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DEVELOPMENT OF HYBRIDS IN COLE CROPS : A REVIEW

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Abstract

The significant global rise in agricultural output over the last few decades has been contributed by hybrid breeding. An efficient pollination control system is required to avoid the unwanted self-pollination or sib-pollination of the female parental line in hybrid breeding programme. With the use of cost effective mechanisms to produce large scale hybrids utilizing selected parental lines ultimately determines the commercial viability of the hybrid varieties. In cole crops, heterosis shown positive response towards high yield, uniform maturity, earliness, tolerance to biotic and abiotic stresses and better quality produce. Although, crosses in cole crops is mainly done by use of controlled pollination and genetic emasculation techniques *viz*., self-incompatibility (SI) and male sterility for commercial hybrid seed production, which is economically feasible. Almost all the cultivars of cole crops grownare F_1 hybrids, mainly developed by male sterility and SI mechanisms have been evolvedfor the development of experimental and commercial hybrids.

Key words : Hybrid, heterosis, combining ability, gene action, *Brassica*.

Introduction

The cole crops (*Brassica oleracea*) consists of numerous plants having chromosomes number (2n=2x=18). These crops are grown from temperate to tropical climatic conditions in different parts of the world. These crops have rich composition of nutrients, which includs several carotenoids like beta-carotene, lutein, zeaxanthin; vitamins C, E and K; folate and minerals (Singh and Devi, 2015). In addition, cruciferous vegetables consists substance 'glucosinolates' which is responsible for its pungent aroma and bitter flavours.

The word 'cole' probably derived from the word 'caulis' means stem/cabbage/stalk. It is known with different names as Kale (English), Kohl (German), Chou (French), Cal (Irish), Col (Spanish), Cavolo (Italian) and Couve (Portuguese) but generally, the word cole is more recognized in the literature worldwide.

The cole crops like, broccoli, brussels sprout, cauliflower, cabbage, kale and kohlrabi at present have evolved after a long time of mutation, natural/artificial hybridization, selection and domestication due the presence of variation within and between subspecies of *B. oleracea*. In the western and southern Europe and North Africa all forms of cole crops are derived from a common kale like ancestor, the wild cabbage (*B. oleracea* L. var. *sylvestris* L.) (table 1). Taxonomically, the cole crops belong to the order *Brassicales* (*Cruciales*), family *Brassicaceae* (*Cruciferae*), tribe *Brassiceae*, subtribe *Brassicinae*, genus *Brassica*, section *Brassica* and species *oleracea* (Singh, 2015).

The economic parts used in cultivated cauliflower (stem), cabbage (leaves), kohlrabi (flower), kale, broccoli and Brussels sprouts(modified) forms which are named as curd, head, knob or leaf. The curd of cauliflower in botanical terms described as pre-floral fleshy apical meristem in which the lateral buds of shoot meristem are elongated and branched, and apices of these branches form the structure of curd of which there will be chances of abort prior to flowering.

In cabbage, once the rosette stage gets completed, new leaves develop with shorter petioles and the leaves begin to form head in cup inward form. Generally it has smooth leaves, while savoy cabbage has attractive crinkled leaves. Furthermore, kohlrabi, grown for its swollen/enlarged stem (knob) which is short duration crop which grows in cool seasonand harvestedat young and tender stage.

The economic partin sprouting broccoli, is 'head' which bears on terminal bud and the 'sprouts' which arise

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from axillary budsconsists of functional flower buds. In Brussels sprout, which bear a resemblance to as small cabbage, which is mainly grown for sprouts *i.e.* swollen axillary buds, which arise along the stem of the plant. Further, crops like kale and collards are non-heading cole vegetables which is grown mostly for tender leaves, mainly used as greens or salad.

The mechanism of bolting and flowering, incole crops usually occurs on mature vegetative plants either in-situ or ex-situ at 5-10°C temperatures which in turn known as vernalization. The temperature and precipitation/ rainfall are two main factors which play major role in selecting the area for seed production of cole crops for vernalization and for season of flowering, seed maturity and harvesting.

The type of inflorescence incole crops except cauliflower is racemose type, the cauliflower havecymose type. The flowers having four sepals, four petals, six stamens (two are short) and two carpels along with superior ovary, septum and two rows of campylotropous ovules. The sepals are green and erect bearing yellow to white colour.

The androecium is tetradynamoushaving two short and four long stamens. Honey bees are pollinating agents. The period from pollination to fertilization generally takes 24-48 hrwith ideal temperature 12-18°C. The lower (less than ideal) temperature affects both fertilization and seed setting. And higher day temperature causes pollen sterility, resulting in poor seed setting and development.

Botanically fruit of crucifersareknown assiliqua, often called pod. The seeds are small, globular, smooth and dark brown in colour. Normally, each pod contains 10-20 seeds and in one gram nearly 300-350 seedsare present. Generally, pod matures at 50-90 days from date of flowering.

Hybrid technology

The technique in which two different parental lines or two inbred lines crossed to develop offsprings is hybrid. Hybrid involves several concepts like heterosis, hybrid vigour, combining ability, gene action etc. The concept of heterosis was first proposed by Shull (1908) signifies the superiority of F_1 hybrid in one or more characters over better parent. Hayes and Jones (1916) first exploited heterosis in cucumber later, extending in various other crops and vegetables including cole crops. In cole crops positive heterosis have been observed especially in yield, earliness, uniform maturity, tolerance to various biotic and abiotic stresses, and better quality produce.

Over period of time the heterosis in cole crops has been greatly facilitated by controlled pollination and genetic emasculation techniques *viz*., self-incompatibility (SI) and male sterility [cytoplasmic male sterility (CMS)] for commercial production of F_1 hybrid seeds.

The advantage of hybrids in cole crops relies ondevelopment of F_1 hybrids and commercial hybrid seeds production.In hybrids proper selection of genotypes/ parental materials has to be done for developing superior F_1 hybrids for better yield, adaptability, quality and tolerance to stresses involveselection of genotypes/ parents, development of inbreds/SI lines/CMS lines, testing for good combinersand evaluation. And hybrid seed production mainly depends on crossing techniques like CMS system and Self-incompatible lines.

In cole crop, the success of cross-pollination varies 40-100% due to presence of SI system due toprotogynus nature of flowers influenced by environmental conditions. In addition, in summer cauliflower (Snowball or Erfurt), there may be self-pollination because of weak SI system.

Inbreds are developd by selecting few plants on the basis of their superiority for desired traits and selfed by bud-pollination or selfing with mixed pollens of selected plantsby repeatingupto 6-8 generations. Doubled haploid (DH) system is an alternative method to produce inbreds by microspore culture, as they generate number of inbred lines with 100% homozygosity in one generation withmore efficient in accelerating breeding programmes to develop new varieties which is tedious in classic breeding approach. With the successful isolation and culture of microspores in *B. napus* by Lichter (1982) and *B. oleracea* var. *italica* by Keller and Armstrong (1983), microspore culture technology has been applied in various breeding programmes for improvement of *Brassicae*. In continuance, Pang *et al*. (2004) and Gu *et al*. (2014) have improved the protocols for efficient production of DHs in cauliflower.

In self-incompatibility self-pollens are recognize and discriminated by stigma thus prevents self-fertilization and inbreeding, and enforces out-crossing. The sporophytic type of SI has been studied by many workers and till date, >70 SI alleles have been isolated in the various cole corps. Watts (1965b) suggested fertility index estimation using following formulae for determining SI lines within and between the progenies.

$$\text{Fertility index (FI)} = \frac{\text{Average no. of seeds per siliqua from natural/compatible cross-pollination}}{\text{Average no. of seeds per siliqua from self-pollination in freshly opened flowers}}$$

If a line having fertility index-

>2 SI line

<1 SC line

1-2 Pseudo-SI.

The use of SI to produce hybrids was suggested by Pearson (1932), it was not until 1950 that they first appeared in Japan and by 1954 in the USA (Wallace, 1979). The advantage of SI system is to produce hybrid seed using two SI lines homozygous for different S-alleles. However, there are several disadvantages which hinder the use of SI like less reliable, inbreeding depression generation after generation and difficulties with reproduction of SI lines.

The second technique is male sterility where the inability of the plant to produce fertile pollen, which provides one of the most efficient and direct controlled pollination for hybrid seed production on large scale. Hence, more attention has been given to isolate the genetic sources of male sterility and use of them in heterosis breeding and hybrid seed production of cole crops.

There are mainly three type of male sterility in cole crops namely, genic male sterility (GMS), cytoplasmic male sterility (CMS) and cytoplasmic genetic male sterility (CGMS). The genetics of GMS is due to monogenic recessive or dominant nuclear genes. The recessive GMS in cole crops have also been reported by Cole (1959), Nieuwhof (1961), Sampson (1966) and Dickson (1970). The practical utility of recessive GMS is limited due to its instability and non-availability of marker genes linked to sterility.

Dominant GMS as a spontaneous mutation has been reported in several *Brassica* crops e.g. Chinese cabbage (Van der Meer, 1987), cauliflower (Ruffio-Chable *et al*., 1993) and cabbage (Fang *et al*., 1997); which have been used to develop homozygous dominant male sterile lines. The dominant GMS type of sterility can be restored, but difficult to maintain. MS lines with superior genes have been used todevelop hybrids in cabbage for commercial seed production.

In CMS type of male sterility, it is controlled by a cytoplasmic male sterile gene (S) where the cytoplasm of zygote comes primarily from the eggs cell resulting in male sterile. The plants showing cytoplasmic male sterility has the characteristics of the cytoplasmic inheritance, maternal inheritance, where sterility is easy to be maintain. This type of sterility is not apparently found in cole crops but has been introduced from several sources. The CMS has been reported in an identified cultivar of Japanese radish by Ogura (1968) and was introduced by transferring to *Brassica oleracea* genome through repeated backcross with broccoli (Bannerot *et al*., 1974 and McCollum, 1981).

Based on GCA and SCA estimates the inbreds/ parents which is to be used in development of F_1 hybrid must be selected. Generally, SCA value of gives better prediction than GCA value of the parents. Combining ability can be studied by adapting single cross, three-way cross, double cross, top cross, diallele cross and polycross mating designs. For SCA single cross, three-way cross

Table 1 : Evolution of cultivated *B. oleracea* crops (Prakash *et al*., 2011; Singh, 2015).

Evolution in order wise	Scientefic name (*B. oleraceae* var.)	Common name	Ancestor
1	var. sylvestri L.	Wild cabbage	-
2	var. ramosa DC.	Thousand-head kale, branching bush kale	1
3	var. gemmifera DC.	Brussels sprout	2
4	var. dalechampii		3
5	var. costata DC.	Portuguese tree kale, tronchuda kale	1
6	var. medullosa Thell.	Marrow-stem kale	1
7	Intermediate between 6 & 8		6
8	var. gongylodes L.	Kohlrabi	7
9	var. sabuda L.	Savoy cabbage	5
10	var. capitata L.	White cabbage	9
11	var. capitata L.	Red cabbage	10
12	var. viridis L., var. sabellica l., var. palmifolia DC.	Kale and Collards	1
13	var. italicaPlencks	Broccoli, calabrase	12
14	var. botryris L.	Cauliflower (biennial)	13
15	var. botryris L.	Cauliflower (annual)	14
16	var. botryris L.	Cauliflower (Indian)) or Tropical cauliflower	15

and double cross are used to study, for GCA polycross; and top cross and diallele cross for GCA and SCA both. All these mating designs are compatible to SI system; while single cross, three-way cross, top cross and polycross mating designs are compatible to male sterility system (CMS).

The promising hybrid combinations are evaluated in replicated trials along with check on the basis of combining ability estimates. Later followed by multi-location testing. The hybridshaving broader adaptability should berecommended for commercial production.

Heterosis

The term heterosis was first used by Shull in 1914. It is superiority of F_1 hybrid over both its parents in terms ofyield and some other character. Usually heterosis is manifested as an increase invigour, size, growth rate, yield or some other characteristic. In several cases, the superior parent of the hybrid may be inferior to thebest commercial variety. In such cases, it will be desirable to estimate heterosis in relation to the best. Hybridization between inbreds developed from the same variety or from closely related varieties produced only a small degree of heterosis.

Singh *et al*. (2009) observed that cabbage crop, exhibited strong heterosis for high yield, better plant stand, early maturity, larger and more uniform heads, uniformity in head compactness and disease tolerance in F_1 hybrids. In addition, the estimate ofheterosisfor mineral elements in cabbage was made for Fe, Zn, Cu and Mn. Significant mean square for parents and hybrids was observed for all minerals under study, which indicated the prevalence of sufficient variation. The parents 83-2, Pride of Asia, Red Cabbage, AC-204 and MR-1 were found to have the potential for use in cabbage quality breeding programme as they exhibited higher hybrid effects for Fe, Zn, Cu and Mn content. The single cross-hybrids, i.e. 83-2 × AC-204; Pride of Asia × C-2 and Pride of Asia × Red Cabbage; Pride of Asia × MR-1; 83-2 × Red Cabbage; and Pride of Asia × AC-204 and 83-2 × MR-1 were the best for Fe and Zn; Fe and Cu; Zn and Mn; Cu and Zn and Cu, respectively. It clearly revealed that none of the hybrids excelled for all the minerals suggesting the significance and need for multiple crossing breeding approaches, *i.e.* three way cross-hybrid, double cross-hybrid, population improvement, synthetics, composites, etc., for increasing the mineral concentration in cabbage head, *i.e.* “Breeding Cabbage for Higher Mineral” (Biofortification) without losing the vigour advantage for yield and other traits of economic importance to combat mineral deficiencies in human beings and plant systems.

Naveen and Tarsem (2005) observed significant and desirable heterobeltiosis for all the characters in cauliflower except plant height, plant spread and days to curd maturity. Best heterobeltiotic effects in desirable direction for stalk length (-13.46%) and curd compactness index (18.62%) were exhibited by PG-26 × D-9. On the other hand, maximum heterobeltiosis for characters *viz*., net curd weight and per cent marketable curds was expressed by Pusa Sharad×D-5320 (74.77%) and PG-26 ×D-91 (14.28%), respectively. Besides, maximum heterosis over the respective better parent for equatorial diameter of curd (21.88%) and curd size index (43.31%) was possessed by Pusa Sharad×D-9-2. Significant and desirable heterosis over the Pusa Synthetic (standard heterosis) was observed for all the characters under study except for stalk length and per cent marketable curds. Pusa Sharad×D-5320 exhibited maximum significant standard heterosis for equatorial diameter of curd (9.36%) and net curd weight (24.25%).

Sernyk and Stefansson (2004) examined the degree of heterosis for seed yield in F_1, hybrids of summer rape (*Brassica napus* L.) in replicated yield trials during two year (1980 and 1981) using intervarietal hybrids produced by manual crossing. The seed yields from the F_1, hybrids of crosses between Marnoo and Regent, and Karat and Regent exceeded those of Regent by 38 and 43V0, respectlely. With the possible exception of maturity, which was one day later than Regent, the agronomic and quality characteristics of these hybrids appeared to be within the ranges acceptable in commercial rapeseed cultivars. However, the successful development of hybrid rapeseed cultivars still depends upon the development of a suitable cytoplasmic, genetic or chemical (male gametocide) pollination control system.

Kibar *et al*. (2015) studied the direction and magnitude of heterosis in twenty-fourhybrids for yield contributing head traits in cabbage (*Brassica oleracea* var. *capitata* L.). A field experiment was conducted during the cabbage growing season of 2011-2012 at the Black Sea Agricultural Research Institute, Samsun, Turkey. Hybrids and parents were evaluated ina randomized block design with three replications. Measurements were performed for headweight, head diameter and head length to estimate mid parent and better parent heterosis in eachhybrid. The direction and magnitude of mid parent and better parent heterosis among hybridsfor all the head traits was found to be highly variable. The maximum and significant heterosisin favorable directions both over mid parent and better parent for head weight (73.6 and 62.3%, respectively), head diameter (39.6 and 39.1%, respectively) and head length (25.3 and 21.6%, respectively) was observed in the hybrid P8 ×P14. In this study, the hybrids P8 ×P14, P3 ×P13, P3 ×P14 and P8 ×P13 were found to be promising hybrid combinations with regard totheir per se performance for head traits and the magnitude of heterosis.

Bondareva and Engalychev (2009) revealed the optimal plant development stages for controlling self-incompatibility and propagating lines by geitonogamous pollination of buds on inbred lines of Chinese cabbage of the pakchoi varietal type. General combining ability is assessed by a complete diallel scheme of crosses of eight inbred lines and the most promising ones producing a high heterotic effect with respect to yielding ability, productivity, and clubroot resistance are identified.

Thakur and Vidyasagar (2016) crossed seven lines (four cytoplasmic male sterile and three self-incompatible) of cabbage with four cabbage testers as per line × tester mating design during 2012-13 to produce 28 F_1 hybrids. These hybrids along with lines and testers were evaluated in randomized block design during 2013-14 to carry out combining ability and gene action studies. The line × tester analysis revealed significant differences due to lines and testers for most of the traits studied. The general combining ability (GCA) effects indicated that the line CMS GAP followed by II-12-4-10 and the tester SC 2008-09 were the best general combiners for net head weight and most of the component traits. On the basis of specific combining ability (SCA) effects, the hybrids CMS GAP × E-1-3, CMS II × E-1-10 and SI 2008-09-03-01× Glory-1 were the most potential specific combiners. The magnitude of dominance variance was higher than additive variance for most of the traits indicating the preponderance of non-additive gene action vis-à-vis exploitation of hybrid vigour in cabbage. The CMS based hybrids have excelled in their heterotic performance for most of the traits whereas for the traits *viz*., gross and net head weight, equatorial diameter and marketable head yield per plot the SI system based hybrids excelled in their performance.

Dey (2014) studied combining ability and heterosis for first time and reported important vitamins and antioxidant plant pigments in cauliflower. Five CMS lines were crossed with 8 male fertile lines in line × tester design to develop 40 hybrids. These hybrids along with parental lines were evaluated for different vitamins and anti-oxidant pigments to reveal extent of heterosis and genetic combining ability. The CMS line Ogu12A was good general combiner (*gca* effect) and Ogu16A was poor general combiner for most of the important traits under study. Most of the heterotic hybrid combinations were associated high specific combing ability (*sca* effect). However, *gca* effect was also important in developing quality heterotic hybrids. The proportions of $\sigma^2 gca/\sigma^2 sca \sigma gca^2/\sigma sca^2$ were less than unity in all the cases indicating the role of non-additive gene action for most of the traits. Highest number of heterotic hybrids in positive direction was recorded for ascorbic acid content followed by anthocyanin content. The accumulated average heterosis of the 40 hybrids was in positive direction for ascorbic acid, anthocyanin and lycopene concentration whereas it was in negative direction for carotenoids and chlorophyll pigments. Very high heterosis for ascorbic acid, anthocyanin and carotenoids in cauliflower indicated the scope for development of F_1 hybrids with higher concentration of these vitamins and anti-oxidant pigments. It is possible to develop heterotic hybrids for different vitamins and anti-oxidant plant pigments through selection of parental lines based on desirable genetic combing ability.

Yang *et al*. (2012)analysedheterosisfor additive × dominant genetic model with genotype × environment (GE) interaction to head weight, head diameter, head height, maturity, plant height, plant spread width and leaf number in cauliflower, based on 2 × year data from 6 × 6 diallel crosses. The results indicated that the effect of environmental deviation of different years on agronomic traits of parents and F_1 was less. The correlation between mean values of agronomic traits in F_1 and parents mean values were significant. These traits could be improved by selection in early generations for head weight, head diameter, head height and maturity which were mainly affected by additive effects. However, the selection effects were prone to be affected by the dominance effects and genotype×environment interaction effects for plant height, plant spread width and leaf number. Therefore the improvement effects would be better for these traits by conducting selections in advanced generations. The total heterosis of head weight, plant height, plant spread width and leaf number was positive value and maturity was negative value for improvement of these traits breeding in cauliflower. There was only genotype × environment interaction heterosis detected for head diameter, the selection effects were easily affected by the various environments. There was no heterosis detected for head height.

Swarup and Pal (1966) studied on the inheritance of curd characters and manifestation of heterosis in cauliflower indicating that dominance and epistasis contributed most towards inheritance of curd maturity, net weight and size of curd. Heterosis manifested in terms of earliness of curd maturity (five to seven days), heavier curd weight (24.55–28.91 per cent.) and larger curd size (22.54–34.85 per cent.) over the better parent. Besides dominance and epistasis, over-dominance was also found in some cases to cause heterosis. Presence of significant additiveness and complementary epistasis found in many crosses may be favourable for improvement of the heterotic hybrids by selection in later generations. Transgressive segregation observed in the F_2 generation may also prove useful for this purpose. The use of F_2 seeds, due to superior performance of some of the hybrids over the better parent and sometimes over the F_1hybrid, may be feasible and economical.

Combining ability

Verma and Kalia (2016) conducted an experiment to identify the superior hybrids in mid-late maturity group of Indian cauliflowerbased on gene action and genetic combining ability. Fifty four F_1 hybrids were developed using self-incompatible linesin line × tester and evaluated along with parental lines for yield and related attributes. The proportions of $\sigma^2 gca/\sigma^2 sca$ were less than unity in all the cases indicating the role of non-additive gene action. Based on generalcombining ability analysis, line cc-35 (64.6 days) and tester HR-12-4 (59.3 days) was found as best general combinerfor earliest to curds maturity. However, line cc-22 (0.83 and 0.67 kg) and tester Pusa Paushja (1.02 and 0.81 kg)was identified as best general combiner for economic traits like marketable and net curd weight, respectively. Similarly, from specific combining ability analysis, hybrids cc-35L×HR-6-5-1-2 (58 days) and cc-35×Pusa Shukti (62 days) were identified as the earliest for days to curd maturity. The high yielding hybrids cc-35L×Pusa Paushja (1.68 kg), cc-22×PalamUphar (1.56 kg), cc-22×SarjuMaghi (1.53 kg) and cc-22×Sl-1-2 (1.53 kg) with maximum SCA effect for marketable curd weight were mid-late in maturity may be utilized for the further testing andcommercial exploitation of heterosis.

Singh *et al.* (2009) evaluated combining ability ofsuperoxide dismutase, peroxidase and catalase activity in cabbage head. Head samples were frozenimmediately in liquid nitrogen and placed at -80 ^{0}C for assay. Less than unity values of $\sigma^2 gca/\sigma^2 sca$ ratiofor all three enzymes indicated predominance of non-additive gene action. The parents CMS-GA and Red Cabbage excelled as good general combiners for all antioxidants and indicated the value and need formultiple crossing. The crosses CMS-GA×Red Cabbage, CMS-GA×C-2, 83-2 ×AC-204, 83-2 × EC-490174, 83-2 × AC-1021, Pride of Asia×C-4, and Pride of Asia×AC-1019 showed significant specificcombining ability, which could be exploited through heterosis breeding. The hybrid combinations withhigh per se performance and favorable SCA estimate and involving at least one of the parents with high GCA estimate could be useful to increase the abundance of favorable alleles for enhancing the antioxidants in cabbage head.

Ram *et al.* (2017) evaluated the combiningability and heterosis for different dietary minerals in snowball cauliflower. Five geneticallydiverse Ogura cytoplasmic male sterile (CMS) lines of cauliflower and seven male fertiletesters were crossed in line × tester mating scheme to obtain 35 F_1 hybrids. The assessment ofthe F_1's along with their parental lines for 8 important macro- and microelements revealed awide range of heterosis. The CMS line, Ogu 13-85 was identified as a good general combinerfor sodium (Na), calcium (Ca), iron (Fe), zinc (Zn) and manganese (Mn) content, whereas Ogu 101 for Mn, Zn, sulphur (S) and magnesium (Mg) contents. The lines with better general combining ability (GCA) produced majority of the heterotic hybrids. However, GCA alone was not sufficient to determine and identify the potential parental lines. The hybrid, Ogu101 × LalchowkMaghi was found to be the best heterotic combination for potassium (K), S and Zn content. The cross Ogu 13-85 × LalchowkMaghi was the best heterotic hybrid for Naand Ca content. The cross-combinations Ogu 13-85 × DB- 187, Ogu 13-01 × DB- 187 and Ogu 13-01 × Sel- 26 showed high heterosis for accumulation of Mg, Fe and Mn, respectively. It was observed that both GCA and specific combining ability were important for heterosis ofmineral content in snowball cauliflower.

Dey *et al.* (2011) selected three CMS lines, Ogu1A, Ogu2A and Ogu3A were among ten lines after BC_7 basedon superior commercial, floral and seed setting traits. Introgression of sterile Oguracytoplasm in cauliflower nuclear background reduced the flower size but did not affect commercial and seed setting traits drastically. Line × Tester analysis was done by taking these three CMS lines free from floral deformities as female parent with nine diverse lines of snowball cauliflower as tester. The parent Ogu2A exhibited highest GCA effect for curd yield (4.51) and harvest index (1.97) while Ogu1A exhibited highest GCA for earliness (–2.73). The parent, Ogu2A exhibited significant GCA for curd length (0.39) while, none of the CMSlines showed significant GCA for curd diameter and depth. Heterosis for curd yield was highest in the hybrid, Ogu2A × Kt-22 (63.5%) followed by Ogu1A × WF (36.9%) and Ogu1A × Kt-15 was the best hybrid for earliness followed by Ogu3A × Kt-22 with heterosis of –14.4% and –11.7%. However, the number of heterotic hybrids for yield and earliness waslow indicating narrow genetic base of the snowball cauliflower.

Singh *et al*. (2002) estimated combining ability effects for six characters in 4 lines × 6 testers crossing programme for cauliflower. Significant variances were observed for lines, testers and line × tester for all the traits except leaf size index for line × tester. Female parents Cauliflower No.1, RSK 1301 and male parents CC 2, CC 3 showed high general combining ability forearliness. Kt 25 was found to be a good general combiner for all the traits except days to 50% curd maturity. High *sca* effects for yield and other traits were showed by the cross combinations, Cauliflower No. I × Janavon, PSB 1 × Janavon and RSK 1301 × Lawyna.

Deepa *et al*. (2005) estimated the general and specific combining ability in earlymaturing cauliflower lines through line × tester analysis involving 6 lines and 6 testers. The combining ability analysis revealed highly significant differences among the treatments for all the parameters studied. The mean squares due to lines and testers were significant for allthe characters except stem length, whereas due to line × tester, it was significant for leafnumber, leaf weight and leaf area. Among the parents, First Early, IIHR-217- 1-4- 6, IIHR-263and IIHR-Sel. 3, IIHR-217-1-4-6, IIHR-305 were the best general combiners for days taken for 50% curd initiation and days taken for 50% curd maturity, respectively. Similarly, First Early and Katki among the lines and IIHR-263 among the testers were the best general combiners for yield contributing characters. The best specific combinations for curd weight were Katki × IIHR-263, IIHR-Sel.3 × IIHR-302, Arka Kanti × IIHR-316, Early Kunwari ×IIHR-250- 4-1- 11, Early Kunwari × IIHR-217- 1-4- 6 and Katki × IIHR-305.

Lal *et al*. (1977) selected six early maturing inbreds from maturity group I of Indian cauliflowers anddiallel crosses were made to study the combining ability of inbreds and identify the desirable parent(s) for hybridization. Seven characters, *i.e.* curd weight, curd size index, maturity, plantheight, number of leaves, leaf size index and plant spread were studied both in F1 and F_2 generations. Though, the estimates of both general and specific combining ability varianceswere highly significant for all the characters, the magnitudes of general combining ability variances were higher than that of specific combining ability variances. The performance ofthe inbreds was in general associated with their general combining ability effects. The inbred 103 was found to be best combiner for all the characters and the cross 105 × 108 showedmaximum yield potential.

Gene action

More and Wallace (1987) estimated of D and H_1 and revealed that manifestation of head weight and head diameter is governed by nonadditive genetic components. Both the additive and non-additive genetic components are involved in the expression of head length, core length, stem length and plant height. Over dominance was recorded for head weight, length and diameter and core length; and dominance for stem length and plant height. Recessive alleles were more frequent than positive alleles in the parents in stem length and plant height. For remaining characters the reverse was true. The studies also revealed that more than one genes controlling head weight, length and diameter exhibited dominance. Summing up the results, heterosis breeding has been recommended for head weight, length and diameter while conventional selection procedure would bring desirable improvement in stem length and plant height.

Prakash *et al*. (2017) made 60 crosses between 5 cytoplasmic male-sterile lines and 12 male-fertile testers during the summer of 2015, as per the line × tester design to study gene effects. The seedlings of all the parents and 60 F_1 crosses, along with three checks, were transplanted during the *Rabi* (winter) season of 2015-2016 and evaluated using a randomized complete-block design. Combining ability, gene action and heterosis were determined for different antioxidant compounds. Experimental results revealed that the range of cupric ion reducing antioxidant capacity (CUPRAC) [parents = 1.26-7.33 and hybrids = 0.04-6.54 μmoltrolox/g], ferric reducing ability of plasma (FRAP) [parents = 1.65-4.76 and hybrids = 0.16-4.67 μmoltrolox/g], β-carotene (parents = 0.44-2.29 and hybrids = 0.04-1.89 μg/100 g) and chlorophyll-a (parents = 0.71-4.08 and hybrids = 0.19-3.08 mg/g f.w.) for hybrids was lower than that of the parents because of outbreeding depression. The parental lines 6A, 208A, 83-5-8, and Sel-5-83-6 were found to be good general combiners for most of the antioxidant compounds studied. Based on the mean performance, specific combining ability effects and heterosis, five hybrid combinations *viz*., 9A × KIRC-8 for CUPRAC and FRAP; 208A × C-122 for ascorbic acid; 6A × Chhaki-2 for total carotenoids and β-carotene; 831A × Chhaki-2 for chlorophyll-a; and 6A × 83-5-8 for chlorophyll-b and total chlorophyll content, were most promising. The ratio of general combining ability (GCA) and specific combining ability (SCA) variances, *i.e.*, [$2\sigma^2 g/(2\sigma^2 g + \sigma^2 s)$], which reflects the relative importance of GCA versus SCA, was less than unity for different antioxidant compounds, which implied that for these traits, nonadditive gene effects were more important than additive effects. The numerical values of range for contribution of lines × testers interaction for different traits (41.47-70.18%) were found to be higher than the individual contribution of lines (11.24-47.22%) and testers (8.31-21.76%).

Singh *et al*. (2013) conducted an experiment with seventy one cabbage genotypes including cultivars, germplasm and F_1 hybrids grown in field. Mineral composition of the genotypes tested differed highly significantly indicating the presence of adequate amount of variability. A high heritability (>80%) accompanied by high genetic advance as percentage of mean (>40%) for uptake and accumula-tion of Fe, Zn, Cu, Mn and Ca indicates the predominance of additive gene, which could be improved by hybridization followed by selection breeding approach. Nevertheless, heterosis breeding would be an imperative in increasing the K content in cabbage heads as indicated by non-additive gene action for K accumulation having high heritability (>80%) and low genetic advance as percentage of mean (<30%). Moreover, both additive and non-additive genes were responsible for individual head weight. A positive correlation for Fe, Zn and Mn contents with other minerals will help in simultaneous selection of mineral elements. Nevertheless, major yield contributing 'head weight' was negatively correlated with minerals content and emphasized the selection of smaller head size to maintain the higher minerals content in tis-sues of cabbage heads.

Singh *et al*. (2015) investigated at Palampur during rabi 2012 and 2013 to gather information on the nature of gene action by following line × tester mating design involving five lines and three testers. The analysis of variance revealed significant differences among treatments for days to marketable curd maturity from date of transplanting, gross weight per plant, marketable yield per plant, curd size index, curd depth, curd diameter, per cent marketable curds, stalk length, number of leaves per plant, plant height, harvest index, ascorbic acid content and total soluble solids. The magnitude of dominance variance was higher than additive variance for all the traits except curd depth and total soluble solids which indicated the involvement of nonadditive gene action which could be utilized through the development of hybrids in cauliflower. A complete correspondence was noticed between per cent contribution of line × tester interaction (crosses) and non-additive gene action (σ^2D), which reaffirm the importance of hybrids in cauliflower.

Verma and Kalia (2015) evaluated eighty crosses derived from line (10) × tester (8) mating design along with their parents to study the combing ability and its relationship to gene action and heterosis for eight yield and related traits in early maturity cauliflower. Analysis of genetic component of variance and variance due to specific combining ability ($\sigma^2 sca$) revealed preponderance of dominant variance and non-additive gene action for all of the traits except for days to 50% curd maturity. In hybrids, contribution of lines was higher over the testers for all the traits. Among the lines cc-32E, 395aa and 14-4-17 and testers Sl-71, 23000 and Pusa Deepali were identified as promising general combiner for gross plant weight and marketable and net curd weight. However, hybrid cc-32E × Pusa Meghna was earliest (52 days) for curd maturity. For leaf area, plant height, curd compactness and gross plant weight the best combination was cc-32E × 23000. Among the hybrids, identified superior crosses with significantly highest level of heterosis over better parents were 395aa × Sel-7 (68.0%), cc-32E × 23000 (48.19%) and 395aa × Pusa Deepali (34.76%) for economic trait marketable curd weight. Hence, these hybrids can be further tested under different agro-climate for commercial production.

Mumtaz *et al*. (2015) used the Hayman and Jinks model to estimate genetic expression (i.e. gene action) on quality-related traits (oil percetange, glucosinolate, protein percentage, erucic acid, lenolenic acid, oleic acid and moisture percentage) using four lines (UAF-11, Toria, BSA and TP-124–1) and their hybrids in a diallel fashion. All traits other than oil percentage and linolenic acid were found to be controlled by dominant gene action. Absence of non-allelic interaction (epistasis) was observed for all traits. Number of frequency of dominant genes was more frequent towards better parents, and recessive genes were greater than dominant genes in all traits, except in the case of lenolenic acid. The best parents were TP-124–1 and UAF-11, which had the maximum dominant and maximum recessive genes, respectively, for the best traits (*i.e.* protein percentage, erucic acid, lenolenic acid and oleic acid); they can be used as parents in future hybrid breeding and other future breeding programs.

Singh and Kumar (2016) investigated 7 × 7 half diallel of cauliflower (*Brassica oleracea* var. *botrytis* L.) including 21 F_1's and 7 parents was undertaken with a view to estimate the extent of genetic variability, correlation, path analysis, manifestation of heterosis, general and specific combing ability effects and genetic components of variance indicating different type of gene effects. The analysis of variance revealed highly significant differences among genotypes for all the attributes under study. High heritability coupled with moderate genetic advance as per cent of mean was recorded for the plant height indicating importance of additive gene action controlling this character. The F_1 cross INB-21-2 × PCF-84 was best heterotic combination for gross plant weight, marketable curd weight, net curd weight, curd diameter, curd depth, curd size index and curd yield per hectare (q) over better parent. PG-3 × PES-1 was best heterotic cross over standard parent. Other combinations showing significant values for all type of heterosis were INB-21-2 × PCF-27, PG-3 × PCF-84, PCF-27 × PES-1 and INB-21-2 × X PES-1. The findings of present investigation revealed that the parent PG-3 (stalk length), INB-21-2 (days to curd initiation and days to curd maturity), PCF-27 (plant height, days to curd initiation, days to 50 per cent initiation, days to curd maturity, gross plant weight, marketable curd weight, net curd weight, curd diameter, curd depth, curd index, harvest index and curd yield), PES-1 (leaf length, leaf width, days to curd initiation, days to 50 per cent curd initiation, days to curd maturity, gross plant weight, marketable curd weight, net curd weight, net curd weight, curd depth, curd index, harvest index and curd yield), PCF-108 (plant height, plant diameter, number of leaves per plant, leaf length, leaf width and stalk length) and DC-98-4-2 (plant diameter, curd diameter and days to 50 per cent curd initiation) were promising donor based on general combining ability. The crosses INB-21-2 × PCF-84 and PG-3 × PES-1 showed maximum *sca* effects hence, these crosses may be advanced to recover desirable segregants for the improvement of yield and yield contributing characters.

Rahman *et al*. (2011) A 7× 7diallel experiment (excluding reciprocal) on Brassica rapa (toria)was conducted to study the nature and magnitude of gene action analysis and inheritance of some elected genotypes for seed yield and other related characters such as days to 50% flowering, days to maturity, plant height, primary branches per plant, secondary branches per plant, length of siliqua, siliquae plant^{-1}, seeds siliqua^{-1}, 1000-seed weight, seed yield plant^{-1}, harvest index and oil content. The components of variation along with the derived genetic ratios for different traits, showed that the D and H components, which measure additive and dominance variation respectively, were significant for all the traits studied. The results indicated the importance of both additive and dominance components for the inheritance of all the traits in Brassica campestris. However, the magnitude of dominance was higher than the additive component for all the traits except days to maturity, siliqua per plant, which indicated that dominance component had a predominant role in the inheritance of these traits. The positive and negative estimation of h_2 indicated mean direction of dominance and respective genes towards positive and negative sides, respectively. The results showed that eight characters*viz*., plant height, primary branches plant^{-1}, 1000-seed weight, secondary branches plant^{-1}, siliquae plant^{-1} and seed yield plant^{-1} possessed positive effects, indicating the mean direction of dominance as well as importance of dominant genes in the expression of these traits. On the other hand, days to flowering, days to maturity, seeds siliqua^{-1}, harvest index and oil content exhibited the values in negative direction, showing the excess of recessive genes for these traits.

Conclusion

The first studies of JG Koelreuterin the eighteenth century that wereconfirmed by Darwin for vegetables (1876) and Beal for maize (1880) the concept ofhybrid vigour gained increasing attention inplant breeding. The success of hybridbreeding will only be realized if reasonably priced technical solutions are available. The benefit characters of hybrids are not only limited to increased seed yield or biomass but also improve physical stability, higher responsiveness to fertilizers, better root penetration and seed filling are valuable advantages as well. The improved toleranceto abiotic stresses (eg drought and heat) inhybrids has been particularly relevant, which is economic. Moreover hybrid seeds are important tools for capturing the value of products that have been created by breeders. They broadened the genetic diversity of parental lines which ensure continued genetic gains.

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