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Epistasis and inheritance of yield contributing traits in Chilli (*Capsicum annuum* L.)

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Abstract

The generation mean analysis for yield contributing traits involving six generations (P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2) was undertaken to study the nature and magnitude of gene effects in Chilli (*Capsicum annuum* L.). The significance of individual scaling test and three parameter genetic model revealed the existence of epistasis and indicated the importance of additive [d], dominance [h] and other three types of non-allelic gene interactions *i.e.* additive × additive [i], additive × dominance [j] and dominance × dominance [l] for five characters *viz.*, plant height (cm), plant canopy width (cm), fruit length (cm), fruit width (cm) and fruit weight (g). The results suggested the presence of duplicate type of epistasis for most of the traits studied indicating that selection for improvement may be successful in later generations of segregating populations. In view of these results, the implementation of population improvement technique such as reciprocal recurrent selection will be more effective with high potential in Chilli.

Keywords: Chilli, epistasis, generation mean, gene effect, scaling test

Introduction

Chilli or hot pepper (*Capsicum annuum* L.) is one of the imperative crops widely cultivated by the farmers as a vegetable as well as spice or condiment in the tropical and sub-tropical regions worldwide. In India, this high value crop is grown commercially in the states of Andhra Pradesh, Telangana, Karnataka, Maharashtra, Orissa and Tamil Nadu which constitute major growing area and total production of chilli. Chilli fruits are rich source of proteins, carbohydrates, minerals and vitamins like A, C and E (Than *et al.*, 2008) [1]. Chilli has broad range of culinary uses from fresh consumption to processed products such as potted chilli pepper, dehydrated flakes and sauces (Moreira *et al.*, 2006) [2]. Capsanthin is the most important pigment of chilli and used as a natural food colour in salad dressings, meat products, cosmetics, and even clothing. The active ingredient, Capsaicin is accountable for pungency and has good medicinal value as an antioxidant, antimutagenic, anticarcinogenic, and immunosuppressive (Welbaum, 2015) [3].

Chilli is comprised of variable cultivated and wild species. Various accessions of chilli differ in many morphological and quality characters which are the major yield attributing traits and an aim of chilli breeding programs (Rego *et al.*, 2009; Rodrigues *et al.*, 2012) [4, 5]. The exploitation of this existing vast variation for the yield and yield contributing characters is limited and has been neglected due to inadequate information about gene action and magnitude of major yield related traits (Ben-Chaim and Paran, 2000; Dhall and Hundal 2010; Goffar *et al.*, 2016; Navhale *et al.*, 2017) [6, 7, 8, 9]. However, the information provided is limited and also biometrical analysis with large population size is required. The potential of a population and selection efficiency for the improvement of cultivars can be examined by means of relative magnitude of additive, dominance and epistatic effects (Goncalves *et al.*, 2011; Hallauer *et al.*, 2010) [10, 11]. The chilli breeding program can be improved to substantial level if information about the nature and magnitude of gene effects is available which will help in designing the proficient breeding program. Further, understanding of the inheritance of yield contributing traits will help to exploit the use of genetic potential in an advance breeding program. Hence, considering the significance of chilli crop and in view of the above-mentioned constraints, the present study was carried out to understand the inheritance pattern of yield related traits in chilli.

Materials and Methods

Genetic Materials

To study the inheritance of plant and fruit related characters, we crossed a chilli accession, IHR 3575 with a bell pepper genotype, IHR 3476. IHR 3575 is characterized by small pungent fruits and resistance to important soil borne pathogen *Phytophthora capsici* whereas; IHR 3476 is blocky type sweet pepper cultivar. The six generations *i.e.* P_1, P_2, F_1, F_2, BC_1P_1 and BC_1P_2 were developed during summer season of the year 2016 (Fig. 1). IHR 3575 (P_1) was crossed with IHR 3476 (P_2) to produce F_1 seeds. The F_1's were self-pollinated to produce F_2 population. The back crosses were made to develop BC_1P_1 (backcross with IHR 3575) and BC_1P_2 (backcross with IHR 3476) populations.

Evaluation of Progenies

All the six generations were evaluated in the randomized block design with three replications at the research farm of Division of Vegetable Crops, ICAR-Indian Institute of Horticultural Research, Bengaluru (latitude 13°58' North, longitude 78°45' East and an altitude of 890 meters above mean sea level) during summer season of the year 2017. Crop management and all other recommended cultural operations were performed as per the standard practices with row- to- row and plant- to- plant distance of 60 and 45 cm, respectively to raise a healthy crop.

Data Collection

The data were recorded on 30 plants in parents and F_1, 250 plants in F_2 and 150 plants in each for BC_1P_1 and BC_1P_2 populations. The observations were recorded for five characters *viz*., plant height (cm), plant canopy width (cm), fruit length (cm), fruit width (cm) and fruit weight (g).

Statistical Analysis

The data recorded were subjected to generation mean analysis as described by Jinks and Mather (1971) [12]. The individual scaling test (Hayman, 1958) [13] along with three parameter genetic model (Jinks and Jones, 1958) [14] was performed to perceive the presence and absence of the gene interactions. The scales (A, B, C and D) were calculated as per the following formula: $A = 2BC_1P_1 - P_1 - F_1 = 0$; $B = 2BC_1P_2 - P_2 - F_1 = 0$; $C = 4F_2 - 2F_1 - P_1 - P_2 = 0$; $D = 2F_2 - BC_1P_1 - BC_1P_2 = 0$. The test of significance of different scales was carried out as described by Jinks and Jones (1958) [14] and the gene interactions were projected as per the following equations:

$m = F_2$

$d = BC_1P_1 - BC_1P_2$

$h = F_1 - 4F_2 - ½ (P_1 + P_2) + 2(BC_1P_1 + BC_1P_2)$

$i = 2BC_1P_1 + 2BC_1P_2 - 4F_2$

$j = (BC_1P_1 - BC_1P_2) - ½ (P_1 - P_2)$

$l = P_1 + P_2 + 2F_1 + 4F_2 - 4(BC_1P_1 + BC_1P_2)$

For the above equations, [m] is the mean of the F_2 generation, and the gene effects are additive [d], dominance [h], additive × additive [i], additive × dominance [j] and dominance × dominance [l]. The presence of the non-allelic interaction was confirmed by the significance of interaction components. The data for generation mean analysis were analyzed using the Statistical Analysis System (SAS) V 9.3 package at both one percent ($P < 0.01$) and five percent ($P < 0.05$) level of significance.

Results and Discussion

Mean Performance of Progenies

The mean values and standard errors of six generations derived from the cross of IHR 3575 and IHR 3476 for five plants and fruit related traits are presented in the Table 1. The parents expressed significant mean differences for most of the traits studied. The hybrid performed better than their respective parents for plant height and plant canopy width. For the traits such as fruit length, fruit width and fruit weight, the hybrid was better performing than P_1 generation while showed inferior performance as compared to P_2 generation. However, all the trait mean values of the F_1 generation were lower than the corresponding values of the F_2 generation. The BC_1P_1 and BC_1P_2 progenies resembled their respective recurrent parents with respect to all the traits whereas, F_2 individuals showed drastic variation for the yield related traits under study. The mean performance of the BC_1P_2 generation was higher than that of BC_1P_1 generation for the traits except for plant height and plant canopy width in the present study. Marame *et al.* (2009) [15] reported that the improved performance of F_1 could be due to an accumulation of favorable dominant alleles whereas, the better performance of the F_2, BC_1P_1 and BC_1P_2 generations might reveal a higher frequency of their transgressive segregants.

Generation mean analysis besides providing estimates of main gene effects (additive and non-additive), also confers precise information on non-allelic interactions *viz*., additive × additive [i], additive × dominance [j] and dominance × dominance [l], the relative magnitude of which will designate the future breeding program. The results acquired on estimates of scaling test and gene effects in regard to plant and fruit characters are presented through Table 2 and 3 and are discussed trait-wise here under.

Table 1: Generation means (±SE) of yield contributing traits of six generations in Chilli

Traits	P_1	P_2	F_1	F_2	BC_1P_1	BC_1P_2
Plant height (cm)	48.10 ± 1.07	33.96 ± 0.56	59.46 ± 1.26	65.63 ± 0.72	69.86 ± 0.78	44.99 ± 0.81
Plant canopy width (cm)	32.41 ± 1.07	28.11 ± 0.61	39.83 ± 1.03	41.67 ± 0.43	43.47 ± 0.52	28.63 ± 0.53
Fruit length (cm)	3.42 ± 0.06	7.51 ± 0.14	5.91 ± 0.11	6.67 ± 0.08	4.19 ± 0.05	8.47 ± 0.11
Fruit width (cm)	1.57 ± 0.05	5.75 ± 0.14	2.57 ± 0.05	2.92 ± 0.03	1.91 ± 0.02	4.52 ± 0.06
Fruit weight (g)	3.90 ± 0.08	104.27 ± 2.33	18.54 ± 0.56	21.36 ± 0.34	7.44 ± 0.25	43.71 ± 1.10

P_1- parent 1; P_2- parent 2; F_1- first filial generation; F_2- second filial generation; BC_1P_1- backcross generation derived from parent 1; BC_1P_2- backcross generation derived from parent 2.

Table 2: Individual scaling test and three parameter genetic model for yield contributing traits in chilli

Traits	A	B	C	D	[m]	[d]	[h]
Plant height (cm)	32.15** ± 2.29	-3.45 ^{ns} ± 2.14	61.53** ± 4.04	16.41** ± 1.85	49.19** ± 5.58	7.07** ± 0.61	-18.50* ± 9.23
Plant canopy width (cm)	14.69** ± 1.83	-10.68** ± 1.61	26.50** ± 2.97	11.25** ± 1.15	45.39** ± 4.43	2.15** ± 0.62	-31.41** ± 6.08
Fruit length (cm)	-0.95** ± 0.18	3.53** ± 0.29	3.93** ± 0.43	0.68** ± 0.21	3.79** ± 0.53	-2.04** ± 0.08	0.32 ^{ns} ± 1.04

Fruit width (cm)	-0.31** ± 0.10	0.73** ± 0.21	-0.78** ± 0.25	-0.60** ± 0.10	1.06** ± 0.29	-2.09** ± 0.08	1.70** ± 0.57
Fruit weight (g)	-7.56** ± 0.77	-35.38** ± 3.26	-59.79** ± 2.94	-8.43** ± 1.33	25.94** ± 3.41	-50.19** ± 1.17	-44.77** ± 8.14

[m] = mean effect; [d] = additive effect; [h] = dominance effect; *significant at $p = 0.05$; **significant at $p = 0.01$; ns = not significant.

Table 3: Estimates of gene effects for yield contributing traits in chilli using six parameter model

Traits	[m]	[d]	[h]	[i]	[j]	[l]	Epistatic gene action
Plant height (cm)	65.63** ± 0.73	24.87** ± 1.14	-14.39** ± 3.95	-32.82** ± 3.69	17.80** ± 1.29	4.12 ^{ns} ± 6.08	–
Plant canopy width (cm)	41.67** ± 0.44	14.84** ± 0.76	-12.92** ± 2.60	-22.49** ± 2.30	12.69** ± 0.97	18.48** ± 4.22	Duplicate
Fruit length (cm)	6.68** ± 0.08	-4.28** ± 0.13	-0.91* ± 0.44	-1.36** ± 0.41	-2.24** ± 0.15	-1.22 ^{ns} ± 0.67	–
Fruit width (cm)	2.92** ± 0.04	-2.61** ± 0.07	0.10 ^{ns} ± 0.23	1.20** ± 0.20	-0.52** ± 0.11	-1.61** ± 0.38	–
Fruit weight (g)	21.37** ± 0.35	-36.28** ± 1.13	-18.69** ± 2.95	16.86** ± 2.65	13.91** ± 1.63	26.09** ± 5.39	Duplicate

[m] = mean effect; [d] = additive effect; [h] = dominance effect; [i] = additive × additive effect; [j] = additive × dominance effect; [l] = dominance × dominance effect; *significant at $p = 0.05$; **significant at $p = 0.01$; ns = not significant.

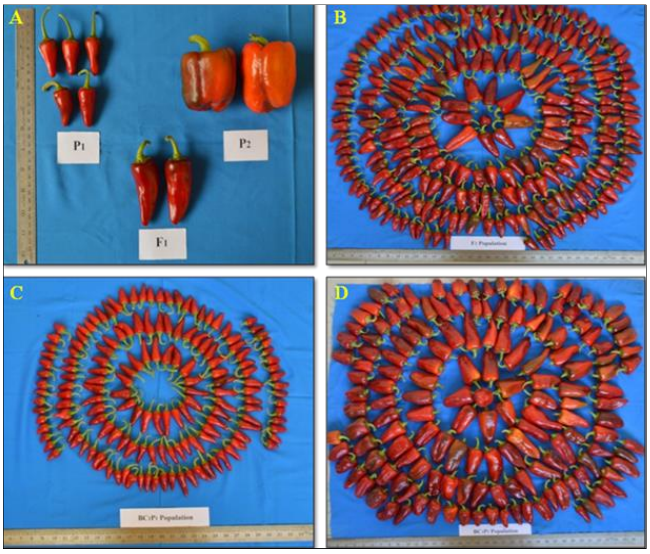

Fig 1: Development of six generations from the cross of IHR 3575 × IHR3476 (A- parent 1, parent 2, F_1 generation; B- F_2 generation; C- BC_1P_1 generation; D- BC_1P_2 generation)

Test for Additive- Dominance Model and Genetic Effects

In the present study, the estimates of simple scaling test manifested that scales A, C and D were significant exhibiting all the three types of non-allelic interactions *viz.*, additive × additive, additive × dominance and dominance × dominance in the inheritance of plant height as confirmed by significant three parameter genetic model. The higher magnitude of additive [d] gene effect was observed as compared to the dominance [h] gene effect. The additive gene effect was positive and significant whereas, dominance gene effect observed negative and significant. The interaction components *i.e.* significance of [i], [j] and [l] revealed that additive × additive, additive × dominance and dominance × dominance non-allelic gene interactions were present, respectively for the trait under study. Additive, dominance and additive × additive, additive × dominance epistatic gene actions controlled the plant height. This result is in close conformity with the previous report by Kamboj *et al.* (2007) [16] in chilli. The significance of [i] and [j] components of gene interaction is in line with the earlier findings of Patel *et al.* (2003) [17] for plant height in chilli. In contrary to this result, Anandhi and Khader (2011) [18] reported duplicate type of epistatic gene action for plant height in chilli. The presence of significant individual scaling test for plant canopy width was confirmed by three parameter genetic model indicating the presence of non-allelic gene interactions and hence, the additive-dominance model was further extended to epistatic effects of gene action. The presence of higher magnitude of additive × additive [i] and dominance × dominance [l] and lower magnitude of additive × dominance [j] type of gene interactions were observed. Among the epistatic effects of gene action, additive × additive [i] gene interaction was negative and significant whereas, additive × dominance [j] and dominance × dominance [l] were observed positive and significant. The contradictory signs of (h) and (l) effects suggested duplicate type of gene action for plant canopy width. Similar result for plant canopy width is also reported by Hasanuzzaman and Golam (2011) [19] in chilli.

The individual scaling test and three parameter genetic model for fruit length were recorded significant thereby, indicating the presence of epistatic interactions. The additive-dominance model was found insufficient as suggested by the significant three parameter model. Among the epistatic effects of gene action for fruit length, additive × additive [i] and additive × dominance [j] were recorded negative and significant type of gene interactions whereas, dominance × dominance [l] effect was found negative and non-significant. The fruit length was controlled by additive and dominance effects along with additive × additive [i] and additive × dominance [j] epistatic gene action. This finding is in accordance with the previous reports by Hasanuzzaman and Golam (2011) [19] in chilli. In contrary to this result the complementary epistatis for fruit length is reported by Somashekhar *et al.* (2008) [20] whereas; Bal and Singh (1999) [21] have reported duplicate epistasis in chilli. The results obtained for significance of scaling test and three parameter genetic model for fruit width revealed the occurrence of all the three types of epistatic interactions. The estimates of the six-parameter model indicated negative and significant additive [d] gene effect while positive and non-significant dominance [h] gene effect for this trait. The significance of additive × additive [i] was positive whereas, additive × dominance [j] and dominance × dominance [l] were observed negative and significant. Additive effect and all three types of non-allelic interactions were found to be involved in the control of fruit width. Sharma (2007) [22] has also reported the significant additive effect along with significant [i], [j] and [l] gene interactions for fruit width in chilli whereas, Patil *et al.* (2012) [23] has reported the duplicate type of gene interaction for fruit width in chilli. The significant values of A, B, C and D were observed in individual scaling test in addition to significant three parameter genetic model for the fruit weight indicating the non-allelic gene interactions for this trait. The additive [d] and dominance [h] components were observed negative and significant. Among the epistatic effects of gene action, additive × additive [i], additive × dominance [j] and dominance × dominance [l] type of gene interactions were found positive and significant. The contrary signs of [h] and

[l] effects suggested duplicate type of gene action for fruit weight. Similar results are also reported by Sharma (2007) [22] for fruit weight in chilli.

The significant simple scaling test and three parameter genetic model revealed the existence of epistatic interactions for all the traits studied hereunder. Further, the six-parameter model was used to assess the presence or absence and nature of the non-allelic gene interactions against the respective standard errors following a conventional ‘t’ test. The significance of [m] effect for all the traits studied implies that these traits are governed quantitatively. All the three types of gene action *i.e.* additive, dominance and epistatic interactions were observed to be involved in the inheritance of all the traits studied. The classification of gene interaction depends on the significance and sign of the estimates of dominance [h] and dominance × dominance [l] effects (Mather, 1982) [24]. The dominance [h] and dominance × dominance [l] effects have contrary signs for traits such as plant canopy width and fruit weight, signifying the presence of the duplicate type of epistasis. Though, duplicate epistasis hinders the expression and selection of traits in early generations of segregating populations. However, such gene effects can be exploited by delayed selection or selection after biparental intermating (Misra *et al.*, 1994) [25]. According to Singh and Narayana (2000) [26] the reciprocal recurrent selection can be used for the improvement of traits when both additive and non-additive gene effects are involved in the expression of the traits.

Conclusions

Significance of the individual scaling test strongly indicates that the various traits studied in the present research work were not under the control of simple additive or dominance gene effects, however epistatic (non-allelic) interactions also seemed to be involved in their inheritance. The information on nature and magnitude of generations mean and gene action for yield attributing traits is essential for the development of the high yielding varieties/ hybrids. Moreover, the presence of the additive [d] and dominance [h] gene effects, estimation of their relative magnitudes and types of epistatic interaction *viz.*, additive × additive [i], additive × dominance [j] and dominance × dominance [l] play an important role in selecting the suitable breeding method for crop improvement program in chilli.

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Compliance with ethical standards

Conflict of interest: The authors declare that there is no conflict of interest.

Author contributions

K. Madhavi Reddy designed the experimental scheme while, Manish Kumar performed the experiments with assistance from T.H. Singh. All the authors have discussed the results and commented on the manuscript.

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