

RESEARCH NOTE

Analysis of embryo, cytoplasmic and maternal correlations for quality traits of rapeseed (*Brassica napus* L.) across environments

C. H. SHI*, H. Z. ZHANG and J. G. WU

Department of Agronomy, College of Agriculture and Biotechnology, Zhejiang University,
Hangzhou 310029, China

Introduction

In recent years, the relationships among some nutrient-quality traits in rapeseed (*Brassica napus* L.) have been studied in terms of phenotypic, genotypic and/or environmental correlations (Kondra and Thomas 1975; Bahram *et al.* 1977; Yadava *et al.* 1983; Chen and Beversdorf 1990; Ecker and Yaniv 1993; Liu *et al.* 2001). It has also been recognized that phenotypic variations for some important quality traits of rapeseed are simultaneously controlled by genetic main effects from embryo, cytoplasm and maternal plant, as well as by their genotype \times environment interaction (G \times E) effects (Zhang *et al.* 1996; Shi *et al.* 2003; Zhang *et al.* 2004a,b; Wu *et al.* 2005). The objectives of the present study were mainly to estimate the genotype correlation components—including genetic main correlations and G \times E interaction correlations—across different genetic systems (embryo, cytoplasm, maternal plant) for fatty acids and other nutrient traits in rapeseed.

Materials and methods

Experiments were conducted in 1998 and 1999. The diallel design was used for this experiment, with eight parents of *Brassica napus*, namely Youcui 601, Gaoyou 605, Huashuang 3, Yunyou 8, Zhongyou 821, Eyouchangjia, Zhong R-888 and Tower. The seeds of parents and F₁s obtained by crossing among the eight parents were sown on October 7 in both years, and 31-day-old seedlings were individually transplanted in 35 cm \times 30 cm spaces in the experimental farm at Zhejiang University. There were 24 plants in one plot and the experiment was laid out in a randomized block design with three field replications. Standard cultural practices were followed throughout the growing season. Seed samples of parents and F₂ seeds on F₁ plants were

derived at maturity from eight plants in the middle part of each plot. Samples of F₁ seeds analysed were obtained by using the method of isolated pollination during the flowering season. Fatty acids—palmitic acid content (PAC), oleic acid content (OAC), linoleic acid content (LAC), linolenic acid content (LLAC), eicosenoic acid content (EIAC) and erucic acid content (EAC)—were determined (%) by gas chromatography (Zhou and Liu 1987) on a Shimadzu GC-9A. Glucosinolate content (GSLC; $\mu\text{mol/g}$), oil content (OC; %) and protein content (PC; %) were also determined by near-infrared reflectance spectroscopy using a NIRSystems model 5000 monochromator (Shenk and Westerhaus 1993), for which about 3 g of each intact sample was scanned in a small ring cup of 36 mm inner diameter.

Since the performance of rapeseed quality traits could be simultaneously controlled by different genetic systems, including diploid embryo, cytoplasm and diploid maternal plant, the genotypic correlation among these seed-quality traits may be further partitioned into different components, including embryo additive and dominance correlations, cytoplasmic correlation, maternal additive and dominance correlations, and their G \times E interaction correlations. The phenotypic correlation ($r_P = C_P / \sqrt{V_{P(X)} V_{P(Y)}}$) and genotypic correlation ($r_G = C_G / \sqrt{V_{G(X)} V_{G(Y)}}$) components among seed-quality traits were estimated by using the genetic model for quantitative traits of the diploid plant (Zhu 1992; Zhu and Weir 1994). r_G was further partitioned into (i) genetic main correlation ($r_{GM} = C_{GM} / \sqrt{V_{GM(X)} V_{GM(Y)}}$) components, including embryo additive ($r_A = C_A / \sqrt{V_{A(X)} V_{A(Y)}}$) and dominance ($r_D = C_D / \sqrt{V_{D(X)} V_{D(Y)}}$) correlations, cytoplasmic correlation ($r_C = C_C / \sqrt{V_{C(X)} V_{C(Y)}}$), and maternal additive ($r_{Am} = C_{Am} / \sqrt{V_{Am(X)} V_{Am(Y)}}$) and dominance ($r_{Dm} = C_{Dm} / \sqrt{V_{Dm(X)} V_{Dm(Y)}}$) correlations; and (ii) G \times E interaction correlation ($r_{GE} = C_{GE} / \sqrt{V_{GE(X)} V_{GE(Y)}}$), including embryo additive ($r_{AE} = C_{AE} / \sqrt{V_{AE(X)} V_{AE(Y)}}$) and dominance

For correspondence. E-mail: chhshi@zju.edu.cn.

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($r_{DE} = C_{DE}/\sqrt{V_{DE(X)}V_{DE(Y)}}$) interaction correlations, cytoplasmic interaction correlation ($r_{CE} = C_{CE}/\sqrt{V_{CE(X)}V_{CE(Y)}}$), and maternal additive ($r_{AmE} = C_{AmE}/\sqrt{V_{AmE(X)}V_{AmE(Y)}}$) and dominance ($r_{DmE} = C_{DmE}/\sqrt{V_{DmE(X)}V_{DmE(Y)}}$) interaction correlations. Residual correlations ($r_e = C_e/\sqrt{V_{e(X)}V_{e(Y)}}$) for these nutrient-quality traits were also estimated. The Jack-knife 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 and discussion

Analysis of relationships among fatty acids

Fatty acid component content was closely related to the nutrient quality of rapeseed oil. Significant relationships among fatty acids, as reflected in r_p and r_g values, were found for most of the pairwise tests (table 1). Significant positive relationships were found between PAC and OAC, PAC and LAC, and OAC and LAC, indicating that simultaneous improvement in these three traits could be achieved by selecting plants with high PAC, OAC and LAC. Since the relationships between PAC and EAC, OAC and EAC, and LAC and EAC were significantly negative, plants with higher PAC, OAC and LAC and lower EAC could be obtained by breeding. But breeding may not achieve simultaneous improvement of PAC and EIAC, OAC and EIAC, or LAC and EIAC because of their significant negative relationships, and may not also be suitable for PAC and LLAC, or EIAC and EAC because of the significant positive relationships. No significant relationship was observed between OAC and LLAC, LAC and LLAC, or LLAC and EIAC, except for r_p between LAC and LLAC at 10% significance level.

For r_g , the results showed that components of r_{GE} for the pairwise tests tended to be higher than r_{G_m} from embryo, cytoplasmic and maternal genetic systems, suggesting that the contributions from different genetic systems to the correlations between quality traits were influenced by environmental factors. For r_{G_m} , all r_D were significant, suggesting that the relationships due to embryo dominance effects were close. Next in importance were relationships examined by r_{Dm} , which in most of the pairwise tests were significant, especially between OAC/ LAC/EAC and other fatty acids. For r_{GE} , the results indicated that r_{DE} , r_{CE} and r_{DmE} were significant, except for r_{DE} between PAC and EIAC or LLAC and EIAC. r_{AmE} was also an important measure because most of the r_{AmE} were significant. Most of the genotypic correlation components and their $G \times E$ interaction correlations were significant for the pairwise tests of PAC and OAC, OAC and LAC, or PAC and EAC, OAC and EAC, LAC and EAC, suggesting that these could be simultaneously improved because of the significant positive or negative relationships.

Analysis of relationships among GSLC, OC and PC

High OC is one of the most important aims in rapeseed breeding. Rapeseed meal with higher PC and lower or no

GSLC is considered as a valuable protein source for animal feed. Information about the contributions from different genetic systems to relationships among GSLC, OC and PC might help breeders to design effective breeding procedures for developing new varieties of rapeseed with high OC and PC and low GSLC. The r_p and r_g values for pairwise tests among GSLC, OC and PC (table 2) indicated that a variety with higher OC and lower GSLC might be obtained in rapeseed breeding because of their significant negative correlations, while it would be difficult to simultaneously improve plants for PC and GSLC, as they were significantly positively correlated. It may be possible to breed for higher OC and PC because all r_p and r_g for this pair of traits were nonsignificant. Among the genotypic correlation components, r_A , r_{CE} , and r_{DmE} were the most important. r_{Am} was also critical in the pairwise tests of GSLC and OC, and GSLC and PC.

Relationships between fatty acid components and other quality traits

Rapeseed breeders are now paying more attention to achieving the combination of higher OC with ideal fatty acid components and higher PC, and lower or no GSLC. It is therefore important to understand the correlations between fatty acid components and other quality traits. The r_p and r_g results in table 3 show that GSLC and OAC/LAC/EAC, and OC and EIAC may be simultaneously improved by selection because of the significant negative or positive relationships for these pairs of traits. But simultaneous improvement is unlikely for the pairs GSLC and EIAC, OC and OAC/LAC/EAC, and PC and OAC/LAC/EAC, since r_p and r_g were all significant for these pairs of traits. So in general, rapeseed breeders could achieve the breeding effect of reducing GSLC and increasing fatty acid components except for EIAC at the same time. But it would be difficult to breed for rapeseed with high OC or PC and ideal fatty acid composition of OAC, LAC and EAC.

Our results also indicate that r_{G_m} components r_A , r_D , r_C , r_{Am} and r_{Dm} were higher for GSLC and fatty acid components pairwise, while r_{GE} components r_{AE} , r_{DE} , r_{CE} , r_{AmE} and r_{DmE} were more important for OC or PC and fatty acids pairwise. These results suggest that the relationships between GSLC and fatty acids are more stable than those between fatty acids and OC or PC under different conditions. The correlations reveal that r_{DE} and r_{CE} may be more important than others, since most of them were significant. In other words, the correlation components that estimate embryo dominance interaction effects and cytoplasmic interaction effects reveal strong relationships and the influence of these effects on the simultaneous performance of the traits. The correlation components that estimate embryo additive effects (r_A), embryo dominance effects (r_D) and maternal additive effects (r_{Am}) are also crucial indicators of relationships between fatty acid components and GSLC, OC or PC. Our results also show that the components r_{G_m} and r_{GE} were mostly significant for the pairs GSLC and PAC/EAC, and PC and OAC/LAC/EAC.

Quantitative genetics of rapeseed

Table 1. Genetic correlations of fatty acids (PAC, OAC, LAC, LLAC, EIAC and EAC) in rapeseed.

Parameter	r_p	r_G	r_{GM}						r_{GE}						r_e
			r_A	r_D	r_C	r_{Am}	r_{Dm}	r_{AE}	r_{DE}	r_{CE}	r_{GE}	r_{AmE}	r_{DmE}	r_e	
PAC & OAC	0.311***	0.310***	0.691***	0.463***	0.549***	0.000	-0.326***	0.000	-0.151***	0.462***	0.523***	0.478***	0.392***		
PAC & LAC	0.250***	0.240***	0.549***	0.426***	0.000	-0.075*	0.000	0.087*	0.412***	0.567***	0.319***	0.504***			
PAC & LLAC	0.166***	0.177***	0.000	-0.147***	0.000	0.000	0.000	0.249***	0.157***	0.266***	0.000	0.146***	0.071		
PAC & EIAC	-0.086**	-0.079*	0.000	-0.353***	0.092*	0.000	-0.013	0.073*	0.026	-0.256***	-0.173***	-0.102**	-0.245***		
PAC & EAC	-0.337***	-0.337***	-0.689***	-0.459***	0.400***	0.000	0.094**	0.182***	0.068*	-0.536***	-0.584***	-0.360***	-0.349***		
OAC & LAC	0.313***	0.314***	0.668***	0.556***	0.000	-0.472***	-0.112***	0.000	-0.124***	0.503***	0.553***	0.415***	0.285***		
OAC & LLAC	0.029	0.049	0.000	-0.153***	0.000	-0.598***	0.000	0.000	-0.068*	0.508***	0.000	0.147***	-0.316***		
OAC & EIAC	-0.241***	-0.243***	0.000	-0.575***	-0.089*	0.000	-0.184***	0.000	-0.335***	-0.475***	-0.357***	-0.161***	-0.187***		
OAC & EAC	-0.475***	-0.473***	-0.803***	-0.598***	-0.157***	0.139***	-0.114***	0.000	0.201***	-0.527***	-0.672***	-0.454***	-0.586***		
LAC & LLAC	0.078*	0.051	0.000	-0.366***	0.000	-0.687***	0.000	0.000	0.348***	0.469***	0.000	0.195***	0.427***		
LAC & EIAC	-0.089**	-0.081*	0.000	-0.498***	0.000	0.000	0.172***	0.000	-0.116***	-0.521***	-0.074*	-0.259***	-0.273***		
LAC & EAC	-0.352***	-0.351***	-0.705***	-0.383***	0.000	0.778***	-0.129***	0.000	-0.155***	-0.537***	-0.569***	-0.360***	-0.400***		
LLAC & EIAC	0.039	0.034	0.000	0.273***	0.000	0.000	-0.252***	-0.051	-0.393***	0.000	-0.168***	0.115***			
LLAC & EAC	-0.074*	-0.078*	0.000	0.309***	0.000	1.000***	0.000	-0.322***	-0.328***	-0.559***	0.000	-0.162***	-0.031		
EIAC & EAC	0.239***	0.242***	0.000	0.551***	0.076*	0.000	0.177***	0.267***	0.160***	0.483***	0.296***	0.125***	0.150***		

Significance: * at 0.10, ** at 0.05, *** at 0.01 level.

See text (Materials and methods) for the names of the correlation components.

Table 2. Genetic correlations of glucosinolate (GSLC), oil (OC) and protein (PC) content in rapeseed.

Parameter	r_p	r_G	r_{GM}						r_{GE}						r_e
			r_A	r_D	r_C	r_{Am}	r_{Dm}	r_{AE}	r_{DE}	r_{CE}	r_{GE}	r_{AmE}	r_{DmE}	r_e	
GSLC & OC	-0.070*	-0.068*	-0.263***	0.000	1.000***	-0.343***	0.000	0.065*	0.058	-0.144***	0.000	-0.132***	-0.121***		
GSLC & PC	0.256***	0.257***	0.217***	0.053	0.000	0.620***	0.275***	0.000	-0.019	0.086***	0.000	0.167***	0.253***		
OC & PC	-0.036	-0.025	0.251***	0.000	0.000	0.041	0.000	0.000	-0.109***	0.499***	-0.597***	-0.183***	-0.213***		

Significance: * at 0.10, ** at 0.05, *** at 0.01 level

Table 3. Genetic correlations between fatty acid components and other quality traits (GSLC, OC and PC) in rapeseed.

Parameter	r_p	r_G	r_{GM}						r_e		
	r_A	r_D	r_C	r_{Am}	r_{Dm}	r_{AE}	r_{DE}	r_{CE}	r_{AmE}	r_{DmE}	
PAC & GSLC	-0.009	-0.001	0.335***	-0.184***	0.710***	0.000	0.146***	-0.006	0.191***	-0.328***	0.000
OAC & GSLC	-0.084**	-0.078*	0.007	-0.250**	0.005	-0.369***	-0.030	0.000	0.181***	-0.026	0.000
LAC & GSLC	-0.118***	-0.120***	-0.164***	-0.235***	0.000	-0.425***	-0.073*	0.000	0.280***	0.044	0.000
LLAC & GSLC	0.019	0.007	0.000	0.307***	0.000	0.906***	0.000	0.114**	0.023	0.159***	0.000
EIAC & GSLC	0.124***	0.131***	0.000	0.205***	0.525***	0.000	0.195	0.041	-0.018	-0.032	0.000
EAC & GSLC	0.116***	0.112***	-0.024	0.231***	0.284***	0.508***	0.106**	-0.204***	-0.238***	0.060*	0.000
PAC & OC	-0.009	-0.001	-0.258***	0.000	-0.706***	0.000	0.000	-0.139***	-0.316***	-0.134***	-0.011
OAC & OC	-0.084**	-0.078*	-0.418***	0.000	-0.363***	0.518***	0.000	0.000	0.422***	-0.005	0.058
LAC & OC	-0.118***	-0.120***	-0.411***	0.000	0.000	0.246***	0.000	0.000	-0.398***	-0.507***	0.119***
LLAC & OC	0.019	0.007	0.000	0.000	0.000	-0.176***	0.000	-0.344***	-0.481***	-0.539***	0.000
EIAC & OC	0.124***	0.131***	0.000	0.000	-0.037	0.000	0.000	0.236***	0.022	0.272***	0.531***
EAC & OC	0.141***	0.139***	0.316***	0.000	0.417***	-0.692***	0.000	0.302***	0.336***	0.425***	-0.061
PAC & PC	-0.068*	-0.059	-0.085**	-0.352**	0.000	0.000	-0.199**	0.000	0.152***	-0.530***	-0.057
OAC & PC	-0.124***	-0.115**	-0.170***	-0.352**	0.000	0.001	-0.070*	0.000	0.190***	-0.402***	-0.259***
LAC & PC	-0.141***	-0.140***	-0.136***	-0.342**	0.000	-0.100**	0.069	0.000	0.221***	-0.312***	-0.294***
LLAC & PC	0.039	0.023	0.000	-0.026	0.000	0.263***	0.000	0.000	0.035	-0.474***	0.000
EIAC & PC	0.031	0.029	0.000	0.376***	0.000	0.000	-0.068*	0.000	-0.073*	0.383***	-0.461***
EAC & PC	0.158***	0.154***	0.164***	0.451***	0.000	-0.123***	0.155***	0.000	-0.307***	0.478***	0.308***

Significance: * at 0.10, ** at 0.05, *** at 0.01 level.

Since most of the residual correlations (r_e) were significant, the pairwise relationships among these nutrient-quality traits were also influenced by sampling errors.

Our results of genotypic correlations might be used in rapeseed nutrient-quality breeding and the analysis method for genotypic correlation components could be applied in other dicotyledonous crops.

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