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Study of β-carotene enhancing '*Or*' gene effects on yield and contributing traits in mid-season Indian cauliflower (*Brassica oleracea* var. *botrytis* L.)

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ABSTRACT

Nature of gene action of EC 625883, an orange curd colour genotype, on yield and contributing traits in cauliflower was studied by using five generation model (P_1, P_2, F_1, F_2 and F_3) in three cross combinations, *viz*., DC-309 × EC 625883, CC-35 × EC 625883 and DC 18-19 × EC 625883 for ten quantitative traits. The orange curd colour *Or* gene donor homozygous line EC 625883 and three divergent recipient mid season (November-January) maturity white curd lines, namely, DC-309, CC-35, and DC 18-19 were involved in hybridization. Generation mean analysis using scaling test indicated that epistasis gene interaction model fitted well for most of the traits under study in all the three cross combinations. The complementary type of gene interaction was observed for number of days to marketable curd maturity, total plant weight, marketable curd weight and net curd weight. The presence of complementary type of interactions and prevalence of high magnitude of non-additive gene effects suggested exploitation of heterosis breeding for improvement in cauliflower using *Or* gene for enhancing of β-carotene and micronutrient simultaneously.

Key words: β-carotene, generation mean analysis, orange cauliflower, quantitative traits, scaling test.

INTRODUCTION

Cauliflower is the most popular crucifer vegetable grown commercially in India on an area of 0.43 million hectares with a production of 8.57 million tonnes and 19.8 t/ ha productivity (Anon, 1). India ranks second in cauliflower production in the world. Major cauliflower growing states in India are West Bengal, Bihar, Odisha, Haryana, Madhya Pradesh, Gujarat, Jharkhand, Assam, Chhattisgarh and Uttar Pradesh. Cauliflower shares about 4.3% of the total area and 4.7% of the total vegetable production in India. The curd is edible part of cauliflower, which consists of proliferating, arrested inflorescence and floral meristems. It contains an appreciable amount of vitamin B, vitamin C, folate, calcium and protein. Vitamin A is essential for vision, gene transcription, immune function, embryonic development, reproduction, bone metabolism, skin health and antioxidant activity. Cauliflower, however, lacks β-carotones a precursor vitamin A the deficiency of which leads to night blindness, keratomalacia, xerophthalmia and retarded physical growth. The β-carotene is present in a wide variety of yellow-orange coloured fruits and dark green and yellow vegetables such as broccoli, spinach, turnip greens, carrots, squash, sweet potatoes and pumpkin (Farre *et al*., 7). The orange curd colour genotype is a spontaneous novel mutant, a rich source of β-carotene, is governed by single dominant gene (*Or*) with few modifier genes (Crisp *et al*., 4). In view of this, the present study was undertaken to study the effect of *Or* gene on yield and contributing traits in mid-season Indian cauliflower through generation mean analysis.

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MATERIALS AND METHODS

The experiment comprised five generations, *viz*., P_1, P_2, F_1, F_2 and F_3 developed from cross combinations of three mid season white curded recipient inbred lines, namely, Pusa Sharad (DC-309), CC-35, DC 18-19 and an *Or* gene homozygous donor line EC 625883. From this, three cross combinations, *viz*., DC-309 × EC 625883, CC-35 × EC 625883 and DC 18-19 × EC 625883 were developed. The experiment was conducted during 2009-2013 in a randomised block design with three replication at the research farm of the Division of Vegetable Science, ICAR-IARI, New Delhi situated at an elevation of about 228 m above mean sea level, 20° 40' N latitude and 77° 13'E longitude. Thirty-day-old seedlings were planted manually at a spacing of 60 × 45 cm between and within rows, respectively. The recommended cultural practices (Singh and Sharma, 16) were followed including recommended rate of 120N-80P-40K kg/ha. The N was from urea, P from single super phosphate, and K from muriate of potash. Half of N and all of P and K fertilizers were applied during land preparation. The remaining N was applied in two splits at 30 and 60 days after planting. The plots were flood irrigated through a furrow system beginning immediately after transplanting and at 12-15 day interval ensuring sufficient moisture. For weed management, the herbicide pendimethalin was

applied 2-3 days prior to transplanting at 3.3 l/ha. One month after transplanting, first earthing up was done and the first split application of nitrogen was applied; after an additional month, the second split application of nitrogen was applied. For managing diseases and insect pests, streptocycline at 0.1 g/ l water + blitox at 2 g/ l water and indoxacarb at 1 ml/ l water were applied 30 days after planting to control black rot disease and *Spodoptera* insect pest, respectively. The observations were recorded on ten plants each in parents and F_1 generations and 20 plants each in F_2 and F_3 generations for ten major traits, such as plant height, stalk length, leaves per plant, leaf length, leaf breadth, days to 50% curd initiation, number of days to marketable curd maturity, total plant weight, marketable curd weight and net curd weight. The quantitative data recorded for each of ten traits were compiled and mean values calculated from the data gathered from three replications for each trait were used for statistical analysis. The genetic effects were estimated using five parameter-model suggested by Hayman (5). The component of gene effects included [m] = mean of F_2 generation, [d´] = additive effect (joint estimates of d and ĵ in 5-parameter model), [h] = dominance effect, [i] = additive × additive effect, [l] = dominance × dominance effect. The scaling tests of Mather (13) were performed to detect non-allelic interactions, and gene effects were estimated according to Jinks and Jones (12).

RESULTS AND DISCUSSION

The mean and standard errors for five generations in respect of ten traits in three crosses have been presented in Tables 1, 2 and 3. The mean effect of all the ten characters studied, *viz.*, plant height, stalk length, leaves per plant, leaf length, leaf breadth, days to 50% curd initiation, number of days to marketable curd maturity, total plant weight, marketable curd weight and net curd weight were positive and significant in all the crosses (DC-309 × EC 625883, CC-35 × EC 625883 and DC 18-19 × EC 625883). The estimates of scaling tests and gene effects on five generation mean in each of the three crosses for all the traits studied are presented in Tables 4 & 5, respectively. In the absence of back cross generation, Hayman (9) and Jinks and Jones (12) prescribed five parameter model for generation mean analysis, which included F_3 as one of the generation in addition to P_1, P_2, F_1 and F_2. However, in the present investigation. C and D scaling test was carried out as suggested by Mather (13) in all the crosses for each trait to examine whether epistatic gene effects exist in the material under study, and its relative importance. Accordingly in interacting crosses, all the five parameters (m. d, h, i & l) were estimated.

Table 1. Generation means ± SE of plant height, stalk length, leaves per plant, leaf length of five generations of three crosses in orange cauliflower.

Trait / Generation	DC-309 × EC 625883	CC-35 × EC 625883	DC 18-19 × EC 625883
Plant height (cm)			
P_1	61.13 ± 2.64	61.20 ± 0.53	71.87 ± 1.80
P_2	62.73 ± 1.00	62.73 ± 1.00	62.73 ± 1.00
F_1	69.53 ± 2.48	68.47 ± 1.53	82.80 ± 0.90
F_2	69.67 ± 0.88	60.13 ± 2.18	65.93 ± 4.58
F_3	61.00 ± 0.58	59.00 ± 2.31	61.73 ± 1.33
Stalk length (cm)			
P_1	2.93 ± 0.44	3.62 ± 0.13	4.42 ± 0.19
P_2	2.53 ± 0.35	2.53 ± 0.35	2.53 ± 0.35
F_1	2.93 ± 0.13	3.31 ± 0.30	7.86 ± 0.27
F_2	3.47 ± 0.17	2.97 ± 0.14	3.19 ± 0.21
F_3	3.25 ± 0.04	2.79 ± 0.11	2.99 ± 0.06
Leaves per plant			
P_1	25.87 ± 0.71	25.07 ± 0.18	22.27 ± 1.55
P_2	23.93 ± 0.13	23.93 ± 0.13	23.93 ± 0.13
F_1	28.13 ± 0.53	25.93 ± 0.68	32.47 ± 1.00
F_2	25.27 ± 0.29	24.67 ± 0.47	25.80 ± 0.64
F_3	25.47 ± 0.18	24.13 ± 0.27	20.87 ± 0.48
Leaf length (cm)			
P_1	43.27 ± 2.66	52.80 ± 1.27	55.07 ± 0.24
P_2	51.40 ± 0.20	51.40 ± 0.20	51.40 ± 0.20
F_1	51.80 ± 2.91	54.80 ± 0.40	61.53 ± 0.85
F_2	57.87 ± 2.56	60.27 ± 2.94	49.53 ± 0.75
F_3	56.67 ± 2.26	58.60 ± 1.59	47.87 ± 0.24

The simple scaling test of Mather was applied to determine the presence of genetic interaction in three cauliflower crosses involving one common donor line carrying beta-carotene enhancing *Or* gene. The perusal of results indicate that C and D were largely significant in all of the crosses for most of the traits studied, suggesting the involvement of either one or both of the epistatic components *i* and *l*. On the basis of simple scaling test for epistasis, the five parameter model was fitted to the observed components of mean in each of the three crosses for all the traits.

In case of plant height, both the scales (C and D) were significant in all the three crosses. Dominance gene effects appeared to play an important role for the inheritance of plant height as it exhibited comparatively higher significant values in all the crosses. All the five components of gene effects (m, d, h, i, l) were significant in cross DC 18-19 × EC 625883 with complementary type of epistasis. In cross CC-35 × EC 625883, two

Table 2. Generation means ± SE of leaf breath, days to 50% curd initiation, number of days to marketable curd maturity of five generations of three crosses in orange cauliflower.

Trait / Generation	DC-309 × EC 625883	CC-35 × EC 625883	DC 18-19 × EC 625883
Leaf breadth (cm)			
P1	16.07 ± 0.27	17.73 ± 0.71	16.13 ± 0.35
P2	17.80 ± 0.12	17.80 ± 0.12	17.80 ± 0.12
F1	19.73 ± 2.32	18.87 ± 1.03	18.67 ± 0.35
F2	16.33 ± 1.19	15.67 ± 1.47	13.13 ± 0.44
F3	14.47 ± 0.37	14.93 ± 0.48	12.17 ± 0.24
Days to 50% curd initiation			
P1	68.80 ± 10.35	91.80 ± 0.31	93.47 ± 0.24
P2	85.40 ± 0.53	85.40 ± 0.53	85.40 ± 0.53
F1	81.87 ± 0.87	94.20 ± 0.31	91.87 ± 0.75
F2	77.00 ± 2.55	72.33 ± 0.24	103.40 ± 0.12
F3	80.93 ± 3.19	73.40 ± 1.29	105.60 ± 0.76
No. of days to marketable curd maturity			
P1	94.20 ± 2.41	108.87 ± 0.18	114.40 ± 0.87
P2	105.33 ± 0.24	105.33 ± 0.24	105.33 ± 0.24
F1	97.13 ± 0.97	113.73 ± 1.04	110.47 ± 0.87
F2	92.80 ± 3.97	86.40 ± 1.60	121.20 ± 0.83
F3	95.00 ± 2.34	91.73 ± 2.29	120.27 ± 0.75

components of genetic effects (m, l) were significant with complementary epistasis and preponderance for additive components, whereas in cross DC-309 × EC 625883, four components of gene effect (m, h, i, l) were significant with duplicate type of epistasis.

In case of stalk length, all the three crosses showed significant values for the scale 'C' only. The dominance component was comparatively higher in all the crosses suggesting its important contribution in inheritance of stalk length. Three components of gene effects (m, h, l) were significant in the cross DC 18-19 × EC 625883 with complementary type of epistasis, which was duplicate in the remaining crosses. In case of leaves per plant, only 'C' scale was significant in two crosses, namely, DC-309 × EC 625883 and DC 18-19 × EC 625883. Dominance component was found to play an important role in inheritance of leaves per plant exhibiting higher values in all the three crosses. Four components of the gene effects (m, h, i, l) in two crosses, namely, DC-309 × EC 625883 and DC 18-19 × EC 625883 were significant with complementary epistasis in the former and duplicate in the latter.

In case of leaf length, all the three crosses showed significant values for the estimates of scaling test C and D except for D in the cross DC 18-19 × EC 625883. Four components of gene effects (m, d, i, l) in cross DC-309 × EC 625883, two (m, l) in CC-35 × EC 625883 and four (m, h, i, l) in DC 18-

Table 3. Generation mean ± SE of total plant weight, marketable curd weight and net curd weight of five generations of three crosses in orange cauliflower.

Trait/ Generation	DC-309 × EC 625883	CC-35 × EC 625883	DC 18-19 × EC 625883
Total plant weight (g)			
P_1	2103.33 ± 171.50	1766.67 ± 52.39	2763.33 ± 38.44
P_2	1926.67 ± 126.67	1926.67 ± 126.67	1926.67 ± 126.67
F_1	3346.67 ± 245.04	3046.67 ± 73.33	4343.33 ± 24.04
F_2	1946.67 ± 238.42	1786.67 ± 150.70	1793.33 ± 173.72
F_3	1778.67 ± 116.17	1600.00 ± 126.62	2156.67 ± 58.40
Marketable curd weight (g)			
P_1	1580.00 ± 240.28	1043.33 ± 8.82	1513.33 ± 44.10
P_2	1314.00 ± 124.13	1314.00 ± 124.13	1314.00 ± 124.13
F_1	2710.00 ± 193.48	2386.67 ± 157.20	3310.00 ± 470.32
F_2	1263.33 ± 162.72	1054.00 ± 49.69	1273.33 ± 184.87
F_3	994.67 ± 90.64	1006.67 ± 66.42	966.00 ± 91.27
Net curd weight (g)			
P_1	1001.33 ± 79.74	653.33 ± 23.33	667.33 ± 15.38
P_2	1060.33 ± 49.77	1060.33 ± 49.77	1060.33 ± 49.77
F_1	2443.33 ± 164.76	1633.33 ± 98.38	3521.33 ± 16.18
F_2	531.33 ± 35.41	479.00 ± 21.22	512.67 ± 61.13
F_3	376.67 ± 44.10	431.33 ± 38.86	330.00 ± 30.55

Table 4. Scaling test for quantitative traits in mid-season orange cauliflower.

Trait	Cross	Simple scaling test	
		C	D
Plant height (cm)	C1	15.73**	-9.33**
	C2	6.71**	2.34**
	C3	2.34**	-3.92**
Stalk length (cm)	C1	2.53**	-0.69
	C2	0.94**	0.38
	C3	2.71**	-1.82
Leaves per plant	C1	-5.00**	-1.60
	C2	1.73	1.07
	C3	-2.88**	-1.49
Leaf length (cm)	C1	33.20**	-15.80**
	C2	12.09**	6.35**
	C3	2.75**	-2.49
Leaf breadth (cm)	C1	-10.33**	-8.43**
	C2	7.67**	3.17**
	C3	-1.35	-2.66**
Days to 50% curd initiation	C1	-22.60**	-3.20**
	C2	14.65**	6.18**
	C3	-0.68	-0.51
No. of days to marketable curd maturity	C1	-22.60**	-3.20**
	C2	16.19**	8.29**
	C3	-1.40	-0.39
Total plant weight (g)	C1	-2936.67**	-1581.33**
	C2	1093.23**	497.94**
	C3	-2.09**	-3.18**
Marketable curd weight (g)	C1	-3260.67**	-966.00**
	C2	804.06**	344.11**
	C3	-4.06**	-2.81**
Net curd weight (g)	C1	-4823.00**	-1317.33**
	C2	370.78**	111.72**
	C3	-13.01**	-11.79**

*,**Significant at 5 and 1% significance levels; Epistasis C1 = DC-309 × EC 625883, C2 = CC-35 × EC 625883, C3 = DC 18-19 × EC 625883

19 × EC 625883 were significant. Leaf length was found to be governed by duplicate type of epistasis in CC-35 × EC 625883 and complementary type in other two crosses.

For leaf breadth, the estimates of scaling test revealed significance for both the scales (C and D) in all the crosses except for scale 'C' in the cross DC 18-19 × EC 625883. Dominance gene effects were significant and predominant in all the crosses. Four components of gene effects (m, h, i, l) were significant in all the crosses except for nonallelic interaction (l) in the cross DC-309 × EC 625883 which also showed duplicate type of epistasis, whereas in others it was complementary type.

In case of days to 50% curd initiation, both the scales (C and D) were significant in two crosses, namely, DC-309 × EC 625883 and CC-35 × EC 625883; however these were non-significant in cross DC 18-19 × EC 625883. Dominance gene effects and dominant × dominant gene interaction 'l' were significant and predominant in all the crosses. Four components of gene effects (m, d, h, l), (m, h, i, l) and (m, d, h, l) in crosses DC-309 × EC 625883, CC-35 × EC 625883 and DC 18-19 × EC 625883, respectively were significant. Duplicate type of gene action was observed in cross DC-309 × EC 625883 and complementary type in the remaining two. For number of days to marketable curd maturity, the estimates of scales C and D were significant in crosses DC-309 × EC 625883 and CC-35 × EC 625883 and non-significant in DC 18-19 × EC 625883. Four components of gene effects (m, d h, i) in the cross C-309 × EC 625883, three (m, h, l) in DC-35 × EC 625883 and five (m, d, h, i, l) in DC 18-19 × EC 625883 were significant. The complementary type of epistasis was found to be predominant in all the crosses.

In case of total plant weight, marketable curd weight and net curd weight significant values were revealed for both the scales (C & D) in all the three crosses, which led to the estimation of all the five type of gene effects (m, d, h, i, l). All the components of the gene effects (allelic and non-allelic) were significant for the three traits in all crosses. Dominance gene effects appeared to play an important role in the inheritance of all the three traits as these revealed comparatively higher significant values as also non-allelic interaction 'l' in all the crosses. Complementary type of epistasis was observed in all the three traits in all the crosses. Since yield being complex polygenic trait resulting from interaction among various inherent traits and environment, it can be further improved through indirect selection on the basis of yield contributing traits (Chandra *et al.*, 2). Sufficient understanding of the inheritance of quantitative traits and information about it is essential to develop breeding strategy. Generation mean analysis is a powerful breeding technique for estimating main gene effects (additive and dominance) and their digenic (additive × additive, additive × dominance and dominance × dominance) interaction responsible for inheritance of quantitative traits. It helps us in understanding the performance of the parents used in the crosses to be used either for heterosis breeding or pedigree selection (Sharma *et al.*, 14). Therefore, the estimates of the relative magnitude of various gene effects including epistasis are of significance, when each cross combination is considered. Since linkage affects the epistatic term in generation mean (Hayman, 9), additive and dominant gene effects cannot be precisely measured in the presence of epistasis (Hayman, 10). Even with these

Table 5. Estimation of gene effects on five generation means for quantitative traits in mid-season orange cauliflower.

Trait	Cross	Gene effect					Type of epistasis
		m	d	h	i	l	
Plant height (cm)	C1	69.67**	-0.80	23.2**	13.82**	-46.58**	D
	C2	60.13**	-0.77	0.71	0.54	16.18**	C
	C3	65.93**	4.57**	22.44**	16.08**	22.58**	C
Stalk length (cm)	C1	3.47**	0.20	0.23	0.43	-2.60	D
	C2	2.97**	0.54	0.71	1.56	-0.05	D
	C3	3.19**	0.94	3.66**	1.17	11.34**	C
Leaves per plant	C1	25.27**	0.97	4.04**	2.74**	3.38**	C
	C2	24.67**	0.57	2.27	1.97	0.53	C
	C3	25.80**	-0.83	17.60**	7.81**	-8.53**	D
Leaf length (cm)	C1	57.87**	-4.07**	-0.84	-13.44**	-22.58**	C
	C2	60.27**	0.70	0.80	-0.50	-23.47**	D
	C3	49.53**	1.83	12.44**	7.81**	23.11**	C
Leaf breadth (cm)	C1	16.33**	-0.87	7.24**	2.71**	-0.89	D
	C2	15.67**	-0.03	4.09**	2.92**	4.62**	C
	C3	13.13**	-0.83	6.27**	2.90**	9.60**	C
Days to 50% curd initiation	C1	77.00**	-8.30**	-7.24**	-28.61	33.96**	D
	C2	72.33**	3.20	11.73**	12.53**	64.00**	C
	C3	103.40**	4.03**	-13.56**	-7.92	-19.02**	C
No. of days to marketable curd maturity	C1	92.80**	-5.57**	-2.98*	-11.48**	-23.29	C
	C2	86.40**	1.77	4.00**	0.90	101.33**	C
	C3	121.20**	4.53**	-4.67**	3.80**	-33.60**	C
Total plant weight (g)	C1	1946.67**	88.33**	1381.33**	226.33**	2837.33**	C
	C2	1786.67**	-80.00**	1337.78**	22.22**	2364.45**	C
	C3	1793.33**	418.33**	731.11**	-430.56**	8737.78**	C
Marketable curd weight (g)	C1	1263.33**	133.00**	1680.89**	683.89**	2424.89**	C
	C2	1054.00**	-135.33**	1014.67**	-464.00**	3301.33**	C
	C3	1273.33**	99.67**	2177.33**	480.33**	3792.00**	C
Net curd weight (g)	C1	531.33**	-29.50**	1687.11**	215.61**	4273.78**	C
	C2	479.00**	203.50**	896.67**	286.83**	2824.00**	C
	C3	512.67**	196.50**	2492.89**	557.61**	7048.89**	C

*, ** Significant at 5 and 1% significance levels; D = Duplicate epistasis C = Complementary epistasis C1 = DC-309 × EC 625883, C2 = CC-35 × EC 625883, C3 = DC 18-19 × EC 625883

limitations, estimates of the several parameters provide indication of the relative importance of various types of gene effects influencing total genetic variation of an attribute (Gamble, 8).

Presence of epistasis / gene interaction varied with the crosses as well as traits, and most of the crosses showed presence of epistasis. The generation mean for most of the traits showed importance of both additive and dominant types of gene effects. However, dominant gene effects were higher than additive gene effects. Several workers have estimated gene effects in cauliflower for different traits (Dixit *et al*., 6; Jindal and Thakur, 11; Singh *et al*., 15; Varalakshmi, 17; Devaraju *et al*., 5; Verma and Kalia, 18) who also reported importance of both additive and dominance components in the control of various traits, however dominance component was preponderant.

In the presence of epistasis, predominance of complementary type of gene action was observed. In such situation, dominance effects tend to be overestimated, while additive component is relatively underestimated. Some crosses showed duplicate type of gene interaction, in such cases intermating or biparental mating between selected plants from early segregating generations could help in improving such traits (Comstock *et al*., 3). Among the epistatic gene effects, dominance × dominance (l) type gene effect was greater in magnitude than additive × additive (i) type. It is evident from the present study that epistasis is important basic mechanism, therefore, while formulating

breeding startegies gene interactions should also be taken into consideration along with main gene effects. In complementary type of gene action, particularly i and l reinforce the effect of dominance component. It is because of this reason that heterosis is expressed with greater magnitude in crosses, where complementary type of interaction is observed (Jinks and Jones, 12), while it may not be observed at all in crosses showing duplicate type of gene action. In the present investigation, complementary type of gene action was exhibited for most of the traits in most of the crosses.

In conclusion, the generation means for most of the characters in the present study showed the importance of both additive and dominance type of gene effects. However, dominance effect, in general, was higher than additive gene effects. Among the epistatic gene effect, dominance × dominance type was greater than additive × additive. In the presence of epistatsis, complementary type of gene interaction was observed in almost all the crosses for most of the traits favouring heterosis breeding.

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