RESEARCH ARTICLE

Comparative mapping reveals similar linkage of functional genes to QTL of yield-related traits between *Brassica napus* and *Oryza sativa*

FUPENG LI, CHAOZHI MA*, QINGFANG CHEN, TOUMING LIU, JINXIONG SHEN, JINXING TU, YONGZHONG XING and TINGDONG FU

National Key Laboratory of Crop Genetic Improvement, National Center of Rapeseed Improvement in Wuhan, National Center of Plant Gene Research, Huazhong Agricultural University, Wuhan 430070, People's Republic of China

Abstract

Oryza sativa and *Brassica napus*—two important crops for food and oil, respectively—share high seed yield as a common breeding goal. As a model plant, *O. sativa* genomics have been intensively investigated and its agronomic traits have been advanced. In the present study, we used the available information on *O. sativa* to conduct comparative mapping between *O. sativa* and *B. napus*, with the aim of advancing research on seed-yield and yield-related traits in *B. napus*. Firstly, functional markers (from 55 differentially expressed genes between a hybrid and its parents) were used to detect *B. napus* genes that co-localized with yield-related traits in an $F_{2:3}$ population. Referring to publicly available sequences of 55 *B. napus* genes, 53 homologous *O. sativa* genes were subsequently detected by screening, and their chromosomal locations were determined using silico mapping. Comparative location of yield-related QTL between the two species showed that a total of 37 *O. sativa* and *B. napus* homologues were located in similar yield-related QTL between species. Our results indicate that homologous genes between *O. sativa* and *B. napus* may have consistent function and control similar traits, which may be helpful for agronomic gene characterization in *B. napus* based on what is known in *O. sativa*.

Introduction

Members of the *Brassica* genus, including *B. oleracea*, *B. rapa*, and *B. napus*, are most closely related to the model plant *Arabidopsis thaliana*, having diverged less than 20 million years ago (Brendel *et al.* 2002); they share about 85% exon sequence similarity (Cavell *et al.* 1998). Genomewide comparative genetic mapping of *A. thaliana* and *B. oleracea* revealed co-linear segments spanning 3.7–49.6 cM (Kowalski *et al.* 1994). Thus, the *Arabidopsis* genome could prove to be a powerful tool for studying *Brassica* genomics.

Wolfe *et al.* (1989) conducted comparative genome analyses between dicots and monocots, which diversified 160–240 million years ago. Paterson *et al.* (1996) speculated that 43–58% of chromosomal tracts of 3 cM or less have remained co-linear between monocots and dicots over the evolutionary time; however, contradictory results have been reported by Gale and Devos (1998). Comparative analysis of a 1.5-Mb genomic region revealed homology between segments of *Arabidopsis* chromosome 4 and *O. sativa* chromosome 2 (van Dodeweerd *et al.* 1999); moreover, comparative mapping has indicated additional homologous segments in the vicinity of markers. Comparisons have shown that about 80.6% of *Arabidopsis* genes have a conserved homologue in *O. sativa*, with a mean extent of homology of 80.1% (60.0% amino acid identity) of the protein length (Yu *et al.* 2002).

A number of important genes have been isolated based on comparative genomics. An *O. sativa* EST with a sequence nearly identical to that of the *Arabidopsis GAI* (gibberellin insensitive) gene was used to investigate homologues in wheat and maize. The proteins encoded by wheat *Rht-1* and maize *d8* are closely related to the *Arabidopsis* GAI protein, and experimental data indicate that they are functional orthologues (Peng *et al.* 1999). This demonstrates the distinguished function of the EST database for establishing the relationship between *Arabidopsis* genes and cereal crops homologues. Recently, *ghd7* was characterized from an elite *O. sativa* hybrid and was found to encode a CTT protein (Xue *et al.* 2008) that is homologous to the conserved domain in

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*For correspondence. E-mail: yuanbeauty@mail.hzau.edu.cn.

Arabidopsis CO that promotes flowering during long days (Robert *et al.* 1998).

Rice and oilseed, respectively, are the first and the fifth largest cultivated crops in China; high seed yield is one of the most important breeding objectives for both crops. As a model plant, *O. sativa* genome has been sequenced, and its functional genomics has been extensively analysed. Compared to *O. sativa*, much less information is available on *B. napus*, and no information is available on homologous genome sequences between the two species. Coding genes of *Arabidopsis* and *O. sativa* are homologous, and extensive co-linear and highly similar gene sequences exist between *B. napus* and *Arabidopsis* (Cavell *et al.* 1998; van Dodeweerd *et al.* 1999). These similarities indicate the possibility of efficiently investigating nonannotated *B. napus* genes by directly using the *O. sativa* functional genomics or by using *Arabidopsis* as a bridge.

In this report, we used the sequences of functional markers in QTL intervals of yield-related traits in *B. napus* to search for homologous genes from *O. sativa*. We compared their functions with *B. napus*, and detected linkage between homologous genes and QTL of yield-related traits by silico mapping and population mapping in *O. sativa*. Our results revealed that *B. napus* and *O. sativa* shared homologous sequences of genes with similar functions, as well as consistent linkage relationships between genes and agronomic traits.

Materials and methods

Plant material

Functional markers (Li *et al.* 2006) were analysed between the *B. napus* lines S-1300 (a Chinese, semi-winter, selfin-compatible line) and Eagle (a spring-type, European line). A 184-plant $F_{2:3}$ population produced from a S-1300 × Eagle cross was used for QTL identification (Li *et al.* 2007). An *O. sativa* near-isogenic line of 186 plants resulting from a Teqing × Zhenxian97 cross were used for QTL location of homologues (Liu *et al.* 2010).

PCR system and sequence validation

PCR was performed in 20-μL reaction containing 50 ng genomic DNA, 1 unit *Taq* polymerase (MBI Fermentas, Vilnius, Lithuania), 2 μL 10× *Taq* buffer with $(NH_4)_2SO_4$, 2 mM $MgCl_2$, 0.2 mM dNTP mix (Sangon, Shanghai, China), and 0.5 μM of each primer. PCR conditions consisted of an initial denaturation for 4 min at 94°C; 30 cycles of 45 s at 94°C, 45 s at the annealing temperature, and 60 s at 72°C; with a final extension of 10 min at 72°C. The SSCP (single-strand conformation polymorphism) fragments were excised from nondenaturing acrylamide gel and incubated in 20 μL TE (10 mM Tris, 1 mM EDTA, pH 8.0) for 10 min at 95°C. After centrifugation, 2 μL of supernatant was used as a template for PCR amplification using the same primers and reaction conditions described above. PCR products were size

separated by 1.2% agarose gel electrophoresis and detected by staining with ethidium bromide.

The expected band was excised from agarose gels and the DNA fragment was purified using the UNIQ-10 column Gel Recovery kit (Sangon, Shanghai, China). Subsequently, each fragment was ligated into the pMD18-T vector (TaKaRa, Dalian, China) and screened for positive transformed clones using M13 universal primers. The clones were sequenced and compared with publicly available EST sequences, which were then used to manually design the functional markers using the SEQMAN application of the DNASTAR software suite (Windows v5.0.2; DNASTAR, Madison, USA).

Comparison of sequences and yield-related QTL between *B. napus* and *O. sativa*

The $F_{2:3}$ population lines of *B. napus*, along with the parental plants, were planted in two test locations (Jingmen and Wuhan) in China, with a randomized complete block design with two replications. Twelve yield-related agronomic traits were evaluated, including plant height (PH), height of primary effective branch (HPB), length of main inflorescence (LMI), effective length of main inflorescence (ELMI), number of siliques on main inflorescence (SMI), silique density on main inflorescence (SDMI), number of first branches (FB), number of siliques on first branches (SFB), number of siliques per plant (SP), number of seeds per silique (SS), 1000-seed weight (SW), and yield per plant (YP). Yield-related QTL were analysed on the basis of linkage mapping (Li *et al*. 2006, 2007).

Homologous *O. sativa* sequences were filtered using the BLASTx search tool (http://blast.ncbi.nlm.nih.gov/Blast.cgi), referring to the publicly available *B. napus* sequences. The threshold value was set to $E \le 10^{-10}$ and the highest scoring sequence of *O. sativa* was confirmed as the homologue. The *O. sativa* homologues were located in relevant chromosomes and we identified yield-related QTL in the vicinity of these genes using the Gramene website (www.gramene.org). The concerned yield-related traits of *O. sativa* were as follows: plant height (PH), culm thickness (CT), tiller number (TN), panicle length (PL), panicle number (PN), panicle weight (PW), number of primary branches (PB), secondary rachis branches (SRB), spikelets per panicle (SPP), spikelet fertility (SF), grains per spike (GPS), 1000-grain weight (GW), grain yield per plant (GYP), and biological yield (BY). We determined the orientation of the *O. sativa* yield-related QTL that harboured homologues, and compared them to the QTL of *B. napus*.

Synchronously, the near-isogenic lines of *O. sativa*, derived from a single-seed descendent of a cross between Teqing and Zhenshan97 (Liu *et al.* 2010), were planted in 2005 and 2006 rice-growing seasons in Wuhan, China. Field experiments were carried out following a randomized complete block design with two replicates, and 10 plants from each plot were harvested to score seed yield-related traits (Liu *et al.* 2010).

Results

Validation of functional markers in B. napus

We previously screened differential *B. napus* gene expression between a hybrid and its parents using IntelliGene II *Arabidopsis* CHIP1 (DXO121; Takara, Dalian, China) (Shen *et al.* 2006). We developed 177 functional markers showing polymorphisms between S-1300 and Eagle lines (Li *et al.* 2006); 108 that presented clear bands were chosen

to validate differential expression genes in *B. napus*. These 108 functional markers were sequenced in either S-1300 or Eagle, and were compared with the publicly available sequences used to design primers; 42 functional markers were identical to the expected sequences, 61 sequences had 1–3-bp insertions/deletions (indels) or repeats, and sequencing failed for the remaining five markers. These results showed that functional primers could amplify the source sequences (see table 1 in electronic supplementary material

Table 1. Homologous sequences by silico mapping and their function in *O. sativa.*

Symbol	*A. thaliana*	*B. napus*	*O. sativa*	Chromosome*	Function description
ABC1	AT1G79600	CD813230	XP_474059	4	ABC1 family
ACT2	AT5G09810	AI352754	NP_001051086	3	Actin 1, interaction with myosin
ANL2[a]	AT4G00730	CD822199	BAD29470	2	GL2-type homeobox genes
APL[a]	AT4G39210	CD827309	AC007858	5	ADP-glucose pyrophosphorylase
APOC[a]	AT5G66530	CD815825	XP_450550	9	Aposory-associated protein C-like
APRR2[a]	AT4G18020	CD821312	EAY89091	3	Hypothetical protein
AT03[b]	AT3G56940	CB686353	NP_913010	1	Unnamed protein product
ATHA	AT4G39350	CD831246	NP_001059487	7	Cellulose synthase-7
ATHB	AT5G05170	CD837508	NP_001059162	7	Cellulose synthase-4
ATPS	AT4G14680	U68218	NP_001051234	3	ATP sulphurylase
AUXDR[b]	AT3G15450	CD839494	CAJ86257	4	Unkown protein
AUXR[a]	AT3G03850	CD840488	XP_479809	8	Hypothetical protein
BGAL9	AT2G32810	CD822546	ABA97653	12	Galactose binding lectin domain containing protein
BKCOAS[a]	AT5G04530	CD813605	NP_001064831	10	Naringenin-chalcone synthase family protein
BSPR[b]	AT4G18890	CD818227	NP_913207	1	Unknown protein
C2H2T	AT3G62240	CD827449	AAS98500	5	Putative zinc-finger protein
CAS1[a]	AT2G07050	CD828014	NP_001045848	2	Cycloartenol synthase
CDKC	AT5G64960	CD814110	NP_914221	1	Cell division cycle 2-like protein kinase 5
CHS	AT5G13930	AF076334	CAA61955	11	Naringenin-chalcone synthase
CPS[a]	U11034	AF258249	NP_001052171	4	Copalyl diphosphate synthetase
CYPRT[a]	AT3G45310	CD825388	BAD38077	9	Putative oryzain gamma chain precursor
CYSD2	AT5G28020	CD823095	NP_914407	1	Putative plastidic cysteine synthase 1
DEAD[a]	AT5G11200	CD836516	BAD88053	1	Putative HLA-B associated transcript 1
DNAPL	AT1G67320	CD826774	NP_001059432	7	DNA primase, large subunit family
EIF-4F	AT5G57870	CD825242	XP_473052	4	Eukaryotic initiation factor 4G (eIF4G)
FBS	AT1G43670	U20179	BAD81916	1	Fructose-1,6-bisphosphatase
FERRITN	AT5G01600	CD820594	NP_001065936	12	Ferritin 1, chloroplast precursor
GAPA	AT3G26650	CB686102	XP_472744	4	Glyceraldehyde-3-phosphate dehydrogenase
GCIP1	AT2G16860	CD830043	BAD54053	6	GCIP-interacting family protein-like
GTL	AT1G33240	CD826243	NP_922337	10	Putative transcription factor
IRONT[a]	AT5G24380	CD832837	NP_001053450	4	Oligopeptide transporter OPT superfamily protein
KEMP	AT1G72250	CD835629	ABA99856	12	Kinesin motor protein, putative
KRCP[a]	AT5G48180	CD830343	NP_001062670	9	Galactose oxidase, central domain containing protein
LADC	AT5G21160	CD825067	NP_001042674	1	RNA-binding protein Lupus La domain containing protein
LHCB4[a]	AT3G08940	CB686060	XP_507368	7	Chlorophyll A–B binding protein
NAM	AT3G10480	CD837251	NP_001062518	8	No apical meristem (NAM) protein domain containing protein
OHP2[a]	AT1G34000	CD828875	NP_917460	1	Hypothetical protein
OMET	AT1G21130	CD814524	XP_480185	8	Putative Caffeic acid 3-O-methyltransferase

Table 1 (*contd*).

Symbol	*A. thaliana*	*B. napus*	*O. sativa*	Chromosome[*]	Function description
P450	AT3G14690	CD815555	NP_917788	7	Putative cytochrome P450
PAP	AT2G35490	CD834713	NP_922856	10	Putative plastid-lipid associated protein
PTPTP	AT5G46110	CB686190	NP_001055001	5	Triose phosphate/phosphate translocator, chloroplast precursor (CTPT)
PTS	AT4G39280	CD815241	ABB47547	10	Phenylalanyl-tRNA synthetase, alpha subunit, putative
RabGAP[a]	AT5G41940	CD823463	NP_922353	10	Similar to GTPase activating protein
RPPOB	AT3G09200	CD815196	XP_479931	8	60S acidic ribosomal protein P0
RPSaA	AT1G72370	CD813694	XP_479167	7	Putative 40S ribosomal protein
SCPS	AT5G20280	CD813732	NP_001061495	8	Sucrose–phosphate synthase 2
SCPT	AT3G48780	CD815627	NP_001067972	11	Serine palmitoyltransferase
SOUL	AT3G10130	CD815508	BAD29282	2	SOUL heme-binding family protein
SRC[a]	AT4G30610	CD831657	XP_550207	1	Putative carboxypeptidase D
SUC1	X75365	AY190281	NP_001048591	2	Sucrose transporter
THRX	AT1G76080	CB686095	NP_001059627	7	Thioredoxin-related domain containing protein
UXS	AT3G53520	CD831259	BAB84333	1	UDP-glucuronic acid decarboxylase
VHSD	AT1G21380	CD814345	NP_001046532	2	VHS domain-containing protein

[a]Different functions between *O. sativa* and *A. thaliana*. [b]Unknown function in *O. sativa*.
[*]Gene location in *O. sativa*.

at http://www.ias.ac.in/jgenet), and therefore the functional markers could be used to amplify publicly available gene sequences from *B. napus*.

Comparing homologous sequences of O. sativa and B. napus

Forty functional genes were found to be linked with *B. napus* agronomic traits QTL in our previous results. In total, 55 publicly available *B. napus* genes were used to screen for *O. sativa* homologues, including the 40 functional genes and 15 genes located outside of QTL intervals. Initially, *O. sativa* homologues were searched using the BLASTn search tool (http://blast.ncbi.nlm.nih.gov/Blast.cgi); however, homologous sequences were not obtained by this method. Homologous genes were subsequently filtered with the BLASTx search tool (http://blast.ncbi.nlm.nih.gov/Blast.cgi). With this method, homologous genes in *O. sativa* were found for 53 *B. napus* genes (table 1); two *B. napus* genes did not have any homologous *O. sativa* sequences. Of the homologous genes, 34 had consistent function between *O. sativa* and *Arabidopsis*, 16 genes had different functions between the two species, and three genes had not been annotated in *O. sativa*.

Comparison of yield-related QTL between O. sativa and B. napus

Yield-related QTL located near 40 *B. napus* genes were identified in an $F_{2:3}$ population. Using the Gramene website tool (http://www.gramene.org), we searched for and determined the physical location and yield-related QTL surrounding 40 homologous *O. sativa* genes by silico mapping. In total, 37 homologous genes were located in the QTL intervals, which primarily involved panicle and grain traits (table 2).

Based on the conservation of EST and genes between these two species, yield-related QTL were compared between *O. sativa* and *B. napus*. In summary, a total of 37 *O. sativa* and *B. napus* homologues were located in similar yield-related QTL. Among these homologues, five genes (*ATHB*, *C2H2T*, *CHS*, *KEMP*, and *RPSaA*) were located in a yield per plant QTL in both species, the *BKCOAS* gene was located in a plant height QTL, and the *C2H2T* gene was situated in QTL of yield per plant and 1000-seed (grain) weight. The *VHSD* gene was located in *B. napus* QTL of yield per plant, plant height, number of siliques per plant, number of siliques on main inflorescence, and number of first branches, and in the *O. sativa* QTL of grain yield per plant, plant height, panicle number, secondary rachis branches, and spikelets per panicle. These results indicated that homologous genes likely have same function and control similar traits between *O. sativa* and *B. napus*.

In order to validate the locations of homologous genes on the genetic map, we chose the most similar sequences between *B. napus* and *O. sativa*, and developed 21 arbitrary degenerate (AD) primers to map them using near-isogenic line populations of *O. sativa*. Ten of these primers presented with polymorphism in the *O. sativa* parents, generating 12 polymorphic bands. Six markers, originated from *CDKC*, *IRONT*, *OHP2*, *RPPOB*, *GTL*, and *GCIP1*, could orientate to *O. sativa* chromosome (figure 1). Two markers (*CDKC* and *GTL*) mapped to the same location compared with silico mapping, at chromosomes 1 and 12, respectively. Yield-related QTL were also compared between *O. sativa* and *B. napus*. *BnCDKC* was mapped to linkage 7 of *B. napus* situated in the SP and SFB QTL regions; *OsCDKC* was mapped to the SPP and GW QTL regions of chromosome 1 in *O. sativa* (figure 2).

Table 2. QTL for yield-related traits around the homologous sequences.

Symbol	Yield-related QTL in *B. napus*	Yield-related QTL in *O. sativa*
ACT2	ELMI	GW,CT,GPS,PH,YP
ANL2	SFB	GW,CT,GPS,PN,PH,SW,GYP
APL	SFB	PB
APRR2	SFB,SP	GYP,PL,TN
AT103	LMI,SDMI,FB	PL,PN,PW,PH,SRB,SPP,TN
ATHA	SFB,SP	GW,GYP,PL,PH,SPP,TN,GYP
ATHB	YP	GW,BY,GPS,GYP,PN,TN
ATPS	FB,YP	GW,CT,GPS,PH,SRB
AUXDR	HPB	PH,CT,GPS,GYP,TN,SPP
AUXR	HPB,SDMI,FB,SFB,YP,SP	CT
BKCOAS	PH,SMI	PH,CT,PN,PL
C2H2T	SW,LMI,ELMI,SDMI,HPB,YP	GW,GYP,GPS,PW
CDKC	SP,SFB	BY,PL,PN,PH,GPS,TN
CHS	YP,SFB	GW,BY,CT,GPS,PN,PW,HP,GYP
CPS	LMI,ELMI,SFB,SP	PL,TN
CYPRT	SDMI	PL,TN,PH,TN,GPS
DNAPL	PH,SDMI,SS	GW,GPS,TN,GYP,PN
EIF-4F	HPB,SMI,SDMI,SFB,YP	CT,PL,PH,PN
FERRIT	LMI,ELMI	GW,SPP,GYP
GAPA	SMI	CT,PL,PH,PN
GCIP1	FB	GW,GYP,GPS,PH,GPS,TN
IRONT	SMI,YP,SP	CT,PL,PH,SPP,TN,BY
KEMP	HPB,LMI,ELMI,SFB,YP	TN,PH,PN,GW,GYP
KRCP	FB	PL,PN
LADC	PH,LMI,ELMI	PL,PN,PW
NAM	PH,LMI,EMLI	CT,PN,TN
OMET	SFB	TN
PTPTP	SMI,SW	PL,PN,SRB,TN
RabGAP	PH,SW,HPB,LMI,SDMI	CT,GW,PN
RPPOB	YP	GW
RPSaA	HPB,LMI,ELMI,SDMI,SFB,SW,YP	PH,PN,GYP,PW,SF,PB
SCPS	SDMI	GW,PL,PN,PH,TN
SCPT	ELMI	GW,CT,GYP,PN,PH,
SUC	SFB,SS,SW,HPB,LMI,ELMI,SFB	PH,TN,GW
THRX	LMI	PL
WXS	SS	GW,BY,CT,GYP,PL,PN,PH
VHSD	PH,SFB,SS,SMI,FB,YP,SP	GYP,PL,PN,PH,SRB
CAS1	FB	–
LD	SS	–
RRM	LMI,ELMI,SDMI,FB,SW	–

QTL in *B. napus*: PH, plant height; HPB, height of primary effective branch; LMI, length of main inflorescence; ELMI, effective length of main inflorescence; SMI, number of siliques on main inflorescence; SDMI, silique density on main inflorescence; FB, number of first branches; SFB, number of siliques on first branches; SP, number of siliques per plant; SS, number of seeds per silique; SW, 1000-seed weight; YP, yield per plant.
QTL in *O. stativa*: PH, plant height; CT, culm thickness; TN, tiller number; PL, panicle length; PN, panicle number; PW, panicle weight; PB, number of primary branches; SRB, secondary rachis branches; SPP, spikelets per panicle; SF, spikelet fertility; GPS, grains per spike; GW, 1000-grain weight; GYP, grain yield per plant; BY, biological yield.

Discussion

In the present study, we performed a comparative mapping between *O. sativa*, a major cereal crop and model species for monocots, and *B. napus*, one of the most important oil crops for dicots. Previous detailed analysis showed that the *Brassica* and *Arabidopsis* genera are closely related (Parkin *et al.* 2005), with significant synteny and about 85% exon

sequence similarity (Cavell *et al.* 1998). Further, *O. sativa* and *Arabidopsis* share 80.6% homologous genes and 80.1% protein homology (Cavell *et al.* 1998). Given these relationships, it seems possible to efficiently perform comparative genomics studies between *O. sativa* and *B. napus* using the EST database of *Arabidopsis* as a bridge (Liang *et al.* 2009). Genes from different species containing same motifs usually present similar or consistent functions, such as the
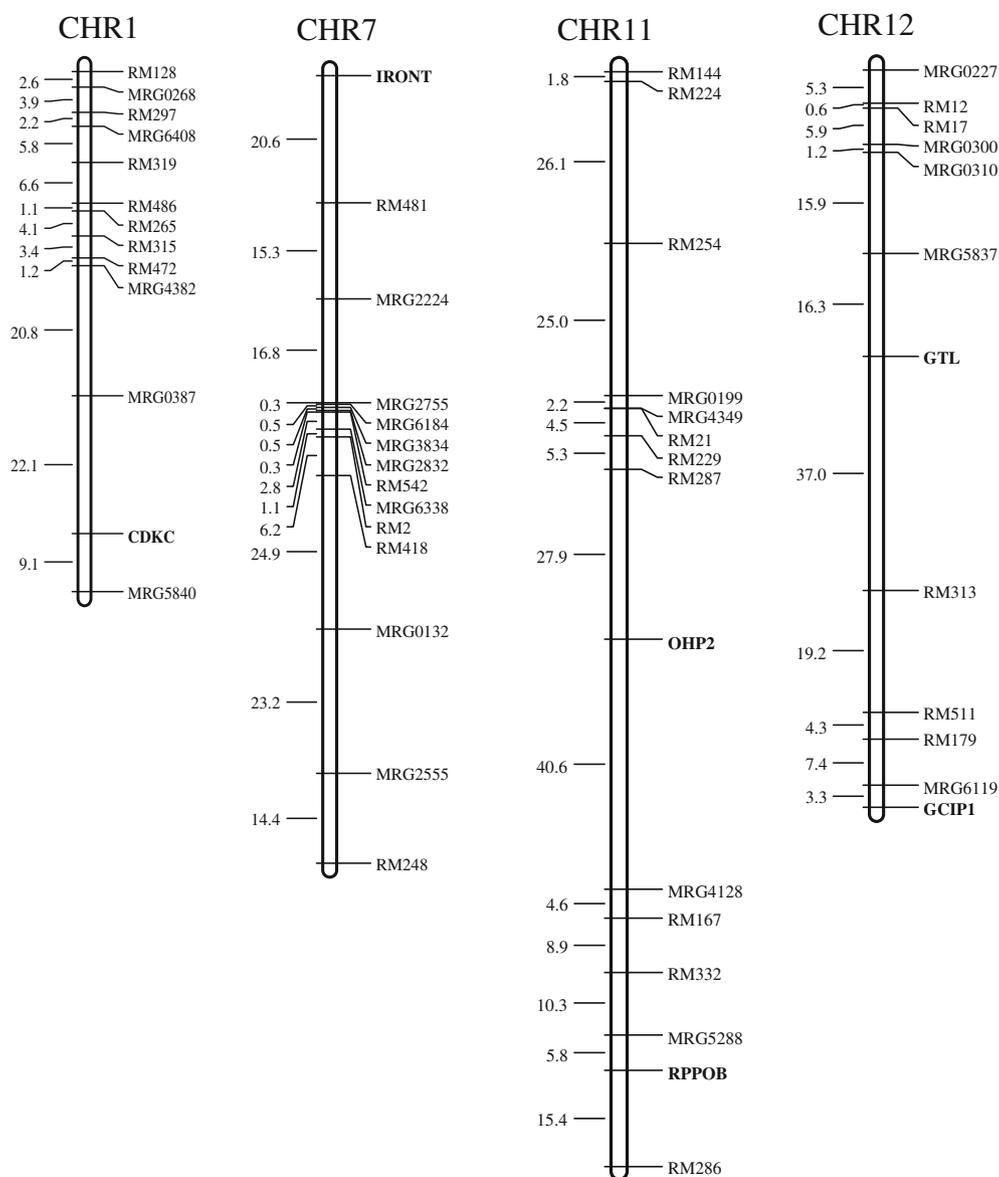
Figure 1. Homologues located in four molecular linkages of the *Oryza sativa* near-isogenic line population. For each group, genetic distance in cM is shown on the left, marker number is presented on the right, and bold markers indicate rice homologous genes.

MADS-box-containing *flowering locus* genes and the OSR domain-harbouring grain shape genes (Reeves *et al.* 2007; Mao *et al.* 2010). Amino acid identification is more effective for cross-species comparison, as indicated in our study by the identification of 53 homologous genes across distantly related species by BLASTx rather than BLASTn.

The strategy of using cross-species domain conservation has been applied in both closely and distantly related species. In *Brassica* research, the *Arabidopsis* EST database is usually used to predict genes with higher sensitivity (>70–80% at gene CDS level). The related species EST data can also be used as cross-species gene prediction; *Arabidopsis* genes were used to predict maize EST function (Brendel *et al.*

2002) and a number of rice genes were separated based on *Arabidopsis* gene information (Xue *et al.* 2008; Bi *et al.* 2011; Gao *et al.* 2011). In the present study, our screening detected 53 homologous genes between *B. napus* and *O. sativa*, 64.2% of which had the same function in both species (table 1), indicating considerable consistency between gene functions of *B. napus* and *O. sativa*.

Both oilseed and rice are globally important crops, and have similar yield component factors. Oilseed plant yield is multiplicatively determined by the following three component traits: number of siliques per plant, number of seeds per silique, and seed weight. Rice plant yield is also determined by three component traits: number of panicles per
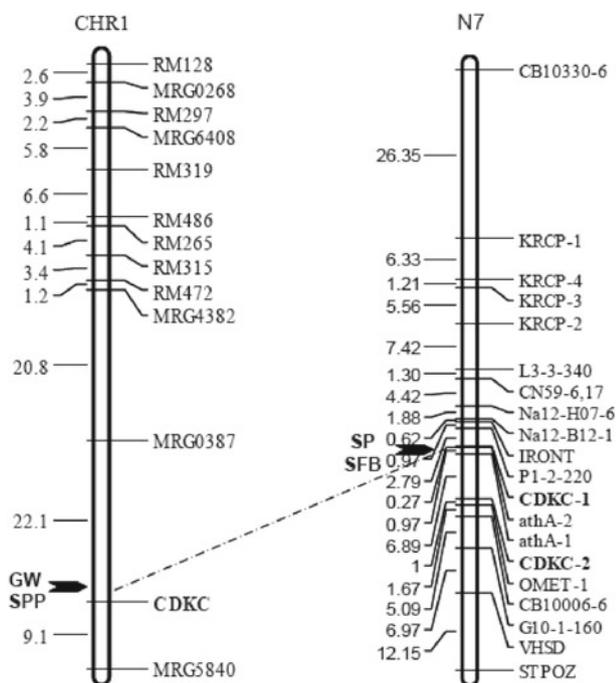
Figure 2. Comparative mapping of *CDKC* between *O. sativa* and *B. napus*. *OsCDKC* is located on chromosome 1 of *O. sativa* and lies around the QTL intervals of GW and SPP. SP, number of siliques per plant; SFB, number of siliques on first branches; SPP, spikelets per panicle; GW, 1000-grain weight.

plant, number of grains per panicle, and grain weight. The rice plant *O. sativa* has been adopted as an important model system for plant science research and has been used for many functional genomics studies (Xing and Zhang 2010); thus, the agronomic traits of *O. sativa* have been greatly advanced and informational resources are conveniently available for this species. In the present study, we conducted preliminary investigation, comparing the locations of QTL between *O. sativa* and *B. napus*, using same function homologues as a criterion. Homologous genes were found to be located around similar QTL intervals, such as plant height, seed/grain weight, branch/tiller number, and silique/panicle traits. These results indicate the possibility for studying complex agronomic traits in *B. napus* according to those in *O. sativa*.

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