



Combining ability analysis for yield component parameters in winter rapeseed genotypes (*Brassica napus* L.)

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Abstract

Eight winter rapeseed genotypes GA096, Geronimo, Okapi, Orient, Sunday, Zarfam, SW0756, and Modena were used as parents of a complete diallel mating design. A set of 56 diallel F_1 hybrids (with reciprocals) including their parents were evaluated in a 8×8 simple lattice design with two replications during 2007/08. Several agronomic traits like Plant height, number of lateral branches per pod, number of pod per main branch, number of seed per pod, 1000 seed weight, seed yield and oil content were recorded. The main objective was to examine the combining abilities of selected canola (*Brassica napus* L.) lines in diallel crosses and to identify candidates for promising hybrid combinations. Significant variances were observed among genotypes for all of the traits (except for seed number per plant). Significant GCA and SCA were observed for 1000 seed weight, oil content and seed yield. Reciprocal effects were significant for oil content. There were significant positive effects for yield and yield components.

Keyword: Diallel analysis, rapeseed, combining ability, yield components

Introduction

The Brassicaceae family consists of many important field crops and vegetables such as rapeseed. Rapeseed rank third in the world most important vegetable oil source with an annual growth rate exceeding that of palm. Rapeseed is the world's second leading source of protein meals. The main rapeseed-producing regions of the world are China, Canada, India and Northern Europe. Worldwide production of rapeseed has increased six fold between 1975 and 2007 by the aim of conventional and modern plant breeding approaches. World production is expected to trend further upward over between 2005 and 2015 (UN Food & Agriculture Organisation (FAO)).

Heterosis has an important role in plant breeding programmes. It is well known that the utilization of heterosis is an effective way to increase crop yield and the major objective of oilseed breeding in recent years has been the development hybrid varieties to use heterosis in term of seed and oil yield (Wang, 2005). The practical exploitation of heterosis in a large number of crops on millions of hectares across the world is indicative of success

of the first category of pursuers. The extent of heterosis in rapeseed has been analyzed in a number of studies with widely varying results, depending on the materials used. In spring rapeseed hybrids an average high parent heterosis of 30% with a range of 20–50% was observed, while for winter rapeseed hybrids an average high parent heterosis of 50% was reported, ranging from 20 to 80% as reviewed by McVetty (1995). Brandle and McVetty (1990) reported a high-parent heterosis with 120% for seed yield in *B. napus*. The value amount of heterosis as well as the GCA and SCA effects is important consideration for hybrid breeding (Hermam, 2007)

Knowledge about the type and amount of genetic effects is required for an efficient use of genetic variability of crops. The concept of good combining ability refers to the potential of a parental form of producing by its crossing with another parent superior offspring for the breeding process and it is widely used in the breeding of cross-pollinated plants. Information and exact study of combining ability can be useful in regard to selection of breeding methods and selection of lines for hybrid combination (Can *et al.*, 1997). Due to the numerous theoretical and

practical advantages of this method, in recent years the choice of parental forms on the basis of combining ability has been extended. Advancement in the yield of brassica requires certain information regarding the nature of combining ability of parents available for use in the hybridization program.

Seed yield is a complex trait that includes various components and finally results in a highly plastic yield structure (Diepenbrock, 2000). Yield per area is the product of population density, the number of pods per plant, the number of seeds per pod and the individual seed weight. While examining the genetic control of grain yield in oilseed rape both additive and non-additive gene effects have been found to be involved (Singh and Yadav, 1980; Singh *et al.*, 2008; Singh and Dixit, 2006; Yadav *et al.*, 2005).

Information regarding the inheritance of grain yield in oilseed rape is limited. Variability of results indicated clearly that the inheritance patterns of plant traits imparting yield varies with the genetic material and the climatic vagaries that suggested exploring the genetic information about the present material before performing selection. The present study was undertaken to examine the combining abilities ability patterns of selected canola (*Brassica napus* L.) lines in a diallel cross, to genetic analysis of some agronomic traits and oil content using a mixed model and to identify candidates for promising hybrid combinations.

Materials and methods

Plant material

The complete diallel design with reciprocals crosses were conducted in 2006/2007. A total of eight genetically diverse and geographically distinct canola quality *Brassica napus* L. lines (cultivars) including GA096, Geronimo, Okapi, Orient, Sunday, Zarfam, SW0756 and Modena were chosen as parents.

Sixty four entries including eight parents and their 56 F_1 hybrids were evaluated during a consecutive growing seasons in an 8×8 simple lattice design with two replications. Seeds were sown in a 30-60 cm furrow system (one row in each furrow and 60 cm spacing between two rows) in the third week of

October 2007 and 2008. Nitrogen fertilizer in the form of urea (46 % N) was applied uniformly on all plots (50 kg N ha⁻¹ at sowing, 50 kg N ha⁻¹ top-dressed at the start of flowering and 50 kg N ha⁻¹ top-dressed at the start of budding). Other fertilizers were applied prior to plowing at the recommended rates of 59 and 100 kg ha⁻¹ for P₂O₅ and K₂O, respectively. A sample of five representative plants were taken from each plot for recording data on plant height, number of lateral branches and number of grains per pod. Furthermore, 1000 grain weight was measured using a sub-sample of the harvested seed from each plot. The oil content (%) was determined using a Foss NIRSystems 5000 near-infrared reflectance spectroscopy (Foss NIRSystems Inc.) according to WinISI III manual instructions for routine analysis (Foss-tecator Infrasoft International LLC).

Statistical analysis

Analysis of variance (ANOVA) was done among hybrid combinations with the GLM procedure using the Statistical Analysis System (SAS) (Zhang *et al.* 2005). All of the genetic effects in the model were considered as random effects. Analysis was carried out by the procedure suggested by Griffing method-II and model-I.

Relative hybrid performance (in %) in comparison with the mean of both parents (mid-parent heterosis, MPH) were calculated as follows: MPH = 100 × ((F₁ – MP) / MP), where F₁ = hybrid performance, MP = mean performance of both parents.

Results and Discussion

Components of genetic variation

Data normality was tested using the Kolmogorov–Smirnov test. The analysis of variance revealed considerable genetic diversity among the genotypes for all of the traits except for seed number per pod (data not shown). The variance due to general and specific combining ability were estimated for assessing the contribution of the additive and non additive types of gene action involved in the inheritance of different characters. GCA and SCA

variances revealed highly significant differences for the most of the characters.

Variation in both GCA and SCA were highly significant ($P < 0.05$) for 1000 seed weight, oil content, and seed yield (table 1) indicating

importance of additive and dominance gene effects in the parental population for these traits. The involvement of non-additive genetic effects in the inheritance of grain yield and some of the yield contributing traits in rapeseed has been previously reported (Akbar *et al.*, 2008; Brandle and McVetty,

Table1: Estimates of GCA effects for yield and yield components in eight parents of *B. napus*.

| Parents | Yield | Oil content | Plant height | Number of silique | Number branch number | Number of seed | 1000 seed weight |
|----------|--------|-------------|--------------|-------------------|----------------------|----------------|------------------|
| GA096 | 0.039 | -0.05 | -4.77* | -2.44 | 0.06 | -0.75** | -0.08 |
| Geronimo | -0.60* | 0.30** | 2.48 | 0.28 | 0.17 | -0.21 | 0.02 |
| Okapi | 0.03 | 1.34** | -03.20 | -5.19** | -0.04 | 0.39 | 0.06 |
| Orient | -0.6* | -0.54* | -3.60 | -1.67 | -0.27* | 0.50 | 0.01 |
| Zarfam | 0.6* | -0.29 | 0.40 | -1.16 | -0.24* | 0.55* | 0.04 |
| Sunday | 0.04 | -0.23 | 3.18 | 4.14** | -0.12 | -0.14 | 0.09 |
| SW0756 | -0.051 | -0.41 | 2.93 | 3.76** | 0.35** | -0.16 | -0.09 |
| Modena | 0.002 | -0.70** | 2.57 | 2.29 | 0.10 | -0.20 | -0.05 |

*, ** Significant at $p < 0.05$ and 0.01 probability levels, respectively.

1990; Sheoran *et al.*, 2000; Singh *et al.*, 2002; Singh *et al.*, 2008; Singh and Dixit 2006, Yadav *et al.*, 2005; Rameah *et al.*, 2003; Cheema and Sadaqat, 2004; Patel *et al.*, 1996; Sheikh, 1998; Singh *et al.*, 2010). Ghosh *et al.* (2002) were of the opinion that for most of the major traits including seed yield had both additive and non-additive gene action of prime importance in Indian mustard. However, other researchers have emphasized the importance of additive genetic effects for some traits such as number of branches and number of pod per plant in this crop (Brandle and McVetty, 1990; Rameah *et al.*, 2003 and Larik and Rajput, 2000).

The magnitude of SCA was higher than GCA for 1000 seed weight, oil content and yield suggesting the performance of dominant gene action. Although several studies have suggested the prevalence of additive genetic effects for oil content in rapeseed

(Engqvist and Becker, 1991; Shen *et al.*, 2005), the results of our study showed dominance effects in oil content. Downey and Rimer (1993) reported the importance of non-additive gene action in controlling the oil content. Both additive and non-additive effects were also found to influence oil content in *B. napus* (Rameah *et al.*, 2003; Cheema and Sadaqat, 2004). Wang *et al.*, 2010 indicated that oil content was mainly influenced by dominant and additive effects, with dominant effect the most important player.

For height, Branch number and pod number only GCA was significant indicating the importance of additive gene action for these traits. The findings of the present investigation of different parameters are in conformity with the findings of following authors. Larik and Rajput (2000) and Sheikh (1998) studied *B. napus* and *B. juncea* and reported the

involvement of additive effects in the plant height. Larik and Rajput (2000); Mishra *et al.* (1983) and Yadav *et al.* (2005) reported additive gene action in controlling number of primary branches which supported the results of present study.

For number of pod per plant on main branch, Larik and Rajput (2000); Rameah *et al.* (2003); Singh *et al.*, 2010; Thakur and Sagwal, 1997 also reported similar GCA effects for pod number which is corroborated of the present study. It can be concluded that for above mentioned traits, breeding programs based on selection will be efficient whereas for 1000 seed weight, oil content, and seed yield, with dominance gene action hybridization based methods and selection of the traits in late segregating generations in genotypes might be fruitful for the improvement can be suggested. A perusal of general combining ability (GCA) effects of parents indicated that none of the parent was found to be good general combiner for the entire traits table (table 1). The estimates showed that Zarfam followed by GA096 and Sunday were the best general combiners for seed yield. Okapi and Geronimo with the positive significant GCA effects were the best combiners for percent oil content.

SW0756 and Sunday with positive GCA effects for height and pod number were considered as good combiners for the traits, simultaneously. The parents Okapi and Sunday had significant positive GCA effects for 1000-seed weight, so they can be considered as good combiners for this trait. SW0756 also has the best positive GCA effects for branch number per plant. Therefore, these cultivars can be used as proper genetic materials in rapeseed breeding programs.

The Orient×SW0756 cross had significant positive SCA effects and were found better crosses for number of pod per plant (table 2). For number of seed per plant, the crosses GA096×Modena and Orient×Modena had high significant positive SCA effects. For plant height, the best combination with a significant positive SCA effect was Sunday×Modena. None of the crosses had significant positive SCA effects for plant height and number of branch per plant. The crosses SW0756×Modena,

Orient×Modena and Sunday×Modena crosses with significant positive SCA effects were good specific combiners for 1000-seed weight. SW0756×Modena, Zarfam×Modena and Zarfam×Sunday were the top four combinations with positive SCA effects for seed yield, respectively. Among these crosses, at least one of their parents had significant positive GCA effects for seed yield expect for first cross. In other studies (Thakur and Sagwal, 1997; Rameah, 2003) similar results were reported. Therefore GCA effects can be considered as a good criterion for predicting SCA effects on seed yield. Aforementioned crosses could be regarded as promising genotypes to be utilized either as F_1 hybrids or as a source population for further selection in rapeseed.

Heterosis

Significant heterosis for yield components and seed yield in *B. napus* and other *Brassica* species have been reported. As grain yield is a complex trait, the highest level of heterosis F_1 heterosis was related to this trait in this experiment. Out of 56 crosses, 46 crosses exhibited positive mid-parent heterosis for seed yield which matched with the results of Radoev *et al.*, 2008. The top five combinations with significant positive mid parent heterosis on seed yield were SW0756×Modena, SW0756×GA096, Sunday×SW0756, Sunday×Zarfam and SW0756×Orient, respectively (table 3). As crosses with high SCA effects for yielded more than those with high heterosis for seed yield, it can be concluded that the SCA effect is a more realistic criterion than mid parental heterosis for seed yield prediction. The crosses Modena×SW0756, Sunday×SW0756, Sunday×Modena, Sunday×Okapi, Okapi×SW0756 exhibited significant positive mid parent heterosis for 1000seed. For height: Sunday×Zarfam, Okapi×Sunday, Modena×Sunday, SW0756×Sunday, Sunday×Orient were the best crosses. For Oil content the crosses Okapi×Modena, Geronimo×Sunday, Geronimo×Modena, Geronimo×Zarfam, GA096×Modena had positive but not significant mid parent heterosis. A number of researchers have indicated that the absence of heterosis for oil content is a common phenomenon in oil seed *Brassicac*s (Brandle and McVetty, 1990;

Table 2: Estimates of SCA effects for yields and yield components in diallel crosses of eight parents of *B. napus*

| Crosses | 1000 seed | Yield | Oil | height | Pod number | Seed number | Branch number |
|------------------|-----------|----------|----------|--------|------------|-------------|---------------|
| GA096×Geronimo | 0.0730 | -0.007 | -3.199** | 5.234 | 2.200 | 0.557 | 0.248 |
| GA096×Okapi | -0.032 | -0.077 | -0.180 | -0.584 | 0.662 | 1.065 | -0.539 |
| GA096×Orient | -0.175 | 0.043 | 0.438 | -2.184 | -2.107 | 0.398 | -0.064 |
| GA096×Zarfam | 0.136 | 0.141 | 0.547 | -6.484 | -6.713 | -0.128 | -0.245 |
| GA096 ×Sunday | 0.081 | -0.016 | 0.649 | -1.816 | 3.083 | -0.202 | -0.008 |
| GA096×SW0756 | -0.248* | 0.149 | -0.148 | 1.241 | -3.881 | 0.300 | -0.177 |
| GA096×Modena | 0.126 | 0.093 | 0.469 | -3.888 | -1.781 | 3.314** | -0.838 |
| Geronimo×Okapi | 0.059 | 0.043 | -0.473 | 3.760 | 0.494 | 0.163 | 0.598 |
| Geronimo×Orient | 0.087 | 0.022 | 0.597 | 3.810 | -3.825 | 0.147 | 0.073 |
| Geronimo×Zarfam | 0.129 | 0.003 | 0.811 | -4.591 | -6.832 | 1.121 | -0.058 |
| Geronimo×Sunday | -0.004 | -0.113 | 1.866** | 1.328 | -0.536 | -0.343 | -0.470 |
| Geronimo× SW0756 | 0.068 | -0.197** | 1.282 | -5.866 | 5.100 | 0.679 | -0.189 |
| Geronimo×Modena | 0.215 | -0.263 | 1.325 | 17.469 | 6.138 | 1.385 | 0.225 |
| Okapi×Orient | 0.011 | 0.014 | -0.596 | -1.009 | -0.913 | -0.676 | 0.536 |
| Okapi×Zarfam | 0.096 | -0.082 | -0.265 | -2.659 | -4.819 | -0.052 | -0.045 |
| Okapi×Sunday | 0.236 | 0.131 | 0.710 | 7.459 | 3.726 | -0.156 | -0.108 |
| Okapi× SW0756 | 0.186 | -0.006 | 1.661** | 2.316 | -0.237 | 0.897 | 0.173 |
| Okapi×Modena | 0.350 | 0.164 | 1.433 | 6.938 | -3.625 | 1.038 | -0.438 |
| Orient×Zarfam | 0.021 | 0.011 | -1.033 | 6.041 | -0.538 | 0.082 | -0.320 |
| Orient×Sunday | 0.004 | -0.085 | -1.240 | 1.359 | 2.258 | 1.328 | 0.067 |
| Orient×SW0756 | 0.151 | 0.059 | -0.262 | -1.285 | 11.894** | -0.760 | 0.098 |
| Orient×Modena | 0.589** | 0.157 | -0.132 | 1.288 | 0.994 | 2.864** | 0.488 |
| Zarfam×Sunday | 0.160 | 0.189** | -0.766 | 5.959 | 4.651 | -0.438 | -0.164 |
| Zarfam×SW0756 | -0.079 | -0.011 | -1.003 | 3.066 | 5.738 | 0.184 | 0.067 |
| Zarfam×Modena | 0.050 | 0.313** | -0.813 | -0.513 | -9.300 | 2.600 | -1.031 |
| Sunday×SW0756 | 0.098 | 0.082 | 0.721 | 1.534 | -3.630 | -0.047 | 0.155 |
| Sunday×Modena | 0.578** | 0.063 | -1.406 | 19.919 | 10.255 | -1.676 | 0.181 |
| SW0756×Modena | 0.80** | 0.365** | -1.652 | 4.5125 | 13.858 | -0.358 | -0.600 |

*, ** Significant at $p < 0.05$ and 0.01 probability levels, respectively.

Table 3: Estimates (%) of mid parent heterosis for yield and yield components in the diallel crosses of eight parents of *B. napus*.

| Crosses | 1000 seed | Yield | Oil | height | Pod number | Seed number | Branch number |
|-----------------|-----------|--------|--------|----------|------------|-------------|---------------|
| GA096×Geronimo | -0.006 | 0.001 | -0.020 | -0.007 | 0.021 | 0.132 | 0.100 |
| GA096×Okapi | -0.030 | 0.112 | 0.001 | -0.039 | -0.197 | 0.132 | -0.162 |
| GA096×Orient | 0.262 | -0.003 | 0.006 | -0.088 | 0.009 | 0.056 | -0.064 |
| GA096×Zarfam | 0.174 | 0.132 | 0.008 | -0.047 | -0.221 | 0.106 | -0.171 |
| GA096×Sunday | 0.089 | 0.005 | 0.039 | 0.050 | 0.203 | 0.059 | -0.153 |
| GA096×SW0756 | 0.652 | 0.040 | 0.001 | 0.037 | 0.066 | 0.103 | -0.016 |
| GA096×Modena | 0.354 | 0.055 | 0.064 | -0.016 | 0.068 | 0.110 | -0.024 |
| Geronimo×Okapi | -0.078 | 0.127 | 0.056 | 0.103 | -0.007 | 0.087 | 0.321 |
| Geronimo×Orient | -0.023 | 0.107 | 0.052 | 0.067 | 0.100 | 0.039 | 0.188 |
| Geronimo×Zarfam | -0.030 | 0.108 | 0.069 | -0.014 | -0.026 | 0.120 | -0.044 |
| Geronimo×Sunday | -0.106 | 0.125 | 0.077 | 0.083 | 0.030 | 0.030 | -0.091 |
| Geronimo×SW0756 | -0.246 | 0.073 | 0.085 | 0.088 | 0.189 | 0.118 | 0.117 |
| Geronimo×Modena | 0.026 | 0.080 | 0.073 | 0.114 | 0.096 | 0.016 | -0.126 |
| Okapi×Orient | 0.551 | 0.060 | 0.033 | 0.067 | 0.101 | 0.061 | 0.306 |
| Okapi×Zarfam | 0.124 | 0.122 | 0.058 | 0.043 | -0.034 | 0.052 | 0.036 |
| Okapi×Sunday | 0.633 | 0.167 | 0.050 | 0.164 | 0.148 | 0.021 | 0.215 |
| Okapi×SW0756 | 0.057 | 0.217 | 0.063 | 0.029 | -0.106 | 0.088 | 0.299 |
| Okapi×Modena | 0.343 | 0.085 | 0.091 | 0.036 | -0.107 | 0.017 | -0.207 |
| Orient×Zarfam | 0.522 | 0.145 | -0.037 | 0.0079 | -0.147 | 0.042 | 0.0000 |
| Orient×Sunday | -0.007 | 0.106 | -0.04 | 0.035 | 0.247 | 0.100 | 0.091 |
| Orient×SW0756 | 0.492 | 0.187 | -0.019 | -0.025 | 0.270 | 0.006 | 0.174 |
| Orient×Modena | 0.309 | 0.076 | 0.046 | 0.006 | 0.165 | 0.119 | 0.130 |
| Zarfam×Sunday | 0.720 | 0.152 | -0.034 | 0.045 | -0.105 | 0.029 | -0.027 |
| Zarfam×SW0756 | 0.576 | 0.044 | -0.018 | -0.0451 | -0.085 | 0.081 | -0.041 |
| Zarfam×Modena | 0.624 | 0.092 | 0.022 | -0.007 | -0.226 | 0.112 | -0.198 |
| Sunday×SW0756 | 0.819 | 0.240 | -0.026 | 0.018 | -0.043 | 0.005 | 0.068 |
| Sunday×Modena | 0.063 | 0.233 | 0.018 | 0.036585 | 0.056 | -0.089 | 0.009 |
| SW0756×Modena | 1.149 | 0.072 | -0.014 | -0.0593 | -0.266 | 0.042 | -0.165 |

Goffman and Becker, 2001, Ofori and Becker, 2008). However, negative or absence of heterosis for oil content is a common phenomenon in oil seed Brassicas (Brandle and McVetty, 1990; Schuler *et al.*, 1992; Falk *et al.*, 1994, Teklewold and Becker, 2005), in this study, certain positive mid-parent heterosis in some of the crosses has been existed.

For Pod number per plant Modena×SW0756, Orient×SW0756, Orient×Sunday, Geronimo×SW0756, Orient×Modena crosses showed positive heterosis and Top five crosses with positive mid parent heterosis for Branch number were belong to Geronimo×Okapi, Okapi×SW0756, Okapi×Sunday, Geronimo×Orient, Orient×SW0756 and for Seed number, the crosses Orient×GA096, GA096×Okapi, GA096×Geronimo, Okapi×GA0756 and Orient×Geronimo have the best mid parent heterosis.

In most of the traits significant differences of the mid-parent heterosis between some crosses and their reciprocals was observed. These differences should be due to the significant cytoplasmic effects of their parents. Significant maternal effects were observed for oil content, branch number and pod number. Therefore, the direction of crosses is important for these traits and it is suggested that genetic improvements could be effective by selection based on the performance of oil content in maternal plant. Significant maternal effects have been reported for oil content (Variath *et al.*, 2009), branch number and pod number in *B. napus* (Campbell and Kondra, 1978) and *B. rapa* (Singh *et al.*, 1980). Wang *et al.*, 2010 pointed out that the maternal effects played a major role on oil content of F₁ hybrid seeds and the oil content of F₁ hybrid seeds in rapeseed (*Brassica napus*) is mainly controlled by maternal accompanied with a minor xenia effect. Therefore, it can be concluded that cytoplasmic effects played an important role on oil content in rapeseed.

Conclusion

Usually it is difficult to obtain high oil content F₁ hybrid when a combination was made between a high oil content parent and a medium or low oil content parent since the heterosis effect was significantly negative in such an occasion (Wang *et*

al. 2009). To get a high oil content hybrid, it is essential to have two parents with high oil content. In addition, cytoplasmic effect is another thing that should be considered seriously in the breeding of high oil content of *B. napus* (Wang *et al.*, 2009). In this study additive effects played the most important roles on seed oil content in *B. napus*. The results of Zhao *et al.*, 2005 depicted that additive effects were main factors contributing to the variation in oil content. Results of this investigation showed that there were significant maternal effects on seed oil content in *B. napus*, which is in agreement with Wu *et al.*, 2006a, b and Wang *et al.*, 2010. In conclusion, seed oil content in rapeseed (*B. napus*) was mainly controlled by the maternal genotype. Wang *et al.*, 2010 suggested that the inheritance of oil content was fitted with an additive-dominant-epistasis model, with dominant and additive effects being the main components. Although combining ability studies in oilseed *Brassica* spp. are inadequate, most of these studies emphasized the predominance effect of GCA on yield and most of the yield components indicating the importance of additive gene action (Brandle and McVetty, 1989; McGee and Brown, 1995; Wos *et al.*, 1999). On the other hand, Pandey *et al.*, (1999) reviewed evidences for the presence of significant SCA effects for yield and yield components. Ramsay *et al.*, (1994) reported that variation for both GCA and SCA were responsible for dry matter yield and other quantitative traits in *B. napus*. In *B. juncea*, predominance of general combining ability effects were observed in seed yield, its components, days to flowering and maturity.

Earlier breeders concluded that the different environment one has to suggest different selection criteria for the improvement in the yield. For those traits that are controlled by additive gene action, simple selection in early generation is suggested, whereas for those traits controlled by non-additive gene action selection in later generation would be more effective (Cheema and Sadaqat, 2004). Rishipal and Kumar (1993) reported that environment and crosses in *B. juncea* considerably influenced the gene effects.

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