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Quantitative trait loci for resistance to fusarium head blight and deoxynivalenol accumulation in Wangshuibai wheat under field conditions

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Wangshuibai is a Chinese landrace wheat with a high level of resistance to fusarium head blight (FHB) and deoxynivalenol (DON) accumulation. Using an F7 population of recombinant inbred lines (RILs) derived from the cross between Wangshuibai and Annong 8455 for molecular mapping of quantitative trait loci (QTL) for FHB resistance, the proportion of scabbed spikelets (PSS) and DON content were assessed under field conditions. Composite interval mapping revealed that two and three QTL were significantly associated with low PSS and low DON content, respectively, over 2 years. QTL on chromosomes 3B and 2A explained 17 and 11·5%, respectively, of the phenotypic variance for low PSS, whereas QTL on chromosomes 5A, 2A and 3B explained 12·4, 8·5 and 6·2%, respectively, of the phenotypic variance for low DON content. The 3B QTL appeared to be associated mainly with low PSS, and the 5A QTL primarily with low DON content in Wangshuibai. The 2A QTL had minor effects on both low PSS and DON content. Microsatellite and AFLP markers linked to these QTL should be useful for marker-assisted selection of QTL for low PSS and low DNA content from Wangshuibai.

Keywords: deoxynivalenol, fusarium head blight, molecular markers, QTLs, *Triticum aestivum*

Introduction

Fusarium head blight (FHB), primarily caused by *Fusarium graminearum*, is a devastating and insidious disease of wheat in humid and semihumid areas worldwide. In China, FHB has affected more than seven million hectares of wheat and caused yield losses of more than one million tonnes in severe epidemics (Yao & Lu, 2000). In the USA, several severe FHB outbreaks on wheat and barley from 1991 to 1997 resulted in about $1·3 billion of direct losses, with a cumulative economic impact of $4·8 billion of losses (Johnson *et al*., 2003), and the disease remains a threat to wheat production in many other countries (Bai & Shaner, 2004).

Infected grain is often contaminated with deoxynivalenol (DON), a mycotoxin mainly produced by *F. graminearum*. As epidemics become more frequent and severe in many countries, DON contamination of wheat and other small grain crops is becoming a major concern for animal production and human health (reviewed by Desjardins, 2006).

The employment of cultivars with high FHB resistance and low DON content is the most economical and effective method to reduce losses caused by FHB (Bai & Shaner, 2004). FHB resistance is quantitatively inherited in wheat. Although germplasm immune to FHB has not been found, resistance to FHB and DON accumulation is well documented in wheat and its relatives (Mesterhazy, 1995; Buerstmayr *et al*., 1996; Bai *et al*., 2001; Miedaner *et al*., 2003; Cumagun *et al*., 2004).

Advances in molecular marker technology allow the dissection of quantitative trait loci (QTL) into individual Mendelian factors and mapping of these QTL to known chromosome regions (Paterson *et al*., 1988). QTL mapping sets the stage for the acceleration of the crop breeding process through marker-assisted selection. In the last few years, QTL for FHB resistance have been extensively studied and most of the resistance alleles are contributed by resistant germplasm, such as Sumai 3 and its derivatives (Bai *et al*., 1999; Waldron *et al*., 1999; Anderson *et al*., 2001; Zhou *et al*., 2002; Buerstmayr *et al*., 2002, 2003; Yang *et al*., 2005), Arina (Paillard *et al*., 2004), Frontana (Steiner *et al*., 2004), Ning7840 (Shen *et al*., 2003a), F201 (Shen *et al*., 2003b), Renan (Gervais *et al*., 2003), Wangshuibai (Lin *et al*., 2004, 2006; Zhou *et al*., 2004; Zhang *et al*., 2004; Mardi *et al*., 2005), etc. However, most previous molecular mapping work mainly focused on FHB symptoms. There is a strong need to identify beneficial QTL for resistance to DON accumulation in wheat grain.

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The objectives of the present study were to identify and map QTL for low PSS and/or low DON content from a recombinant inbred line (RIL) population that originated from a cross between Wangshuibai and Annong 8455.

Materials and methods

Plant materials

A total of 118 F7 recombinant inbred lines (RILs) were derived from the cross of Wangshuibai × Annong 8455 by single-seed descent. Wangshuibai is a landrace originating from Jiangsu, China. It is one of the best scab-resistant sources and has been used in many breeding programmes. Annong 8455 (NPFP 73/Annong 1) is a FHB-susceptible wheat cultivar released from Anhui Agricultural University in China with superior grain quality.

The two parents and their F7 RILs were evaluated in the field with three replicates during the 2003 and 2004 growing seasons at the Jiangsu Academy of Agricultural Sciences experimental station in Nanjing. Thirty seeds per line were sown in a 1 m row in each replicate.

Evaluation of FHB

Conidial inoculum was produced from a mixture of local highly pathogenic isolates of *F. graminearum* using mung bean liquid medium (Bai *et al*., 2001). A droplet of conidia (approximately 1000 spores) was injected into a central floret of selected spikes at anthesis with a hypodermic syringe. Approximately 15 spikes per replicate were inoculated. Following inoculation, each spike was covered with a plastic bag for 24 h. Scabbed spikelets and the total number of spikelets in each inoculated spike were counted on day 21 after inoculation. Disease severity was calculated as the proportion of scabbed spikelets (PSS) in an inoculated spike.

DON analysis

Seeds of inoculated spikes from each replicate were ground for DON analysis. The flour sample was extracted by shaking with acetonitrile-water (86/16, v/v) using 5 mL solvent per 1 g sample for 2 h. Extracts were purified by filtration on a column (containing active carbon, aluminium and diatomite) and twice washed with 2 mL acetonitrile water. DON in the extract was measured by high-pressure liquid chromatography (HP1100 HPLC-system; Hewlett-Packard). A Spherisorb S5 ODZ2250 × 4·6 mm reverse-phase column (Waters) was used. The mobile phase used was methanol-water (25/75, v/v) at a flow rate of 1 mL min^{-1}. The detection wavelength was set at 220 nm.

SSR and AFLP analysis

DNA from parents and 104 F7 RILs were extracted from young leaves using the CTAB method (Saghai-Maroof *et al*., 1984) with minor modifications.

A total of 504 pairs of simple sequence repeat (SSR) primers were used for parental screening, including 265 GWM SSR primers (Röder *et al*., 1998) and 239 BARC primers (Song *et al*., 2005). PCR was performed in a volume of 25 μL in a Perkin-Elmer 9600 Thermal Cycler. The reaction mixture contained 250 nm of each primer, 0·2 mM of each deoxynucleotide, 1·5 mM $MgCl_2$, 1 unit *Taq* polymerase and 50–100 ng of template DNA. For PCR amplification, the reaction was incubated at 94°C for 3 min, then continued for 45 cycles each of 1 min of denaturing at 94°C, 1 min of annealing at 50, 55 or 60°C (depending on the SSR primers) and 2 min of extension at 72°C, with a final extension at 72°C for 10 min

For AFLP analysis, genomic DNA was double-digested with *Eco*RI and *Mse*I restriction enzymes and ligated to corresponding AFLP adaptors. A 30 μL aliquot of preamplified PCR mixture consisted of 1 × PCR buffer, 2·5 mM $MgCl_2$, 0·2 mM dNTP mix, 75 ng of each adapter-derived primer and 10 μL diluted template DNA. PCR was run for 29 cycles at 94°C for 30 s, 56°C for 1 min and 72°C for 1 min. The preamplified PCR product was then used as a template for further selective amplification. A total of 130 combinations of *Mse*I and *Eco*RI primers were screened between parents for polymorphism. For selective PCR, each 10 μL of PCR mixture contained 3 μL 10-fold-diluted preamplified DNA, 1 × PCR buffer, 2·5 mM $MgCl_2$, 0·2 mM dNTP mix, 10 ng *Mse*I primer, 0·35 pmol *Eco*RI primer and 0·2 unit of *Taq* polymerase. PCR was run for 13 cycles of 94°C for 30 s, 65°C for 30 s with a temperature reduction of −0·7°C per cycle in each following cycle, and 72°C for 60; this was followed by 23 cycles at 94°C for 30 s, 56°C for 30 s and 72°C for 60 s.

The amplified products from SSR and AFLP were separated in 6% denaturing polyacrylamide gels running at 80 W. The gel was visualized by silver staining.

Data analysis

Analyses of variance and correlation were carried out using SAS software ver.8·2 (SAS Institute Inc). JOINMAP 3·0 was used to create a genetic linkage map of SSR and AFLP markers (Van Ooijen & Voorrips, 2001) and MapQTL 5 (Van Ooijen, 2004) was used to identify the locations and effects of QTL. The threshold logarithm of the odds (LOD) value for claiming a significant QTL was selected based on a permutation test with 1000 runs.

Results

Phenotypic performance of RILs

The mean, range and distributions of PSS and DON content for the RIL population and their parents are summarized in Table 1 and Fig. 1. A wide range of PSS values on the 21st day after inoculation was observed among the RILs, from 2·4 to 79·0% over 2 years. Wangshuibai exhibited PSS values of 26·4 and 9·3% in 2003 and 2004, respectively, compared with 62·0 and 51·9% for Annong 8455. The population also segregated for DON content, with a

Table 1 Variation of proportion of scabbed spikelets (PSS) and deoxynivalenol (DON) content in wheat parents and recombinant inbred lines (RILs), 21 days after inoculation with *Fusarium graminearum*

				RIL population			
Trait	Year	Wangshuibai	Annong 8455	Max	Min	Mean	h^{2a}
PSS (%)	2003	26·4	62·0	79·0	15·7	41·7	
	2004	9·3	52·0	72·8	2·4	13·2	
	Mean	18·0	57·0	75.	9·0	27·4	0·74
DON content (mg kg^{-1})	2003	2·4	119·2	284·5	0·0	83·4	
	2004	5·6	36·4	47·4	0·0	15·1	
	Mean	4·0	87·8	166·0	0·0	49·2	0·78

[a]Broad-sense heritability.

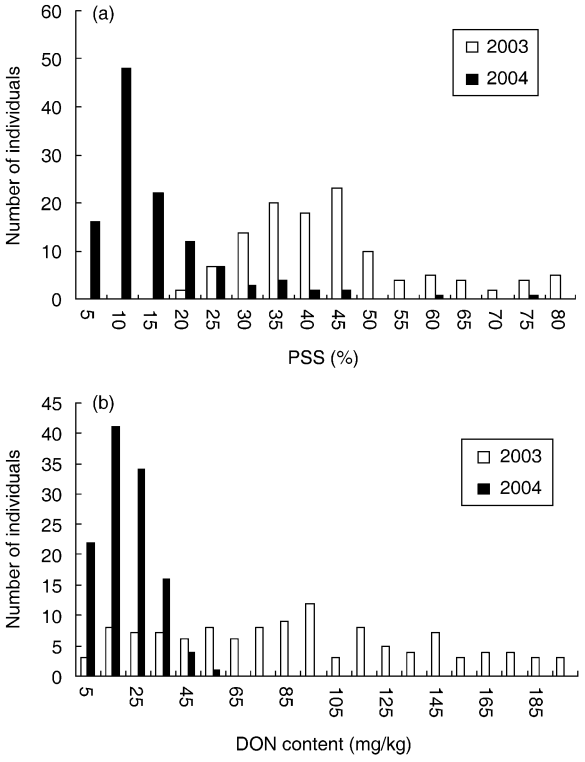

Figure 1 Distribution of proportion of scabbed spikelets (PSS) (a) and deoxynivalenol (DON) content (b) of F_7 recombinant inbred wheat lines (derived from a cross between Wangshuibai and Annong 8455) in 2003 and 2004, 21 days after inoculation with *Fusarium graminearum*.

range of 0–284·5 mg kg^{-1} over 2 years. The DON content of Wangshuibai was 2·4 mg kg^{-1} in 2003 and 5·6 mg kg^{-1} in 2004. Annong 8455 had a DON content of 119·2 mg kg^{-1} in 2003 and 36·4 mg kg^{-1} in 2004.

The mean PSS and DON content for the RIL population were significantly higher in 2003 than in 2004. This was mainly because the more humid weather in 2003 caused a more severe FHB epidemic in the Yangtze river valley area than in 2004 (Zhu *et al*., 2003). However, the correlation between the 2 years was significant at $P < 0·01$, with $r = 0·49$ for PSS and $r = 0·59$ for DON content. PSS was also weakly correlated with DON content, with correlation coefficients of 0·31 in 2003 and 0·35 in 2004.

ANOVA results showed that genotypic variation was significant for both PSS and DON content over 2 years (Table 2). The effects of year and genotype × year interaction were also significant. Broad-sense heritabilities for PSS and DON content were 0·74 and 0·78, respectively, over 2 years (Table 1).

Molecular markers

After 504 pairs of SSR primers and 130 AFLP primer combinations were screened for polymorphism between parents, 112 SSR and 347 AFLP fragments were identified as polymorphic between the two parents. Among them, 353 markers were mapped on 38 linkage groups covering a genetic distance of 1594 cM. Of the linkage groups, 29 could be associated to 19 chromosomes according to previously published map information (Röder *et al*., 1998; Somers *et al*., 2004; Song *et al*., 2005). Only chromosomes

Table 2 Analysis of variance for proportion of scabbed spikelets (PSS) and deoxynivalenol (DON) content in wheat parents (Wangshuibai and Annong 8455) and recombinant inbred lines (RILs), 21 days after inoculation with *Fusarium graminearum*

		PSS			DON content		
Source	d.f.	MS	*F*-value	*P*	MS	*F*-value	*P*
Years	1	40 654	160·69	< 0·001	127 010	159·5015	< 0·001
Replications (within year)	4	253	1·67	0·15	796	2·05	0·09
Genotypes	117	1 247	4·28	< 0·001	4 893	5·12	< 0·001
Genotypes/Years	117	291	1·92	< 0·001	955	2·46	< 0·001
Error	468	151			389		
Total	707						

Table 3 Quantitative trait loci associated with resistance to fusarium head blight and deoxynivalenol (DON) accumulation detected by composite interval mapping in the F_7 recombinant inbred line wheat population derived from the cross Wabgshuibai × Annong 8455

			2003			2004			Mean over 2 years		
Trait[a]	Chr.	Flanking marker	LOD	R^2	Add.[b]	LOD	R^2	Add.	LOD	R^2	Add.
PSS	3B	*Xgwm533·1-Xbarc133*	5·03**	17·9	−16·31	2·52**	13·3	−7·07	4·97**	17·0	−13·42
	2A	*Xgwm425-XmCCT.eAAG.2*	2·56**	11·9	−4·85	2·03*	10·0	−4·11	2·48**	11·5	−4·37
	5A	*Xgwm186-XmCCA.eAAG.2*	–	–	–	1·92*	6·4	−3·81	–	–	–
DON	5A	*XmCCA.eAAG.2-Xgwm156*	2·46**	12·7	−5·08	2·28**	11·1	−8·17	2·40**	12·4	−7·34
	2A	*Xgwm425-XmCCT.eAAG.2*	2·01*	9·9	−4·75	1·96*	7·4	−6·02	1·98*	8·5	−5·96
	3B	*Xbarc102-Xgwm533·1*	–	–	–	1·83*	5·7	−5·60	–	–	–
		Xgwm533·1-Xbarc133	–	–	–	–	–	–	1·89*	6·2	−4·82

*,**, correspond to 0·05 and 0·01 significance levels, respectively, for the closest marker based on 1000 permutations.
[a]PSS, proportion of scabbed spikelets, DON, deoxynivalenol content; 21 days after inoculation with *Fusarium graminearum*.
[b]Additive effect of Wangshuibai allele.

1D and 4D had no mapped SSR markers. Eleven AFLP linkage groups did not contain any SSR markers and therefore their chromosome identity was not determined.

QTL mapping

Composite interval mapping was used to detect putative QTL for low PSSs and low DON content. Three QTL for low PSS were detected on chromosomes 3B, 2A and 5A (Table 3, Fig. 2). The QTL on chromosome 3B was mapped on the short arm and positioned in the 5 cM interval between SSR markers *Xgwm533·1* and *Xbarc133* in both years. This QTL explained the largest portion of the phenotypic variance, with R^2 values of 17·9 and 13·3% for 2003 and 2004, respectively. The QTL on chromosome 2A was also consistent over 2 years. It was located between SSR marker *Xgwm425* and AFLP marker *XmCCT.eAAG.2* and explained 11·9 and 10·0% of the total phenotypic variance in 2003 and 2004, respectively. The third QTL was located on chromosome 5A and flanked by SSR marker *Xgwm186* and AFLP marker *XmCCA.eAAG.2*, but it showed a minor effect, with only a marginally significant LOD value detected in 2004. All these QTL were from the resistant parent Wangshuibai and demonstrated reduced PSS.

Composite interval mapping indicated that the three QTL on chromosomes 5A, 2A and 3B also contributed to low DON content in Wangshuibai. However, the rank of QTL effects on low DON content for each QTL was different from that for low PSS. The QTL on chromosome 5A had the largest effect on low DON content across 2 years, accounting for 12·7 and 11·1% of the total phenotypic variance for low DON content in 2003 and 2004, respectively. This QTL was positioned in the 5 cM interval between *Xgwm156* and *XmCCA.eAAG.2*, the same region as the minor QTL associated with low PSS on chromosome 5A in 2004. The QTL on chromosomes 2A and 3B explained smaller portions of phenotypic variation for low DON content than the 5A QTL. The QTL on 2A was located on the same chromosome region for low PSS and explained 8·5% of phenotypic variation of low mean DON content over 2 years. The QTL on chromosome 3B was linked to different, but closely linked, markers in 2 years. It was significant only in 2004, when it explained 5·7% of the phenotypic variation for low DON. When the means were averaged over 2 years, this QTL explained 6·2% of the phenotypic variation and mapped to the same chromosome region for low PSS. All marker alleles for low-DON QTL were from the resistant parent Wangshuibai.

Discussion

In the present study, the F_7 RIL population derived from Wangshuibai × Annong 8455 was evaluated for the proportion of scabbed spikelets (PSS) and DON content under field conditions over 2 years. The frequency distributions of the RILs for PSS and DON content revealed that FHB resistance and low DON content were quantitatively inherited in this population. Similar findings were reported in previous studies for both traits (Bai & Shaner, 2004). Phenotypic expression of FHB is affected by environmental factors. PSS and DON content in 2003 were much higher than in 2004 because a more severe epidemic occurred in 2003 in the Yangtze river valley of China. Significant effects of year and genotype × year interaction for both traits were also found. Despite this, broad-sense heritabilities over 2 years were high for PSS and DON content (Table 1), indicating that assessments of FHB resistance and DON accumulation are reproducible.

Correlations between PSS and DON content have been extensively studied, but the results from different reports are inconsistent. High correlations between FHB severity and DON content were reported in some wheats (Teich *et al.*, 1987; Miedaner *et al.*, 2001, 2003), but most studies revealed only low to moderate associations and correlation coefficients that were strongly influenced by location and year (Miedaner & Perkowski, 1996; Mesterhazy *et al.*, 1999; Bai *et al.*, 2001; Somers *et al.*, 2003). Phenotypic correlation between PSS and DON content was weak (r = 0·31–0·35) in the present study, indicating that there are different components of

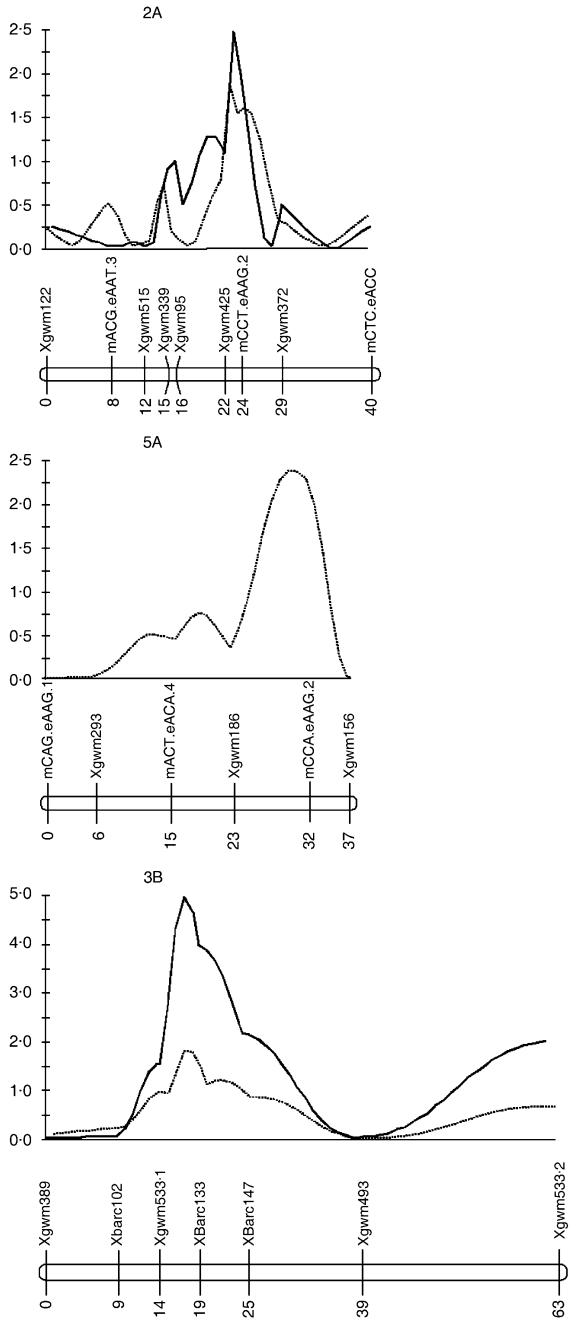

Figure 2 Portion of genetic linkage map derived from F_7 recombinant inbred wheat lines showing chromosome positions of putative quantitative trait loci (QTL) associated with resistance to fusarium head blight and deoxynivalenol (DON) accumulation over 2 years. Solid lines show QTL associated with low average proportion of scabbed spikelets (PSS) over 2 years; dotted lines show QTL associated with low average DON content over 2 years.

resistance: resistance to disease spread and to toxin accumulation.

In the Wangshuibai × Annong 8455 population, putative QTL associated with resistance to FHB were detected on chromosomes 3B, 2A and 5A. The QTL on chromosome 3B showed the largest effect on phenotypic FHB resistance and explained 17·0% of the phenotypic variance over 2 years. This QTL was previously identified as a main-effect QTL for FHB resistance in Wangshuibai (Lin *et al*., 2004; Zhou *et al*., 2004; Zhang *et al*., 2004; Mardi *et al*., 2005). A QTL from a similar chromosome region with a major effect on FHB resistance was also reported in several other cultivars from China, such as Sumai3, Ning 894037 and Huapei 57-2. (Waldron *et al*., 1999; Anderson *et al*., 2001; Buerstmayr *et al*., 2002; Zhou *et al*., 2002, 2004; Bourdoncle & Ohm, 2003; Shen *et al*., 2003b). In Sumai 3 and its derivatives, this QTL for FHB resistance was mapped to the distal end of chromosome 3BS (Waldron *et al*., 1999; Zhou *et al*., 2002). Based on its linked markers, the QTL from Wangshuibai also located in the same region and is likely to be the same QTL as that of Sumai 3. However, the QTL in Wangshuibai had less effect on FHB resistance than that from Sumai 3, and the banding pattern of linked SSR markers was different from that in Sumai 3, suggesting that the 3BS QTL in Wangshuibai is most likely allelic to the 3BS QTL in Sumai 3. Wangshuibai has no evident association with Sumai 3 in its pedigree. Some researchers showed that the resistance QTL on chromosome 3BS in Sumai 3 was derived from Taiwan wheat (Zhou *et al*., 2002); therefore the possibility cannot be ruled out of a potential genetic relationship between the two varieties, because Wangshuibai and Taiwan wheat both originated from the Yangtze river valley in China.

In addition to the QTL on chromosome 3BS, QTL with smaller, but significant, effects for phenotypic FHB resistance were located on chromosomes 2A and 5A. QTL associated with FHB resistance on chromosome 2A were found from other wheat varieties (Waldron *et al*., 1999; Anderson *et al*., 2001; Zhou *et al*., 2002; Paillard *et al*., 2004; Steiner *et al*., 2004). However, the chromosome location was not consistent between studies. The FHB QTL was mapped at the end of chromosome 2AS of Ning7840 (a derivation from Sumai3) (Zhou *et al*., 2002), but on the end of chromosome 2AL in Stoa and Arina (Waldron *et al*., 1999; Anderson *et al*., 2001; Paillard *et al*., 2004). In the present study, the QTL was located near the centromere of chromosome 2A and had a smaller effect than the QTL on chromosome 3BS, which suggests that the QTL from divergent sources are different. The QTL on chromosome 5A was only detected in 2004, indicating that the QTL has a minor effect on PSS. Lin *et al*. (2006) identified a QTL associated with spread resistance to FHB on chromosome 5A in Wangshuibai, but it seemed to be in a different region on chromosome 5A from that in the present study.

QTL for low DON content were detected on chromosomes 5A, 2A and 3B. The QTL on chromosomes 3B and 2A were mapped to the same genomic region as for low PSS. The QTL on chromosome 5A overlapped with the QTL for low PSS in 2004. This QTL for low PSS was also reported in CM-82036 (Buerstmayr *et al*., 2002), DH181 (Yang *et al*., 2005), Frontana (Steiner *et al*., 2004), Renan (Gervais *et al*., 2003) and Patterson (Shen *et al*., 2003a).

Somers *et al.* (2003) reported a QTL controlling DON accumulation on chromosome 5AS linked to marker *Xgwm96* in Maringa. The SSR marker *Xgwm96* was located on chromosome 5AL near the centromere on the consensus map (Somers *et al.*, 2004), about 6 cM from *Xgwm156*. *Xgwm156* was the closest marker to the LOD peak of the QTL for low DON content in present study. The 3B and 5A QTL had contrasting effects on resistance to phenotypic FHB and DON accumulation. The 3B QTL had a much larger effect than the 5A QTL for FHB resistance, whereas 5A QTL had a much larger effect than the 3B QTL for resistance to DON accumulation. This indicates that the 3B QTL may contribute more to phenotypic FHB resistance, whereas the 5A QTL appears to play an important role in resistance to DON accumulation. However, whether resistance to DON accumulation is independent of resistance to disease severity is still equivocal, because disease severity may affect kernel development. DON is usually measured from harvested grains; if infected, the ovary may never develop into a mature kernel, and thus the DON content in the harvested grain may be lower than might be expected based on intensity of head blight symptoms.

In this study, several SSR markers were identified as associated with QTL for both low PSS and low DON on chromosomes 2A, 3B and 5A. Their availability will facilitate marker-assisted selection to obtain improved lines by pyramiding both resistances to phenotypic FHB and DON accumulation in wheat breeding and enabling transfer of the resistance genes from Wangshuibai.

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