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ORIGINAL PAPER

QTL analysis of resistance to Fusarium head blight in the novel wheat germplasm CJ 9306. I. Resistance to fungal spread

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Abstract Fusarium head blight (FHB or scab) caused by *Fusarium* species is a destructive disease in wheat and barley worldwide. The objectives of our study were to identify quantitative trait loci (QTLs) for resistance to FHB spread (Type II resistance) and to quantify the magnitude of their effects in a novel highly resistant wheat germplasm, CJ 9306. A set of 152 F_7 recombinant inbred lines (RILs) derived from a cross Veery/CJ 9306 and two parents were evaluated for FHB resistance by single-floret inoculation in three greenhouse experiments in 2002 and 2004. Percentage (PSS) and number (NSS) of scabby spikelets at 25 days post-inoculation were analyzed. In total 682 simple sequence repeat (SSR) markers were screened for polymorphism between the two parents, and a genetic linkage map was constructed with 208 polymorphic markers. Ten QTLs associated with FHB resistance were detected, five from CJ 9306 and five from Veery. The major QTL on 3BS (*QFhs.ndsu–3BS*) was validated in CJ 9306, exhibiting greatest additive effects and explained 30.7% of phenotypic variation for PSS on the overall average of three experiments. Another major QTL on 2DL (*QFhs.nau–2DL*) from CJ 9306 explained 9.9–28.4% of phenotypic variation, with a significant QTL × environment interaction. *QFhs.nau–1AS* and *QFhs.nau-7BS* showed lower additive effects and explained lower variance (4.5–9.5%). A QTL on 5AS, decreasing PSS by 10.3% on average, was validated by simple marker analysis and joint trait/experiment IM/CIM analysis despite insignificance for single-experiment IM and CIM analyses. Likewise, *QFhs.nau-2BL* and *QFhs.nau-1BC* from Veery could reduce PSS by 13.2 and 11.4%, respectively. The effects of other three minor QTLs from Veery were significant for one experiment and combined analysis. Comparisons of two- and three-locus combinations suggested that the effects of FHB resistance QTLs/genes could be accumulated, and the resistance could be feasibly enhanced by selection of favorable alleles for multiple loci. Four two-locus combinations and two three-locus combinations were suggested as the preferential choices in practical marker-assisted selection program.

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Introduction

Fusarium head blight (FHB or scab) caused by *Fusarium* species is one of the most destructive diseases in wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) worldwide. During the past decades, frequent epidemics of this disease resulted in substantial economic loss (Bai and Shaner 2004; Windels 2000). Not only can the disease

cause dramatic decrease of grain yield and quality, but may also lead to serious mycotoxin contamination in the infected grains, which is detrimental to the health of human beings and livestock. Agronomic approaches and fungicide applications now available are far from effective prevention of the disease epidemics, although they can reduce the damage to some extent. Developing and growing resistant cultivars is the most economic, effective and environment-friendly approach to control this disease.

Breeding for resistance to FHB has received increasing attention in China since the 1980s (Wu et al. 1984), and in Europe and North America since the 1990s (Miedaner 1997; Rudd et al. 2001). So far significant progress in wheat research has been achieved and some resistant varieties have been released (Jin 1996; Bai and Shaner 2004; McKendry et al. 2004; Mergoum et al. 2005). However, the development of FHB resistant cultivars is still a great challenge as the progress in plant breeding is still hampered by lack of elite germplasm resources as well as limited understanding of the underlying genetic mechanisms of the resistance, particularly for novel improved germplasms. Quantitative trait locus (QTL) mapping and marker-assisted selection (MAS) could largely enhance the efficiency of utilizing elite germplasms and breeding resistant cultivars.

Previous studies suggested that FHB resistance in wheat is inherited predominantly as a quantitative trait in an additive-dominance model (Bai et al. 2000; Snijders 1990; Jiang and Ward 2006). Multiple loci or genes were involved in the resistance, and each had low expressivity or low contribution to heritability and was sensitive to genetic background (Gervais et al. 2003; Shen et al. 2003; Somers et al. 2003; Klahr et al. 2004; Mardi et al. 2005). To date, all 21 chromosomes have been reported to carry QTLs for FHB resistance, and approximately 30 QTLs have been identified. However, most of these studies were focused on a few resistant cultivars, such as Sumai 3 and its derivatives (Waldron et al. 1999; Anderson et al. 2001; Buerstmayr et al. 2002; Zhou et al. 2002; Yang et al. 2005b), Wangshuibai (Jia et al. 2005; Lin et al. 2004, 2006; Zhang et al. 2004; Zhou et al. 2004; Mardi et al. 2005). QTL analysis on more extensive resources of resistance, especially those novel improved germplasms, is of great importance and significance for acceleration of the development of resistant cultivars.

CJ 9306 is a novel wheat germplasm superior to Sumai 3 in both FHB resistance and agronomic performance (Jiang et al. 2006a). It was developed through multiple-parent crossing and recurrent selection combined with modified pedigree methods with the aid of a dominant male-sterile gene *Ta1* (*ms2*). The original parentage included five local superior cultivars and 15 important resources of resistance to FHB and/or other major diseases from China and other countries (such as Sumai 3, Ning 7840, Wangshuibai, Fanshanxiaomai, Wenzhouhongheshang, Emai 9, Zhen 7495, Nobeokabuzu, Shinchunaga, Frontana, Jinzhou 1, etc.). Recurrent selection has a special advantage in accumulating multiple genes and creating desired gene combinations (Jiang et al. 1994). Conventional genetic studies indicated that the resistance in CJ 9306 was inherited as a quantitative trait with both major and minor genes/QTLs (Jiang and Ward 2006). Because of its excellent resistance, unique history of breeding, and complex parentage, characterization of its FHB resistance by DNA markers is very useful and significant for understanding of the underlying genetic basis and effective utilization of this novel elite germplasm. Therefore, the objectives of our study were: (1) to identify and localize QTLs for resistance to FHB in CJ 9306, and (2) to quantify the magnitude of their effects as both individual genes alone and gene combinations for multiple loci, with the ultimate goal to develop tools and approaches (MAS procedures) utilizable in practical breeding programs. The results of QTL analysis of resistance to fungal spread (Type II resistance) are reported in this paper only. The data for resistance to mycotoxin accumulation, and resistance to yield loss will be presented in the following report.

Materials and methods

Plant materials and experimental design

A set of 152 F_7 recombinant inbred lines (RILs) derived from a wheat cross Veery/CJ 9306 and two parents were used to evaluate FHB resistance. CJ 9306, developed at Nanjing Agricultural University (NAU), China through multiple-parent crossing and recurrent selection combined with modified pedigree methods with the aid of a dominant male-sterile gene *Ta1* (*ms2*), has a very high level of FHB resistance and good agronomic traits (Jiang et al. 2006a). Previous experiments consistently demonstrated that it was superior to Sumai 3 and Ning 7840 in both Type II resistance to FHB and agronomic performance. Veery [Kavkaz/Buho//KAL/BB (CM33027)], developed at CIMMYT, Mexico, is susceptible to FHB. The cross (Veery/CJ 9306) was made at Nanjing, China in 1998, and F_2 seeds were randomly harvested in 1999. Subsequently, the RILs were developed in the greenhouse at Michigan State University by single seed decent (SSD). The 152 RILs were grown in the greenhouse at Michigan State University in a completely randomized design with two replications. For each line, six plants were planted in two square pots (11 × 11 cm) per replication, each pot having three plants. The two parents were planted as the controls many times at an interval of 1 week. Sown in December

of 2001, January of 2002 and November of 2003, the experiments were repeated three times in different greenhouse compartments, and designated as Experiment 02, 02a and 04, respectively.

Disease inoculation and resistance evaluation

Single-floret inoculation was conducted immediately before or after initial anthesis (around Zadoks growth stage 60) (Jiang et al. 2006b). The inoculum was *F. graminearum* isolate PH-1 for Experiment 02 and 02a, and a mixture of two isolates PH-1 and WF-1 for Experiment 04. Six to eight spikes of each RIL were inoculated per replication. For each single batch of inoculation, the checks were included. The inoculated plants/pots were mist-irrigated in a misting chamber at 22–26°C for 3 days. Then the pots were transferred to another greenhouse compartment. The number of scabby spikelets (NSS) on the inoculated spikes was visually counted multiple times at different days post-inoculation (dpi). At 25 dpi, the total spikelets were also estimated to calculate the percentage of scabby spikelets (PSS) for each observation. Only the PSS and NSS at 25 dpi are presented as the measurements of Type II resistance in this paper. In addition, since these two measures were highly correlated ($r = 0.978–0.986$, $P < 0.01$), the presentation and discussion were focused on the results for PSS, but the results for NSS were occasionally mentioned as well.

DNA markers and genotyping

In 2004, all the RILs and the two parents were planted in the greenhouse, with each having about 20 seedlings in a pot. At Zadoks growth stage 11, the leaves were harvested and stored in a freezer at –80°C. The sample leaves were dried by vacuum drying at –50°C and then ground for DNA extraction. CTAB extraction was adopted to isolate DNA. A total of 682 simple sequence repeat (SSR) primer pairs (http://wheat.pw.usda.gov) were screened for polymorphism between the two parental lines. PCRs were performed on a DNA Engine Dyad Peltier Thermal Cycler (MJ Research, Inc., Waltham, MA, USA). Polymorphic markers were used to genotype the mapping population with a simple and high throughput polyacrylamide gel electrophoresis system (Wang et al. 2003). The segregating data of 208 SSR markers in total were used to construct a genetic linkage map using JoinMap version 3.0 (van Oijen and Voorrips 2001) and referring to high-density linkage maps (Shi and Ward 2004; Somers et al. 2004). A logarithm of odds (LOD) threshold value of 3.0 was used for grouping.

QTL mapping and statistical analysis

On the basis of replication means, ANOVA was performed for single experiment and over all combination (Sokal and Rohlf 1981), respectively, and then broad-sense heritability on a line mean basis was estimated (Fehr 1987). The exact confidence intervals for heritability were calculated following Knapp et al. (1985). QTL analysis was performed in Windows QTL Cartographer version 2.0 (Wang et al. 2001–2004), based on the genotype means. Single marker analysis (SMA), interval mapping (IM), and composite interval mapping (CIM) were performed. Multiple interval mapping (MIM) was performed to detect the QTL × QTL interaction (epistasis). The QTL × environment (E) interaction was detected using the JZmapqtl program. A LOD value of 2.5 was set as the threshold value, but all the QTLs with a LOD value above 2.0 were presented and claimed. Only the results of CIM were presented here. Because the investigated FHB-resistant line CJ 9306 was developed by NAU and the cross Veery/CJ 9306 was also originally made at NAU, the symbols of QTLs were designated as *QFhs.nau* followed by corresponding chromosomes, except the well-known major QTL on 3BS (*QFhs.ndsu-3BS* or the gene *Fhb1*) which is already catalogued in the Wheat Gene Catalog and GrainGenes. To verify the validation of QTLs/markers (including those with a LOD value smaller than 2.5 for CIM), and to provide information for marker-assisted selection, a comparison between two groups of RILs carrying marker allele from Veery and CJ 9306 was conducted based on the results of ANOVA for group comparison of QTL/marker alleles. Likewise, a comparison of different QTL/marker combinations for multiple loci was also computed. *Q*-test (Tukey–Kramer method) was used to examine the significance of differences (Sokal and Rohlf 1981).

Results

Phenotypic analysis

ANOVA indicated that the differences among RILs were highly significant for both single experiment data and combined analysis over all three experiments ($F = 8.1–15.0$, $P < 0.01$). The environmental differences and RIL × environment interactions were also significant ($F = 11.6$ and 3.7 for PSS, and 27.0 and 3.9 for NSS, respectively, $P < 0.01$). Over all three experiments, the average of Veery and CJ 9306 was 85.0 and 6.8% for PSS, respectively, and 15.6 and 1.2 for NSS (Table 1). The average of PSS for the RIL population was 50.3% with a range of 5.9–100%. The average of the RIL population for NSS was 8.9 ranging from 1.2 to 19.5. Frequency

Table 1 Average, range and coefficient of variation, and broad-sense heritability of Type II resistance to Fusarium head blight based on percentage (PSS) and number (NSS) of scabby spikelets for an F_7 RIL population derived from the wheat cross Veery/CJ 9306 over three experiments/environments

Population	PSS	NSS
Veery	85.0 ± 4.4	15.6 ± 0.8
CJ 9306	6.8 ± 1.1	1.2 ± 0.2
RILs		
Mean ± SE	50.3 ± 2.2	8.9 ± 0.4
Range	5.9–100	1.2–19.5
CV %	53.8	54.1
$LSD_{5\%}$	14.3	2.6
h_B^2	0.87	0.85
h_B^2 90% confidence interval	0.83–0.90	0.81–0.88

distributions were continuous, and transgressive segregation was evident toward susceptibility (Fig. 1). The estimates of heritability in broad sense for single experiments were 88–93%. Based on a three-year combined analysis, the estimates of heritability were 85–87% after eliminating the variance of RIL × environment interaction.

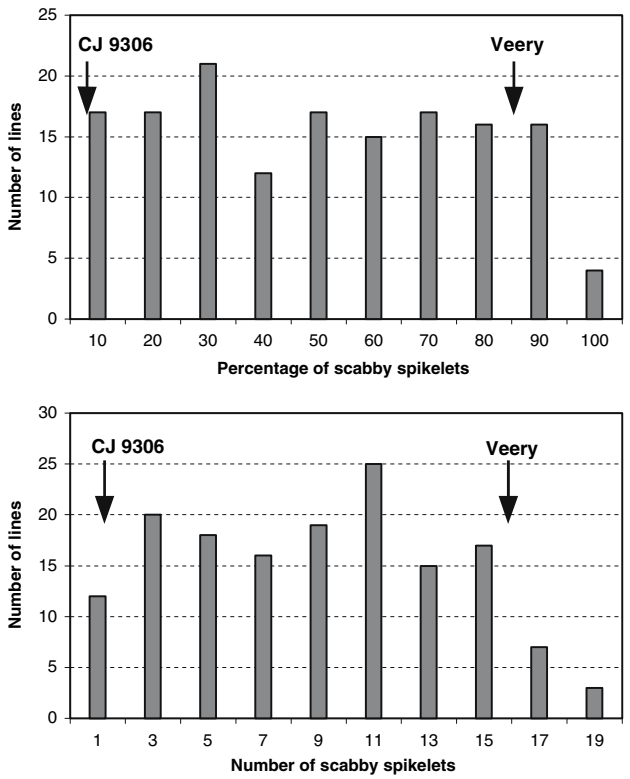

Fig. 1 Frequency distribution of 152 F_7 RILs derived from a wheat cross Veery/CJ 9306 for Type II resistance to FHB (PSS and NSS over three experiments)

QTL mapping and analysis

Interval mapping (IM) and composite interval mapping (CIM) analyses detected four QTLs contributing to Type II resistance to FHB in CJ 9306. They were located on 3BS, 2DL, 1AS and 7BS, respectively, and all showed positive additive effects on the resistance (Table 2). The major QTL on 3BS (*QFhs.ndsu-3BS*) was consistently detected by three individual experiments and the overall average data. It explained 18.2–27.8% of phenotypic variation for a single experiment, and 30.7% for the overall average of three experiments. The QTL on 2DL (*QFhs.nau-2DL*) explained 9.9–28.4% of phenotypic variation, except insignificance in Experiment 04. In comparison, the QTLs on 1AS (*QFhs.nau-1AS*) and 7BS (*QFhs.nau-7BS*) showed lower additive effects and explained lower variance (4.5–9.5%). The mappings for these four QTLs based on CIM for PSS are shown in Fig. 2. CIM for Experiment 02a or 04 also detected two minor QTLs in the susceptible parent Veery (Table 2). One was located on 2AL, but another could not be localized due to insufficient marker data for linkage mapping.

Four additional minor QTLs located on 5AS, 1BC (centromeric region), 2BL and 5BL, respectively, were detected by simple marker analysis and joint trait IM/CIM analysis (i.e. the data from individual experiments were treated as separate traits) (Table 3), although they were not significant for single-experiment CIM and IM analyses.

Multiple interval mapping (MIM) analysis did not detect significant epistatic interactions between the QTLs detected by CIM. However, by ZJmapqtl program and ANOVA of marker alleles, significant QTL × E interactions were detected for the QTLs *QFhs.nau-2DL*, *QFhs.nau-1BC* and *QFhs.nau-2AL*, indicating that their effects were dependent on experimental conditions (including different isolates used) (Table 3).

Phenotypic effects and comparison of QTL/marker alleles

The averages of alternative QTL alleles (SSR markers) associated with FHB resistance and the differences between them are listed in Table 3. For the five QTLs on 3BS, 2DL, 1AS, 7BS and 5AS, favorable alleles from CJ 9306 significantly enhanced the resistance, except for *QFhs.nau-2DL* and *QFhs.nau-5AS* in Experiment 04. The CJ 9306 alleles for markers *Xgwm533a*, *Xgwm533b* or *Xgwm493* linked to *QFhs.ndsu-3BS* could decrease PSS by 17.2–28.1% or reduce NSS by 3.2–4.9. For the QTLs on 2DL, 1AS and 7BS, on three experiments, the averages of RILs with alleles from CJ 9306 for PSS and NSS were14.3–17.2% and 2.2–2.8 lower than those of Veery-

Table 2 QTLs for Type II resistance to FHB in the novel wheat germplasm CJ 9306 detected by composite interval mapping (CIM) of an F_7 RIL population derived from the cross Veery/CJ 9306, based on the data of percentage of scabby spikelets (PSS)

Experiment	QTL	Interval	Chromosome	Region length (cM)	LOD	Additive effects[a]	R^2 (%)
2002	*QFhs.ndsu-3BS*	*Xgwm533b–Xgwm493*	3BS	15.5	8.1	12.7	18.2
	QFhs.nau-2DL	*Xgwm157–Xwmc041*	2DL	27.1	3.3	9.3	9.9
	QFhs.nau-1AS	*Xwmc024–Xbarc148*	1AS	15.3	2.5	7.9	6.8
2002a	*QFhs.ndsu-3BS*	*Xgwm533b–Xgwm493*	3BS	15.5	9.1	16.7	25.3
	QFhs.nau-2DL	*Xgwm157–Xwmc041*	2DL	27.1	10.5	17.9	28.4
	QFhs.nau-7BS	*Xgwm400–Xgwm573*	7BS	29.7	3.1	9.8	8.5
	QFhs.nau-2AL	*Xgdm093–Xgwm265*	2AL	13.0	2.2	–6.6	4.1
2004	*QFhs.ndsu-3BS*	*Xgwm533b–Xgwm493*	3BS	15.5	11.7	16.0	27.8
	QFhs.nau-1AS	*Xwmc024–Xbarc148*	1AS	15.3	2.1	6.5	4.5
	QFhs.nau-?[b]	*Xbarc068–Xwmc175R*	?[b]	18.0	3.0	–7.6	6.3
Average (3 year)	*QFhs.ndsu-3BS*	*Xgwm533b–Xgwm493*	3BS	15.5	11.2	15.7	30.7
	QFhs.nau-2DL	*Xgwm157–Xwmc041*	2DL	27.1	3.5	10.8	15.5
	QFhs.nau-1AS	*Xwmc024–Xbarc148*	1AS	15.3	2.9	8.5	9.5
	QFhs.nau-7BS	*Xgwm400–Xgwm573*	7BS	29.7	2.5	7.7	7.3

[a] The positive values indicate that the alleles of QTLs from CJ 9306 positively contributed to the resistance or reduced the severity of disease, but in contrast the negative symbol means that the alleles from Veery had positive effects on the resistance

[b] The chromosome was not determined due to insufficient marker data for linkage mapping

allele RILs, respectively. The QTL on 5AS reduced PSS by 10.3% or NSS by 1.5.

For *QFhs.nau-2BL* and *QFhs.nau-1BC*, the favorable alleles from Veery significantly decreased the severity of disease (by 13.2 and 11.4% for PSS, on average, and by 2.3 and 1.5 for NSS) (Table 3). The remaining three QTLs from Veery reduced PSS by 6.0–8.1% or NSS by 1.0–1.4 on average, but their effects were significant only for one experiment and combined analysis.

The data also suggested a small difference between the two measurements of resistance in the efficiency of identifying the QTLs. PSS was a little more powerful than NSS for detecting minor QTLs.

Comparison of QTL/marker combinations for two or three loci

The mean PSS and NSS of RILs bearing favorable alleles at two loci were smaller ($P < 0.01$) than those of the reciprocal genotypes in all cases, and in most cases lower than those of RILs with favorable alleles at only one locus (Table 3). Furthermore, in most cases, for three-locus combinations, the averages of PSS and NSS of RILs carrying favorable alleles at all three loci were smaller than those of the genotypes with favorable alleles at only two loci.

Among all the two-locus combinations, the genotypes bearing favorable alleles at *QFhs.ndsu-3BS* + *QFhs.nau-2DL*, *QFhs.ndsu-3BS* + *QFhs.nau-1AS*, *QFhs.ndsu-3BS* + *QFhs.nau-7BS* and *QFhs.ndsu-3BS* + *QFhs.-nau-2BL* were the best, leading to a decrease of 38–40% for PSS or 6.5–7.2 for NSS relative to the genotype without favorable alleles at either locus. Among all the three-locus combinations, genotypes *QFhs.ndsu-3BS* + *QFhs.nau-2DL* + *QFhs.nau-1AS* and *QFhs.ndsu-3BS* + *QFhs.nau-2DL* + *QFhs.nau-2BL* were the best combinations, showing the lowest disease severity (19–20% for PSS or 3.2–3.4 for NSS).

Discussion

QTLs for FHB resistance

The present study identified five favorable QTLs for Type II resistance to FHB in the novel wheat germplasm CJ 9306. In a DH population derived from W14, a sister line to CJ 9306, Chen et al. (2006) detected only two QTLs. In comparison, enhanced efficiency of QTL identification in our study might be attributed to larger population (or more RILs) and more markers used in the experiments. The QTL on 3BS for FHB resistance has been widely validated in various resources of resistance in wheat, including some of the original parents of CJ 9306, Sumai 3 and its derivatives (Anderson et al. 2001; Buerstmayr et al. 2002; Zhou et al. 2002; Yang et al. 2005b), Wangshuibai (Jia et al. 2005; Lin et al. 2004, 2006; Zhang et al. 2004; Zhou et al. 2004; Mardi et al. 2005), Frontana and its derivatives (Somers et al. 2003; Han et al. 2005), W14 (Chen et al. 2006), etc.

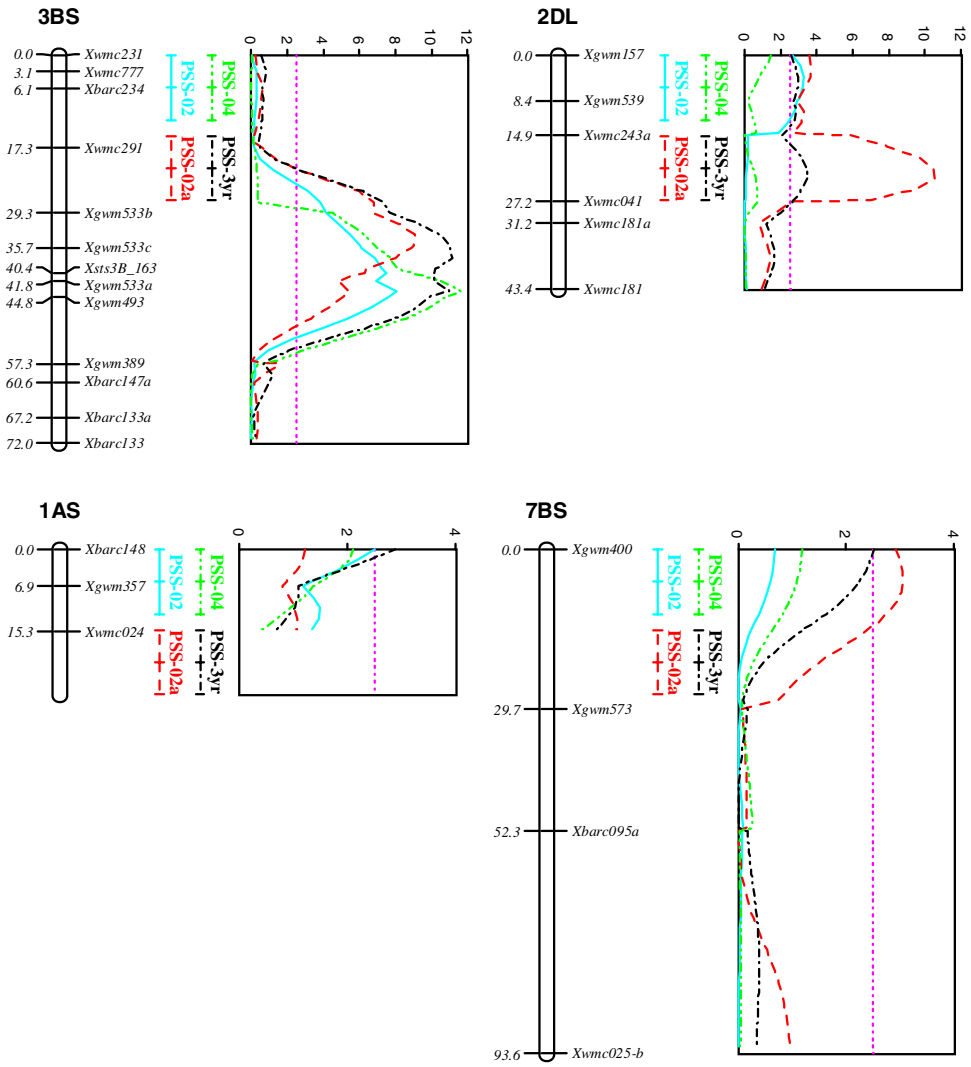

Fig. 2 QTL mapping for FHB Type II resistance in an F_7 RIL population derived from the wheat cross Veery/CJ 9306 based on CIM analysis of the percentage of scabby spikelets (PSS) after single-floret inoculation in the greenhouse

The explained phenotypic variations varied from 4–60%, depending on specific experiments, sources of resistance, and parameters and types of resistance. Yang et al. (2005a) suggested that the QTL (*Qfhb.ksu-3BS1*) had only marginal significance in a population derived from the Korean FHB-resistant cultivar Chokwang. In our study, this QTL (*QFhs.ndsu-3BS*) could explain 18.2–27.8% of phenotypic variance for individual experiments, but up to 30.7% for the overall average of three experiments. Based on the SSR markers associated with the QTL and their effects as well as explained phenotypic variation, we assume that this major QTL in CJ 9306 might be derived from one of the resistant varieties Sumai 3, Ning 7840 and Wangshuibai. Haplotype analysis might produce more detailed clarification. A comparison of alternative groups of RILs with marker alleles from Veery and CJ 9306 also indicated that, on average, the favorable alleles from CJ 9306 for the markers *Xgwm533a*, *Xgwm533b* or *Xgwm493* within the flanking region for this QTL could lead to a reduction of 17.2–28.1% for PSS or 3.2–4.9 for NSS, further indicating its important role as a major QTL in the inheritance of FHB resistance. Therefore, selection of this QTL would significantly increase the resistance of offspring.

In this study, another major QTL on 2DL was detected by CIM in two of three experiments and combined analysis, explaining 9.9–28.4% of phenotypic variation for PSS. There was a significant interaction between this QTL and environments. Over all three experiments, it could decrease the PSS by 14.3% and NSS by 2.8, respectively. Somers et al. (2003) reported a QTL having peak marker *Xgwm539* on 2DL in Wuhan-1, which was assigned the designation *QFhs.crc-2D* in GrainGenes. Yang et al. (2005b) from the same laboratory detected a QTL on 2DS with peak marker *Xwmc144* in DH181 (a derivative of Sumai 3), but did not consistently confirm the peak marker *Xgwm539*. In their study, the QTL on 2DL was detected for Type II resistance (SFI) in only one of two experiments, and not significant for DON accumulation and field infection (Somers et al.

Table 3 Means of RILs carrying different alleles of QTLs and QTL combinations for FHB resistance in the F_7 RIL population derived from the wheat cross Veery/CJ 9306 for average percentage of scabby spikelets (PSS) over three experiments

QTL (marker)	Allele[a]	PSS	QTL combination	Allele[a]	PSS
QFhs.ndsu-3BS	V	63.8 ± 3.1	*3BS + 2DL*	V + V	70.4 ± 4.1
(*Xgwm533a*)	CJ	40.5 ± 3.0		V + CJ	55.4 ± 4.4
	Difference[b]	23.2****		CJ + V	46.9 ± 3.9
				CJ + CJ	31.0 ± 4.3
QFhs.nau-2DL	V	56.9 ± 2.9		R^2 (%)	26.6**
(*Xgwm539*)	CJ	42.5 ± 3.3	*3BS + 1AS*	V + V	67.9 ± 4.3
	Difference	14.3****		V + CJ	54.5 ± 4.5
				CJ + V	46.6 ± 4.7
QFhs.nau-1AS	V	56.2 ± 3.3		CJ + CJ	28.0 ± 3.5
(*Xbarc148*)	CJ	39.0 ± 3.4		R^2 (%)	30.2**
	Difference	17.2****	*3BS + 7BS*	V + V	71.0 ± 3.1
				V + CJ	49.9 ± 5.7
QFhs.nau-7BS	V	55.7 ± 2.7		CJ + V	45.4 ± 3.9
(*Xgwm400*)	CJ	40.4 ± 3.5		CJ + CJ	32.3 ± 4.1
	Difference	15.3****		R^2 (%)	25.9**
			3BS + 2BL	V + V	51.7 ± 5.7
QFhs.nau-5AS	V	57.5 ± 3.6		V + CJ	66.5 ± 5.4
(*Xgwm425*)	CJ	47.2 ± 3.1		CJ + V	26.9 ± 5.0
	Difference	10.3****		CJ + CJ	44.4 ± 4.6
				R^2 (%)	27.4**
QFhs.nau-1BC	V	42.0 ± 3.7	*3BS + 2DL + 1AS*	CJ + CJ + V	41.1 ± 7.8
(*Xbarc1160*)	CJ	53.4 ± 2.7		CJ + CJ + CJ	19.1 ± 3.4
	Difference	–11.4****		R^2 (%)	34.8**
			3BS + 2DL + 7BS	CJ + CJ + V	39.0 ± 8.1
QFhs.nau-2BL	V	40.3 ± 3.9		CJ + CJ + CJ	24.4 ± 3.8
(*Xbarc128*)	CJ	53.5 ± 3.7		R^2 (%)	33.6**
	Difference	–13.2****	*3BS + 2DL + 5AS*	CJ + CJ + V	41.0 ± 7.8
				CJ + CJ + CJ	25.2 ± 4.9
QFhs.nau-2AL	V	46.4 ± 3.1		R^2 (%)	31.7**
(*Xgwm356*)	CJ	54.5 ± 3.1	*3BS + 2DL + 2BL*	CJ + CJ + V	19.6 ± 7.7
	Difference	–8.1***		CJ + CJ + CJ	50.8 ± 9.3
				R^2 (%)	27.1**
QFhs.nau-5BL	V	46.5 ± 3.3	3BS + 1AS + 5AS	CJ + CJ + V	39.1 ± 6.9
(*Xgwm408*)	CJ	52.9 ± 3.0		CJ + CJ + CJ	22.5 ± 4.4
	Difference	–6.4**		R^2 (%)	31.3**

, *, ****: Significant at $P < 1$, 0.1 and 0.01%, respectively

[a] V = Homozygous alleles for Veery, and CJ = Homozygous alleles for CJ 9306, respectively

[b] The positive value indicates that the favorable allele was from CJ 9306, whereas the negative value indicates that the favorable allele was from Veery. The significance of differences was on the basis of ANOVA results

2003). In our experiments, however, the QTL on 2DL in CJ 9306 was also detected for DON accumulation (detail will be presented in the next paper). Moreover, there were not direct relationships between CJ 9306 and Wuhan-1 in the pedigrees. CJ 9306 was developed through multiple-parent crossing and recurrent selection, with five agronomic parents and 15 resistant varieties included originally (Jiang et al. 2006a). The exact pedigree of Wuhan-1 is unknown (Somers et al. 2003). We suppose that the QTL on 2DL in CJ 9306 is most likely the same as the QTL reported by Somers et al. (2003) since both had the same marker *Xgwm539*, but they may have different alleles and different functions/expressions in the resistance. Therefore, we assign a new designation *QFhs.nau-2DL* to this QTL in CJ 9306. Jia et al. (2005) and Mardi et al. (2005) separately reported a QTL on 2D in the Chinese landrace

Wangshuibai, but the associated intervals were different. So far, except for Wangshuibai, no other parents of CJ 9306 have been reported to carry a QTL on 2DL. Therefore, we suppose that this QTL (*QFhs.nau-2DL*) in CJ 9306 was most likely derived from Wangshuibai or another uninvestigated parent of CJ 9306, but not from Sumai 3, Ning 7840 and Frontana.

For the markers linked to QTLs on 1AS and 7BS, the average of RILs with favorable alleles from CJ 9306 for PSS and NSS was 11.7–21.2% and 1.6–3.4 lower than that of Veery-allele RILs, respectively. No SSR markers associated with FHB resistance on chromosome 1AS have been reported to date, although a QTL on 1AL was detected by Guo et al. (2006). *QFhs.nau-1AS* identified in this study is the first one localized on 1AS contributing to FHB resistance in wheat, and thus its origin is unclear. Although Wangshuibai was reported to have a QTL on chromosome 7B (Jia et al. 2005), it was still not assured that Wangshuibai was the original source of *QFhs.nau-7BS* in CJ 9306 since the flanking intervals were not the same in these two resistant germplasms.

Previous studies suggested that there were QTLs on 5A or 5AS for Type II resistance (Buerstmayr et al. 2002; Chen et al. 2006), Type I resistance (Yang et al. 2005b), and field resistance (including Type I and II resistance) (Gervais et al. 2003; Jia et al. 2005; Yang et al. 2005b; Chen et al. 2006); but no uniform designation was assigned, and the explained phenotypic variances were very variable (4–26%). In our study, this QTL was so weak that it could not be detected by CIM in all cases. Its effects were smaller than the effects of other QTLs in CJ 9306, and significant only for Experiment 02 and a combined analysis over all three experiments. The reason for this might be because of different backgrounds, lack of enough linked markers and/or possible masking of other major QTLs. Even so, the favorable allele of QTL on 5AS (designated as *QFhs.nau-5AS*) from CJ 9306 could reduce PSS by 10.3%, or NSS by 1.5. In the same experiments or populations, the QTLs on 5AS were not detected for Type II resistance but for Type I resistance (Yang et al. 2005b; Lin et al. 2004, 2006), or its effects and explained phenotypic variations for Type II resistance were smaller than those for the field resistance (Chen et al. 2006). Therefore, it might be supposed that the QTL on 5AS played a more important role in field/Type I resistance than in Type II resistance. Based on reported studies and data now available, the source of *QFhs.nau-5AS* in CJ 9306 is still not determined although it might likely be Wangshuibai or Sumai 3.

In addition to the favorable QTLs from CJ 9306, five minor QTLs were also detected in the susceptible cultivar Veery, and were localized on 1BC (centromeric region), 2BL, 2AL and 5BL, respectively, with one not localized because of insufficient marker data. Previous studies suggested that the QTLs on these four chromosomes could be derived from either resistant or susceptible varieties/lines. For instance, the QTLs on 2B and/or 2A were identified in the resistant Ning 7840 (Zhou et al. 2002) and Renan (Gervais et al. 2003), and in the susceptible Nanda 2419 (Lin et al. 2004) or Stoa (Waldron et al. 1999; Anderson et al. 2001) as well. Likewise, the QTLs on 1B and/or 5B were detected in resistant variety Wangshuibai (Lin et al. 2004; Jia et al. 2005) and susceptible Alondra's (Zhang et al. 2004) or Patterson (Bourdoncle and Ohm 2003). This may provide some underlying elaboration on the evident transgressive segregation toward susceptibility in the RIL and F_2 populations (Jiang and Ward 2006). Comparatively speaking, *QFhs.nau-2BL* and *QFhs.nau-1BC* exhibited larger effects than the other three QTLs, which showed significant effects for one of three experiments as well as the overall average data. Waldron et al. (1999) detected a QTL on 2AL in the RIL population Sumai 3/Stoa using RFLP markers, and named it *QFhs.ndsu-2A*. Because different DNA markers (SSR markers) were used in the present study, the relationship or allelism between our QTL on 2AL (*QFhs.nau-2AL*) and *QFhs.ndsu-2A* could not be compared. In other words, it is currently difficult to determine if they are the same or different. Therefore, we would use a new name instead. For the QTLs associated with FHB resistance on 1BC, 2BL and 5BL, formal naming was not done until now. Thus we would propose our names for reference.

It is problematic to directly compare validation results between different studies (Pumphrey et al. 2007). As discussed above, the effects and explained variations of a QTL varied usually with different backgrounds/populations, resistance types and parameters, inoculation techniques and disease pressures, and the types and numbers of DNA markers. Therefore, it could be expected that the amounts of variation accounted for by a QTL were different in the literature. This point should be taken into account in the practical application of marker-assisted selection.

QTL × E and QTL × QTL interactions

Conventional genetic studies showed that the Type II resistance to FHB in CJ 9306 was inherited in an additive-dominance model, and there were significant differences in the expression of resistance between years and a significant interaction between genotypes and environments (Jiang and Ward 2006; Jiang et al. 2006b). In this study, significant QTL × E interactions were detected for *QFhs.nau-2DL*, *QFhs.nau-1BC* and *QFhs.nau-2AL*. In addition, the differences in QTL effects between years/experiments

were significant for most of the QTLs. Therefore it would be necessary that the effects of the QTLs and selection responses were validated repeatedly under different environments. QTL × QTL interactions were reported in some studies (Jia et al. 2005; Yang et al. 2005b; Guo et al. 2006; Lin et al. 2006; Ma et al. 2006). In this study, however, no significant epistasis was detected for major QTLs. As for epistatic interactions among the minor QTLs, further investigations are needed.

Marker-assisted selection for two or more loci

The cumulative effects of two QTLs for FHB resistance were investigated (Buerstmayr et al. 2002, 2003; Somers et al. 2003; Steiner et al. 2004; Guo et al. 2006). Genotypes fixed for two resistance QTLs had the lowest disease severity compared with the other three possible genotypes. Somers et al. (2003) suggested that marker-assisted selection (MAS) for favorable alleles at two loci was not significantly different from MAS for favorable alleles at either locus alone. However, other results suggested that the average of the lines with favorable alleles at both loci for disease severity was significantly lower than that of the lines with favorable alleles at either locus alone (Buerstmayr et al. 2002, 2003; Steiner et al. 2004; Guo et al. 2006). In our study, the averages of PSS and NSS of RILs bearing favorable alleles at two loci were not only significantly smaller than those of the reciprocal genotypes (without favorable alleles at both loci) in all cases, but also significantly smaller than those of RILs with favorable alleles at only one locus in most cases. This implies that the effects of MAS for favorable alleles at two loci would be greater than those of MAS for either locus alone in the improvement of FHB resistance.

Furthermore, we first tried a comparison of three-locus combinations. The averages of PSS and NSS of RILs carrying favorable alleles at all three loci were the lowest among all possible combinations at three loci in most cases. In other words, the resistance of genotypes with favorable alleles at two loci could be further enhanced by an additional favorable allele at the third locus (Table 3). For QTL/marker combinations at three loci, the average levels of resistance from low to high in genotypes were: no favorable allele—one favorable allele—two favorable alleles—three favorable alleles, except for the non-reciprocal comparisons. When four or five loci carrying favorable alleles from CJ 9306 were considered simultaneously, the coefficients of determination between the accumulated effects of alleles for different combinations and the averages of PSS or NSS for the corresponding RILs were 0.329–0.409 ($P < 0.01$). Therefore, we conclude that the effects of FHB resistance QTLs/genes could be accumulated, and the resistance could be feasibly enhanced by selection of favorable alleles for multiple loci in breeding programs.

Our results also suggest that the following two- and three-locus QTL combinations could be the preferential choices in practical MAS programs: *QFhs.ndsu-3BS* + *QFhs.nau-2DL*, *QFhs.ndsu-3BS* + *QFhs.nau-1AS*, *QFhs.ndsu-3BS* + *QFhs.nau-7BS* and *QFhs.ndsu-3BS* + *QFhs.nau-2BL*, and *QFhs.ndsu-3BS* + *QFhs.nau-2DL* + *QFhs.nau-1AS* and *QFhs.ndsu-3BS* + *QFhs.nau-2DL* + *QFhs.nau-2BL*. Selection of favorable alleles for these QTL combinations would result in the best efficiency of improvement of FHB resistance. In addition, among the best resistant RILs with a resistance similar to CJ 9306, none had all of the same alleles as CJ 9306 for the ten QTLs described above. In other words, some QTL combinations different from CJ 9306 could also reach a very high level of resistance. As such, is it possible to develop a cultivar/line with a higher resistance than CJ 9306 by selecting the favorable alleles at all ten loci simultaneously? In the present population, no such segregant or RIL was produced due to the limited size of population. Clearly, it deserves an attempt. Pyramiding different resistance genes/QTLs should be a feasible approach to this goal.

Utilization of CJ 9306

As most of the highly FHB resistant varieties, such as Wangshuibai, Sumai 3 and its derivatives, have many inferior agronomic characteristics, breeders were reluctant to use such sources in breeding programs (Buerstmayr et al. 2002). The success of their utilization in practical breeding has been limited. Because of its superior performance in FHB resistance as well as well-improved agronomic traits, CJ 9306 is a valuable alternative (Jiang et al. 2006a). This study and previous experiments (Jiang and Ward 2006) suggested that around 10% of RILs or 40% of F_2 individuals derived from CJ 9306 exhibited a high level of resistance (PSS < 15% or NSS < 2.5). Recent breeding practice indicated that CJ 9306 and its sister line CJ W14 were highly effective sources and had excellent combining ability with US winter wheats although they are spring types. Moreover, CJ 9306 also had an excellent resistance to mycotoxin accumulation and exhibited good field resistance similar to that of Sumai 3, besides a very high level of Type II resistance (Jiang et al. 2006a, b). By pyramiding different QTLs through MAS, the efficiency of utilizing CJ 9306 in breeding would be accelerated. QTL analysis for these types of resistance will provide further elaborations on the underlying genetic basis of resistance and helpful information for breeding.

In breeding practice, however, the effects of a QTL vary significantly with different backgrounds, even for the

strongest QTL on 3BS (or *Fhb1*). For instance, in the recent data presented by Pumphrey et al. (2007), the QTL *Fhb1* varied from no effects to substantial effects among 19 pairs of near-isogenic lines (NILs), although the reduction in FHB disease parameters was significant overall. Moreover, different QTLs/genes might mask the effects of each other due to epistatic interactions in some cases, although the additivity of QTLs was convincingly demonstrated in our study. A line with moderate resistance due to the presence of other resistance QTL may not benefit as much by the addition of another resistance locus as a line without other resistance genes (Pumphrey et al. 2007). Therefore, it is not necessarily expected that the effects of the validated QTLs in this population derived from Veery/CJ 9306 would be so evident in other populations.

In addition, this study also demonstrated a successful example of integrating multiple QTLs for FHB resistance by recurrent selection. In CJ 9306, an excellent multiple-QTL combination produced a high level of resistance. CJ 9306 could serve as the evidence that recurrent selection has been successful not only phenotypically (Jiang et al. 1994, 1995), but also genotypically. It was well demonstrated that pyramiding multiple favorable genes from different parents or varieties could be realized through recurrent selection, even without markers. Of course, MAS could enhance the efficiency of recurrent selection and accelerate the progress of the procedure. Therefore, it should be a valuable strategy to incorporate MAS into recurrent selection programs as well.

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