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ORIGINAL PAPER

Identification of a major QTL for silique length and seed weight in oilseed rape (*Brassica napus* L.)

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Abstract Silique length (SL) and seed weight (SW) are two important yield-related traits controlled by quantitative trait loci (QTL) in oilseed rape (*Brassica napus* L.). The genetic bases underlying these two traits are largely unknown at present. In this study, we conducted QTL analyses for SL and SW using 186 recombinant inbred lines (RILs) derived from a cross between S1, an EMS mutant with extremely long siliques and large seeds, and S2, an inbred line with regular silique length and seed size. RILs were grown in Wuhan in the 2008/09 (SS09) and 2009/10 (SS10) growing seasons, and mean SL and SW for each line were investigated. Ten non-redundant QTL were identified for SL. Of these, a major QTL, *cqSLA9*, consistently explained as much as 53.4% of SL variation across environments. The others are minor QTL and individually explained less than 10% of the SL variation. Nine non-redundant QTL were identified for SW. Of which, one major QTL, *cqSWA9*, explained as much as 28.2% of the total SW variation in the SS09 and SS10 environments. In addition, three additive by additive interactions with small effects were detected for SL, and no interactions were detected for SW. Interestingly, the two major QTL, *cqSLA9* for SL and *cqSWA9* for SW colocalized in the same chromosomal region and were integrated into a unique QTL, *uqA9*. The S1 allele at this locus increases both SL and SW, suggesting that *uqA9* has pleiotropic effects on both SL and SW. The existence and effect of *uqA9* was confirmed in genetically different RILs derived from the cross between S1 and No2127, a resynthesized DH line having regular silique length and seed size. Individuals in one residual heterozygous line for *cqSLA9* showed significant difference in silique length. The results in this study revealed that silique length in the S1 mutant is mainly controlled by the *cqSLA9* locus, which will be suitable for fine mapping and marker-assisted selection in rapeseed breeding for high yield.

Introduction

Oilseed rape (*Brassica napus* L.) is one of the most important oil crops worldwide. It has become the world's third leading source for both vegetable oil and oil meal (Snowdon et al. 2007). In China, oilseed rape is the most important oil crop and provides about 50% of the vegetable oil supply (Yin et al. 2009). Rapeseed meal is a high-protein animal feed, competitive with soybean meal. In addition, rapeseed oil has been used as biofuel, a desirable alternative for fossil oil worldwide. However, due to the rapid increase of world population and the consumption for biofuel in recent years, the production of oilseed rape is unable to satisfy the global demand. Development of high yield varieties is one of the most important ways to solve the shortage of rapeseed supply.

Yield is one of the most important and complex traits in crops. Seed yield per unit area in oilseed rape is usually considered a function of siliques. Siliques per plant (SPP), seeds per silique (SPS) and seed weight (SW) are three important components which determine seed yield per plant (Chen et al. 2007). Thus, rapeseed yield is directly and indirectly influenced by silique or silique-related traits. As one of the most important organs, siliques play a paramount role in the survival of a species. Siliques serve to

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encapsulate the developing seeds and protect them from biotic and abiotic stresses (Bennett et al. 2011). It has been proven that silique is not only an important source organ which provides photosynthates to the developing seeds contained therein (Allen et al. 1971), but also an important sink organ which intakes the carbohydrates synthesized in the vegetative parts of the plant such as leaves and stem (Schiltz et al. 2005). Physiological analyses indicated that approximately 30% of dry matter of siliques and seeds contained in siliques being attributed to assimilates produced by siliques (Brar and Thies 1977; Samizadeh et al. 2007). In addition, it had been revealed that signals originating from the silique act to coordinate seed filling and regulate the reallocation of reserves (Bennett et al. 2011). The length of siliques is significantly correlated with SPS and SW variation and independent with SPP (Chay and Thurling 1989; Lebowitz 1989; Diepenbrock 2000). In general, longer siliques produce more seeds and greater seed weight than short siliques (Chay and Thurling 1989; Lebowitz 1989; Özer et al. 1999). Therefore, long silique has been characterized as a desirable trait in rapeseed breeding programs (Chay and Thurling 1989; Aytac and Kinaci 2009), suggesting that it could be used as an indirect indicator of selection in breeding for high seed yield. In addition, the development of siliques also influences the oil and protein content (Bennett et al. 2011). Seed weight, determined by seed size, is one of the most important traits in *Brassica* species, because it was not only positively correlated with plant productivity (Clarke and Simpson 1978; Butruille et al. 1999; Shi et al. 2009), but was also positively correlated with oil content (Singh et al. 1996). Given their importance in determining grain yield and quality in oilseed rape, therefore, understanding the genetic bases of SL and SW is of great importance for yield improvement in rapeseed breeding.

With the advent of DNA molecular markers, the genetic bases of yield and its related traits have been extensively analyzed in rice, maize, barley, sorghum and other crops and a great achievement had been gained (Bernardo 2008; Takeda and Matsuoka 2008). In rapeseed, a large number of quantitative trait loci (QTL) controlling yield and yield components have been genetically mapped (Quijada et al. 2006; Udall et al. 2006; Chen et al. 2007; Shi et al. 2009; Basunanda et al. 2010). SL and SW are the two important silique-related traits and are quantitatively inherited (Chen et al. 2007; Fan et al. 2010). Genetic analysis indicated that SL is stably inherited with a broad-sense heritability of more than 90% (Chen et al. 2007), while SW was more sensitive to environments, the broad-sense heritability was ranging from 46 to 91% (Radoev et al. 2008; Shi et al. 2009; Basunanda et al. 2010; Fan et al. 2010). More than 20 QTL distributed on 15 chromosomes of *B. napus* were identified for SL, and individual QTL explained 5.5–25.3% of the phenotypic variation (Udall et al. 2006; Chen et al. 2007; Zhang et al. 2011). The genetic basis of SW is more complicated. More than 80 QTL distributed on all the 19 chromosomes of the *B. napus* genome had been identified for SW and individual QTL explained 2.0–23.0% of the phenotypic variation (Quijada et al. 2006; Udall et al. 2006; Shi et al. 2009; Basunanda et al. 2010; Fan et al. 2010; Zhang et al. 2011). At the present time, little is known about the control of SL and SW in rapeseed at the molecular level, and no gene controlling SL and SW has yet been cloned because of the complexity of the rapeseed genome, namely the abundance of homologous regions derived from genome duplication (Parkin et al. 2005).

The primary objectives of this study were to identify QTL controlling SL and SW using RILs derived from crosses among varieties with very different SL and SW, and to evaluate the effects of reproducible QTL. We identified a major QTL on chromosome A9, which pleiotropically controls both SL and SW. The effect of this QTL was validated in a different set of RILs and a residual heterozygous line.

Materials and methods

Plant material

Two semi-winter type inbred lines, S1 and S2, and one spring type double-haploid (DH) line, No2127, were selected for dissecting the genetic bases of SL and SW in *B. napus*. S1 is a DH line with long siliques and large seeds regenerated from EMS (ethylmethane sulfonate)-treated microspore cultures of a breeding line 92-B10 with regular silique length and seed weight (Shi et al. 1995), and has been self-pollinated for more than 10 generations. S2 is an inbred line with regular silique length and seed size. The DH line No2127 has regular silique length and seed size, which is derived from an interspecific cross between a light brown seeded *B. alboglabra* (a form of *B. oleracea*) and a yellow-seeded *B. rapa* var. trilocularis (yellow sarson) (Chen et al. 1988), and has been self-pollinated for at least 20 generations. Two F_2 populations were developed from the crosses between S1 and S2 and between No2127 and S1, respectively. The two F_2 populations were selfed to F_6 and F_4 generations, respectively, using the single seed descendant (SSD) method. The RILs derived from S1 and S2 were named as the SS population, and the RILs derived from No2127 and S1 were named as the NS population.

Experiment design and traits measurement

The 186 SS RILs were grown using a randomized complete block design with three replications in the experimental

farm at Huazhong Agricultural University, Wuhan, China, in the 2008/09 (SS09) and 2009/10 (SS10) winter–spring growing seasons. The 192 NS RILs were planted in the summer of 2010 (NS10) in Lanzhou, China, and in the 2010/11 (NS11) winter-spring growing season in Wuhan using a randomized complete block design with one replication. Each line was grown in a plot with two rows and 10–12 plants in each row, with a distance of 20 cm between plants within each row and 30 cm between rows. The SS RILs were used to mapping QTL for SL and SW and NS RILs were used for validation of QTL.

The average length of 10 well-developed siliques (not including the beak) from the middle of the main inflorescence was used to represent the SL for each plant, and the average silique length of 10 plants from the center of each plot in each replicate was used to represent SL for each RIL. The average weight of 1,000 well-filled open-pollinated seeds was measured to represent SW for each plant, and the average seed weight of 10 plants was measured to represent for SW of each RIL. The phenotypic data for SL were surveyed in the SS RILs in the SS09 and SS10 environments and in the NS RILs in the NS10 and NS11 environments, and the phenotypic data for SW were surveyed in the SS RILs in the SS09 and SS10 environments and in the NS RILs in the NS11 environments.

Polymorphism screening and map construction

Genomic DNA was extracted from leaf tissues of 10 plants within each RIL in the SS and NS populations, respectively. Two groups of SSR markers from different sources were used for polymorphism screening. The first group of SSR markers was selected from previously published papers (Lagercrantz et al. 1993; Kresovich et al. 1995; Szewc-McFadden et al. 1996; Uzunova and Ecke 1999; Lowe et al. 2002; Lowe et al. 2004; Piquemal et al. 2005; Suwabe et al. 2006; Choi et al. 2007; Hasan et al. 2008; http://brassica.agr.gc.ca/index_e.shtml; http://ukcrop.net/ace/search/BrassicaDB; http://www.osbornlab.agronomy.wisc.edu/research/maps/ssrs.html). The second group of SSR markers was developed from publicly available *Brassica* sequences by our laboratory (Cheng et al. 2009; Fan et al. 2010; Li et al. 2011; Xu et al. 2010; Wang et al. 2011). PCR reactions were performed as previously described (Cheng et al. 2009). SSR markers with clear polymorphisms between S1 and S2 and between No2127 and S1 were selected to genotype the SS and NS RILs for the construction of linkage maps. For markers detected at more than one polymorphism locus, the loci were named by including an alphabetic letter to distinguish them. The Pearson's Chi-square test was used to assess the goodness-of-fit to the expected 1:1 segregation ratio for each locus ($P < 0.05$).

Genetic linkage maps were constructed using the Joinmap 3.0 software (Van Ooijen and Voorrips 2001) with the maximum recombinant frequency of 0.4 and minimum logarithm of odds (LOD) scores of 3.0. The recombinant ratio was converted to genetic distance by Kossambi map function (Kosambi 1944). Linkage groups were aligned with the reference linkage maps based on the common markers (Lowe et al. 2004; Piquemal et al. 2005; Chen et al. 2007; Suwabe et al. 2008; Cheng et al. 2009), and the linkage groups from the A and C genome were designated A1–A10 and C1–C9, respectively.

Genetic analysis and QTL mapping

Phenotypic correlation coefficients between SL and SW were calculated using the procedure CORR in the SAS software (SAS Institute Inc. 2000), and the genetic correlation coefficient was calculated as described by Kashiani and Saleh (2010). The broad-sense heritability was calculated as: $H_B^2 = \sigma_g^2/(\sigma_g^2 + \sigma_{gl}^2/n + \sigma_e^2/nr)$, where σ_g^2 is genotypic variance, σ_{gl}^2 is the variance due to genotype by environment interaction, σ_e^2 is error variance, n is the number of environments, and r is the number of replications. Year-location combinations were treated as different environments. Components of variance (σ_g^2, σ_{gl}^2 and σ_e^2) were estimated using the mixed linear models (MIXED) procedure in the SAS software (SAS Institute Inc. 2000) with environment considered as a random effect.

QTL analyses for SL and SW were performed separately in each population and environment. The software Windows QTL Cartographer 2.5 (http://statgen.ncsu.edu/qtlcart/WQTLCart.htm) was used to conduct the composite interval mapping (CIM) (Zeng 1994). The forward regression method based on model 6 (standard model) in the software was selected to get cofactors; the number of control markers, windows size and walk speed was set to 5, 10 and 2 cM, respectively. To determine a significant QTL, the marker distance was set to 5 cM. LOD threshold value of 3.5 was used to declare the presence of a QTL. In addition, QTL that repeatedly detected at a LOD value below the threshold but higher than 2.5 were also considered as a significant QTL. The nomenclature of QTL was similar to that described by Udall et al. (2006) with the codes 1 and 2 representing for QTL detected in the SS RILs in the SS09 and SS10 environments, and 3 and 4 for the QTL detected in the NS RILs in the NS10 and NS11 environments, respectively. If two or more QTL for the same trait were identified in the same linkage group in the same environment, an alphabetical letter is added at the end of the QTL. For example, if two QTL for SL were detected on C3 in SS09 environment, they were named as *qSLC3.1*a and *qSLC3.1b*, respectively.

QTL repeatedly detected in different environments and located in the same chromosomal region, either for the

same or different traits, were subjected to meta-analysis to estimate the position of the underlying meta-QTL (Goffinet and Gerber 2000). Meta-analyses were conducted using the BioMercator 2.1 software (Arcade et al. 2004). QTL repeatedly identified for the same trait in different environments were first integrated into consensus QTL, which were then designated with initial letters "*cq*" followed by trait names and linkage groups. An alphabetical letter is added if more than one consensus QTL is located on the same linkage group. Then the QTL for different traits were further integrated into unique QTL and designated with initial letters "*uq*" followed by the linkage groups.

Analysis of digenic interaction effect

Genome-wide digenic interactions in the SS09 and SS10 environments were analyzed in the SS RILs using the software QTLNetwork 2.0 (Yang et al. 2008) based on the mixed-model based composite interval mapping (MCIM) method. The critical *F* value was estimated using 1,000 times of permutation test and the detected epistatic effect were estimated by a full-QTL model (Yang et al. 2008). The significant level for the experimental-wise type I error, testing windows, filtration windows and walk speed were set to 0.05, 10, 10 and 1 cM, respectively.

Results

Trait performance of the S1 mutant

In both winter/spring and summer growing environments, S1 showed extremely long siliques and large seeds. The average silique length of S1 was 10.7 ± 0.61 cm, which was significantly longer than that of S2 and No2127 (4.04 ± 0.37 and 4.40 ± 0.45 cm, respectively). In addition, the average seed weight of S1 was 4.66 ± 0.58 g, which was significantly higher than that of S2 and No2127 (3.36 ± 0.59 and 3.10 ± 0.27 g, respectively). Furthermore, the S1 mutant had an average seed number of 24.11 ± 1.89 per silique, while the S2 and No2127 had an average seed number of 15.64 ± 5.10 and 16.39 ± 4.01 per silique, respectively. However, the seed density of S1 was 2.30 ± 0.16 seeds/cm, which is significantly lower than that of S2 and No2127 (3.65 ± 1.01 and 3.75 ± 0.80 seeds/cm, respectively).

Phenotypic variation of the SL and SW

SL and SW were surveyed in the SS RILs in the SS09 and SS10 environments (Fig. 1). Both SL and SW showed a continuous distribution in the two environments, which suggested a quantitative inheritance pattern for both SL and SW. Two-way ANOVA of SL and SW across environments indicated that genotype of each RIL (G), growing environment (E) and genotype-environment interactions (G × E) had significant effects on both SL and SW (Table 1). However, the G × E effects were ignorable because they were minor when compared to the effects of genotypes and environments.

Correlation analyses were performed between SL and SW for SS RILs in each environment. The phenotypic correlation coefficients between SL and SW were 0.45 and 0.40 ($P < 0.01$), and the genetic correlation coefficients were 0.47 and 0.42 ($P < 0.01$) in the SS09 and SS10 environments, respectively, indicating that SL is significantly correlated with SW and the correlation is mainly determined by genetic factors. The positive correlation suggested that longer silique could produce larger seeds. The broad-sense heritability (H_B^2) was also calculated for SL and SW (Table 1). SL has an H_B^2 of 96.4%, suggesting that it is stable and insensitive to the environment impact. While the SW has an H_B^2 of 69.6%, indicating that the SW is relatively sensitive and plastic to environment variation.

Marker polymorphism and genetic map construction

A total of 1,773 SSR markers were screened for polymorphisms between the parental lines S1 and S2. Of which, 387 (21.8%) showed polymorphism. From which, 300 markers that showed stable amplification and clear polymorphic bands were selected to genotype the SS RILs and generated 326 loci. A genetic map containing 289 loci was constructed, which covered a total length of 1,381.3 cM of the *B. napus* genome and has an average distance of 4.8 cM between adjacent loci. All the loci were assigned to the 19 *B. napus* linkage groups (LGs), which were designated as A1–A10 corresponding to the A genome and C1–C9 corresponding to the C genome by aligning the markers to the previously published linkage maps (Lowe et al. 2004; Piquemal et al. 2005; Suwabe et al. 2006; Cheng et al. 2009; Li et al. 2011; Xu et al. 2010). Segregation distortion of each locus was estimated by the goodness-of-fit test, 77 loci (26.6%) showed distorted segregation ($P < 0.05$). The distorted segregation markers are unevenly distributed in the genome and clustered on A1, A4, A9, C3 and C9, which is a common phenomenon in *B. napus* (Chen et al. 2007; Li et al. 2011). None or only a few distorted markers located on A2, A8, A10, C4, C5, C7 and C8.

The segmental components derived from each parent were analyzed for each RIL. The genotype frequency showed a normal distribution. In individual lines, 18–68% of the genome was derived from the S1 chromosomal segments and 24–68% of the genome was derived from the S2 chromosomal segments. On average, about 45% of the genomic segments originated from S1 and 46% from S2, which correspond to the expected 1:1 ratio by a Chi-square test.

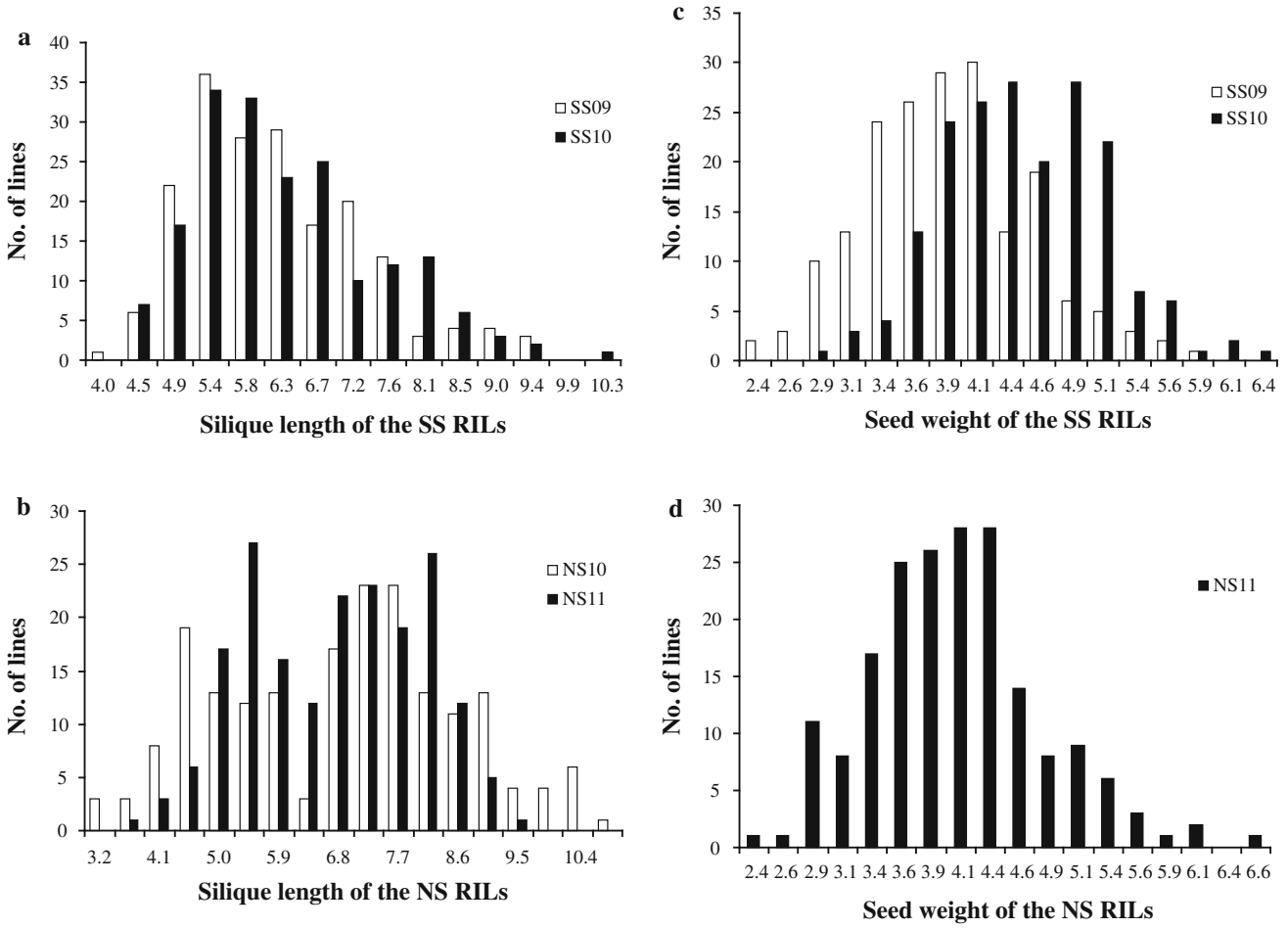

Fig. 1 Distribution of silique length and seed weight. **a** distribution of silique length of the 186 SS RILs grown in the SS09 and SS10 environments in Wuhan; **b** distribution of silique length of the 192 NS RILs grown in the NS10 environment in Lanzhou and in the NS11 environment in Wuhan; **c** distribution of seed weight of SS RILs in SS09 and SS10 environments in Wuhan; **d** distribution of seed weight of NS RILs in NS11 environment in Wuhan

Table 1 Two-way ANOVA and the broad-sense heritability (H_B^2) of silique length and seed weight in the SS RILs grown in the SS09 and SS10 environments

Trait	Source	Sum of square	*df*	Mean square	*F* value	*P*	H_B^2 (%)
SL	Genotype	1371.51	185	7.41	51.94	0.00	96.4
	Environment	4.63	1	4.63	32.41	0.00	
	Genotype × environment	48.93	185	0.26	1.85	0.00	
	Error	106.20	744	0.14			
SW	Genotype	409.60	185	2.21	26.60	0.00	69.6
	Environment	92.70	1	92.70	1113.51	0.00	
	Genotype × environment	34.95	185	0.19	2.27	0.00	
	Error	61.94	744	0.08			

QTL mapping for SL and SW

Genome-wide QTL analysis was performed separately using the phenotypic data of SL obtained from the SS RILs grown in the SS09 and SS10 environments. Eight QTL, *qSLA1.1*, *qSLA6.1*, *qSLA7.1*, *qSLA9.1*, *qSLC2.1a*, *qSLC2.1b*, *qSLC3.1a* and *qSLC3.1b* that located on six LGs (A1, A6, A7, A9, C2 and C3) were detected in the SS09 environment. In the SS10 environment, eight QTL, *qSLA2.2*, *qSLA6.2*, *qSLA7.2*, *qSLA9.2*, *qSLC2.2*, *qSLC3.2a*,

qSLC3.2b and *qSLC4.2* that located on seven LGs (A2, A6, A7, A9, C2, C3 and C4) were detected (Table 2; Fig. 2). To examine if the QTL detected in two environments are reproducible, we compared the confidence intervals of QTL located on the same LGs and found that the confidence intervals of *qSLA9.1* and *qSLA9.2*, *qSLA6.1* and *qSLA6.2*, *qSLA7.1* and *qSLA7.2*, *qSLC2.1b* and *qSLC2.2*, *qSLC3.1a* and *qSLC3.2a*, and *qSLC3.1b* and *qSLC3.2b* overlapped each other, respectively. Meta-QTL analyses integrated these reproducible QTL into six consensus QTL, which were thus renamed as *cqSLA9*, *cqSLA6*, *cqSLA7*, *cqSLC2*, *cqSLC3a* and *cqSLC3b*, respectively (Table 4). *qSLA1.1* and *qSLC2.1a* were only detected in the SS09 environment, and *qSLA2.2* and *qSLC4.2* were only detected in the SS10 environment. The S1 alleles in all the QTL increase SL. Individual QTL explained 1.9–53.4% of the phenotypic variation of SL. The six consensus QTL collectively explained as much as 73.1% of the SL variation in the SS09 and SS10 environments. Of these consensus QTL, five minor QTL (*cqSLA6*, *cqSLA7*, *cqSLC2*, *cqSLC3a*, *cqSLC3b*) each explained less than 10% of the phenotypic variation in each environment. It is worth noting that *cqSLA9* located at the position of 92.2 cM on A9 had the largest LOD scores (36.5 and 39.5) (Table 2) and explained as much as 53.4% of the SL variation in the SS09 and SS10 environments, suggesting that it is a major QTL for SL. To evaluate the effect of *cqSLA9*, RILs were classified into two groups (AA and BB) based on the genotype of the most tightly linked marker Na10-B07. Lines carrying the S1 alleles (AA) had an average SL of 7.25 ± 0.92 and 7.49 ± 0.91 cm in the SS09 and SS10 environments, respectively, which are significantly ($P < 0.01$) longer than those carrying the S2 alleles (BB) with an average SL of 5.51 ± 0.59 and 5.61 ± 0.59 cm (Table 5).

QTL analysis was also conducted for SW in the SS RILs grown in the SS09 and SS10 environments. Seven QTL, *qSWA1.1a*, *qSWA1.1b*, *qSWA6.1*, *qSWA7.1*, *qSWA9.1*, *qSWC9.1a* and *qSWC9.1b* that located on five LGs (A1, A6, A7, A9 and C9), were detected in the SS09 environment. Seven QTL, *qSWA1.2a*, *qSWA1.2b*, *qSWA6.2*, *qSWA9.2a*, *qSWA9.2b*, *qSWA9.2c* and *qSWC9.2* that located on four LGs (A1, A6, A9 and C9), were detected in the SS10 environment (Table 3; Fig. 2). The S1 alleles at *qSWA6.1*, *qSWA9.1*, *qSWC9.1b*, *qSWA6.2*, *qSWA9.2c* and *qSWC9.2* increase seed weight, while the S2 alleles at the other loci increase seed weight. The confidence intervals of *qSWA1.1a*, *qSWA1.1b*, *qSWA6.1*, *qSWA9.1* and *qSWC9.1b* overlapped with that of *qSWA1.2a*, *qSWA1.2b*, *qSWA6.2*, *qSWA9.2c* and *qSWC9.2*, respectively. Meta-QTL analyses integrated these five pairs of QTL into five consensus QTL (Table 4), which were renamed as *cqSWA1a*, *cqSWA1b*, *cqSWA6*, *cqSWA9* and *cqSWC9*. The other four QTL were only detected in one of the environments. These consensus QTL individually explained 4.2–28.2% of phenotypic variation, and collectively explained 50.1 and 57.3% of the SW variation in two environments, respectively. Of these consensus QTL, four minor QTL (*cqSWA1a*, *cqSWA1b*, *cqSWA6* and *cqSWC9*) each explained an average phenotypic variation of about 7% across environments. Interestingly, the major consensus QTL *cqSWA9* explained 28.2 and 21.7% of the total phenotypic variation of seed weight in the SS09 and SS10 environments, respectively. The effect of *cqSWA9* on SW was also evaluated by classifying RILs into two groups (AA and BB) based on the genotype of the most tightly linked marker Na10-B07. Lines carrying the S1 alleles (AA) had an average SW of 4.32 ± 0.60 and 4.80 ± 0.62 g in the SS09 and SS10 environments, respectively, which are significantly ($P < 0.01$) longer than those carrying the S2 alleles (BB) with an average SL of 3.61 ± 0.51 and 4.26 ± 0.53 g (Table 5).

Correlated trait pairs tended to share a higher proportion of QTL than uncorrelated traits did (Latta and Gardner 2007). The positive correlation between SL and SW prompted us to examine if the confidence intervals of QTL for SL and SW overlapped each other. Interestingly, the confidence intervals of *cqSLA9* and *cqSWA9*, the two major QTL for SL and SW, respectively, overlapped each other in the two environments (Fig. 2). In addition, the confidence intervals of *cqSLA6* and *cqSWA6* also overlapped each other (Fig. 2). Meta-QTL analyses integrated these overlapped QTL into two unique QTL, *uqA6* and *uqA9*, indicating that these two QTL have pleiotropic effects on both SL and SW. Moreover, the S1 alleles at these two unique QTL increase SL and SW, which is consistent with the positive correlation between these two traits.

Epistasis analysis for SL and SW

Genome-wide digenic interactions were analyzed in the SS RILs in the SS09 and SS10 environments to identify potential epistasis for SL and SW. Three pairs of additive by additive interactions (A × A) involving six loci distributed on 6 LGs (A6, A7, A9, C2, C3 and C7) were identified to have significant effects on SL. Two of the interactions occurred between two pairs of QTL, *cqSLA6* and *cqSLC3a*, and *cqSLA9* and *cqSLC2*. The remaining interaction involved a pair of non-QTL loci located in the intervals of CNU331-BrGMS337 on A7 and BRAS019-BoGMS710b on C7. These interactions in total explained 2.4% of the phenotypic variation, suggesting that the effects of digenic interactions are very low and SL is primarily controlled by additive effect. No digenic interaction was detected for SW, which is consistent with previous result (Fan et al. 2010), and suggested that the variation of SW is primarily controlled by additive effect.

Table 2 QTL for silique length detected in the SS and NS RILs across four environments

Environment	Population	LG	QTL	Pos.	CI	LOD	A	R^2 (%)
SS09	SS	A1	*qSLA1.1*	60.3	52.1–66.0	3.6	0.25	3.6
		A6	*qSLA6.1*	23.7	13.8–33.3	3.0	0.19	2.8
		A7	*qSLA7.1*	37.2	33.5–40.3	3.5	0.21	3.3
		A9	*qSLA9.1*	92.2	92.0–95.8	36.5	0.82	46.8
		C2	*qSLC2.1a*	12.1	9.8–16.1	3.4	0.16	1.9
			qSLC2.1b	30.9	23.6–36.6	7.3	0.32	7.3
		C3	*qSLC3.1a*	60.1	50.6–66.5	2.8	0.18	2.3
			qSLC3.1b	98.5	96.5–100.5	3.5	0.22	3.4
SS10	SS	A2	*qSLA2.2*	72.8	66.1–80.8	4.5	0.30	5.9
		A6	*qSLA6.2*	21.7	17.0–26.5	5.0	0.25	4.1
		A7	*qSLA7.2*	39.5	35.0–41.5	4.0	0.23	3.8
		A9	*qSLA9.2*	92.2	91.9–94.1	39.5	0.92	53.4
		C2	*qSLC2.2*	30.9	22.0–36.7	4.8	0.25	4.2
		C3	*qSLC3.2a*	58.1	54.9–62.8	6.3	0.28	5.4
			qSLC3.2b	98.5	84.8–100.5	2.5	0.19	2.3
		C4	*qSLC4.2*	17.9	10.9–22.8	4.4	0.23	3.7
NS10	NS	A9	*qSLA9.3*	70.7	68.2–79.8	32.6	1.56	65.6
NS11	NS	A9	*qSLA9.4*	70.7	69.7–72.7	29.7	1.11	55.0

QTL were designated as "*q*" for QTL followed by the initial of trait name, LG and numerical code of trial (trial code 1 and 2 after the dot represent for QTL detected in the SS RILs in the SS09 and SS10 environments, respectively, and 3 and 4 for the QTL detected in the NS RILs in the NS10 and NS11 environments, respectively). An alphabetical letter is added at the end of the QTL when two or more QTL for the same trait are identified on the same LG in the same environment

LG the linkage group the QTL located in, *Pos.* map position of the peak of the LOD score, *CI* confidence interval, flanking marker nearest the 95% confidence interval was used for significant QTL, *A* additive effect, R^2 percentage of the phenotypic variation explained by the QTL

Validation of the major QTL for SL and SW on A9 in different genetic background

To examine the stability of the unique QTL (*uqA9*) on A9, a new set of RILs (NS RILs) derived from the cross between No2127 and S1 was used to detect QTL for SL and SW in the NS10 and NS11 environments. SL showed a similar continuous bimodal distribution in the NS10 and NS11 environments and SW showed a unimodal distribution (Fig. 1). The phenotypic correlation coefficient between SL and SW is 0.47 ($P < 0.05$). A genetic linkage map of A9 covered a total length of 86.0 cM was constructed using 13 SSR markers as used in the SS RILs and BnaNZDH population (Cheng et al. 2009) (Fig. 2). Two QTL, *qSLA9.3* and *qSLA9.4* located at 70.7 cM on the linkage map were detected in the NS10 and NS11 environments, respectively, and explained 65.6 and 55.0% of the SL variation, respectively (Table 2). Based on the confidence intervals of the QTL, we declared that *qSLA9.3* and *qSLA9.4* corresponded to *uqA9* mentioned above. Two QTL for SW were detected on A9 in the NS11 environment. Of which, *qSWA9.4b* explained 14.9% of the SW variation (Table 3; Fig. 2). The S1 alleles increase both SL and SW. The confidence intervals of *qSLA9.3*, *qSLA9.4* and *qSWA9.4b* also overlapped each other, and overlapped with that of *uqA9*, further indicating that *uqA9* has pleiotropic effects on both SL and SW.

Validation of *uqA9* for SL using residual heterozygous line

To further examine the effect of *uqA9* on SL under identical genetic background, we screened the SS RILs to identify residual heterozygous lines (RHLs) (Yamanaka et al. 2005) that segregate at the *uqA9* region. One recombinant inbred line, L133, was identified to be heterozygous in the genomic region from BrGMS1093 to BnEMS300 that encompassed the *uqA9* locus but homozygous for the other QTL except for the minor QTL *qSLA1.1*. Eight individuals in L133 were genotyped using nine co-dominant markers (BrGMS1093, BrGMS1037, BrGMS1039, BrGMS1041, Na10-B07, BnEMS799a, BoGMS116, sN11670 and BnEMS300) that flanked the target region of *uqA9* (Fig. 3). Of these, four individuals were homozygous for the S1 allele and the others were homozygous for the S2 allele based on the closest marker Na10-B07. The S1 homozygous allele individuals had SL longer than 9.06 cm, and the S2 homozygous individuals had SL shorter than 7.78 cm (Fig. 3). From the eight individuals, one S1 homozygous individual, L133-2, and two S2 homozygous individuals,

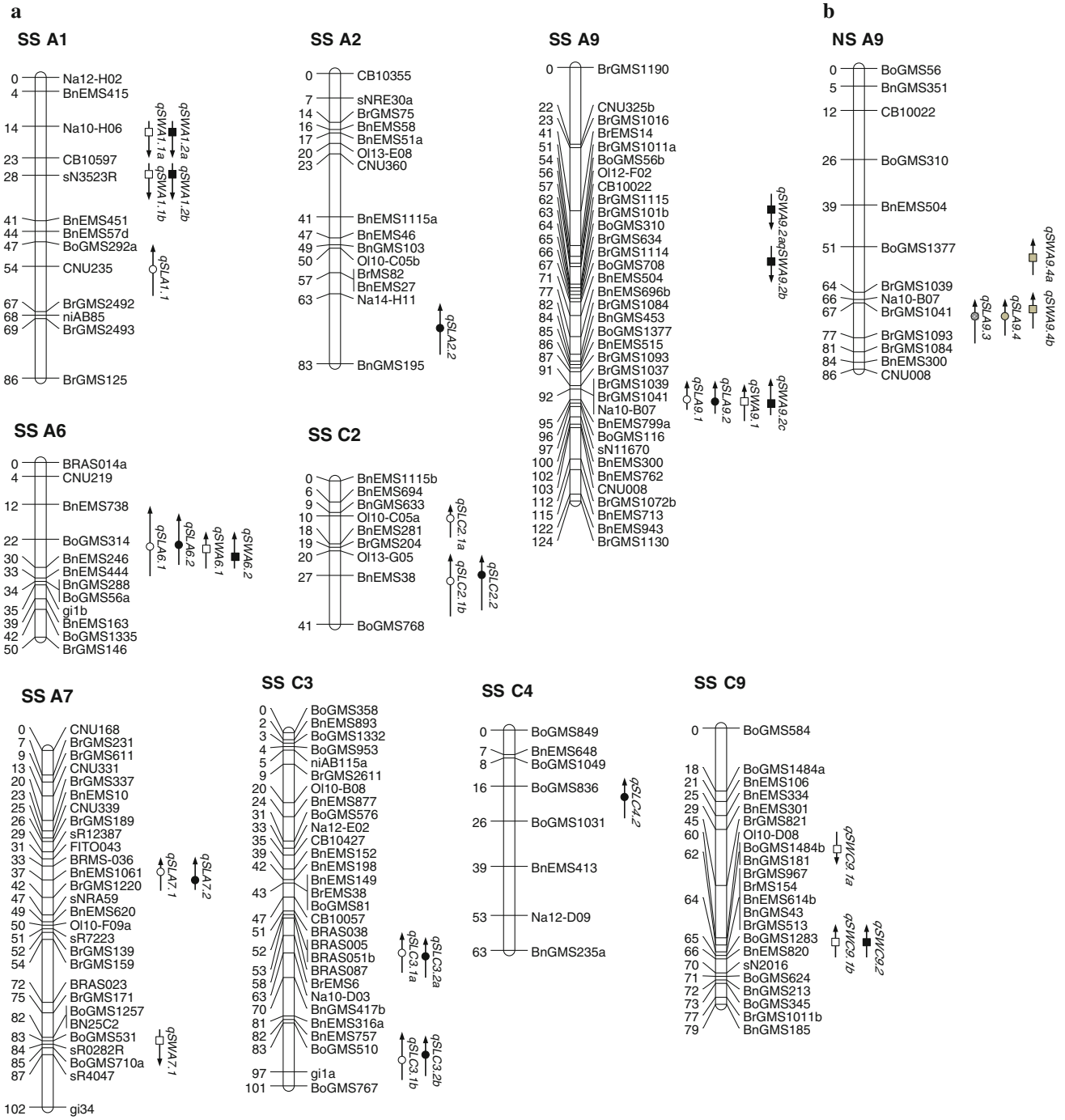

Fig. 2 Map locations of QTL for silique length and seed weight. **a** QTL for silique length and seed weight detected in the SS RILs grown in the SS09 and SS10 environments; **b** QTL for silique length and seed weight on the A9 linkage group detected in the NS RILs grown in the NS10 and NS11 environments. The *arrow* to the right of the linkage groups denotes the confidence intervals for the QTL. The symbols of *circles* and *squares* represent the positions of the QTL peak. *Blank*, *black*, *hatched black* and *gray* circles indicate QTL for silique length detected in the SS09, SS10, NS10 and NS11 environments, respectively. *Blank*, *black* and *gray squares* indicate QTL for seed weight detected in the SS09, SS10 and NS11 environments, respectively. *Upward arrows* indicate S1 as the donor of the increasing allele; *downward arrows* indicate S2 as the donor of the increasing allele

L133-3 and L133-7, were selfed to further examine the silique length in their progenies. The L133-2 progenies had an average silique length of 9.98 ± 0.65 cm, which is significantly longer than that of the L133-3 and L133-7 progenies (6.79 ± 0.40 cm), which further demonstrated that *uqA9* significantly increase silique length.

Table 3 QTL for seed weight in the SS and NS RILs across three environments

Environment	Population	LG	QTL	Pos.	CI	LOD	A	R^2 (%)
SS09	SS	A1	*qSWA1.1a*	19.5	13.8–23.4	4.4	−0.19	7.2
			qSWA1.1b	28.4	23.4–33	4.6	−0.15	5.0
		A6	*qSWA6.1*	25.7	15.7–35.9	3.8	0.14	4.2
		A7	*qSWA7.1*	83.3	77.2–84.2	4.1	−0.16	5.6
		A9	*qSWA9.1*	91.8	91.1–93.6	17.1	0.37	28.2
		C9	*qSWC9.1a*	37.0	26.1–56.3	3.6	−0.08	1.3
			qSWC9.1b	65.5	64.7–69.5	4.0	0.17	5.5
SS10	SS	A1	*qSWA1.2a*	19.5	14.4–23.4	4.4	−0.19	7.7
			qSWA1.2b	27.4	26.1–34.1	5.4	−0.18	7.3
		A6	*qSWA6.2*	29.7	23.8–33.3	6.5	0.21	10.7
		A9	*qSWA9.2a*	44.8	42.8–50.9	4.1	−0.15	4.9
			qSWA9.2b	56.5	52.6–59.3	4.6	−0.14	4.0
			qSWA9.2c	91.5	90–93.3	12.0	0.33	21.7
		C9	*qSWC9.2*	65.5	65.2–70.5	6.1	0.29	9.9
NS11	NS	A9	*qSWA9.4a*	53.2	51.2–54.8	3.6	0.21	4.5
			qSWA9.4b	66.7	65.6–71.5	6.9	0.35	14.9

Footnotes are the same as Table 2

Table 4 Consensus QTL for silique length and seed weight obtained by meta-analysis in all the environments in the SS RILs

Trait	Consensus QTL	LG	Position	CI
SL	*cqSLA6*	A6	22.1	17.8–26.4
	cqSLA7	A7	38.4	36.1–40.8
	cqSLA9	A9	92.2	91.3–93.2
	cqSLC2	C2	30.9	26.0–35.8
	cqSLC3a	C3	58.5	55.0–62.0
	cqSLC3b	C3	98.5	96.6–100.5
SW	*cqSWA1a*	A1	19.5	16.2–22.8
	cqSWA1b	A1	27.8	24.8–30.9
	cqSWA6	A6	29.0	24.7–33.3
	cqSWA9	A9	92.0	90.7–92.7
	cqSWC9	C9	65.5	63.7–67.3

LG linkage group, *CI* confidence interval for the consensus QTL

Table 5 Effects of the major QTL *uqA9* on SL and SW in the SS RILs grown in the SS09 and SS10 environments

Environment	Na10-B07	N[a]	SL (cm)			SW (g)		
			Range	Mean ± SD	P[b]	Range	Mean ± SD	P[b]
SS09	AA	66	5.18–9.62	7.25 ± 0.92	0.00	3.20–5.81	4.32 ± 0.60	0.00
	BB	104	3.96–7.23	5.51 ± 0.59		2.39–4.99	3.61 ± 0.51	
SS10	AA	66	5.74–10.15	7.49 ± 0.91	0.00	3.11–6.42	4.80 ± 0.62	0.00
	BB	104	4.27–7.86	5.61 ± 0.59		2.94–5.50	4.26 ± 0.53	

[a] Number of RILs for each group (AA and BB) classified according to the genotype of the marker Na10-B07 that closely linked to the major QTL *uqA9*

[b] P values obtained by t test between groups

Discussion

Silique length and seed weight are two important yield-related traits. The genetic bases of these two traits are largely unclear at present. In this study, we dissected the genetic bases of SL and SW using RILs derived from S1 and S2, two parents with significant differences of silique length and seed size. In this population, SL showed a high broad-sense heritability, which is consistent with previous results (Chen et al. 2007), suggesting that SL is stable across environments. QTL analysis identified ten non-redundant QTL for SL, and six consensus QTL were reproducibly identified across the two environments. It is worth noting that *cqSLA9* explained as much as 53% of the SL variation in both environments. The positive allele at *cqSLA9* is from S1, an EMS mutant with extraordinary long siliques mutagenized from a short silique inbred line 92-B10 (Shi et al. 1995). Previous studies did not identify QTL for SL in this chromosomal region (Chen et al. 2007; Zhang et al. 2011), suggesting that the S1 allele at *cqSLA9* is a novel mutation probably caused by the EMS mutagen in the process of microspore culture. In addition, nine non-redundant QTL were detected for SW from the same RILs, and five consensus QTL were reproducibly detected across environments. A major QTL, *cqSWA9*, explained more than 20% of the SW variation in each year. Meta-analysis integrated *cqSLA9* for SL and *cqSWA9* for SW into a single *uqA9* locus, which has pleiotropic effects on both SL and SW. The pleiotropy and position of *uqA9* was confirmed using RILs derived from S1 and No2127, a DH line with regular silique length and seed size. In addition to *uqA9*, another unique QTL, *uqA6*, was identified to pleiotropically control both SL and SW with a relatively small effect. The pleiotropic QTL genetically explained, at least partially, the phenotypic correlation between SL and SW.

Fine mapping and map-based cloning have been demonstrated to be one of the most efficient ways to dissect the genetic bases of quantitative traits and to identify genes underlying these traits (Takeda and Matsuoka 2008; Miura et al. 2011). QTL with large and stable effects on target traits were more suitable for fine mapping and map-based cloning. In general, most of the yield-related QTL cloned in crops so far can explain a large proportion of phenotypic variation and their effects are stable across environments (Bernardo 2008; Takeda and Matsuoka 2008; Xing and Zhang 2010). In oilseed rape, most of the QTL identified so far individually explained less than 10% of the phenotypic variation of SL and SW (Quijada et al. 2006; Udall et al. 2006; Chen et al. 2007; Shi et al. 2009). In this study, *uqA9* was confirmed to be a major QTL with an effect of over 50% on SL. To our knowledge, this is a QTL with the largest effect on SL identified in *B. napus* so far and is suitable for map-based cloning to uncover the molecular mechanisms of silique development.

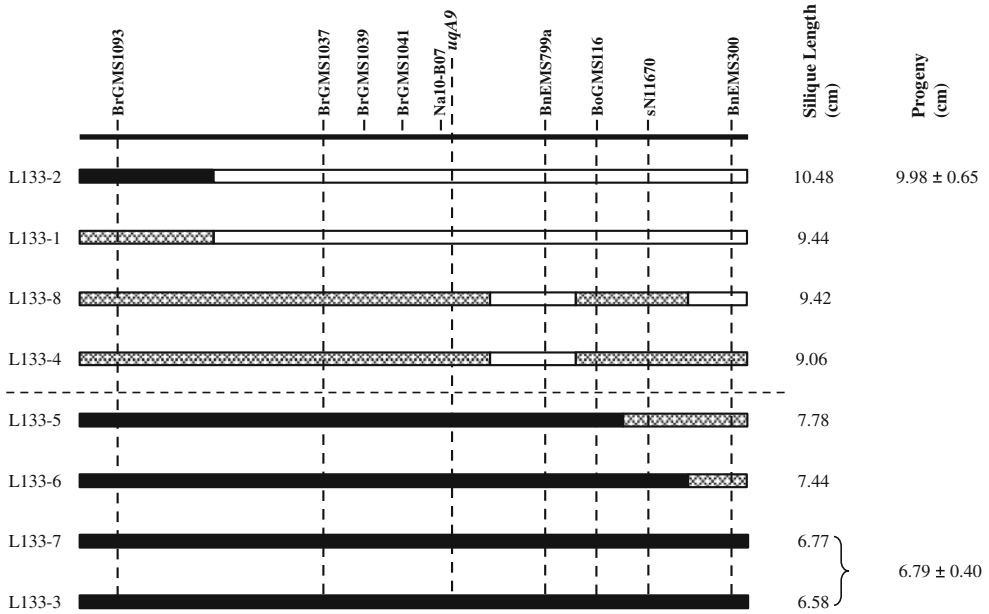

Fig. 3 Schematic chromosomal components of individuals in the L133 family revealed by SSR markers in the *uqA9* region. The individuals in L133 family were genotyped using nine co-dominance markers flanking *uqA9*. *Each bar* represents an independent individual. The average length of 10 well-developed siliques from the middle of the main inflorescence was used to represent the SL for each plant. *Hollow* bars indicate the S1 homozygous regions. *Solid* bars indicate the S2 homozygous regions, and the *hatched black* bars indicate the heterozygous regions. L133-2, L133-3 and L133-7 were selfed and the average silique lengths of their progenies were significantly different ($P < 0.01$)

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