

Diallel analysis of oil content and some agronomic traits in rapeseed (*Brassica napus* L.) based on the additive-dominance genetic model

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Abstract

Development of high oil content varieties is one of the most important aims of current rapeseed breeding programs. A set of 36 diallel F1 hybrids, their parents and four additional cultivars were evaluated in the breeding nurseries during 2008 and 2009. Plant height (PH), number of lateral branches per pod (NBP), main stem length, number of grains per pod, days to start of flowering (DSF), 1000 grain weight (GW), harvest index (HI), and oil content (OC) were measured. Diallel analysis was carried out considering the additive-dominance genetic model to estimate variance and covariance components. The additive genetic variance component was significant for NBP and DSF, the dominance genetic variance for PH and the additive by year interaction for PH and OC. GW However, dominance by year interaction was significant for all characters under investigation and played a major role in the inheritance of these traits. This implies that the utilization of heterosis could be effective for the genetic improvement of oil content and agronomic traits in rapeseed in specific environments. Positive dominance effects of oil content were seen in Okapi × Orient and SLM046 × Opera crosses followed by SLM046 × Colvert and Fornax × Okapi combinations. Fornax, Talaye and Modena proved good general combiners and could be used for the improvement of oil content and agronomic characters. NBP, NGP and HI had significant effects on the oil content. These characters should be given more attention as the main traits of selection for the purpose of improving oil content in rapeseed.

Keywords: additive × year interaction, *Brassica napus* L., dominance × year interaction

Abbreviation: ANOVA, analysis of variance; DSF, days to start of flowering ; HI, harvest index; LUP, linear unbiased prediction; MINQUE, minimum norm quadratic unbiased estimation; MSL, main stem length; NBP, number of lateral branches per pod; NGP, number of grains per pod; PH, plant height; SPII, Seed and Plant Improvement Institute; GW, 1000 grain weight

Introduction

The oilseed *Brassicaceae* are the world's third most important source of oils and their production has witnessed a steady upward movement (Beckman, 2005) by the aim of conventional and modern plant breeding approaches. The main objective of rapeseed breeding programs is the development of varieties with high grain and oil contents per area unit. Although presently planted cultivars are capable of achieving high oil content, interest still exists in pursuing further improvement of both oil percent and grain yield through breeding activities, because genetic gains can be accomplished without a concomitant increase in crop management costs. Rapeseed breeding strategies primarily deal with developing new genotypes for human consumption, characterized by high and stable grain yield and oil content as well as low glucosinolate and erucic acid. Grain yield oil content and oil content are quantitative traits affected by the genotype, environment and genotype by environment interaction (Huhn and Leon, 1985). The complexity of these traits is a result of diverse processes that occur during plant development. Exploitation of genetic variability in any crop species is considered to be critical for

making further genetic improvement in grain yield as well as other economically important traits (Rehman et al., 2009). For an efficient use of genetic variability, knowledge about the type and amount of genetic effects is required. In the past, the statistical analysis of fixed and random effects has been practically impossible for some genetic models with mixed effects. Cockerham (1980) resolved this problem and proposed methodology for constructing general genetic models, as well as for setting up fundamental principles to develop several complicated genetic models. Although, Griffing's methods of diallel analysis (Griffing, 1956) have been widely used to provide reliable information on the nature and magnitude of gene effects that contribute to the expression of quantitative traits Mohammadi et al., 2010) but mixed linear models developed by statisticians (Hartley and Rao, 1967; Rao, 1970; Miller 1974) can be applied in quantitative genetics for estimating genetic parameters in plant breeding. These procedures overcame the shortcomings of ANOVA methods for handling unbalanced data and complicated models (Rao, 1971). Zhu and Weir (1994) proposed a genetic model of diallel

crosses based on the mixed models for estimating variance and covariance components of additive, dominance and cytoplasmic effects, as well as direct additive and dominance effects. Zhu and Weir (1994) used a minimum norm quadratic unbiased estimation (MINQUE) method to estimate the variance components for a single trait and covariance components for multiple traits of random factors. The linear unbiased prediction (LUP) method was used to predict the random effects including additive, dominance, paternal, and environment effects, etc. For the analysis of the phenotypic variation, Abderrahmane and Zhu (2001) focused particularly on the influence of the environment and on the interaction between genetic and environment effects. They declared that an understanding of the inheritance of these effects is of fundamental significance in the study of evolution and in the application of genetics to animal and plant breeding. The objectives of the present study were: 1) genetic analysis of some agronomic traits and oil content using a diallel mating system through mixed models and 2) to investigate the genetic contribution of the agronomic traits to oil content, using the additive-dominance method of Zhu and Weir (1996) and multivariable conditional analysis of Atchley and Zhu (1997).

Materials and methods

Plant materials

A nine parent diallel cross without the reciprocals was made in 2007. The cultivars, SLM046, Okapi, Orient, Fornax, Colvert, Zarfam, Opera, Modena and Talaye were used as parents. These genotypes were chosen based on their considerable variability in oil, grain yield and yield related traits.

Experiment

Forty nine entries including nine parents, their 36 F1 hybrids and four additional genotypes, Hayola 401, RGS003, Licord and Opera, were evaluated during two consecutive growing seasons using a 7×7 simple lattice design with two replications. Seeds were sown in a 30-60 cm furrow system (one pair of rows in each furrow with 30 cm spacing and 60 cm spacing between two paired rows) in the third and second week of October 2008 and 2009, respectively. Therefore, a plot had four pairs of 3 m length rows and a size of 7.2 m². Plots were overplanted and thinned to a 10 cm within row spacing for the establishment of 16.67 plants per m². 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. Weeds were controlled by hand as needed. Plant height (PH), number of lateral branches per pod (NBP), main stem length (MSL) and number of grains per pod (NGP) were measured on 10 random plants. Furthermore, days to start of flowering (DSF) were recorded and 1000 grain weight (GW) was measured using a sub-sample of the harvested seed from each plot. The area harvested was 4.5 m²; however, only the middle six rows were harvested for measuring grain yield and biological yield at physiological maturity. Then, grain yield was adjusted to 12.5% seed moisture content. Harvest index (HI) was calculated by the ratio of grain yield to biological yield. The oil content (OC) was determined using an Inframatic 8620

near infrared spectroscopy analyzer (Perten Instruments, Inc., Springfield, IL).

Statistical analysis

A genetic model including additive and dominance effects (Zhu et al., 1993) and their interaction effects with year (Zhu, 1996) was employed grain yield as follows:

$$y_{ijkl} = \mu + Y_i + A_j + A_k + D_{jk} + AY_{ij} + AY_{ik} + DY_{ijk} + B_{l(i)} + e_{ijkl}$$

Where y_{ijkl} is the yield of hybrid jk for replicate l and year i ; μ is the grand mean; Y_i is the i th year effect; A_j is the additive effect of parent j ; A_k is the additive effect of parent k ; D_{jk} is the dominance effect of parent jk combination with parent j ; AY_{ij} and AY_{ik} are the additive \times year interaction effects of parents k and j ; DY_{ijk} is the dominance \times year interaction effects of parent k in combination with parent j ; $B_{l(i)}$ is the block effect and e_{ijkl} is the residual effect. All of the genetic effects in the model were considered as random effects. For conditional analysis, OC|T represented the grain yield given the other traits (Shi et al., 2003), which is computed by further calculating conditional variance components and conditional genetic effects. Phenotypic correlation coefficients (r_{ph}), correlation coefficients due to the additive effect (r_A), correlation coefficients due to the dominance effect (r_D) and correlation coefficients for the corresponding $G \times Y$ interactions ($r_{A \times Y}$ and $r_{D \times Y}$) were also calculated. All of the statistical analyses were carried out using QGASStation developed by Chen and Zhu (2003).

Results

Anderson and Darling test using MINITAB (2005) 14 software indicated the normality of datasets. Analysis of variance showed significant differences among genotypes for all of the traits under study (data not shown). Both year and genotype \times year interaction effects were significant, which suggested that the traits were influenced by the year in which the genotypes were grown. Values of phenotypic variance and genetic variance components are presented in Table 1 for oil content and other measured traits. The additive genetic variance component (V_A) was significant for NBP, HI, GW and DSF and the dominance variance (V_D) was significant for PH. Furthermore, low ratios of additive genetic variance to phenotypic variance (V_A/V_{ph}) were obtained for NBP (4%), HI (1%), GW (5%), and DSF (8%). However, dominance by year interaction variance ($V_{D \times Y}$) was significant for all of the studied traits (Table 1). High ratios of $V_{D \times Y}/V_{ph}$ for PH and OC and relatively high values for NBP, GW and DSF were also observed. Significant positive phenotypic correlations (r_{ph}) were observed between oil content and all measured traits except for GW and DSF (Table 2). These findings are in agreement with those of Pospisil and Mustapic (1995) but contrast with those of Ozer et al. (1999) and Marjanovic-Jeromela et al. (2007) who reported positive correlations of oil content with days to flowering start and 1000 grain weight. The estimated correlation coefficients of genetic components between oil content and other traits are presented in Table 2. There were no significant additive correlations (r_A) and dominance correlations (r_D) between the oil content and other traits. No additive \times year interaction correlations ($r_{A \times Y}$) were found between oil content and agronomic traits, except PH. However, significant positive dominance \times year interaction

Table 1. Estimated phenotypic variance, genetic variance components and their proportion of variance for seven agronomic traits and oil content in rapeseed

GP†	PH	NBP	MSL	NGP	HI	GW	DSF	OC
V _A	0.00 ^{ns}	0.03 ^{**}	0.00 ^{ns}	0.00 ^{ns}	0.16 ^{**}	0.01 ^{**}	7.11 ^{**}	0.00 ^{ns}
V _D	28.95 ^{**}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}
V _{A×Y}	13.72 ^{**}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.23 ^{**}
V _{D×Y}	218.45 ^{**}	0.39 ^{**}	10.60 ^{**}	9.91 ^{**}	9.47 ^{**}	0.07 ^{**}	40.41 ^{**}	7.77 ^{**}
V _R	66.39 ^{**}	0.33 ^{**}	22.74 ^{**}	17.02 ^{**}	14.91 ^{**}	0.07 ^{**}	37.81 ^{**}	3.17 ^{**}
V _{ph}	327.52	0.75	33.34	26.92	24.54	0.15	85.33	11.17
PV‡								
V _A /V _{ph}	0.00	0.04	0.00	0.00	0.01	0.05	0.08	0.00
V _D /V _{ph}	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00
V _{A×Y} /V _{ph}	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.02
V _{D×Y} /V _{ph}	0.67	0.52	0.32	0.37	0.39	0.47	0.47	0.70

V_A, additive variance; V_D, dominance variance; V_{A×Y}, additive × year interaction variance; V_{D×Y}, dominance × year interaction variance; V_R, residual variance and V_{ph}, phenotypic variance. **, * and ^{ns}, significant at 1% and 5% probability level and non-significant, respectively. † GP, Genetic parameters; PH, plant height; NBP, number of lateral branches per pod; MSL, main stem length; NGP, number of grains per pod; HI, harvest index; GW, 1000 grain weight; DSF, days to start of flowering; OC, oil content. ‡ PV; Proportion of variance.

Table 2. Estimated correlation coefficients of genetics components between oil and seven agronomic traits and oil in rapeseed

Parameters	PH† vs. Oil	NBP vs. Oil	MSL vs. Oil	NGP vs. Oil	HI vs. Oil	GW vs. Oil	DSF vs. Oil
r _A	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}
r _D	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}
r _{A×Y}	100.00 ^{**}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}
r _{D×Y}	-30.88 [*]	33.81 [*]	39.79 [*]	42.49 [*]	68.16 ^{**}	67.05 ^{**}	-58.66 ^{**}
r _{ph}	24.26 [*]	29.63 [*]	25.51 [*]	70.29 ^{**}	48.20 ^{**}	10.89 ^{ns}	-18.95 ^{ns}

r_A, additive correlation; r_D, dominance correlation; r_{A×Y}, additive × year interaction correlation; r_{D×Y}, dominance × year interaction correlation and r_{ph}, phenotypic correlation. **, * and ^{ns}, significant at 1% and 5% probability level and non-significant, respectively. † PH, plant height; NBP, number of lateral branches per pod; MSL, main stem length; NGP, number of grains per pod; HI, harvest index; GW, 1000 grain weight; DSF, days to start of flowering

correlations ($r_{D \times Y}$) were obtained between oil content and NBP, MSL, NGP, HI and GW, while there were significant negative dominance \times year interaction correlations ($r_{D \times Y}$) between oil content and PH and DSF. The ratios of genetic contribution of different traits to oil content are summarized in Table 3. Although there were no significant contributions of genetic main effects (CR_A and CR_D) and additive \times year interaction ($CR_{A \times Y}$) of all traits to oil content, a large contribution of dominance \times year interaction ($CR_{D \times Y}$) was found. The phenotypic contribution ratios were also significant for all of the seven agronomic characters. It means that phenotypic variation in oil content was significantly influenced by these traits, especially by HI and GW (Table 3). Furthermore, conditional residual variances were observed (data not shown) that indicated the role of sampling errors in explaining the conditional effect of agronomic traits on the oil content. Predicted additive genetic effects of oil content and contributed additive effects of seven agronomic traits to oil are given in Table 4. For Fornax, Talaye and Modena, the positive and large additive effects of oil content resulted from all traits, while for Orient, the positive additive effects of oil resulted from MSL, NGP, HI, GW and DSF. On the other hand, Okapi, SLM046, Colvert, Zarfam and Opera had negative additive effects for oil content and contributed negative additive effects through all agronomic traits (Table 4). In this study, different values for oil content were observed and the hybrids had somewhat increased value compared with their parents (data not shown). For all F1 crosses, the predicted dominance effects of oil content and contributed dominance effects of seven agronomic traits to oil are presented in Table 5. There were positive dominance effects of oil content for 18 combinations (50%). The positive dominance effect of oil content for different crosses resulted from different traits and most of the positive dominance effect of oil was resulted mainly from all traits. However, for most of the F1 crosses, the highest contributed dominance effects among the agronomic traits were due to NBP and HI, followed by MSL, NGP and GW. Furthermore, the negative dominance effect of oil was observed for 18 other combinations (50%). For most of the F1 crosses presented in Table 5, the highest contributed negative dominance effects were due to PH, NBP, MSL, NGP and GW. NBP had a considerable participation in both positive and negative dominance contributions to oil content. Oil content no significant dominance effects were obtained for most of the agronomic traits in seven combinations consisting of 2×3 , 2×6 , 3×8 , 3×9 , 4×5 , 6×8 and 6×9 crosses (Table 5). Only one of the 36 crosses (3×8), that did not show any significant dominance effects for agronomic traits, had dominance effects for oil content. There were high positive dominance effects of oil content in 2×4 (Okapi \times Orient) and 3×7 (SLM046 \times Opera) followed by 3×5 (SLM046 \times Colvert) and 1×2 (Fornax \times Okapi) crosses. These combinations may be used for the breeding of high oil cultivars.

Discussion

In the present investigation, genetic effects due to dominance \times year interaction played a major role in the inheritance of all agronomic traits under study in rapeseed. These results showed that the genotype by environment interactions are not avoidable in agriculture investigations (Allard and Bradshaw, 1964; Yan and Kang, 2003). The dominance \times year interaction provides a measure of the stability of the effects of dominance interaction

over years (Allard, 1956). Its variance ratio in the present instance suggested moderate instability for most of the agronomic characters and relatively high instability for plant height and oil content. Thus, dominance relationships in the genetic control of these traits appeared to shift with environmental changes. The observation of a major role for dominance \times year interaction in controlling most of the agronomic traits and oil content suggests that selection in early segregating generations is not likely to be effective in bringing about desirable changes in these traits. Furthermore, high ratios of $V_{D \times Y}/V_{ph}$ for PH and relatively high values for NBP, GW and DSF, indicated that utilization of heterosis in rapeseed could be feasible when selection is based on the evaluation of plant materials in a number of environments. The involvement of non-additive genetic effects in the inheritance of grain yield and yield components in rapeseed has been previously reported (Lefort-Buson and Dattee, 1982; Brandle and McVetty, 1989; Singh et al., 1995; Rameah et al., 2003; Marjanovic-Jeromela et al., 2007). However, other researchers have emphasized the importance of additive genetic effects for some traits such as NGP and GW in this crop (Brandle and McVetty, 1989; Singh et al., 1995; Rameah et al., 2003). Oil content of rapeseed is a typical quantitative trait and can be easily influenced by environmental factors (Pai and Kumar, 1991; Shi et al., 2003; Wang et al., 2010). Although the absolute oil content may vary considerably due to the environment, a high stability of the relative oil content, i.e., the range of oil in different cultivars relative to each other, appears to occur (Hauska et al., 2007). Oil content in rapeseed has also been reported as highly heritable in some experiments (Becker et al., 1999; Wu et al., 2006). A large difference in the oil content of parents, such as the case of present study, is necessary for the genetic basis of this trait to be accurately determined. Similar to the agronomic traits, dominant \times year interaction played the most important role in seed oil content in this crop and accounted for 70% of the total variation, while additive \times year interaction, as well as residual variances, were also significant. Although several studies have suggested the prevalence of additive genetic effects for oil content in rapeseed (Engqvist and Becker, 1991; Shen et al., 2005) and a number of researchers have indicated that the absence of heterosis for oil content is a common phenomenon in oil seed *Brassicaceae* (Brandle and McVetty, 1990; Schuler et al., 1992; Goffman and Becker, 2001; Ofori and Becker, 2008), we found the importance of dominance, but not additive, effects. Downey and Rimer (1993) and Thakur and Sagwal (1997) reported the importance of non-additive gene action in controlling the oil content. Krzymanski et al. (1994) observed significant heterosis for this trait. Both additive and non-additive effects were also found to influence oil content in *B. napus* (Rameah et al., 2003; Marjanovic-Jeromela et al., 2007) and *Brassica juncea* (Mahmood et al., 2006). Furthermore, the results of QTL mapping indicated that genotype \times environment interactions (both non-additive and additive types) involve in the determination of the oil content (Zhao et al., 2005). Since dominant \times environment and interaction contributed a substantial amount of the total variance in our research, this implied the utilization of heterosis could be effective for the genetic improvement of oil content in rapeseed provided that genetic materials are evaluated in several environments. The response of a genotype to environmental changes is determined by phenotypic plasticity, which is shown by the genotype when its phenotype for a given character can be altered by environmental factors (Allard and

Table 3. Estimated phenotypic and genetic contribution ratios of agronomic traits to oil content in rapeseed

Parameters	PH vs. Oil	NBP vs. Oil	MSL vs. Oil	NGP vs. Oil	HI vs. Oil	GW vs. Oil	DSF vs. Oil
CR_A	3.94 ^{ns}	0.74 ^{ns}	3.31 ^{ns}	2.59 ^{ns}	2.35 ^{ns}	0.11 ^{ns}	3.27 ^{ns}
CR_D	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}
$CR_{A \times Y}$	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}	0.00 ^{ns}
$CR_{D \times Y}$	45.96 ^{**}	40.29 ^{**}	48.92 ^{**}	48.82 ^{**}	21.42 [*]	15.29 ^{ns}	40.56 ^{**}
CR_{ph}	50.10 ^{**}	58.97 ^{**}	47.77 ^{**}	48.60 ^{**}	76.23 ^{**}	84.60 ^{**}	56.16 ^{**}

CR_A , additive contribution ratios; CR_D , dominance contribution ratios; $CR_{A \times Y}$, additive \times year interaction contribution ratios; $CR_{D \times Y}$, dominance \times year interaction contribution ratios and CR_{ph} , phenotypic contribution ratios. **, * and ^{ns}, significant at 1% and 5% probability level and non-significant, respectively. † PH, plant height; NBP, number of lateral branches per pod; MSL, main stem length; NGP, number of grains per pod; HI, harvest index; GW, 1000 grain weight; DSF, days to start of flowering

Table 4. Predicted additive effects of oil content and contributed additive effects of agronomic traits to oil in rapeseed

Parents	Contributed additive effects of traits to Oil							OC
	PH [†]	NBP	MSL	NGP	HI	GW	DSF	
Fornax	0.475 ^{**}	0.471 ^{**}	0.425 ^{**}	0.402 ^{**}	0.468 ^{**}	0.440 ^{**}	0.499 ^{**}	0.459 ^{**}
Okapi	-0.419 ^{**}	-0.462 ^{**}	-0.434 ^{**}	-0.291 ^{**}	-0.423 ^{**}	-0.392 ^{**}	-0.417 ^{**}	-0.441 ^{**}
SLM046	-0.249 ^{**}	-0.119 [*]	-0.259 ^{**}	-0.215 ^{**}	-0.271 ^{**}	-0.204 ^{**}	-0.337 ^{**}	-0.278 ^{**}
Orient	0.092	0.064	0.163 ^{**}	0.249 ^{**}	0.167 ^{**}	0.121 [*]	0.211 ^{**}	0.148 ^{**}
Colvert	-0.167 ^{**}	-0.175 ^{**}	-0.158 ^{**}	-0.212 ^{**}	-0.144 ^{**}	-0.217 ^{**}	-0.189 ^{**}	-0.177 ^{**}
Zarfam	-0.484 ^{**}	-0.473 ^{**}	-0.521 ^{**}	-0.460 ^{**}	-0.497 ^{**}	-0.500 ^{**}	-0.446 ^{**}	-0.506 ^{**}
Opera	-0.124 [*]	-0.205 ^{**}	-0.157 ^{**}	-0.278 ^{**}	-0.201 ^{**}	-0.201 ^{**}	-0.180 ^{**}	-0.140 ^{**}
Talaye	0.361 ^{**}	0.410 ^{**}	0.408 ^{**}	0.442 ^{**}	0.399 ^{**}	0.426 ^{**}	0.430 ^{**}	0.437 ^{**}
Modena	0.516 ^{**}	0.489 ^{**}	0.535 ^{**}	0.364 ^{**}	0.502 ^{**}	0.527 ^{**}	0.429 ^{**}	0.498 ^{**}

**and *, significant at 1% and 5% probability level, respectively† PH, plant height; NBP, number of lateral branches per pod; MSL, main stem length; NGP, number of grains per pod; HI, harvest index; GW, 1000 grain weight; DSF, days to start of flowering; OC, oil content

Table 5. Predicted dominance effects of oil content and contributed dominance effects (%) of agronomic traits to oil content for F₁ crosses in rapeseed

Crosses	Contributed dominance effects of agronomic traits to oil content							
	PH [†]	NBP	MSL	NGP	HI	GW	DSF	OC
1 × 2	1.615**	1.675**	1.773**	1.199**	1.655**	1.726**	1.469**	1.669**
1 × 3	-1.153**	-0.730**	-0.691**	-0.579**	-0.813**	-0.584**	-0.760**	-0.748**
1 × 4	1.231**	1.470**	1.211**	1.987**	1.468**	0.490**	1.385**	1.460**
1 × 5	-0.211 ^{ns}	-0.277**	-0.135**	-0.327**	-0.297**	0.689**	-0.037 ^{ns}	-0.277**
1 × 6	0.842**	0.954**	0.851**	0.594**	0.971**	0.940**	0.989**	0.942**
1 × 7	-0.716**	-1.049**	-0.949**	-1.082**	-0.967**	-0.973**	-1.133**	-1.027**
1 × 8	-1.404**	-1.286**	-1.568**	-0.855**	-1.141**	-1.938**	-1.318**	-1.294**
1 × 9	-1.059**	-1.130**	-0.899**	-1.058**	-1.168**	-1.219**	-0.983**	-1.099**
2 × 3	0.144 ^{ns}	0.151 ^{ns}	0.030 ^{ns}	-0.025 ^{ns}	0.096 ^{ns}	0.091 ^{ns}	-0.076 ^{ns}	0.133 ^{ns}
2 × 4	2.095**	1.972**	2.040**	1.792**	2.072**	1.534**	2.173**	1.992**
2 × 5	-0.444**	-0.931**	-1.023**	-0.742**	-0.909**	-0.513**	-0.842**	-0.916**
2 × 6	-0.272 ^{ns}	-0.063 ^{ns}	-0.105 ^{ns}	0.312**	-0.111 ^{ns}	-0.103 ^{ns}	-0.104 ^{ns}	-0.078 ^{ns}
2 × 7	-1.873**	-1.740**	-1.815**	-1.756**	-1.665**	-1.439**	-1.670**	-1.736**
2 × 8	-0.743**	-0.101 ^{ns}	-0.172 ^{ns}	-0.479**	-0.001 ^{ns}	-0.612**	-0.179 ^{ns}	-0.110 ^{ns}
2 × 9	-1.036**	-1.467**	-1.492**	-1.090**	-1.578**	-0.741**	-1.481**	-1.485**
3 × 4	-0.993**	-1.030**	-0.924**	-0.842**	-1.012**	-0.632**	-1.263**	-1.061**
3 × 5	1.255**	1.644**	1.587**	1.725**	1.601**	1.391**	1.471**	1.632**
3 × 6	-0.172 ^{ns}	-0.499**	-0.797**	-0.095 ^{ns}	-0.561**	-0.291*	-0.245**	-0.519**
3 × 7	2.274**	1.932**	1.881**	1.401**	1.906**	1.642**	2.143**	1.930**
3 × 8	0.049 ^{ns}	-0.062 ^{ns}	-0.011 ^{ns}	0.112 ^{ns}	-0.003 ^{ns}	0.077 ^{ns}	0.136 ^{ns}	-0.061 ^{ns}
3 × 9	-0.202 ^{ns}	-0.084 ^{ns}	-0.029 ^{ns}	0.348**	-0.050 ^{ns}	-0.421**	-0.080 ^{ns}	-0.093 ^{ns}
4 × 5	-0.102 ^{ns}	0.233*	0.199**	0.123 ^{ns}	0.192*	0.095 ^{ns}	0.186*	0.213*
4 × 6	1.432**	1.485**	1.624**	0.843**	1.381**	1.469**	1.500**	1.489**
4 × 7	0.463**	0.635**	0.598**	1.041**	0.756**	0.448**	0.479**	0.660**
4 × 8	-1.292**	-1.599**	-1.625**	-1.396**	-1.647**	-1.002**	-1.428**	-1.597**
4 × 9	0.599**	0.542**	0.612**	0.503**	0.532**	0.691**	0.643**	0.573*
5 × 6	1.238**	1.480**	1.380**	1.280**	1.485**	1.087**	1.345**	1.482**
5 × 7	-0.046 ^{ns}	-0.276*	-0.137 ^{ns}	0.179**	-0.400**	-0.001 ^{ns}	-0.043 ^{ns}	-0.276**
5 × 8	1.340**	1.023**	0.839**	0.535**	1.001**	0.566**	1.033**	1.037**
5 × 9	-0.571**	-0.366**	-0.470**	-0.214**	-0.279**	-0.692**	-0.378**	-0.374**
6 × 7	-2.033	-2.043**	-1.924**	-2.068**	-2.105**	-1.951**	-2.003**	-2.022**
6 × 8	-0.158 ^{ns}	-0.214 ^{ns}	0.008 ^{ns}	0.248**	-0.234**	-0.147 ^{ns}	-0.383**	-0.229**
6 × 9	-0.194 ^{ns}	0.067 ^{ns}	0.221**	-0.285**	0.058 ^{ns}	0.289**	-0.188**	0.055*
7 × 8	0.104 ^{ns}	-0.231*	-0.272**	0.130 ^{ns}	-0.349**	0.382**	-0.272*	-0.238**
7 × 9	1.412**	1.539**	1.501**	1.058**	1.585**	1.887**	1.478**	1.558**
8 × 9	0.045 ^{ns}	0.560**	0.524**	0.277**	0.615**	0.523**	0.354**	0.561**

** , * and ^{ns}, significant at 1% and 5% probability level and non-significant, respectively. †† PH, plant height; NBP, number of lateral branches per pod; MSL, main stem length; NGP, number of grains per pod; HI, harvest index; GW, 1000 grain weight; DSF, days to start of flowering; OC, oil content.

Bradshaw, 1964; Bradshaw, 1965). This concept can be applied to genetic effects that consist of additive and dominance effects. Witcombe and Whittington (1971) found that when the physical effects of environmental factors on germination of rapeseed were dissimilar, such as between temperature and water potential, every genotype had different phenotypic plasticities of germination speed and each plasticity was specific to a particular environmental factor. If GE interactions depend on the physical nature of the environments, separate analyses, corresponding to each of the environmental factors to be tested, might be useful for studying the phenotypic plasticity (Miura et al., 1988). According to additive-dominance genetic model and conditional genetic effects, the genotypes Fornax, Talaye, and Modena proved to be good general combiners for oil content improvement based on all measured traits. Therefore, these cultivars, followed by Orient can be used as proper genetic materials in rapeseed breeding programs. On the other hand, Okapi, SLM046, Colvert, Zarfam and Opera had negative

additive effects for oil content and contributed negative additive effects through all agronomic traits, so they are not regarded as good contributors of additive effects to oil content (Table 4). The crosses Okapi × Orient and SLM046 × Opera followed by SLM046 × Colvert and Fornax × Okapi were found to be the best specific combiners for all of the studied traits. These crosses could be regarded as promising genotypes to be utilized either as F₁ hybrids or as a source population for further selection in rapeseed. Conditional analysis was developed to estimate conditional variance components and conditional genetic effects (Zhu, 1995; Atchley and Zhu, 1997). This method can be used to evaluate in more detail the genetic variation and genetic effects of target traits such as oil content and grain yield, conditional on given variables such as yield components (Xiao et al., 2007). Thus, the contribution of one agronomic trait to the oil content of seeds can be measured by conditional analysis. This method can uncover not only the contributed genetic variances but also the contributed genetic

effects of the traits for an individual parent or an F1 cross. Oil content is an important target for oilseed production and all seven traits in this study, especially NBP, HI and NGP, had significant effects on this character. Therefore, NBP, HI and NGP should be given more attention as the main traits of selection for oil content indirectly. NBP is a component of grain yield and oil content in rapeseed. New cultivars with a modern plant habit have more branches than the old cultivars and high heterosis values of lateral branching were found in an analysis of different generations of winter and spring rapeseeds (Pospisil and Mustapic, 1995). Also, some researchers suggested that HI is one of the most important traits in determining rapeseed oil content (Li et al., 2001; Zhang and Zhu, 2006). Furthermore, presence of significant conditional residual variances indicated that the performance of oil content due to other traits was also influenced by sampling errors (data are not shown). Similar results for significant conditional residual variances were reported by the other researchers, for example, Shi et al. (2002) in paddy rice and Zhang et al. (2007) in sponge gourd.

Conclusion

In this study, the inheritance of oil content and several agronomic characters was fitted to an additive-dominant model, with additive \times year and dominant \times year interactions were the main components. Since interaction of dominance effects with environment constituted the substantial amount of the total variance, this implies that the utilization of heterosis could be effective for the genetic improvement of oil content in rapeseed in specific environments. NBP, NGP and HI had significant effects on the oil content. These characters should be given, therefore, more attention as the main traits of selection for the purpose of improving oil content in rapeseed.

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