

Genetic analysis of grain yield, days to flowering and maturity in oilseed rape (*Brassica napus* L.) using diallel crosses

H. Amiri-Oghan^a, M.H. Fotokian^b, F. Javidfar^{a,*}, B. Alizadeh^a

^a*Oilseeds Research Department, Seed and Plant Improvement Institute, Mahdasht Avenue, Karaj, Iran.*

^b*Department of Agronomy and Plant Breeding, College of Agriculture, University of Shahed, Iran.*

*Corresponding author; E-mail: fjavidfar@gmail.com

Received 1 July 2008; Accepted after revision 25 March 2009; Published online 28 April 2009

Abstract

Twenty one F₂ progenies derived from a 7×7 diallel crosses along with parents were evaluated for grain yield, flowering and maturity time. Due to significant genotypic effects for all traits, genetic analyses were performed on F₂ progenies including analyses of combining ability and genetic components. The Analysis of variance revealed that both additive and non-additive genetic effects were involved in controlling these traits. GCA/SCA ratios were 0.91 for days to flowering, 0.95 for days to maturity and 0.83 for grain yield which indicated that the additive gene effects were more important than non-additive gene effects for all these traits. Narrow-sense heritability was high for days to flowering (73.12%) and days to maturity (81.99%) and low for grain yield (30.15%). Heterosis in hybrids seemed to be largely determined by complementary epistasis as well as genetic distance between the parents. The spring-type varieties Tower and Regent appeared as the best parents for earliness whereas winter-type varieties D.R. and Ceres were best parents for high grain yield. It could be concluded from the study that S₁ recurrent selection would be effective to improve the performance of these genotypes for grain yield, flowering and maturity time. The selected S₁ lines from each cycle can be used in a pedigree-breeding program to identify superior genotypes.

Keywords: Breeding; GCA; Heritability; Heterosis; SCA

Introduction

F₁ data is mostly used to estimate gene action and combining ability with Griffing's method II (1956), but it is usually difficult to obtain sufficient F₁ seeds especially for multi-location testing in self-pollinated crops where hand emasculation must be done. Due to easiness of production of large quantity of F₂ seeds, many researchers use F₂ data for diallel analysis to estimate combining ability and gene action (Cho and Scott, 2000; Kao and Mc Vetty, 1987; Verhalen and Murray, 1969). These studies all reported that F₂ analysis provide reliable and better information than F₁ generation.

Flowering is the most critical stage influencing the yield of oilseed rape. The onset of flower initiation can have strong influence on flower, pod and seed number (Diepenbrock, 2000). Habekotte (1997) used a sensitivity analysis within a crop growth model to study options for increasing seed yield in winter oilseed rape. The most promising crop type for high seed yield combined late maturity with early flowering. Various studies on spring cultivars of oilseed rape (*Brassica napus* L.) have shown flowering time to be a highly heritable character determined by genes that exhibit some degree of dominance (Laosuwan, 1969; Campbell and Kondra 1978; Olivieri and Parrini 1979; Thurling and Vijendra Das 1979; Singh and Yadav 1980; Lefort-Buson and Dattee 1982a, b). Likewise, studies with winter (i.e. autumn-sown) cultivars of this species (Olivieri and Parrini 1979) showed both additive and dominance gene effects to have a significant role in the inheritance of flowering time. Thukral and Singh (1987) and Singh and Yadav (1980) showed that only non-additive gene actions were important in controlling the days to maturity in oilseed rape.

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. Hence, seed yield is a complex trait that includes various components and finally results in a highly plastic yield structure (Diepenbrock, 2000). Singh and Yadav (1980) and Thakur and Sagwal (1997) while examining the genetic control of grain yield in oilseed rape found both additive and non-additive gene effects to be involved.

In Iran, oilseed rape is edible oil crop and has recently been exploited to boost its production. Iran has diverse agro-ecological region in order to increase area and production of oilseed rape (Ali et al., 2003). Oilseed rape is well adapted to these agro-ecological regions but commercial cultivation is limited in some regions due to short growing season that may be due to quick weather change or limited period from planting to harvesting time, as the second crop must be planted on the same land. Moreover, in some areas, terminal drought occur as a common environmental stress which adversely affects the growth and development of oilseed rape crop in Iran (Moghanni Nasri et al., 2006). Thus early maturing and high yielding cultivars of oilseed rape are necessary for successful cultivation in this country. Information regarding the inheritance of grain yield, flowering and maturity time in oilseed rape is limited. Thus, present study was designed to determine gene actions and combining abilities of oilseed rape cultivars for grain yield, flowering and maturity time.

Materials and Methods

Field experiment

In order to produce F_2 seeds, twenty one F_1 populations from a 7×7 diallel cross were selfed in a winter nursery in Karaj, Iran ($35^\circ 59' N$ and $51^\circ 6' E$) during winter 2003-04. Since sufficient F_1 seeds were not available to conduct yield trials in the field, the F_2 seeds were used for evaluations.

F_2 progenies along with 7 parents (Ceres, Cobra, Yantar, A.W., D.R, Regent and Tower) were grown in a randomized complete block design with two replications at Seed and Plant Improvement Institute (SPII), Karaj during winter 2004-05. The selected parents

with diverse agronomic and morphological characteristics had been maintained through five generations of selfing in greenhouse.

The plots consisted of three rows 3 m long and 50 cm apart. The distance between plants on each row was 5 cm resulting in approximately 450 plants per plot, which were sufficient for F₂ genetic analysis. The recommended rates of NPK fertilizers and irrigations were applied during growing season. All the plant protection measures were adopted to make the crop free from insects and weeds. The data on days to 50% flowering and physiological maturity time were recorded during growing phase and grain yield (t ha⁻¹) was measured after harvesting based on whole plot.

Statistical analysis

The combining ability analysis was performed using mean values following Model I Method II of Griffing's method (1956). The statistical t-student test was applied to examine the effects of general combining ability (GCA) and specific combining ability (SCA). The diallel component analysis was done according to Hayman's method (1954). Narrow-sense heritability (h_n^2) estimates were obtained using formula suggested by Verhalen and Murray (1969) as follows:

$$h^2 = [0.25D / (0.25D + 0.0625H_1 - 0.125F + E)] \times 100$$

Where D=additive gene effects, H₁=dominance gene effects, E=environmental effects, and F=directional dominance effects. For F₂ data, these parameters resemble to F₁ data with small modifications due to reduced heterozygosity (Jinks, 1956).

GCA/SCA ratios with a theoretical maximum of unity were computed according to Baker (1978) as follows:

$$GCA/SCA = 2S_{g_i}^2 / (2S_{g_i}^2 + S_{s_{ij}}^2)$$

Where g_i is the GCA effect of parent i and s_{ij} is the SCA effect of the Cross i×j.

All the analyses were performed using a sub-program written and attached to MS-Excel software.

Results and Discussion

Analysis of variance

The analysis of variance for days to flowering, maturity and grain yield revealed highly significant differences among progenies. The mean squares due to GCA and SCA were highly significant ($P < 0.01$) for all the traits under study (Table 1) indicating that both additive and non-additive gene effects are important components of combining ability. GCA/SCA ratios were 0.91, 0.95 and 0.83 for days to flowering, days to maturity and grain yield, respectively. These ratios very close to unity confirmed the predominance of additive effects over non-additive effects and provided additional evidence that selection may be effective in the F₂ and later generations for studied traits. Singh et al., (1992) suggested that when SCA effects are predominant in self-pollinated crops then the major portion of the variability is due to additive×additive effects and selection should be delayed to later

generations. Bhullar et al., (1979) pointed out that this could also be due to divergence among progenies in the same parental array.

Table 1. Mean squares for days to flowering and maturity and grain yield according to Griffing's method II, 1956.

SOV	df	Days to flowering	Days to maturity	Grain yield (t ha ⁻¹)
GCA	6	291.856**	68.081**	0.256**
SCA	21	58.439**	7.664**	0.103**
Error	27	20.869	0.661	0.001
GCA/SCA		0.91	0.95	0.83

** : Significant at the 1 % level of probability.

General combining ability and performance of parents

The estimates of GCA effects of the parents showed that Tower followed by Regent were the best general combiners for early flowering and maturity as indicated by their highest negative GCA effect and shortest flowering and maturity time (Table 2). The varieties Ceres and D.R. were the best combiners for grain yield as they had the highest the grain yield and GCA estimates. The positive correlation between GCA estimates and parental performances (Table 2) suggested the possibility of further selection of parents for these traits on the basis of *per se* performance.

The *per se* performance and SCA effects for all the traits indicated that ranking of the crosses on the basis of SCA effects did not necessarily match the ranking on the basis of *per se* performance. Hence, high mean performance will not necessarily be inherited in crosses.

Table 2. Estimates of general combining abilities (GCA) and means for phenological traits and grain yield in a 7×7 diallel cross of oilseed rape.

Parent	Days to flowering		Days to maturity		Grain yield (t ha ⁻¹)	
	GCA	mean	GCA	mean	GCA	mean
Ceres	4.159**	193.0	1.540**	242.5	0.262**	4.905
Regent	-7.397**	142.0	-2.349**	201.5	-0.286**	3.189
Cobra	1.659*	176.0	-0.571*	228.5	0.150**	4.126
Yantar	5.603**	183.0	3.929**	229.5	-0.274**	3.821
A.W.	1.603*	173.5	0.873**	232.0	0.169**	4.412
D.R.	3.103**	190.5	1.040**	233.5	0.193**	4.690
Tower	-8.730**	143.0	-4.460**	204.5	-0.214**	3.063
r (GCA, mean)	0.96**		0.81*		0.91**	

* and **: significant at the 5 % and 1 % levels of probability, respectively.

r: coefficient of correlation

Components of genetic variation

Additive (D) and non-additive (H_1 and H_2) components were significantly deviated from zero for all three traits indicating that both additive and dominance effects are important components of genetic variation for these traits (Table 3). Similar results were recorded by Thukral and Singh (1987) and Sharma (1978). Another study (Dahanayake and Galwey, 1999) indicated that the days to flowering in spring genotypes of *B. napus* were controlled by both additive and dominance effects. However dominance (H_1 and H_2) effects were larger than additive (D) components in all cases suggested that non-additive gene action played a predominant role in the inheritance of flowering, maturity and grain yield. This was also revealed by degree of dominance $(H_1/4D)^{0.5}$, which indicated presence of partial dominance for flowering time and maturity and over-dominance for grain yield. Thus over-dominance of loci may not be the true cause of heterosis; instead, complementary epistasis (Comstock and Robinson, 1952) coupled with genetic diversity in parents involved might cause heterosis for grain yield.

The low estimate of E component indicated least influence of environment in the expression of these traits. The estimates of H_1 effect was larger than H_2 in all cases but estimates of $H_2/4H_1$ were smaller than 0.25 (the theoretical maximum) for flowering, indicating that alleles for early and late flowering were not equal in proportion in the parents. Such an allelic distribution may be the result of selection forces for flowering, causing differential distribution of dominant and recessive alleles in these parental lines. The estimates of $H_2/4H_1$ for maturity time and grain yield were closer to 0.25, indicating more equal distribution of dominant and recessive alleles among the parents.

The significant positive values of F components for flowering and maturity further suggested that dominant alleles were more frequent than recessive alleles in the parental lines. Results from a diallel cross among 10 spring oilseed rape cultivars indicated that late-flowering parents had more dominant alleles than early-flowering parents when temperature during early development was low. However, a higher frequency of recessive alleles was obtained when temperature was higher at this stage (Thurling and Vijendra Das 1979a). Negligible value of F for grain yield suggested that there were equal frequencies for positive and negative alleles in the parents or there is bidirectional dominance of genes involving in the control of the trait. These results are completely agreed with the findings of Thukral and Singh (1987). They reported that non-additive gene effects for maturity and grain yield are more important than additive gene effects whereas for flowering time additive gene effects are more important. In this study, it was found that non-additive gene effects are also important for flowering as reported by Sharma (1978). This disagreement may be due to use of different parental lines in these studies. The dominance effect, i.e. sum total over all loci at heterozygous state (h^2 not heritability) was significant only for flowering and maturity time traits. This suggests that substantial heterogeneity could remain hidden under the facade of phenotypic uniformity for both flowering and maturity time. However, the ratio of total dominant and recessive alleles pooled over all parents, i.e. $[(DH_1)^{0.5} + \frac{1}{2} F / (DH_1)^{0.5} - \frac{1}{2} F]$ was more than 1, indicating marginal to maximal prevalence of dominant over recessive genes for flowering and maturity time and grain yield.

The estimate of heritability for flowering time (73.12 %) and maturity time (81.99 %) were in the range of high heritability (>30%) and that for grain yield (30.15 %) in the range of intermediate category, i.e. between 20 to 30 percent. This indicated that rapid progress will be achieved through selection for the flowering and maturity time than grain yield.

Table 3. Genetic components (\pm SE) for days to flowering and maturity time and grain yield in a 7 \times 7 diallel crosses of oilseed rape.

Variance components and parameters	Days to flowering	Days to maturity	Grain yield (t ha ⁻¹)
D	204.047 \pm 9.203	42.897 \pm 1.769	0.174 \pm 0.037
H ₁	781.013 \pm 88.631	102.121 \pm 17.042	1.702 \pm 0.357
H ₂	507.241 \pm 78.097	98.124 \pm 15.017	1.656 \pm 0.314
F	385.802 \pm 44.017	38.008 \pm 8.464	0.064 \pm 0.707
h ²	472.374 \pm 52.453	100.110 \pm 10.086	0.000 \pm 0.127
E	20.869 \pm 3.254	0.661 \pm 0.625	0.001 \pm 0.010
$\frac{H_2}{4D}$	0.162	0.240	0.243
$\left(\frac{H_1}{4D}\right)^{0/5}$	0.978	0.771	1.564
$\frac{[(DH_1)^{0.5} + 0.5F]}{[(DH_1)^{0.5} - 0.5F]}$	2.886	1.805	1.125
$[h^2 \text{ (Heritability, \%)}]$	73.12	81.99	30.15

It is concluded from the diallel analysis that both additive and non-additive gene effects were involved in the controlling of flowering and maturity time and grain yield. However, additive gene effects were more important than non-additive gene effects in all these traits. Hence both types of gene effects would safely be employed in developing the superior genotypes. Although combining ability studies in oilseed *Brassica* spp. are scanty, most of these studies emphasized the preponderance 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 *Brassica juncea*, predominance of general combining ability effects were observed in seed yield, its components, days to flowering and maturity. Although, specific combining ability effect was significant for days to flowering (Teklewold and Becker, 2005)

The highest yielding parents namely Ceres and D.R. were late in flowering and maturity, whereas the lowest yielding parents namely Tower and Regent were early in flowering and maturity. To combine earliness in high-yielding background, such an undesirable linkage can be broken by intermating the individuals in segregating populations generated from combinations of such parents and then following improvement by selecting superior genotypes for yield accompanied with early maturity in this crop.

Acknowledgments

We would like to thank the Seed and Plant Improvement Institute (SPII), Karaj, Iran for financial support of this work.

References

- Ali, N., Javidfar, F., Mirza, M.Y., 2003. Selection of stable rapeseed (*Brassica napus*) genotypes through regression analysis. Pak. J. Bot. 35, 175-180.
- Baker, R.J. 1978. Issues in diallel analysis. Crop Sci. 18, 533-536.
- Bhullar, K.S., Gill, K.S., Khehra, A.S., 1979. Combining ability analysis over F1-F5 generations in diallel crosses of bread wheat. Theor. Appl. Genet. 55, 77-80.
- Brandle, J.E., McVetty, P.B.E., 1990. Geographic diversity, parental selection, and heterosis in oilseed rape. Can. J. Plant Sci. 70, 935-940.
- Campbell, D.C., Kondra, Z.P., 1978. A genetic study of growth characters and yield characters of oilseed rape. Euphytica, 27, 177-183.
- Cho, Y., Scott, R.A., 2000. Combining ability of seed vigor and grain yield in soybean. Euphytica, 112, 145-150.
- Comstock, R.E., Robinson, H.F., 1952. Estimation of average dominance of genes. In: Gowen, J.W. (ed.) Heterosis. Hafner Pub. Co. New York, London. Pp: 494 -535.
- Dahanayake, S.R., Galwey, N.W., 1999. Diallel analysis of vernalization responses in spring rape (*Brassica napus* L.): a basis for adaptation to a Mediterranean environment. Aust. J. Agric. Res. 50, 1417-1423.
- Diepenbrock, W., 2000. Yield analysis of winter oilseed rape (*Brassica napus* L.): A review. Field Crop Res. 67, 35-49.
- Griffing, B., 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9, 463-493.
- Habekotte, B., 1997. Evaluation of seed yield determining factors of winter oilseed rape (*Brassica napus* L.) by means of crop growth modeling. Field Crops Res. 54, 137-151.
- Hayman, B.I., 1954. The theory and analysis of diallel crosses. Genetics, 39, 789-809.
- Jinks, J.L., 1956. The F2 and backcross generations from a set of diallel crosses. Hered. 10, 1-30.
- Kao, H.M., McVetty, B.E., 1987. Quantitative genetic studies of yield, yield components, and phenological and agronomic characteristics in spring faba beans. Genome, 29, 169-173.
- Laosuwan, P., 1969. Inheritance of number of days from seedling to first bloom and number of leaves in rapeseed (*Brassica napus* L.). MSc Thesis, University of Manitoba.
- Lefort-Buson, M., Dattee, Y., 1982a. Genetic study of some agronomic characters in winter oilseed rape (*Brassica napus* L.). I. Heterosis. Agron. 2, 315-321.
- Lefort-Buson, M., Dattee, Y., 1982b. Genetic study of some agronomic characters in winter oilseed rape (*Brassica napus* L.). II. Genetic parameters. Agronomie, 2, 323-331.
- McGee, K.P., Brown, J., 1995. Investigation of F1 hybrids performance in fall- and spring-planted canola. p. 116-118. In Proc. 9th Int. Rapeseed Conf., 4-10 July 1995. Cambridge, U.K.
- Moghanni Nasri, M., Heidari Sharif Abad, H., Shirani Rad, A.H., Majidi Hervean, E., Zamanizadeh, H.R., 2006. Performance of the effect water stress on physiological characters of rapeseed cultivars. J. Agr. Sci. 12, 127-133.
- Olivieri, A.M., Parrini, P., 1979. Earliness of flowering in winter and summer rapeseed. Cruciferae Newsl. 4, 22-23.
- Pandey, L.D., Singh, B., Sachan, J.N., 1999. *Brassica* hybrid research in India: Status and prospect. Paper 263. In Proc. 10th Int. Rapeseed Confr. [CD-ROM]. 26-29 Sep. 1999, Canberra, Australia.
- Ramsay, L.D., Bradshaw, J.E., Kearsey, M.J., 1994. The inheritance of quantitative traits in swedes (*Brassica napus* L. spp. rapifera) diallel analysis of dry matter yield. J. Genet. Breed. 48, 253-257.
- Sharma, J.R., 1978. Graphical analysis and variance components of flowering time and synchrony of flowering in brown-seeded Indian colza. Indian J. Agric. Sci. 48, 437-444.
- Singh, H., Yadav, C.K., 1980. Gene action and combining ability for grain yield, flowering and maturity in rapeseed. Indian J. Agric. Sci. 50, 655-658.
- Singh, O., Gowda, C.L., Sethi, S.C., Dasgupta, T., Smithson, J.B., 1992. Genetic analysis of agronomic characters in chickpea. I. Estimates of genetic variances from diallel designs. Theor. Appl. Genet. 83, 956-962.
- Teklewold, A., Becker, H.C., 2005. Heterosis and Combining Ability in a Diallel Cross of Ethiopian Mustard

- Inbred Lines. *Crop Sci.* 45, 2629–2635.
- Thakur, H.L., Sagwal, J.C., 1997. Heterosis and combining ability in rapeseed (*Brassica napus* L.). *Indian J. Genet. Plant Breed (Abstract)*.
- Thukral, S.K., Singh, H., 1987. Genetic analysis of seed yield, flowering and maturity in rapeseed. *Indian J. Agric. Sci.* 57, 298-302.
- Thurling, N., Vijendra Das, L.D., 1979. Genetic control of pre-anthesis development of spring rape (*Brassica napus* L.). I. Diallel analysis of variation in the field. *Aust. J. Agric. Res.* 30, 251-259.
- Verhalen, L.M., Murray, J.C., 1969. A diallel analysis of several fiber property traits in upland cotton (*Gossypium hirsutum* L.) *Crop Sci.* 9, 311-315.
- Wos, H., Bartkowiak-Broda, I., Budzianowski, G., Krzymanski, J., 1999. Breeding of winter and spring oilseed rape hybrids at Malyszyn. Paper 544. In Proc. 10th Int. Rapeseed Conf. [CD-ROM]. 26–29 Sep. 1999, Canberra, Australia.