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Heterosis and combining ability analysis for oil yield and its components in rapeseed

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Abstract

The occurrence of heterosis for oil percent, oil yield and some yield components has been studied in 36 F_1 combinations derived from nine parental genotypes (from France, Denmark, Sweden, Germany and Iran) of rapeseed according to a diallel design. In the 2008 and 2009 seasons the F_1 hybrids and the parental genotypes were sown according to simple lattice design. In both years, the mean squares due to general combining ability (GCA) and specific combining ability (SCA) were also highly significant. SCA genetic variances were greater than GCA and more important for the traits, showing the predominance of non-additive gene action. The results of combined analysis over year indicated SCA × year interactions were significant sources of variation in the inheritance of all traits while GCA × year interactions were significant only for number of seeds per pod of plant and oil percent. Significant positive heterotic effects including mid-parent and high parent heterosis were observed for all the triats studied but for different number of crosses. Parental genotypes with best GCA (Opera and Talaye) and its utilization as one of the parents produced excellent hybrid combinations having valuable SCA determination for oil yield. F_1 hybrids like Orient × Zarfam, Orient × Talaye, Opera × Talaye performed well in GCA and SCA determination and heterosis. This outcome could be a good indicator to identify the most promising genotypes to be utilized either as F_1 hybrids or as a resource population for further selection in rapeseed improvement.

Keywords*: Brassica napus*, F_1 hybrids, General and specific combining ability, Heterotic effects

Abbreviations: GCA_general combining ability; GCA × Y_GCA × year interactions; SCA_specific combining ability; SCA × Y_SCA × year interactions; NBP_number of lateral branches per plant; NPP_number of pods per plant; NSP_number of seeds per pod of plant; LP_ length pod of plant; SW_thousand seed weight; OP_oil percent; OY, oil yield

Introduction

Rapeseed (*Brassica napus* L.) oil ranks third behind soybean and oil palm showing the importance of this product. Apart from direct human and animal consumption, indutria1 uses include the manufacture of rapeseed oi1 and convert biomass to bioenergy have been developed in the recent years in world (Ofori and Becker 2008). Thus considering that the rapeseed oil, beside its use for food, feed and industrial purposes, is also used for metilester, which is important component for biodiesel production, it can be expected that the rapeseed production area will continue expanding in the next years. Rapeseed breeding strategies are mostly dealing with developing cultivars characterized by high and stable seed and oil yield, as well as by low content of glucosinolates and erucic acids for human consumption. Seed yield, oil yield and oil percent are quantitative traits, which expressions are the result of genotype, environmental effect and genotype-environment interaction (Huhn and Leon 1985). Complexity of these traits is a result of diverse processes that occur during plant development. Iran has been facing a chronic shortage of edible oil; a large quantity of edible oil is imported annually from other countries to fill the gap between local production and consumption (Dehghani et al. 2008). Iran has had an important rapeseed breeding program in recent years, supported by the Seed and Plant Improvement Institute (SPII). Increasing the genetic potential of yield, tolerance to biotic and abiotic stresses and early maturity are important objective of rapeseed breeding programs in Iran and other countries. The phenomenon of heterosis of F_1 hybrids can also reflect special combining ability (SCA) and general combining ability GCA of parental lines. Combining ability concepts are the basic tools for improved production of crops in the form of F_1 hybrids. Identifying parental combinations with strong heterosis for yield and obtain genetic parameters are the most important steps in the development of new cultivars (Diers et al. 1996; Becker et al. 1999; Melchinger 1999), and heterosis effects are generally more pronounced in crosses between genetically distinct materials. The ultimate goal would be the development of hybrid cultivars of rapeseed that can potentially utilize the total amount of heterosis available. Griffing's biometrical analysis (Griffing 1956) has been widely used to aid plant geneticists in the selection of parents for hybridization. In most instances, the analysis provides reliable information on the combining ability of parents, i.e., the potential of parents to produce superior progenies following hybridization, and the magnitude of additive and non-additive gene action (Shattuck et al. 1993). According to Singh and Chaudhary (1985), it is appropriate to use the square components of the effects to

Table 1. Mean squares for ANOVA and combining ability in a 9×9 diallel cross of rapeseed across two years

S.O.V.	D.F.	NBP	NPP	NSP	LP	SW	OP	OY
Year (Y)	1	4.12**	527.16^{ns}	7.78^{ns}	1.64**	4.26**	0.25^{ns}	0.58**
REP/Y	2	1.26	452.53	1.08	0.26	0.02	0.02	0.97
Genotype (G)	44	1.00^{ns}	600.16^{ns}	36.30^{ns}	0.23**	0.18^{ns}	1.92^{ns}	0.11^{ns}
GCA	8	1.06**	900.94**	18.80^{ns}	0.18^{ns}	0.17*	1.89**	0.12**
SCA	36	0.99**	547.13**	24.42^{ns}	0.62**	0.17**	1.78**	0.11**
G × Y	44	1.00**	600.16**	36.30**	0.23**	0.18**	1.92**	0.18**
GCA × Y	8	0.51^{ns}	286.72^{ns}	33.93**	0.15^{ns}	0.06^{ns}	2.12**	0.05^{ns}
SCA × Y	36	1.11**	669.81**	36.83**	0.25**	0.21**	1.87**	0.21**
Error	88	0.31	238.89	17.38	0.11	0.07	0.32	0.03
σ_A^2		2.89	3.77	1.91	1.12	3.32	1.93	4.10
σ_D^2		0.90	0.82	0.66	2.48	0.82	0.95	0.50
σ_{Ph}^2		6.12	66.14	8.90	5.37	5.88	6.90	8.23
h_B^2		61.82	6.93	28.89	66.90	70.58	41.73	55.92
h_N^2		47.19	5.70	21.44	20.82	56.55	27.92	49.81
		0.76	0.82	0.74	0.31	0.80	0.67	0.89

*, ** and ^{ns}: Significant at 0.05 and 0.01 probability levels, respectively and non-significant

indicate the corresponding type of gene activity. The genetic ratio, proposed by Backer (1978), shows how much of the observed variance can be explained by additive and non-additive effects. Genetic ratio values near the unit indicate a preponderance of additive effects. The purpose of this paper was to study the main genetic components involved in the characters of oil yield, oil percent and some important yield component traits including number of lateral branches per plant (NBP) , number of pods per plant (NPP), number of seeds per pod of plant (NSP), length pod of plant (LP), thousand seed weight (SW), oil percent (OP) and oil yield (OY) by means of a diallel cross among nine parents chosen international rapeseed cultivars.

Materials and methods

Plant materials and design of field experiments

Nine parental rapeseed cultivars containing Fornax, Okapi, SLM046, Orient, Colvert, Zarfam, Opera, Talaye, and Modena. The parental cultivars were crossed in all combinations based on half diallel scheme in 2007 and 36 possible F_1 crosses were obtained. The seeds from the 36 crosses and the nine parents were in addition to Hayola 401, RGS003, Licord and Opera cultivars sown in two growing season 2008 and 2009, in layout of a simple lattice design with two replicates. Plots consisted of eight rows 3 m long and the distance between rows was 30 cm and between sown seeds along the row 5 cm. The plot size was 7.2 m^2 but at the time of harvest, in order to control boarder effects, plants from the sides of each plot were removed and harvest area decrease to 4.5 m^2. Weeds were removed by hand weeding during growth stages. Appropriate pesticides were used to control insects and diseases were applied at the recommended rates as usual in the environment. At the time of harvest, in order to control boarder effects, plants from the sides of each plot were removed. To measure yield components and other morphological traits including number of lateral branches per plant (NBP), number of pods per plant (NPP), number of seeds per pod of plant (NSP) and length pod of plant (LP), ten plants were harvested from each plot at the time of maturity. Thousand seed weight (SW) was measured using a sub-sample of the harvested seed from each plot. Seed yield was measured at physiological maturity and yield was adjusted to 12.5% seed moisture content. The oil content of each genotype was calculated by using Inframatic 8620 (Perten Instruments, Inc., Springfield, IL). Oil yield (OY) was calculated according to oil percent and seed yield.

Statistical procedures and data analysis

General combining ability among parents and SCA among combinations was calculated separately for each environment. Combined analysis of variance for determining Environment, Genotype, GCA, SCA and their interaction was using the following statistical model:

$$X_{ijkl}=\mu+E_i+R_{j(i)}+G_k+G_l+S_{kl}+EG_{ik}+EG_{il}+ES_{ikl}+\varepsilon_{ijkl}$$

where X_{ijkl} is the observed value of the combination between *k*th and *l*th parent in the *i*th replication; μ is the mean of all observation values; E_i is the environment effect; R_k is the replication effect; G_k and G_l are the GCA values of the *k*th and *l*th parents, respectively; S_{kl} is the SCA for the cross involving *k*th and *l*th parent; EG_{ik} is the interaction effect between *i*th environment and GCA values of the *k*th parent; EG_{il} is the interaction effect between *i*th environment and GCA values of the *l*th parent; ES_{ilk} is the interaction effect between *i*th environment and SCA for the cross involving *k*th and *l*th parent and Eijkl is the error. DIALLEL-SAS program developed by Zhang et al. (2005) was used for analyzing diallel cross data. The general combining ability and specific combining ability variance components and estimation of combining ability effects on each trait was done according to Model 1, Method 2 of Griffing (1956).

Table 2. Estimates of components of variance due to GCA in a 9×9 diallel of rapeseed across two years

Parent	NBP	NPP	NSP	LP	SW	OP	OY
Fornax	-0.027	5.644**	0.376	-0.067	0.027	0.008**	0.033
Okapi	0.048	0.405	-0.981*	0.026	-0.069*	-0.007**	-0.082**
SLM046	-0.354**	-7.333**	-0.408	-0.017	-0.105**	-0.005	-0.065**
Orient	0.187**	4.856**	-0.658	-0.001	0.038	0.002	0.029
Colvert	-0.006	-0.603	0.229	-0.056	0.057	-0.003	-0.011
Zarfam	-0.072	-4.681**	-0.299	-0.057	-0.008	-0.008**	-0.035
Opera	0.145*	1.224	0.901	0.105**	0.088**	-0.002	0.062**
Talaye	0.058	4.152**	-0.033	0.094*	0.015	0.007**	0.057**
Modena	0.020	-3.663	0.873	-0.028	-0.043	0.008**	0.012

* and ** Significant at 0.05 and 0.01 probability levels, respectively

Results

The combined analysis of variance (ANOVA) for seven traits of 45 studied genotypes over the two years revealed highly significant differences between the years for NBP, LP, SW and OY but not for NPP, NSP and Oil (Table 1). The year × genotype interaction was highly significant for all traits but the genotype main effect was not significant except LP. Although genotype main effect was highly significant separately in each year (data are not shown). The significant year × genotype interaction indicates the differences among studied genotypes from the first year to the second year had no constant process in all measured traits. Thus the rustles of this research indicated this fact that the G × Y interactions are not avoidable in agriculture investigations (Yan and Kang 2003). The variation in the performance of the genotypes across environments can be ascribed to significant changes in the GCAs of the parents and SCAs of crosses across the environments. Mean squares due to GCA and SCA were also highly significant (Table 1), which allowed arbitrating the components of genetic variations due to GCA and SCA and their effect on the hybrids. However, GCA effect was not significant for LP. Since GCA and SCA provide an estimate for additive and non-additive gene actions, respectively (Sprague and Tatum 1942), our results were in good agreement with those of Rameah et al. (2003) and Marjanovic et al. (2007), who found that most of the total genetic variability for a number of agronomic traits in rapeseed crosses were due to both additive and non-additive gene effects. The results of combined analysis of diallel experiment over year was indicated SCA × year interactions were significant sources of variation in the inheritance of all traits while GCA × year interactions were significant only for NSP and OP. This implies that different genes are involved in controlling these measured traits. In other word, the significance of SCA × year for all traits and significance of GCA × year in NSP and OP traits, indicating that oil percent, oil yield and other yield component traits were was sensitive to environmental conditions and that data from additional environments or seasons would make SCA effects more precise. Indeed GCA × year and SCA × year interactions though significant, were not very high to relative main effects; thus genotype × year interactions would presumably not hinder identification of better plants. However the significances of GCA × E effects for some traits suggest that it is necessary to select parental genotypes to obtain hybrids in specific environments. Broad sense heritability varied from medium (41.73) for oil percent to high (70.58) for SW with the exception of NPP which broad-sense heritability is very low (6.93). Relatively higher broad sense heritability showed the effectiveness of selection of transgressive segregants in late generations in the crosses depicting heterobeltiosis (over dominance type of gene action). Among these traits thousand seed weight had higher value for broad sense heritability. The broad sense heritability estimate for studied traits were consistent with the estimates given by Rameah et al. (2003), Akbar et al (2008) in evaluation of heterosis for seed yield of rapeseed. The narrow sense heritability varied from low (5.70) for NPP to medium (56.55) for SW. Both broad- and narrow sense heritabilities were medium for oil yield (Table 1). The relatively high values indicate the possibility of genetic gain in selection for high thousand seed weight and oil yield based on selection. The narrow sense heritability estimate for SW (56.55) and NPP (5.7) presented here were consistent with the estimates given by Rameah et al. (2003) 0.61 and 0.20, respectively but inconsistent with the estimates presented for Akbar et al. (2007) who found low narrow sense heritability for 1000-seed weight (3.92). The GCA to SCA variance ratio or genetic ratio ($2\sigma^2_{GCA}/[2\sigma^2_{GCA}+\sigma^2_{SCA}]$) exhibited that all the traits were pre-dominantly controlled by non-additive type of gene action (Backer, 1978). Therefore, selection might be fruitful for the improvement of the traits in late segregating generations in genotypes, which had highly significant genotypic mean squares. However, among the studied traits, NPP, SW and oil yield had comparatively better fixable variation due to higher GCA/SCA variance ratio but selection for the LP trait would not bring about significant improvement due to non-significant variation existed in genotypic mean square (Table 1). The genetic variance ratio for many the traits depicted that these were controlled by additive type of gene action because its values near the unit to indicate a preponderance of additive effects. Rameah et al. (2003) have achieved similar results in estimation of genetic parameters for yield, yield components in rapeseed but Dhillon et al. (1990) and Akbar et al. (2008) who found GCA/SCA ratio estimates for traits low, confirmed the importance of non-additive gene action. Parent Talaye had significant positive GCA effects for NPP, LP, OP and oil yield traits are the good combiner for having high oil percent and oil yield, simultaneously (Table 2). Parent Orient had significant positive GCA effects for NBP and NPP and was considered as good combiner for having these traits, simultaneously. Thakur and Sagwal (1997) also reported similar GCA effects for NPP and seed yield. Parent Opera with significant positive GCA effects for NBP and LP and also significant positive GCA effects for SW and oil yield were considered as good combiner for these traits (Table 2) and parent Fornax had significant positive GCA effects for NPP and OP. These results agree with

Table 3. Estimates of components of variance due to SCA in a 9×9 diallel cross of rapeseed across two years

Genotype	NBP	NPP	NSP	LP	SW	OP	OY
G1×G2	0.200	-1.603	3.383*	0.150	0.027	0.029**	-0.006
G1×G3	0.055	18.148**	-1.187	0.876**	0.078	-0.013**	0.117
G1×G4	0.535*	9.811	-3.696	0.124	-0.477**	0.025**	-0.145
G1×G5	-0.056	14.485**	0.296	-0.022	0.480**	-0.005	0.198**
G1×G6	0.252	4.923	2.452	0.179	-0.001	0.017**	0.057
G1×G7	-0.554*	-27.045**	0.265	-0.369*	0.030	-0.018**	-0.139
G1×G8	0.320	8.848	-3.137	-0.108	-0.317**	-0.024**	-0.333**
G1×G9	-0.875**	-17.101**	0.604	-0.583**	0.060	-0.015	0.118
G2×G3	0.177	-0.453	1.247	0.044	-0.026	0.003	0.097
G2×G4	-0.339	-0.353	1.570	-0.058	-0.227	0.035**	0.064
G2×G5	-0.428	-6.256	-1.155	-0.838**	0.199	-0.015	-0.070
G2×G6	0.460	13.477**	-2.632	-0.022	-0.015	0.001	-0.159**
G2×G7	0.114	3.852	0.153	1.101**	0.147	-0.029**	-0.053
G2×G8	0.430	6.507	2.710	1.039**	-0.250*	-0.002	-0.098
G2×G9	0.041	-11.794	-4.029*	-0.211	0.255	-0.024**	0.189**
G3×G4	0.793**	11.363	-1.438	-0.260	0.210	-0.018**	-0.078
G3×G5	-0.099	-12.140	-0.638	0.303*	-0.121	0.029**	0.007
G3×G6	0.105	3.653	-2.927	-0.096	0.109	-0.008	0.199**
G3×G7	-0.229	-2.985	3.69*	-0.276	-0.143	0.034**	-0.013
G3×G8	-0.438	-3.038	-1.181	-0.342*	0.065	-0.001	-0.034
G3×G9	-0.260	-8.268	-0.365	-0.341*	-0.170	-0.014	-0.218**
G4×G5	0.905**	23.698**	0.678	0.359*	-0.055	0.004	0.062
G4×G6	0.023	-9.824	4.658**	0.130	-0.009	0.027**	0.212**
G4×G7	-0.368	-12.532	-2.721	0.300*	-0.101	0.012	-0.254**
G4×G8	0.270	8.818	-1.357	-0.207	0.296*	-0.029**	0.188**
G4×G9	-1.280**	-20.794**	1.389	-0.259	0.211	-0.023**	0.059
G5×G6	-0.151	-10.022	1.433	0.633**	-0.194	0.027**	0.060
G5×G7	0.182	15.480	-3.326	-0.142	0.140	-0.004	0.191**
G5×G8	-0.394	-19.530**	3.525*	-0.116	-0.230	0.018**	0.123
G5×G9	0.164	1.044	-1.026	-0.049	-0.188	-0.030**	-0.347**
G6×G7	-0.602*	-3.095	0.272	-0.189	0.037	-0.034**	0.079
G6×G8	0.462	13.940	-3.335	-0.258*	0.041	-0.004	0.040
G6×G9	-0.102	-2.901	1.211	-0.097	0.073	-0.012	-0.214**
G7×G8	0.501*	0.015	-2.684	-0.340*	0.309**	-0.005	0.370**
G7×G9	0.271	16.285**	3.857*	0.396*	-0.128	0.036**	-0.055
G8×G9	-0.550	-12.275	3.691*	0.559**	0.033	0.028**	-0.205**

* and ** Significant at 0.05 and 0.01 probability levels, respectively

those of Rameah et al. (2003) and Akbar et al. (2008) who reported that positive GCA effects was obtained for the above mentioned traits in rapeseed. The cross G4 × G6 (Orient × Zarfam), had significant positive SCA effects for NSP, OP percent and oil yield .The crosses G4×G8 and G7×G8 had significant positive SCA effects for SW and oil yield and can be considered as good combinations for having these traits, simultaneously (Table 3). Also G1×G2, G3×G7 and G5×G8 combinations had the positive and significant SCA effects for NSP and oil percent while G3×G5, G5×G6 and G7×G9 crosses had significant positive SCA effects for LP and oil percent. It had been observed before that crossing a parent with high GCA values with a parent with low GCA values may produce a hybrid combination with high SCA values (Marinkovic 2004). However, in this research this phenomenon was seen for oil yield of G4×G8, SW of G7×G8, NSP of G1×G2 and etc. The hybrids showed both positive and negative mid-parent heterotic effects for the measured traits (Table 4). Cross G3×G7 (SLM046 × Opera) showed the highest significant positive heterosis (38.5) for number of lateral branches per plant (NBP). Also crosses G2×G7, G5×G7 and G1×G7 showed the significant positive heterosis over 30. In NBP trait, heterosis ranged from -16.1 to +38.5% and 61% of hybrids attained positive heterosis. This may suggest a possible advantage of these hybrids in term is of capacity for high number of lateral branches per plant. The high-parent heterosis values are given in Table 5 and the magnitude of heterosis was variable for the different traits and cross combinations. The high-parent heterosis was -27.72 to 27.62 for NBP as G3×G7 and G4×G7 crosses had the maximum amounts. Number of lateral branches per plant (NBP) is a component of seed yield and oil yield in rapeseed. New cultivars with a modern plant habit have more branches than the old cultivars (Pospisil and Mustapic 1995) and high heterosis values of lateral branching were found in an analysis of different generations of winter and spring rapeseeds. Number of pods per plant (NPP) is the most important factor of seed yield in rapeseed therefore more pods per plant would certainly results in greater oil yield per unit area. Hence, positive heterosis is desirable for NPP. Heterosis effects over mid parent concerning to NPP indicated that out of 36 crosses, 23 crosses (about 64%) exhibited positive heterosis and the values ranged from -29.7 to 47.9%. Among these crosses, the

Table 4. Estimates of mid-parent heterosis in a 9×9 diallel of rapeseed across two years

Genotype	NBP	NPP	NSP	LP	SW	OP	OY
G1×G2	-7.8	-2.5	-16.5	2.2	-6.4	-3.9	-14.2
G1×G3	-14.0	-29.7	17.9	6.2	-5.4	-6.0	-21.2
G1×G4	2.0	0.6	2.1	2.6	8.1	-7.3	-7.2
G1×G5	2.7	-10.5	9.2	0.5	3.7	-7.8	-24.4
G1×G6	-8.6	-27.6	-6.7	-2.5	-0.7	-7.9	-33.1
G1×G7	30.1	19.8	20.0	19.1	-2.4	0.1	-3.1
G1×G8	-5.9	8.7	16.1	4.4	3.7	6.9	2.5
G1×G9	18.6	1.8	14.7	3.9	-6.0	4.1	-1.7
G2×G3	-11.3	-18.7	0.6	4.1	-5.9	-5.0	-18.3
G2×G4	5.3	16.4	-12.9	0.6	7.5	-6.4	-3.9
G2×G5	6.0	3.6	-6.8	-1.5	3.1	-6.8	-21.7
G2×G6	-5.6	-16.2	-20.4	-4.4	-1.2	-6.9	-30.7
G2×G7	34.3	38.6	2.4	16.8	-2.9	1.1	0.4
G2×G8	-2.9	25.8	-1.0	2.3	3.1	8.1	6.2
G2×G9	22.4	17.8	-2.2	1.8	-6.5	5.3	1.9
G3×G4	8.5	17.7	-7.2	-1.7	6.6	-0.7	8.1
G3×G5	9.3	4.8	-0.7	-3.7	2.3	-1.2	-11.9
G3×G6	-2.7	-15.3	-15.2	-6.6	-2.0	-1.3	-22.0
G3×G7	38.5	40.2	9.1	14.1	-3.7	7.3	12.9
G3×G8	0.1	27.3	5.5	0.0	2.3	14.6	19.4
G3×G9	26.2	19.1	4.2	-0.5	-7.2	11.6	14.6
G4×G5	0.4	-5.8	3.4	-1.0	-2.1	-0.3	-10.2
G4×G6	-10.7	-23.8	-11.7	-4.0	-6.2	-0.4	-20.5
G4×G7	27.2	26.0	13.6	17.3	-7.8	8.3	15.1
G4×G8	-8.1	14.4	9.8	2.8	-2.1	15.7	21.7
G4×G9	15.9	7.1	8.5	2.3	-11.2	12.7	16.8
G5×G6	-5.8	-10.6	-7.9	-1.5	-2.1	-0.1	-6.1
G5×G7	34.1	47.9	18.5	20.3	-3.9	8.6	36.0
G5×G8	-3.1	34.3	14.6	5.4	2.1	16.1	43.8
G5×G9	22.2	25.7	13.3	4.9	-7.4	13.0	38.1
G6×G7	17.5	24.6	12.5	10.0	-0.9	4.2	18.3
G6×G8	-15.1	13.2	8.8	-3.6	5.3	11.3	25.1
G6×G9	7.1	5.9	7.5	-4.1	-4.5	8.4	20.1
G7×G8	-16.1	-4.8	-1.7	-6.6	3.0	3.3	2.8
G7×G9	5.8	-10.9	-2.8	-7.1	-6.5	0.6	-1.3
G8×G9	11.5	-3.3	-0.6	-0.3	-4.9	-1.3	-2.0

maximum positive value was recorded in cross G5×G7 (Colvert ×Talaye) followed by G3×G7, G5×G8 and G2×G7 crosses (Table 4). The high-parent heterosis was -31.44 to 33.81 for number of pods per plant and G5×G7 cross had the maximum amount (Table 5). In earlier genetic studies, (Gupta 1991; Leon J. 1991; Thakur and Sagwal 1997; Rameah et al. 2003 and Akbar et al. 2008) significant heterosis for yield components especially for number of pods per plant (NPP) in B. *napus* and other *Brassica* species have been reported. Number of seeds per pod would directly contribute in higher yields; therefore, positive heterosis is useful NSP. The hybrids showed both positive and negative mid-parent heterotic effects NSP (Table 4). Cross G1×G7 (Fornax × Opera) showed the highest significant positive heterosis (20.0) for number of seeds per pod and heterosis of NSP ranged from -20.4 to +20.0%. This may suggest a possible advantage of these hybrids in term is of capacity for high number of seed per pod. The high-parent heterosis was -28.37 to 9.88 for NBP while G5×G7 and G5×G7 crosses had the maximum amounts (Table 5). The results of this study are in agreement with Leon, J. 1991; Thakur and Sagwal, 1997 and Rameah et al. (2003) who reported positive and significant heterosis for number of seeds per pod. Longer pod would contain more and bulky seeds which would directly contribute in higher yields; therefore, positive heterosis is useful for pod length. Heterosis effects showed that 21 crosses (58%) presented positive effects over mid parent for pod length and the values ranged from -7.1 to 20.3%. although, more than of half crosses showed significant positive effects but the maximum estimate was observed in cross G5×G7 and G1×G7. The high-parent heterosis was -12.81 to 18.53 for number of pods length as G5×G7, G1×G7 and G4×G7 combinations had the maximum amounts (Table 5). Present results are similar to the findings of Satwinder et al. (2000), who reported that F_1 generations expressed significant heterosis for all yield components including length of pods. Thousand seed weight (SW) is one of the most important factors of seed and oil yield in rapeseed therefore more values of this trait would certainly results in greater oil yield per unit area. Positive heterosis is desirable for NPP. Heterosis effects over mid parent concerning to NPP indicated that out of 36 crosses, only 12 crosses (about 33%) exhibited positive heterosis and the values ranged from -11.2 to 8.1%. Among these F_1 combinations, the maximum positive value was recorded in cross G1×G4 followed by G2×G4 and G3×G4 crosses (Table 4). The high-parent heterosis was -12.99 to 4.33 for number of pods length and G6×G8 combination had the maximum amount. These results

Table 5. Estimates of mid-parent heterosis in a 9×9 diallel of rapeseed across two years

Genotype	NBP	NPP	NSP	LP	SW	OP	OY
G1×G2	-14.44	-4.90	-28.37	0.00	-12.05	-7.58	-24.85
G1×G3	-20.23	-31.44	1.21	3.95	-11.07	-9.61	-30.98
G1×G4	-5.39	-1.87	-12.36	0.42	1.55	-10.85	-18.76
G1×G5	-4.70	-12.69	-6.27	-1.64	-2.59	-11.32	-33.82
G1×G6	-15.19	-29.37	-19.94	-4.56	-6.64	-11.42	-41.43
G1×G7	20.74	16.83	2.99	16.58	-8.31	-3.72	-15.18
G1×G8	-12.72	6.06	-0.40	2.16	-2.59	2.89	-10.27
G1×G9	10.03	-0.70	-1.57	1.64	-11.64	0.20	-13.87
G2×G3	-20.23	-31.44	0.00	0.00	-11.07	-9.61	-30.98
G2×G4	-5.39	-1.87	-13.41	-3.39	1.55	-10.85	-18.76
G2×G5	-4.70	-12.69	-7.39	-5.38	-2.59	-11.32	-33.82
G2×G6	-15.19	-29.37	-20.89	-8.18	-6.64	-11.42	-41.43
G2×G7	20.74	16.83	1.76	12.16	-8.31	-3.72	-15.18
G2×G8	-12.72	6.06	-1.59	-1.72	-2.59	2.89	-10.27
G2×G9	10.03	-0.70	-2.74	-2.21	-11.64	0.20	-13.87
G3×G4	0.00	0.00	-13.41	-3.39	0.00	-1.38	0.00
G3×G5	0.73	-11.03	-7.39	-5.38	-4.08	-1.89	-18.54
G3×G6	-10.36	-28.03	-20.89	-8.18	-8.07	-2.00	-27.90
G3×G7	27.62	19.06	1.76	12.16	-9.71	6.52	4.41
G3×G8	-7.75	8.08	-1.59	-1.72	-4.08	13.82	10.45
G3×G9	16.29	1.19	-2.74	-2.21	-12.99	10.85	6.02
G4×G5	0.00	-11.03	0.00	-2.06	-4.08	-0.52	-18.54
G4×G6	-11.00	-28.03	-14.59	-4.96	-8.07	-0.63	-27.90
G4×G7	26.70	19.06	9.88	16.09	-9.71	8.00	4.41
G4×G8	-8.42	8.08	6.26	1.73	-4.08	15.41	10.45
G4×G9	15.45	1.19	5.01	1.22	-12.99	12.40	6.02
G5×G6	-11.00	-19.11	-14.59	-2.96	-4.15	-0.11	-11.50
G5×G7	26.70	33.81	9.88	18.53	-5.87	8.57	28.16
G5×G8	-8.42	21.48	6.26	3.87	0.00	16.01	35.58
G5×G9	15.45	13.73	5.01	3.34	-9.29	12.98	30.14
G6×G7	0.00	0.00	0.00	0.00	-1.79	0.00	0.00
G6×G8	-27.72	-9.22	-3.29	-12.37	4.33	6.86	5.79
G6×G9	-8.88	-15.01	-4.42	-12.81	-5.36	4.07	1.54
G7×G8	-27.72	-9.22	-3.29	-12.37	0.00	0.00	0.00
G7×G9	-8.88	-15.01	-4.42	-12.81	-9.29	-2.61	-4.01
G8×G9	0.00	-6.38	-1.17	-0.51	-9.29	-2.61	-4.01

were consistent with the estimates given by Nassimi et al. (2006) while Rameah et al. (2003) were reported only negative heterosis values of thousand seed weight in the analysis of winter rapeseed generations. The oil percent is one of the important traits of rapeseed because it is useful in food and industrial applications. Therefore, positive heterosis is desirable for oil percent. Heterosis effects over mid parent concerning to OP indicated that out of 36 crosses, 20 crosses (about 55.6%) exhibited positive heterosis and the values ranged from -7.9 to 16.1%. Among these crosses, the maximum positive value was recorded in cross G5×G8 cross (Table 4). The high-parent heterosis was -11.42 to 16.01 for oil percent while G5×G8 and G4×G8 combinations had the maximum amount (Table 5). Although we found positive heterosis for oil percent and also Krzymanski et al. (1997) found significant heterosis for oil content but some other researchers were reported that negative or absence of heterosis for oil content is a common phenomenon in oil seed *Brassicas* (Brandle and McVetty 1990; Schuler et al. 1992; Goffman and Becker 2001, Ofori and Becker 2008). Similar to the other crops, oil yield is considered to be the main contributor towards favorability in rapeseed; therefore, positive heterosis is considered useful for selecting hybrids for oil yield. Effects of heterosis over mid parent for OY showed that out of 36 crosses, only half of them (18 crosses) exhibited positive heterosis and the values ranged from -33.1 to 43.8%. The variations among this trait heterosis values were vey high due to complex and quantitative nature of seed yield and oil percent which make the OY. The high-parent heterosis was -41.43 to 35.58 for oil percent as G5×G8, G5×G9 and G5×G7 combinations had the maximum amounts (Table 5). In this study, different values of oil yield were registered and the hybrids had somewhat increased value compared with their parents. Similar results were reported by Pospisil and Mustapic (1995) and Marinkovic (2004).

Discussion

On the basis of the present results would appear possible to conclude that heterosis in rapeseed can occur as expression of high GCA as well as SCA as long as parents differ in the expression of the traits for which heterosis is expected. Significant levels of heterosis for agronomic and quality related traits have been obtained in F_1 hybrids of both spring and winter forms of rapeseed (Lefort-Buson and Dattee 1982; Brandle and McVetty 1989; Leon 1991; Downey and Rimer

1993; Goffman and Becker 2001). Under such situation, one of the improvement strategies might be hybrid breeding.

The diallel analysis by Griffing's method proved useful in the identification of parents for hybrid combinations, as the high correlation between the performance of the parents and estimates of the effects of their GCA and SCA seem to indicate. Significant mean squares for GCA and SCA confirm the presence of combining ability; however, SCA mean squares were larger than GCA. Combining ability can play a better role in identifying the precious genotypes for having specific cross combinations which can be used for heterosis and for further selection in segregating generations. Significant mean squares for GCA and SCA in number of lateral branches per plant (NBP), number of pods per plant (NPP), number of seeds per pod of plant (NSP), length pod of plant (LP), thousand seed weight (SW), oil percent (OP) and oil yield (OY) have been revealed by earlier researchers (Satwinder et al. 2000; Rameah et al. 2003; Marinkovic 2004; Nassimi et al. 2006; Akbar et al. 2008). None of the 36 crosses showed significant positive heterosis for oil yield components simultaneously, indicating compensatory effects of yield components. However, according to mid parent heterosis and regarding oil percent and oil yield traits as the final goal, some crosses including G3×G7, G3×G8, G3×G9, G5×G7, G5×G8, G5×G9, G6×G7, G6×G8 and G6×G9 crosses had significant positive heterosis for both mentioned traits, and some of the other studied traits, simultaneously. Crosses G5×G7 (Colvert × Opera) and G5×G9 (Colvert × Modena) indicated significant positive high parent heterosis for oil percent and oil yield traits and the other component except thousand seed weight. The maximum mid parent heterosis for NBP (38.5), NPP (47.9), NSP (20), LP (20.3), SW (8.1), OP (16.1) and OY (43.8) in this study is comparable to the 53% (Lee et al. 1980), 43% (Lefort-Buson et al. 1985) and 15% (Leon 1991) in seed yield but was less than the 81% of Diers et al. (1996) and 89% of Riaz et al. (2001). Although the average heterosis for oil content was virtually zero in the other Brassica species and some researches reported that negative or absence of heterosis for oil content (Banga and Labana 1984; Brandle and McVetty 1990; Falk et al. 1994) but heterosis for oil content could be much appealing in the rapeseed (*Beassica napus* L.). On the other word, the available experience of heterosis in rapeseed indicates that it is an essential prerequisite for the success of hybrids. The results of genetic analysis showed that most of the studied traits were revealed to be predominantly influenced by the over dominant gene. Similar results have been reported by Varsha et al. (1999) and Ghosh and Gulati (2001). The narrow-sense heritability of number of pods per plant were low and it was high for number of lateral branches per plant and thousand seed weight, and so defining an index for selection based on these traits will be effective in a breeding program. The preponderance of SCA variance for all traits demonstrates the predominance of dominance gene effects. Hence, non-additive gene effects were largely influencing the expression of these traits, and selection will bring no or slow genetic improvement. The lack of significant GCA variance for NPP, LP, SW and OY may be partly explained by the very high GCA × year interaction variance. The primary criteria for choosing parents that might have high heterotic response and subsequently produce superior F_1 crosses would be the GCA effect of the parents. GCA variance was not predominant for the studied traits and so parents with high values did not tend to produce superior F_1 combinations. Parental genotypes with best GCA (Opera and Talaye) and its utilization as one of the parents produced excellent hybrid combinations having valuable SCA determination for oil yield. Parent Talaye was found as the best general combiner for most important traits including NPP, oil percent and oil yield followed by Opera. F_1 hybrids like Orient × Zarfam, Orient × Talaye, Opera × Talaye performed well in GCA and SCA determination and heterosis. Results also revealed that yield components governed by non-additive type of gene action and selection in such promising hybrids could be used in hybrid rapeseed production for increased oil yield and oil percent. Moreover, simple selection in top performing hybrids can also be studied in further segregating generations. The observed heterosis indicates the potential for increasing oil yield and oil percent by a systematic search for heterotic groups and testing parents for their combining ability. Finally the results of breeding research presented in this paper show that both oil percent and oil yield of important properties for industrial use can be improved.

References

Akbar M, Tahira BM, Hussain M (2007) Combining heterosis for seed yield and its components in rapeseed. J Agric Res 45: 95–104.

Akbar M, Tahira BM, Hussain M (2008) Combining ability studies in *Brassica napus* L. Int J Agri Biol 10: 205–208.

Backer RJ (1978) Issues in diallel analysis. Crop Sci 18: 533–536.

Banga SS, Labana KS (1984) Heterosis in Indian mustard (*Brassica juncea* (L.) Coss). Plant Breed 92: 61–70.

Becker HC, Loptien H, Roebbelen G (1999) Breeding: An overview. p. 413–460. *In* C. Gomez-Campo (ed.) Biology of *Brassica coenospecies*. Elsevier Science BV, Amsterdam.

Brandle JE, McVetty PBE (1989) Heterosis and combining ability in hybrids derived from oilseed rape cultivars and inbred lines. Crop Sci 29: 1191–1195.

Brandle JE, McVetty PBE (1990) Geographic diversity, parental selection, and heterosis in oilseed rape. Can J Plant Sci 70: 935–940.

Dehghani D, Omidi H, Sabaghnia N (2008) Graphic analysis of trait relations of canola (*Brassica napus* L.) using biplot method. Agron J 100: 760–764.

Dhillon SS, Labana KS, Banga SK (1990) Studies on heterosis and combining ability in Indian mustard. J Res PAU 27: 1–8.

Diers BW, McVetty PBE, Osborn TC (1996) Relationship between heterosis and genetic distance based on restriction fragment length polymorphism markers in oilseed rape (*Brassica napus* L.). Crop Sci 36: 79–83.

Downey RK, Rimer SR (1993) Agronomic Improvement in Oilseed *Brassicas*. Advan Agron 50: 1–150.

Falk KC, Rakow GFW, Downey RK, Spurr DT (1994) Performance of inter-cultivar summer turnip rape hybrids in Saskatchewan. Can J Plant Sci 74: 441–445.

Ghosh SK, Gulati SC (2001) Genetic variability and association of yield components in Indian mustard (*Brassica juncea* L.). Crop Res Hisar 21: 345–9.

Goffman FD, Becker HC (2001) Diallel analysis for Tocopherol content in seeds of rapeseed. Crop Sci 41: 1072–1079.

Griffing B (1956) Concept of general and specific combining ability in relation to diallel systems. Aust J Biol Sci 9: 463–493.

Gupta VP, Sehon MS, Satiga DR (1991) Studies of genetic diversity, heterosis and combining ability in indian mustard [*Brassica juncea* L. (Czern & Cross)]. Indian J Genet 51: 448–453.

Huhn M, Leon J (1985) Phenotypic Yield Stability Depending on Plant Density and on Mean Yield per Plant of Winter Rapeseed Varieties and of Their F_1 and F_2-Generations. J. Agron. Crop Sci 162: 172–179.

Krzymanski J, Pietka T, Krotka K, Bodnaryk RP, Lamb RJ, Pivnick KA (1997) Resistance of hybrid canola (*Brassica napus* L.) to flea beetle (Phyllotreta sp.) damage during early growth. Post Nauk Rolnic 45: 41–52.

Lefort-Buson M, Dattee Y (1982) Genetic study of some agronomic characters in winter oilseed rape (*Brassica napus* L.) II. genetic parameters. Agronomie 2: 323–332.

Lefort-Buson M, Guillot-Lemoine B, Dattee Y (1985) Heterosis and genetic distance in rapeseed (*Brassica napus* L.): Crosses between European and Asiatic selfed lines. Genome 29: 413–418.

Leon J (1991) Heterosis and mixing effect in winter oilseed rape. Crop Sci. 31, 281–284.

Marinkovic R, Marjanovic-Jeromela A (2004) Combining ability in some varietes of winter oil rape (*Brassica napus* L.). Bioteh Biotech Equip 18: 110–114.

Marjanovic-Jeromela A, Marinkovic R, Miladinovic AD (2007) Combining abilities of rapeseed (*Brassica napus* L.) varieties. Genetika 39: 53–62.

Melchinger AE (1999) Genetic diversity and heterosis. In: C. G. Coors, and S. Pandey (Eds), Genetic and Exploitation of Heterosis in Crops, 99–118. American Society of Agronomy, Madison.

Nassimi AW, Raziuddin R, Ali N (2006) Heterotic studies for yield associated traits in *Brassica napus* L. Using 8 × 8 Diallel Crosses. Pak J Biol Sci 9: 2132–2136.

Ofori A, Becker HC (2008) Breeding of *Brassica rapa* for biogas production: heterosis and combining ability of biomass yield. Bioenerg Res 1: 98–104.

Pospisil M, Mustapic Z (1995) Evaluacija novih OO-kultivara uljane repice. Sjemenarstvo 12: 273–282.

Rameah V, Rezai A, Saeidi G (2003) Estimation of genetic parameters for yield, yield components and glucosinolate in rapeseed (*Brassica napus* L.). J Agric Sci Technol 5: 143–151.

Riaz A, Li G, Quresh Z, Swati M.S, Quiros CF (2001) Genetic diversity of oilseed *Brassica napus* inbred lines based on sequence-related amplified polymorphism and its relation to hybrid performance. Plant Breed 120: 411–415.

Satwinder K, Paramjit S, Gupta VP, Kaur S, Sirigh P (2000) Combining ability analysis for oil yield and its components in *Brassica napus* L. Cniciferae Newslet 22: 67–68.

Schuler TJ, Hutcheson DS, Downey RK (1992) Heterosis in inter-varietal hybrids of summer turnip rape in Western Canada. Can J Plant Sci 72: 127–136.

Shattuck VI, Christie B, Corso C (1993) Principles of Griffing's combining ability analysis. Genetica 90: 73–77.

Singh TP, Chaudhary BD (1985) Biometrical methods in quantitative genetics. Kaliani Publishers, New Dehli 318 pp.

Sprague GF, Tatum LA (1942) General vs specific combining ability in single crosses of corn. J Am Soc Agron 34: 923–932.

Thakur HL, Sagwal JC (1997) Heterosis and combining ability in oilseed rape (*Brassica napus* L.). Indian J Genet 57: 163–167.

Varsha I, Satija DR, Singh P (1999) Gene effects for seed yield and its components in crosses involving exotic parents in *Brassica napus*. Crop Imp 26: 188–92.

Yan W, Kang MS (2003) GGE Biplot Analysis: A graphical tool for breeders, geneticists, and agronomists. CRC Press, Boca Raton, FL.

Zhang Y, Kang MS, Lamkey KR (2005) DIALLEL-SAS05: A comprehensive program for Griffing's and Gardner-Eberhart analysis. Agron J 97: 1097–1106.