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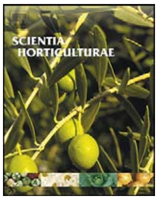

Combining ability for superoxide dismutase, peroxidase and catalase enzymes in cabbage head (*Brassica oleracea* var. *capitata* L.)

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ABSTRACT

Antioxidant enzymes have been touted as beneficial for enhancing the fitness, preventing disorders, and mitigating the effects of aging and senescence. Our objective was to evaluate combining ability of superoxide dismutase, peroxidase, and catalase activity in cabbage head. Head samples were frozen immediately in liquid nitrogen and placed at −80 °C for assay. Less than unity values of $\sigma^2_{gca}/\sigma^2_{sca}$ ratio for 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 for multiple 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 specific combining ability, which could be exploited through heterosis breeding. The hybrid combinations with high *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.

1. Introduction

Cabbage (*Brassica oleracea* var. *capitata* L.) is economically an important cole crop grown and consumed worldwide. There are various biotic, abiotic and environmental stresses/problems responsible for reducing the productivity as well as quality of the head (Maggio et al., 2005; Khattab, 2007). Most of the disorders/illness in aerobic organisms including plants and humans are aroused through production of deleterious free radicals/active oxygen species (AOS) such as singlet oxygen ($^1O_2$), superoxide radical (*$O^-{}_2$), hydrogen peroxide (H_2O_2), hydroxyl ion (OH^-), and free Hydroxyl radical (*OH) which are invariably produced in mitochondria, endoplasmic reticulum, micro-bodies, plasma membranes, chloroplasts, etc. during normal or aberrant metabolic processes as well as a consequence of exposure to various stresses (Marschner, 1995). However, conditions when free radical production is excessive, or when the antioxidant system is insufficient may favor an oxidative damage to aerobic life.

AOS are highly reactive and, therefore, harmful. Aerobic organisms would not survive without antioxidant systems that counteract the detrimental effects of free radicals (Devasagayam et al., 2004). The system includes enzymes such as superoxide dismutase (SOD), peroxidase (POX), and catalase (CAT); vitamins like beta-carotene (a vitamin-A precursor), vitamin-C, and vitamin-E; phytochemicals such as phenol, flavinoid, and phenylopropanoid; and minerals like selenium and zinc (McKersie, 1996; Singh et al., 2006). SOD is regarded as the key enzymatic antioxidant, localized in cytosol, chloroplast, mitochondria and peroxisomes, catalyses the scavenging of *$O_2{}^-$ to H_2O_2. However, POX, an iron heme protein, accelerates the reduction of H_2O_2 with a concurrent oxidation of a substrate, mostly located in cell wall, and involved in oxidation of phenol compounds towards the synthesis of lignin. CAT, the third enzyme, also scavenges H_2O_2 to water and molecular oxygen, localized in mitochondria and peroxisomes, and absent in chloroplast (Kuk et al., 2003; Starzynska et al., 2003).

In humans and plants, if not neutralised, the free radicals damage various cells and organs causing many degenerative diseases and susceptibility to biotic and abiotic stresses. An inherent or inbuilt antioxidant system has the ability to scavenge these free radicals and contribute not only towards plant defence system (Bowler et al., 1992; Gay and Tuzun, 2000; Zambounis et al., 2002; Yiu and Tseng, 2005) and longer life (Dhindsa et al., 1981; Lesham, 1988; Toivonen and Sweeney, 1998; Kuk et al., 2003; She et al., 2003) but also towards human health, i.e. for prevention of illnesses such as heart disease and cancer, and even mitigating the effects of ageing (Adams and Best, 2002; Dorge, 2005; Petersen et al., 2005).

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McKersie (1996) classified cole crops (cabbage, broccoli, Brussel sprouts, collard, kale, etc.), and mustard and turnip leaves as 'Super Food' because of the robust oxidative defence systems. Cabbage is gaining popularity worldwide due to wider adaptability, cheaper and round the year availability, and an integral part of fast food. There is, therefore, a need to evaluate the parents for general combining ability (GCA) and specific combining ability (SCA) to determine relative magnitude of additive and non-additive effects for enzymatic antioxidant activity, which would be very useful while selecting superior parents and determining the breeding strategies for developing the productive cultivars having better inbuilt defence system and longer shelf life.

Based on available literature, very little information is available on enzymatic antioxidants activity in vegetable crops and none of the studies describe the combining ability of enzymatic antioxidants either in cabbage or other vegetable crops. Thus, the objective of this study was to identify promising genotypes and crosses on the basis of GCA and SCA performance and to suggest suitable breeding approaches for increasing the SOD, POX and CAT concentration in cabbage head.

2. Materials and methods

2.1. Basic experimental materials

Sixteen cabbage genotypes including five lines *viz*., CMS-GA, Golden Acre, 83-1, 83-2 and Pride of Asia (respective code used hereafter as L_1, L_2, L_3, L_4, and L_5); and 11 testers *viz*., AC-204, EC-490174, Pusa Mukta, C-4, Red Cabbage, C-2, AC- 1019, EC-490192, MR-1, AC-208 and AC-1021 (respective code used hereafter as T_1, T_2, T_3, T_4, T_5, T_6, T_7, T_8, T_9, T_{10}, and T_{11}) comprised basic experimental materials for present investigation.

2.2. Development of cross seeds

The parents were chosen on the basis of the variability and their practical applicability in heterosis breeding. Parents were crossed in line × tester mating design during 2005–2006 to obtain approximately 15 g of cross seeds. The standard procedure of hand emasculation and pollination was followed to produce the cross seeds. Appropriate buds likely to open within the next 48 h on the female parents were emasculated and covered with butter paper bags in the evening and were pollinated by using the previously bagged mixed pollen from at least 8–10 plants of male parent before noon on the following day and were again covered with butter paper bags. Since cabbage is a highly cross pollinated crop, all the breeding work (emasculation, pollination and selfing) was carried out by isolating the flower buds with butter paper bags. The siliques were harvested 30–35 days after pollination, air dried for 3–5 days, hand threshed, packed individually, placed in moisture proof envelope and stored safely.

2.3. Field experiment

Thirty days old seedlings of 16 parents and their 55 F_1 crosses were transplanted in the following year at Naggar Farm of Indian Agricultural Research Institute Regional Station, Katrain, Kullu Valley, Himachal Pradesh, India. The farm is located at 32.12°N latitude and 77.13°E longitude with an altitude of 1690 m above the mean sea level. There were 36 plants per plot at the spacing of 45 cm × 45 cm. Plots were triplicated in a randomized block design. Crops were well raised and fed to have better phenotypic as well as morphological expression. The crop was fertilized @120 kg N, 60 kg P_2O_5 and 50 kg K_2O per ha supplied as urea, single super phosphate and murate of potash, respectively. Half of the N, and full P_2O_5 and K_2O were applied as basal dressing at time of transplanting while remaining half dose of N was side-dressed at 50 days after transplanting. Need based irrigation was applied in the experimental plots. Following was the range of variation for temperature and relative humidity (RH) during the crop growth period (August–December), $T_{\max}$ (°C) 27.45–13.55; $T_{\min}$ (°C) 20.06–5.10 and RH (%) 88.6–70.23. Cumulative rainfall during the growth period was 656 mm. The crop attracted three major pests, i.e., cabbage butter fly (*Pieris brassicae*), diamond back moth (*Plutella xylostella*) and cutworm (*Agrotis ipsilon*) which were taken care of following recommended pesticides (Anonymous, 2000).

2.4. Sampling and laboratory assay

Head of each genotype in replicated trial was harvested at fresh marketable stage, chopped, homogenized, sample of 2 g fresh weight (FW) frozen immediately in liquid nitrogen and kept at $-80\,^{\circ}\mathrm{C}$ for enzymatic assay. For estimating SOD, POX and CAT activities, the tissue was extracted in 20 ml cold 0.1 M potassium phosphate buffer (pH 7.5) containing 0.5 mM ethylenediaminetetra acetic acid.

SOD activity (unit of SOD $\mathrm{min}^{-1}\,\mathrm{g}^{-1}$ FW) was determined using the method of Dhindsa et al. (1981) which is based on formation of blue colored formazone by nitro-blue tetrazolium chloride (dye) and O_2^{-} radical. A complete reaction mixture containing 1.5 ml of 100 mM potassium phosphate buffer (pH 7.8), 0.2 ml of 200 mM methionine, 0.1 ml of nitro-blue tetrazolium chloride (NBT), 0.1 ml of ethylenediaminetetra acetic acid (EDTA), 0.1 ml of 1.5 M sodium carbonate (Na_2CO_3), 0.1 ml of enzyme extract and 0.8 ml of double distilled water (DDW) is mixed and the reaction is initiated by adding 0.1 ml of 2 μM riboflavin with 15 min incubation under fluorescent light (30 W). Following which the reaction tubes were covered with a black cloth to stop the reaction. A non-irradiated reaction mixture containing enzyme extract, which did not develop color, was used as control. Illumination of complete reaction mixture without enzyme, developed maximum color, served as blank. The absorbance was read at 560 nm in a visible-spectrophotometer (ECIL, India). A 50% inhibition of enzyme activity was taken as one activity unit of SOD per gram per minute.

POX activity (μmol tetraguaiacol $\mathrm{min}^{-1}\,\mathrm{g}^{-1}$ FW) in the extract was assayed as described by Castillo et al. (1984). This method is based on an increase in optical density due to the oxidation of guaiacol to tetraguaiacol on addition of H_2O_2 monitored over a period of 1 min at 470 nm. A complete reaction mixture contains 1.0 ml of 100 mM potassium phosphate buffer (pH 6.1), 0.5 ml of 96 mM guaiacol, 0.5 ml of H_2O_2, 0.1 ml of enzyme extract and 0.4 ml of DDW. The enzyme activity was calculated using the extinction coefficient (ε) of tetraguaiacol (26.6 mM/cm).

CAT activity (mM H_2O_2 reduced $\mathrm{min}^{-1}\,\mathrm{g}^{-1}$ FW) was determined following the method of Aebi (1984), based on decrease of absorption due to breakdown of H_2O_2 by the enzyme measured at 240 nm on UV spectrophotometer (ECIL, India). A complete reaction mixture contains 1.5 ml of 100 mM potassium phosphate buffer (pH 7.0), 0.5 ml of 75 mM H_2O_2, 0.2 ml of enzyme extract and 0.8 ml of DDW.

2.5. Statistical analyses

Analysis of variance was performed and estimates of variance components were calculated for each enzyme. The GCA effects of the parents, the SCA effects of the crosses, variance components and various types of gene effects were estimated as per the method given by Kempthorne (1957) using Statistical Package for Agricultural Research data analysis (SPAR).

Table 1
Mean squares and estimates of variance components for antioxidant enzymes.

Source of variation	Mean square Superoxide dismutase	Peroxidase	Catalase
Replication	0.21	40,802	145.6
Line	4.29**	10,371,115**	26,648**
Tester	3.04*	1,597,644	15,057**
Line × tester	1.10**	1,255,336**	3,921**
Error	0.09	53,657	88.4

Variance component	Estimates of variance component Superoxide dismutase	Peroxidase	Catalase
σ^2_{gca}	0.11	197,043	705.5
σ^2_{sca}	0.33	400,560	1277.4
$\sigma^2_{\text{gca}}/\sigma^2_{\text{sca}}$	0.33	0.49	0.55
σ^2_{A}	0.43	788,173	2821.95
σ^2_{D}	1.34	1,602,239	5109.8

* $P < 0.05$.
** $P < 0.01$.

3. Results

The mean squares due to GCA (lines and testers) and SCA (line × tester interactions) were observed to be significant for all biochemical traits except GCA effect of tester for peroxidase activity (Table 1). The estimates of variance components for various enzymatic antioxidants indicated a lower value of σ^2_{gca} and σ^2_{A} than the respective σ^2_{sca} and σ^2_{D} for all parameters (Table 1). The estimates of GCA effects of lines and testers (Table 2) revealed that among five lines only L_1 was good general combiner for all three antioxidants, however L_2 for SOD and CAT activity, and L_4 for CAT activity. Nevertheless, L_3 showed poor combining ability to all three antioxidants. Among the 11 testers, only one tester T_5 showed good GCA for all antioxidants, nevertheless T_1, T_3, T_6, T_8 and T_{11} were poor general combiners for SOD, POX and CAT activity. T_9 had good GCA for SOD and CAT activity.

Although SCA effects for antioxidant activity were estimated among 55 crosses in their heads, only cross combinations with significant SCA effect along with their respective mean SOD, POX and CAT activities are presented in Table 3. Significant positive SCA effects were observed in 19, 20 and 18 crosses for SOD, POX, and CAT activity, respectively. Only seven cross combinations namely, $L_1 \times T_5$, $L_1 \times T_6$, $L_4 \times T_1$, $L_4 \times T_2$, $L_4 \times T_{11}$, $L_5 \times T_4$, and $L_5 \times T_7$ showed good specific combination for SOD, POX and CAT activity.

4. Discussion

Significant mean squares for parents (lines and testers) indicate pervasiveness of additive variance. The line × tester interaction also showed significant mean squares for all the enzymatic antioxidants indicating the prevalence of non-additive variance. Less than unity value of $\sigma^2_{\text{gca}}/\sigma^2_{\text{sca}}$ ratio indicates predominance of non-additive gene action for the activity of SOD, POX and CAT. Further, lower value of the σ^2_{A} than the σ^2_{D} for all enzymatic activity suggests greater significance of dominant gene action. Dominance effect of SOD, POX and CAT activity has also been reported by Shuxun et al. (2004) in short seasoned cotton cultivars.

The high GCA effects of parents *viz.*, L_1, L_2, T_5 and T_9 signify the importance of additive and additive × additive gene effects which could be exploited through hybridization followed by selection programmes. Out of 16 parents, only two parents, i.e. L_1 and T_5 excelled for higher GCA effects for all enzymatic antioxidants, which indicate the value and need for multiple crossing in a suitable mating system to develop antioxidant rich genotypes and cultivars. For antioxidant activity, parents showing the best *per se* performance always were not the best general combiners which indicate that the selection of parents on the basis of their *per se* performance or GCA effect alone will not suffice the purpose. Thus, selection of parental lines for breeding on the basis of both *per se* performance and GCA effect is suggested.

Table 2
Estimates of general combining ability effects and *per se* performance for superoxide dismutase, peroxidase and catalase activity.

S. No.	Parent	Superoxide dismutase GCA effect	Mean (activity unit $\text{min}^{-1}\,\text{g}^{-1}$ FW)	Peroxidase GCA effect	Mean (μmol tetraguaiacol $\text{min}^{-1}\,\text{g}^{-1}$ FW)	Catalase GCA effect	Mean (mM H_2O_2 reduced $\text{min}^{-1}\,\text{g}^{-1}$ FW)
	Line						
1	L_1	0.15**	7.34	580.69**	1788	36.91**	23.1
2	L_2	0.51**	7.10	−568.34**	927	14.03**	90.4
3	L_3	−0.30**	6.11	−456.79**	901	−15.96**	134.8
4	L_4	−0.38**	7.01	−158.22**	3966	2.57*	157.8
5	L_5	0.02	7.11	602.66**	2583	−37.55**	24.8
	SE	0.04		31.74		1.29	
	Tester						
1	T_1	−0.05	5.92	−48.29	2013	−24.69**	47.9
2	T_2	0.14*	6.95	−269.36**	1816	−3.07	16.0
3	T_3	−0.39**	6.17	−244.56**	2285	−9.09**	17.8
4	T_4	0.29**	5.81	−219.29**	698	−32.85**	14.2
5	T_5	0.88**	7.09	579.91**	4536	68.23**	213.3
6	T_6	−0.27**	6.41	45.91	559	−10.87**	55.0
7	T_7	−0.40**	6.66	486.98**	1583	43.38**	40.8
8	T_8	−0.49**	6.60	−529.36**	1870	−25.40**	26.7
9	T_9	0.64**	7.24	76.44	1238	21.05**	65.6
10	T_{10}	−0.01	7.01	142.38**	1499	−4.49*	203.9
11	T_{11}	−0.33**	4.86	−20.76	415	−22.21**	14.2
	SE	0.07		50.19		2.04	

* $P < 0.05$.
** $P < 0.01$.

Table 3
Estimates of significant specific combining ability effects and *per se* performance for superoxide dismutase, peroxidase and catalase activity.

S. No.	Superoxide dismutase			Peroxidase			Catalase		
	Cross	SCA effect	Mean (activity unit min^{-1} g^{-1} FW)	Cross	SCA effect	Mean (μmol tetraguaiacol min^{-1} g^{-1} FW)	Cross	SCA effect	Mean (mM H_2O_2 reduced min^{-1} g^{-1} FW)
1	$L_1 \times T_5$	0.35**	7.93	$L_1 \times T_5$	1665.24**	4160	$L_1 \times T_5$	56.67**	264.2
2	$L_1 \times T_6$	0.79**	7.22	$L_1 \times T_6$	251.58*	2212	$L_1 \times T_6$	20.54*	148.9
3	$L_4 \times T_1$	0.47**	6.59	$L_4 \times T_1$	1072.02**	2199	$L_4 \times T_1$	11.94**	92.2
4	$L_4 \times T_2$	0.69**	7.00	$L_4 \times T_2$	261.42*	1167	$L_4 \times T_2$	15.14**	117.0
5	$L_4 \times T_{11}$	0.91**	6.77	$L_4 \times T_{11}$	429.82**	1585	$L_4 \times T_{11}$	16.58**	99.3
6	$L_5 \times T_4$	0.80**	7.67	$L_5 \times T_4$	1111.14**	2828	$L_5 \times T_4$	33.64**	65.6
7	$L_5 \times T_7$	0.65**	6.81	$L_5 \times T_7$	447.87**	2871	$L_5 \times T_7$	97.45**	205.7
8	$L_1 \times T_4$	0.37**	7.36	$L_1 \times T_1$	377.44**	2244	$L_1 \times T_9$	63.08**	223.4
9	$L_2 \times T_7$	0.34**	7.00	$L_1 \times T_9$	913.71**	2905	$L_1 \times T_{10}$	10.59*	145.4
10	$L_2 \times T_8$	0.55**	7.12	$L_2 \times T_5$	401.27**	1747	$L_1 \times T_{11}$	17.71**	134.8
11	$L_2 \times T_{11}$	0.26*	7.27	$L_2 \times T_8$	309.54**	546	$L_2 \times T_9$	39.90**	177.3
12	$L_3 \times T_2$	0.50**	6.89	$L_2 \times T_{10}$	596.81**	1504	$L_2 \times T_{10}$	49.47**	161.3
13	$L_3 \times T_9$	0.35**	7.23	$L_2 \times T_{11}$	515.94**	1261	$L_3 \times T_1$	19.87**	81.6
14	$L_4 \times T_8$	0.64**	6.32	$L_3 \times T_2$	308.33**	916	$L_3 \times T_3$	55.69**	133.0
15	$L_4 \times T_9$	0.45**	7.26	$L_3 \times T_6$	432.73**	1356	$L_3 \times T_4$	20.92**	74.5
16	$L_5 \times T_3$	0.55**	6.74	$L_3 \times T_7$	725.33**	2089	$L_3 \times T_6$	25.54**	101.1
17	$L_5 \times T_6$	0.49**	6.79	$L_4 \times T_4$	367.35**	1324	$L_4 \times T_3$	12.33**	108.2
18	$L_5 \times T_9$	0.29*	7.49	$L_5 \times T_1$	1426.53**	462	$L_4 \times T_8$	28.64**	108.2
19	$L_5 \times T_{10}$	0.76**	7.32	$L_5 \times T_3$	365.74**	2058			
20				$L_5 \times T_{10}$	418.14**	2497			
	SE	0.13			100.38			4.07	

* $P < 0.05$.
** $P < 0.01$.

The SCA effect represents dominance and epistatic gene effects (non-additive effects) which can be used as an index to determine the usefulness of a particular cross combination for exploitation through heterosis breeding and hybridization programme. The crosses $L_1 \times T_5$, $L_1 \times T_6$, $L_4 \times T_1$, $L_4 \times T_2$, $L_4 \times T_{11}$, $L_5 \times T_4$ and $L_5 \times T_7$ have significant SCA effects for SOD, POX and CAT activity provide an opportunity to exploit through heterosis breeding. Significant performance of the cross $L_1 \times T_5$ for all enzymatic antioxidants resulted from good general combiner parents indicating the role of cumulative effects of additive and additive × additive genes. By restoring the population improvement, modified pedigree breeding programme and heterosis breeding, the $L_1 \times T_5$ cross may be exploit to improve antioxidant level of cabbage head. The cross $L_1 \times T_6$ also has significant positive SCA effects for SOD, POX and CAT activity and resulted from one good and one poor general combiner. Heterosis breeding and recurrent selection may be useful to harness both additive as well as non-additive gene effects using above cross. Also majority of the cross combinations exhibiting desirable SCA effects had at least one of the parents as good general combiner. Heterosis breeding and recurrent selection was recommended to improve the net head weight of cabbage by Singh (2007).

Positive and significant SCA effects for SOD activity in the crosses $L_4 \times T_1$, $L_4 \times T_{11}$, $L_5 \times T_7$, etc.; for POX activity in $L_4 \times T_1$, $L_4 \times T_{11}$, etc.; and for CAT activity in $L_5 \times T_4$ resulted from parents showing poor combining ability. It might be due to presence of high magnitude of non-additive especially complementary epistatic effects which could be harnessed through heterosis breeding.

Some of the resultant crosses, e.g. $L_1 \times T_2$, $L_1 \times T_9$, $L_2 \times T_2$, $L_2 \times T_4$, $L_2 \times T_5$ and $L_2 \times T_9$ for SOD; $L_1 \times T_7$, $L_1 \times T_{10}$ and $L_5 \times T_5$ for POX activity; and $L_1 \times T_7$ and $L_2 \times T_5$ for CAT activity exhibit low SCA effects despite both of their parents having high GCA effects. This is possible only in the absence of any interaction among favorable alleles contributed by the parents. Thus, it is evident that two parents with high GCA effects for a trait may not always result in a combination showing high SCA effects.

Likewise the parents, the crosses revealing the best *per se* performance always was not showing the best SCA effects. Moreover, selection of parents for hybrid breeding only on the basis of SCA effects has limited value. Therefore, hybrid combination with high *per se* performance, with favorable SCA estimates and involving at least one of the parents with high GCA estimates would be beneficial to increase the concentration of favorable alleles for enhancing the antioxidant activity in cabbage head. These results also show that SCA is more important than GCA in predicting hybrid combinations having high activity of enzymatic antioxidants in cabbage head. The present study, further, emphasizes the significance of assessing the combining ability for SOD, POX and CAT activity, and identifying prospective parents and appropriate breeding techniques to develop productive, potential and antioxidant rich cabbage cultivars, synthetics and hybrids for better stress tolerance ability of plants, shelf life of produce, and eventually, healthy lifestyle to consumers by enjoying antioxidants.

5. Conclusion

Significant mean squares of parents and crosses for SOD, POX and CAT indicated the prevalence of additive and non-additive variance, respectively. Less than unity value of $\sigma^2_{gca}/\sigma^2_{sca}$ and σ^2_A/σ^2_D ratio indicated the predominance of non-additive gene action and dominant gene action, respectively for antioxidant activity. The parents *viz*., L_1, L_2, T_5 and T_9 expressed additive and additive × additive gene effects which could be exploited through hybridization followed by selection programmes. The crosses such as $L_1 \times T_5$, $L_1 \times T_6$, $L_4 \times T_1$, $L_4 \times T_2$, $L_4 \times T_{11}$, $L_5 \times T_4$ and $L_5 \times T_7$ showed significant SCA effects for all three enzymes and provide an opportunity to improve the antioxidant concentration through heterosis breeding. The information gained from this study, therefore, could be used in future breeding programmes to enhance the stress tolerance ability of plants, and quality and shelf life of produce by harnessing antioxidants.

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