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Conditional QTL mapping of oil content in rapeseed with respect to protein content and traits related to plant development and grain yield

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Abstract Oil content in rapeseed (*Brassica napus* L.) is generally regarded as a character with high heritability that is negatively correlated with protein content and influenced by plant developmental and yield related traits. To evaluate possible genetic interrelationships between these traits and oil content, QTL for oil content were mapped using data on oil content and on oil content conditioned on the putatively interrelated traits. Phenotypic data were evaluated in a segregating doubled haploid population of 282 lines derived from the F_1 of a cross between the old German cultivar Sollux and the Chinese cultivar Gaoyou. The material was tested at four locations, two each in Germany and in China. QTLMapper version 1.0 was used for mapping unconditional and conditional QTL with additive (*a*) and locus pairs with additive × additive epistatic (*aa*) effects. Clear evidence was found for a strong genetic relationship between oil and protein content. Six QTL and nine epistatic locus pairs were found, which had pleiotropic effects on both traits. Nevertheless, two QTL were also identified, which control oil content independent from protein content and which could be used in practical breeding programs to increase oil content without affecting seed protein content. In addition, six additional QTL with small effects were only identified in the conditional mapping. Some evidence was apparent for a genetic interrelationship between oil content and the number of seeds per silique but no evidence was found for a genetic relationship between oil content and flowering time, grain filling period or single seed weight. The results indicate that for closely correlated traits conditional QTL mapping can be used to dissect the genetic interrelationship between two traits at the level of individual QTL. Furthermore, conditional QTL mapping can reveal additional QTL with small effects that are undetectable in unconditional mapping.

Introduction

Oil yield, the most important trait in rapeseed production, is the result of seed oil content and seed yield. Simultaneous increases of seed oil content and seed yield are difficult to achieve in practical breeding programs. Both traits are the products of complex interdependencies between plant developmental traits and yield components. The relationships between plant development, plant organ growth and the accumulation of oil, protein and other components in the seed has been well documented by Mendham and Salisbury (1995) in oilseed rape. Each developmental process is to a greater or lesser extent under genetic control, and is affected to varying degrees by environmental factors (reviewed by Leon and Becker 1995).

Oil content in *B. napus* is generally regarded as a character with high heritability (Lööf and Appelqvist 1972; Röbbelen and Thies 1980; Becker et al. 1999). Several mapping experiments for oil content in different *Brassica* species were conducted (Ecke et al. 1995; Cheung and Landry 1998; Sharma et al. 1999; Gül et al. 2003). QTL with additive effects and epistatic as well as environmental interactions were presented by Zhao et al. (2005). However, the relationships of the mapped QTL with individual developmental traits like flowering time or grain filling period were not examined although QTL for flowering time have been extensively studied in *Arabidopsis* and *Brassica* (Koornneef et al. 1994; Ferreira et al. 1995; Osborn et al. 1997; Butruille et al. 1999; Axelsson et al. 2001; Kole et al. 2001). Mapping QTL for yield components in oilseed rape is rare (Upadhyay et al. 1996;

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Butruille et al. 1999; Gül 2002) and their genetic relationships with oil content at the QTL level is still poorly understood. On the other hand, oil and protein synthesis in the seed share basic resources in the metabolic pathways and are partly controlled by the same genes, which causes significant negative correlation between the two traits (Grami and Stefansson 1977; Stefansson and Kondra 1975; Röbbelen and Thies 1980). Gül et al. (2003) identified six QTL for seed oil content and four of them showed a close linkage with QTL for protein content. In three cases the allele increasing oil content was in coupling phase with the allele decreasing protein content and vice versa, explaining the negative correlation between the two traits.

Our objective was to evaluate the genetic influence of variation in protein content, plant developmental traits and yield components on oil content. In a previous experiment, QTL for oil content were mapped in a DH population derived from a cross between a European and a Chinese variety (Zhao et al. 2005). To investigate the genetic relationship between these QTL for oil content and other traits, a statistical procedure for analyzing conditional genetic effects (Zhu 1995) was combined with the QTL mapping method of Wang et al. (1999). If oil content is genetically correlated with a secondary trait like protein content, the conditioning of oil content on protein content allows the analysis of oil content independently of variation in protein content. The conditional values are estimated for the situation of no variation for the secondary trait, a method that is very similar to the estimation of adjusted values in a covariance analysis. The oil content conditioned on the various other traits can be analysed by QTL mapping in the same way as the original oil content. By comparing unconditional and conditional QTL for oil content, the genetic interdependencies between oil and seed protein content, between oil content and different developmental traits or with yield components can be identified at the level of individual QTL. The results might provide valuable information for marker assisted selection to improve oil content without negative effects on protein content, developmental features and seed yield.

Materials and methods

Plant materials and genetic map

A doubled haploid (DH) population of 282 lines derived from microspores of F_1 plants of a cross between ‘Sollux’ and ‘Gaoyou’ was used in this study (Zhao et al. 2005). The parental lines differed strongly in many morphological and developmental traits like yield components, flowering time and maturity. Both lines were high in erucic acid and glucosinolate content, and exhibited high oil contents in seeds. A linkage map comprising 125 microsatellite markers (SSRs) covering a total length of 1,196 cM of the rapeseed genome was used for mapping (Zhao et al. 2005).

Field trials and trait evaluation

Four experiments were conducted in 2000/2001 at two locations in China, Xian and Hangzhou, and two locations in Germany, Reinshof and Weende, both located near Göttingen. The details of the field trials were described by Zhao et al. (2005).

Data were collected both on morphological and seed attributes. Plant development was monitored, including begin of flowering (50% of plants showing first flowers), end of flowering (50% of plants having no open flowers) and maturity (silique colour changed to yellow). The traits analysed were days to flowering (DTF, days from sowing to begin of flowering), duration of flowering (DOF, days from begin of flowering to end of flowering), grain filling period (GFP, days from end of flowering to maturity). At the maturity stage, five representative plants from the centre of each plot were sampled for evaluating single seed weight (SSW), number of seeds per silique (NSS) and analysis of seed quality. The NSS was measured based on ten siliques, two from each plant, taken from the lower part of the main raceme. Around 10 g of seeds were bulk harvested from the terminal raceme and the two uppermost primary branches. Seed weight was measured and seed oil and protein (SP) content were determined by near-infrared reflectance spectroscopy (NIRS, Tillmann 1997), adjusted to 9% seed moisture.

Data analysis and QTL mapping

All seven traits were first analysed with the MINQUE method (Zhu 1992) to estimate variance and covariance components. Based on these components genetic correlation coefficients were estimated between oil content and the other traits. Significance levels of the genetic correlation coefficients were derived by a jackknife resampling procedure. Conditional phenotypic values $y_{hk(T1|T2)}$ were obtained by the mixed model approach for the conditional analysis of quantitative traits described by Zhu (1995) where $T1|T2$ means trait 1 conditioned on trait 2 (for example oil|SP = oil content conditioned on seed protein content). Phenotypic variances were calculated from trait means over four locations.

QTL mapping was performed using the program QTLMapper version 1.0 (Wang et al. 1999). The genetic model used and the detailed mapping procedure was described previously (Wang et al. 1999; Zhao et al. 2005). The significance threshold was chosen at $\alpha = 0.005$ for declaring a putative QTL and its associated genetic effects.

Results

Phenotypic variation of traits and correlations to oil content

Table 1 shows mean, maximal and minimal trait values calculated from averages over four locations for seed oil and seed protein content and the three developmental as well as the two yield related traits. Strong transgressive segregations were observed for all traits with the exception of days to flowering, indicating that alleles with positive effects are distributed among the parents. The evaluation of the genetic and phenotypic correlations between oil content and the different traits (Table 2) showed highly significant negative correlations with a high correlation coefficient to seed protein content and a smaller correlation coefficient to DOF, significant positive correlations to seeds per silique and DTF and no significant correlation with GFP. For SSW only the phenotypic correlation was significant with a small positive correlation coefficient. Conditioning oil content on protein content led to a strong reduction of variance (Table 2) while oil content conditioned on the remaining traits showed variances nearly as high as the unconditioned oil content.

Relationship of QTL for oil content to the other evaluated traits

Table 3 compares the results of unconditional and conditional QTL mapping for oil content for loci with significant additive effects. Unconditional mapping identified eight QTL for oil content with additive effects ranging in absolute size from 0.55 to 0.22% oil content, together explaining 45% of the variance of the trait. When oil content was conditioned on seed protein content, five of the eight QTL failed to show significant effects and the QTL on linkage group 1 showed a strongly reduced effect, indicating a strong genetic association between these two traits. In the conditional mapping six additional QTL were detected with additive effects ranging in absolute size from 0.24 to 0.14%, giving a total of nine QTL. Together these QTL still explained 40.5% of the variance of the conditional trait.

QTL mapping for oil content conditioned on the three developmental traits showed five QTL on linkage groups 1, 7, 9, 18 and 19 to be independent from these traits. On the other hand, the QTL on linkage group 14-1 failed to show significant effects when conditioned on developmental traits. The remaining two QTL on linkage groups 11-1 and 12 were influenced by only one or two of the developmental traits.

Table 1 Phenotypic values of parental lines, F_1 and the DH population in the mean across four environments

Traits	Parents		F_1	DH population ($n=282$)			
	Sollux	Gaoyou		Max	Min	Mean	SD
Oil	48.0	47.2	49.1	52.1	41.7	48.0	1.54
SP	20.1	20.8	19.1	23.0	17.1	19.8	1.46
DTF	211	186	203	211	186	202	4.72
DOF	28	36	31	41	26	31	2.43
GFP	31	34	33	37	28	31	1.63
SSW	4.49	3.76	4.24	5.21	2.92	3.88	0.40
NSS	19.1	21.7	25.3	27.8	12.7	20.9	2.47

Oil Seed oil content (%), *SP* seed protein content (%), *DTF* days to flowering (day), *DOF* duration of flowering (day), *GFP* grain filling period (day), *SSW* single seed weight (mg), *NSS* number of seeds per silique

Table 2 Genetic and phenotypic correlations between oil content and the other traits and phenotypic variances of oil content and oil content conditioned on the other traits

Trait	Correlations		Variances	
	Genetic	Phenotypic	Direct	Conditioned on
Oil	–	–	2.36	
SP	−0.812**	−0.852**		0.91
DTF	0.172*	0.233*		2.24
DOF	−0.354**	−0.347**		2.19
GFP	0.049	0.018		2.30
SSW	−0.211	0.172*		2.30
NSS	0.468*	0.421**		2.04

For abbreviation, see Table 1
*$P \leq 0.05$; **$P \leq 0.01$

Only one QTL, on linkage group 11-1, was influenced by seed weight but three QTL on linkage groups 1, 9 and 14-1 failed to show significant effects when oil content was conditioned on seeds per silique. The other QTL for oil content were independent of the two yield related traits.

With the exception of oil content conditioned on seeds per silique the QTL mapped for the conditional traits explained between 38.3 and 44.1% of the variance of the respective trait, values close to the 45% that was found for the unconditioned oil content. Only the variance explained by the QTL for oil content conditioned on seeds per silique was with 27.4% significantly smaller.

The close genetic relationship between seed oil and protein content was also reflected in the mapping of locus pairs with additive × additive epistatic effects (Table 4). Of nine locus pairs with absolute effects ranging from 0.38 to 0.20% identified in the unconditional mapping only one showed a significant, albeit reduced effect when oil content was conditioned on protein content. Three new locus pairs were detected in the conditional mapping, with absolute effects ranging from 0.25 to 0.13%. One of the new locus pairs, the pair on linkage groups 3 and 11-1 is comprised of two loci that had already shown significant additive effects in the unconditional respectively conditional QTL mapping. In the remaining two new locus pairs a locus with significant additive effects is paired with a locus without significant additive effects. With only 17.6% the variance explained by the locus pairs mapped for oil content conditioned on protein content is strongly reduced compared to the 30.3% that is explained by the epistatic locus pairs mapped for unconditioned oil content.

Discussion

In 1995 Zhu introduced a new methodology for conditional genetic analysis. This method was later used to study developmental quantitative genetics in mice (Atchley and Zhu 1997), rice (Shi et al. 2001) and cotton

Table 3 QTL with significant additive effects for oil content and for oil content when conditioned on the other traits

Linkage group	Marker interval	Additive effect (%)	Conditional additive effect (%)					
		Oil[a]	Oil | SP[b]	Oil | DTF	Oil | DOF	Oil | GFP	Oil | SSW	Oil | NSS
1	HMR292/ HMR327	0.373**	0.200**	0.396*	0.374**	0.346**	0.390**	
1	HMR274b/HMR430		−0.166*					
2	HMR066/HMR087c		0.243**					
3	HMR085/HMR440		0.143**					
7	HMR300c/MR133.2	−0.551**		−0.471**	−0.453**	−0.490**	−0.480**	−0.400**
8	HMR388/HMR577		−0.180**					
9	HMR438a/HMR310	0.338**		0.516**	0.343**	0.333**	0.387**	
9	HMR284a/HMR359c		−0.213**					
11-1	MR148/HMR407a	−0.257*		−0.236*				−0.175*
12	HMR299c/HMR403a	0.271*	0.229**		0.383*	0.464**	0.358**	0.330**
14-1	HMR403b/MR229	0.221**	0.222**				0.324**	
15	MR97/MR54		−0.205**					
18	HMR335a/HMR588	−0.517**		−0.444**	−0.404**	−0.467**	−0.455**	−0.290**
19	HMR615a/HMR288	0.224**		0.227*	0.258*	0.199**	0.206**	0.418*
Variance explained (%)[c]		45.0	40.5	42.4	38.3	41.0	44.1	27.4

*$P \leq 0.005$; **$P \leq 0.001$

[a] The QTL effect is the phenotypic effect due to the substitution of a ‘Gaoyou’ allele by an allele of ‘Sollux’

[b] Oil | SP, Oil | DTF, Oil | DOF, Oil | GFP, Oil | SSW and Oil | NSS indicates oil content conditioned on SP, DTF, DOF, GFP, SSW and NSS, respectively (abbreviations see Table 1)

[c] Percentage of phenotypic variance (see Table 2) explained by the additive effects of the mapped QTL

(Zhu 1995; Ye et al. 2003) and more recently a method for multivariable conditional analysis was proposed for analysing the contributions of component traits to a complex trait (Wen and Zhu 2005). Furthermore, by combining the conditional genetic analysis method with QTL mapping, it was extended to map conditional QTL for a molecular dissection of the development of traits like plant height and tiller number during plant growth in several studies on rice (Yan et al. 1998a, b; Cao et al. 2001; Wu et al. 2002) and to evaluate the genetic contributions of yield components to yield (Guo et al. 2005). In the present study, this methodology was used to analyse the interrelationships between oil content and protein content as well as between oil content and developmental and yield related traits in rapeseed (*Brassica napus* L.).

QTL for seed oil and protein content have been reported before to be closely linked, indicating loci with pleiotropic effects on both traits. Gül et al. (2003) identified six QTL for oil content in *B. napus* with four of these QTL being closely linked to QTL for protein content. At three of these loci the allele increasing oil content was in coupling phase with the allele decreasing protein content and vice versa. However, another two QTL for oil content and one additional QTL for protein content were detected on separate linkage groups, unlinked to QTL for the other trait. In soybean, Shoemaker et al. (1996) reported QTL for seed protein and oil content in corresponding regions and Lee et al. (1996) identified various common markers on five linkage groups, which were associated with both, seed protein and oil content. The close relationship and

Table 4 Estimated additive × additive epistatic effects (*aa*) of locus pairs on oil content calculated from oil content and from oil content conditioned on seed protein content

Linkage group	Marker interval	Linkage group	Marker interval	aa effect[a] (%)	Conditional *aa* effect (%)
1	HMR407b/HMR292	2	HMR300a/HMR066	−0.294**	
1	HMR274b/HMR430	10	HMR643b/HMR615b		0.252**
1	HMR295c/ HMR293	12	HMR353b/HMR364b	0.384**	0.141*
2	HMR300a/HMR066	10	HMR625/HMR643b	0.323**	
3	HMR449a/ MR12	7	HMR300c/ HMR133.2	−0.195**	
3	HMR085/ HMR440	11-1	MR148/ HMR407a		−0.246**
3	HMR449a/MR12	18	HMR335a/ HMR588	−0.199**	
4	HMR637/ MD2.2	12	HMR353b/HMR364b	−0.291**	
7	MR133.2/MD20	17	HMR318/HMR349		0.128**
11-1	MR148/HMR407a	12	HMR299c/HMR403a	0.323**	
11-1	MR148/HMR407a	16	HMR348/MR133	0.205*	
13	HMR314b/HMR090b	15	MR97/MR54	0.263**	
Variance explained (%)[b]				30.3	17.6

*$P \leq 0.005$; **$P \leq 0.001$

[a] A positive sign of the epistatic effect indicates that parental allele combinations and a negative sign that recombinant allele combinations increase phenotypic values

[b] Percentage of phenotypic variance (see Table 2) explained by the epistatic effects of the mapped locus pairs

negative correlation between oil and protein content in the seed can be expected since the biochemical pathways for oil and protein synthesis compete for the same basic substrates. In addition, oil and protein are major constituents of the seed whose contents are usually expressed in relation to total seed mass; increasing one compound has to decrease another compound.

In the present study the close relationship between seed oil and protein content was reflected in the strong negative correlation between the two traits and in the strong reduction of variance when oil content was conditioned on protein content. Accordingly, five of the initially mapped QTL for oil content and eight of the nine epistatic locus pairs failed to show significant effects in the conditional data. These QTL and locus pairs are likely to represent genes involved in protein synthesis with only indirect effects on oil content or genes controlling substrate partitioning between oil and protein synthesis. On the other hand, one additive QTL and one epistatic locus pair showed reduced but still significant effects in the conditional mapping. This may indicate that the effects of these QTL observed in the unconditional mapping were partially due to genetic effects on protein content. However, there were two other QTL with very small reduction in conditional additive effects. These should represent genes that influence oil content independently from protein content. Such genes are of special interest in rapeseed breeding since they would allow to increase oil content without a concomitant decrease in protein content. Increasing oil content without decreasing protein content is an important objective in rapeseed breeding because it would increase oil yield without decreasing the value of the meal.

Six additional QTL and three epistatic locus pairs for oil content that were not apparent in the unconditional mapping could be detected in the conditional mapping. In QTL mapping, the likelihood to detect a QTL is dependent on the ratio between the variance caused by the QTL's effect and the total variance of the trait as well as the size of the mapping population (Lander and Botstein 1989). For QTL with small effects the likelihood of detection may be well below 1 and QTL with effects below a certain threshold become virtually undetectable. The QTL for oil content initially mapped in the unconditioned data showed effects ranging from 0.22 to 0.55%, indicating a detection threshold at about 0.2%. With allelic effects ranging from 0.14 to 0.24% the effects of the QTL detected only in the conditional mapping are on average smaller and in part well below the detection threshold from the unconditional mapping. The strong reduction in variance observed after conditioning oil content on protein content has obviously allowed the mapping of QTL with smaller effects, indicating that, in the case of two strongly correlated traits like oil and protein content, conditional mapping can be used to reveal additional QTL that would remain below the detection threshold in unconditional mapping.

The DH population analysed showed broad segregation in the developmental traits, due to parental lines that were strongly divergent in these traits. Despite this broad variation the evidence for a genetic interrelationship between oil content and the developmental traits was weak. While DTF and DOF still showed significant genetic correlations to oil content the reduction in variance when oil content was conditioned on the developmental traits was negligible, indicating that most of the variation in oil content occurred independent from the variation in the developmental traits. Furthermore, from the eight QTL for oil content only three failed to show significant effects when oil content was conditioned on the developmental traits, but these three QTL were the QTL with the smallest effects. As mentioned above, the likelihood to detect a QTL is, among other parameters, dependent on the size of the effect of the QTL and will be well below 1 for QTL with small effects. In repeated experiments such QTL will be detected in one experiment but not necessarily in another. The mapping of QTL for oil content after conditioning oil content on different traits can be regarded as different experiments, leaving the possibility that the failure to consistently detect three of the QTL with the smallest effects in all of the conditional data sets is just due to chance. Similar observations were made when oil content was conditioned on seed weight. The reduction in variance was again negligible and only one QTL, a QTL with one of the smallest effects, failed to show significant effects in the conditional mapping.

Apart from protein content, oil content showed the strongest correlations to seeds per silique in the segregating DH population. While the reduction in variance was small when oil content was conditioned on seeds per silique, three QTL failed to show significant effects in the conditional mapping, including some QTL with intermediate effects. These QTL may be involved in an interaction between oil content and seeds per silique. Since the correlation between oil content and seeds per silique was positive, the QTL involved in the interaction between the two traits identified here could be a valuable resource in rapeseed breeding. They would allow a simultaneous increase in oil content and seeds per silique, with the latter trait being a component of seed yield. In several studies it was shown that seeds per silique are positively correlated with seed yield, whereas no consistent correlation exists between SSW and seed yield (for review see Léon and Becker 1995).

In conclusion, conditional QTL mapping can contribute to a better understanding of the interdependence of various traits and, in the case of closely correlated traits, can lead to the detection of additional QTL with smaller effects.

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