Euphytica (2015) 205:647–657
DOI 10.1007/s10681-015-1379-2

QTL identification on two genetic systems for rapeseed glucosinolate and erucic acid contents over two seasons

J. F. Xu · Y. Long · J. G. Wu · H. M. Xu · Z. G. Zhao · J. Wen · J. L. Meng · C. H. Shi

Received: 27 April 2014 / Accepted: 27 January 2015 / Published online: 8 February 2015

Abstract Glucosinolate and erucic acid are important plant compounds in rapeseed believed to have numerous functions in rapeseed-environment interactions. However, little is known about the QTL information related to the two different genetic systems including the embryo nuclear chromosomes and maternal plant nuclear chromosomes for glucosinolate content (GSLC) and erucic acid content (EAC) in rapeseed. Differences in QTL distribution between these two genetic systems, which control the performance of GSLC and EAC across different environmental conditions, were analyzed in the present study. A set of 202 DH populations derived from an elite hybrid cross of 'Tapidor' × 'Ningyou7' and their two backcross populations BC_1F_1 1 (DHs × Tapidor) and BC_1F_1 2 (DHs × Ningyou7) generated in two years were used as experimental materials for the study. A total of nine loci for GSLC and three loci for EAC with significant embryo additive main effects, embryo dominant main effects and/or maternal additive main effects, explaining 83.8 and 89.7 %, respectively, of their phenotypic variation, were identified. Although QTL × environment interaction effects were also detected in the present experiment, they played a minimum role in influencing the phenotypic variation. It was noted that *qEAC-7-1* for EAC mapped on linkage group A7 was detected as the major QTL and could explain 68.32 % of the phenotypic variation for this trait. These results could be useful for the molecular maker-assisted breeding of GSLC and EAC quality traits based on the influence of two genetic systems.

Keywords *Brassica napus* L. · Quantitative trait · Quantitative trait locus (QTL) · Genetic main effect · QTL × environment interaction effect

J. F. Xu · H. M. Xu · J. Wen · C. H. Shi (✉)
Department of Agronomy, Zhejiang University, Hangzhou 310058, China
e-mail: chhshi@zju.edu.cn

Y. Long · J. L. Meng
College of Plant Science & Technology, Huazhong Agriculture University, Wuhan 430070, China

J. G. Wu
Department of Horticulture, Zhejiang A&F University, Lin'an 311300, China

Z. G. Zhao
State Key Laboratory Breeding Base, Qinghai Academy of Agricultrual and Forestry Sciences, Xining 810016, China

Introduction

Brassica napus, an important worldwide edible oil crop, is often used within many biological research fields including plant pathology, crop science and biomass energy (Cardoza and Stewart 2007). Glucosinolate and erucic acid are both important agronomic traits within the oil quality of rapeseed, and achieving

lower glucosinolate content (GSLC) and erucic acid content (EAC) is the important goal in rapeseed production and quality improvement due to the toxicity of glucosinolate after its enzymic breakdown (Mawson et al. 1994) and the antinutritional qualities of erucic acid (Badawy et al. 1994). However, gucosinolate can be used as biopesticides (in pest control and prevention or for the treatment of fungal diseases in plants), in the prevention of cancer in human or as flavor compounds (Halkier and Gershenzon 2006). Rapeseed oil with high erucic acid content is desired as raw material for these applications (Lühs and Friedt 1993).

Since GSLC and EAC are quantitative traits, they have complex genetic mechanisms and might be sensitive to environmental factors. To date many scientists have done numerous studies on these two traits in rapeseed based on the QTL mapping models developed by Lander and Bostein (1989), Zeng (1993), and Wang et al. (1999). For the QTL analysis of these two traits, the inheritance of seed glucosinolate accumulation in different *Brassica* species, some QTLs detected for GSLC have been described (Uzunova et al. 1995; Toroser et al. 1995; Howell et al. 2003; Sharpe and Lydiate 2003; Zhao and Meng 2003; Basunanda et al. 2007; Hasan et al. 2008; Feng et al. 2012). The genetic control of EAC is relatively simpler and only two alleles located separately in A and C genome chromosomes in *B. napus* were found. These correspond to homologous copies of the *Arabidopsis* fatty acid elongase gene *FAE1* (Jönsson 1977; Anand and Downey 1981; Fourmann et al. 1998; Lemieux et al. 1990; James et al. 1995; Lassner et al. 1996). The results of the mentioned-above studies demonstrated that a number of QTLs are located on different chromosomes in allotetraploid rapeseed and all of the identified QTLs were in consideration of QTLs expressed only in the embryo nuclear genome. Although rapeseed is a new generation from its seed-producing plant which supplies assimilates for the seed development, there is currently a thought that glucosinolates are synthesized mainly in maternal vegetative organs such as young leaves and silique walls, and then transported actively to the embryo (Magrath and Mithen 1993). Recently, some models have been constructed to dissect the nuclear genetic effects for the seed quality traits on the different parts from maternal and offspring tissues (Foolad and Jones 1992; Zhu and Weir 1998; Wang et al. 1999; Cui et al. 2004, 2005). Previous studies have shown that the performance of most rapeseed quality traits were simultaneously affected by the expression of nuclear genes in the embryo and maternal plant genetic systems (Shi et al. 2003, 2006; Zhang et al. 2004a, b, 2011a, b; Wu et al. 2005, 2006; Variath et al. 2009, 2010; Wang et al. 2010; Chen et al. 2011a, b; Zhang et al. 2011a, b). Besides, some QTLs divided into different genetic systems across environments were identified for rice (Zheng et al. 2008; Shi et al. 2009a, b) and cotton (Liu et al. 2012, 2013). There is however, little work done on QTL identification simultaneously considering the effects of the maternal nuclear genome and their stability over different seasons in rapeseed which could further improve our understanding of the gene expression mechanism of quality traits in rapeseed.

In the present study, a DH population and newly-developed software named as QTL Network-CL-2.0-Seed, which can divide the total genetic effect of QTLs into embryo additive main effect, embryo dominant main effect, maternal additive main effect as well as their environmental interaction effects, were utilized to identify and dissect the QTLs for GSLC and EAC of rapeseed. A total of nine QTL loci for GSLC and three QTL loci for EAC with significant embryo additive main effects, embryo dominant main effects and/or maternal additive main effects were identified and could explain 83.8 and 89.7 % of their phenotypic variation, respectively. The results of this study could help to clarify further the nature of glucosinolate and erucic acid contents in rapeseed at the molecular level and provide a theoretical basis for the molecular marker-assisted selection (MAS) breeding for quality improvement under the influence of embryo and maternal plant genetic systems, and provide more reliable information for future cloning of the relevant genes.

Materials and methods

Materials

A doubled haploid (DH) segregating population of 202 lines (named as TN DH) was derived from a hybrid of Tapidor and Ningyou7. Tapidor is a kind of European winter cultivar with low GSLC and low EAC, whereas Ningyou7 is a Chinese semi-winter cultivar with

higher GSLC and EAC (Qiu et al. 2006). The two parents Tapidor and Ningyou7 and 202 TN DHs which were kindly supplied by Huazhong Agricultural University, Wuhan, China, have different contents of rapeseed nutrition traits, especially GSLC and EAC.

Field experiments

The experiment was conducted on randomized block designed plots with two replications. The seeds of 204 materials including TN DHs and their parents were sown at the experimental farm of Zhejiang University in October of 2011 and 2012, respectively. After 40 days they were individually transplanted at a spacing of 25 cm × 25 cm, and each line contained 32 individual plants (8 rows with 4 plants per row). 177 BC_1F_1 1 (DHs × Tapidor) and 181 BC_1F_1 2 (DHs × Ningyou7) were derived from every TN DH by crossing each of the parents with hand emasculation in the spring of 2012 and 2013, respectively. Mature seeds of the parental lines, and of BC_1F_1 1 and BC_1F_1 2 materials were harvested for further analysis of quality traits.

Trait measurement

Spectral measurements and trait determination were performed using a Near Infrared Scanning Monochromator (Model 5000 NIRS Systems Inc, Silver Spring, MD, USA) and the WinISI II software (v1.5, FOSS NIRSystems, Silver Springs, MD, USA) to determine GSLC and EAC in rapeseed with about 3 g/sample in a small ring cup of 36-mm (inner diameter) (Wu et al. 2002).

Genetic linkage map for QTL mapping

The linkage map was constructed with different molecular markers, including restriction fragment length polymorphism (RFLP), amplified fragment length polymorphism (AFLP), methylation sensitive AFLP (MS-AFLP), simple sequence repeats (SSR), single nucleotide polymorphism (SNP), sequence-tagged site (STS), single-strand conformational polymorphism (SSCP) and cleaved amplified fragment length polymorphism (CAPS). The 786 molecular makers cover 19 linkage groups (A1-A10 and C1-C9), with a total genome size of 2117.2 cm and an average distance of 2.7 cm between marker pairs (Shi et al. 2009a, b).

Data analysis and QTL mapping

Statistics used for phenotypic analysis including mean, standard deviation, the minimum value, the maximum value, skewness and kurtosis of the target traits were calculated with the SAS 9.1 (SAS Institute, Cary, North Carolina, USA).

QTL analysis with environmental interaction effects was carried out on GSLC and EAC of two backcross populations in rapeseed by using the QTL Network-CL-2.0-Seed software and the mixed-model based composite interval mapping (MCIM) method with a 10 cM window size and a 1 cm walking speed (Yang et al. 2007). A logarithm of odds (LOD) threshold of 3 was used to indicate the existence of a putative QTL associated with a target trait. A maximum of 10 background makers were used to control genetic background and 1,000 permutations to estimate the LOD threshold used to declare significant QTL (Doerge and Churchill 1996). The confidence interval was set to 95 %. The QTL main effects including the embryo additive main effect, embryo dominance main effect and maternal additive main effect, QTL × environment interaction effects and corresponding *P* values were estimated by the Markov Chain Monte Carlo (MCMC) (Zheng et al. 2008; Liu et al. 2013). QTL were named based on the McCouch standard nomenclature (McCouch et al. 1997).

Result

Phenotypic variation for glucosionlate and erucic acid contents

Glucosinolate content (GSLC) and erucic acid content (EAC) of the two parents and two backcross populations (BC_1F_1 1 and BC_1F_1 2) are listed on Table 1. The results show that there were significant differences between parents in the performance of GSLC and EAC. In both years, GSLC and EAC in the oilseed of Ningyou7 were all significantly higher than those of Tapidor. Unlike GSLC, the average EAC of BC_1F_1 2 was greater than that of BC_1F_1 1. The influence of parents in backcross populations was relatively weak on GSLC, as could be observed in the results where the average GSLC in BC_1F_1 1 was only slightly higher than that in BC_1F_1 2 in both years. Transgressive segregation for GSLC and EAC was found in different

Table 1 The quality traits of *Brassica napus* L. including GSLC (μmol/g) and EAC (%) of parents and two backcross populations

Growth year	Trait	Parent		BC_1F_1 1 (DH × Tapidor)							BC_1F_1 2 (DH × Ningyou7)						
		Tapidor	Ningyou7	n	Mean	SD	Minimum	Maximum	Skewness	Kurtosis	n	Mean	SD	Minimum	Maximum	Skewness	Kurtosis
2012	GSLC	37.387	68.914**	177	69.422	18.746	24.150	117.684	−0.421	−0.410	181	66.612	18.458	19.170	111.411	−0.677	−0.099
	EAC	7.280	45.068**	177	17.280	9.528	0.280	41.483	−0.048	−0.816	181	35.239	5.601	22.339	45.563	−0.394	−0.729
2013	GSLC	39.545	80.821**	177	58.341	17.933	12.517	99.342	−0.433	−0.296	181	52.303	16.198	3.903	83.208	−0.744	0.136
	EAC	8.973	45.278**	177	21.051	10.933	0.000	44.452	−0.290	−0.849	181	40.283	5.143	29.274	51.779	−0.162	−0.810

** Indicates significant difference between parents Tapidor and Ningyou7 according to *t* test ($P < 0.01$). GSLC = glucosinolate content, EAC = erucic acid content

backcross poupulations under two years, while GSLC was in bidirectional transgressive segregation and EAC was in unidirectional transgressive segregation (Fig. 1). The skewness and kurtosis of GSLC and EAC were all lower than 1, which showed that their distributions were normal. The results revealed that the distributions of these two quality traits were presented in an almost continuously variable manner (Fig. 1), showing that GSLC and EAC of rapeseed are quantitative traits, and confirming that they had complex genetic basis from the phenotype. The frequency distribution of GSLC showed one peak with continuous distribution, while the frequency distribution of EAC showed multiple peaks in continuous distribution. Furthermore, the significant correlation coefficient between GSLC and EAC ($r = -0.232$**) suggested that they were negatively correlated.

QTL mapping for glucosinolate and erucic acid contents

It was observed that twelve QTLs for GSLC and EAC were distributed in different linkage groups (Table 2; Fig. 2). All QTLs had extremely significant embryo and maternal additive main effects, in which three were found with slightly significant QTL × environment effects. The results showed that QTLs controlling the performance of GSLC and EAC were basically the genetic main effects and weakly influenced by environmental factors of the two seasons. QTLs associated with glucosinolate and erucic acid contents were, therefore, relatively stable over two years.

Mapping QTL controlling glucosinolate content

Nine QTLs controlling GSLC in the present experiment were detected to locate in A3, A4, A8, A9, C1, C2, C2, C7 and C9 linkage group, namely *qGSLC-3-1*, *qGSLC-4-2*, *qGSLC-8-3*, *qGSLC-9-4*, *qGSLC-11-5*, *qGSLC-12-6*, *qGSLC-12-7*, *qGSLC-17-8* and *qGSLC-19-9*, respectively (Table 2; Fig. 2). All QTLs could explain 83.8 % of phenotypic variation in GSLC (Table 2). The genetic effects from the allele of Ningyou7 could increase GSLC, while that from Tapidor could decrease the GSLC. Compared with other, *qGSLC-19-9* had the larger genetic contribution (24.8 %) in Table 2 suggesting that it was the major

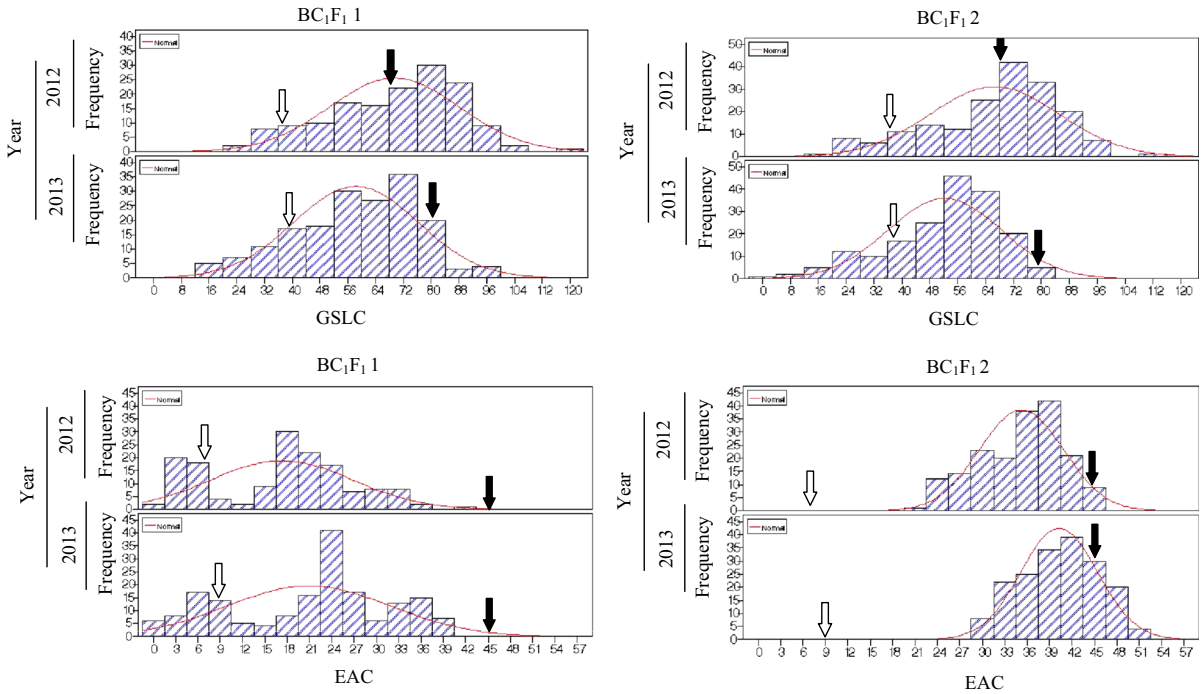

Fig. 1 Frequency distributions of GSLC and EAC for BC1F1 1 and BC1F1 2 in 2012 and 2013. *White* and *black arrows* indicate the average *values* of the parents Tapidor and Ningyou7, respectively

QTL controlling the performance of GSLC in rapeseed and was very important for improving GSLC in oilseed breeding. *qGSLC-3-1* and *qGSLC-4-2* displayed significant embryo additive main effects, embryo dominant main effects and maternal additive main effects. While for *qGSLC-3-1* the maternal additive main effect was larger than the embryo additive main effect, the opposite was true for *qGSLC-4-2*. *qGSLC-12-6* and *qGSLC-12-7* were located between the molecular markers HG-FT-C2 and HR-TP2-110 (63.9 cm), and between EM18ME6-220 and NA12C03 (124.3 cm) on the same linkage group C2, respectively. They both had significant embryo additive main effects, embryo dominant main effects and maternal additive main effects, but *qGSLC-12-6* showed positive embryo dominant main effects and maternal additive main effects, while *qGSLC-12-7* only had positive embryo main effects. *qGSLC-8-3*, *qGSLC-11-5* and *qGSLC-17-8* were all with the positive maternal additive main effects coming from the parent Ningyou7 and the negative embryo additive main effects from Tapidor. In contrast, the embryo additive main effect from *qGSLC-17-8* was positive and the maternal additive main effect was negative. In addition, no environmental interaction effects of QTLs for GSLC were detected in this study except for *qGSLC-9-4* in which the embryo and maternal additive interaction effects ($AeE_2 = -1.010$*, $AmE_2 = 1.005$*) in 2013 were both significant. Therefore, the QTL × environment interaction of *qGSLC-9-4* could not be ignored when analyzing the performance of GSLC under the conditions of 2013.

Mapping QTL controlling erucic acid content

Three QTL loci for EAC, named as *qEAC-7-1*, *qEAC-8-2* and *qEAC-13-3*, could explain 89.7 % of the phenotypic variation. The phenotypic contribution rate of single QTL ranged from 5.7 to 68.3 %. Among them, *qEAC-7-1* located between maker HG-WRI1-A7 and CNU168 in the linkage group A7 had a higher genetic contribution (68.3 %), indicating that it was a major QTL controlling the EAC. Its embryo additive main effects ($Ae = -62.123$) and maternal additive main effects ($Am = 63.380$) of *qEAC-7-1* were the largest among the three QTLs, while its embryo and

Table 2 QTL locations and the genetic effect components for GSLC and EAC of rapeseed under different years

QTL	Linkage group	Maker interval	R^2	Position	Range	*Ae*	*De*	*Am*	AeE_1	DeE_1	AmE_1	AeE_2	DeE_2	AmE_2
qGSLC-3-1	A3	B085J21-2/ H069E01-1	0.097	106.6	105.5–108.6	−103.516**	1.097^{+}	106.775**	−0.000	−0.000	0.000	−0.149	0.000	0.161
qGSLC-4-2	A4	HS-K02-2/ HBR094	0.018	18.5	16.2–19.4	−46.518**	1.960**	42.505**	−0.000	0.000	0.000	−0.017	−0.000	0.019
qGSLC-8-3	A8	HAU327/ HBR010	0.212	32.7	28.3–40.4	−154.202**	0.287	156.249**	0.132	0.002	−0.129	0.000	−0.002	−0.000
qGSLC-9-4	A9	H055O17-4/ B005E24-3	0.009	115.5	114.1–117.5	28.266**	0.460	−36.726**	0.254	0.000	−0.254	1.005*	−0.000	−1.010*
qGSLC-11-5	C1	EM09ME10-420/ ZNS08M15-80	0.024	37.3	36.7–39.8	−51.647**	−0.178	53.811**	−0.000	0.000	0.000	−0.150	0.000	0.155
qGSLC-12-6	C2	HG-FT-C2/ HR-TP2-110	0.007	63.9	58.6–66.9	−30.057**	1.862**	26.191**	0.331	0.000	−0.343	0.000	0.000	−0.000
qGSLC-12-7	C2	EM18ME6-220/ NA12C03	0.023	124.3	117.3–124.3	49.332**	−1.352*	−52.790**	0.109	−0.000	−0.110	0.000	0.000	−0.000
qGSLC-17-8	C7	HBR080/HS-AU39A	0.200	64.3	62.1–66.8	149.096**	−0.047	−152.777**	0.083	0.000	−0.078	0.000	0.000	−0.000
qGSLC-19-9	C9	CB10064/HR-TP3-360	0.248	25.0	21.0–29.0	164.156**	1.212^{+}	−172.000**	−0.000	0.000	0.000	−0.219	0.000	0.223
qEAC-7-1	A7	HG-WRI1-A7/ CNU168	0.683	90.4	85.7–93.4	−62.123**	-0.530^{+}	63.380**	0.000	0.000	−0.000	0.000	0.000	0.000
qEAC-8-2	A8	HBR015/ CNU090	0.156	70.3	69.7–71.3	27.854**	3.042**	−32.330**	0.000	-0.668^{+}	0.000	−0.121	0.692^{+}	0.121
qEAC-13-3	C3	OL13C12/ JICB0633	0.057	133.4	131.4–134.4	16.165**	2.553**	−20.358**	0.000	-0.652^{+}	0.000	−0.076	0.646^{+}	0.075

The subscript number 1 and 2 indicate the environment of 2012 and 2013, respectively

Ae embryo additive main effect, *De* embryo dominance main effect, *Am* maternal additive main effect, AeE_1 embryo additive interaction effect in environment 1, DeE_1 embryo dominance interaction effect in environment 1, AmE_1 maternal additive interaction effect in environment 1, AeE_2 embryo additive interaction effect in environment 2, DeE_2 embryo dominance interaction effect in environment 2, AmE_2 maternal additive interaction effect in environment 2

**, * and $^{+}$ indicate significant at the level of 1, 5 and 10 %, respectively

Fig. 2 **a, b** Mapping of QTL with embryo and maternal effects for GSLC and EAC of rapeseed under different years

maternal additive main effects were opposite, showing that its expression in the embryo and maternal nuclear genomes was different. Besides, *qEAC-8-2* and *qEAC-13-3* with significant embryo additive main effects, embryo dominant main effects, maternal additive main effects and slight QTL × year effects, were distributed on different linkage groups.*qEAC-8-2* with the second largest genetic effects located on linkage group A8 had the narrowest confidence interval and a genetic contribution of 15.59 % in the phenotypic variation of EAC. The positive effects of its embryo additive main effects were mainly from the allele of Tapidor, while its negative maternal additive main effects were from Ningyou7. *qEAC-13-3* was different for its position in the linkage group C3, and its negative maternal additive main effects (decreasing EAC) were also larger than positive embryo additive main effects (increasing EAC). It was found that the embryo dominant main effects of *qEAC-8-2* and *qEAC-13-3* were larger than that of *qEAC-7-1*, which could explain 0.02 and 0.01 % of the total phenotypic variation, respectively. The environmental interaction effects of *qEAC-8-1* and *qEAC-13-2* were similar, both having the significant embryo dominant interaction effects under different environmental conditions.

Discussion

Glucosinolate is a kind of sulfur-containing anionic hydrophilic secondary metabolite widely found in the roots, stems, leaves and seeds of cruciferous plants, especially in *Brassica* species (Barbara and Jonathan 2006). It is the main bioactive component in rapeseed and other cruciferous plants, which determines the flavor and nutritional quality of plants. Though it is the major secondary metabolite in *Brassica* plants, current knowledge on glucosinolate is mainly through the genetic studies of this metabolite in the model plant *Arabidopsis*. To a certain extent, it had revealed the mechanism of glucosinolate biosynthesis (Grubb and Abel 2006). Erucic acid is a kind of unique fatty acid in cruciferous plants (Ecke et al. 1995). It is of low nutritional value, because its carbon chain (C21:1) is longer than other fatty acids such as palmitic (C16:0), oleic (C18:1), linoleic (C18:2), linolenic (C18:3) and eicosenoic (C20:1) acids and cannot be easily decomposed and absorbed by the human body (Das et al. 2002). Erucic acid is also an important industrial raw material (Lühs and Friedt 1993). Therefore, the level of erucic acid in rapeseed oil will not only affect the nutritional value of edible rapeseed oil, but also influence the value of the use of rapeseed oil for industrial purposes.

For rapeseed, the current studies of glucosinolate and erucic acid contents are mainly focused on their accumulation, while their genetic research still in the developing stage. Previous QTL mapping results for GSLC and EAC were only focuses on the seed embryo genetic system (Toroser et al. 1995; Uzunova et al. 1995). However, the studies conducted by Kondra and Stefasom (1970) and Zhang et al. (1996) revealed that these quality traits could be controlled by the genetic effects from the genes of maternal plant, embryo or cytoplasm, while no environmental factors were considered. Shi et al. (2003) and Zhang et al. (2011a) found that the embryo and maternal main effects and their genotype × environmental interaction effects could simultaneously affect the performance of GSLC and EAC. In the present experiment, a newly-developed multi genetic system model for dicotyledonous seed quality traits was used to identify QTLs controlling the performance of GSLC and EAC from the different angle. As a result, twelve QTLs associated with GSLC and EAC were detected which could simultaneously express in embryo and maternal genetic linkage groups. Some of them with weak environment interaction effects indicated that GSLC and EAC were mainly controlled by genetic main effects from embryo and maternal plant genomes. The results showed that GSLC and EAC of rapeseed were mostly based on the embryo and maternal additive main effects in correspondence with the results got by Shi et al. (2003) and Zhang et al. (2011a, b). For GSLC, five QTLs (*qGSLC-9-4*, *qGSLC-12-6*, *qGSLC-12-7*, *qGSLC-17-8* and *qGSLC-19-9*) corresponded to those mapped in previous researches on rapeseed (Toroser et al. 1995; Uzunova et al. 1995; Howell et al. 2003; Quijada et al. 2006; Feng et al. 2012), and *qGSLC-9-4* might have been previously detected on A genome linkage groups of *Brassica juncea* L. (Ramchiary et al. 2007; Bisht et al. 2009). Besides, *qGSLC-8-3*, *qGSLC-17*-8 and *qGSLC-19-9* had larger genetic contributive values and the GSLC of oilseed might be improved according to the molecular markers closely linked to these three QTL during early generations. For EAC, one major QTL, *qEAC-7-1* was detected with the largest genetic contribution with embryo and

maternal additive effects. This QTL might offer a new insight into cloning related genes for reducing EAC in rapeseed breeding. The other two QTLs (*qEAC-8-2* and *qEAC-13-3*) located on linkage groups A8 and C3 were corresponded with the genes/QTLs had already been identified (Jourdren et al. 1996, Thormann et al. 1996; Fourmann et al. 1998; Qiu et al. 2006; Amar et al. 2008), which might be closely linked with a *Brassica FAE1* homologue controlling erucic acid biosynthesis.

On the other hand, we compared the QTLs detected in this study and the previously mapped ones by using TN DH mapping population. It was found that there were some QTLs, *qGSLC-9-4* and *qGSLC-12-6* for GSLC, *qEAC-8-2* and *qEAC-13-3* for EAC being repeatedly detected for each detection (Qiu et al. 2006; Feng et al. 2012), while the others have not been reported. The interesting thing is that the maternal additive effects of these four QTLs were negative, which mean that alleles from Tapidor could decrease the content in seeds, and the maternal effects were higher than the embryo effects. More importantly, this study firstly verified that the QTLs of rapeseed quality traits were related to two different genetic systems and their environmental interaction effects at the same time. QTL × environment interaction effect was also an important part enjoying different influence on the phenotypic variation of glucosinolate and erucic acid contents. During the rapeseed growing season, rainfall in 2013 was more than that in 2012, while the temperature in 2012 higher than that in 2013. The weak environmental interaction would be a useful guide for its stable performance when selecting glucosinolate content across environments in rapeseed breeding, while the strong QTL × environment interaction effect for erucic acid contents showed that it could be influenced by the interaction of rainfall, temperature and soil water availability during seed development under different years. This could provide a new approach for the future breeding of rapeseed quality traits by molecular marker-assisted selection to improve the breeding efficiency, and also offer a new theoretical basis for cloning related genes in future.

Acknowledgments The project was financially supported from Zhejiang Provincial Key Laboratory of Crop Germplasm Resources, Foundation for University Key Teacher by the Ministry of Education of China and by the 151 Program for the Talents of Zhejiang Province. We are grateful to A. Quampah for providing good suggestion when revising this paper.

References

Amar S, Ecke W, Becker HC, Möllers C (2008) QTL for phytosterol and sinopate ester content in *Brassica napus* L. collocate with the two erucic acid genes. Theor Appl Genet 116:1051–1061

Anand I, Downey R (1981) A study of erucic acid alleles in digenomic rapeseed (*Brassica napus* L.). Can J Plant Sci 61:199–203

Badawy IH, Atta B, Ahmed WM (1994) Biochemical and toxicological studies on the effect of high and low erucic acid rapeseed oil on rats. Nahrung 38(4):402–411

Barbara AH, Jonathan G (2006) Biology and biochemistry of glucosinolates. Annu Rev Plant Biol 57:303–333

Basunanda P, Spiller TH, Hasan M, Gehringer A, Schondelmaier J, Lühs W, Friedt W, Snowdon RJ (2007) Marker-assisted increase of genetic diversity in a double-low seed quality winter oilseed rape genetic background. Plant Breed 126:581–587

Bisht NC, Gupta V, Ramchiary N, Sodhi YS, Mukhopadhyay A, Arumugam N, Pental D, Pradhan AK (2009) Fine mapping of loci involved with glucosinate biosynthesis in oilseed mustard (*Brassica juncea*) using genomic information from allied species. Theor Appl Genet 118:413–421

Cardoza V, Stewart CN (2007) Canola. Biotechnol Agr Forest 61:29–37

Chen GL, Zhang B, Wu JG, Shi CH (2011a) Nondestructive assessment of amino acid composition in rapeseed meal based on intact seeds by near-infrared reflectance spectroscopy. Anim Feed Sci Tech 165:111–119

Chen G, Wu J, Shi C (2011b) Dynamic genetic effects on threonine content in rapeseed (*Brassica napus* L.) meal at different developmental stages. Czech J Genet Plant Breed 47(3):101–113

Cui YH, Wu RL (2005) Statistical model for characterizing epistatic control of triploid endosperm triggered by maternal and offspring QTLs. Genet Res Camb 86:65–75

Cui YH, Casella G, Wu RL (2004) Mapping quantitative trait loci interactions from the maternal and offspring genomes. Genetics 167:1017–1026

Das S, Roscoe TJ, Delseny M, Srivastava PS, Lakshmikumaran M (2002) Cloning and molecular characterization of the *Fatty Acid Elongase* 1 (*FAE* 1) gene from high and low erucic acid lines of *Brassica campestris* and *Brassica oleracea*. Plant Sci 162:245–250

Doerge RW, Churchill GA (1996) Permutation tests for multiple loci affecting a quantitative character. Genetics 142: 285–294

Ecke W, Uzunova M, WeiBleder K (1995) Mapping the genome of rapeseed (*Brassica napus* L.). II. Localization of genes controlling erucic acid synthesis and seed oil content. Theor Appl Genet 91:972–977

Feng J, Long Y, Shi Shi JQ, Barker G, Meng JL (2012) Characterization of metabolite quantitative trait loci and metalbolic networks that control glucosinolate concentration in the seeds and leaves of *Brassica napus*. New Phytol 193:96–108

Foolad MR, Jones RA (1992) Models to estimate maternally controlled genetic variation in quantitative seed characters. Theor Appl Genet 83:360–366

Fourmann M, Barret P, Renard M, Pelletier G, Delourme R, Brunel D (1998) The two genes homologous to *Arabidopsis FAE1* co-segregate with the two loci governing erucic acid content in *Brassica napus*. Theor Appl Genet 96:852–858

Grubb CD, Abel S (2006) Glucosinolate metabolism and its control. Trends Plant Sci 11:89–100

Halkier BA, Gershenzon J (2006) Biology and biochemistry of glucosinolates. Annu Rev Plant Biol 57:303–333

Hasan M, Friedt W, Pons-Kühemann J, Freitag NM, Link K, Snowdon RJ (2008) Association of gene-linked SSR markers to seed glucosinolate content in oilseed rape (*Brassica napus* ssp. *napus*). Theor Appl Genet 116: 1035–1049

Howell PM, Sharpe AG, Lydiate DJ (2003) Homoeologous loci control the accumulation of seed glucosinolates in oilseed rape (*Brassica nap*us). Genome 46:454–460

James DW Jr, Lim E, Keller J, Plooy I, Ralston E, Dooner H (1995) Directed tagging of the arabidopsis fatty acid elongation *1* (*FAE1*) gene with the maize transposon activator. Plant Cell 7:309–319

Jönsson R (1977) Erucic-acid heredity in rapeseed (*Brassica napus* L. and *Brassica campestris* L.). Hereditas 86:159–170

Jourdren C, Barret P, Horvais R, Foisset N, Delourme R, Renard M (1996) Identification of RAPD markers linked to the loci controlling erucic acid level in rapeseed. Mol Breed 2:61–71

Kondra IP, Stefasom BR (1970) Inheritance of the major glucosinolates of rapeseed (*Brassica napus*). Canad J Plant Sci 50:643–647

Lander ES, Bostein D (1989) Mapping Mendelian factors underlying quantitative traits using RFLP linkage maps. Genetics 121:185–199

Lassner M, Lardizabal K, Metz J (1996) A jojoba β-ketoacyl-CoA synthase cDNA complements the canola fatty acid elongation mutation in transgenic plants. Plant Cell 8:281–292

Lemieux B, Miquel M, Somerville C, Browse J (1990) Mutants of Arabidopsis with alterations in seed lipid fatty acid composition. Theor Appl Genet 80:234–240

Liu HY, Quampah A, Chen JH, Li JR, Huang ZR, He QL, Shi CH, Zhu SJ (2012) QTL analysis for gossypol and protein contents in upland cottonseeds with two different genetic systems across environments. Euphytica 188(3):453–463

Liu HY, Quampah A, Chen JH, Li JR, Huang ZR, He QL, Zhu SJ, Shi CH (2013) QTL mapping based on different genetic systems for essential amino acid contents in cottonseeds in different environments. PLoS ONE 8(3):e57531. doi:10.1371/journal.pone.0057531

Lühs W, Friedt W (1993) Non-food uses of vegetable oils and fatty acids. In: Murphy DJ (ed) Designer oil crops: breeding, processing and biotechnology. VCH, Cambridge, pp 73–130

Magrath R, Mithen R (1993) Maternal effects on the expression of individual aliphatic glucosinolates in seeds and seedlings of *Brassica napus*. Plant Breed 111:249–252

Mawson R, Heaney RK, Zdunczyk Z, Kozlowska H (1994) Rapeseed meal-glucosinolates and their antinutritional effects Part 4. Goitrogenicity and internal organs abnormalities in animals. Nahrung 38(2):178–191

McCouch SR, Cho YG, Yano M, Paul E, Blinstrub M (1997) Report on QTL nomenclature. Rice Genet Newslett 14:11–13

Qiu D, Morgan C, Shi J, Long Y, Liu J, Li R, Zhuang X, Wang Y, Tan X, Dietrich E, Weihmann T, Everett C, Vanstraelen S, Beckett P, Fraser F, Trick M, Barnes S, Wilmer J, Schmidt R, Li J, Li D, Meng J, Bancroft I (2006) A comparative linkage map of oilseed rape and its use for QTL analysis of seed oil and erucic acid content. Theor Appl Genet 114:67–80

Quijada PA, Udall JA, Lambert B, Osborn TC (2006) Quantitative trait analysis of seed yield and other complex traits in hybrid spring rapeseed (*Brassica napus* L.): 1. Identification of genomic regions from winter germplasm. Theor Appl Genet 113:549–561

Ramchiary N, Bisht NC, Gupta V, Mukhopadhyay A, Arumugam N, Sodhi YS, Pental D, Pradhan AK (2007) QTL analysis reveals context-dependent loci for seed glucosinolate trait in the oilseed *Brassica juncea*: importance of recurrent selection backcross scheme for the identification of 'true' QTL. Theor Appl Genet 116:77–85

Sharpe AG, Lydiate DJ (2003) Mapping the mosaic of ancestral genotypes in a cultivar of oilseed rape (*Brassica napus*) selected via pedigree breeding. Genome 46:461–468

Shi CH, Zhang HZ, Wu JG, Li CT, Ren YL (2003) Genetic and genotype × environment interaction effects analysis for erucic acid content in rapeseed (*Brassica napus* L.). Euphytica 130(2):249–254

Shi CH, Zhang HZ, Wu JG (2006) Analysis of embryo, cytoplasmic and maternal correlations for quality traits of rapeseed (*Brassica napus* L.) across environments. J Genet 85(2):147–151

Shi CH, Shi Y, Lou XY, Xu HM, Zheng X, Wu JG (2009a) Identification of endosperm and maternal plant QTLs for protein and lysine contents of rice across different environments. Crop Pasture Sci 60(3):295–301

Shi JQ, Li RL, Qiu D, Jiang CC, Long Y, Morgan C, Bancroft I, Zhao JY, Meng JL (2009b) Unraveling the complex trait of crop yield with quantitative trait loci mapping in *Brassica napus*. Genetics 182:851–861

Thormann CE, Romero J, Mantet J, Osborn TC (1996) Mapping loci controlling the concentrations of erucic and linolenic acids in seed oil of *Brassica napus* L. Theor Appl Genet 93:282–286

Toroser D, Thormann CE, Osborn TC, Mithen R (1995) RFLP mapping of quantitative trait loci controlling seed aliphatic-glucosinolate content in oilseed rape (*Brassica napus* L.). Theor Appl Genet 91:802–808

Uzunova M, Ecke W, Weissleder K, Röbbelen G (1995) Mapping the genome of rapeseed (*Brassica napus* L.). I. Construction of an RFLP linkage map and localization of QTLs for seed glucosinolates content. Theor Appl Genet 90:194–204

Variath MT, Wu JG, Li YX, Chen GL, Shi CH (2009) Genetic analysis for oil and protein contents of rapeseed (*Brassica napus* L.) at different developmental times. Euphytica 166:145–153

Variath MT, Wu JG, Zhang L, Shi CH (2010) Analysis of developmental genetic effects from embryo, cytoplasm and maternal plant for oleic and linoleic acid contents of rapeseed. J Agr Sci 148:375–391

Wang DL, Zhu J, Li ZK, Paterson AH (1999) Mapping QTLs with epistatic effects and genotype × environment interactions by mixed linear model approaches. Theor Appl Genet 99:1255–1264

Wang XF, Liu GH, Yang Q, Hua W, Liu J, Wang HZ (2010) Genetic analysis on oil content in rapeseed (*Brassica napus* L.). Euphytica 173:17–24

Wu JG, Shi CH, Fan LJ (2002) Calibration optimization for analysing erucic acid and glucosinolate contents of rapeseed by near infrared reflectance spectroscopy (NIRS). J Chin Cer Oils Assoc 17(2):59–62

Wu JG, Shi CH, Zhang HZ (2005) Genetic analysis of embryo, cytoplasmic and maternal effects and their environment interactions for protein content in *Brassica napus* L. Aust J Agr Res 56(1):69–73

Wu JG, Shi CH, Zhang HZ (2006) Partitioning genetic effects due to embryo, cytoplasm and maternal parent for oil content in oilseed (*Brassica napus* L.). Genet Mol Biol 29(3):533–538

Yang J, Zhu J, Williams RW (2007) Mapping the genetic architecture of complex traits in experimental populations. Bioinformatics 23:1527–1536

Zeng ZB (1993) Theoretical basis for separation of multiple linked gene effects in mapping quantitative trait loci. Proc Natl Acad Sci USA 90:10972–10976

Zhang SF, Song WG, Ren RJ, Tian BM, Wen YC, Liu JM, Wang JP (1996) Studies on hereditary capacity of quantitative characters and gene effects of CMS double low *Brasscica napus*. Oil Crops Chin 18(3):1–3

Zhang HZ, Shi CH, Wu JG, Ren YL, Li CT, Zhang DQ, Zhang YF (2004a) Analysis of genetic and genotype × environment interaction effects from embryo, cytoplasm and maternal plant for oleic acid content of *Brassica napus* L. Plant Sci 167:43–48

Zhang HZ, Shi CH, Wu JG, Ren YL, Li CT, Zhang DQ, Zhang YF (2004b) Analysis of genetic effects and heritabilities for linoleic and linolenic acid content of *Brassica napus* L. across environments. Eur J Lipid Sci Technol 106(8): 518–523

Zhang HZ, Shi CH, Wu JG (2011a) Analysis of embryo, cytoplasmic and maternal effects for heterosis of erucic acid and glucosinolates contents in rapeseed (*Brassica napus* L.). Sci Agr Sin 10(9):1525–1531

Zhang L, Chen GL, Wu JG, Variath MT, Shi CH (2011b) Developmental genetic analysis for crude fiber content and crude ash content of rapeseed meal in two different growing years. J Food Qual 234(4):284–297

Zhao J, Meng J (2003) Detection of loci controlling seed glucosinolate content and their association with *Sclerotinia* resistance in *Brassica napus*. Plant Breed 122:19–23

Zheng X, Wu JG, Lou XY, Xu HM, Shi CH (2008) The QTL analysis on maternal and endosperm genome and their environmental interactions for characters of cooking quality in rice (*Oryza sativa* L.). Theor Appl Genet 116(3):335–342

Zhu J, Weir BS (1998) Mixed model approaches for genetic analysis of quantitative traits. In: Chen LS, Ruan SG, Zhu J (eds) Proc Inter Conf on Mathematical Biol. World Scientific Publishing Co., Singapore, pp 321–330