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ORIGINAL PAPER

Detection of QTL for six yield-related traits in oilseed rape (*Brassica napus*) using DH and immortalized F_2 populations

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Abstract The inheritance of yield-related traits in rapeseed (*Brassica napus*) is poorly understood, and the investigations on mapping of quantitative trait loci (QTL) for such traits are only few. QTL related to six traits were mapped which include plant height (PH), height of lowest primary effective branch (HPB), length of main inflorescence (LMI), silique length (SL), number of primary branches (FB) and silique density (SD). A set of 258 doubled haploid (DH) lines derivatives of a cross between a canola variety Quantum and a resynthesized *B. napus* line No.2127-17, and a fixed immortalized F_2 (designated as IF_2) population generated by randomly permutated intermating of these DHs were investigated. A genetic linkage map was constructed using 208 SSR and 189 SRAP markers for the DH population. Phenotypic data were collected from three environments for the two populations. Using composite interval mapping analyses, 30 and 22 significant QTL were repeatedly detected across environments for the six traits in the DH and IF_2 populations, respectively. Twenty-nine QTL were common between the two populations. The directions of parental contribution for all common QTL were the same, showing a great potential for marker-assisted selection in improving these traits. Some chromosomal regions harbor QTL for multiple traits, which were consistent with significant phenotypic correlations observed among traits. The results provided a better understanding of the genetic factors controlling yield-related traits in rapeseed.

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Introduction

Rapeseed—*Brassica napus* is cultivated as an oilseed crop worldwide. Development of high yielding varieties is a major goal in rapeseed breeding. The seed yield in rapeseed is determined by three yield components, viz. siliques per plant (SP), seeds per silique (SS) and seed weight (SW). The first two components determine the total number of seed per plant. An increase in these components is the major contributing factors in rapeseed yield improvement. SP and SS are determined concurrently by a number of plant and silique characteristics such as plant height, silique length, number of branches, number of siliques per branch and silique density. These are complex quantitative traits controlled by several genes and highly influenced by environmental conditions. The genetic basis for most of these traits in rapeseed is not well elucidated.

The application of molecular marker techniques for quantitative trait locus (QTL) analysis has proved to be an effective approach to dissect complicated quantitative traits. Although several investigations on traits such as seed quality (Howell et al. 2003; Zhao et al. 2006; Marwede et al. 2005; Delourme et al. 2006), flowering time (Ferreira et al. 1995; Osborn et al. 1997) and disease resistance (Dreyer et al. 2001; Zhao et al. 2006) are available, only

few studies on QTL mapping for yield-related traits have been carried out in rapeseed. Butruille et al. (1999) detected four QTLs (located on N2, N3, N12, and N13) for plant height. Yi et al. (2006), employing a DH population in a single environment, identified 3, 4, 3 and 2 QTL for plant height, height of first primary effective branch, length of main inflorescence and number of primary branches, respectively. More recently, Udall et al. (2006) and Quijada et al. (2006) carried out QTL mapping for plant height and other traits in four rapeseed crosses using DH lines and their testcrosses. They detected a number of QTL with stable effects across populations and environments.

Hua et al. (2002) proposed a novel experimental design which was referred to as "immortalized F_2" (IF_2) population. It could be generated by an artificial random intermating of DH lines or recombinant inbred lines (RILs). The IF_2 population has several distinct advantages for QTL analysis as the genotypes and their proportions are similar to those in an F_2 population. Also the IF_2 population allows trials at multiple locations over several years. Moreover, molecular marker data for an IF_2 population can be deduced from that of corresponding DHs (or RILs), so it is easy to obtain. These facts indicate the efficacy of IF_2 population an ideal choice for complete genetic analysis and very suitable for QTL mapping of quantitative traits.

In the present study, QTL associated with six yield-related traits were identified in two oilseed rape populations. The QTL detected in the two populations will be useful for marker-assisted selection of higher seed yields in rapeseed.

Materials and methods

Plant materials

The 258 DH lines were developed by microspore culture from the cross between two *B. napus* lines viz. variety Quantum and line No.2127-17 (Liu et al. 2005). The IF_2 population was created following the design of Hua et al. (2002). In this design, crosses were made between the DHs chosen by random permutations of the 258 lines. In each round of permutation, the 258 DHs were randomly divided into two groups, and the lines in the two groups were paired up at random without replacement to provide parents for 129 crosses. Each of the 258 lines was used only once in each round of pairing and crossing. This procedure was repeated two times, resulting in a population consisting of 258 crosses.

Trait evaluation

Replicated field trials were carried out at a single site (Hezheng, Gansu Province) in 2004, and at two sites (Hezheng, Gansu Province; Xining, Qinghai Province) in 2005 in the spring rapeseed area, northwest of China. The field planting followed a randomized complete block design with four replications for the DH population and two replications for the IF_2 population in each trail. Each plot consisted of six rows: two rows for a cross in the IF_2 population and two rows for each of its respective parents (DH lines). There were 12 plants in each row, with a distance of 20 cm between plants within each row and 30 cm between rows. Five check plots consisting of Quantum, No.2127-17, and their F_1 hybrid were randomly arranged in each trial. The field management followed essentially normal agricultural practice.

Two partly dominant traits of No.2127-17, white petal and yellow seed coat color, were helpful to easily determining hybrid plants in crosses of the IF_2 populations (Liu et al. 2005). There were 145 crosses (white petal × yellow petal; yellow seed coat × black seed coat) for which hybrid plants can be determined by these two morphological characters. For the remainder crosses, a selected set of co-dominant SSR markers were used based on the genotype of their parents to determine hybrid plants for each cross.

Ten matured plants in the middle of rows were selected from each material for trait evaluation which included: plant height (PH), measured from ground level to the tip of the main inflorescence; height of lowest primary effective branch (HPB), measured from ground level to the base of lowest primary effective branch; length of main inflorescence (LMI), measured from the base of highest primary effective branch to the tip of the main inflorescence; silique density (SD), measured as the number of effective silique on main inflorescence divided by effective length of main inflorescence; silique length (SL), measured by the average length of ten siliques selected from the middle part of main inflorescence (not including the beak); and number of primary branches (FB), measured as the number of effective primary branches. All of the trait evaluations were done at harvest maturity for each material.

Molecular marker and linkage map

Two classes of molecular markers, simple sequence repeat (SSR) and sequence related amplified polymorphism (SRAP), were used in assaying the polymorphisms of the DH population. The genotypes of the IF_2 population were deduced on the basis of genotypes of DH lines. SSR analysis followed the methods of Piquemal et al. (2005). Most of SSR primer pair sequences were obtained from public sources: http://www.ukcrop.net/perl/ace/search/BrassicaDB (Lowe et al. 2004), http://www.brassica.info/ssr/SSRinfo.htm (prefixed by Ra, Ol, Na, BN, MB, BRMS- and MR), and

http://www.osbornlab.agronomy.wisc.edu/research/maps/ssrs.html (prefixed by FITO). Primer pairs prefixed by "BRAS" and "CB" were from the electronic supplementary material of Piquemal et al. (2005). Primer pairs prefixed "s" were obtained from Agriculture and Agri-Food Canada (http://www.brassica.agr.gc.ca/ind ex_e.shtml). Primer pairs prefixed "P" were from private communication.

SRAP analysis followed the methods of Li and Quiros (2001). Ten forward primers and 17 reverse primers were employed, which resulted in 170 primer combinations (Table 1). Polymorphic pairs were named by combining the name of forward and reverse primers.

When a primer pair generated more than one polymorphic locus, the name of pair was eventually followed by a letter to distinguish the different loci. For instance, primer pair Ra2-F11 corresponded to three genetic loci Ra2-F11A, Ra2-F11B and Ra2-F11C.

The χ^2 test was used to assess goodness-of-fit to the expected segregation ratio for each marker. Linkage analysis was performed with all markers using Mapmaker Exp/3.0b (Lander et al. 1987). A minimum LOD score of 5.0 and a maximum distance of 30 cM were used to group loci into the linkage groups (LG). The *three-point* command was utilized for multi-point analysis. The order within each LG was determined at LOD 3.0 by the commands *order*, *try*, *and ripple* (all with the *error detection* command on). Map distances were calculated by means of the Kosambi mapping function (Kosambi 1944).

Table 1 SRAP primers used in this study

Forward primer 5′–3′		Reverse primer 5′–3′	
Name	Sequence	Name	Sequence
ME1	ME-ATA	EM1	EM-AAT
ME2	ME-AGC	EM2	EM-TGC
ME3	ME-AAT	EM3	EM-GAC
ME4	ME-ACC	EM4	EM-TGA
ME5	ME-AAG	EM5	EM-AAC
ME6	ME-TAG	EM6	EM-GCA
ME7	ME-TTG	EM7	EM-ATG
ME8	ME-TGT	EM8	EM-AGC
ME9	ME-TCA	EM9	EM-ACG
ME10	ME-TAC	EM10	EM-TAG
		EM11	EM-TCG
		EM12	EM-GTC
		EM13	EM-GGT
		EM14	EM-CAG
		EM15	EM-CTG
		EM16	EM-CGG
		EM17	EM-CCA

ME- 5′-TGA GTC CAA ACC GG-3′; *EM*- 5′-GAC TGC GTA CGA ATT-3′

Statistical analysis and QTL mapping

Year-location combinations were treated as independent environments. Estimates of means and variances for the traits were conducted using SAS software (SAS Institute Inc. 1999). Pearson's correlation coefficients between traits were calculated using the procedure CORR of SAS. The heritability (h^2) was calculated as: $h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{ge}^2/n + \sigma_e^2/nr)$, where σ_g^2 is genotypic variance, σ_{ge}^2 variance due to genotype by environment interaction, σ_e^2 error variance, n number of environments; r number of replications. The estimates of σ_g^2, σ_{ge}^2, σ_e^2, were obtained from an analysis of variance (ANOVA) with environment considered as a random effect.

QTL analysis was performed separately for the DH and IF_2 populations. The Windows version of QTL Cartographer V2.0 (Wang et al. 2003) was used to conduct composite interval mapping (CIM) analysis. As all traits fitted to normal distribution according to skewness and kurtosis (data not shown), these were directly subjected to analysis. Model 6 of the Zmapqtl procedure was employed. The likelihood of a QTL and its corresponding effect at every 2 cM was estimated. Forward stepwise regression and backward elimination regression methods were used to choose significant markers for each trait (cofactor in for $P < 0.01$; cofactor out for $P > 0.05$). Cofactors within 10 cM on either side of the QTL test site were not included in the Zmapqtl QTL model. A 1,000-permutation test of shuffling the phenotypes means with the genotypes was performed to estimate a significance threshold of the test statistic for a QTL based upon a 5% experiment-wise error rate (Doerge and Churchill 1996) in every trial. On a genome-wide basis by permutation, the LOD thresholds for significance were 2.56–3.12 and 3.36–3.84 for the six traits in the DH and IF_2 population, respectively. For each putative QTL, a 1-LOD confidence interval (CI) was constructed according to Lander and Bostein (1989). QTL with similar positions (overlapping 1-LOD confidence intervals) were assumed to be the same ones between environments or populations. When a QTL was significant in other environments or another population but its LOD value was below the significance threshold of permutation test in the current environment, the LOD thresholds 2.5 and 3.0 were used for significance in the DH and IF_2 population, respectively.

Results

Construction of the linkage map

Only the marker data in the DH population was used to construct the linkage map because it has less missing marker data than the IF_2 population. A total of 397

molecular markers, including 208 SSR loci, 189 SRAP loci, were mapped on 20 linkage groups, covering 1,747.4 cM according to the Kosambi function (Fig. 1). The 19 main LGs were assigned to the public linkage maps by SSR markers. The marker order in our map was in good agreement with the map of Piquemal et al. (2005) and Qiu et al. (2006).

A high proportion of loci showed segregation distortion in the DH populations: 70 SSR loci (17.6%) and 59 SRAP loci (14.8%) showed distorted segregation ratio ($P < 0.01$), respectively. Most of loci with distorted segregation (103 loci) skewed towards the Quantum (female parent). Loci with skewed segregation tended to cluster on N1, N2, N3, N5, N7, N11, N12, N13, N15, and N18. All loci with skewed segregation in the DH population also showed segregation distortion in the IF_2 population.

Phenotypic analysis

The measurements of six traits for both populations as well as two parents are listed in Table 2. Quantum had higher phenotypic values than No.2127-17 for all of the traits measured. The performance of the IF_2 population was higher than those of the DH population for all six traits, which is reasonable considering the heterosis effects. For all traits both populations showed transgressive and continuous distribution except for PH in the IF_2 population, suggesting polygenic inheritance of the traits.

DH population showed higher heritability for all traits as compared to IF_2 population. In both populations, SL showed the highest heritability of all traits investigated. The heritability of FB was much smaller in the IF_2 population than in the DH population. The difference in heritability between the two populations may have been due to more replications in field tests of the DH population.

The correlation coefficients between six traits were calculated for the DH and IF_2 population (Table 3) across environments. Most of the traits were significantly correlated with each other. LMI showed significant positive correlation with PH, but it showed significant negative correlation ($P < 0.01$) with other traits with the exception of SL. SL was relatively independent of other traits as it showed significant correlation with PH and HPB

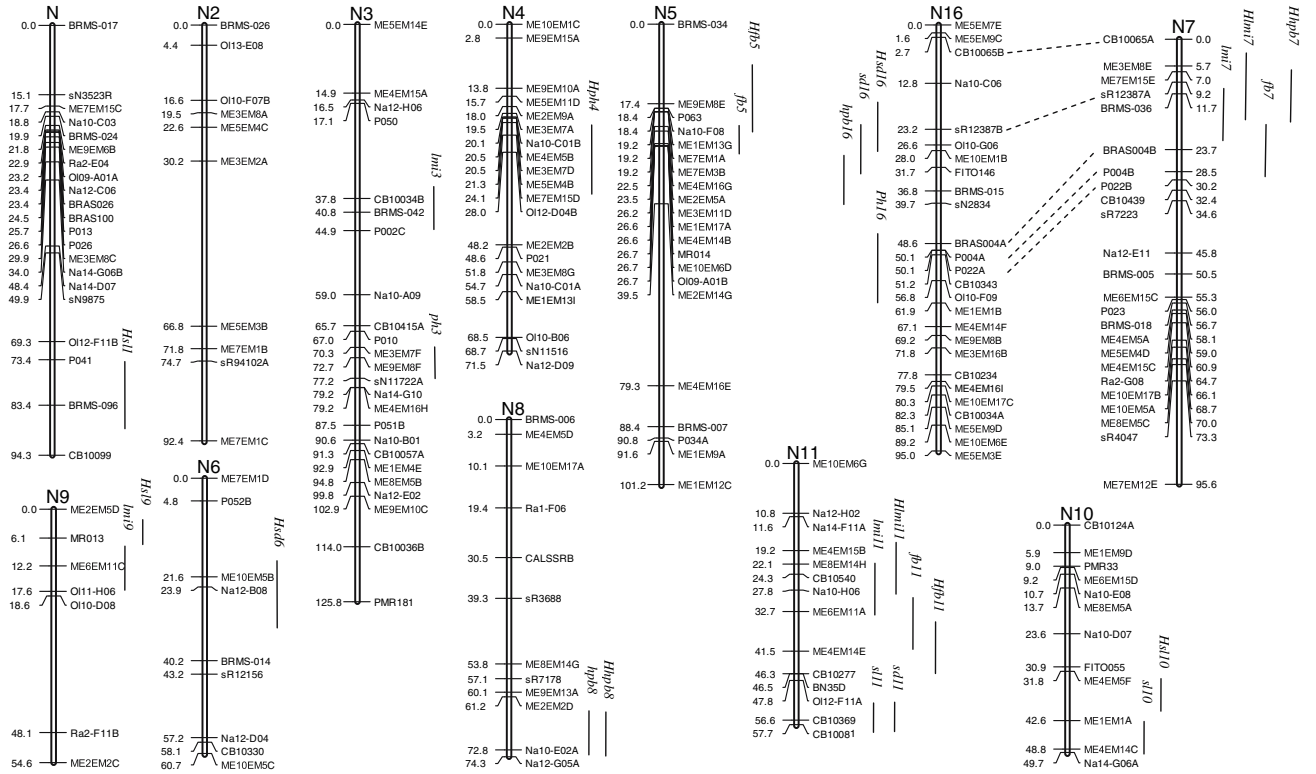

Fig. 1 Genetic map and QTL position in the DH and IF_2 populations. Linkage group (LG) designations follow the convention of Parkin et al. (1995). The average values of three environments were used as input data in QTL mapping. QTL were designated using the trait name initials followed by a number identifying the LG. The number of LG was followed by a letter to distinguish QTL on the same LG. For the QTL detected in the IF_2 population, an "H" was added before the trait name initials to distinguish these designations from those used in the DH population. The *vertical lines* beside linkage groups indicate 1-LOD score confidence intervals of QTL. *Broken lines* between linkage groups N7 and N16 represent homoeologous polymorphic marker locis

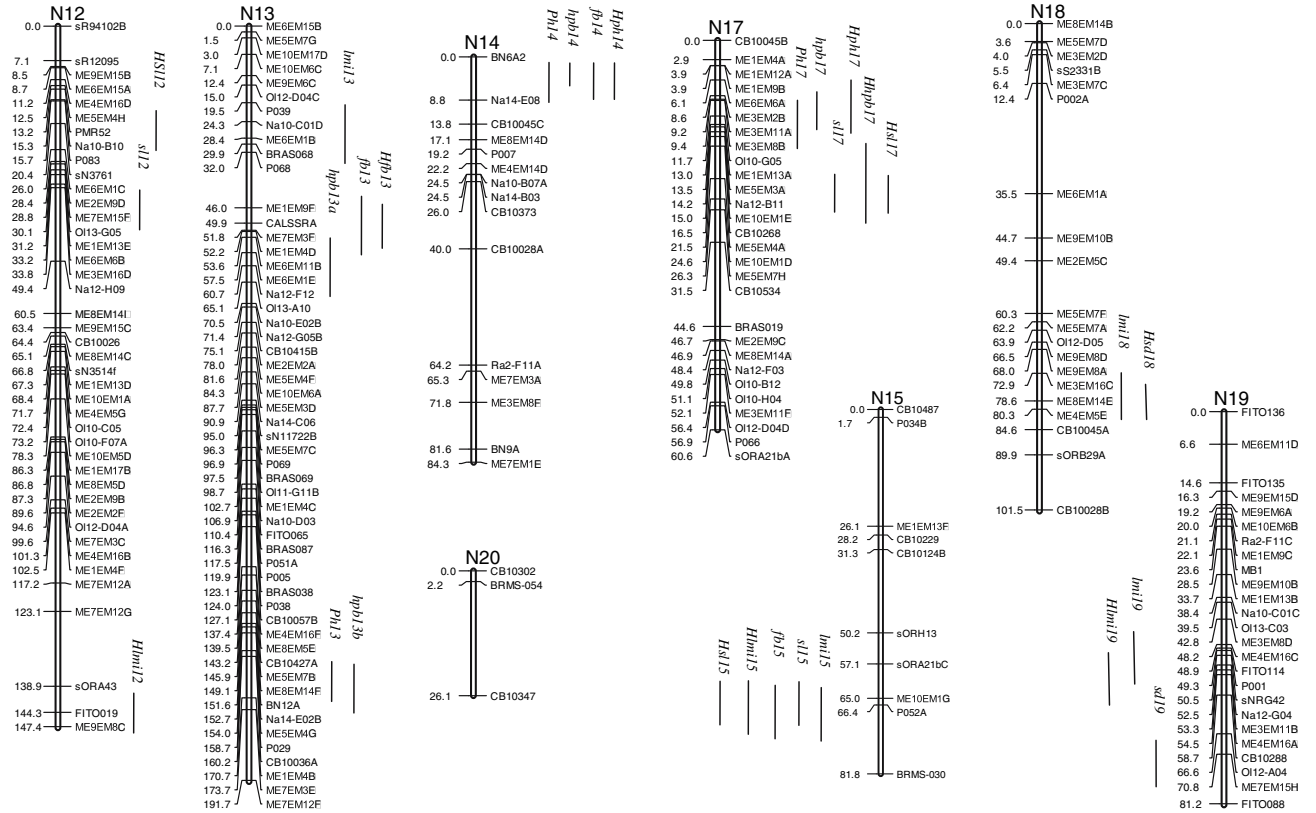

Fig. 1 continued

($P < 0.05$) with low correlation coefficients. For crosses in the IF_2 population, mid-parental values showed significant correlations with F_1 values for all traits examined, with correlation coefficient ranging from 0.52 (for SD) to 0.73 (for LMI).

QTL mapping

Analyses across environments revealed significant genotype × environment interactions for all traits in both populations [see Tables S1, S2 of the Electronic Supplementary Material (ESM)]. For each trait, the analysis was carried out for the data in individual environments as well as using the pooled data averaged over all environments. Detailed information of QTL detected in individual environment is presented in Tables S3, S4 (EMS). Though the QTL × environment interaction effects may be significant for some QTL, most of repeatedly detected QTL across environments were also significant when using average values of three environments (see Tables 4, 5; Fig. 1).

Twelve QTL were detected for PH, and they were distributed on ten linkage groups. The QTL on N3, N10, N13, N16 and N17 were both detected in the two populations. The QTL on N3 was only detected in the trial 2005Xining, while the QTL on N10 was only significant in the trail 2005Hezheng. The QTL on N14 were detected in all three environments in the DH population, but it was only significant when using average value of three environments in the IF_2 population. The QTL on the top of N4 was only detected in the IF_2 population, though it had the highest additive effect and accounted for the largest portion of phenotypic variance in the IF_2 population.

Ten QTL were identified for HPB. The QTL on N2, N8, N16 and N17 were both detected in the two populations. The QTL on N17 was detected in all trials, though it did not show the largest effect in most of environments. In the DH population the QTL on N14 was detected in all trials, but it was not significant in the IF_2 population. Similarly, the effect of *hpb13a* was significant in two trails in the DH population, but it was not detected in the IF_2 population. *Hlmi7* was detected in the two trials of 2005 in the IF_2 population, but it did not show significant effect in the DH population.

Twelve chromosome regions were associated with LMI in the three trials. Seven QTL were both detected in the two populations, and of them the QTL on N7 and N15 were significant in all environments. In the DH population the QTL on N9 was detected in all trials, but it was not significant in any of trials in the IF_2 population. On the

Table 2 Phenotypic summary of plant height (PH), height of lowest primary effective branch (HPB), length of main inflorescence (LMI), silique length (SL), number of primary branches (FB) and silique density (SD) for Quantum (P_1), No.2127-17 (P_2), the DH population and the IF_2 population of Quantum × No.2127-17 in 2004 and 2005

	Trial	PH (cm)	HPB (cm)	LMI (cm)	SL (cm)	FB	SD
P_1	1[a]	115.37	21.6	58.23	6.32	4.61	0.89
	2[b]	113.77	22.79	59.38	6.56	3.6	0.85
	3[c]	124.23	17.69	64.91	6.5	4.28	0.74
P_2	1	97.24	15.59	52.17	5.27	3.33	0.78
	2	99.88	21.22	57.02	5.73	2.36	0.78
	3	112.13	5.85	57.13	5.52	4.11	0.71
DH	1	108.7 ± 10.7[d]	21.5 ± 9.3	58.0 ± 7.4	5.7 ± 0.5	4.1 ± 0.7	0.9 ± 0.1
		80.2–135.2[d]	4.5–56.5	42.1–83.2	4.4–7.3	2.5–6.1	0.6–1.2
	2	20.0 ± 12.7	32.7 ± 11.8	59.9 ± 8.3	6.2 ± 0.6	3.5 ± 0.7	0.9 ± 0.1
		88.2–150.0	6.3–66.6	38.4–83.7	4.7–8.0	1.9–6.1	0.5–1.2
	3	131.2 ± 14.9	28.6 ± 16.0	60.7 ± 8.8	5.8 ± 0.6	4.5 ± 0.8	0.8 ± 0.1
		92.9–171.2	2.0–85.4	35.4–85.4	4.0–7.2	2.9–7.3	0.6–1.2
IF_2	1	120.6 ± 8.2	26.3 ± 7.5	60.7 ± 4.4	6.0 ± 0.3	4.3 ± 0.5	0.9 ± 0.1
		98.0–140.4	8.7–49.2	49.9–70.3	5.1–6.7	3.2–5.9	0.7–1.2
	2	129.2 ± 9.9	34.5 ± 12.4	63.4 ± 6.7	6.5 ± 0.5	3.9 ± 0.7	1.0 ± 0.1
		104.2–154.9	2.7–76.5	46.0–80.7	5.1–7.8	2.3–6.0	0.7–1.2
	3	139.2 ± 12.0	27.5 ± 13.3	63.4 ± 6.9	6.1 ± 0.5	5.1 ± 0.7	0.9 ± 0.1
		104.1–166.7	0.0–64.3	44.6–83.0	4.9–7.1	3.0–6.9	0.6–1.1
h^2	DH	0.84	0.83	0.87	0.93	0.84	0.83
	IF_2	0.77	0.71	0.76	0.82	0.66	0.79

h^2 Heritability

[a] Environment: 2004Hezheng

[b] Environment: 2005Hezheng

[c] Environment: 2005Xining

[d] Trait values are given as mean value ± standard deviation (upper) and as a range (lower)

contrary, the QTL on the bottom of N12 was only detected in the IF_2 population.

Thirteen QTL were identified for SL in the two populations. The QTL on N1, N3, N10, N12, N15 and N17 were both detected in the two populations. The QTL on N17 was detected in all environments for the both populations, but it only had largest contribution rates in the trial 2005Hezheng. Two QTL were detected on N14 in the DH population (*sl14a*, *sl14b* in Table S3), but neither of them was significant in the IF_2 population. On the contrary, two QTL on N3 and N12 (*Hsl3a* and *Hsl12b* in Table S4) were repeatedly detected in the IF_2 population, but they were not detected in the DH population.

Table 3 Phenotypic correlations among traits in the DH population (below diagonal) and the IF_2 population (above diagonal) of Quantum × No.2127-17

Trait	PH	HPB	LMI	SL	FB	SD
PH		0.67**	0.23**	0.20**	0.32**	0.32**
HPB	0.81**		−0.26**	0.15*	0.15*	0.55**
LMI	0.27**	−0.14*		−0.01	−0.40**	−0.33**
SL	0.15*	0.15*	−0.10		0.07	0.01
FB	0.16*	0.27**	−0.66**	0.09		0.30**
SD	0.22**	0.49**	−0.35**	−0.02	0.30**	

* Significance at 0.05 level of probability and ** significance at 0.01 level of probability, respectively

Fourteen QTL were detected for FB, but only three of them were common between the two populations. The QTL on N13 were detected in all trails, and it had largest effect in the both population when using average values of three trials. *fb7* and *fb15* were repeatedly detected in the DH population, but they were not significant in the IF_2 population.

Fifteen QTL were detected for SD. The QTL on N6, N15, N16 and N18 were common between the two populations. The QTL on N11 (*sd11*) was only significant in the DH population, while the QTL on N10 was only repeatedly detected in the IF_2 population.

Totally, 76 QTL were identified for the six traits for the two mapping populations, and they were detected on all main LGs (N1-N19). The distribution of QTL was not well proportioned between linkage groups: on groups N2, N4, N6 and N9 no more than three QTL were detected, while

seven QTL were detected on groups N3, N12 and N13. Twenty-nine QTL were both detected between the two populations, and for all of them the direction of parental contribution was the same across environments and populations. Thirty QTL were repeatedly detected in the DH population, and 22 ones in the IF_2 population. Some QTL were only repeatedly detected in one population, which means their effects could be specified by allele situation or genetic background.

Discussion

It is essential to use appropriate experimental designs and materials for QTL mapping. Strenuous efforts have been made to construct experimental populations for detecting and analyzing QTL in the last decade. Plant populations with various genetic structures have been developed to achieve these goals and mainly consist of F_2/F_3, BC (backcross), DHs, RILs, and BILs (backcross inbred lines).

Table 4 Putative QTL for six traits detected in the DH population of Quantum × No.2127-17

Trait	QTL[a]	Position[b] (cM)	Marker[b]	CI[b] (cM)	LOD	A	R^2 (%)[c]	Trial[d]
PH	*ph3*	75.2	sN11722A	70.3–77.2	3.8	−2.89	6.2	3
	ph13	164.2	CB10036A	162.2–168.2	3.6	−3.10	6.9	2,3
	ph14	0.0	BN6A2	0.0–8.0	6.7	−3.89	10.8	1,2,3
	ph16	50.1	P004A	43.7–60.8	7.4	3.98	11.8	1,2,3
	ph17	13.0	ME1EM13A	8.1–18.5	7.6	4.08	12.0	1,2,3
HPB	*hpb8*	72.8	Na10-E02A	67.2–72.8	3.6	−2.60	5.6	2,3
	hpb13a	57.5	ME6EM1E	53.6–69.1	3.9	2.74	5.9	1,2
	hpb13b	166.7	ME1EM4B	160.2–172.2	3.5	−2.58	5.4	3
	hpb14	0.0	BN6A2	0.0–4.8	3.1	−2.11	4.3	1,2,3
	hpb16	33.7	FITO146	28.0–35.7	9.7	4.44	16.2	1,2,3
	hpb17	9.4	ME3EM8B	5.9–11.7	7.6	3.80	12.0	2,3
LMI	*lmi3*	38.8	CB10034B	33.8–42.9	5.7	−2.29	9.1	2,3
	lmi7	15.7	BRMS-036	9.7–21.7	5.4	2.57	9.4	1,2,3
	lmi9	17.6	Ol11-H06	8.1–18.6	7.1	2.34	9.2	1,2
	lmi11	24.1	CB10540	21.2–32.7	3.6	−1.70	4.9	2,3
	lmi13	29.9	BRAS068	19.5–36.0	4.5	−1.85	6.1	
	lmi15	68.4	P052A	63.1–72.4	8.5	−2.89	13.8	1,2,3
	lmi18	76.9	ME8EM14E	72.9–82.3	9.5	2.99	15.1	1,3
	lmi19	48.9	FITO114	44.8–56.5	8.0	−2.58	11.6	1,2
SL	*sl10*	46.6	ME4EM14C	42.6–48.8	3.5	0.13	5.5	2,3
	sl11	56.6	CB10369	53.8–57.7	3.9	0.16	5.6	1
	sl12	33.8	ME3EM16D	31.2–39.8	11.2	−0.24	17.1	1,2,3
	sl15	65.0	ME10EM1G	61.1–72.4	5.8	0.17	8.6	2,3
	sl17	20.5	ME5EM4A	16.5–23.5	10.5	0.23	16.8	1,2,3
FB	*fb5*	21.2	ME4EM16G	18.4–22.5	3.7	−0.16	5.8	2,3
	fb7	28.5	P004B	15.7–30.4	6.1	−0.19	8.5	1,2,3
	fb11	36.7	ME6EM11A	29.8–41.5	6.7	0.22	10.6	1,2,3
	fb13	51.8	ME7EM3F	42.0–55.6	15.0	0.31	22.4	1,2,3
	fb14	0.0	BN6A2	0.0–6.8	5.8	0.23	11.5	1
	fb15	65.0	ME10EM1G	63.1–72.4	7.2	0.20	10.1	2,3
SD	*sd11*	53.8	CB10369	49.8–56.6	8.5	0.05	15.7	1,2,3
	sd16	25.2	Ol10-G06	20.8–31.7	8.4	0.04	14.2	1,2,3
	sd19	70.8	ME7EM15H	68.6–74.8	4.5	0.02	7.0	1

A Additive effect; positive additive effects indicate that the Quantum allele increases the value of the trait

[a] QTL names are abbreviations of the trait followed by its respective linkage group number. An alphabetical letter a or b was added if more than one QTL were found in one linkage group

[b] Peak effect of the QTL, the closest marker and the 1-LOD score confidence interval (CI)

[c] Proportion of the phenotypic variation explained by the QTL

[d] Number indicating the environment in which QTL were significant: *1* 2004Hezheng, *2* 2005Hezheng, *3* 2005Xining

Table 5 Putative QTL for six traits detected in the IF_2 population of Quantum × No.2127-17

Trait	QTL[a]	Position[b] (cM)	Marker[b]	CI[b] (cM)	LOD	A	D	R^2 (%)[c]	Trail[d]
PH	*Hph4*	32.0	Ol12-D04B	26.1–38.0	7.4	−5.37	4.91	13.5	2,3
	Hph14	0.0	BN6A2	0.0–6.0	3.9	−4.39	−0.15	7.2	
	Hph17	11.7	Ol10-G05	5.9–18.5	4.7	2.21	1.95	8.1	1,3
HPB	*Hhpb7*	11.7	ME7EM15E	7.2–15.7	7.4	−4.42	2.73	11.0	2,3
	Hhpb8	71.2	Na10-E02A	67.2–72.8	7.1	−4.09	−0.65	10.5	1,2,3
	Hhpb17	26.3	ME5EM7H	18.5–30.3	6.0	3.49	0.19	7.9	1,2,3
LMI	*Hlmi7*	7.0	ME7EM15E	3.7–17.7	9.4	2.56	−1.33	12.7	1,2,3
	Hlmi11	22.1	ME8EM14H	17.6–29.8	4.9	−1.94	0.31	6.5	2,3
	Hlmi12	144.3	FITO019	140.9–146.3	8.4	−2.98	2.71	11.0	2,3
	Hlmi15	65.0	ME10EM1G	61.1–70.4	9.9	−3.17	2.01	13.5	1,2,3
	Hlmi19	58.5	CB10288	53.3–62.7	6.1	−2.45	1.17	8.3	2
SL	*Hsl1*	79.4	BRMS-096	75.4–89.4	4.4	−0.01	−0.19	8.7	1
	Hsl9	4.0	MR013	2.0–8.1	4.2	−0.01	0.19	9.3	3
	Hsl10	33.8	ME4EM5F	31.8–37.8	4.9	0.03	0.17	8.2	1
	Hsl12	20.4	sN3761	17.7–22.4	7.3	−0.14	−0.09	11.0	1,2,3
	Hsl15	65.0	ME10EM1G	61.1–68.4	5.2	0.09	0.06	7.3	2,3
	Hsl17	20.5	ME5EM4A	16.5–23.5	9.9	0.14	0.09	15.3	1,2,3
FB	*Hfb5*	12.0	ME9EM8E	6.0–21.2	6.3	−0.23	0.06	10.9	1,2
	Hfb11	41.5	ME4EM14E	36.7–46.3	6.1	0.24	−0.11	8.7	2,3
	Hfb13	51.8	ME7EM3F	46.0–52.2	7.2	0.30	0.09	10.1	1,2,3
SD	*Hsd6*	21.6	ME10EM5B	16.8–31.9	5.8	−0.03	0.01	8.4	3
	Hsd16	23.2	sR12387B	18.8–25.2	6.6	0.04	−0.03	9.3	1,3
	Hsd18	80.3	ME4EM5E	76.9–82.3	7.9	0.01	0.04	11.1	2,3

A Additive effect, *D* dominance effect. Positive additive effects indicate that the Quantum allele increases the value of the trait

[a] QTL names are abbreviations of the trait followed by its respective linkage group number. An alphabetical letter "H" was added before names to distinguish QTL detected in the DH population

[b] Peak effect of the QTL, the closest marker and the 1-LOD score confidence interval (CI)

[c] Proportion of the phenotypic variation explained by the QTL

[d] Number indicating the environment in which QTL were significant: *1* 2004Hezheng, *2* 2005Hezheng, *3* 2005Xining

F_2 population provides the most comprehensive genetic information. However, each genotype in an F_2 population is represented by only one individual. In rapeseed, DHs have been used most often, because of their inherent advantages of providing a constant DNA supply and phenotyping opportunities for many different studies. However, allelic differences are limited because of absence of heterozygous locus in DHs, since only two types of alleles segregate at each polymorphic locus. In some cases, TC progenies populations have been used (Udall et al. 2006; Quijada et al. 2006). In this study two permanent populations, DH population and IF_2 population, derived from a single cross were used. DH lines were maintained by selfing, while IF_2 population could be replicated by intermating of DH lines, which means they both could provide constant phenotyping opportunities for many different studies. Our experimental designs have increased scope for identifying QTL and facilitated the comparisons of QTL between different types of populations.

B. napus is hypothesized to have originated by hybridization of *B. rapa* and *B. oleracea* (Song and Osborn 1992; UN 1935). Homoeologous regions were identified between and among the A genome linkage groups originating from the *B. rapa* ancestor and the C genome linkage groups originating from the *B. oleracea* ancestor in the amphidiploid genome of *B. napus* (Parkin et al. 1995; Piquemal et al. 2005). QTL duplications may exist in these homoeologous regions (Delourme et al. 2006). In our study, *Hhpb7* and *hpb16* could be a pair of putatively homoeologous QTL, because the former was located near marker sR12387A and the latter was near marker sR12387B (Fig. 1). Interestingly, Zhao et al. (2006), Udall et al. (2006) and Quijada et al. (2006) found QTL in the genomic regions having chromosomal rearrangement between N7 and N16. According to the results of Parkin et al. (2005) and Qiu et al. (2006), *hpb8* and *hpb13a* should be another pair of putatively homoeologous QTL. *hpb8* is located near SSR markers Na10-E02A and Na12-G05A, and *hpb13a* is

located near SSR markers Na10-E02B and Na12-G05B. Unfortunately, alignment of linkage groups to the *A. thaliana* genomes is not possible in the present study, so in the future common markers between the two species should be developed in order to ascertain the paralogous relationships of these QTL regions.

Most pairs of traits showed significant correlation in the present study, which is also reflected by the genomic location and effects of QTL detected. Some QTL clusters were found on the linkage map, and they were mainly located on LGs N7, N11, N13, N14, N15, N16 and N17. As mentioned above, LMI showed significant negative correlations with most of other traits. In the QTL clusters on N7, N11 and N15, QTL for LMI showed opposite direction of parental contribution compared to QTL of other traits. Most QTL for SL were not located in the QTL clusters, which again indicated that SL was an independent trait from other traits investigated.

Appropriate plant height, low height of branches, long main inflorescence, long silique, more branches and high silique density are main objectives of rapeseed breeding in China. However, significant correlations for some pairs of traits make difficult simultaneous improving these traits by conventional breeding. For example, it is normally difficult to increase the length of main inflorescence without decreasing number of primary branches. QTL detected in the present study may provide useful information for improving these traits by MAS. For LMI and FB, four genomic locations (on linkage groups N7, N11, N13 and N15) were found affecting both traits with opposite direction of effects. Fortunately, for each trait there were some QTL whose effects were independent of the other trait. Thus, improving the two traits simultaneously is likely to be possible by manipulating these loci in MAS.

In the present study, we identified some QTL which were only significant in one mapping population. In MAS, QTL are usually identified in early generations and their flanking markers are used for selecting lines during advanced generations. Thus, employing QTL only detected in the DH population is most suitable for MAS. For QTL only detected in the IF_2 population, MAS based on them might sometimes produce poor effect or even no effect. But genomic information of these QTL would be valuable in hybrid cultivar breeding, and be helpful to analyze QTL expression in different environments and different backgrounds.

The present investigation is the first comprehensive report on using molecular markers to dissect the genetic control of the six yield-related traits using a repeatable IF_2 population that has the genetic structure similar to F_2 in rapeseed. QTL mapping for the six traits has not been reported earlier with the exception of PH. Characterization of stable QTL in different environments, and common QTL from different types of populations promise to increase information on the genetic basis and their distribution of valuable QTL in the rapeseed genomes and facilitating application of MAS in improving seed yield in this crop.

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