Chicago, IL).

Results and Discussion

Genetic effects for different characters

The analysis of variance for combining ability based on Griffing's Model 1 and Method 2 illustrated that components of gca and sca mean squares were highly significant for fruit yield per plant along with all other quantitative traits in F_1 generation (Table 1), indicated equal importance of both additive and non-additive gene actions in the inheritance of studied traits. The relative importance of genetic effects for quantitative traits is generally ascertained by the predictability ratio [24]. Preponderance of additive gene effects for days to 50% flowering was reflected as their predictability ratios were approaching unity (more than 0.80). In contrast, node number at first flowering, fruit diameter, fruit weight and PDI of YVMV disease

were controlled by both additive and non-additive gene action as their predictability ratios were between >0.50 and <0.80. On the other hand, the ratios <0.50 for fruit length, number of fruits per plant, and fruit yield per plant were indicative of non-additive genetic control of these traits (Table 2). In the present study, the GCA effects could not be considered to predict the performance of the parents, because most of the values of predictability ratio were much lower than the unity. Low predictability ratio highlighted the importance of SCA variance, and hence late selection would be practised based on better heterotic combinations rather than the performance of the parents involved in crossing programmes. Overwhelming response of non-additive gene action for the control of fruit length, number of fruits per plant and fruit yield per plant has been observed, hence selection will bring no or slow genetic improvement. In such case, heterosis breeding could be used to harness it by producing and marketing hybrids affordable to the resource-poor farmers of tropics for increasing okra productivity. The effects of non-additive gene actions for such traits are in a harmony with the findings of Das et al. [12]. On the other hand, selection for traits, such as node at first flowering, fruit weight, fruit diameter, and PDI of YVMV disease, that were governed by both additive and non-additive type of gene actions, might be deferred to later generations to allow a decrease in dominance, additive × dominance, and dominance × dominance effects [25]. The use of reciprocal recurrent selection could improve these traits [26]. Preponderance of both additive and non-additive gene action for the control of node number at first flowering was earlier reported by Jindal et al. [11]. The greater importance of additive gene effects (α^2a) in case of days to 50% flowering suggested the use of breeding systems that emphasize mainly α^2a. The amount of α^2aa contribution to the non-additive variance estimated for such traits is not known. However, if additive × additive epistatic variance was of importance, breeding system would change very little because additive × additive epistatic variance can be exploited by pedigree method. This type of epistatic variance increases during the selfing process so that selection of traits governing earliness of the crop in early generations should be handled accordingly as suggested by Singh et al. [25]. Previous studies also suggested additive genetic control for days to 50% flowering [27].

Standard heterosis and dominance effect of F_1 hybrids

The number of F_1 hybrids displaying either significantly positive or negative heterosis over two standard commercial hybrids (Shakti and Abantika) is presented in Table 3. The cross BCO-1 × Arka Anamika expressed the maximum standard heterosis for fruit yield per plant and PDI of YVMV disease over Shakti (4.62%, -71.28%, respectively) and Abantika (17.59%, -72.28%, respectively). However, the hybrid VRO-6 × 11/RES-6 also exhibited desired significant standard heterosis for fruit yield per plant and PDI of YVMV disease over Abantika (12.00%, -55.82%, respectively) and also showed heterosis for PDI of YVMV disease over Shakti (-54.24 %). In general, high yielding crosses exhibited low severity of YVMV disease and less population density of whiteflies as revealed from the Figures 1-2. The correlation study also depicted that fruit yield expressed strong inverse relations with PDI of YVMV disease and average whitefly population per leaf (Table 4). The highest mean (*per se*) performance for fruit yield per plant along with low severity of YVMV disease was recorded in BCO-1 followed by 11/RES-6 (Table 2). Thus, two promising crosses involved at least one parent having high yield potential with low disease severity. The hybrids with negative estimates of heterosis for days to 50% flowering, node number at first flowering and PDI of YVMV disease are desirable and could always be exploited. Our results are in well comparable with Jagan et al. [28] for node number at first flowering. Significant negative standard heterosis for PDI of YVMV disease has also been reported [29]. Fruit yield of crosses were highly influenced by YVMV disease severity and whitefly population density. The inverse relationships between yield and disease causing factors have also been reported from the Gangetic plains of eastern India [30]. On the other hand, positively significant standard heterosis for fruit length, fruit diameter, fruit weight, number of fruits per plant and fruit yield per plant found in our study, have also been reported [12,13,29,31,32] and could be useful for selection of high yielding hybrids. No problem of cross compatibility has been observed between cultivated (*A. esculenta*) and two wild species (*A. manihot* and *A. caillei*) as well as between two wild species. However, the expression of two wild species in a series of hybrid combinations with parents of cultivated species (*A.esculenta*) did not show any promise with regard to fruit yield and YVMV disease tolerance. These wild species might have acted as symptomless carrier of YVMV disease as reported earlier by Nariani and Seth [18]. Therefore, utilization of wild parent belonging to these species may be discouraged in hybrid development programme of okra.

The values of dominance estimates illustrated in 45 F_1 hybrids are presented in Table 5. Preponderance of partial dominance was reflected in most of hybrids in days to 50% flowering and fruit diameter. Overwhelming response of over dominance in majority of the hybrids was evident in conditioning of characters like node at first flowering, fruit length, number of fruits per plant, fruit yield per plant and PDI of YVMV disease. Thus the present study reflected various degrees of dominance; i.e., complete, partial to over-dominance or absence of dominance which involved in the inheritance of characters studied. To the best of our knowledge no previous works have been documented so far in okra to support our findings.

Table 1: Analysis of variance (mean square) for combining ability of eight characters in okra.

Source of variation (d.f.)	D50F	NFF	FL	FD	FW	NFPP	FYPP	PDI
GCA (9)	433.64**	24.67**	5.80**	0.53**	45.40**	65.08**	7659.30**	1501.19**
SCA (45)	4.30**	1.75**	0.64**	0.02**	3.16**	15.88**	1133.74**	109.41**
Error (108)	1.98	0.02	0.0014	0.0007	0.11	0.09	6.24	6.61
α^2a	35.97	2.05	0.48	0.04	3.77	5.42	637.76	124.55
α^2na	2.32	1.73	0.64	0.02	3.05	15.80	1127.50	102.80
Predictability ratio $\alpha^2a/(\alpha^2a + \alpha^2na)$	0.94	0.54	0.43	0.73	0.55	0.26	0.36	0.55

D50F= Days to 50% flowering, NFF= Node at 1st flowering; FL= Fruit length (cm), FD=Fruit diameter (cm),

FW= Fruit weight (g), NFPP= Number of fruits per plant, FYPP= Fruit yield per plant (g),

PDI= Percent Disease Index (%) of YVMV disease.

** Significant at 1% level

Table 2: Mean (*per se*) performance of 10 parents for eight characters of okra.

Parents	D50F	NFF	FL	FD	FW	NFPP	FYPP	PDI
BCO-1	47.33	6.50	8.35	1.45	9.01	25.07	177.53	9.56
VNR Green	49.00	5.03	6.93	1.46	9.90	12.17	113.88	17.25
VRO-6	46.67	4.07	7.86	1.52	9.02	13.33	111.09	60.23
11/RES-6	49.00	5.07	5.87	1.28	5.58	16.80	170.00	14.40
10/RES-6	46.00	4.50	7.72	1.60	9.59	16.40	111.80	45.86
10/RES-4	47.00	6.50	7.90	1.46	8.21	18.33	108.79	55.40
Pusa Sawani	48.00	6.03	9.00	2.20	8.75	5.63	48.46	74.29
Arka Anamika	49.67	6.00	8.20	1.42	7.40	6.47	55.18	64.02
A. manihot	75.00	9.00	6.16	1.46	5.61	27.57	32.64	27.72
A. caillei	79.67	11.03	12.00	2.73	21.02	7.67	95.43	25.46

D50F= Days to 50% flowering, NFF= Node number at 1st flowering; FL= Fruit length (cm),
FD= Fruit diameter (cm), FW= Fruit weight (g), NFPP= Number of fruits per plant,
FYPP= Fruit yield per plant (g), PDI= Percent Disease Index (%) of YVMV disease.

Table 3: Selected crosses with high standard heterosis (%), their corresponding gca and sca effects, and type of cross combinations.

Characters	Cross (es) with high standard heterosis (%) over Shakti	Cross (es) with high standard heterosis (%) over Abantika	Parents with gca effects	Sca effects of crosses with *per se* performance	Type of combinations
Days to 50% flowering	BCO-1 × VNR Green (-10.39%**)	BCO-1 × VNR Green (-9.80*)	BCO-1 (-2.64**), VNR Green (-2.69**), Arka Anamika (-2.19**)	-1.88 (46.00)	H x H
	BCO-1 × Arka Anamika (-9.87%*)	BCO-1 × Arka Anamika (-9.28*)		-2.32* (46.27)	H x H
Node number at first flowering	VRO-6 × Pusa Sawani (-53.33%**)	VRO-6 × Pusa Sawani (-36.36%**)	VRO-6 (-0.97**), Pusa Sawani (-1.07**), 10/ RES-4 (-0.77**)	-1.33** (3.50)	H x H
	VRO-6 × 10/RES-4 (-40.00 %**)	VRO-6 × 10/RES-4 (-18.18 %**)		-0.62** (4.50)	H x H
Fruit length (cm)	None	*A. caillei* × Arka Anamika (25.24% **)	*A. caillei* (1.07**). Arka Anamika (0.37**), BCO-1 (0.39**)	0.52 (10.07)	H x H
		BCO-1 × *A. caillei* (20.93%**)		0.15 (9.73)	H x H
Fruit diameter (cm)	10/RES-4 × *A. caillei* (44.70 %**)	10/RES-4 × *A. caillei* (72.70 %**)	10/RES-4 (-0.08**), *A. caillei* (0.57**), Pusa Sawani (0.08**)	0.19 (2.32)	L x H
	Pusa Sawani × *A. caillei* (43.66 %**)	Pusa Sawani × *A. caillei* (71.46 %**)		0.01 (2.30)	H x H
Fruit weight (g)	BCO-1 × *A. caillei* (4.94 %)	BCO-1 × *A. caillei* (125.69 %**)	BCO-1 (0.50**), *A. Caillei* (3.84**)	2.09** (16.37)	H x H
Number of fruits per plant	BCO-1 × Arka Anamika (48.41 %**)	BCO-1 × Arka Anamika (23.03 %**)	BCO-1 (2.83**), Arka Anamika (-0.64**), VRO-6 (0.55**), 11/RES-6 (1.29**)	8.61** (23.40)	H x H
	VRO-6 × 11/RES-6 (43.55%**)	VRO-6 × 11/RES-6 (25.55%**)		8.21** (22.63)	H x H
Fruit yield per plant (g/plant)	BCO-1 × Arka Anamika (4.62 %**)	BCO-1 × Arka Anamika (17.59 %**)	BCO-1 (34.44**), Arka Anamika (2.15*), VRO-6 (14.61**), 11/ RES-6 (21.44**)	108.42** (257.21)	H x H
	VRO-6 × 11/ RES-6 (2.35 %)	VRO-6 × 11/ RES-6 (12.00 %**)		96.73** (245.0)	H x H
PDI (%) of YVMV disease	BCO-1 × Arka Anamika (-71.28 %**)	BCO-1 × Arka Anamika (-72.28 %**)	BCO-1 (-19.20**), Arka Anamika (6.54**), VRO-6 (10.82**), 11/ RES-6 (-14.28**)	-22.39** (7.23)	H x L
	VRO-6 × 11/ RES-6 (-54.24 %**)	VRO-6 × 11/ RES-6 (-55.82 %**)		-27.30** (11.52)	L x H

Data in parentheses indicate *per se* values.

* Significant at 5% level, ** Significant at 1% level.

Choosing of good general and specfic combiners

Two parents, BCO-1 and 11/RES-6 exhibited significant gca effects in desired direction in most of the heterotic hybrids for fruit yield per plant followed by number of fruits per plant, fruit weight, fruit length, days to 50% flowering, node number at first flowering and PDI of YVMV disease (Table 3). They also exhibited the highest *per se* performance for fruit yield per plant along with number of fruits per plant. Thus, these two parental lines were found most promising as general combiner because they produced the maximum frequency of high yielding hybrids with appreciable YVMV disease tolerance when crossed with other parents. Significantly positive gca effects for fruit yield per plant and other yield component characters have also been reported by previous workers [12,31].

Two crosses, BCO-1 × Arka Anamika and VRO-6 × 11/RES-6 expressed the maximum significant sca effects for fruit yield per plant along with number of fruits per plant, days to 50% flowering, and PDI of YVMV disease in desired directions (Table 3). Among the forty five hybrids, the *per se* performance of the hybrid BCO-1 × Arka Anamika was found to be the highest for fruit yield per plant and could be identified as potential specific combiner for certain important traits. The negative SCA effects observed in some of the crosses for different characters might be due to the presence of unfavourable gene combinations in the parents for the respective traits. These best specific combiners having the highest magnitude of significant SCA effects in desired direction are recommended for heterosis breeding. The inter-crossing of these materials could, therefore, generate a population with a large gene pool, where genetic linkages and genetic blocks could be broken [33]. Significant sca effects in desired direction

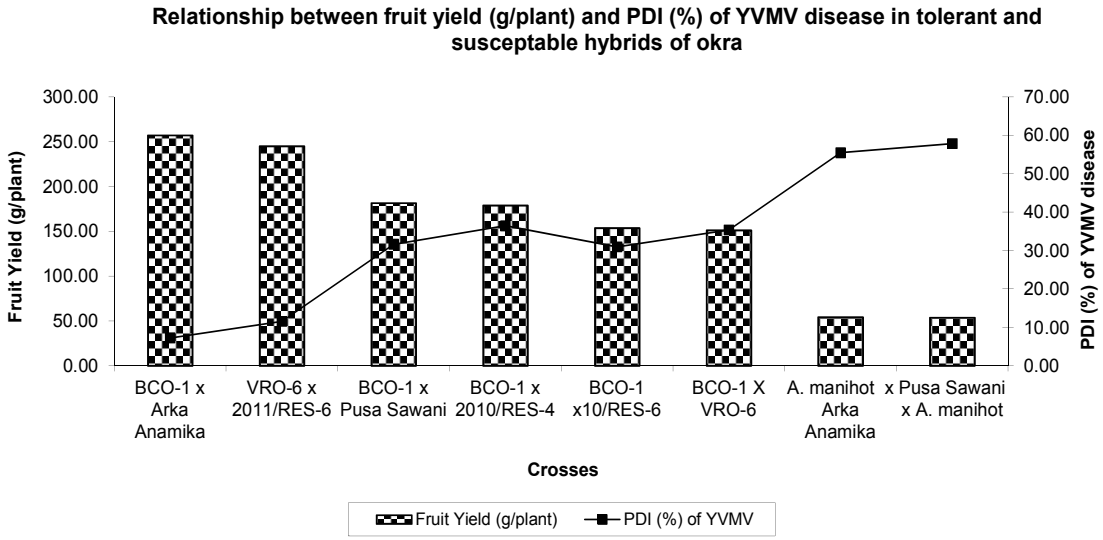

Figure 1: Relationship between fruit yield (g/plant) and PDI (%) of YVMV disease in tolerant and susceptible hybrids of okra.

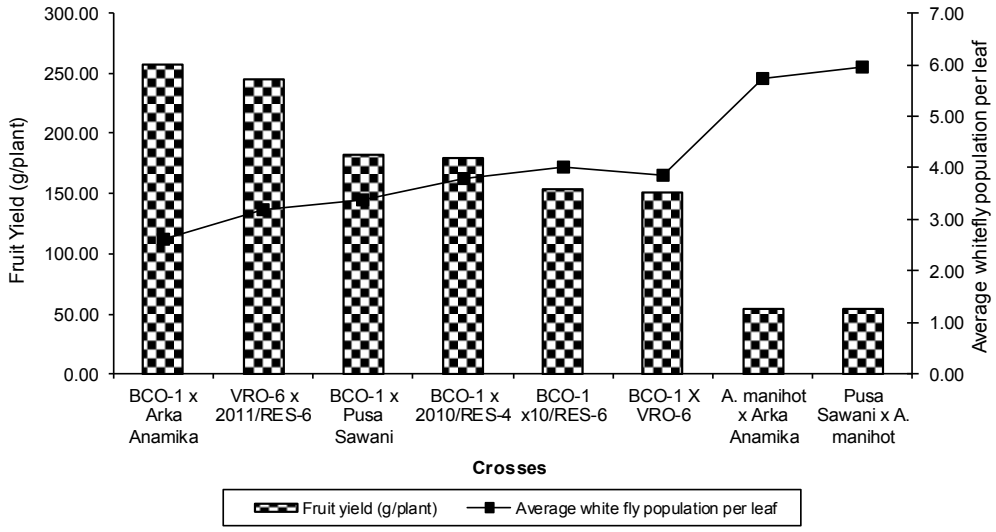

Figure 2: Relationship between fruit yield (g/plant) and average whitefly population per leaf in tolerant and susceptible hybrids of okra.

for node at 1st flowering [34] number of fruits per plant [35-37]; fruit length, fruit diameter, fruit weight and fruit yield per plant [10]; PDI of YVMV disease [12] involving various combinations of gca effects of the parents have also been reported. These two promising hybrids along with one most susceptible hybrid (BCO-1 × VRO-6) were grown under artificial inoculation condition to confirm the tolerance against this virus. Out of twenty plants inoculated with whiteflies none of the plants of the hybrid (BCO-1 × Arka Anamika) were developed any symptom of YVMV even after 30 and 45 days of inoculation and grow normally even after feeding by the vectors. Only one plant after 60 days of inoculation showed 5.00 % disease incidence in BCO-1 × Arka Anamika as compared to another promising hybrid VRO-6 × 11/RES-6 which showed 15.00 % disease incidence. However, the susceptible hybrid BCO-1 × VRO-6 exhibited 80.00 % disease incidence after 60 days of inoculation (Table 6).

The perusal of different cross combinations revealed that the crosses involved three types of combinations namely, H × H type; H × L type and L × H type, where H stands for significant gca effect and L for non-significant gca effect in desired direction of the parents (Table 3). The result depicting the type of cross combinations for the genetic control of the characters under study, both additive as well as additive × additive type of epistatic interactions were involved in H × H type cross combinations and thus, can be exploited effectively for the improvement of the traits through pedigree method of selection [38]. On the other hand, crosses of H × L type or L × H type involved one parent having either positive or negative significant gca effect indicated that predominantly additive effect was present in good combiner and possibly complementary epistatic effect in poor combiner and these two gene actions acted in complementary fashion to maximize the expression as suggested by Salimath and Bahl [26].

Table 4: Dominance estimate (DE) of F_1 hybrids for eight traits of okra.

Crosses	D50F	NFF	FL	FD	FW	NFPP	FYPP	PDI
BCO-1 × VNR Green	2.60	0.32	0.43	7.67	1.42	-1.12	-1.01	1.29
BCO-1 × VRO-6	-5.00	-0.64	2.11	-0.30	367.67	-0.90	0.20	-0.02
BCO-1 ×11/RES-6	1.40	-0.49	0.23	2.47	1.30	-2.27	-16.98	1.36
BCO-1 × 10/RES-6	-1.00	0.47	4.73	-0.06	8.69	-1.77	0.27	-0.18
BCO-1 × 10/RES-4	-1.00	0.00	6.66	3.00	8.52	-2.02	1.04	-0.17
BCO-1 × Pusa Sawani	1.00	7.29	0.51	-0.87	13.36	0.18	1.06	0.32
BCO-1 × *A. caillei*	-0.09	-1.44	-0.25	0.31	0.23	-1.26	-1.18	-1.22
BCO-1 × *A. manihot*	-0.20	0.20	-0.97	13.50	-1.35	-11.72	-0.64	-1.22
BCO-1 x Arka Anamika	1.91	3.13	14.78	4.43	3.56	0.82	2.30	1.09
VNR Green × VRO-6	0.14	-3.00	4.80	-0.60	5.88	-1.63	21.83	-0.68
VNR Green × 11/RES-6	0.00	-27.00	1.08	0.62	0.85	-1.80	-1.57	-0.21
VNR Green × 10/RES-6	0.33	-2.75	4.36	0.77	8.61	-0.46	32.38	-1.13
VNR Green × 10/RES-4	0.33	-0.36	2.97	3.00	2.39	-0.57	14.79	1.17
VNR Green × Pusa Sawani	1.67	-1.93	0.10	-0.98	0.48	1.73	1.86	-0.29
VNR Green × *A. caillei*	0.09	-0.32	-0.43	0.20	-0.22	-1.95	-2.87	-3.53
VNR Green × *A. manihot*	0.15	-0.53	-0.48	0.00	-0.94	-1.26	-0.43	-3.96
VNR Green × Arka Anamika	2.00	-3.14	2.35	1.40	1.89	1.19	1.93	-0.19
VRO-6 × 11/RES-6	0.71	-2.93	1.69	0.97	2.03	4.37	3.55	1.13
VRO-6 × 10/RES-6	-1.00	-3.62	-3.14	-1.33	6.19	-1.78	62.01	-1.97
VRO-6 × 10/RES-4	1.00	0.64	-3.83	-2.16	2.08	-1.15	12.38	-7.46
VRO-6 × Pusa Sawani	1.50	1.58	-2.06	-1.28	-0.60	1.36	1.60	-1.77
VRO-6 × *A. caillei*	0.19	-0.71	-0.82	-0.30	-0.60	-1.45	-3.80	0.14
VRO-6 × *A. manihot*	0.08	-0.39	-0.64	7.95	-0.77	-1.51	-0.44	-0.46
VRO-6 ×Arka Anamika	0.33	-2.10	1.26	-2.21	1.48	1.22	1.78	1.34
11/RES-6 × 10/RES-6	0.11	0.88	2.14	0.60	2.20	-25.00	-0.05	-0.80
11/RES-6 × 10/RES-4	1.00	1.79	1.38	0.58	1.91	-3.26	0.08	-0.40
11/RES-6 × Pusa Sawani	2.33	4.24	0.88	-0.54	2.81	0.21	0.59	0.21
11/RES-6 × *A. caillei*	0.15	-1.99	0.14	-0.01	-0.09	-1.27	-1.41	-2.80
11/RES-6 × *A. manihot*	0.03	-1.03	-1.28	3.60	-1.00	-1.33	-0.69	-2.86
11/RES-6 × Arka Anamika	1.00	-2.14	0.82	-0.43	2.79	0.72	0.45	0.40
10/RES-6 × 10/RES-4	-7.00	-0.57	5.33	-1.23	1.01	-5.34	4.57	-1.00
10/RES-6 × Pusa Sawani	0.67	1.00	-0.08	-0.63	11.71	-0.37	1.45	0.62
10/RES-6 × *A. caillei*	-0.15	-1.62	-0.64	0.42	0.05	-1.47	-1.97	-1.45
10/RES-6 × *A. manihot*	0.08	-0.59	-1.11	1.47	-1.62	-1.56	-0.41	-1.75
10/RES-6 × Arka Anamika	0.09	-2.42	1.60	-1.15	1.03	0.18	1.23	0.23
10/RES-4 × Pusa Sawani	2.33	7.57	1.52	-0.66	14.53	-0.43	1.21	1.18
10/RES-4 × *A. caillei*	-0.41	0.32	-0.70	0.35	-0.41	-1.31	-4.43	-1.32
10/RES-4 × *A. manihot*	0.21	0.60	-0.91	0.00	-1.11	-0.93	-0.38	-1.10
10/RES-4 × Arka Anamika	1.00	-3.27	6.73	4.09	8.68	-0.42	1.16	1.18
Pusa Sawani × *A. caillei*	0.22	-0.59	-1.50	-0.62	-0.29	-1.13	0.01	-0.23
Pusa Sawani × *A. manihot*	0.04	-0.66	-1.04	0.09	-2.49	-0.02	1.66	-0.29
Pusa Sawani × Arka Anamika	3.40	57.00	-1.61	-1.09	0.92	5.16	4.10	1.64
A. caillei × *A. manihot*	4.00	-1.46	-0.70	-0.19	-0.94	-0.56	0.26	2.67
A. caillei × Arka Anamika	-0.02	-0.01	-0.01	-0.05	-0.31	0.20	0.04	-0.30
A. manihot × Arka Anamika	0.00	0.02	0.00	5.18	-0.23	-0.71	0.90	-0.53

D50F= Days to 50% flowering, NFF= Node number at 1st flowering, FL= Fruit length (cm), FD= Fruit diameter (cm), FW= Fruit weight (g), NFPP= Number of fruits per plant, FYPP= Fruit yield per plant (g), PDI= Percent Disease Index (%) of YVMV disease.
* LSD at 5% and ** LSD at 1%.

Table 5: Correlation comparison matrix between disease causing variables and fruit yield among tolerant and susceptible crosses of okra.

Parameter	Fruit yield per plant (g)	PDI (%) of YVMV disease	Average whitefly population per leaf
Fruit yield per plant (g)	1.000	-0.976**	-0.972**
PDI (%) of YVMV disease		1.000	0.940**
Average whitefly population per leaf			1.000

** LSD at 1%.

Table 6: Per cent infection of YVMV disease in tolerant/susceptible hybrids after cross inoculation.

Tolerant/Susceptible Crosses	Number of plants inoculated with whiteflies	Plants infected at 30 days after inoculation	Plants infected at 45 days after inoculation	Plants infected at 60 days after inoculation	Percentage of plants infected at 60 days after inoculation
BCO-1 x Arka Anamika	20	0	0	1	5.00
VRO-6 x 11/RES-6	20	0	1	3	15.00
BCO-1 × VRO-6	20	5	11	16	80.00

Conclusion

The present study demonstrated the prevalence of non-additive gene effects in governing traits like fruit length, number of fruits per plant, and fruit yield per plant which could be improved through heterosis breeding. Pedigree method of selection is suggested for the improvement of days to 50% flowering controlled by additive gene effects. Reciprocal recurrent selection is ascertained to improve node number at first flowering, fruit weight, fruit diameter, and PDI of YVMV disease influenced by both additive and non-additive gene effects. Two parents, BCO-1 and 11/RES-6 could be utilized as promising donors in future okra breeding programme for improvement in fruit yield and YVMV disease tolerance. Exploitation of parents belonging to wild species (*A. manihot* and *A. caillei*) for the development of desirable hybrids should not be encouraged. The cross BCO-1 × Arka Anamika emerged as outstanding hybrid in respect of fruit yield and level of tolerance against YVMV disease, and could be exploited at commercial level in the tropics after its critical evaluation. The dominance effects clearly demonstrated partial- to over-dominance reactions for the inheritance of fruit yield and other economically important traits in okra.

Acknowledgements

First author wishes to acknowledge the Department of Science and Technology, Government of India for financial help in the form of Inspire Fellowship to conduct the entire study and ICAR-NBPGR, New Delhi, India for providing wild species of okra.

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