RESEARCH ARTICLE

Genetic analysis of amino acid content in wheat grain

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Abstract

Complete diallel crosses with five parents of common wheat (*Triticum aestivum* L.) were conducted to analyse inheritance of 17 amino acid contents by using the genetic model including seed, cytoplasmic, maternal and environment interaction effects on quantitative traits of seeds in cereal crops. The results showed that inheritance of 17 amino acid contents, except tyrosine, was controlled by several genetic systems including seed, cytoplasmic, and maternal effects, and by significant gene × environment interaction effects. Seed-direct additive and maternal effects constituted a major part of genetic effects for lysine, tyrosine, arginine, methionine, and glutamic acid content. Seed-direct additive effect formed main part in inheritance of isoleucine and serine contents. Threonine content was mainly governed by maternal additive effect. The other nine amino acid contents were almost entirely controlled by dominance effects. High general heritability of tyrosine (36.3%), arginine (45.8%), lysine (24.7%) and threonine (21.4%) contents, revealed that it could be effective to improve them by direct selection in progenies from appropriate crosses. Interaction heritability for phenylalanine, proline, and histidine content, which was 36.1%, 39.5% and 25.7%, respectively, was higher than for the other amino acids.

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Introduction

Wheat, the most important cereal crop (Peña *et al.* 2006), is the principal source of energy, protein and dietary fibre for a major portion of the world's population (Abdel-Aal and Huclw 2002). Wheat protein quality is mainly dependent on the protein content and the balance of amino acid composition in the wheat grain (Li and Zhang 2000; Liu *et al.* 2002). Amino acid composition in wheat protein is unbalanced, especially the total essential amino acid (TEAA) content, which is only 42% in egg and milk protein (Zhai 1988). In particular, lysine, threonine and isoleucine are the main limiting amino acids in wheat. Hence, people cannot meet their nutritional needs through wheat alone (Myer *et al.* 1996). Therefore, it is important to enhance the level of nutrition in food by increasing the protein content of wheat, especially improving the amino acid composition of protein.

Contents of wheat grain amino acids are quantitative traits, controlled by many genes, and their genetic basis was studied by several researchers (Zheng 1989; Zhou and Cai 1990; Dong *et al.* 1993). However, those genetic models could only analyse additive, dominant and epistatic effects. As we know, wheat seed belongs to a new generation, different from maternal plants that provide grain nutrients. Consequently, maternal and cytoplasmic effects can be important components of the total genetic effect for the performance of grain traits. Moreover, the diploid embryo might also have genetic effects affecting the performance of quality traits in wheat (Shi *et al.* 1999; Zhu and Xu 1994). Hence, seed, cytoplasmic and maternal effects should be considered when analysing the inheritance of quantitative traits of seeds in wheat. Recently, several studies indicated that protein (Chen and Zhu 1999a) and lysine content (Shi and Zhu 1999) in rice, and amino acid content in barley (Xu *et al.* 1996) and rapeseed (Ren 2004) are governed by several genetic systems, i.e. seed, cytoplasmic and maternal effects. However, similar studies in wheat have not been reported till date.

Therefore, it is very important to study the inheritance of amino acid content in wheat by using a genetic model including seed, cytoplasmic and maternal effects and

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gene × environment (G × E) interaction effects on quantitative traits of seeds in cereal crops (Zhu 1996). We report results from a study here in which we also estimated heritability and genetic effects for 17 amino acids. The results provide useful information for wheat breeders to improve the nutritional quality of wheat grain.

Materials and methods

Material and field experiment

A 5×5 diallel cross was conducted in 2008 using five wheat varieties (P_1, 07A415; P_2, Bainong AK58; P_3, Liangxing66; P_4, Luo3429; P_5, Zhoumai 98100). Seeds of the progeny (F_1) and the parents were obtained and grown at two locations (Jiyuan, Henan province and Tai'an, Shandong province, China). The field experiment was conducted by a completely randomized block design with two replications in two environments, and all materials were grown in 2-m-long, three-row plots (25 cm apart). Crop management was carried out following local practices. The lines were harvested individually at maturity, and cleaned prior to milling.

Method

Milling and determination of the amino acid content: Whole wheat meals were prepared by milling the wheat with a 3100 Mill (Stockholm, Perten, Sweden). Wheat grain (200 g) was added into the feeder, then the mill was started and continued to run for 1 min after all the wheat pasted the roller. Amino acid compositions was obtained using an amino acid analyser (Biochram 30; Cambridge, UK). In a test tube, 10 mL of 6 N HCl were added to a 50 mg sample. The test tube was evacuated and flushed with nitrogen, sealed, and placed in an oven at 110°C for 24 h, then cool to room temperature. The hydrolysate was filtered to remove the visible sediments and evaporated under vacuum at 60°C. The hydrolysate was dissolved in 1 mL of buffer (pH 2.2). A known volume (20 μL) was injected into the amino acid analyser to estimate the amino acid profile for each sample (Chinese standard GB7649-87 1987). Two replicates per sample was tested.

Data analysis

A genetic model including seed, cytoplasmic and maternal effects and (G×E) interaction effects on quantitative traits of seeds in cereal crops (Zhu and Xu 1994) was used by means of the QGA station software (J. Zhu, Zhejiang University, Hangzhou, China) to analyse the inheritance of 17 amino acids in wheat grain. According to the model, MINQUE (0/1) method was used to estimate the variance and covariance. Partitioning for the phenotypic variance is given by:

$$\begin{aligned} V_P &= V_G + V_{GE} + V_e \\ &= V_A + V_D + V_C + V_{Am} + V_{Dm} + V_{AE} + V_{DE} + V_{CE} + V_{AmE} \\ &\quad + V_{DmE} + 2(C_{A.Am} + C_{D.Dm}) + 2(C_{AE.AmE} + C_{DE.DmE}) + V_e, \end{aligned}$$

where V_A is direct additive variance, V_D is direct dominance variance, V_C is cytoplasmic variance, V_{Am} is maternal additive variance, V_{Dm} is maternal dominance variance, V_{AE} is direct additive × environment variance, V_{DE} is direct dominance × environment variance, V_{CE} is cytoplasmic × environment variance, V_{AmE} is maternal additive × environment variance, V_{DmE} is maternal dominance × environment variance, $C_{A.Am}$ is covariance between the direct and maternal additive effects, $C_{D.Dm}$ is covariance between the direct and maternal dominance effects, $C_{AE.AmE}$ is covariance between the direct and maternal additive × environment effects, $C_{DE.DmE}$ is covariance between the direct and maternal dominance × environment effects, and V_e is the residual variance. Meanwhile, components of total heritabilities $\left(h^2 = h^2_G + h^2_{GE} = h^2_{Go} + h^2_{Gc} + h^2_{Gm} + h^2_{GoE} + h^2_{GcE} + h^2_{GmE}\right)$ were also estimated by the following method:

$$\begin{aligned} h^2_{Go} &= (V_A + C_{A.Am})/V_P \\ h^2_{Gc} &= V_C/V_P \\ h^2_{Gm} &= (V_{Am} + C_{A.Am})/V_P \\ h^2_{GoE} &= (V_{AE} + C_{AE.AmE})/V_P \\ h^2_{GcE} &= V_{CE}/V_P \\ h^2_{GmE} &= (V_{AmE} + C_{AE.AmE})/V_P \end{aligned}$$

where h^2_{Go} is the direct component of heritability, h^2_{Gc} is the cytoplasm component of heritability, h^2_{Gm} is the maternal component of heritability, h^2_{GoE} is the direct × environment component of heritability, h^2_{GcE} is the cytoplasmic × environment component of heritability, h^2_{GmE} is the maternal × environment component of heritability, h^2_G is general heritability, and h^2_{GE} is interaction heritability (Chen and Zhu 1999b). Contribution of genetic main effect variance to total genetic variance (C_1) and the contribution of environment interaction variance to total genetic variance (C_2) were calculated by the following method:

$$\begin{aligned} C_1 &= (V_A + V_D + V_C + V_{Am} + V_{Dm}) / (V_P - V_e) \\ C_2 &= (V_{AE} + V_{DE} + V_{CE} + V_{AmE} + V_{DmE}) / (V_P - V_e) \end{aligned}$$

Standard errors of the statistics were obtained by jackknife procedures (Miller 1974), and *t*-tests were performed for testing null hypothesis of zero parameters.

Results

Phenotypic performance of parents and F_2

The phenotypic data of five parents and F_2 generation under two environments are provided in tables 1 & 2. Table 1

Table 1. Amino acid contents (mg/g) for five parents in two growing environments.

	P_1		P_2		P_3		P_4		P_5	
Trait	Tai'an	Jiyuan	Tai'an	Jiyuan	Tai'an	Jiyuan	Tai'an	Jiyuan	Tai'an	Jiyuan
Lys	2.77	2.36	2.82	2.84	2.59	2.62	2.46	2.37	2.65	1.92
Thr	3.23	2.90	3.41	3.05	3.24	2.50	3.14	2.68	3.46	2.44
Ile	8.49	8.34	9.31	7.68	9.56	8.06	8.49	6.02	8.86	7.36
Phe	6.82	5.62	7.27	6.30	6.68	6.04	5.62	5.99	5.62	5.33
Val	8.53	8.45	9.54	7.99	9.58	7.67	8.55	4.68	8.97	7.50
Mat	8.61	10.36	7.77	7.16	8.70	9.61	9.50	5.28	10.15	9.86
Leu	12.50	10.60	12.61	10.06	12.10	9.70	10.24	8.36	11.96	9.45
Glu	34.04	27.54	32.30	28.88	32.92	25.09	29.69	25.2	32.99	24.57
Pro	8.99	12.90	15.80	12.00	7.73	1.67	10.91	3.93	17.54	12.65
Cys	7.99	8.52	9.56	8.76	8.80	7.92	7.72	6.86	8.63	9.06
Asp	6.12	5.49	6.20	5.47	5.83	5.02	5.57	5.00	6.15	4.52
Ser	5.08	4.45	5.07	4.46	5.14	3.82	4.59	3.89	5.42	3.65
Gly	4.53	4.33	5.04	4.56	4.91	3.86	4.51	3.44	5.06	4.09
Ala	4.74	4.99	5.47	5.12	5.59	4.27	5.10	3.39	5.51	4.51
Tyr	4.95	4.30	5.30	4.86	5.01	4.41	4.73	5.05	4.75	4.16
His	2.58	2.06	2.88	2.69	2.52	2.71	2.11	1.95	2.55	1.69
Arg	4.81	3.94	5.03	4.64	4.82	3.89	4.61	3.93	4.71	3.39

Table 2. Amino acid contents (mg/g) for five parents and their F_2 seeds in two growing environments.

		Parent		F_2	
Trait	Location	Average	Variation range	Average	Variation range
Lys	Tai'an	2.66	2.46–2.82	2.72	2.37–3.02
	Jiyuan	2.42	1.92–2.84	2.45	2.16–2.92
Thr	Tai'an	3.30	3.14–3.46	3.22	2.84–3.55
	Jiyuan	2.71	2.44–3.05	2.96	2.60–3.31
Ile	Tai'an	8.94	8.49–9.56	8.72	7.46–9.62
	Jiyuan	7.49	6.02–8.34	8.14	6.29–10.15
Phe	Tai'an	6.40	5.62–7.27	6.68	4.75–7.77
	Jiyuan	5.86	5.33–6.30	6.06	3.93–7.67
Val	Tai'an	9.03	8.53–9.58	8.71	7.68–9.59
	Jiyuan	7.26	4.68–8.45	8.22	5.94–9.67
Mat	Tai'an	8.95	7.77–10.15	8.88	6.78–11.06
	Jiyuan	8.45	5.28–10.36	8.65	4.77–10.54
Leu	Tai'an	11.88	10.24–12.61	11.52	9.78–13.01
	Jiyuan	9.63	8.36–10.60	10.70	8.08–13.31
Glu	Tai'an	32.39	29.69–34.04	31.93	29.82–35.15
	Jiyuan	26.26	24.57–28.88	28.94	25.98–34.31
Pro	Tai'an	12.19	7.73–17.54	9.86	2.53–16.40
	Jiyuan	8.63	1.67–12.90	9.45	3.59–17.76
Cys	Tai'an	8.54	7.72–9.56	8.35	7.42–9.49
	Jiyuan	8.22	6.86–9.06	8.00	6.02–9.31
Asp	Tai'an	5.97	5.57–6.20	5.91	5.27–6.42
	Jiyuan	5.10	4.52–5.49	5.55	4.88–6.20
Ser	Tai'an	5.06	4.59–5.42	4.89	4.54–5.58
	Jiyuan	4.05	3.65–4.46	4.45	3.92–5.06
Gly	Tai'an	4.81	4.51–5.06	4.69	4.26–5.21
	Jiyuan	4.06	3.44–4.56	4.34	3.66–5.18
Ala	Tai'an	5.28	4.74–5.59	5.16	4.50–5.86
	Jiyuan	4.46	3.39–5.12	4.80	3.84–5.63
Tyr	Tai'an	4.95	4.73–5.30	4.88	3.61–5.74
	Jiyuan	4.56	4.16–5.05	4.47	3.26–5.34
His	Tai'an	2.53	2.11–2.88	2.65	2.23–3.19
	Jiyuan	2.22	1.69–2.71	2.37	2.01–3.09
Arg	Tai'an	4.80	4.61–5.03	4.70	4.08–5.29
	Jiyuan	3.96	3.39–4.64	4.19	3.71–4.76

shows that there were differences among amino acid contents of five parents. Moreover, phenotypic values of amino acid content differed largely among different generations over two environments. The means of F_2 generation and parents planted in Tai'an were all higher than those planted in Jiyuan.

Genetic variance and covariance components analysis

Estimated proportions of genetic variance and covariance of wheat grain amino acid content are provided in table 3. All the residual variances of amino acid content reached significant level. This revealed that the variation of amino acid content in wheat grain could be affected by genotype effects as well as G×E interaction effects and residual error.

The contribution of genetic main effects variance for lysine and isoleucine to total genetic variance were 57.7% and 11.8%, and their contributions of environment interaction variance were 35.8% and 77.5%, respectively. Therefore, expression of genes for lysine could be mainly affected by genetic main effects and expression of genes for isoleucine could be mainly affected by environment interaction effects. Direct additive variance, maternal additive and dominance variance for lysine and isoleucine were highly significant, which indicated that these two amino acid content was mainly affected by seed-direct effect as well as maternal effect. Contributions of direct additive effect, maternal additive effect and maternal dominance effect to total genetic variance were 46.8%, 41.5%, 11.7% and 51.0%, 9.8%, 39.2%, respectively. It was suggested that lysine content was affected by direct additive and maternal additive effects, whereas isoleucine content was controlled by direct and maternal dominance effects. At the same time, direct dominance × environment interaction effects of lysine and isoleucine contents were highly significant too. It was also suggested that direct dominance × environment interaction effects should not be neglected.

For threonine and serine, the contributions of genetic main effects variance to total genetic variance were 41.8% and 17.7%, respectively, and their contributions of environment interaction variance were 56.9% and 70.9%, respectively. This suggested that amino acid content of threonine and serine was mainly affected by circumstances. Direct additive and dominance variance, maternal additive variance for the two amino acids reached extreme significant level, which suggested that they were mainly affected by direct effect as well as maternal effect. The contributions of direct additive effects, direct dominance effects and maternal additive effects to total genetic variance were 2.0%, 6.8%, 81.7% and 37.0%, 10.4%, 7.4%, respectively, which suggested that threonine content was affected by maternal additive effect, whereas serine content was affected by direct additive effects. The covariances between direct additive and maternal additive effects were also highly significant, indicating that direct additive variance was related to maternal additive variance at the same increment function.

The content of tyrosine and arginine was affected by genetic main effects. Their direct additive variance, cytoplasmic variance, maternal additive and dominance variance reached extreme significant level, which expressed that their contents were affected by seed-direct, cytoplasmic and maternal effects at the same time. The contributions of direct additive and maternal additive variance to total genetic variance were 41.9%, 26.2% and 32.8%, 36.0%, respectively. The results suggest that tyrosine and arginine contents were mainly affected by direct additive and maternal additive effects.

The contribution of genetic main effects variance of phenylalanine, cysteine and alanine to total genetic variance were 10.2%, 46.5% and 7.2%, respectively, and their contributions of environment interaction variance were 65.9%, 53.5% and 92.8%, respectively, implying that these amino acid contents were mainly affected by circumstances. Futher, only maternal dominance variance of genetic main effect reached extremely significant level which suggested that amino acid content of phenylalanine, cysteine and alanine was mainly affected by maternal dominance effects. At the same time the direct additive × environment interaction effects of phenylalanine, direct dominance × environment interaction effects of cysteine and alanine contents were all extremely significant.

For leucine, aspartic acid and valine, the contributions of environment interaction variance were 57.7%, 83.6% and 95.1%, respectively, which suggested that these amino acid contents were mainly affected by circumstances. Only the direct dominance effect of genetic main effects reached extreme significant level which suggested that these amino acid contents were mainly controlled by direct dominance effect. Direct dominance × environment interaction effects of leucine and aspartic acid contents while cytoplasmic × environment interaction effects of valine content were all extremely significant.

For proline, the ratios of genetic main effect variance and environment interaction variance to total genetic variance were 41.5% and 46.0%, respectively. It suggested that amino acid content of proline was affected by circumstances. Only direct dominance effect of proline reached extreme significant level which suggested that its content was mainly controlled by seed direct dominance effect. Meanwhile, direct additive × environment interaction effects and maternal additive × environment interaction effects of proline contents were also extremely significant.

For glycine, contributions of genetic main effects variance and environment interaction variance to total genetic variance were 5.7% and 87.2%, respectively. It suggested that glycine content was mainly affected by environment interaction. Direct dominance variance and maternal dominance variance for glycine were extremely significant which expressed that glycine was controlled by direct dominance and maternal dominance effects at the same time. Further, the ratios of the two variances to genetic main effects variance were 66.7% and 33.3%, respectively, which suggested

Table 3. Estimated proportions of genetic variance and covariance for wheat grain amino acid content.

Trait	V_A/V_P	V_D/V_P	V_C/V_P	V_{Am}/V_P	V_{Dm}/V_P	V_{AE}/V_P	V_{DE}/V_P	V_{CE}/V_P	V_{AmE}/V_P	V_{DmE}/V_P	$C_{A\cdot Am}/V_P$	$C_{D\cdot Dm}/V_P$	$C_{A\cdot AmE}/V_P$	V_e/V_P
Lys	0.116**	0.000	0.000	0.103**	0.029**	0.000	0.154**	0.000	0.000	0.000	0.014	0.000	0.000	0.571**
Thr	0.005**	0.040**	0.000	0.201**	0.000	0.000	0.335**	0.000	0.000	0.000	0.004	0.000	0.000	0.411**
Ile	0.026**	0.000	0.000	0.005**	0.020**	0.000	0.335**	0.000	0.000	0.000	0.023	0.000	0.000	0.568**
Phe	0.000	0.000	0.000	0.000	0.041**	0.154**	0.000	0.000	0.111**	0.000	0.000	0.000	0.048	0.597**
Val	0.000	0.025**	0.000	0.000	0.000	0.000	0.456**	0.025**	0.000	0.000	0.000	0.000	0.000	0.493**
Mat	0.011**	0.000	0.000	0.002**	0.000	0.000	0.400**	0.040**	0.000	0.000	0.010	0.000	0.000	0.484**
Leu	0.000	0.190**	0.000	0.000	0.000	0.000	0.259**	0.000	0.000	0.000	0.000	0.000	0.000	0.550**
Glu	0.047**	0.078**	0.015**	0.009**	0.000	0.000	0.220**	0.000	0.000	0.000	0.041	0.000	0.000	0.548**
Pro	0.000	0.314**	0.000	0.000	0.000	0.053**	0.000	0.285**	0.010**	0.000	0.000	0.000	0.047	0.245**
Cys	0.000	0.000	0.000	0.000	0.231**	0.000	0.266**	0.000	0.000	0.000	0.000	0.000	0.000	0.503**
Asp	0.000	0.063**	0.000	0.000	0.000	0.000	0.322 **	0.000	0.000	0.000	0.000	0.000	0.000	0.615**
Ser	0.030**	0.045**	0.000	0.006**	0.000	0.000	0.324**	0.000	0.000	0.000	0.026**	0.000	0.000	0.542**
Gly	0.000	0.016**	0.000	0.000	0.008**	0.000	0.367**	0.000	0.000	0.000	0.000	0.015	0.000	0.577**
Ala	0.000	0.000	0.000	0.000	0.034**	0.000	0.439**	0.000	0.000	0.000	0.000	0.000	0.000	0.528**
Tyr	0.203**	0.000	0.053**	0.101**	0.127**	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.512**
His	0.000	0.052**	0.040**	0.000	0.000	0.086**	0.000	0.000	0.017**	0.095**	0.000	0.000	0.077	0.557**
Arg	0.123**	0.000	0.093**	0.024**	0.135**	0.000	0.060**	0.000	0.000	0.000	0.109	0.000	0.000	0.346**

**Significant at 0.01 level.

V_A/V_P, ratio of direct additive variance to phenotypic variance; V_D/V_P, ratio of direct dominance variance to phenotypic variance; V_C/V_P, ratio of cytoplasmic variance to phenotypic variance; V_{Am}/V_P, ratio of maternal additive variance to phenotypic variance; V_{Dm}/V_P, ratio of maternal dominance variance to phenotypic variance; V_{AE}/V_P, ratio of direct additive × environment variance to phenotypic variance; V_{DE}/V_P, ratio of direct dominance × environment variance to phenotypic variance; V_{CE}/V_P, ratio of cytoplasmic × environment variance to phenotypic variance; V_{AmE}/V_P, ratio of maternal additive × environment variance to phenotypic variance; V_{DmE}/V_P, ratio of maternal dominance × environment variance to phenotypic variance; $C_{A\cdot Am}/V_P$, ratio of additive covariance to phenotypic variance; C_{DDm}/V_P = ratio of dominance covariance to phenotypic variance; $C_{A\cdot AmE}/V_P$ = ratio of additive × environment covariance to phenotypic variance; V_e/V_P, ratio of residual variance to phenotypic variance.

that glycine content was mainly affected by direct dominance effect. Meanwhile, the direct dominance × environment interaction effects and maternal dominance × environment interaction effects for glycine reached extremely significant level.

For histidine, the contributions of genetic main effects variance and environment interaction variance to total genetic variance were 20.7% and 44.6%, respectively, which suggested that the histidine content was mainly affected by circumstances. Direct dominance variance and cytoplasm variance for histidine were highly significant, which accounted for 56.5% and 43.5% of genetic main effects, respectively. It was suggested that histidine content was also mainly controlled by direct additive and cytoplasm effects. Meanwhile, direct additive × environment interaction, maternal dominance × environment interaction and maternal additive × environment interaction variances for histidine were all extremely significant.

For methionine, the ratios of genetic main effects variance and environment interaction variance to total genetic variance were 2.7% and 93.0%, respectively, which implied that methionine content was mainly affected by circumstances. Direct additive variance and maternal additive variance for methionine were highly significant which expressed that methionine was also controlled by the direct additive and maternal additive effects. Direct dominance × environment interaction and cytoplasm × environment interaction effects for methionine content reached extreme significant level.

For glutamic acid, the contributions of genetic main effects variance and environment interaction variance to total genetic variance were 33.0% and 48.8%, respectively. Further, direct additive and dominance variance, cytoplasm variance and maternal additive variance were all extremely significant. To genetic main effect variance, the contributions of direct additive, dominance and cytoplasm variance were 31.5%, 52.3% and 10.1%, respectively, which suggested that glutamic acid content was also mainly controlled by direct additive and dominance effects.

Heritability analysis

Heritability estimates are presented in table 4, and significant heritabilities were only detected for the contents of 12 amino acids. Heritabilities were mainly composed of general components for lysine, threonine, isoleucine, glutamic acid, serine, tyrosine and arginine, which indicated that selection for these traits would be generally effective for various environments. Among them, general heritability of tyrosine and arginine was as high as 36.3% and 45.8%, respectively, which was mainly composed of direct and maternal effects; and interaction heritability was not observed. For lysine, threonine and glutamic acid, general heritabilities were 24.7%, 21.4% and 15.3%, which were mainly composed of direct and maternal effects. Heritabilities of isoleucine and serine were lower, which was decided by direct and maternal effects.

For methionine and histidine, highly significant general and interaction heritabilities were observed. Moreover, interaction heritability of histidine was also higher (25.7%), which was mainly composed of direct × environment interaction heritability.

Only highly significant interaction heritabilities were observed for phenylalanine, valine and proline. Among them, the interaction heritabilities for phenylalanine and proline were higher, which were 36.1% and 39.5%, respectively. Meanwhile, the inheritance of phenylalanine was mainly controlled by direct × environment interaction and maternal × environment interaction effects while that of proline was mainly controlled by direct × environment interaction and cytoplasm × environment interaction effects. Maternal plant and hybrid seeds should be mainly chosen in specific environment to improve them.

Table 4. Estimation of heritability for wheat amino acid content.

Heritability (%)	Lys	Thr	Ile	Phe	Val	Mat	Glu	Pro	Ser	Tyr	His	Arg
h^2_{Go}	13.0**	0.9**	4.9**	0.0	0.0	2.1**	8.8**	0.0	5.6**	20.6**	0.0	23.2**
h^2_{Gc}	0.0	0.0	0.0	0.0	0.0	0.0	1.5**	0.0	0.0	5.3	4.0**	9.3**
h^2_{Gm}	11.7**	20.5**	2.8**	0.0	0.0	1.2**	5.0**	0.0	3.2**	10.4**	0.0	13.3**
h^2_{GoE}	0.0	0.0	0.0	20.2**	0.0	0.0	0.0	10.0**	0.0	0.0	16.3**	0.0
h^2_{GcE}	0.0	0.0	0.0	0.0	2.5**	4.0**	0.0	28.5**	0.0	0.0	0.0	0.0
h^2_{GmE}	0.0	0.0	0.0	15.9**	0.0	0.0	0.0	1.0	0.0	0.0	9.4**	0.0
h^2_{G}	24.7**	21.4**	7.7**	0.0	0.0	3.3**	15.3**	0.0	8.8**	36.3**	4.0**	45.8**
h^2_{GE}	0.0	0.0	0.0	36.1**	2.5**	4.0**	0.0	39.5**	0.0	0.0	25.7**	0.0

**Significant at 0.01 level.
h^2_{Go}, direct heritability; h^2_{Gc}, cytoplasmic heritability; h^2_{Gm}, maternal heritability; h^2_{GoE}, direct interaction heritability; h^2_{GcE}, cytoplasmic interaction heritability; h^2_{GmE}, maternal interaction heritability; h^2_{G}, general heritability; h^2_{GE}, interaction heritability.

The inheritances of leucine, cysteine, glycine, aspartic acid and alanine were mainly controlled by dominant effects, suggesting that heterosis could be utilized for their improvement.

Discussion

Improving nutritional quality is one of the major objectives in wheat breeding. Most researchers focussed on content of protein and starch for nutritional quality of wheat in previous studies (Zlatska 2005; Cavanagh *et al.* 2010; Hristov *et al.* 2010; Sun *et al.* 2010; Zhang *et al.* 2011). As we all know, amino acid, is the material for protein synthesis and is the main form for making use of protein in human and animal bodies. Wheat protein quality mainly depend on the type and ratio of amino acids. Amino acid composition in proteins is very unbalanced in most cereal. For example, wheat protein mostly lacks lysine, which seriously affects absorption and utilization of wheat protein. Since, determination of amino acid content using an amino acid analyzer, is operationally complex, time consuming and expensive, few studies have focussed on genetic analysis of amino acid content in wheat. In this study, magnitude of direct, cytoplasmic and maternal genetic effects as well as G×E interaction effects were estimated, illustrating the genetic mechanism of amino acid content, which are of importance in improving wheat quality through breeding.

For wheat, nutritional ingredients such as proteins and amino acids are mainly stored in endosperm of the grain. So, genes of seed and maternal plant could affect the performance of these traits. Meanwhile, plasmagene could also indirectly control these traits by affecting the synthesis of chloroplast and mitochondria. However, in previous studies, inheritance of wheat amino acid content was analysed by diploid genetic models, which could only analyse additive and dominance effects for amino acid content, but failed to separate relative components of different genetic systems such as direct, maternal and cytoplasmic effects as well as G×E interaction effects.

The results of this study revealed that the genetic control of 17 amino acids content in wheat involved direct genetic effects, maternal genetic effects and cytoplasmic genetic effects. All these amino acids except tyrosine were significantly influenced by the G×E interaction effects. So, different environmental conditions should be considered during breeding.

For lysine, glutamic acid, tyrosine, methionine and arginine, the additive (including direct and maternal additive) variances were highly significant. The parent material with high content should be chosen and single seed or individual plant seed considered first in hybrid offspring.

The contents of isoleucine and serine in wheat were mainly controlled by the direct additive effects, whereas threonine content was mainly governed by maternal additive effect. Hence, choosing parent with high threonine content will observe obvious effect during improvement. However, the other nine amino acids content was mainly controlled by dominance effects, and importance should be given to utilization of heterosis for improvement.

The results of estimates of heritability showed that general heritabilities for tyrosine, threonine, arginine and lysine were higher, which implied the effectiveness of selection in early generations. However, G×E interaction heritabilities for proline, phenylalanine and histidine were higher, which revealed that these amino acids were obviously influenced by environment.

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