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ORIGINAL PAPER

Mapping and validation of quantitative trait loci associated with wheat yellow mosaic bymovirus resistance in bread wheat

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Abstract Wheat yellow mosaic (WYM) caused by wheat yellow mosaic bymovirus (WYMV) has been growing as one of the most serious diseases affecting wheat production in China. In this study, the association of quantitative trait loci (QTLs) governing WYMV resistance with molecular markers was established using 164 recombinant inbred lines (RILs) derived from 'Xifeng Wheat' (highly resistant) × 'Zhen 9523' (highly susceptible). Phenotypic data of WYMV resistance of the RILs were collected from 4-year, two-location replicated field trials. A molecular marker-based linkage map, which was comprised of 273 non-redundant loci and represented all the 21 wheat chromosomes, was constructed with the JoinMap 4.0 software. Using the Windows QTL Cartographer V2.5 software, three QTLs associated with WYMV resistance, *QYm.njau-3B.1*, *QYm.njau-5A.1* and *QYm.njau-7B.1*, were detected on chromosomes 3BS, 5AL, and 7BS, respectively. The favorable allele effects were all contributed by 'Xifeng Wheat'. Among the three QTLs, *QYm.njau-3B.1* and *QYm.njau-5A.1* were detected in all the four trials and the overall mean, and could explain 3.3–10.2% and 25.9–53.7% of the phenotypic variation, respectively, while *QYm.njau-7B.1* was detected in one trial and the overall mean and explained 4.9 and 3.3% of the phenotypic variation, respectively. A large portion of the variability for WYMV response was explained by a major QTL, *QYm.njau-5A.1*. The relationship of the molecular markers linked with *QYm.njau-5A.1* and the WYMV resistance was further validated using a secondary F_2 population. The results showed that three markers, i.e., *Xwmc415.1*, *CINAU152*, and *CINAU153*, were closely linked to *QYm.njau-5A.1* with the genetic distances of 0.0, 0.0, and 0.1 cM, respectively, indicating they should be useful in marker-assisted selection (MAS) wheat breeding for WYMV resistance. A panel of germplasm collection consisting of 46 wheat varieties with known WYMV response phenotypes was further used to validate the presence and effects of *QYm.njau-5A.1* and the above three markers. It was found that *QYm.njau-5A.1* was present in 12 of the 34 WYMV-resistant varieties.

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Introduction

Wheat yellow mosaic bymovirus (WYMV) and wheat spindle streak mosaic bymovirus (WSSMV) are two closely related soil-borne bymovirus, which cause very similar symptoms and severely affect the production of bread

wheat. However, sequence data indicate that WYMV was a distinct species from WSSMV within the genus *Bymovirus* of the family *Potyviridae* (Clover and Henry 1999; Yu et al. 1999). WSSMV is mainly distributed in Europe and America, while WYMV is dominant in Asia, such as Japan and China. WYMV was first found in Japan in 1927 (Sawada 1927), and very similar disease was detected in Canada in the early 1960s (Slykhuis 1960). Since then, WYMV has been reported in different wheat growing areas worldwide. In China, WYMV is widespread in the winter wheat growing regions including Shanxi, Sichuan, Hubei, Shandong, Henan, Anhui, Jiangsu and Zhejiang Provinces and causes grain yield losses ranging from 20 to 70% in individual fields depending on the variety and severity of symptoms in plants (Liu et al. 2004, 2005b).

WYMV is often transmitted to the root of its hosts the soil-borne fungus vector, *Polymyxa graminis* (Inouye 1969). Thus, the soil with WYMV may preserve infectivity for many years. Delayed planting date and crop rotation may help reducing the infection and limiting the incidence of WYMV. However, rotations may reduce the population of *Polymyxa graminis* in the soil, but has difficulty in eliminating it. It has been reported that some fields without planting wheat for 10 years still harbor the bymovirus and its fungus vector (Ruan et al. 1991; Chen 2005). Therefore, the disease is best controlled by growing wheat varieties with WYMV resistance.

Although a number of wheat varieties with both high yield potential and high level of resistance to WYMV have been developed and released, the genetic and molecular mechanism underlying the WYMV resistance is still poorly understood. WYMV resistance in wheat was reported to be controlled by one to three genes (Qin et al. 1986; Liu et al. 2004) with one major gene being associated with homoeologous group 2 chromosome (Liu et al. 2005a, b; Nishio et al. 2010). However, due to the differences of plant materials and population types, the major genes were mapped to different chromosomes of homoeologous group 2, i.e., 2A and 2DL. In addition, due to the use of different standards of phenotypic evaluation and different molecular genetic maps, the marker intervals on chromosome 2DL were also not fully consistent.

The wheat variety, 'Xifeng Wheat', originally introduced from Japan into China in 1985, has high resistance against WYMV. Several new wheat varieties with high level of resistance to WYMV have been released using 'Xifeng Wheat' as breeding parents directly or indirectly in China (e.g., 'Ningmai 9', 'Ningmai 16' and 'Yangmai 18') (Qian et al. 1999; Yao et al. 2009; Zhang 2009). So far, results on the genetics of resistance to WYMV in 'Xifeng Wheat' have not yet been reported. In the present research, a recombinant inbred line (RIL) population derived from 'Xifeng Wheat' was developed and used to construct a molecular marker-based linkage map. The RIL population was evaluated for WYMV resistance in 4-year, two-location replicated field trials. QTLs responsible for WYMV resistance were identified, and the molecular markers flanked the major QTL were validated for their effectiveness in MAS of WYMV resistance in wheat breeding.

Materials and methods

Plant materials and field experimental design

A mapping population of 164 RILs was developed by a single-seed descent (SSD) method from a cross between the two elite winter varieties 'Xifeng Wheat' (highly resistant) and 'Zhen 9523' (highly susceptible). The F_6 lines, when all individuals of each line showed relatively uniform phenotype of agronomic traits, were used for evaluation of WYMV resistance.

The 164 RILs and their parents were grown and evaluated for resistance to WYMV. A randomized block design was used. In year 2007, the disease nursery for WYMV resistance evaluation was located in Maan County of Jiangsu Province [designated as trial E1 (F_6 population)]. In years 2008, 2009, and 2010, the disease nursery was located in the Institute of Agricultural Sciences in Lixiahe District of Jiangsu Province [designated as trials E2 ($F_{6:7}$), E3 ($F_{6:8}$) and E4 ($F_{6:9}$), respectively]. Both nurseries showed severe and uniform infection of WYMV. It was indicated by the fact that the highly susceptible parent 'Zhen 9523' showed 100% infection evenly without any additional artificial inoculation. Two replications were used for trials E1 and E2, and three replications were used for trials E3 and E4. For each trial, 20 seeds per plot were planted for each line in a 1.5-m row and spaced 0.25 m apart.

In order to validate the relationship of the molecular markers linked with the major QTL *QYm.njau-5A.1* and the WYMV resistance, a highly WYMV-resistant RIL (named as 'RILV-6'), which only carries the major QTL *QYm.njau-5A.1*, was selected for marker analysis and used to construct a secondary F_2 population by crossing with 'Zhen 9523'. The obtained 280 F_2 individuals and their derived 276 $F_{2:3}$ lines (Due to extremely severe WYMV damages, 4 of 77 susceptible F_2 individuals failed to produce any progeny) were evaluated for WYMV resistance.

A panel of germplasm collection consisting of 46 wheat varieties with known WYMV response phenotypes (data shown in Table S1) was used to further validate the presence and effects of *QYm.njau-5A.1* and its linked markers by associated analysis strategy and identify the distributions of different resistance loci in these wheat varieties.

WYMV resistance evaluation of the secondary F_2 population (Year 2010), the derived $F_{2:3}$ population (Year 2011), and the panel of germplasm collection (Year 2011)

were performed in the natural disease nursery of Institute of Agricultural Sciences in Lixiahe District of Jiangsu Province. A randomized block design and two replications were used for the $F_{2:3}$ population and the panel of germplasm collection. Twenty seeds per plot were planted for each material in a 1.5-m row and spaced 0.25 m apart.

All the materials were planted in late October each year, and were grown under normal field conditions with standard cultivation practice.

Evaluation of WYMV resistance

For the RIL population, the WYM responses were recorded three times in year 2007 (each on February 9th, 23rd, and March 6th), once in year 2008 (on March 6th), and twice in years 2009 (each on March 6th and 24th) and 2010 (each on February 25th and March 11th). WYM responses of the secondary F_2 population were recorded twice in year 2010 (each on February 25th and March 11th). WYM responses of the derived $F_{2:3}$ population and the panel of germplasm collection were recorded once in year 2011 (on March 9th). The infection types (ITs) were scored according to Liu et al. (2005b) with minor modification. A 0–5 scale was used to represent different ITs (Fig. 1), where

0 = no visible symptom;
1 = leaves showed light mosaic with no distinct paled streak spot;
2 = leaves showed light mosaic and distinct paled streak spot, but no dwarfing of plant;
3 = leaves showed both distinct mosaic and paled streak spots, infected leaf with >50% paled streak spots, diseased plant was lightly dwarfed with a few yellow mosaic leaves died, and the tillers dwarfed;
4 = leaves showed both serious mosaic and paled streak spots, infected leaf had >75% paled streak spots, infected plant dwarfed obviously, with its heart leaf distorted or curled and part of the infected leaves, and tillers died; and
5 = infected plant dwarfed seriously, most infected leaves and tillers or even the whole plant died.

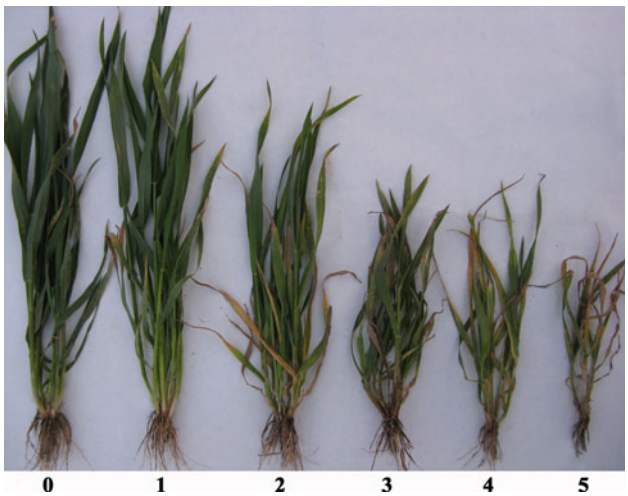

Fig. 1 Symptoms of the 0–5 scale individual plants caused by WYMV in the 'Xifeng Wheat × Zhen 9523' RIL population in nursery at trial E4 on March 11 in the year 2010

For the RIL population, all individual plants for each line were scored in all the four trials. For each line in each block, a disease index (DI) was calculated using the formula: $DI\ (\%) = \sum(DS \times N_i) \times 100/(5 \times N)$, where DS was a disease scale which represented an IT, N_i was the number of plants of the relevant DS, and N was the total number of plants observed per line. Then the mean of the DI for each line was calculated in each trial.

For the F_2 population, ITs were scored for all individuals. For the derived $F_{2:3}$ population and the panel of germplasm collection, ITs of all individual plants were scored and the mean of the ITs was calculated for each $F_{2:3}$ line or variety in each block, and then the overall mean of the ITs for each $F_{2:3}$ line or variety was calculated.

Data processing and statistical analysis

For each year, the phenotype data collected on the day, when all the tested materials showed the most typical WYMV symptoms, were chosen for QTL analysis or marker analysis, i.e., March 6th in years 2007, 2008 and 2009 and March 11th in year 2010 for the DI of the 164 RILs, March 11th in year 2010 for the ITs of the 280 F_2 individuals, and March 9th in year 2011 for the ITs of the derived $F_{2:3}$ lines and 46 wheat varieties.

All the phenotypic data for the WYM responses were calculated using the Statistical Analysis System version8.1 (SAS v8.1) (SAS Institute Inc, Raleigh, USA). For the RIL population, analyses of variance (ANOVA) for environment, genotype, and genotype by environment interaction effects were carried out using the PROC GLM; Variance components were estimated in a model using the PROC VARCOMP; and the broad-sense heritability (h^2) was calculated using the variance components. Pearson correlations among trials were calculated using the PROC CORR.

DNA extraction and molecular marker analysis

Genomic DNA was extracted using the sodium dodecyl sulfate (SDS) method according to Sharp et al. (1988) and Devos et al. (1992).

A total of 1,558 wheat genomic SSR, EST-SSR, and EST-STS primer pairs from different sources (Röder et al. 1998; Pestsova et al. 2000; Gupta and Roy 2002; Paillard et al. 2003; Somers et al. 2004; Song et al. 2005; Xue et al.

2008) were used to screen the polymorphisms between the two parents of the RIL population. In addition, 228 EST-STS primer pairs were designed using the online software Primer3 V0.4.0 (http://frodo.wi.mit.edu/primer3/) or ConservedPrimers 2.0 (http://probes.pw.usda.gov/ConservedPrimers/) according to the published sequences of wheat ESTs, which were cytogenetically mapped to specific deletion bins by Qi et al. (2004). All these primer pairs were synthesized by Shanghai Invitrogen Biotechnology Company Limited (the forward and reverse primers of EST-STS marker *CINAU152* are 5′-CTTGGTTTCGG TGTGTGTAT-3′ and 5′-CCATTCTGATGGAAGCAAT A-3′, and the forward and reverse primers of EST-STS marker *CINAU153* are 5′-GCAAAAATGTAATGCAC CAT-3′ and 5′-GTTGCTATTGCCTTCAGTTG-3′). Those markers, which were polymorphic between the two parents, were further used for genotyping of the RILs. The six markers linked with the major QTL detected in the RIL population, which were polymorphic between the 'RILV-6' and 'Zhen 9523', were further used for amplification in the F_2 population, and the three markers flanked the major QTL were further used for amplification in the panel of germplasm collection.

PCR amplification was carried out in a 10-μl reaction containing 40 ng genomic DNA, 2 μM each of the primer pairs, 2.5 mM each dNTPs, 2.5 mM $MgCl_2$, 1× PCR buffer (10 mM Tris–HCl, pH 8.5, 50 mM KCl), and 0.5 U *Taq* DNA polymerase with a PTC-200 thermal cycler (BioRad, Hercules, CA, USA). Amplification was conducted at 94°C for 3 min, followed by 35 cycles at 94°C for 30 s, annealing of different primers at 50, 55, or 60°C for 50 s at a ramp rate of 0.5°C/s, 72°C for 1 min 10 s, and a final extension at 72°C for 10 min. PCR products were resolved in 8% non-denaturing poly-acrylamide gels (Acr:Bis = 19:1 or 39:1) and were visualized by silver staining (Bassam and Gresshoff 2007).

Linkage map construction

Linkage analysis was performed using the JoinMap 4.0 software (Van Ooijen 2006). The Kosambi mapping function (Kosambi 1944) with a minimum LOD (Logarithm of the odds) threshold of 3.0 and a linkage threshold significance of $P = 0.05$ was applied to transform the recombination frequencies into the genetic distances in centiMorgans. Linkage groups were assigned to chromosomes based on the published genetic maps of wheat (available at GrainGenes website at http://wheat.pw.usda.gov).

QTL analysis and estimation of epistatic interactions of the RIL population

QTLs were detected with the Windows QTL Cartographer V2.5 software (Wang et al. 2006) by composite interval mapping (CIM) method (Zeng 1993, 1994) using the Zmapqtl model 6 with a window size of 10 cM and a 2 cM walk speed. The statistical significance thresholds used to declare the presence of QTLs were determined by 1,000 random permutations with a genome-wide type I error rate of 5% (Doerge and Churchill 1996). The 95% confidence intervals of the QTL locations were determined by one-LOD intervals surrounding the QTL peak (Mangin et al. 1994). According to the partial correlation of the putative QTL with the target trait adjusted for cofactors in the multilocus model, the additive value and the coefficient of determination (R^2) were estimated based on the most significant dataset.

The epistatic interactions among QTLs and of QTL by environment were examined with the QTLNetwork 2.0 (Yang et al. 2007, 2008). The 1D search for the main effect QTL was done with a 10-cM testing window, 1-cM walking speed, and a 10-cM filtration window. Both the 1D and 2D genome scans were conducted with $P = 0.05$ significance threshold based on 1,000 permutations. The total effects of two examined QTLs must have a P value less than 1×10^{-5} and the interaction effects must have a P value less than 0.01.

Results

Linkage map construction of the RIL population

In the survey of using 1,786 primer pairs to detect polymorphisms between the two parents, 316 primer pairs (17.7%) amplified polymorphic band(s). Among them, 270 markers representing 273 non-redundant loci, which amplified clear and reproducible bands, were used to assemble the linkage groups in the RIL population. The obtained linkage map contained 33 linkage groups spanning a total genetic length of 1,673.4 cM with an average marker density of 9.8 cM (data shown in Fig. S1). All the 21 wheat chromosomes were represented by at least one linkage group.

Evaluation and statistical analysis of WYMV resistance of the RIL population

General statistics for the DI of the RILs and their two parents in the population are summarized in Table 1. For all the four trials and the overall mean, the means of the DI and variation coefficients of 'Xifeng Wheat' were zero (Table 1). For the susceptible parent 'Zhen 9523', the means of the DI in trials E1, E2, E3, and E4 were 58.61, 72.13, 75.27, and 69.03%, respectively, and its variation coefficients were 0.06, 0.05, 0.03, and 0.04, respectively. Shapiro–Wilk test confirmed that the distributions of the DI

Table 1 General statistics for the DI of the RILs and their two parents in the 'Xifeng Wheat × Zhen 9523' RIL population

Trials	Parents (Mean ± SD)		RIL population		One-sample *t*-test	*F* test			h^2 (%)
	Xifeng Wheat	Zhen 9523	Mean ± SD	Range	Zhen 9523	Genotypes	Genotype × environment	Environments	
E1	0.00	58.61 ± 3.24	17.45 ± 16.11	0.00–68.10	51.92***	30.27***	2.03***	109.19***	84.08
E2	0.00	72.13 ± 3.77	22.90 ± 24.31	0.00–77.50	54.14***				
E3	0.00	75.27 ± 2.43	13.54 ± 22.77	0.00–80.00	119.29***				
E4	0.00	69.03 ± 2.87	10.36 ± 18.38	0.00–71.00	64.91***				
Mean	0.00	68.76 ± 3.79	16.02 ± 18.61	0.00–71.83	100.65***				

*** $P = 0.001$. *E1* the trial for the disease nursery experiment in Maan County of Jiangsu Province in year 2007; *E2*, *E3,* and *E4* the trials for the disease nursery experiments in the Institute of Agricultural Sciences in Lixiahe District of Jiangsu Province in years 2008, 2009, and 2010, respectively; Mean the overall mean across the four trials. The same as given below

of 'Zhen 9523' were normal ($P > 0.05$), One-sample *t* test for mean of the DI of 'Zhen 9523' confirmed that its differences to zero were significant at the $P = 0.001$ level, i.e., WYMV differences represented by the DI between the two parents were significant at the same level (Table 1). The mean values for the DI of the RILs were between those of the two parents in all the four trials with transgessive segregation within the population (Table 1, Fig. 2). The DI in the RILs showed a continuous distribution but skewed toward the resistant parent. Shapiro–Wilk test confirmed that the distributions were non-normal ($P < 0.001$). These results suggested that there were major loci controlling the WYMV resistance in the population.

ANOVA revealed that the variances of genotypes, environments, and genotype by environment interaction were significant at the $P = 0.001$ level (Table 1). However, the mean correlation coefficient (*r*) for the DI of the RILs among different trials was 0.77; and positive correlation coefficients between any two trials ranged from 0.70 to 0.95 and all were significant at the $P = 0.001$ level (Table 2). Therefore, the detection of QTLs was carried out not only on the DI of the RILs in each trial, but also on the overall mean of the four trials. The estimated broad-sense inheritability for all the data was 84.08% (Table 1), which suggested that the major loci controlling WYMV resistance had very high effects on the phenotype of WYMV resistance.

QTL analysis and estimation of epistatic interactions of the RIL population

Three different QTLs associated with WYMV resistance were detected in at least one trial and the overall mean

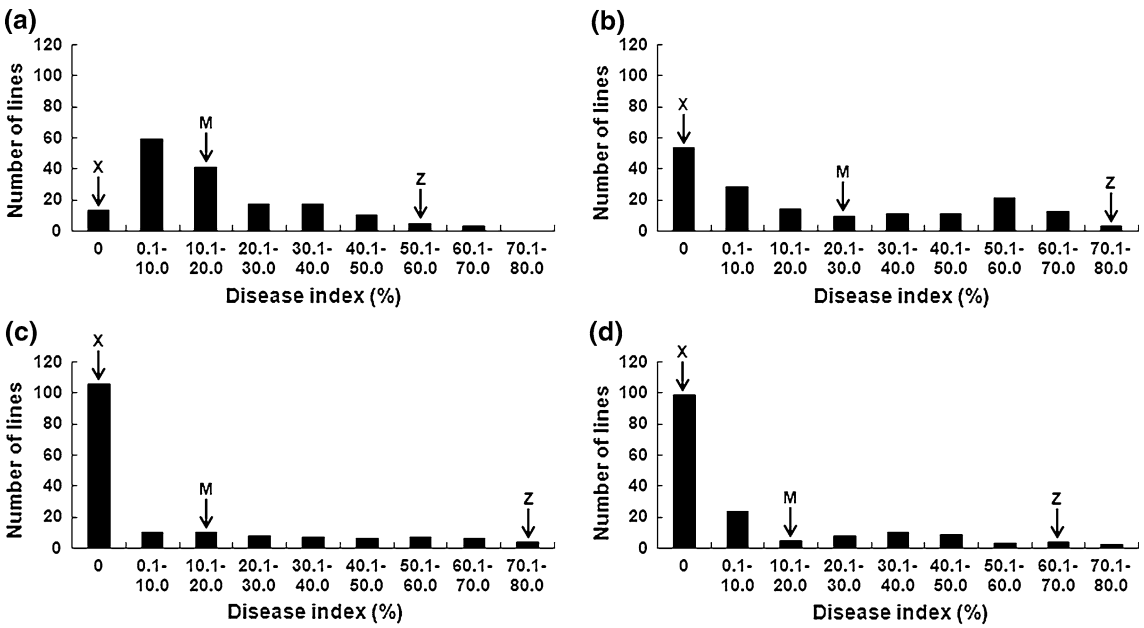

Fig. 2 Frequency distribution for the DI of the RILs in the 'Xifeng Wheat × Zhen 9523' RIL population. **a**, **b**, **c**, and **d** represent the frequency distribution of the DI in trials E1, E2, E3, and E4, respectively. *X*, Xifeng wheat; *Z*, Zhen 9523; *M*, Means of the population

using the significance ($P < 0.05$) LOD thresholds at 3.0, 3.1, 3.1, 3.0, and 3.0 in trials E1, E2, E3, E4, and the overall mean, respectively. They were mapped to chromosomes 3BS, 5AL, and 7BS (Fig. 3) and the favorable alleles conferring resistance were inherited from the resistant parent 'Xifeng Wheat'. The QTL *QYm.njau-5A.1* had the LOD scores of 13.8–35.9 and explained the most phenotypic variation, i.e., 25.9–53.7% (Table 3). The QTLs *QYm.njau-3B.1* and *QYm.njau-5A.1* with LOD scores of 3.2–35.9 were detected in all the four trials and the overall mean, while the QTL *QYm.njau-7B.1* with a LOD score of 3.1 was detected only in trial E1 and the overall mean (Table 3). For each trial, these three putative QTLs totally explained 33.7–57.0% of the observed phenotypic variance in the population.

QYm.njau-3B.1, which was in the marker interval between *Xwmc754* and *Xwmc623,* had the negative additive effects ranging from −4.44 to −7.44 and explained the phenotypic variation from 3.3 to 10.2% (Table 3, Fig. 3). The peaks of the *QYm.njau-3B.1* slightly varied among different trials, from 11.8 cM in trials E2, E4 and the overall mean to 16.6 cM in trial E1 (Table 3, Fig. 4). However, the QTLs detected on chromosome 3BS in all the four trials and the overall mean were treated as a unique QTL based on the overlapping confidence intervals.

QYm.njau-5A.1 explained the most phenotypic variations in all the four trials and the overall mean, which was 53.7% in E2 (Table 3). It was mapped to a 9.9 cM marker interval between *CINAU151* and *Xwmc327* on chromosome 5AL. In all the four trials and the overall mean, its peak was located at a 0.4 cM interval delimited by two co-segregating markers, *Xwmc415.1* and *CINAU152* (at 52.1 cM), and an EST-STS marker *CINAU153* (at 52.5 cM) (Table 3, Figs. 3, 5).

QYm.njau-7B.1, which was detected only in trial E1 and the overall mean and explained 4.9 and 3.3% of the phenotypic variation, respectively (Table 3), was located between markers *Xgwm46* and *Xwmc476* on chromosome 7BS.

The software program QTLNetwork 2.0 was used to detect the interactions among QTLs and of QTL by environment. Significant ($P < 1 \times 10^{-5}$) additive by additive negative interaction was observed between QTLs *QYm.njau-3B.1* and *QYm.njau-5A.1*, with the value of interaction effect being 5.16 and the interaction explaining 5.0% of the

Table 2 Pearson's correlation coefficients for the DI of the RILs in the 'Xifeng Wheat × Zhen 9523' RIL population among different trials

Trials	E1	E2	E3	E4
E1	1			
E2	0.77***	1		
E3	0.70***	0.78***	1	
E4	0.70***	0.74***	0.95***	1

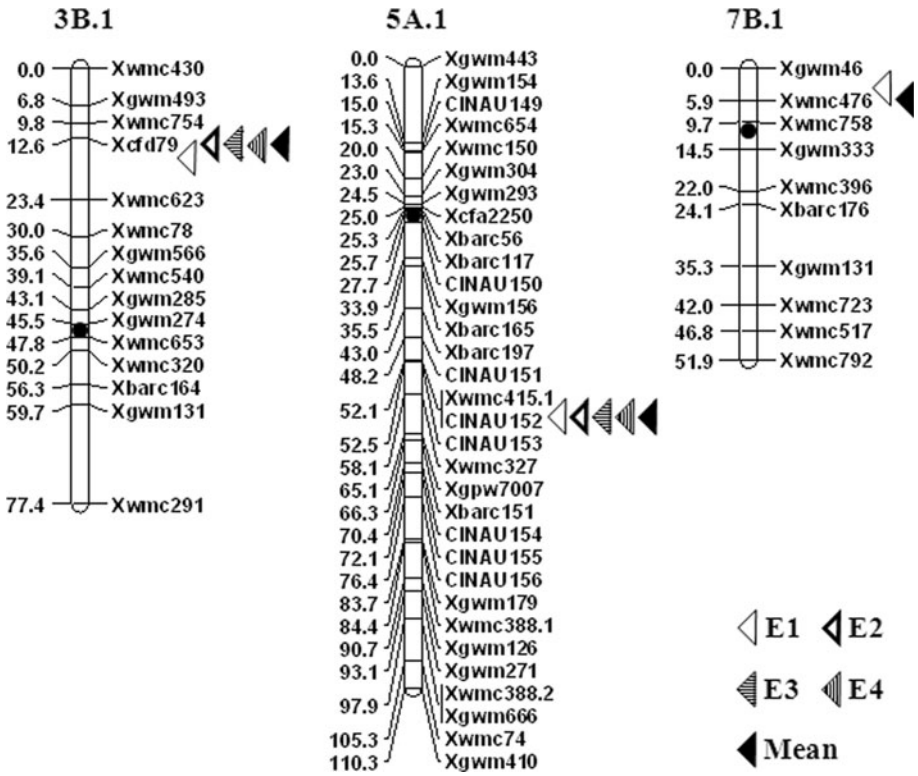

Fig. 3 Linkage maps and the detected QTLs associated with the DI of the RILs on chromosomes 3B, 5A, and 7B in the 'Xifeng Wheat × Zhen 9523' RIL population. Numbers to the left show the genetic distances in centiMorgans. Locations of QTL peaks are indicated with different *triangles* in all the four trials and the overall mean

phenotypic variation. These indicated that the phenotypic variation in the 'Xifeng Wheat × Zhen 9523' RIL population was not controlled by simple additive effects. The interactions of QTL *QYm.njau-5A.1* with three environments (E1, E2, and E4), which explained in total 2.9% of the phenotypic variation, were significant at $p = 0.01$, 1×10^{-5} and 0.01, respectively, with the effective values being 2.97, −5.81, and 3.07, respectively. These results showed that the stably expressed major QTL, *QYm.njau-5A.1*, was also slightly affected by environments.

Inheritance analysis and validation of *QYm.njau-5A.1* using a secondary F_2 population

The obtained ('RILV-6' × 'Zhen 9523') F_1 individuals all showed high level of WYMV resistance same as 'RILV-6' (resistant; IT0) (March 9th in year 2009, Yangzhou). The derived F_2 population of 280 individuals showed segregation for WYMV resistance, of which 203 had the similar resistant level as 'RILV-6' and 77 as 'Zhen 9523'. The segregation ratio was in accordance with 3:1

Table 3 QTL analysis for the DI of the RILs in the 'Xifeng Wheat × Zhen 9523' RIL population by CIM method

QTLs	Trials	Locations	Marker intervals	Peak positions	Confidence intervals	LOD critical scores	LOD scores	R^2 (%)	Additive effects
QYm.njau-3B.1	E1	3B	*Xcfd79*[a]*-Xwmc623*	16.6	10.9–21.5	3.0	4.5	7.6	−4.47
	E2	3B	*Xwmc754-Xcfd79*[a]	11.8	9.8–16.2	3.1	3.2	3.3	−4.44
	E3	3B	*Xcfd79*[a]	12.6	10.8–15.0	3.1	6.7	10.2	−7.44
	E4	3B	*Xwmc754-Xcfd79*[a]	11.8	10.9–18.5	3.0	4.6	7.8	−5.19
	Mean	3B	*Xwmc754-Xcfd79*[a]	11.8	9.8–16.7	3.0	6.0	6.9	−4.95
QYm.njau-5A.1	E1	5A	*Xwmc415.1* [a]*/CINAU152*[a]	52.1	50.2–55.0	3.0	18.6	30.0	−9.16
	E2	5A	*Xwmc415.1* [a]*/CINAU152*[a]	52.1	50.0–55.5	3.1	35.9	53.7	−18.00
	E3	5A	*Xwmc415.1* [a]*/CINAU152*[a]	52.1	49.7–53.8	3.1	15.9	27.6	−12.23
	E4	5A	*Xwmc415.1* [a]*/CINAU152*[a]	52.1	50.0–54.9	3.0	13.8	25.9	−9.48
	Mean	5A	*Xwmc415.1*[a]*/CINAU152*[a]	52.1	50.2–52.7	3.0	29.5	45.9	−12.76
QYm.njau-7B.1	E1	7B	*Xgwm46-Xwmc476*[a]	4.0	1.1–8.2	3.0	3.1	4.9	−3.66
	Mean	7B	*Xwmc476*[a]	5.9	1.2–8.2	3.0	3.1	3.3	−3.49

[a] The nearest markers of the putative QTLs

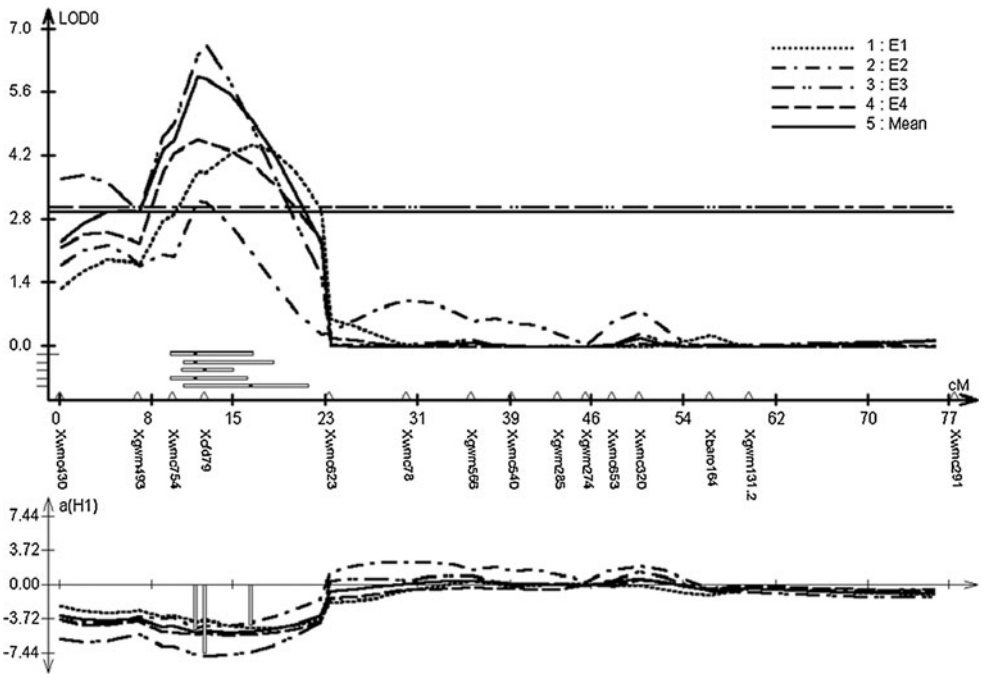

Fig. 4 QTL location on chromosome 3B detected by CIM method in all the four trials and the overall mean in the 'Xifeng Wheat × Zhen 9523' RIL population

($\chi^2 = 0.93 < \chi^2_{0.05,\ 1} = 3.84$), indicating that *QYm.njau-5A.1* responsible for WYMV resistance in 'RILV-6' acted as a dominant gene (Table 4).

Six molecular markers linked with *QYm.njau-5A.1* (i.e. *Xbarc197*, *CINAU151*, *CINAU153*, *Xwmc415.1*, *CINAU152*, and *Xwmc327*) were found to be polymorphic between 'RILV-6' and 'Zhen 9523' and were further used for amplification in the F_2 individuals. The results indicated that three co-dominant markers *Xbarc197*, *Xwmc415.1,* and *CINAU152* showed a segregation ratio of 1:2:1, and two dominant markers *CINAU151* and *CINAU153* both showed a segregation ratio of 3:1 (Table 4). However, segregation ratio of the co-dominant marker *Xwmc327* deviated from 1:2:1 (Table 4). The obtained 276 $F_{2:3}$ lines were further evaluated for WYMV resistance, and the segregation ratio of the homozygous dominant, heterozygous dominant, and homozygous recessive alleles of the F_2 individuals was in accordance with 1:2:1. Linkage analysis using the F_2 population validated that the markers *Xbarc197*, *CINAU151*, *CINAU153*, *Xwmc415.1*, *CINAU152*, and *Xwmc327* were linked to *QYm.njau-5A.1* with the genetic distances of 9.2, 5.2, 0.1, 0.0, 0.0, and 9.7 cM, respectively (Fig. 6).

Validation of the presence and effectiveness of *QYm.njau-5A.1* and the distribution of different resistance loci in 46 wheat varieties

A panel of germplasm collection consisting of 46 wheat varieties was evaluated for WYMV resistance; it was found that 34 were resistant to WYMV, and 12 were susceptible. Three markers, *Xwmc415.1*, *CINAU152,* and *CINAU153* closely linked with *QYm.njau-5A.1* identified in the present study, and one marker, *Xwmc41* linked with the gene *YmYF* or *YmIb* mapped on chromosome 2DL previously reported by Liu et al. (2005b) and Nishio et al. (2010), were used for marker analysis of the 46 wheat varieties.

Of the 34 wheat varieties which showed high level of WYMV-resistance, 12 varieties could only amplify the

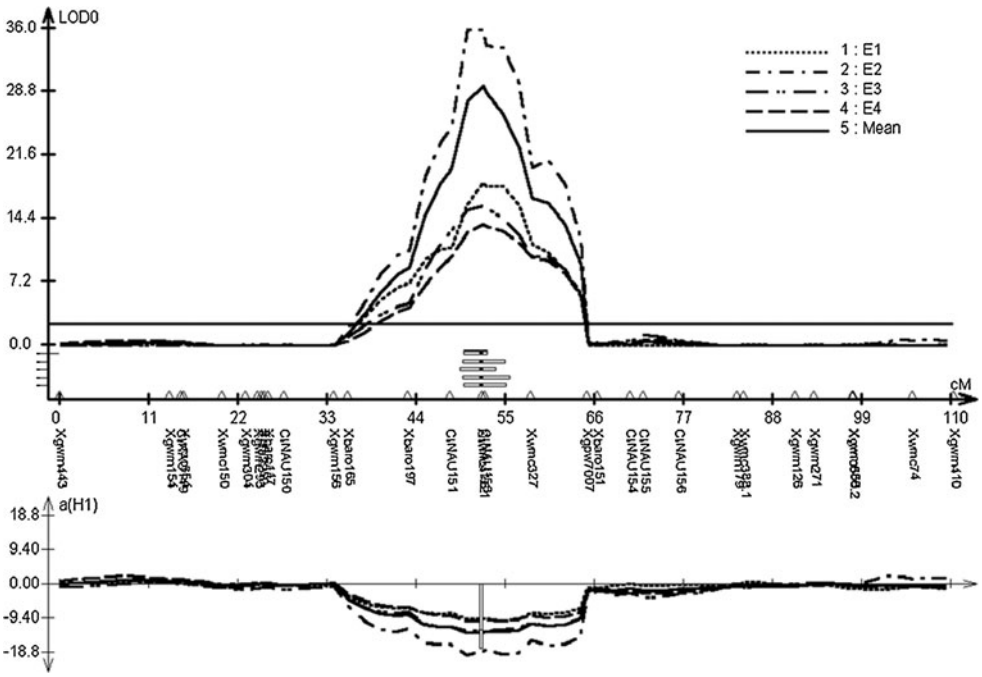

Fig. 5 QTL location on chromosome 5A detected by CIM method in all the four trials and the overall mean in the 'Xifeng Wheat × Zhen 9523' RIL population

Table 4 Segregation analysis for the WYMV-resistance gene *QYm.njau-5A.1* and markers in the 'RILV-6 × Zhen 9523' secondary F_2 population

Gene or markers	No. of F_2 population	Observed number			Expected ratio	χ^2
		A[a]	H	B		
QYm.njau-5A.1	280	60	143	77	1:2:1	2.19
Xbarc197	280	66	134	80	1:2:1	1.91
CINAU151	280	202[b]		78	3:1	1.22
CINAU153	280	203[b]		77	3:1	0.93
Xwmc415.1	280	60	143	77	1:2:1	2.19
CINAU152	280	60	143	77	1:2:1	2.19
Xwmc327	280	52	133	95	1:2:1	13.91

[a] Genotype: A = RILV-6; H = heterozygous; B = Zhen 9523

[b] No. of A and H classes

$\chi^2_{0.05,\ 3:1} = 3.84$, $\chi_{0.05,\ 1:2:1}{}^2 = 5.99$

same specific bands as in 'Xifeng Wheat' using three markers closely linked with *QYm.njau-5A.1* (Fig. 7a, b and c, lanes 1–12, respectively), 19 varieties could only amplify the same specific bands as in 'Yangfu 9311' using the marker *Xwmc41* linked with *YmYF* or *YmIb* (Fig. 7d, lanes 11–29, respectively), and the remaining 5 resistant varieties failed to amplify any marker alleles associated with the above WYMV resistance QTL/gene. It was proposed that 10 WYMV-resistant varieties only have the resistance QTL *QYm.njau-5A.1* (Fig. 7, lanes 1–10), 17 WYMV-resistant varieties only have the resistance gene *YmYF* or *YmIb* (Fig. 7, lanes 13–29), and 2 varieties with WYMV-resistance have both resistance alleles (Fig. 7, lanes 11–12), while the remaining 5 resistant varieties may contain other novel resistant gene(s).

All the 12 WYMV-susceptible varieties amplified the same specific band as in 'Zhen 9523' using the three markers closely linked with *QYm.njau-5A.1* (Fig. 7a, b and c, lanes 35–46, respectively). While using the marker *Xwmc41* linked with *YmYF* or *YmIb*, 11 of 12 amplified the same specific band as in 'Zhen 9523' (Fig. 7d, lanes 35–40 and 42–46, respectively) and the remaining one amplified the same specific band as in 'Yangfu 9311' (Fig. 7d, lane 41).

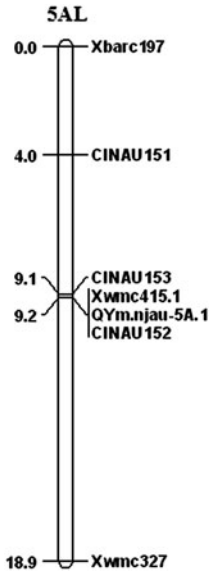

Fig. 6 Molecular marker-based linkage map of *QYm.njau-5A.1* associated with WYMV resistance on chromosomes 5AL in the 'RILV-6 × Zhen 9523' secondary F_2 population. *Numbers* to the *left* show the genetic distances in centiMorgans (cM)

Discussion

The WYMV resistance of the RILs showed high broad-sense heritability (84.08%), which indicated the high accuracy and reproducibility of both the field natural infection nursery and the scoring method for WYMV resistance. The disease index (DI) was used to estimate the WYMV resistance of the RILs. Although the DI of the RILs showed a continuous distribution, there was an obvious tendency of skewness toward the resistant parent in each trial (Fig. 2), suggesting that, although WYMV

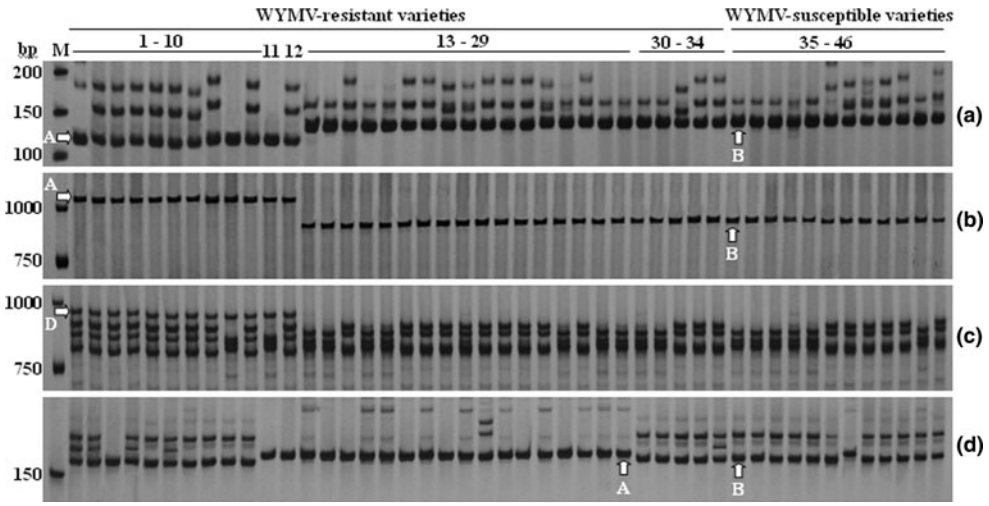

Fig. 7 Polymorphism of the markers linked with WYMV-resistance QTL/gene in the 34 WYMV-resistant varieties (lanes 1–34) and the 12 WYMV-susceptible varieties (lanes 35–46). **a–c** represent the amplified bands in 39:1 non-denaturing poly-acrylamide gels using the markers *Xwmc415.1*, *CINAU152*, and *CINAU153* closely linked with *QYm.njau-5A.1*, respectively; **d** represents the amplified bands in 19:1 non-denaturing poly-acrylamide gel using the marker *Xwmc41* linked with *YmYF* or *YmIb*. Note: When using the three markers closely linked with *QYm.njau-5A.1*, the variety 'Xifeng Wheat' that amplified the specific band was marked as *A*/*D*, while 'Zhen 9523' amplified the specific band was marked as *B*; When using the marker *Xwmc41*, the variety 'Yangfu 9311' that amplified the specific band was marked as *A*, and 'Zhen 9523' that amplified the specific band was marked as *B*. *Arrows* indicate the polymorphic bands of marker alleles. *M* marker

resistance in 'Xifeng Wheat' was inherited as a quantitative trait, there were dominant major gene effects in this population. WYMV resistance was reported to be controlled by one, two or three genes in different wheat varieties (Qin et al. 1986; Liu et al. 2004). In this study, two QTLs (*QYm.njau-5A.1* and *QYm.njau-3B.1*) could be stably detected in all the four trials, suggesting that WYMV resistance of 'Xifeng Wheat' is controlled by at least two genes.

Liu et al. (2005a) mapped a WYMV-resistance gene *YmNM* to chromosome 2A in Chinese wheat variety 'Ningmai 9' by a bulk segregant analysis (BSA) method using an F_2 population. The *YmNM* gene was flanked by an AFLP marker *E2/M5* and a SSR marker *Xgwm328* with a genetic distance of 23.0 cM apart. Using an F_2 population derived from the Chinese wheat variety 'Yangfu 9311', Liu et al. (2005b) mapped the resistance gene *YmYF* on chromosome 2DL at the region with a genetic distance of 8.1 cM from SSR marker *Xwmc41* and 11.6 cM from SSR marker *Xgwm349*. Using a F_1-derived doubled-haploid (DH) lines involving the Holland wheat variety 'Ibis', Nishio et al. (2010) mapped the resistance gene *YmIb* in a cluster of SSR markers including *Xcfd16*, *Xwmc41*, *Xcfd168,* and *Xwmc181* at the genetic distances of 2.0, 4.0, 7.1, and 12.4 cM, respectively. However, the relationship of *YmYF* and *YmIb* need to be further clarified. We identified three different QTLs associated with WYMV resistance in 'Xifeng Wheat' on chromosomes 3BS, 5AL, and 7BS, respectively. All have not been reported and should be new gene resources in wheat breeding for WYMV resistance. Among them, one major QTL *QYm.njau-5A.1* and one minor QTL *QYm.njau-3B.1* were all identified to be consistently expressed across seasons. *QYm.njau-5A.1* was mapped close to SSR marker *Xwmc415.1* and two EST-STS markers (*CINAU152* and *CINAU153*) on chromosome 5AL, and these markers had genetic distances of 0.0, 0.0, and 0.4 cM from the QTL peak (52.1 cM), respectively. However, the peaks (11.8–16.6 cM) of the *QYm.njau-3B.1* slightly varied among different trials. The relationships of the significant ($P < 1 \times 10^{-5}$) additive by additive negative interaction (the value of interaction effect being 5.16) between *QYm.njau-3B.1* and *QYm.njau-5A.1* and of the significant ($P < 0.01$) interactions of *QYm.njau-5A.1* with three environments (E1, E2, and E4) would possibly explain for the almost negative fluctuations of the effects between *QYm.njau-3B.1* and *QYm.njau-5A.1* in all the four trials (Figs. 4, 5), and the decreased effect of *QYm.njau-5A.1* ($R^2 = 27.6\%$, LOD score = 15.9) maybe one of the causes of the increase of the effect for *QYm.njau-3B.1* ($R^2 = 10.2\%$, *LOD* score = 6.7) in trial E3. Therefore, the resistance effect of the minor QTL *QYm.njau-3B.1* increased when the resistance effect of QTL *QYm.njau-5A.1* reduced or was completely absent. Vice versa, the effect of QTL *QYm.njau-5A.1* will be more prominent when the minor QLT *QYm.njau-3B.1* reduced or was completely absent. However, these need to be further validated in the wheat breeding for WYMV resistance.

The high level of WYMV resistance contributed by the major QTL *QYm.njau-5A.1* was further confirmed by construction and characterization of a secondary F_2 population, in which *QYm.njau-5A.1* was identified as a single dominant gene. In the RIL population, significant ($P < 1 \times 10^{-5}$) additive by additive negative interaction was observed between QTLs *QYm.njau-3B.1* and *QYm.njau-5A.1*, and the interaction effect among environments was also significant ($P < 0.001$). The lack of polymorphisms of two *QYm.njau-3B.1* linked markers *Xcfd79* and *Xwmc754* between 'RILV-6' and 'Zhen 9523' indicated that 'RILV-6' lacks the resistance allele *QYm.njau-3B.1* (data not shown). This resulted in the decrease or loss of the interaction effect between *QYm.njau-3B.1* and *QYm.njau-5A.1*. There was no interaction effect of environment by environment because the WYMV resistance of the F_2 population was evaluated in a single environment, and the dominant effect of *QYm.njau-5A.1* was dominant in the F_2 population. In addition, although the segregation ratio of resistant and susceptible F_2 individuals was 2.64:1, which was deviated from 3:1, the chi-square (χ^2) test failed to detect the slight deviation due to its less insensitivity. This is one of the reasons why the major QTL *QYm.njau-5A.1* was treated as a single dominant gene in the secondary F_2 population.

Three markers flanked *QYm.njau-5A.1* in the RIL population, *Xwmc415.1*, *CINAU152*, and *CINAU153*, were found to be closely linked with *QYm.njau-5A.1* in the F_2 population and they should be useful in MAS wheat breeding for WYMV resistance. Based on the amplification pattern of the markers closely linked with *QYm.njau-5A.1* or linked with *YmYF* or *YmIb* in the panel of germplasm collection consisting of 46 wheat varieties, 5 varieties with WYMV-resistance failed to amplify any marker alleles associated with the above-known WYMV-resistance QTL/gene. We suggested that there exits a new resistance gene(s) or it was attributed to recombination occurred between the molecular markers and the resistance QTL/gene. The WYMV-susceptible variety 'Virgilio' (Fig. 7d, lane 41) amplified the same specific band as in the WYMV-resistant variety 'Yangfu 9311' using the marker *Xwmc41* linked with the resistance gene *YmYF* or *YmIb*, which further confirmed the presence of recombinant event(s) in the processes of wheat breeding due to the genetic distance of the marker(s) and the resistance gene(s).

Closely related to WYMV is WSSMV, which is of importance in many European and American wheat growing areas (Ordon et al. 2009). WSSMV resistance was also reported to be controlled by one to three genes (Wiese et al. 1974; Van Koevering et al. 1987; Yao et al. 1999;

Zhou et al. 2000; Ren et al. 2008). Two QTLs related to WSSMV resistance were previously detected also on chromosome 2DL using the F_5 recombinant inbred lines derived from the USA cultivar 'Geneva' (Khan et al. 2000) and the F_9 recombinant inbred lines involving the México wheat cultivar 'ARz' (Yan et al. 2008). According to the consensus map constructed by Somers et al. (2004), marker interval *Xgwm608–Xgwm539* of the QTL detected by Yan et al. (2008) for WSSMV resistance perhaps overlap the resistance gene *YmYF* or *YmIb*. The genes or QTLs for WYMV or WSSMV resistance repeatedly detected in chromosome 2DL by different researchers using different materials indicated that such chromosome regions should be very important for virus disease resistance. However, whether these loci in group 2 chromosomes and the QTLs detected in the present study confer resistances to both viruses need to be further studied.

It has been found that many resistance genes were present as gene clusters. Dilbirligi et al. (2004) reported the presence of five major *R* gene clusters (short arm of groups 1, 2, and 3 and long arm of groups 5 and 6) that spanned only ~3% of the wheat genome but contained ~47% of the candidate *R* genes. By an approach of map-based cloning, Krattinger et al. (2009) cloned a gene, *Lr34/Yr18/Pm38/Ltn1*, at the gene-rich island of chromosome 7DS, which confers durable resistance against several diseases. In the present study, the stably expressed minor QTL, *QYm.njau-3B.1*, was located distally on chromosome arm 3BS in the marker interval *Xwmc754–Xwmc623*, which was 3.0 cM distant from the marker interval *Xgwm533–Xgwm493*, tagging a chromosome region enriched with disease resistance genes (Paux et al. 2008; Choulet et al. 2010), including a stably expressed major QTL, *QFhs.ndsu-3BS*, related to *Fusarium* head blight resistance (Anderson et al. 2001; Jiang et al. 2007a, b). Although the two marker intervals of *QYm.njau-3B.1* and *QFhs.ndsu-3BS* were all located at the distal deletion bin 3BS8-0.78-0.87 (Paux et al. 2008), *QYm.njau-3B.1* and *QFhs.ndsu-3BS* were mapped in two different marker intervals on chromosome 3BS. The stably expressed major QTL, *QYm.njau-5A.1*, was mapped on chromosome 5AL in the marker interval flanked by *Xwmc415.1*, *CINAU152* and *CINAU153* (Figs. 3, 5), and the marker interval is probably in one of the five main areas of *R* gene clusters (Dilbirligi et al. 2004).

For the purpose of fine mapping and further cloning of the major resistance QTL *QYm.njau-5A.1*, a further ('RILV-6' × 'Zhen 9523') F_2 population composed of 6,002 individuals has been developed. The phenotyping and genotyping of this population is in progress. The classical map-based cloning seems to be most appropriate approach for the cloning of *QYm.njau-5A.1* at present, but is a long-term goal without the genome sequences of common wheat or its related species available.

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