RESEARCH ARTICLE

Analysis of embryo, cytoplasmic and maternal genetic correlations for seven essential amino acids in rapeseed meal (*Brassica napus* L.)

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Abstract

Genetic correlations of nutrient quality traits including lysine, methionine, leucine, isoleucine, phenylalanine, valine and threonine contents in rapeseed meal were analysed by the genetic model for quantitative traits of diploid plants using a diallel design with nine parents of *Brassica napus* L. These results indicated that the genetic correlations of embryo, cytoplasm and/or maternal plant have made different contribution to total genetic correlations of most pairwise nutrient quality traits. The genetic correlations among the amino acids in rapeseed meal were simultaneously controlled by genetic main correlations and genotype × environment (GE) interaction correlations, especially for the maternal dominance correlations. Most components of genetic main correlations and GE interaction correlations for the pairwise traits studied were significantly positive. Some of the pairwise traits had negative genetic correlations, especially between valine and other amino acid contents. Indirect selection for improving the quality traits of rapeseed meal could be expected in rape breeding according to the magnitude and direction of genetic correlation components.

Introduction

Brassica oil crops are mainly grown for the production of vegetable oils. However, the byproduct obtained after oil extraction is a rich protein source comprising about 40% of crude protein. Protein of rapeseed meal contains rational amino acid composition and is an important source of nutrition for feeding livestock (Goding *et al*. 1972; Huisman and Tolman 1990). Compared to soybean and peanut, rapeseed meal has higher contents of most essential amino acids, especially methionine and cysteine. Thus, the nutritive value of rapeseed meal is not less than soybean meal (Josefesson and Muhlenberg 1968; Simbaya *et al*. 1995). (Röbbelen 1981) emphasized that the development of high-protein cultivars in rapeseed is an important breeding objective, because the rapeseed meal can be changed into an economically viable feed for livestock. Condensed proteins from rapeseed meal have been applied to high-valued animal feed ingredients. Several results have confirmed that plant protein is more beneficial to humans than animal protein (Friedman

1996; Millward 2006). Besides building blocks of proteins and polypeptides, some amino acids are important regulators of key metabolic pathways which are necessary for growth, maintenance, reproduction and immunity in farm animals (Wu 2009). An accurate adjustment of amino acid contents in compound feed is very important, because lack of lysine, methionine, threonine and other essential amino acids can restrict the growth of livestock (Fontaine *et al*. 2002). Therefore, breeders are interested in improving the protein content and rational amino acids composition in rapeseed.

For breeding a new rapeseed variety, breeders are concerned with the combination of quantitative traits in the selection process. An understanding of the nature of relationships among traits can be useful in multiple trait improvement programmes. For example, Hu (1997) found that there were high significant positive relationships between individual plant yield and pod number, 1st branch number, 2nd branch number, pod density, plant height and pod number of main anthotaxy. Researches have further revealed that the correlations of some pairwise quality traits were significantly negative, such as between glucosinolate content and oil content, erucic acid content and oleic acid content or

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linoleic acid, or protein content and oil content (Downey and Harvey 1963; Downey and Craig 1964; Krzymanski and Downey 1968; Grami and Stefansson 1977a, b; Velasco *et al.* 1999), while that between oil content and oleic acid content (Schierholt and Becker 2001; Möllers and Schierholt 2002) was significantly positive. Yadava *et al.* (1983) and Getinet *et al.* (1996) pointed out that indirect selection effects could be expected according to the correlations among agronomic and quality traits in crop plants. However, until now, most of the phenotypic correlation coefficients were only acquired through simple correlation formula among agronomic traits or quality traits in previous studies.

It is well known that phenotypic variations for many important rapeseed quality traits are simultaneously controlled by genetic main effects and genotype × environment interaction effects from the different genetic systems including diploid embryo nuclear genes, cytoplasmic genes and diploid maternal plant nuclear genes (Zhang *et al.* 1996; Shi *et al.* 2003; Zhang *et al.* 2004a, b; Wu *et al.* 2005). So, the genotypic correlation among quality traits can also be further divided into genetic main correlation and their G × E interaction correlation components. Genetic correlation studies can reveal the magnitude and nature of genetic association among different rapeseed quality traits. Further, the partitioning of the genetic correlation across different genetic systems can provide a deeper understanding of the nature of gene interactions occurring in different pairwise traits. Genetic correlation studies among the fatty acid components or between the fatty acids and other seed quality traits in rapeseed has revealed significant correlations deriving from the different genetic systems among the quality traits of rapeseed and some of the quality traits could be simultaneously improved by selection because of their significant negative or positive relationships (Shi *et al.* 2006). In spite of the importance being given to improve the amino acid composition of rapeseed meal, little attention has been paid to analyse the relationship between the amino acids content in rapeseed meal. Till date, no knowledge is available on genetic correlation components of embryo additive and dominance effects, cytoplasmic effects, maternal additive and dominance effects for individual amino acids content traits of rapeseed meal across environments. The main objective of the present study was to investigate the genetic correlation components including genetic main correlations and G × E interaction correlations from embryo, cytoplasm, and maternal plant genetic systems among amino acids traits in rapeseed meal and to use the information for providing new avenues for improving the amino acids composition in rapeseed meal.

Materials and methods

Field experiment

Experiments were conducted from 2005 to 2008 in the experimental farm of Zhejiang University, Hangzhou, People's Republic of China (120°11′27″E, 30°16′28″N). A complete diallel mating design was used and included nine parents of *B. napus*; namely Youcai 601, Double 20–4, Huashuang 3, Gaoyou 605, Zhongyou 821, Eyouchangjia, Zhong R-888, Tower and Zheshang 72. Seeds of the nine parents were sown in October 2005, and the seeds of parents were self-pollinated and F$_1$ were obtained by crossing among nine parents with hand emasculation in the spring of 2006. The seeds of parents and F$_1$ were sown in October 9 in 2006 and October 13 in 2007, respectively. The 38-day-old seedlings were individually transplanted at a spacing of 35 cm × 30 cm, and there were 32 plants in each plot. The experiment was laid out in a randomized block design with two field replications and standard cultural practices were followed throughout the growing season. The selfpollinated seeds samples of parents and F$_2$ seeds on F$_1$ plants were derived at maturity from 12 plants in the centre part of each plot, in which several anthotaxys were randomly set in the photic bag before anthesis. Samples of F$_1$ seeds for all crosses were obtained by crossing females to males using the method of isolated pollination during the same growing season in both environments.

Calibration equations for seven essential amino acids contents

For developing the calibration equations of amino acids content of rapeseed meal, 621 rapeseed samples with different amino acid contents were selected in the present experiment. About 3 g of each intact sample were scanned in a 36 mm inner-diameter ring cup (Shenk and Westerhaus 1993) using a NIRSystems model 5000 near-infrared reflectance spectroscope (NIRSystems, Silver Spring, USA) according to the WinISI II manual instructions for routine analysis (FOSS NIRSystems/TECTOR, Infrasoft International, LLC). Two hundred and twenty-six rapeseed samples which comprised the calibration set were screened out from 621 primary samples, using CENTER and SELECT algorithm based on the spectra variation. After defatting by Soxhlet extractive method GB2906–82 of China with crude fat analyzer model SZF-06 (Xinjia Electronic, Shanghai, P. R. China), an amino acid auto-analyzer model L-8900 (Hitachi High-Technologies, Tokyo, Japan) was used to estimate amino acids contents of rapeseed meal. The calibration equation was finally developed using a standard normal variant + detrending scatter correction and a 2, 4, 4, 1 mathematical treatment and a modified partial least square (MPLS) regression method. Equation was achieved for lysine (Lys), methionine (Met), leucine (Leu), isoleucine (Ile), phenylalanine (Phe), valine (Val), and threonine (Thr) with RSQ of 0.972, 0.800, 0.966, 0.914, 0.931, 0.620 and 0.964. Their corresponding standard error of cross-validation (SEC) was 0.100, 0.062, 0.094, 0.085, 0.070, 0.512 and 0.061, respectively.

Determination for seven essential amino acids contents

The seven essential amino acids content for each of the samples were determined using the calibration equation

developed as above. All samples from each parent, F_1 and F_2 were measured with two replications.

Statistical analysis methods

As the performance of rapeseed quality traits could be simultaneously controlled by diploid embryo nuclear, cytoplasmic and diploid maternal plant nuclear genetic systems, the genetic correlation among the quality traits could be further divided into different components, including embryo additive and dominance correlations, cytoplasmic correlation, maternal additive and dominance correlations, and their GE interaction correlations. The phenotypic correlation $\left(r_{P(XY)} = C_{P(XY)}/\sqrt{V_{P(X)}V_{P(Y)}}\right)$ and genotypic correlation $\left(r_{G(XY)} = C_{G(XY)}/\sqrt{V_{G(X)}V_{G(Y)}}\right)$ components among seed quality traits were estimated by using the genetic model for quantitative traits of seeds in diploid plant (Zhu 1992; Zhu and Weir 1994). $r_P = \sqrt{H_X^2 * H_Y^2} * r_G + \sqrt{\left(1 - H_X^2\right) * \left(1 - H_Y^2\right)} * r_e$, where H_X^2 and H_Y^2 represent broad-sense heritability for X and Y traits, respectively. r_G was further partitioned into genetic main correlation (r_{GM}) components, including embryo additive main correlation $\left(r_{A(XY)} = C_{A(XY)}/\sqrt{V_{A(X)}V_{A(Y)}}\right)$ and dominance main correlation $\left(r_{D(XY)} = C_{D(XY)}/\sqrt{V_{D(X)}V_{D(Y)}}\right)$, cytoplasmic main correlation $\left(r_{C(XY)} = C_{C(XY)}/\sqrt{V_{C(X)}V_{C(Y)}}\right)$, maternal additive main correlation $\left(r_{Am(XY)} = C_{Am(XY)}/\sqrt{V_{Am(X)}V_{Am(Y)}}\right)$ and dominance main correlation $\left(r_{Dm(XY)} = C_{Dm(XY)}/\sqrt{V_{Dm(X)}V_{Dm(Y)}}\right)$; and GE interaction correlation (r_{GE}) components including embryo additive interaction correlation $\left(r_{AE(XY)} = C_{AE(XY)}/\sqrt{V_{AE(X)}V_{AE(Y)}}\right)$ and dominance interaction correlation $\left(r_{DE(XY)} = C_{DE(XY)}/\sqrt{V_{DE(X)}V_{DE(Y)}}\right)$, cytoplasmic interaction correlation $\left(r_{CE(XY)} = C_{CE(XY)}/\sqrt{V_{CE(X)}V_{CE(Y)}}\right)$, maternal additive interaction correlation $\left(r_{AmE(XY)} = C_{AmE(XY)}/\sqrt{V_{AmE(X)}V_{AmE(Y)}}\right)$ and dominance interaction correlation

$\left(r_{DmE(XY)} = C_{DmE(XY)}/\sqrt{V_{DmE(X)}V_{DmE(Y)}}\right)$. Residual correlations $\left(r_{e(XY)} = C_{e(XY)}/\sqrt{V_{e(X)}V_{e(Y)}}\right)$ arising from experimental errors or microenvironment influences were also estimated. The terms X and Y in the equation represent two different amino acids, C stands for covariance and V is the variance. The Jackknife technique (Miller 1974; Zhu and Weir 1996) was applied by sampling generation means of entries for estimating the standard errors of estimated components of correlations.

Results

Phenotypic and genotypic correlations among seven essential amino acids content

The estimates of r_P, r_G and r_e among seven essential amino acid traits of rapeseed meal are presented in table 1. Lysine showed significant relationships with other essential amino acids, as reflected in their r_P and r_G values. Significant positive r_P and r_G were found between Lys and Met/Leu/Ile/Phe/Thr, indicating that genetic improvement in these five pairwise amino acids could be achieved at the same time by selecting plants with higher Lys content. However, the r_P between Lys and Val was significantly negative, while the r_G was not significant. For r_G between lysine and other amino acids, the results from tables 2 and 3 showed that the components of r_{GE} for these pairwise traits were more important than that of r_{GM} from embryo, cytoplasmic and maternal genetic systems, suggesting that the correlations could be easily influenced by environmental factors. So, while selecting for lysine and other amino acids, due consideration must be given to the effect of the prevailing environment on the relationship between the traits.

Significant r_P and r_G values were noted between Met and other essential amino acids except between Met and Val. The relationships between Met and Leu/Ile/Phe/Thr/Lys were

Table 1. Phenotypic, genotypic and residual correlations among seven essential amino acids content of rapeseed meal.

Parameter		Lys	Met	Leu	Ile	Phe	Val	Thr
Lys			r_P 0.126**	0.122**	0.160**	0.171**	−0.089*	0.213**
			r_G 0.097*	0.115**	0.139**	0.158**	−0.033	0.175**
Met	r_e	0.801**		r_P 0.084*	0.094*	0.113**	−0.007	0.118**
				r_G 0.075$^+$	0.086*	0.102*	0.016	0.100*
Leu	r_e	0.200**	0.281**		r_P 0.181**	0.258**	0.022	0.227**
					r_G 0.143**	0.193**	0.029	0.175**
Ile	r_e	0.433**	0.318**	0.621**		r_P 0.234**	0.018	0.229**
						r_G 0.189**	0.018	0.184**
Phe	r_e	0.310**	0.368**	0.915**	0.790**		r_P 0.025	0.283**
							r_G 0.031	0.232**
Val	r_e	−0.641**	−0.421**	−0.039	0.024	−0.035		r_P −0.041
								r_G −0.004
Thr	r_e	0.653**	0.542**	0.762**	0.788**	0.852**	−0.392**	

[a]The numbers in lower left corner are the residual correlations. [b]The numbers in the upper and lower line in the upper right corner are phenotypic and genotypic correlations, respectively. $^+$Significant at $P < 0.10$. *Significant at $P < 0.05$. **Significant at $P < 0.01$.

Table 2. Additive and cytoplasmic correlations among seven essential amino acids content of rapeseed meal.

Parameter	Lys	Met	Leu	Ile	Phe	Val	Thr
Lys		r_A 0.000	0.000	0.000	0.000	0.000	0.000
		r_C 0.000	0.000	0.000	0.000	0.000	0.000
		r_{Am} 0.318**	0.180**	0.048	0.165**	0.000	0.192**
Met	r_{AE} 0.091*		r_A 0.266**	−0.040	0.246**	0.436**	0.115**
	r_{CE} 0.345**		r_C 0.000	0.000	0.000	−0.028	0.000
	r_{AmE} −0.056		r_{Am} 0.210**	0.175**	0.213**	0.000	0.249**
Leu	r_{AE} 0.000	0.000		r_A 0.164**	0.239**	0.063+	0.173**
	r_{CE} 0.000	0.000		r_C 0.000	0.000	0.000	0.000
	r_{AmE} 0.000	0.000		r_{Am} 0.124**	0.175**	0.000	0.219**
Ile	r_{AE} 0.154**	0.072+	0.000		r_A 0.207**	0.207**	0.093*
	r_{CE} 0.209**	0.192**	0.000		r_C 0.000	0.000	0.000
	r_{AmE} 0.036	0.066+	0.000		r_{Am} 0.206**	0.000	0.188**
Phe	r_{AE} 0.000	0.000	0.000	0.000		r_A 0.218**	0.208**
	r_{CE} 0.000	0.000	0.000	0.000		r_C 0.000	0.000
	r_{AmE} 0.000	0.000	0.000	0.000		r_{Am} 0.000	0.299**
Val	r_{AE} −0.106**	−0.178**	0.000	0.093*	0.000		r_A 0.038
	r_{CE} −0.327**	−0.229**	0.000	−0.264**	0.000		r_C 0.000
	r_{AmE} −0.052	−0.031	0.000	0.097*	0.000		r_{Am} 0.000
Thr	r_{AE} 0.000	0.000	0.000	0.000	0.000	0.000	
	r_{CE} 0.000	0.000	0.000	0.000	0.000	0.000	
	r_{AmE} 0.000	0.000	0.000	0.000	0.000	0.000	

[a]The numbers in the upper, middle and lower line in lower left corner are the embryo additive, cytoplasmic and maternal additive interaction correlations, respectively. [b]The numbers in the upper, middle and lower line in the upper right corner are the embryo additive, cytoplasmic and maternal additive correlations, respectively. +Significant at $P < 0.10$. *Significant at $P < 0.05$. **Significant at $P < 0.01$.

significantly positive, suggesting that a variety with higher contents of these five amino acids might be obtained in rapeseed breeding. The r_G from tables 2 and 3 showed that components of r_{GM} for the pairwise traits between Met and other amino acids were more visible than their corresponding components of r_{GE}.

For Leu, significant positive r_P and r_G were found with the other essential amino acids (except for Val). No significant relationship between Ile and Val, Phe and Val, Thr and Val were detected in the experiment (table 1). So breeders could simultaneously improve essential amino acid in rapeseed through selection except for Val. For the pairwise traits of Ile and other amino acids, and also Phe and other amino acids, contribution from components of r_{GM} tend to be larger than that of r_{GE}, indicating that the genetic main effects role from different genetic systems to the correlations for the

Table 3. Dominance correlations among seven essential amino acids content of rapeseed meal.

Parameter	Lys	Met	Leu	Ile	Phe	Val	Thr
Lys		r_D 0.044	0.143**	0.277**	0.159**	0.039	0.220**
		r_{Dm} −0.079*	0.203**	0.207**	0.173**	0.058	0.139**
Met	r_{DE} 0.309**		r_D 0.083*	0.249**	0.091*	0.208**	0.091*
	r_{DmE} 0.185**		r_{Dm} 0.055+	0.119**	0.027	0.057	−0.012
Leu	r_{DE} 0.157**	0.247**		r_D 0.122**	0.082*	0.236**	0.061
	r_{DmE} −0.029	0.018		r_{Dm} 0.295**	0.260**	0.014	0.251**
Ile	r_{DE} 0.107**	0.193**	0.268**		r_D 0.159**	0.160**	0.186**
	r_{DmE} −0.713**	−0.574**	1.000**		r_{Dm} 0.357**	0.108**	0.340**
Phe	r_{DE} 0.191**	0.272**	0.338**	0.298**		r_D 0.198**	0.097*
	r_{DmE} 0.055	0.065+	0.268**	0.965**		r_{Dm} 0.054	0.324**
Val	r_{DE} −0.032	−0.034	−0.035	−0.071+	−0.027		r_D 0.211**
	r_{DmE} 0.000	0.000	0.000	0.000	0.000		r_{Dm} 0.104**
Thr	r_{DE} 0.134**	0.221**	0.321**	0.256**	0.328**	−0.112**	
	r_{DmE} 0.132**	0.090*	0.287**	0.879**	0.272**	0.000	

[a]The numbers in the upper and lower line in lower left corner are the embryo dominance and maternal dominance interaction correlations, respectively. [b]The numbers in the upper and lower line in the upper right corner are the embryo dominance and maternal dominance correlations, respectively. +Significant at $P < 0.10$. *Significant at $P < 0.05$. **Significant at $P < 0.01$.

pairwise quality traits were stronger than that of the corresponding GE interaction effects. On the whole, components of r_{GM} for the pairwise traits among seven essential amino acids content were more evident than that of r_{GE}.

Significant positive r_P and r_G were found among seven essential amino acid contents except for those between Val and other amino acids. On the whole, the results indicated that selection of plants with high Lys content tends to increase the contents of most essential amino acids, while the selection of plants with higher Val content tends to decrease the contents of other essential amino acids.

Since most of the residual correlations (r_e) were significant, the pairwise relationships among these amino acid traits were also influenced by sampling errors or microenvironments.

Additive and cytoplasmic correlations among seven essential amino acid contents

Additive and cytoplasmic correlations are closely related to indirect selection in crop breeding. The results of additive and cytoplasmic correlations are summarized in table 2. Between Lys and other essential amino acids, no significant r_A or r_C were detected. Significant positive r_{Am} between Lys and Met/Leu/Phe/Thr indicated that the visible relationships existed for these pairwise traits and the genetic improvement for these pairwise traits could be expected by selection according to the holistic performance of maternal plants with higher contents of these amino acids. Significant positive r_{AE} or r_{CE} between Lys and Met/Ile and significant negative r_{AE} or r_{CE} between Lys and Val indicated that environmental effects can influence the relationship for these pairwise traits. As compared with r_{AE} or r_{CE}, no significant r_{AmE} was observed between Lys and other amino acids. Thus, except for the pairwise trait of Lys and Val, all the others can be simultaneously improved by selection because of their significant positive r_{GM} and r_{GE}.

For the pairwise trait of Met and other amino acids, significant positive r_A and r_{Am} were found (except for Ile), while the r_C values were not significant. No significant r_{AE}, r_{CE} and r_{AmE} were observed between Met and Leu/Phe/Thr (except between Ile and Val for r_{AE} or r_{CE}) and so the relationships between these traits were stable under diverse environments.

The results in table 2 further revealed that the components of r_A and r_{Am} between Leu and Ile/Phe/Thr were significantly positive while no significant r_C, r_{AE}, r_{CE} and r_{AmE} were detected for the different pairwise traits. Thus, the relationships between Leu and Ile/Phe/Thr were stable in different environments.

Among the additive main correlation components, r_A and r_{Am} between Ile and other amino acids were significantly positive (except r_{Am} for Val) while no significant r_C were detected. Also, r_{AE}, r_{CE} and r_{AmE} were not found except for the pairwise trait of Ile and Val, which indicated that the relationship between Ile and Phe/Thr was stable. Between Phe

and Val/Thr, only the components of r_A and r_{Am} were found significant (except for r_{Am} between Phe and Thr).

Dominance correlations among seven essential amino acids in rapeseed meal

For the dominance correlation components, which are depicted in table 3, between Lys and other amino acids, r_{Dm} was the most important followed by r_D. Most of the observed significant r_{Dm} or r_D was positive, except for r_{Dm} between Lys and Met which was significantly negative. For interaction relationships, r_{DE} was significantly positive between Lys and Met/Leu/Ile/Phe/Thr, and r_{DmE} was significantly positive between Lys and Met/Thr, whereas it was significantly negative between Lys and Ile. This indicated that performance under different environments must be considered for better improvement of these pairwise traits.

For the relationships between Met and other essential amino acids, significant positive r_{Dm} were found only between Met and Leu/Ile; all r_D were significant positive, suggesting that the relationships were very compact due to embryo dominance main effects, as compared with r_{Dm} (table 3). Most of r_{DE} and r_{DmE} between Met and Ile/Phe/Thr were significant and so the relationship could be influenced by the prevailing environment.

For r_D and r_{Dm} between Leu content and other essential amino acids, the results from table 3 showed that most of r_D and r_{Dm} were significantly positive while the r_{DE} and r_{DmE} between Leu and Ile/Phe/Thr were significantly positive.

The r_D and r_{Dm} between Ile and other essential amino acids were all significantly positive, suggesting that the relationships due to embryo/maternal dominance effects were close (table 3). Besides significant positive r_{DE} and r_{DmE} was also observed between Ile and Phe/Thr. With respect to r_D and r_{Dm} among Phe, Thr and Val content, the results revealed that all components were significantly positive except for r_{Dm} between Phe and Val, suggesting that the dominance correlations contributions from embryo and maternal dominance effects were important. Significantly positive r_{DE} and r_{DmE} between Phe and Thr and significantly negative r_{DE} between Val and Thr were also found. Since dominance correlations are more evident in F_1 generation, the correlations of these pairwise quality traits might be used for the heterosis application. In other words, pairwise quality traits might be simultaneously improved through F_1 heterosis, such as pairwise quality traits between Phe and Thr.

Indirect selection and genetic improvement for seven essential amino acid contents

Results (tables 1, 2 and 3) show that highly significant ($P < 0.01$) positive r_P and r_G existed between Lys and Leu, Lys and Phe, Lys and Thr; Met and Leu, Met and Phe, Met and Thr; Leu and Ile; Leu and Phe, Leu and Thr; Ile and Phe, Ile and Thr, and Phe and Thr. All genetic correlation components were significantly positive. Pairwise traits between

Lys and Leu, Lys and Phe, Lys and Thr; Leu and Thr; Ile and Phe, and Ile and Thr were mainly controlled by dominance correlation and maternal additive correlation, suggesting that selection effects would be expected by single plant selection in later generations. Pairwise traits between Leu and Ile, Leu and Phe; and Phe and Thr were mainly affected by dominance correlation and embryo additive correlation, indirect selection effects would be obtained through single seed selection in later generations. Pairwise traits between Met and Thr were mainly controlled by maternal additive correlation and could be improved through single plant selection in early generations. Pairwise traits between Met and Leu or Met and Phe were mainly governed by embryo additive correlation; simultaneous improvement could be achieved by single seed selection in early generations.

Significant ($P < 0.05$ or $P < 0.01$) positive r_P and r_G were found between Lys and Met, Lys and Ile; Met and Ile, but there existed some significant negative correlation components which could reduce the impact of indirect selection. These pairwise traits, whose additive correlations were relatively weak, were strongly controlled by dominance correlation. So, the improvement for the quality traits could be expected through single plant or single grain selection in later generations. Negative r_P and r_G were found between Val and other essential amino acids. Therefore, increasing Val content in rapeseed meal would inevitably lead to a decrease in the contents of other essential amino acids.

Discussion

The relationship existing among different quality traits of rapeseed is complex because of genetic linkage and the 'pleiotropic' function of genes, causing difficulties in selecting appropriate genotypes from subsequent generations. Correlation analysis of pairwise traits tends to broaden our understanding of the interrelationships and facilitate multiple traits selection in breeding programme. Genotypic correlation is an important statistical parameter which is superior to phenotypic correlation and the analysis can get rid of the interference caused by random error. But, the genotypic correlation is the overall relationship between genetic effects of two traits. So the indirect selection in terms of genotypic correlation sometimes does not give ideal results, since the performance of some nutrient traits could be affected by the genetic effects from embryo, cytoplasm and maternal plant as well as their G × E interaction effects (Shi *et al.* 2003). The genotypic correlation for the quality traits could be further partitioned into components of genetic main correlation arising from genetic main effects and GE interaction correlation arising from GE interaction effects across different genetic systems. Using the genetic models developed by Zhu (1992); Zhu and Weir (1994), different genetic correlation components could be measured for the desired pairwise traits. According to nature of various components, genetic correlations controlled by different genetic effects could

be classified into three types, namely additive correlation, cytoplasmic correlation and dominance correlation.

Additive correlation was defined as all coefficients arising from additive main effects and additive interaction effects, including embryo additive correlation (r_A), embryo additive interaction correlation (r_{AE}), maternal additive correlation (r_{Am}) and maternal additive interaction correlation (r_{AmE}). The additive main effects and their GE interaction effects are accumulative for selection; and the cytoplasm effect can be handed down through maternal plants. It will be easy to achieve simultaneous improvement by indirect selection for the pairwise traits with high positive maternal additive and cytoplasmic correlations. When the relationships of the pairwise seed quality traits were mainly controlled by maternal genetic correlations, there was no obvious separation in F_2 seeds grown on F_1 plants and so the indirect selection for quality traits can be made based on general performance of maternal plant. However, if the relationships of the pairwise seed traits were mainly controlled by seed additive correlation, indirect selection should be made based on the performance of single seed, due to larger separation among seed genotypes. So, different selection methods such as single plant and/or single grain selection could be followed to suit different additive correlations.

Dominance correlation was defined as all coefficients arising from dominance main effects and dominance interaction effects, including embryo dominance correlation (r_D), embryo dominance interaction correlation (r_{DE}), maternal dominance correlation (r_{Dm}) and maternal dominance interaction correlation (r_{DmE}). Since the dominance effects are strongly observed in F_1 generation, dominance correlation can be useful in hybrid breeding. The dominance correlation tends to become weaker with increasing generation, and so selection strategies need to be devised accordingly.

Most of previous correlation analyses about the seed quality traits in different crops belonged to simple correlation estimates due to the nonavailability of suitable genetic models. Analysis of correlation may be carried out on the level of r_P and r_G. However, the selection strategies based only on r_P and r_G values sometimes does not yield desired results for multiple traits improvement in crop breeding. The real genetic association for pairwise traits could be better described by components of additive, dominance and cytoplasmic correlations. Generally, additive and cytoplasmic correlations are effective and important for selection on pairwise traits. Based on the genetic model for quantitative traits of seeds in diploid plant (Zhu 1992; Zhu and Weir 1994), various genetic correlation components including embryo additive and dominance correlations, cytoplasmic correlation, maternal additive and dominance correlations, and their G × E correlations were calculated, the results confirmed that the genetic correlations among different amino acid traits in rapeseed were simultaneously affected by genetic main effects and G × E interaction effects from different genetic systems. Estimated components of genetic correlation are useful to decipher the mechanism of relationship for quality

traits of rapeseed. Therefore, the analysis method on classifying genetic correlation makes it possible to design a scheme for indirect selection. After analysis of genetic correlation for pairwise traits, suitable indirect selection procedure for multiple traits can be established depending on the nature of genetic correlations. The disturbance caused by dominance correlations could be better eliminated for various genetic correlations combination. When a group of additive and dominance correlations were significantly positive/negative at the same time, such as between Lys and Leu, indirect selection effects in early generation would be interfered by dominance correlation; so indirect selection should be delayed to later generations. When pairwise traits were mainly controlled by significant positive/negative additive correlation, indirect selection could be made in early and/or middle generations. For example, pairwise traits between Met and Thr were mainly controlled by maternal additive correlation and could be improved through single plant selection in early generations.

Genetic correlation analysis tends to broaden our understanding of the interrelationships of pairwise traits and facilitates multiple traits selection in breeding programme. It is possible to increase essential amino acids content by breeding methods, including indirect selection. To improve some essential amino acids content of rapeseed meal simultaneously, indirect selection can be used in rapeseed breeding according to the magnitude and direction of genetic correlation components acquired through the present study. In addition, the analysis method for genetic correlation components will play important roles in genetic improvement among quality traits of crops.

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