

Gene actions involved in yield and yield contributing traits of chilli (*Capsicum annuum* L.)

M. Hasanuzzaman¹ and Faruq Golam^{*2}

¹Department of Genetics and Plant Breeding, Hajee Mohamad Danesh Science and Technology University, Dinajpur, Bangladesh

²Genetics and Molecular Biology, Institute of Biological Sciences, University of Malaya, Malaysia

*Corresponding author: faruq@um.edu.my

Abstract

Gene action for yield and yield contributing traits in Chilli (*Capsicum annuum* L.) was studied in four selected crosses, involving five parents, including their F₁'s, F₂'s and first back crosses generations. The significant scaling tests (one or more scales in A, B and C) and joint scaling test indicated the presence of digenic epistasis for all the studied traits. Number of fruits and yield per plant were controlled by additive, dominance and epistatic gene action. Complex genetic behavior was observed in all traits. Since the segregating generations did not follow a simple Mendelian inheritance, high selection pressure is expected in later generations due to probable successful exploitation of additive and dominance components. From these observations it is suggested that the selection for the improvement of all traits, particularly yield per plant, should be delayed to the later generations of segregating population in this plant. The modified bulk method of selection is recommended, in which selection is performed after attaining the homozygosity for maximum heterozygous loci. Presence of complementary gene action and prevalence of the high magnitude of non-additive gene effects were found in most of the traits, indicating that heterosis breeding is more effective with high potential in chilli.

Keywords: Generation mean, Gene action, Chilli (*Capsicum annuum* L.), Yield components.

Introduction

Chilli (*Capsicum annuum* L.) is grown worldwide both as a spice and as a vegetable crop and world's second most important solanaceous vegetable after tomato. Owing to its high cash value and consumption rate the annual trade of chilli is approximately 17% of total spice trade in the world (Ahmed et al., 2000). In India, its introduction is believed to be through the Portuguese in the 16th century (Singh et al., 2004). Chilli is grown in all over the Bangladesh and in most areas, land races are cultivated. The yield of these land races is very low. But, these landraces are heterogeneous and serve as a reservoir of genetic variability for the plant breeder. During 1998-1999 to 2005-2006, average yield was 0.89 ton/ha (BBS, 2007), which is much lower than other neighboring countries such as India. Improving of chilli through developing high-yielding varieties with desirable qualities could reverse the existing trend of low productivity of this crop (Verma et al., 2004; Sreelathakumary and Rajamony, 2002). In Bangladesh, no pure line variety has been developed through gene recombination and very few hybrid varieties have been developed by private seed companies. The efforts of crop improvement have been constrained mainly by a lack of adequate information on the genetic control of characteristics of the yield and yield related traits in Bangladeshi chilli landraces. To increase the yield, genetic information and efficient breeding methods are required. The explanations for the relative importance of additive and non-additive gene effects in planning more efficient breeding programs could be obtained from a comparative assessment of the linear components, viz., additive (d), dominance (h), additive by additive (i), additive by dominance (j) and dominance by dominance (l) gene

effects (Jadhav and Dhupal, 1994). Understanding of the inheritance of yield and yield related traits in advance would be important to maximize the use of genetic potential in an effective breeding program. Such a genetic information about Bangladeshi chilli germplasm is rarely available, so that it creates a problem for the planning of a sound breeding program to improve the basic yield and associated plant traits of the crop. Very few studies have been conducted to find the inheritance pattern of yield and yield related traits in chilli. Considering the importance of chilli and in view of the above-mentioned constraints, the present study was undertaken aiming to study the inheritance pattern of quantitative traits related to yield.

Results and Discussion

Analysis of generation means

The mean performances of different generations of the selected four crosses are presented in Table 2. Expressions of the parents differed significantly as (P₁ and P₂) for most of the traits. Although the parents were significantly different for most of the traits but the number of days to fruit maturity (ripe) and yield per plant in cross CCA 5 × CCA 15, fruit width in crosses BARI Morich 1 × CCA 19 and cross CCA 15 × CCA 19, and days to 50% flowering in cross CCA 5 × CCA 11 did not show any significant variability.

Significant positive heterosis over mid parent in F₁ were observed in fruit length, fruit weight, number of fruits per plant, plant height, plant canopy width, yield per plant and significant negative heterosis was observed in days to fruit

Table 1. List of chilli accessions used in this study.

Parent	Accession	Place of Collection	Center of Origin
1	CCA 5	Bangladesh	Landrace of Bangladesh
2	BARI Morich 1	Bangladesh	Sri Lanka
3	CCA 11	Thailand	Unknown
4	CCA 15	Bangladesh	Landrace of Bangladesh
5	CCA 19	Bangladesh	Landrace of Bangladesh

maturity (green and ripe) in all four crosses. This indicates the unidirectional dominance of these traits. Significant positive and negative heterosis over mid parent in F_1 was observed for days to 50% flowering, fruit width and number of seeds per fruit, which indicate the bidirectional dominance. Significant and negative heterosis over mid parent in F_2 observed in all the traits, indicating that transgressive segregants may be present in positive and negative directions, respectively. Transgressions in segregating generations could occur due to a wider genetic distance between genotypes of their parents and segregation and recombination of increasing and decreasing alleles. Highly significant mean difference between BC_1P_1 and BC_1P_2 was observed in number of fruits per plant and yield per plant in all four crosses. This may be due to increasing alleles associated with one parent and decreasing in the other parent in different magnitudes. The difference between BC_1P_1 and BC_1P_2 in the rest of the traits was not very high in all four crosses. This may be due to dispersion of increasing and decreasing alleles among the parents as well (Mather and Jinks, 1982). An experiment on genetic analysis in hot pepper was conducted by Marame et al. (2009) in Ethiopia and observed that the mean of F_1 , F_2 , B_1 , B_2 were significantly higher in some crosses (not in all crosses) in number of fruits per plant, fruit weight, number of seeds per fruit and dry fruit yield per plant. Similar result was also observed in the present study. Marame et al. (2009) reported that the superiority of F_1 could be due to an accumulation of favorable dominant alleles while the superiority in performance of segregating generations (F_2 , B_1 and B_2) might suggest a higher frequency of their transgressive segregants.

Transgressions in segregating generations could occur due to a wider genetic distance among genotypes and their parents. The particular cases, in which the backcross generations (B_1 and B_2) were superior to their matching generations, might also indicate an accumulation of some favorable alleles. The reverse case, in which the F_2 generation was inferior to its matching progeny generations (F_1 , B_1 and B_2), could be due to the maximum segregation of desirable alleles which may result in higher frequency of inferior segregants in some crosses. Considering the pattern of generation means in the current study, a simple selection method would not be effective. The generation mean did not specify the gene action and inheritance pattern of yield and yield related traits, by which a breeding procedure can be adopted for the yield improvement in chilli.

Analysis of gene effects

The scaling tests A, B and C of Mather and Jinks, (1982) were applied in the present study to test the presence of non-allelic gene interactions. The significant scaling tests (one or

more scales in A, B and C) and joint scaling test indicated the presence of digenic epistasis for all the traits studied except number of seeds per fruit in cross CCA 5 \times CCA 11 (Table 3). However, significant epistasis in six parameter model was observed (Table 4). This may be due to difference in t and χ^2 distribution. In these cases, the epistatic model was suitable for study of gene action of these traits. Non-significance of the scaling tests and joint scaling test for the trait indicated the absence of non-allelic interactions and the three-parameter additive dominance model was adequate for the estimation of gene effects. The six-parameter model of Jinks and Jones, (1958) was used for further tests of the absence or presence and nature of non-allelic gene interactions through the parameters against the respective standard errors following a conventional 't' test. The gene effects are represented in Table 4.

In cross CCA 5 \times CCA 15, additive \times additive, additive \times dominance, dominance \times dominance gene actions controlled days to 50% flowering. Fruit length was controlled by additive \times additive and dominance \times dominance epistatic gene action. Additive, dominance and all types of epistatic gene actions controlled the fruit width. Fruit weight was controlled by additive, additive \times additive and dominance \times dominance gene actions. Number of seeds per plant was controlled by dominance, additive \times additive and dominance \times dominance gene actions. Additive, dominance and all type of epistatic gene actions controlled the number of fruits per plant. Days to maturity (green) was controlled by dominance and all epistatic gene actions. Additive, dominance and all epistatic gene actions controlled the days to fruit maturity (ripe). Additive, dominance, additive \times additive, dominance \times dominance gene actions controlled the plant height. Additive, additive \times additive, dominance \times dominance gene actions controlled the plant canopy width. Yield per plant was controlled by additive, dominance, additive \times dominance, dominance \times dominance.

In BARI Morich 1 \times CCA 19 cross, dominance, additive \times additive, additive \times dominance, dominance \times dominance gene actions controlled the days to 50% flowering. Fruit length was controlled by additive, dominance and all possible epistatic gene actions. Dominance, additive \times additive, and dominance \times dominance epistatic gene actions controlled the fruit width. Fruit weight was controlled by additive, dominance and additive \times dominance gene actions. Number of seeds per plant was controlled by additive, dominance, additive \times dominance and dominance \times dominance gene actions. Additive, dominance and all type of epistatic gene actions controlled the number of fruits per plant. Days to maturity (green) was controlled by dominance, additive \times additive and dominance \times dominance epistatic gene actions. Dominance and all epistatic gene actions controlled the days to fruit maturity (ripe). Additive, and all epistatic gene actions controlled the plant height. Additive and dominance

Table 2. Generation Means (\pm SE) of yield and yield contributing traits of six generations in chili including parents.

Trait	Cr	P ₁	P ₂	F ₁	F ₂	BC ₁ P ₁	BC ₁ P ₂	F ₁ -MP	F ₂ -MP	P ₁ -P ₂
Days to flowering	C ₁	35.50±0.40	43.70±0.40	35.40±0.32	45.91±0.50	47.79±0.42	48.07±0.45	-4.20**	6.31**	-8.20**
	C ₂	36.00±0.45	45.60±0.38	54.43±0.54	52.26±0.44	45.42±0.44	45.56±0.44	13.63**	11.46**	-9.60**
	C ₃	35.50±0.40	34.70±0.42	35.80±0.41	52.70±0.41	47.18±0.42	43.53±0.46	0.7	17.60**	-0.8
	C ₄	43.70±0.40	45.60±0.38	49.93±0.53	57.41±0.33	52.49±0.42	47.83±0.46	5.28**	12.76**	1.90**
Fruit length (cm)	C ₁	7.11±0.06	7.50±0.06	8.50±0.09	8.34±0.07	7.86±0.08	8.04±0.10	1.20**	1.04**	-0.39**
	C ₂	6.51±0.06	7.42±0.06	6.88±0.06	6.07±0.07	7.32±0.09	6.34±0.09	-0.08	-0.89**	-0.92**
	C ₃	7.11±0.06	9.32±0.07	8.53±0.06	7.46±0.10	7.43±0.10	7.68±0.09	0.32**	-0.75**	2.21**
	C ₄	7.50±0.06	7.42±0.06	7.75±0.07	7.01±0.07	7.55±0.09	7.49±0.10	0.29**	-0.45**	-0.08
Fruit width (mm)	C ₁	7.48±0.11	9.85±0.12	9.36±0.11	7.37±0.07	7.66±0.09	8.42±0.10	0.39**	0.54**	2.47**
	C ₂	9.71±0.13	9.85±0.12	9.80±0.11	9.14±0.07	9.78±0.09	9.64±0.10	0.01	-0.64**	-0.14
	C ₃	9.95±0.09	11.43±0.13	10.13±0.09	9.71±0.11	8.72±0.10	9.37±0.09	-0.56**	-0.98**	1.47**
	C ₄	9.95±0.09	7.48±0.11	9.11±0.11	9.25±0.08	8.22±0.09	7.55±0.10	0.69**	-1.30**	2.38**
Fruit weight (g)	C ₁	1.79±0.03	2.79±0.01	3.33±0.04	2.50±0.04	2.55±0.05	2.42±0.05	0.86**	0.56**	1.02**
	C ₂	3.05±0.03	2.79±0.01	3.19±0.03	3.02±0.04	3.29±0.06	2.94±0.06	0.28**	0.10*	0.26**
	C ₃	2.81±0.03	5.97±0.05	4.51±0.04	3.53±0.08	3.55±0.06	3.42±0.06	0.12*	-0.86**	3.17**
	C ₄	2.81±0.03	1.79±0.03	3.16±0.03	2.86±0.04	2.92±0.06	2.50±0.06	1.04**	0.21**	1.00**
Number of seeds per fruit	C ₁	58.50±2.21	69.33±1.96	83.07±2.16	61.16±1.32	66.14±1.81	71.93±1.63	7.12*	0.65	6.37*
	C ₂	42.03±2.39	69.33±1.96	77.70±2.08	70.71±1.21	77.36±1.67	70.17±1.66	22.02**	15.03**	-27.30**
	C ₃	64.87±1.95	89.80±2.09	69.20±1.66	73.68±1.29	68.80±1.67	75.32±1.92	-8.13**	-3.66	24.93**
	C ₄	64.87±1.95	58.50±2.21	68.80±2.40	62.34±1.20	57.48±1.53	56.43±1.55	19.15**	-2.76	10.83**
Number of fruits per plant	C ₁	181.17±4.23	137.97±3.70	177.87±3.25	131.08±3.22	149.36±4.27	162.73±4.50	78.22**	-22.98**	-40.97**
	C ₂	82.53±2.94	137.97±3.70	284.67±3.89	125.29±3.61	102.00±3.80	184.30±3.57	174.42**	15.04**	-55.43**
	C ₃	140.20±4.36	76.07±1.64	171.40±3.54	96.31±3.06	123.78±3.40	105.37±3.57	63.27**	-11.83**	-64.13**
	C ₄	140.20±4.36	181.17±4.23	238.90±3.91	137.70±3.21	112.01±3.39	189.98±4.30	18.30**	-28.49**	-43.20**
Days to fruit maturity (green)	C ₁	33.17±0.27	36.50±0.30	33.33±0.21	40.38±0.29	34.80±0.37	34.26±0.34	-1.50**	5.55**	-3.33**
	C ₂	38.87±0.38	41.40±0.29	35.83±0.30	42.15±0.28	36.28±0.35	36.86±0.37	-4.30**	2.01**	-2.53**
	C ₃	33.17±0.27	41.43±0.28	33.20±0.22	41.39±0.33	38.21±0.31	35.63±0.31	-4.10**	4.09**	8.27**
	C ₄	36.50±0.30	41.40±0.29	38.53±0.27	38.53±0.34	35.33±0.38	38.21±0.33	-0.42	-0.42	4.90**
Days to fruit maturity (ripe)	C ₁	51.17±0.45	50.83±0.30	51.33±0.21	53.71±0.29	50.12±0.37	48.53±0.35	0.33	2.71**	0.33
	C ₂	54.30±0.45	59.73±0.29	50.57±0.32	56.47±0.28	51.58±0.35	51.16±0.38	-6.45**	-0.55	-5.43**
	C ₃	51.17±0.45	57.77±0.28	51.20±0.22	55.74±0.34	51.21±0.31	49.97±0.31	-3.27**	1.27**	6.60**
	C ₄	50.83±0.30	59.73±0.29	53.43±0.29	52.86±0.33	51.10±0.39	52.54±0.33	-1.85**	-2.43**	8.90**
Plant height (cm)	C ₁	63.16±1.38	51.89±1.25	56.63±1.09	55.07±0.76	63.27±1.02	58.64±1.12	-0.9	-2.45*	11.28**
	C ₂	35.09±1.28	64.23±1.36	49.05±1.29	49.01±0.74	49.43±1.03	52.77±1.10	-0.61	-0.65	-29.14**
	C ₃	63.16±1.38	53.71±1.28	66.23±1.33	51.95±0.74	60.07±1.04	53.38±1.00	7.79**	-6.49**	-9.45**
	C ₄	51.89±1.25	64.23±1.36	59.74±1.34	66.03±0.71	63.64±1.04	63.84±0.99	1.68	7.97**	12.35**
Plant canopy width (cm)	C ₁	69.76±1.12	60.35±1.14	71.93±1.22	65.93±0.80	65.26±1.04	59.69±1.08	6.88**	0.88	9.41**
	C ₂	62.66±1.24	73.58±1.18	71.10±1.23	66.17±0.78	64.67±1.10	68.48±1.06	2.99	-1.95	-10.92**
	C ₃	69.76±1.12	59.35±1.30	78.49±1.21	64.39±0.80	67.41±1.10	56.81±1.08	13.93**	-0.16	-10.41**
	C ₄	60.35±1.14	73.58±1.18	69.86±1.05	69.58±0.81	60.54±1.08	67.56±1.08	2.89*	2.62*	13.23**
Yield per plant (g)	C ₁	315.63±10.0	315.43±7.39	740.17±10.0	383.05±8.91	314.16±8.67	463.81±10.5	424.63**	67.51**	0.2
	C ₂	246.70±8.83	375.73±9.20	901.50±12.1	371.79±10.7	275.53±10.0	534.72±10.3	590.28**	60.57**	-129.03**
	C ₃	315.63±10.0	283.57±9.75	748.93±10.1	331.83±10.5	375.78±10.0	306.48±9.89	449.33**	32.23*	-32.07*
	C ₄	315.43±7.39	375.73±9.20	589.23±10.7	319.57±7.88	371.74±10.6	387.17±10.6	243.65**	-26.02*	60.30**

C₁= CCA 5×CCA 15, C₂=BARI Morich 1×CCA 19, C₃=CCA 5×CCA 11, C₄=CCA 15×CCA 19. * P<0.05, ** P<0.01 respectively

× dominance gene actions controlled the plant canopy width. Yield per plant was controlled by additive, dominance, and all epistatic gene actions.

In cross CCA 5 × CCA 11, additive, dominance and all epistatic gene actions controlled days to 50% flowering. Fruit length was controlled by additive × dominance and dominance × dominance epistatic gene actions. Additive, dominance, additive × additive and dominance × dominance epistatic gene actions controlled fruit width. Fruit weight was controlled by additive × dominance and dominance × dominance gene actions. Number of seeds per plant was controlled by additive and additive × dominance gene actions. Additive, dominance, additive × additive and additive × dominance epistatic gene actions controlled the number of fruits per plant. Days to maturity (green) was controlled by additive, dominance and all epistatic gene actions. Additive, dominance and all epistatic gene actions controlled the days to fruit maturity (ripe). Additive, dominance and additive × additive epistatic gene action controlled the plant height. Additive and all epistatic gene actions controlled the plant canopy width. Yield per plant was controlled by additive, dominance, and additive × dominance, dominance × dominance epistatic gene actions.

In cross CCA 15 × CCA 19, additive, dominance and all epistatic gene actions controlled days to 50% flowering. Fruit length was controlled by dominance, additive × additive and dominance × dominance epistatic gene actions. Additive, dominance, additive × additive and additive × dominance epistatic gene actions controlled fruit width. Fruit weight was controlled by dominance, additive × dominance and dominance × dominance gene actions. Number of seeds per plant was controlled by additive, dominance and additive × additive gene actions. Additive, dominance, additive × additive and additive × dominance epistatic gene actions controlled the number of fruits per plant. Days to maturity (green) was controlled by additive, dominance and additive × additive, dominance × dominance epistatic gene actions. Additive, dominance and all epistatic gene actions controlled the days to fruit maturity (ripe). Additive × additive and additive × dominance epistatic gene action controlled the plant height. Additive, dominance, additive × additive and dominance × dominance epistatic gene actions controlled the plant canopy width. Yield per plant was controlled by additive, dominance, and additive × additive epistatic gene actions.

The analyses of gene actions of the selected four crosses revealed that six parameter model fitted in all traits in all four crosses except for CCA 5 × CCA 11 cross in the number of seeds per fruit, which found to be fitted with three parameter model. Significant digenic epistatic gene action was present in all the traits in all four crosses with very few exceptions. Additive, dominance or both the components play an important role in the inheritance of these traits under study. Those in which [h] and [l] have the same sign which is refer to as complementary type and those in which [h] and [l] have opposite signs which is refer to as duplicate types (Mather and Jinks, 1982). Complementary gene action was observed in fruit weight, number of fruits per plant and yield per plant, complementary and duplicate gene actions in days to 50% flowering and duplicate gene action in fruit length and width, number of seeds per fruit, days to fruit maturity (green and ripe), plant height and plant canopy width. Complementary gene action, acts in favor of heterosis causes the increase of heterosis, and duplicates gene action, which acts against the heterosis, causes decrease of heterosis.

A number of researchers reported the gene action of chilli yet. All the three types of gene action i.e., additive, dominance and interaction components were found to play a role in the inheritance of fruit length, fruit width, fruit number, and dry chilli yield. However, their degree differed with crosses. This could be due to differences in magnitude of the gene effects and genetic background of the parents (Murthy and Deshpande, 1997).

Some gene effects such as additive and dominance × dominance in fruit length; dominance and dominance × dominance in fruit length, fruit diameter, number of fruits per plant; additive, dominance and dominance × dominance in fruit width; and additive, dominance, additive × additive and dominance × dominance in fruit weight, number of seeds per fruit plant height and dry fruit yield/plant were also observed with high importance (Jadhav and Dhumal, 1994; Dhall and Hundal, 2006; Sarma and Talukdar, 1998; Somashekhar et al., 2008). The dominance (h) and dominance × dominance (l) components had opposite signs in almost all the crosses in fruit weight and number of fruits per plant indicating the presence of the duplicate type of epistasis. This will reduce the net gain occurring from heterozygosity due to the cancellation of dominance and epistatic effects (Dhall and Hundal, 2006).

The generation mean analysis revealed that individual crosses greatly differed for the gene action and on an overall basis, all the types of gene action, additive, dominance and epistasis are important. The latter two types predominating for many characters thereby indicating that epistasis cannot be ignored. Similar conclusions have been reported by Martin and Lippert (1975), Sharma and Saini (1977) and Jagadeesha (2000) in chilli. Since epistasis was present in many cases, success of selection, which should be undertaken in advanced generations, will depend on the epistasis type. Selection for epistatic interactions warrants inbreeding following by selection. In other words, when epistatic interactions are present, selection between inbred families is the most effective method. However, the rate of inbreeding must be regulated in such a manner that it may ward off natural selection of homozygotes (at slow inbreeding) interfering with allelic fixation. At the same time, it should not be so rapid, which may cause extinction of many lines. Inter-line selection favors either originally more heterozygous lines or those that can manage to preserve overdominant loci or blocks in a heterozygous state by some or other mechanism (Sharma, 1994).

The additive × additive or any other digenic complementary gene interaction are fixable and thus can be exploited effectively for the improvement of the traits through pedigree method of selection (Ram, 1994). Pedigree method was used in developing of cultivars such as Andhra Jyoti, Pusa Jwala, Pusa Sadabahar, X 235, K2, Pant C1, Punjab Lal and Jawahar 218 in India (Ram, 1998). However, Jindal et al. (1993) and Amawate and Behl, (1995) suggested that duplicate epistasis might restrict the expression, and selection of a trait in early segregating generations. The selection in early generations would not be effective for fixable components of variation. Such gene effects can however be exploited by intermating the selected segregants and delaying the selection to the advanced generations (Jindal et al., 1993). Delayed selection (Sharma and Sharma, 1995) or selection after biparental intermating (Misra et al., 1994) would be more effective to get a good response in such cases.

Table 3. Scaling and joint scaling test for yield and yield contributing traits in chilli.

Trait	Cross	A	B	C	χ^2
Days to flowering	C ₁	24.68**	17.03**	33.64**	913.71**
	C ₂	0.41	-8.92**	18.59**	207.14**
	C ₃	16.57**	23.06**	69.01**	1504.65**
	C ₄	0.13	11.34**	40.48**	587.14**
Fruit length (cm)	C ₁	-0.20	-0.15	-2.38**	60.63**
	C ₂	1.25**	-1.62**	-3.41**	235.21**
	C ₃	-2.48**	-0.77**	-3.65**	194.30**
	C ₄	0.11	0.08	1.76**	29.40**
Fruit width (mm)	C ₁	-2.36**	-1.51**	-6.56**	288.73**
	C ₂	0.06	-0.37	-2.58**	48.73**
	C ₃	-2.81**	-2.63**	-2.80**	235.45**
	C ₄	-2.61**	-1.49**	1.38**	218.22**
Fruit weight (g)	C ₁	-0.11	0.06	0.53**	10.47*
	C ₂	0.34**	-0.10	-0.15	10.34*
	C ₃	-3.64**	-0.21	-3.69**	758.75**
	C ₄	-1.28**	-0.02	-1.23**	172.15**
Number of seeds per fruit	C ₁	-18.71**	-14.43**	-11.62	24.98**
	C ₂	34.98**	-6.70	16.09*	68.05**
	C ₃	-8.36	3.53	1.64	4.70
	C ₄	-8.53	-9.28	-49.33**	44.95**
Number of fruits per plant	C ₁	-155.08**	-40.11**	-248.37**	402.47**
	C ₂	-163.20**	-54.03**	-288.68**	489.94**
	C ₃	-36.73**	-64.04**	-173.84**	151.09**
	C ₄	9.63	-60.32**	-150.54**	119.08**
Days to fruit maturity (green)	C ₁	3.10**	-1.32	25.19**	401.93**
	C ₂	-2.14*	-3.52**	16.66**	231.61**
	C ₃	-3.37**	10.06**	24.54**	493.15**
	C ₄	-3.51**	-4.37**	-0.83	43.11**
Days to fruit maturity (ripe)	C ₁	-2.26*	-5.10**	10.19**	136.41**
	C ₂	-1.71	-7.99**	10.71**	201.71**
	C ₃	-9.03**	0.06	11.63**	261.91**
	C ₄	-8.08**	-2.07*	-6.01**	114.12**
Plant height (cm)	C ₁	6.74*	8.77**	-8.02	31.32**
	C ₂	14.71**	-7.76**	-1.40	46.11**
	C ₃	-13.19**	-9.25**	-41.52**	91.05**
	C ₄	3.70	15.65**	28.52**	57.46**
Plant canopy width (cm)	C ₁	-11.17**	-12.90**	-10.25*	33.34**
	C ₂	-4.42	-7.73**	-13.76**	13.34**
	C ₃	-24.21**	-13.43**	-28.52**	92.76**
	C ₄	-8.31**	-9.12**	4.69	28.91**
Yield per plant (g)	C ₁	-427.49**	-127.98**	-579.21**	427.98**
	C ₂	-597.13**	-207.79**	-938.28**	708.01**
	C ₃	-419.54**	-313.01**	-769.75**	491.52**
	C ₄	-190.63**	-161.18**	-591.37**	232.47**

C₁= CCA 5×CCA 15, C₂=BARI Morich 1×CCA 19, C₃=CCA 5×CCA 11, C₄=CCA 15×CCA 19, i= additive x additive type gene interaction, j= additive x dominance type gene interaction and l= dominance x dominance type gene interaction, Significant value of A and B indicates the presence of i, j and l type of gene interaction. Significant value of C indicates the presence of l type of gene interaction. A significant χ^2 value indicates the inadequacy of three parameter model. * P<0.05, ** P<0.01 respectively

Table 4. Estimates of gene effects for yield and yield contributing traits in chilli using six parameter model

Trait	Cross	m	d	h	i	j	l	Epistatic Gene action
Days to flowering	C ₁	45.91**	-0.28	3.87	8.07**	3.82**	-49.78**	-
	C ₂	52.26**	-0.13	-13.46**	-27.10**	4.67**	35.61**	Duplicate
	C ₃	52.70**	-3.64**	-28.69**	-29.39**	-3.24**	-10.23**	Complementary
	C ₄	57.41**	-4.66**	-23.72**	-29.00**	-5.61**	17.52**	Duplicate
Fruit length (cm)	C ₁	8.34**	-0.18	-0.37	-1.57**	0.02	1.38*	-
	C ₂	6.07**	0.97**	2.96**	3.04**	1.43**	-2.67**	Duplicate
	C ₃	7.46**	0.25	0.71	0.40	-0.85**	2.86**	-
	C ₄	7.01**	-0.06	2.33**	2.04**	-0.03	-1.70**	Duplicate
Fruit width (mm)	C ₁	9.25**	0.68**	-5.08**	-5.47**	-0.56**	9.57**	Duplicate
	C ₂	9.14**	0.14	2.28**	2.27**	0.22	-1.95**	Duplicate
	C ₃	9.71**	0.65**	-3.21**	-2.65**	-0.09	8.09**	Duplicate
	C ₄	7.37**	0.76**	3.38**	2.69**	-0.42**	1.19	-
Fruit weight (g)	C ₁	2.86**	0.42**	0.28	-0.58**	-0.08	0.64	-
	C ₂	3.02**	0.35**	0.68**	0.40	0.22**	-0.65	-
	C ₃	3.53**	-0.13	-0.04	-0.16	-1.72**	4.00**	-
	C ₄	2.50**	-0.13	0.97**	-0.08	-0.63**	1.38**	Complementary
Number of seeds per fruit	C ₁	61.16**	5.79*	50.67**	31.52**	0.37	-13.71	Duplicate
	C ₂	70.71**	7.19**	34.20**	12.19	20.84**	-40.46**	Duplicate
	C ₃	73.68**	6.52*	-14.60	-6.47	-5.94*	11.29	-
	C ₄	62.34**	1.04	-14.41*	-21.53**	-2.14	54.67**	-
Number of fruits per plant	C ₁	137.70**	-77.97**	131.39**	53.18**	-57.48**	142.01**	Complementary
	C ₂	125.29**	-82.30**	245.86**	71.44**	-54.58**	145.79**	Complementary
	C ₃	96.31**	-18.41**	136.33**	73.07**	13.66*	27.71	-
	C ₄	131.08**	13.38*	118.15**	99.85**	34.98**	-49.16	-
Days to fruit maturity (green)	C ₁	40.38**	0.54	-24.91**	-23.41**	2.21**	21.64**	Duplicate
	C ₂	42.15**	-0.58	-26.63**	-22.33**	0.69	27.99**	Duplicate
	C ₃	41.39**	-2.58**	-21.95**	-17.85**	-6.71**	11.16**	Duplicate
	C ₄	38.53**	2.88**	-7.46**	-7.04**	0.43	14.92**	Duplicate
Days to fruit maturity (ripe)	C ₁	53.71**	1.59**	-17.21**	-17.55**	1.42*	24.90**	Duplicate
	C ₂	56.47**	0.42	-26.86**	-20.41**	3.14**	30.11**	Duplicate
	C ₃	55.74**	-1.24**	-23.87**	-20.61**	-4.54**	29.59**	Duplicate
	C ₄	52.86**	1.44**	-5.98**	-4.13*	-3.01**	14.28**	Duplicate
Plant height (cm)	C ₁	55.07**	4.62**	22.64**	23.54**	-1.01	-39.06**	Duplicate
	C ₂	49.01**	-3.34*	7.75	8.35*	11.23**	-15.31*	-
	C ₃	51.95**	-6.69**	26.87**	19.08**	-1.97	3.36	-
	C ₄	66.03**	0.20	-7.49	-9.16*	-5.97**	-10.19	-
Plant canopy width (cm)	C ₁	65.93**	5.57**	-6.94	-13.82**	0.86	37.89**	-
	C ₂	66.17**	-3.80*	4.59	1.60	1.66	10.55	-
	C ₃	64.39**	-10.60**	4.81	-9.12*	-5.39**	46.77**	-
	C ₄	69.58**	7.02**	-19.22**	-22.12**	0.41	39.55**	Duplicate
Yield per plant (g)	C ₁	383.05**	-149.66**	448.37**	23.74	-149.76**	531.73**	Complementary
	C ₂	371.79**	-259.19**	723.64**	133.36*	-194.67**	671.57**	Complementary
	C ₃	331.83**	-69.30**	486.53**	37.19	-53.27**	695.36**	Complementary
	C ₄	319.57**	15.42	483.21**	239.56**	-14.73	112.26	-

C₁= CCA 5 X CCA 15, C₂=BARI Morich 1 X CCA 19, C₃=CCA 5 X CCA 11, C₄=CCA 15 X CCA 19. m=mean, d=additive effect, h= dominance effect, i= additive x additive type gene interaction, j= additive x dominance type gene interaction and l= dominance x dominance type gene interaction. * P<0.05, ** P<0.01 respectively

The biparental hybridization between recombinants in early segregating generation (F_2) would produce better genetic combinations, through which the accumulations of desirable genes could be achieved for high yield potential in the individual lines. The other possibilities could be diallel selective mating system as proposed by Jensen (1970) or the recurrent selection procedures (Singh and Pawar, 1990) for the exploitation of non-additive genetic variability.

According to Comstock et al. (1949), use of reciprocal recurrent selection could improve the traits when both additive and non-additive gene effects are involved in the expression of the characters. Heterosis breeding in chilli is feasible because presence of complementary gene action and prevalence of the high magnitude of non-additive gene effects for most of the traits studied. Lippert, (1974) also observed significant heterosis in his developed crossing chilli materials but he concluded that additive effects (GCA) were more important than non-additive (SCA) in explaining variability among F_1 's for different fruit characters. All the traits examined in the present study have shown complex genetic behavior. The simple selection procedure in the early segregating generation may not significantly contribute for the improvement of these traits. The complex genetic behavior particularly additive and dominance components could be successfully exploited in later generation. Therefore, the selection for the improvement of all these traits particularly yield per plant should be delayed to the latter generation of segregating population in chilli.

Taking all together, the modified bulk method of selection is recommended for varietal improvement of chilli, in which selection is performed after attaining the homozygosity for maximum heterozygous loci.

Materials and methods

Plant Materials

Four selected crosses covering 5 selfed parents (Table 1) with their 4 F_1 's, 4 F_2 's and 8 backcrosses were used in this study. The six generations (P_1 , P_2 , F_1 , F_2 , BC_1P_1 and BC_1P_2) were developed in 2006-2007 to 2007-2008.

Experimental design and growing conditions

The present study was conducted at the Research and Development (R & D) Farm of Lal Teer Seed Limited at Basan (North 23.9763° and East 090.3539°), Gazipur, Bangladesh from the period of October 2006 to July 2009. The soil of the experimental land was clay loam, slightly acidic in reaction (soil pH=6-6.5) and low in nitrogen content.

Six generations, P_1 , P_2 , F_1 , F_2 , BC_1P_1 and BC_1P_2 of all four crosses were sown in seedling tray at R & D farm of Lal teer seed limited, Gazipur in September, 2008. Each treatment was replicated three times using RCB design. The transplantation of seedlings completed in October 2008. Raised beds were prepared for transplanting. The width of raised bed was 1.5 meter. Plant to plant distance was 50 cm and row to row distance was 70 cm. Bed to bed distance was 1.0 meter that was used as drain.

Data collection and analysis

The number of plants selected for data recording per cross were 10 for P_1 , 10 for P_2 , 10 for F_1 , 90 for F_2 , 35 for BC_1P_1 and 35 for BC_1P_2 in each replication. The plants were tagged

randomly at flowering stage and data were taken from these selected plants. To find out the presence of gene interaction scaling test and joint scaling test were performed following the method of Mather and Jinks, (1982) and Cavalli, (1952), respectively. The three-parameter model of Jinks and Jones, (1958) was used to test the adequacy of the additive-dominance model in the absence of non-allelic gene interaction and the six-parameter model of Hayman (1958) and Jinks and Jones, (1958) were used to estimate various gene effects including the non-allelic interaction.

References

- Ahmed J, Shivhare US, Raghavan GSV (2000) Rheological characteristics and kinetics of color degradations of green chilli puree. *J Food Eng.* 44:239-244.
- Amawate JS, Behl PN (1995) Genetic analysis of some quantitative components of yield in bread wheat. *Ind J Genet.* 55: 120-125.
- BBS (Bangladesh Bureau of Statistics) (2007) Statistical year book 2006. Bangladesh bureau of statistics, Ministry of Planning, GOB. Dhaka, Bangladesh. ISBN 984-508-814-7.
- Cavalli LL (1952) An analysis of linkage in quantitative inheritance. In: Reeve ECR, Waddington CH (eds). *Quantitative inheritance.* HMSO, London, p.135-144.
- Comstock RE, Robinson HF, Harvey PH (1949) A breeding procedure designed to make maximum use of both general and specific combining ability. *Agron J.* 41:360-367.
- Dhall RK, Hundal JS (2006) Genetics of yield attributes in chilli (*Capsicum annuum*). *Ind J Agric Sci.* 76(11):699-701.
- Hayman BI (1958) The separation of epistasis from additive and dominance variation in generation means. *Heredity.* 12:371-390.
- Jadhav MG, Dhupal SA (1994) Genetic studies of some quantitative characters in chilli. *Journal of Maharashtra Agricultural University* 19(1):62-64.
- Jagadeesha RC (2000) Genetics of yield, yield components and fruit quality parameters in chilli (*Capsicum annuum* L.). Ph.D. thesis, Univ. of Agric. Sci., Dharwad, India.
- Jensen NF (1970) A diallel selective mating system for cereal breeding. *Crop Sci.* 10:629- 635.
- Jinda Y, Behl RK, Singh KP (1993) Gene effects for grain yield and its components in two wheat crosses. *Inter J Trop Agric.* 11 (2): 123-126.
- Jinks JL, Jones RM (1958) Estimation of the components of heterosis. *Genetics* 43: 223-234.
- Lippert LF (1974) Heterosis and Combining Ability in Chili Peppers by Diallel Analysis. *Crop Sci.* (15) 3: 323-325
- Maramba F, Desalegne L, Fininsa C, Sigvald R (2009) Genetic analysis for some plant and fruit traits, and its implication for a breeding program of hot pepper (*Capsicum annuum* var. *annuum* L.). *Hereditas.* 146: 131-140.
- Martin VC, Lippert LF (1975) Combining ability analysis of anatomical components of the dry fruit in pepper. *Crop Sci.* 15: 326-329.
- Mather K, Jinks JL (1982) *Biometrical genetics.* 3rd edition. Chapman and Hall, London.
- Misra SC, Rao VS, Dixit RN, Surve VD, Patil VP (1994) Genetic control of yield and its components in bread wheat. *Ind J Genet.* 54:77-82.
- Murthy HMK, Deshpande AA (1997) Genetics of yield attributes in chilli (*Capsicum annuum* L.). *Vegetable Sci.* 24(2):118-122.
- Ram T (1994) Genetics of yield and its components in rice (*Oryza sativa* L.). *Indian J Genet* 54: 149-154.

- Ram HH (1998) Vegetable breeding: principles and practices. Kalyani publishers, Ludhiana, India.
- Sarma A, Talukdar P (1998) Gene effects in chilli (*Capsicum annum* L.). Crop Improvement 25(2): 220-222.
- Sharma PP, Saini SS (1977) Heterosis and combining ability for yield and agronomic characters in pepper (*Capsicum annum* L.). Vegetable Sci. 4 (1): 43-48.
- Sharma JR (1994) Principles and practice of plant breeding. Tata McGraw-Hill publishing company Limited, New Delhi, India.
- Sharma SN, Sharma RK (1995) Genetic architecture of harvest index in tetraploid wheat (*T. durum* Desf.). Ind J Genet. 55 (3): 233-237.
- Singh BD (2005) Plant Breeding - Principles and Methods. Kalyani Publishers, Ludhiana, India.
- Singh S, Pawar IS (1990) An appraisal of selection methods in self fertilized crops. Trends Crop Improvement. 44 (1): 17-26.
- Singh PK, Dasgupta SK, Tripathi SK (2004) Hybrid vegetable development. International book distribution co. Lucknow, India.
- Singh RK, Chaudhary BD (1985) Biometrical methods in quantitative genetic analysis. Kalyani publishers, Ludhiana, India.
- Somashekhar, Patil SA, Salimath, PM (2008) Estimation of gene effects for fruit yield and its components in chilli (*Capsicum annum* L.) Karnataka J Agric Sci. 21(2): 181-183.
- Sreelathakumary I, Rajamony L (2002) Variability, heritability and correlation studies in chilli (*Capsicum* spp.) under shade. Indian J Hort. 59: 77-83.
- Verma SK, Singh RK, Arya RR (2004) Genetic variability and correlation studies in chillies. Progressive Hort. 36: 113-117.