Research Article

Partitioning genetic effects due to embryo, cytoplasm and maternal parent for oil content in oilseed rape (*Brassica napus* L.)

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Abstract

Analysis of genetic main effects and genotype x environment (GE) interaction effects on the oil content of oilseed rape (*Brassica napus* L.) was conducted by using a genetic model for the quantitative traits of seeds in diploid plants. The experiments were carried out over two years with 8 parents and a diallel mating design, which produced F_1 and F_2 generations. We found that the oil content of rape was simultaneously controlled by embryo genetic effect, cytoplasmic effects and maternal genetic effect as well as GE interaction effects, with the cytoplasmic and maternal effects playing the main role. The results indicate that selection of maternal plants for high oil content would be more efficient than selection based on single seeds. Since the GE interaction effects accounted for 73.69% of the total genetic effects and were more important than the genetic main effects it seems that selection might be influenced by environmental conditions. The estimate of narrow-sense heritability for oil content was 73.52% with the interaction heritability being larger than the general heritability, indicating that the early generations can be used for selection for high oil content. The prediction of genetic effects suggested that the parent cultivars Youcai 601 and Gaoyou 605 were better than the other cultivars for increasing oil content during the breeding of *B. napu*s. The implications for the quantitative trait loci mapping of seed traits interfered by these three genetic systems is also discussed.

Key words: breeding selection, environmental interactions, heritability, QTL.

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Introduction

High oil content is always one of the most important aims in oilseed rape (*Brassica napus* L.) breeding programs, and genetic information on the quantitative traits involved will help breeders construct effective breeding procedures for developing new rape varieties with high oil content. The oil content of rape is an important quantitative trait influenced by environmental conditions (Jensen *et al.*, 1996; Gutierrez Boem *et al.*, 1996) but phenotypic variation in oil content is also mainly controlled by the genotype and genetic and environmental (GE) interaction effects.

It has been pointed out (Grami *et al.*, 1977) that in summer rape broad-sense heritability for oil content is low (0.263), as is narrow-sense heritability (0.163), but for winter rape broad-sense heritability (0.812) and narrow-sense heritability (0.309) are relatively high (Han, 1990), with broad-sense heritability having been reported to be as high as 0.875 (Hu 1987).

Seed genetic components, including additive and dominance effects, play an important role in the inheritance of oil content traits in oilseed rape (Brandle and McVetty,

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1988; Pai and Kumar, 1991; Han 1990) but this trait can also be significantly affected by GE interaction effects across environments (Brandle and McVetty, 1988; Pai and Kumar, 1991; Shafii *et al.*, 1992). As in all plants, rape seeds represent a new generation which is different from the parental plants. However, the maternal plant provides nutrients for seed development, so not only embryo nuclear genes but genetic effects from the nuclear and cytoplasmic genes of the maternal plant could all be important components for the performance of rapeseed traits across environments.

Wang (1992) found that the F_1s oil content shows a significant positive correlation with the female parent (*i.e.* the maternal plant) and highly significant correlations between pollen parents (paternal plant genes) and F_1s oil content have also been were observed as have significant genetic effects for pollen genotype (Hom *et al.*, 2003; Hom, 2004 and Hom *et al.*, 2004). However, detailed genetic information on oil content inheritance in the three genetic systems is still lacking and there is a need to study genotype x environment (GE) interaction effects as well as the genetic main effects for rapeseed traits in three genetic systems (*i.e.* embryo, cytoplasm and maternal plants).

Although it has been shown that the erucic acid content of rapeseeds is controlled by both genetic main effects and GE interaction effects (Shi *et al.*, 2003), the genetic behavior from different oil content genetic systems has not been studied. In the present paper we used genetic models for quantitative traits of seeds in diploid plants to evaluate both the genetic main effects and GE interaction effects of embryo, cytoplasm and maternal plants and to estimate the heritabilities and breeding merit of parents used for improving the oil content of rape.

Materials and Methods

Plant material, cultivation and experimental delineation

The experiments were carried out from 1997 to 2000. A diallel design was used in experiments with the following eight *Brassica napus* L parents: Youcai 601, Gaoyou 605, Huashuang 3, Yunyou 8, Zhongyou 821, Eyouchangjia, Zhong R-888 and Tower. Seeds of the parents were sown in 1997 and F_1 seeds obtained by crossing the eight parents using hand emasculation in the spring of 1998. Two environments were used in this study. For the first environment the parent and F_1s seeds were sown on 7th October 1998 and 31-day-old seedlings individually transplanted at a spacing of 35 x 30 cm with 24 plants in each plot for parents and F_1. Before transplanting the seedlings any false F_1 seedlings were removed, producing a false seedling ratio of about 0.5% among the F_1 generation. The experiment was laid out in a randomized block design with three field replications. Seed samples of parents and F_2s on the F_1 plants were collected at maturity from eight plants in the middle part of each plot. Samples of F_1 seeds used for oil content analysis were obtained during the flowering season of 1999 using the isolated pollination method. The second environment experiment was started on 7th October 1999 using the same procedure as described above.

Oil content analysis

The percentage oil content (OC%, w/w) of the rape seeds was analyzed using a NIRSystems model 5000 near-infrared reflectance spectroscope (NIRSystems, Inc., Silver Spring, MD, USA) according to the WinISI II manual instructions for routine analysis (FOSS NIRSystems/TECTOR, Infrasoft International, LLC.). In excess of 3 g of each intact sample were scanned in a 36 mm inner-diameter ring cup. The oil content calibration equation was developed using a standard normal variant + de-trending scatter correction and a 2, 4, 4, 1 mathematical treatment and a modified partial least square (MPLS) regression method (Wu *et al.*, 2002a). When using such calibration parameters, the regression equations were used to estimate the oil content with a standard error of calibration (SEC) as low as 0.83% and a coefficient of determination (It is described by the r^2 or RSQ) as high as 0.95.

Genetic analysis

The genetic model used was an extension of the diploid plant seeds method for the analysis of cytoplasmic and maternal effects (Zhu and Weir, 1994) by including GE interaction effects for quantitative traits (Zhu, 1996). For a diallel mating design from a set of inbred lines, the generation mean (y_{hijkl}) of mating type k from maternal line i and paternal line j in block l of environment h was partitioned as,

$$y_{hijkl} = \mu + E_h + G_{ijk} + GE_{hijk} + B_{l(h)} + ehijkl$$

These six partitions were grouped into two parts, fixed values of μ (population mean) and E_h (environmental effect), random values of G_{ijk} (genetic main effect with components of embryo additive (A) and dominance (D) effects, cytoplasmic effect (C), maternal additive (Am) and dominance (Dm) effects), GE_{hijk} (GE interaction effect with components of embryo additive interaction (AE) and dominance interaction (DE) effects, cytoplasmic interaction effect (CE), maternal additive interaction (AmE) and dominance interaction (DmE) effects), $B_{l(h)}$ (block effect), and e_{hijkl} (residual effect).

The MINQUE (0/1) method (Zhu and Weir, 1994) was used to estimate variances and covariances. Phenotypic variance (V_P) of the oil content trait was composed of the following genetic components,

$$V_P = V_G + V_{GE} + 2C_{Go.Gm} + 2C_{GoE.GmE} + V_e = (V_A + V_D + V_C + V_{Am} + V_{Dm}) + (V_{AE} + V_{DE} + V_{CE} + V_{AmE} + V_{DmE}) + 2(C_{A.Am} + C_{D.Dm}) + 2(C_{AE.AmE} + C_{DE.DmE}) + V_e$$

where V_G is the genetic main variance including V_A (embryo additive variance), V_D (embryo dominance variance), V_C (cytoplasmic variance), V_{Am} (maternal additive variance), V_{Dm} (maternal dominance variance) and V_{GE} was GE interaction variance including V_{AE} (embryo additive interaction variance), V_{DE} (embryo dominance interaction variance), V_{CE} (cytoplasmic interaction variance), V_{AmE} (maternal additive interaction variance), V_{DmE} (maternal dominance interaction variance). $C_{Go.Gm}$ (covariance between embryo and maternal main effect) could be divided into $C_{A.Am}$ (covariance between embryo and maternal additive effect) and $C_{D.Dm}$ (covariance between embryo and maternal dominance effect), and $C_{GoE.GmE}$ (covariance between embryo and maternal interaction effect) be partitioned into $C_{AE.AmE}$ (covariance between embryo and maternal additive interaction effect), $C_{DE.DmE}$ (covariance between embryo and maternal dominance interaction effect). V_e was residual variance.

Since oil content performance might be simultaneously controlled by genetic main effects and GE interaction effects of genes, the estimated total narrow-sense oil content heritability (h^2) was further partitioned into two

parts of general heritability (h_G^2) which had components of embryo general heritability ($h_{Go}^2 = (V_A + C_{A.Am})/V_p$), cytoplasmic heritability ($h_{Gc}^2 = V_C/V_P$), maternal general heritability ($h_{Gm}^2 = (V_{Am} + C_{A.Am})/V_p$) and interaction heritability (h_{GE}^2) which had components of embryo interaction heritability ($h_{GoE}^2 = (V_{AE} + C_{AE.AmE})/V_p$), cytoplasmic interaction heritability ($h_{GcE}^2 = V_{CE}/V_p$) and maternal interaction heritability ($h_{GmE}^2 = (V_{AmE} + C_{AE.AmE})/V_p$).

The components of genetic main effects and GE interaction effects, including embryo additive effect (A), cytoplasmic effect (C), maternal additive effect (Am), embryo additive interaction effect (AE), cytoplasmic interaction effect (CE) and maternal additive interaction effect (AmE) were predicted by using an adjusted unbiased prediction method (Zhu, 1993; Zhu and Weir, 1996). Sampling generation means of entries, the standard errors of estimated variances, heritabilities and predicted genetic effects were derived using the Jackknife method (Miller, 1974; Zhu and Weir, 1996).

Results

Phenotypic variant of the generations

There was great variation in the mean and range of the oil content of the parent plants and the F₁ and F₂ generations (Figure 1). The oil content of the parent plants ranged from 34.1 to 43.8% in the 1999 trials and 30.5 to 40.3% in the 2000 trials, these values being suitable for genetic crossing designs. A similar situation occurred with the F₁ and F₂ generations and since the ranges and the means of the each generation fluctuated between the two years (Figure 1), the performance of the generations in terms of oil content could be affected by the genotype and influenced by environmental conditions. The means of F₂ generation in both years were larger than those of their parents their parents in Figure 1, indicating that high oil content of F₂ seeds could be improved through the utilization of hybrid vigor rape from hybrid seed (F₁).
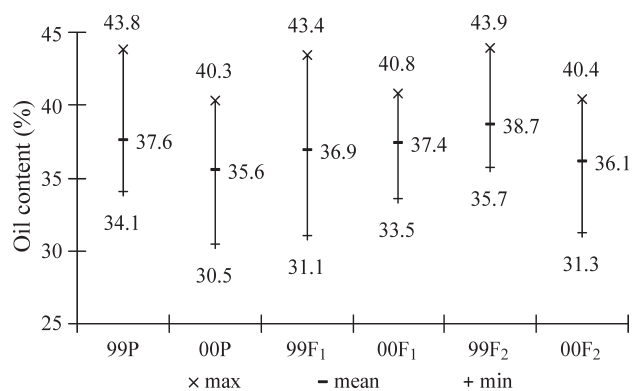
Estimation of components for genetic main variance and GE interaction variance

The oil content variance components of rape seeds are shown in Figure 2. The genetic main variances and GE interaction variances for embryo, cytoplasm and maternal effects were significant, except for V_D and V_{Dm}. Since the proportion of V_{GE} to total genetic variance (73.69%) was larger than that of V_G (26.31%) for oil content, environments could mainly affect the expression of genes controlling this trait. It was suggested that GE interaction effects could not be neglected in high oil content breeding of rapeseed. For genetic main effects, there existed significant components of embryo additive variance (V_A), cytoplasmic variance (V_C) and maternal additive variance (V_{Am}), whereas embryo dominant variance (V_D) and maternal dominant variance (V_{Dm}) were not found. The genetic main effects for oil content were mostly contributed by maternal effects because V_{Am} was larger than V_C and V_A. Since maternal interaction effects, including additive (33.86%) and dominant (22.43%) interaction effects, were accounted for 56.29% of total GE interaction variances, the maternal interaction effects had played a much more important role for oil content than the other interaction components among GE interaction effects. It was revealed, by the larger additive and cytoplasm main variances (($V_A + V_C + V_{Am}$)/V_G = 100.00%), and additive and cytoplasm interaction variances (($V_{AE} + V_{CE} + V_{AmE}$)/$V_{GE}$ = 69.97%), that additive and cytoplasmic effects were more important than other genetic effects. Thus breeding aim of high oil content could be achieved by selection in early generations.

Although the residual variances (V_e) were significant and the performance of oil content of rapeseed could be influenced by sampling errors such as false hybrid seed in F₁ generation, it was concluded that oil content was mainly controlled by genetic main effects and GE interaction effects from different genetic systems, because of the small estimated residual variance. Since $C_{A•Am}$, $C_{D•Dm}$, $C_{AE•AmE}$ and $C_{DE•DmE}$ were all not significant in the present experiment (not shown in Figure 2), no significant relationship

Figure 1 - Phenotypic distribution of generations for rape oil content. Parents = 99P (1999) and 00P (2000), F₁ = 99F₁ (1999) and 00F₁ (2000); F₂ = 99F₂ (1999) and 00F₂ (2000).
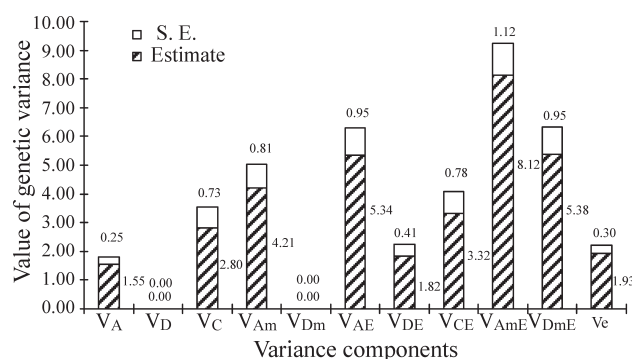

Figure 2 - Estimates of genetic variance components for rape oil content. Values on the upper and right side of the columns are standard error (SE) and variance component estimates. All estimates except for V_D and V_{Dm} were significant at p = 0.01.

between the embryo and maternal main effects or between embryo and maternal interaction effects were found.

Estimation of heritability components

The estimate of the total narrow-sense heritability (h^2) was 73.52% for oil content (Figure 3), while the interaction heritability (h^2_{GE}) (48.68%) for oil content was found to be larger than the general heritability (h^2_G) (24.84%). Therefore, selection efficiency of seeds could be influenced by the environment conditions. The total of maternal and cytoplasm heritabilities including maternal general heritability (h^2_{Gm}), cytoplasmic general heritability (h^2_{Gc}), maternal interaction heritability (h^2_{GmE}) and cytoplasm interaction heritability (h^2_{GcE}) was found as high as 53.54%, while the total embryo heritability including embryo general heritability (h^2_{Go}) and embryo interaction heritability (h^2_{GoE}) was smaller one with 19.98%. Thus, improving oil content of rape seeds would be more efficient when selection was based on maternal plants than on early generations of seeds. The above analysis shows that oil content heritability was so complicated that it was composed of six heritability components all of which were significant, although maternal heritability was the most important.

Analysis of genetic effects for parents

Oilseed rape breeders are mainly interested in the genetic merits of parents because they need better parents in the breeding schedule. The genetic effect of oilseed rape parents was successfully divided between the embryo additive effect, the cytoplasmic effect, the maternal additive effect and their corresponding environmental interaction effects. Our results showed that the genetic main effects (A, C and Am) as well as GE interaction effects (AE, CE and AmE) of parents could affect oil content performance in offspring and detectable differences were found for the genetic main effects and GE interaction effects among parents (Table 1). In 1999 the total genetic effects of oil content for
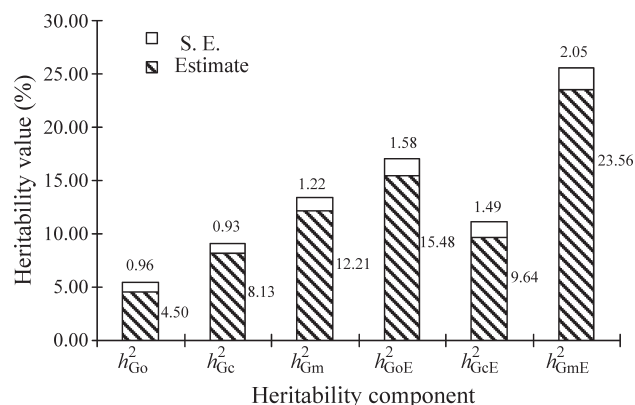

Figure 3 - Estimates of percentage oil content heritability components for oilseed rape. Values on the upper and right side of the columns are standard error (SE) and variance component estimates. All estimates were significant at p = 0.01.

the Youcai 601 parent was 1.19% and 4.37% for the Gaoyou 605 parent (G_t I $= A + AE$ I $+ C + CE$ I $+ Am + AmE$ I) but in 2000 it was 1.56% for the Youcai 601 parent and 5.47% for the Gaoyou 605 parent (G_t II $= A + AE$ II $+ CE$ II $+ Am + AmE$ II). Therefore, they could be used as parents for increasing oil content in rape quality breeding because of their stability for oil content performance in different environments (years). The oil content of the progenies of some parents was low, *e.g.* Yunyou 8 (Oil contents were negative 3.20% for 1999 and 1.96% for 2000), Zhongyou 821 (negative 0.99% for 1999 and 0.05% for 2000) and Zhong R-888 (negative 2.93% for 1999 and 1.38% for 2000) and these varieties do not appear to be suitable parents for improving the oil content of progenies in high oil content breeding programs.

Discussion

Oil is always the main product from rape varieties and it is one of main breeding aims to increase it. There is wide

Table 1 - Predication of genetic main effects and GE interaction effects for oil content (%) of rape seeds.

Parent	Embryo additive effect			Cytoplasmic effect			Maternal additive effect			G_t I	G_t II
cultivar	A	AE I	AE II	C	CE I	CE II	Am	AmE I	AmE II	1999	2000
Youcai 601	0.16	3.29***	-2.60***	1.55	1.73	-0.43	-0.78	-4.77***	3.66***	1.19	1.56
Gaoyou 605	-0.11	-2.68**	2.64**	3.26*	3.12	0.04	-0.41	1.19	0.04	4.37	5.47
Huashuang 3	-0.04	-2.22***	0.40	-0.28	-0.65	0.41	0.12	1.38*	-0.30	-1.68	0.31
Yunyou 8	-0.02	-2.67***	1.71***	-1.91**	-0.38	-1.13	0.31	1.47***	-0.92	-3.20	-1.96
Zhongyou 821	-0.04	1.90***	-2.05***	-0.33	-2.09**	1.93*	0.14	-0.58	0.30	-0.99	-0.05
Eyouchangjia	0.28	6.57**	-2.53**	-1.72	-1.86	0.05	0.21	-2.80***	1.18	0.67	-2.53
Zhong R-888	-0.18	-2.62**	0.85	-0.74	-1.32	0.92	0.25	1.68**	-2.48***	-2.93	-1.38
Tower	-0.05	-1.57***	1.57***	0.17	1.44	-1.80	0.15	2.42***	-1.47**	2.56	-1.44

* = significant at 0.10; ** significant at 0.05; significant at 0.01***; A = embryo additive effect; AE = embryo additive interaction effect; C = cytoplasmic effect; CE = cytoplasmic interaction effect; Am = maternal additive effect; AmE = maternal additive interaction effect; G_t I $= A + AE$ I $+ C + CE$ I $+ Am + AmE$ I ; G_t II $= A + AE$ II $+ C + CE$ II $+ Am + AmE$ II.

variability in the oil content of rape germplasm, which provides the opportunity for improving the quality of rape varieties via breeding (Bhardwaj and Hamama, 2000). In order to increase the efficiency of rape breeding, breeders are now paying much more attention to elucidating the genetic mechanism, which control for oil content in rape seeds.

Most genetic research on the oil content of oilseed rape has focused on the genetic information contained in nuclear genes and has found that the oil content performance is controlled by additive and dominance effects as well as their environment effects (Brandle and McVetty, 1988; Pai and Kumar, 1991), although some research has also found that cytoplasmic or maternal effects could also influence the oil content performance (Wang, 1992). However, there was no information appears to be available on how the oil content of rape can be simultaneously affected by the genetic main effects from the different genetic systems (*i.e.* diploid embryo nuclear genes, cytoplasmic genes and diploid maternal plant nuclear genes) and genotype x environment (GE) interaction effects. If the seed traits were controlled by the genes of the three genetic systems at the same time then the genetic estimations for seed traits obtained from only one genetic system without excluding the influences of other genetic systems would be biased and might mislead breeders. Recently, quantitative trait locus (QTL) mapping has been conducted on oilseed rape to dissect the effects of individual loci for seed traits in terms of rape-oil yield (Tanhuanpää *et al*., 1996; Thormann *et al*., 1996; Zhao *et al*., 2005). QTL analysis in which the molecular marker near the available locus can be screened is important in molecular breeding strategies such marker associated selection (MAS) used to screen the target materials precisely and improve selection efficiency for quantitative traits (Tanhuanpää *et al*., 1996; Somers *et al*., 1998; Gupta *et al*., 2004). So far, QTL mapping for seed traits has been based on the maternal plant because of the QTL method used to map agriculturally plant traits. Due to the nutrient and physiological substances related to the three genetic systems operating during the growth and development of seeds, QTL mapping for seed traits should consider not only maternal effects but also interference embryo and cytoplasm genetic effects.

In this paper we have successfully produced genetic information on the embryo nuclear genes, cytoplasmic genes and diploid maternal plant nuclear genes and their GE interaction effects in respect of the oil content of dicotyledon rape. We found that although oil content performance was affected both by genetic main effects from nuclear genes and GE interaction effects, in which all the individual components could be even more important than those in the main effects in terms of oil content performance.

Our genetic analysis found that the oil content of rapeseed was mainly controlled by maternal and cytoplasm genetic effects with high respective heritabilities, suggesting that improving oil content of rapeseed would be more efficient when selection was based on maternal plants than on seeds from early generations. It thus seems that selection methods might be designed based on maternal single plant performance because the single seed selection method for oil content had low efficiency for rapeseed breeding. The two problems, large amounts of sample and the small size of each sample tested, should be resolved when screening single plants in breeding programs. Also, non-invasive analysis techniques such as nuclear-magnetic resonance (NMR) and near-infrared reflectance spectroscopy (NIRS) techniques could be applied to screen single plant seeds in early generation in breeding programs (Brühl and Matthäus, 1999; Wu *et al*., 2002a, b). When using the NIRS calibration equation to select single seeds, Hom (2004) found that the selection of single seeds has certain responses to selection for oil.

It is very important for breeders worldwide to select suitable parents in rapeseed pure-line breeding programs for improving breeding efficiency. Good parent plants which have the best genetic effects and are suited to different environments for rapeseed quality breeding may be able to be selected by predicting breeding values. Additionally, the approach outlined in this paper appears to give the most detailed genetic information on embryo, cytoplasmic and maternal additive effects as well as their environments interactions for the rape oil content trait and allows breeders to make this work. In this study we found that all parents possessed the appropriate genetic components and that some parents such as Youcai 601 and Gaoyou 605 had better breeding values, which could increase the oil content of rape in different environments (years), and that these two parents perform consistently across environments and could be used as parents in rapeseed quality breeding for increasing oil content.

Acknowledgments

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