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Original article

A triple test cross analysis to detect epistatic gene effects in cabbage (*Brassica oleracea* var. *capitata L.*): An updated methodology

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ABSTRACT

The cross-pollinated crop *Brassica oleracea* var. *capitata L.* shows good heterotic heterosis at high output; better standing of the plants; early maturity; larger and more homogeneous heads; consistency of head compactness; and disease-tolerance in F1 hybrids. There is very limited information documented on the epistasis of essential cabbage characters. We expand the research in this study to include an upgraded test to cross-design for enrolling and estimating epistasis and other genetic variance components controlling head yield and component traits in cabbage. The data was obtained from 45 families produced by crossing 15 lines with three testers; SC 2008–09, E-1-3-1&2, and their single cross F1, was subjected to triple test cross analysis. The current study results confirmed "j + 1" form of epistasis which is a major component for all traits. The plant spread, non-wrapper leaves, nethead/grossweight, polar/equatorial diameter, marketable head yield per plot, iron content and dry matter lugged both "j + 1" and 'i' type with the predominance of the 'i' type of interaction. Except for head shape index, equatorial diameter, head compactness was more noticeable when observed in dominance component. The degree of dominance is in the partial range, but both the head shape index/compactness and equatorial diameter showed over dominance. For maximum part, superiority was shown in both the directions. Appropriate breeding procedures are proposed to exploit the different forms of gene effects discovered for genetic improvement of head yield and quality traits.

1. Introduction

One of the most widely grown and widely eaten Brassica family vegetables is the cabbage (*Brassica oleracea* var. *capitata* L.) (Singh et al., 2021). Several brassicas (cabbage and others) are grown throughout the world. It is a good source of dietary fiber, minerals, including beta-carotene, vitamin C, and glucose, as well as folic acid and fructokinase (Liao et al., 2021). It is an essential component of culinary dishes throughout the world, eaten as a fresh salad and preserved by freezing, dehydration, or pickling (Posta and Berar, 2006). Besides being nutritionally rich, cabbage has medicinal uses as well like, anticarcinogenic properties, anti-inflammatory potential due to the presence of chemical compounds like glucosinolates, glutathione, isothiocyanates (Ghebramlak et al., 2006; Kopsell et al., 2004; Singh et al., 2009). Recognizing the importance and scope of cabbage as a commercial crop around the world, research efforts to improve and develop high yielding cabbage varieties/hybrids are needed. Crop enhancement programs' effectiveness is highly reliant on the quality and scale of genetic components of variation. The selection of breeding procedure is primarily determined by knowledge of gene action regulating economic character. As a result, accurate estimates of such components are needed in order to construct an efficient breeding strategy. Many mating designs make the assumption that epistatic interactions are absent, which is often incorrect. The triple test-cross (TTC) research proposed by Kearsey and Jinks (1968) and their adaptation proposed by Jinks *et al* as are the most important design for the study of population genetic architecture (Jinks and Perkins, 1970). Based on TTC, there are few options for reliable tests and epistasis with unbiased estimation of both additive and dominant genetic components in the absence of epistasis with the widely used tests. Pooni and Jinks (1976) demonstrated that the triple test cross strategy outperformed the alternative

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strategies for detecting epistasis. Furthermore, the method is unaffected by gene correlation, mating mechanism, or allelic frequency. This study was documented in limited studies and present study was to investigate the function of various genetic components within the head yield of inheritance and another horticulturally significant characters in cabbage.

2. Materials and methods

2.1. Precise location, materials and test design

This study was carried out within the premises of our department. The location of the research department was located at 32°6́ N latitude, 76°3́E longitude and 1290.80 m at mean sea level. Agrochemically, the site is in Himachal Pradesh's mild hill region (Zone-II) with the humid climate i.e., sub-temperature and a high rainfall of 2500 mm throughout the annum. Experimental materials used in this study 45-TTC progenies resulting from the mating of 15 inbred lines (females) with three testers (males), namely SC 2008–09 (P1), E-1-3-1&2 (P2), and their single cross F1. Table 1 shows the basic material used for producing triple test cross progenies, as well as their distinguishing characteristics. Jinks and Perkins (1970) suggested an updated TTC design, which was used for the crosses. SC 2008–09 and E-1-3-1&2 were crossed to each other and with 15 lines, resulting in plenty of F1 seeds, and 30 single crosses. Similarly, F1 as the male parent was crossed with 15 lines (females) to create 15 three-way crosses, yielding 45 triple test cross families (L1i, L2i, and L3i). During 2019–2020, this material was raised in triplets using Randomized Complete Block Design (October-March). Inter cultural operations were performed within the accordance with prescribed sets for vegetable crops (Sharma and Sirohi, 2003).

2.2. Observations on quantitative characteristics

The observations were made on ten competitive plants that were marked at random through the replications in each entry on distinct quantitative traits such as days to harvest, plant spread (cm), net weight of head (g), grossweight (g), non-wrapper leaves (n), stalk-length (cm), polar/equatorial diameter (cm), heading (%), head shape-index, compactness of head (g/cm^3), marketable heads per plot (n) and and marketable head yield (kg/plot).

Table 1
Salient features of parents used for developing triple test cross progenies.

Lines/Testers	Internal colour of head	Shape of head in longitudinal section	Shelf life (in days)
I-105 (L_1)	Cream	Broad elliptic	30
I-Suhasini (L_2)	Yellowish	Transverse elliptic	30
I-Madhuri (L_3)	Yellowish	Transverse elliptic	32
II-105 (L_4)	Yellowish	Transverse narrow elliptic	33
II-Suhasini (L_5)	Yellowish	Transverse elliptic	34
II-Madhuri (L_6)	Cream	Transverse elliptic	30
III-105 (L_7)	Yellowish	Transverse elliptic	33
III-Madhuri (L_8)	Whitish	Transverse elliptic	28
Glory-I-Suhasini (L_9)	Yellowish	Transverse elliptic	30
Glory-I-Madhuri (L_{10})	Yellowish	Transverse elliptic	33
Glory-7-Suhasini (L_{11})	Cream	Broad elliptic	33
Glory-7-Madhuri (L_{12})	Cream	Transverse elliptic	30
GA(P)-105 (L_{13})	Cream	Transverse elliptic	30
GA(P)-Suhasini (L_{14})	Yellowish	Broad elliptic	30
GA(P)-Madhuri (L_{15})	Whitish	Transverse elliptic	33
SC 2008–09 (P_1)	Yellowish	Transverse elliptic	30
E-1–3-1&2 (P_2)	Whitish	Transverse elliptic	32
F_1 ($P_1 \times P_2$)	Yellowish	Transverse elliptic	28

2.3. Examination in a laboratory

In fresh marketable heads, total soluble solids (°B), ascorbic acid (mg/100gs), iron content (mg/100gs), carotenoids (µg/100gs), vitamin B1 (µg/100gs), and dry matter (percent) were measured. TSS was determined using a hand refractometer. According to Rangnna (2007), ascorbic acid was measured using a colorimetric system with 2, 6-dichlorophenol indophenol dye. Rangnna (2007) developed a system for estimating iron content that used absorbance at 480 nm and iron requirements for the calibration curve. Carotenoids were collected in acetone solution, and spectrophotometer measurements were taken at 480, 663, and 645 nm OD. Sadasivam (1996) suggested a spectrophotometric approach for determining vitamin B1. The dry matter was calculated using the procedure described by Arora et al. (2008).

2.4. Statistical analysis

The statistical analysis for epistasis detection was performed with the existence of non-allelic interaction and epistasis can be calculated as the described method (Kearsey and Jinks, 1968). The testing and estimation of additive and dominance elements were performed with Jinks and Perkins (1970) and Singh and Chaudhary (1977) studies. The other stats were performed as per the documented study (Khan et al., 2019).

3. Results

In this current study, 15 lines and 3 testers of combined study variance for the parents and their specific 45 TTC hybrids were showed elevated substantial genotype variations for all traits (Table 2). The results obtained for 45 TTC hybrids were correlated with TTC analysis to estimate the numerous genetic variance components. The results which was showed in Table 3 was TTC analysis of variances confirmed the mean-square attributable to hybrids were highly important for all traits tested, indicating the existence of sufficient heterogeneity in the triple test cross progenies for detecting the breeding of recombination.

For all traits, the mean squares due to epistasis showed the existence of major non-allelic interactions (L1i + L2i −2L3i) (Table 4). The existence of 'i' form of interaction (additive additive) for plant

Table 2
Analysis of variance for the Randomized Complete Block Design for head yield and related traits in cabbage.

	Mean squares due to		
Source of variation Traits df	Replications 2	Treatments 62	Error 124
Days to harvest	7.871	162.782*	2.708
Plant spread (cm)	2.116	25.212*	2.423
Stalk length (cm)	0.095	0.807*	0.102
Number of non-wrapper leaves	13.334	3.127*	1.018
Gross weight (g)	635.069	80626.990*	65.085
Net head weight (g)	57.815	47486.950*	43.761
Polar diameter (cm)	0.135	2.636*	0.059
Equatorial diameter (cm)	0.102	2.003*	0.054
Head shape index	0.003	0.012*	0.002
Head compactness (g/cm^3)	0.637	89.781*	0.725
Marketable heads per plot	0.958	1.607*	0.592
Heading (%)	66.498	111.601*	41.100
Marketable head yield per plot (kg)	0.252	5.884*	0.249
Ascorbic acid content (mg/100 g)	0.876	26.476*	1.139
Total soluble solids (°Brix)	2.271	1.735*	0.148
Carotenoid content (µg/100 g)	30.820	18946.970*	53.916
Iron content (mg/100 g)	0.000	0.012*	0.000
Dry matter (%)	0.020	0.622*	0.010
Vitamin B_1 content (µg/100 g)	4.658	109.639*	1.889

Table 3
Analysis of variance for triple test cross hybrids for head yield and related traits in cabbage.

Source of variation	Mean squares due to		
	Replications	Hybrids	Error
Traits df	2	44	88
Days to harvest	1.844	152.196*	2.996
Plant spread (cm)	1.057	26.892*	2.669
Stalk length (cm)	0.075	0.667*	0.104
Number of non-wrapper leaves	19.788	3.865*	1.121
Gross weight (g)	369.252	61526.000*	64.615
Net head weight (g)	24.067	23836.060*	52.188
Polar diameter (cm)	0.043	2.600*	0.032
Equatorial diameter (cm)	0.031	1.434*	0.028
Head shape index	0.001	0.015*	0.001
Head compactness (g/cm^3)	0.090	60.382*	0.797
Marketable heads per plot	1.096	1.416*	0.611
Heading (%)	76.098	98.344*	42.443
Marketable head yield per plot (kg)	0.343	2.864*	0.299
Ascorbic acid content (mg/100 g)	1.501	29.250*	1.054
Total soluble solids (°Brix)	3.110	1.699*	0.155
Carotenoid content (µg/100 g)	79.954	22136.570*	54.114
Iron content (mg/100 g)	0.000	0.050*	0.000
Dry matter (%)	0.015	0.635*	0.011
Vitamin B$_1$ content (µg/100 g)	4.946	113.988*	1.942

* Significant at $P \leq 0.05$.

spread, gross weight, non-wrapper leaves , net head-weight, polar-diameter, equatorial-diameter, marketable head yield per plot, head shape-index, iron content, and dry matter was discovered by more mean square partitioning due to epistasis into 'i' and 'j + l'. On the other hand, all of the characters examined had 'j + l' form of relationship (additive dominance and dominance dominance). As a result, it is obvious that the role of epistasis should not be overlooked when developing a breeding program to enhance commercially relevant traits. Epistasis is an essential for genetic variance: it's zygosity cannot be accurately calculated if it is neglected. If that is the case, multiplicative and dominant parameters will be underestimated, as well as additive and dominant/dominant conclusions will be erroneously estimated.

4. Discussion

Earlier researchers, such as Sharma *et al*, Atter *et al*, Meena *et al.*, and Singh *et al*, have documented considerable variability in their respective cabbage materials for the various collection of characters studied (Sharma, 2001; Atter et al., 2009; Meena et al., 2009; Singh et al., 2013). Estimates of mean squares due to quantities (measuring D component) and disparities (measuring H component) revealed that additive and dominance genetic variances were important for all characters except marketable heads per plot and heading percentage, for which the D component was non-significant. This demonstrated the significance of both components in regulating these characteristics. Because of the greater magnitude of additive gene action, fixable gene action was observed for the majority of the traits. However, due to the higher magnitude of the dominance variable, the non-fixable form of gene action was predominant for equatorial diameter, head shape index, and head compactness. The average degree of dominance (H/D) 1/2 for the majority of the traits was in the range of partial dominance. Overdominance was observed for equatorial diameter, head shape index, and head compactness, indicating the significance of both additive and non-additive gene effects. For most of the characters examined, the r estimates indicated ambi-directional dominance, with declining alleles more frequently dominant than increasing alleles (Table 5). Solieman (2002), Thakur, and Vidyasagar (Reshma et al., 2018) have all expressed similar viewpoints.

Where gene activity is involved in the expression of traits in both additive and non-additive forms, the proposal was made to use reciprocal recurrent selection to improve the characteristics. The main additive action in head yield and most of its constituent characteristics was successfully established in this paper, which is contrary to previous reports that non-additive gene action was dominant in head yield and in most of its traits through diallel and line testing designs (Parkash et al., 2003; Pathak and Kumar, 2007; Singh et al., 2011, 2018; Kibar et al., 2015). As a result, this demonstrates the dependability of the triple test cross mating design in accurately evaluating gene action of biometrical traits.

Table 4
Analysis of variance for the detection of epistasis for head yield and related traits in cabbage.

Source of variation	Epistasis	i-type interaction	(j + l) type interaction	Epistasis × replication	i-type × replication	(j + l) type × replication
Traits df	15	1	14	30	2	28
Days to harvest	754.405*	449.500	776.542*	24.294	44.564	22.846
Plant spread (cm)	164.854*	426.703*	146.150*	18.618	14.311	18.925
Stalk length (cm)	3.581*	2.218	3.678*	0.434	2.007	0.321
Number of non-wrapper leaves	27.681*	101.971*	22.375*	8.076	4.205	8.353
Gross weight (g)	483014.333*	2566622.250*	334185.196*	531.867	2330.108	403.420
Net head weight (g)	195279.044*	1883752.125*	74673.824*	337.978	965.437	293.159
Polar diameter (cm)	23.289*	149.459*	14.276*	0.256	0.272	0.255
Equatorial diameter (cm)	5.661*	11.430*	5.258*	0.276	0.323	0.273
Head shape index	0.122*	0.527*	0.093*	0.006	0.006	0.006
Head compactness (g/cm^3)	373.135*	60.112	395.494*	5.976	22.597	4.788
Marketable heads per plot	8.133*	10.755	7.946*	2.800	0.822	2.941
Heading (%)	564.715*	747.130	551.685*	194.402	56.949	204.211
Marketable head yield per plot (kg)	18.175*	130.629*	10.143*	1.480	0.636	1.540
Ascorbic acid content (mg/100 g)	89.832*	526.817	58.619*	6.013	30.080	4.294
Total soluble solids (°Brix)	2.894*	0.131	3.091*	0.973	0.602	0.999
Carotenoid content (µg/100 g)	5299.827*	415.386	5648.716*	342.895	928.522	301.064
Iron content (mg/100 g)	0.042*	0.045*	0.041*	0.002	0.001	0.002
Dry matter (%)	1.462*	2.832*	1.365*	0.051	0.140	0.054
Vitamin B$_1$ content (µg/100 g)	57.162*	3.755	60.977*	8.216	5.589	8.404

* Significant at $P \leq 0.05$.

Table 5
Analysis of variance for sums ($L_{1i} + L_{2i} + L_{3i}$) and differences ($L_{1i} - L_{2i}$) and the estimates of genetic parameters for head yield and related traits in cabbage.

Mean squares due to Estimates of genetic parameters								
Source of variation	Sums	Sums × Rep.	Differences	Diff. × Rep.	D	H	$(H/D)^{1/2}$	r
Traits df	14	28	14	28				
Days to harvest	322.419*	0.562	319.934*	7.288	423.732*	421.668*	0.998	0.529*
Plant spread (cm)	68.056*	0.015	57.407*	5.259	83.922*	69.139*	0.907	0.643*
Stalk length (cm)	1.621*	0.385	1.401*	0.264	1.815*	1.576*	0.932	−0.175
Number of non-wrapper leaves	9.989*	21.481	7.087*	3.675	10.544*	7.533*	0.845	0.298
Gross weight (g)	110146.286*	1472.000	101784.214*	4.691	146654.476*	135631.465*	0.961	0.406
Net head weight (g)	44878.857*	252.000	41312.232*	45.355	59695.238*	54989.358*	0.959	0.110
Polar diameter (cm)	3.592*	0.006	1.973*	0.018	4.768*	2.610*	0.740	0.445
Equatorial diameter (cm)	2.347*	0.026	4.320*	0.009	3.114*	5.749*	1.359	0.432
Head shape index	0.018*	0.001	0.019*	0.000	0.023*	0.024*	1.015	0.114
Head compactness (g/cm^3)	88.725*	3.734	116.686*	0.827	116.442*	154.452*	1.151	0.140
Marketable heads per plot	3.031*	1.088	2.231	0.955	2.305*	1.416	0.784	0.665*
Heading (%)	210.402*	74.937	154.933	66.359	159.881*	98.321	0.784	0.665*
Marketable head yield per plot (kg)	6.236*	0.186	5.787*	0.469	7.518*	7.066*	0.969	0.262
Ascorbic acid content (mg/100 g)	104.194*	2.782	18.019*	0.417				
	134.703*	22.167*	0.406	−0.008				
Total soluble solids (°Brix)	7.707*	3.315	0.563*	0.349	10.037*	0.453*	0.212	0.148
Carotenoid content (μg/100 g)	85629.714*	312.000	6020.344*	81.069	114035.809*	7902.110*	0.263	−0.092
Iron content (mg/100 g)	0.060*	0.000	0.015*	0.002	0.079*	0.019*	0.486	0.246
Dry matter (%)	1.674*	0.056	0.898*	0.047	2.206*	1.169*	0.728	−0.010
Vitamin B_1 content (μg/100 g)	455.274*	3.203	28.031*	1.151	602.422*	30.985*	0.227	0.280

D = Additive component, H = Dominance component, $(H/D)^{1/2}$ = Degree of dominance, r = Correlation coefficient.

[*] Significant at $P \leq 0.05$.

5. Conclusion

The present study was concluded as the analysis of variance shows that the material under study produced a significant amount of genetic variability. The presence of non-allelic interactions stressed that it is difficult to imagine a case in which epistasis might be considered missing and thus should not be overlooked as this would lead to either over or under estimation of additive and dominance components of variation. In the early generations, breeding procedures such as selection could be useful for improving those characters that showed a preponderance of additive gene effects. The current result also demonstrated the significance of additive dominance (j) and dominance (l) epistasis in the inheritance of head yield and related traits. Since they are non-fixable, the dominance part, as well as the 'i' and 'j' types of epistasis, can be exploited by developing high yielding hybrids through heterosis breeding.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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