Theor Appl Genet (2011) 122:1497–1502
DOI 10.1007/s00122-011-1549-0

ORIGINAL PAPER

Quantitative trait loci for resistance to fusarium head blight in a Chinese wheat landrace Haiyanzhong

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Received: 31 October 2010 / Accepted: 31 January 2011 / Published online: 23 February 2011

Abstract Fusarium head blight (FHB) of wheat causes not only significant reduction in grain yield and end-use quality, but also the contamination of the grain with mycotoxins that are detrimental to human and animal health after consumption of infected grain. Growing resistant varieties is an effective approach to minimize the FHB damage. The Chinese wheat landrace Haiyanzhong (HYZ) shows a high level of resistance to FHB. To identify quantitative trait loci (QTL) that contribute to FHB resistance in HYZ, 136 recombinant inbred lines (RIL) were developed from a cross of HYZ and Wheaton, a hard spring wheat cultivar from the USA. The RIL and their parents were evaluated for percentage of scabbed spikelets (PSS) in both greenhouse and field environments. Five QTL were detected for FHB resistance in HYZ with one major QTL on 7DL. The 7DL QTL peaked at SSR marker *Xwmc121*, which is flanked by the SSR markers *Xcfd46* and *Xwmc702*. This QTL explained 20.4–22.6% of the phenotypic variance in individual greenhouse experiments and 15.9% in a field experiment. Four other minor QTL on 6BS (two QTL), 5AS and 1AS each explained less than 10% of the phenotypic variance in individual experiments. HYZ carried the favorable alleles associated with FHB resistance at the QTL on 7DL, 6BS and 5AS, and the unfavorable allele at the QTL on 1AS. The major QTL on 7D can be used to improve the FHB resistance in wheat breeding programs and add diversity to the FHB resistance gene pool.

Communicated by D. Mather.

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Introduction

Fusarium head blight caused by *Fusarium graminearum* is a destructive disease in wheat (*Triticum aestivum* L.) worldwide (Bai and Shaner 2004). It reduces grain yield and quality and it contaminates grains with fungal toxic metabolites such as deoxynivalenol (DON), rendering the grain unsuitable for human or animal consumption (Trail 2009). Growing resistant varieties is the most economic, effective, and environmentally friendly approach to control the disease.

The quantitative nature and multiple components of FHB resistance increase the complexity of FHB research. Quantitative trait loci (QTL) have been reported for four of the five types of FHB resistance: type I, resistance to initial infection; type II, resistance to fungal spread within the spike; type III, resistance to DON accumulation; and type IV, resistance to Fusarium-damaged kernels (FDK) (Mesterhazy 1995; Schroeder and Christensen 1963). To date, QTL associated with FHB resistance have been reported on 21 chromosomes of 46 different wheat accessions (Liu et al. 2009). QTL on chromosomes 1B, 2D, 3BS,

3A, 5A, 5B, 6B and 7A have been mapped in at least two populations (Liu et al. 2009). QTL on chromosomes 2BL, 2D, 3A, 3BS, 4B, 6AL and 7BS have been introduced into commercial cultivars by combining phenotypic selection with marker-assisted selection (Wilde et al. 2007, 2008). The Sumai3-derived resistance allele at the *Fhb1* locus on 3BS has been extensively used, due to its relatively consistent major effect (Anderson et al. 2001; Buerstmayr et al. 2002; von der Ohe et al. 2010; Zhou et al. 2002). Excessive reliance on a single resistance allele is not a wise breeding practice because it may not provide sufficient protection under severe FHB epidemics. A combination of *Fhb1* with additional major-effect genes/QTL could provide a high level of resistance and help maintain the genetic diversity of the FHB resistance gene pool. Therefore, there is a continuous need to identify effective resistance genes/QTL with major effects and pyramid them with *Fhb1* into commercial cultivars to minimize FHB losses in severe FHB epidemics.

Several Chinese landraces have been reported to show a high level of resistance (Yu et al. 2006, 2008). The QTL for FHB resistance harbored in these landraces have not been investigated. Haiyanzhong (HYZ) is a Chinese spring wheat landrace with superior resistance to FHB (Yu et al. 2006, 2008). The objectives of this study were to investigate QTL for FHB resistance in HYZ and quantify the effects of the QTL in a population of HYZ/Wheaton recombinant inbred lines (RIL).

Materials and methods

Plant materials and FHB evaluation

A population of 136 F_8-derived RIL was developed by single-seed descent from a cross between a susceptible US wheat variety Wheaton and a single plant from the Chinese resistant wheat landrace HYZ. The RIL were grown in 4″ × 4″ plastic pots in a greenhouse at 17 ± 2°C (night) and 22 ± 5°C (day) with supplemental light for 12 h and evaluated for FHB resistance in three consecutive greenhouse experiments and one field experiment at Manhattan, KS. An *F. graminearum* conidial spore suspension was prepared following Bai et al. (1999). The wheat spikes were inoculated by injecting 10 µL of the conidial spore suspension (100 spores/µL) into a floral cavity between the lemma and palea of a floret of middle spikelets of a spike using a syringe. Inoculated plants were maintained at 100% relative humidity for 48 h in a mist chamber, then returned to the greenhouse bench for further FHB development. Each greenhouse experiment was arranged in a randomized complete block design with two replicates (pots) of 5 plants per pot. In the field experiment, the RIL population and both parents were arranged in a randomized complete block design with two replications (blocks) in the KSU FHB Nursery, with about50 seeds per entry sown in a one-row plot in each replication. At anthesis, five spikes per row were inoculated by single-floret injection as described for the greenhouse experiments. Between heading and the late dough stage, plants in the FHB nursery were misted for 10 min every h using sprinklers. In both field and greenhouse experiments, the total number of spikelets and the number of scabbed spikelets were counted for each inoculated spike at 21 days after inoculation. The percentage of scabbed spikelets (PSS) was calculated.

DNA extraction and genotyping

Genomic DNA was isolated from 2-week-old wheat leaves of each RIL using a modified CTAB method (Maguire et al. 1994). Harvested leaf tissue was dried in a freeze dryer (ThermoSavant, Holbrook, NY) for 48 h and ground using a Mixer Mill (MM 300, Retsch, Germany) for DNA isolation.

A total of 1,125 SSR primer pairs including primer sets of BARC, WMC, GWM, KSM, CFA, CFD and DUP (http://wheat.pw.usda.gov) were used to screen the parents. Primer pairs that detected polymorphism between the parents were used to a resistant bulk constructed by mixing equal amounts of DNA from 10 highly resistant RIL and a susceptible bulk constructed by mixing equal amounts of DNA from 10 highly susceptible RIL. Primer pairs that detected polymorphism between the contrasting bulks were used to genotype the RIL population. For SSR analysis, a 10-uL PCR mixture contained 40 ng template DNA, 1 mM each of reverse and M13-tailed forward primers and fluorescence-labeled M13 primer for PCR detection, 0.2 mM of each dNTP, 1X PCR buffer, 2.5 mM $MgCl_2$, and 0.6 U Taq polymerase. A touchdown PCR program was used for PCR amplification, in which the reaction mixture was incubated at 95°C for 5 min, then fie cycles of 45 s of denaturing at 95°C, 5 min of annealing at 68°C with a decrease of 2°C in each subsequent cycle, and 1 min of extension at 72°C; For another five cycles, the annealing temperature started at 58°C for 2 min with a decrease of 2°C for each subsequent cycle; PCR continued through an additional 25 cycles of 45 s at 94°C, 2 min at 50°C, and 1 min at 72°C with a final extension at 72°C for 5 min. Amplified PCR fragments were separated in an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, CA). All marker data were scored using GeneMarker 1.6 (Softgenetics Inc. LLC, State College, PA), and double checked visually to remove ambiguous data.

Genetic map construction and QTL analysis

A genetic linkage map was constructed with SSR markers using JoinMap version 3.0 (Van Ooijen and Voorrips 2001)

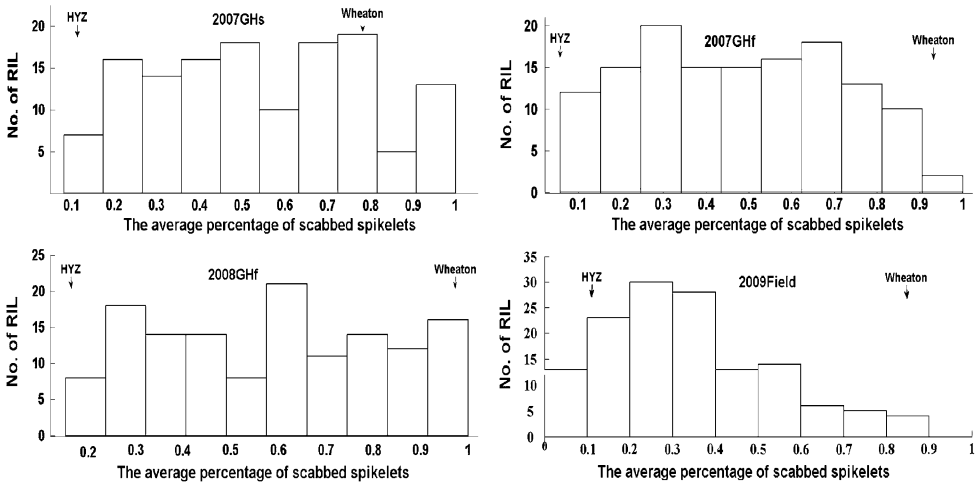

Fig. 1 The frequency distributions of PSS for RIL evaluated in greenhouse experiments of spring 2007 (2007GHs), fall 2007 (2007GHf), spring 2008 (2008GHs) and field experiment of spring 2009 (2009field)

and the Kosambi function (Kosambi 1944). The threshold value of LOD (logarithm of odds) score was set at 3.0 to claim linkage between markers with a maximum fraction of recombination at 0.4.

For QTL analysis, composite interval mapping (CIM) was performed with WINQTL Cartographer Version 2.5 (Wang et al. 2007) using Model 6, and five markers were used as controls with a window size of 10 cM. Multiple interval mapping (MIM) was performed to reveal the epistatic effects between the identified QTL. QTL analysis was done on the basis of line means from individual experiments. Permutation was performed 1,000 times to determine the LOD threshold to claim the significance of QTL ($P < 0.05$).

Statistic analysis

Broad-sense heritability (h^2) was computed as $\sigma g^2/(\sigma g^2 + \sigma e^2)$ based on the estimates of genetic and error variances derived from the analysis of variance (ANOVA). Matlab software (MathWorks Inc, Natick, Massachusetts, USA) was used to perform statistical analysis and to draw boxplots.

Results

Variation in resistance against FHB

The parent HYZ showed a high level of resistance in all three greenhouse experiments with an average PSS of 9.2%, ranging from 6.4 to 11.9%; whereas the parent Wheaton was highly susceptible with an average PSS of 98.8%, ranging from 97.5 to 100%. Similar FHB reactions were observed for the parents in the field experiment. The PSS for the RIL from the three greenhouse experiments ranged from 9.2 to 92.6% with an average of 53.2% and ranged from 6.9 to 87.4% with an average of 34.2% in the field experiment. The correlations of PSS were positive and highly significant among the three greenhouse experiments ($P < 0.0001$) and between the mean PSS from the greenhouse experiments and the field experiment ($P < 0.001$). Frequency distributions of PSS were continuous for both greenhouse and field data (Fig. 1). Transgressive segregation was not evident in the greenhouse experiments and the most resistant RIL showed a similar level of resistance as HYZ. In the field experiment, the majority of the RIL demonstrated moderate resistance. The environmental variation among four experiments was highly significant ($F = 80.39$, $P = 8.10\text{E-}41$), as was the variation for PSS among the 136 RIL ($F = 7.93$, $P = 1.49\text{E-}59$). The broad sense heritability estimate was 61.9% for means over the three greenhouse experiments and 50.1% for the mean over all experiments.

QTL for FHB resistance

Of 1,125 primer pairs were screened, 462 were found to be polymorphic between the parents. Among these, 15 markers from four chromosomes were polymorphic between the contrasting bulks. Therefore, all markers from those chromosomes that had exhibited polymorphism between the parents were used to genotype the RIL. The resulting data were used to construct maps for four linkage groups, covering a total genetic distance of 133.4 cM. Composite interval mapping (CIM) detected one major QTL on 7D, designated *QFhb.hyz-7D,* at which the allele from HYZ contributed to low PSS. This QTL was flanked by the SSR markers *Xcfd46* and *Xwmc702* with a peak near the marker *Xwmc121*. It was consistently significant in all four experiments (Fig. 2). This QTL explained 20.4–22.6% of the phenotypic variation in the three individual greenhouse experiments and 15.9% in the field experiment, with additive effects ranging from 8.8 to 13.1 (Table 1). CIM also detected four minor QTL on 6BS, 5AS and 1AS, and

designated *QFhb.hyz-6B.1*, *QFhb.hyz-6B.2, QFhb.hyz-5A* and *QFhb.hyz-1A*, respectively (Fig. 3). *QFhb.hyz-6B.1* peaked at the SSR marker *Xgwm705* and was detected in the greenhouse experiment in the spring cycle of 2007, which explained ~4.2% of phenotypic variation. *QFhb.hyz-6B.2* was discovered only in 2008 greenhouse experiment and explained 7.2% of PSS variance. *QFhb.hyz-5A* was identified in the spring 2007 greenhouse experiment and in the field experiment, which accounted for 3.9 and 7.4% of PSS variance, respectively. *QFhb.hyz-1A* was flanked by SSR markers *Xwmc120.1* and *Xwmc24,* and peaked at *Xwmc120.2*. This QTL was detected in the spring cycle of 2007 and the fall cycle of 2008, and explained 5.4 and 5.5% of PSS variation, respectively (Fig. 3, Table 1). HYZ contributed the favorable alleles at *QFhb.hyz-7D*, *QFhb.hyz-6B.1*, *QFhb.hyz-6B.2* and *QFhb.hyz-5A* but the unfavorable allele at *QFhb.hyz-1A*. Multiple interval mapping (MIM) analysis did not detect significant epistatic interactions among the four QTL in any individual experiment or in combined data.

To compare the effects of QTL/combinations of interest, the RIL were classified into six groups with a cut-off of five RIL in each group using the PSS data across three greenhouse experiments. Field data was not included due to the availability of data from only one season. The differences in PSS were significant among the six genotype combinations ($F = 12.36$, $P = 3.23E\text{-}07$) (Fig. 4). The group with HYZ alleles at the QTL combination of *QFhb.hyz-7D* + *QFhb.hyz-5A* had lower PSS than the group carrying HYZ-allele at *QFhb.hyz-7D*. These two groups showed significant differences ($LSD_{.05}$) from the groups carrying HYZ-allele either at *QFhb.hyz-6B.1*, or at *QFhb.hyz-5A*, or at *QFhb.hyz-1A* or from the group carrying none of HYZ-allele. The group carrying HYZ-alleles at *QFhb.hyz-6B.1* or *QFhb.hyz-5A* alone displayed moderate to high susceptibility. The RIL with HYZ-allele at *QFhb.hyz-1A* alone showed the highest PSS.

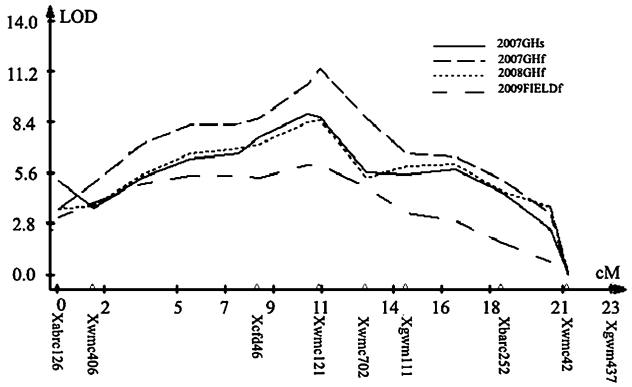

Fig. 2 LOD profiles from composite interval mapping for markers on chromosome 7D using percentage of scabbed spikelets (PSS) data from three greenhouse experiments (2007GHs, 2007GHf and 2008GHf), one field experiment (2009FIELDf)

Discussion

The current study identified five QTL for FHB resistance on chromosomes 7D, 6BS, 5AS and 1AS in the Chinese wheat landrace HYZ. The QTL *QFhb.hyz-7D* explained the largest proportion of variation using both greenhouse and field PSS data, demonstrating this major QTL was stable across different experiments. QTL on chromosome 7DL have also been reported in an Arina/Riband population (Draeger et al. 2007) and a Nanda2419/Wangshuibai population (Li et al. 2008), but they displayed only minor and inconsistent effects. Meta-analysis has indicated that the 7D QTL in those two populations may correspond with each other (Liu et al. 2009). The QTL detected on 7D in the

Table 1 QTL positions, LOD values and thresholds, coefficients of determination (R^2) and additive effects of the QTL under CIM method

QTL	Experiment	LOD	LOD Threshold	Flanking markers	Interval distance	R^2	Additive
QFhb.hyz-7D	2007GHs	9.53	2.11	*Xcfd46-Xwmc702*	4.5	0.217	−13.1
	2007GHf	10.63	2.31	*Xcfd46-Xwmc702*	4.5	0.226	−12.7
	2008GHf	8.72	2.29	*Xcfd46-Xwmc702*	4.5	0.204	−12.4
	2009Field	6.88	2.12	*Xcfd46-Xwmc702*	4.5	0.159	−8.8
QFhb.hyz-6B.1	2007GHs	2.24	2.11	*Xgwm705-Xwmc104*	0.9	0.041	−6.0
QFhb.hyz-6B.2	2008GHf	3.17	2.29	*Xgwm644-Xbarc223.1*	6.0	0.072	−9.0
QFhb.hyz-5A	2007GHs	2.19	2.10	*Xbarc56-Xgwm129*	3.8	0.039	−5.5
	2009field	2.42	2.12	*Xbarc141-Xgwm129*	16.2	0.074	−5.9
QFhb.hyz-1A	2007GHs	2.73	2.10	*Xwmc120.1-Xwmc24*	9.1	0.054	6.7
	2008GHf	2.85	2.26	*Xwmc120.1-Xwmc24*	9.1	0.055	6.5

2007GHs, 2007GHf and 2008GHf: three single greenhouse experiments conducted at Kansas State University, Manhattan, KS, in spring 2007, fall 2007 and fall 2008, respectively. 2009Field: the field experiment conducted at KSU Rocky Ford FHB Nursery at Manhattan, KS in 2009; LOD threshold in each experiment was determined by 1,000-permutation times using WINQTL Cartographer 2.5

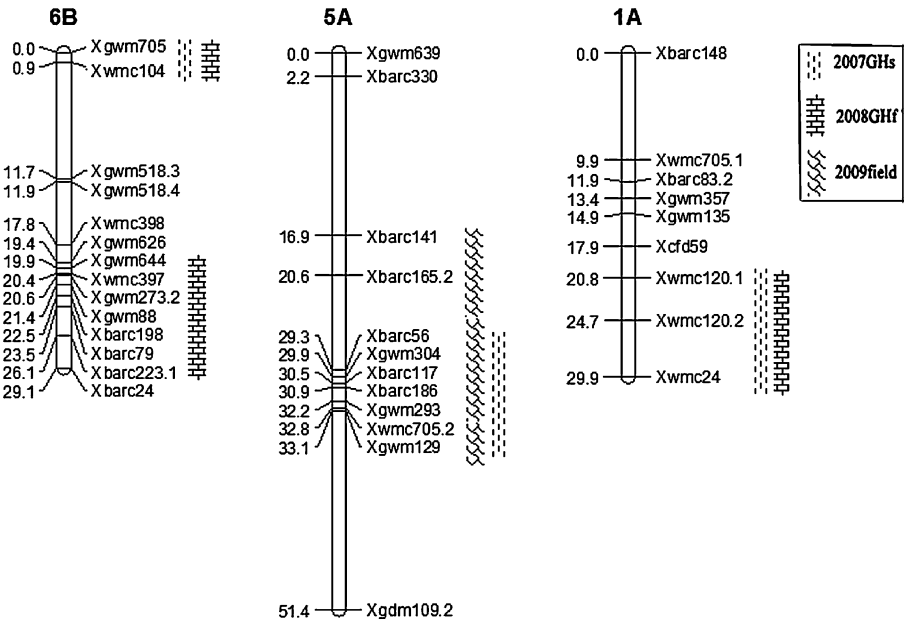

Fig. 3 Locations of minor-effect QTL on chromosomes 6BS, 5AS and 1AS for two greenhouse experiments (2007GHs and 2008GHf), one field experiment (2009Field). None of these minor-effect QTL were detected in the fall cycle of 2007 experiment (2007GHf)

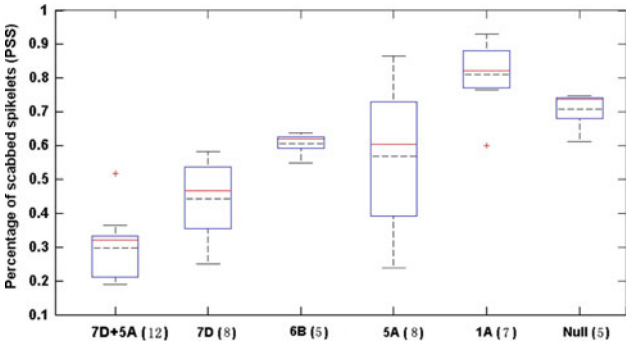

Fig. 4 Boxplots for single QTL and QTL combinations from mean percentage of scabbed spikelets (PSS) over three greenhouse experiments. Boxplots were drawn using Matlab software. The *central dashed line* in the box is the mean PSS value of a group and the *central solid line* is a median. The *top* and *bottom edges* of a box indicate 75th and 25th percentiles of each group. *Whiskers* (*vertical lines* outside of the box) extend to the most extreme data points that algorithm does not consider to be outliers. Outliers (extreme values, symbol +) are individually plotted if they are larger than Q3 + 1.5*(Q3 − Q1) or smaller than Q1 − 1.5*(Q3 − Q1), where Q1 and Q3 are the 25th and 75th percentiles, respectively. This figure includes only those QTL that were significant in at least two experiments. The RIL without any known QTL were counted as susceptible reference. Those groups with fewer than five RIL or those RIL that had either heterozygous or missing marker data at the SSR loci representing known QTL were not included in the analysis. *The number* in parenthesis on the horizontal axis is the number of RIL analyzed in each group

HYZ/Wheaton population may be the same locus as the one detected on 7D in Nanda2419/Wangshuibai, as both are near the common marker *Xcfd46* Therefore, *QFhb.hyz-7D* in HYZ could be a new allele with a major effect on FHB resistance.

QFhb.hyz-6B.1 was associated with *Xgwm705* and *Xwmc104*. This QTL has not been reported before and might be a novel one but the stability of this QTL needs to be further verified. *QFhb.hyz-6B.2* was assigned to the region between *Xgwm644* and *Xbarc223.1*, and was detected only in one greenhouse experiment. This QTL most likely is the same QTL as *Fhb2* since they share the common marker *Xgwm644* (Cuthbert et al. 2007). Several QTL with varied effects on type II resistance (R^2 = 4–24%) have been reported at a similar chromosome location to *Fhb2* (*QFhb.hyz-6B.2*) in different populations derived from Chinese sources (Lin et al. 2004; Loffler et al. 2009; Shen et al. 2003; Yang et al. 2005).

QFhb.hyz-5A was recovered both in greenhouse and field data. More than 12 QTL on chromosome 5A have reported to affect FHB, with the phenotypic variation explained varying from 4 to 26%, depending on experiments, sources and types of resistance in several sources (Buerstmayr et al. 2002; Chen et al. 2006; Jiang et al. 2007a, b; McCartney et al. 2007; Yang et al. 2005). The locations of these QTL did not always concur with each other, and the allelic relationship between 5A QTL in HYZ/Wheaton population and the previously documented QTL remains to be untangled.

The HYZ-allele at the QTL on 1AS increased FHB susceptbility, with the RIL with that allele having 5.6–12.1% higher PSS than the RIL with Wheaton allele. HYZ might have a susceptibility factor or resistance suppressor in this QTL region or Wheaton carries a resistance allele. In a CJ 9306/Veery population, a QTL on 1A chromosome explained 11.7–21.2% of phenotypic variation (Jiang et al. 2007a, b). The QTL region on 1AS in this study had common marker *Xbarc148* with the QTL detected in CJ 9306/Veery population, suggesting they might be same locus.

In summary, the FHB resistance in HYZ was largely due to a QTL on chromosome 7D, with minor effects from QTL on chromosomes 5A and 6B. The QTL on 7D may represent

a locus at which minor effects have been reported previously but importantly, HYZ seems to carry a new allele with a major effect. Identification of this allele may facilitate breeding for FHB improvement. Further study on its effects in different genetic backgrounds and its interaction with *Fhb1* may facilitate validation of the QTL and pyramiding of QTL to improve the level of FHB resistance in commercial cultivars. In addition, QTL on 6BS and 5AS also contributed to the resistance in HYZ, but the QTL on 1A in HYZ enhanced susceptibility. Therefore, when HYZ is used as a resistant parent, selection should be focused on 7D QTL. The HYZ allele at the QTL on 1AS should be avoided during the selection.

Acknowledgment This project is partly funded by US Wheat and Barley Scab Initiative and by the Jiangsu Provincial Natural Science Foundation of China (grant No. BK2010312). Mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. Contribution No. 11-180-J from the Kansas Agricultural Experiment Station, Manhattan, KS, USA.

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