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ORIGINAL ARTICLE

Mapping and validation of a new QTL for adult-plant resistance to powdery mildew in Chinese elite bread wheat line Zhou8425B

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Abstract

Key message **Four QTLs for adult-plant resistance to powdery mildew were mapped in the Zhou8425B/Chinese Spring population, and a new QTL on chromosome 3B was validated in 103 wheat cultivars derived from Zhou8425B.**

Abstract Zhou8425B is an elite wheat (*Triticum aestivum* L.) line widely used as a parent in Chinese wheat breeding programs. Identification of genes for adult-plant resistance (APR) to powdery mildew in Zhou8425B is of high importance for continued controlling the disease. In the current study, the high-density Illumina iSelect 90K single-nucleotide polymorphism (SNP) array was used to map quantitative trait loci (QTL) for APR to powdery mildew in 244 recombinant inbred lines derived from the cross Zhou8425B/Chinese Spring. Inclusive composite interval mapping identified QTL on chromosomes 1B, 3B, 4B, and 7D, designated as *QPm.caas-1BL.1*, *QPm.caas-3BS*, *QPm.caas-4BL.2,* and *QPm.caas-7DS*, respectively. Resistance alleles at the *QPm.caas-1BL.1*, *QPm.caas-3BS,* and *QPm.caas-4BL.2* loci were contributed by Zhou8425B, whereas that at *QPm.caas-7DS* was from Chinese Spring. *QPm.caas-3BS*, likely to be a new APR gene for powdery mildew resistance, was detected in all four environments. One SNP marker closely linked to *QPm.caas-3BS* was transferred into a semi-thermal asymmetric reverse PCR (STARP) marker and tested on 103 commercial wheat cultivars derived from Zhou8425B. Cultivars with the resistance allele at the *QPm.caas-3BS* locus had averaged maximum disease severity reduced by 5.3%. This STARP marker can be used for marker-assisted selection in improvement of the level of powdery mildew resistance in wheat breeding.

Keywords APR · *Blumeria tritici* f. sp. *tritici* · STARP marker · *Triticum aestivum* · Wheat 90K SNP array

Abbreviations

ANOVA	Analysis of variance
APR	Adult-plant resistance
BLUEs	Best linear unbiased estimates
CAPS	Cleaved amplified polymorphic sequences
QTL	Quantitative trait locus (loci)
ICIM	Inclusive composite interval mapping
IT	Infection type
KASP	Kompetitive allele-specific PCR
LOD	Logarithm of odds
MAS	Marker-assisted selection

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MDS	Maximum disease severity
PVE	Phenotypic variance explained
RFLP	Restriction fragment length polymorphism
RIL	Recombinant inbred line
SNP	Single-nucleotide polymorphisms
STARP	Semi-thermal asymmetric reverse PCR

Introduction

Wheat is one of the most important staple crops, but its production is constrained by many biotic and abiotic factors. Powdery mildew, caused by *Blumeria graminis* f. sp. *tritici* (*Bgt*), is a devastating rapidly spreading fungal disease that affects all aerial plant parts including stems, leaves, glumes, and awns. Powdery mildew prevails in many wheat growing regions of eastern Asia, southeastern USA, northeastern Africa, and northern Europe (Saari and Wilcoxson 1974; Roelfs 1977; Selter et al. 2014). The severity and prevalence of powdery mildew has increased in recent decades due to increasing applications of nitrogen fertilizer and irrigation (Olesen et al. 2000). Since the 1980s, this disease has become widespread in most wheat growing regions of China (Li and Zeng 2002) where it affects around 8 million ha of wheat annually (Zhao et al. 2013). In comparison to chemical control, the use of resistant cultivars is a more comprehensive, economical, and environmentally friendly approach to control the disease (Petersen et al. 2015).

To date, 85 powdery mildew resistance genes (*Pm1–Pm58*) at 54 loci have been catalogued in wheat (Hao et al. 2015; Liu et al. 2017; McIntosh et al. 2017; Wiersma et al. 2017). These genes were derived from 20 Triticeae species including *Triticum aestivum*, *T. monococcum*, *T. dicoccum*, *T. spelta*, and *Aegilops speltoides*; 21 loci were from *T. aestivum*. Many of these genes are race-specific and the majority of them have lost effectiveness. However, adult-plant resistance genes, such as *Lr34/Yr18/Pm38*, *Lr46/Yr29/Pm39,* and *Lr67/Yr46/Pm46*, continue to confer race-non-specific resistance to powdery mildew (Lillemo et al. 2008; Herrera-Foessel et al. 2014; Moore et al. 2015), although levels of protection are often less than adequate when such genes are deployed alone and they do not control the disease at early growth stages.

With recent developments in genotyping arrays, such as the high-density wheat 90K SNP chip platform (Wang et al. 2014), SNP markers are being used increasingly in genetic mapping. Due to co-dominance, abundance, and even distribution of SNP across the genome, high-density genome-wide genotyping arrays further improve the construction of high-resolution genetic maps and QTL mapping. In recent years, QTL of different traits were identified from the whole genome using the wheat 90K iSelect array, e.g., for wheat quality (Colasuonno et al. 2014), flag leaf and grain (Wu et al. 2015a, b, 2016), yield and related traits (Gao et al. 2015), and disease resistance (Liu et al. 2016; Zhang et al. 2017). In addition, the SNPs from arrays can be transferred into KASP (Kompetitive allele-specific PCR, Semagn et al. 2014; Thomson 2014) or STARP (Long et al. 2017) markers that can be easily used in marker-assisted selection (MAS). It is expected that the STARP technique, with the major advantages of simple assay design, flexible throughputs, high accuracy, platform compatibility, and low operational costs, will be applied increasingly in MAS and genetic mapping (Long et al. 2017).

Wheat cultivar Zhou8425B developed by the Zhoukou Academy of Agricultural Sciences in Henan province has good resistance to stripe rust, leaf rust, and powdery mildew (http://wheatpedigree.net/sort/show/92642, ZHOU-MAI-8425-B in CIMMYT Genebank). It carries all-stage resistance genes *YrZH84* (Li et al. 2006) and *LrZH84* (Zhao et al. 2008), and 4 leaf rust APR QTL (Zhang et al. 2017). Zhou8425B is an elite wheat cultivar and has been widely used as a parent in breeding programs in the Yellow and Huai Valleys Autumn-sown Wheat Zone since 1984. More than 100 cultivars derived from this line have been grown on an accumulated area of more than 33 million ha in China during the past 20 years. Although stripe rust and leaf rust resistance genes in Zhou8425B were identified previously (Li et al. 2006; Zhao et al. 2008; Yin et al. 2009; Xiao et al. 2011; Zhang et al. 2017), resistance to powdery mildew has not been studied. The objective of the present study was to identify QTL for APR to powdery mildew in Zhou8425B, validate a major QTL on chromosome 3B, and develop a tightly linked STARP marker for MAS in wheat breeding.

Materials and methods

Plant materials

The 244 F_8 recombinant inbred lines (RILs) derived from a cross between Zhou8425B and Chinese Spring were used for construction of a whole-genome high-density linkage map and QTL mapping. One hundred and three cultivars derived from Zhou8425B were used for QTL validation. The highly susceptible wheat cultivar Jingshuang 16 was used as the susceptible control. The resistant wheat line Zhou8425B will be available in CIMMYT Genebank from March, 2018 on (http://wheatpedigree.net/sort/show/92642), and it is also available in the Genebank of Chinese Academy of Agricultural Sciences by the accession number ZM29072 (http://www.cgris.net).

Powdery mildew tests in the greenhouse

Seedlings of 244 F_8 RILs and parents were tested for powdery mildew response in the greenhouse following inoculation with prevalent *Bgt* isolates E09 and E20 obtained from the Plant Protection Institute, CAAS. About 15 seeds of each RIL were planted, and the infection types (IT) based on a 0–4 scale (Liu et al. 1999) were scored 10 days after inoculation when the susceptible control Jingshuang16 showed severe symptoms.

Powdery mildew evaluation in the field

The RILs and parents were evaluated for powdery mildew response at the adult–plant stage in the field at Beijing and Zhengzhou during the 2014–2015 and 2015–2016 cropping seasons following artificial inoculation. The field trials were conducted in randomized complete blocks with three replicates. Each plot consisted of a single 1.5 m row with 20 cm between rows. Approximately 50 seeds were uniformly sown in each row. The highly susceptible cultivar Jingshuang 16 was planted at every tenth row as a control, and also perpendicular and adjacent to the test rows as a spreader for even infection.

The highly susceptible cultivar Jingshuang 16 was planted in 9 cm × 9 cm (diameter × height) plastic pots and inoculated with the virulent isolate E20 at the two-leaf stage in the greenhouse; the fully infected Jingshuang 16 seedlings were then transplanted among the spreader lines with one pot every 50 cm in the field at the stem elongation stage by the end of March. Disease severity on each line was scored as the average percentage of leaf area covered by powdery mildew. The first assessment occurred when the susceptible control Jingshuang 16 was severely diseased about 6 weeks after inoculation. The maximum disease severity (MDS) for each line was evaluated when the disease severity on the control reached a maximum level around 1 week later, which was used for subsequent analysis.

To validate the effect of the new QTL on chromosome 3B, 103 cultivars derived from crosses involving Zhou8425B were planted at Beijing, and at Zhengzhou and Xingyang in Henan province during the 2016–2017 cropping season. The field trials and powdery mildew evaluations in the field were similar to those described above.

Statistical analysis

Phenotypic correlation coefficients, analysis of variance (ANOVA), and *t* tests were conducted using SAS 9.4 software (SAS Institute, Cary, NC). Broad-sense heritability (H^2) of powdery mildew response was calculated following Nyquist and Baker (1991).

QTL analysis

Genomic DNA were extracted from healthy seedling leaves of the RILs and parents by the CTAB method (Saghai-Maroof et al. 1984). Molecular genotyping was performed using the wheat 90K iSelect SNP array and genetic linkage maps were constructed. Twenty-one linkage groups corresponding to all 21 hexaploid wheat chromosomes were assembled from 5636 high-quality polymorphic SNP markers (Gao et al. 2015). QTL analysis was performed by the inclusive composite interval mapping with the ICIM-ADD function using the software QTL IciMapping 4.1 (Li et al. 2007; Meng et al. 2015). Phenotypic values of RILs averaged from three replicates in each environment and BLUEs (best linear unbiased estimates) values of the genetic effects from four environments of RILs by R package lme4 (Bates et al. 2015) were used for QTL detection. QTL were mapped at a logarithm of odds (LOD) threshold of 2.5 based on 1000 permutations and a walk speed of 1.0 cM, with $P = 0.001$ in stepwise regression. QTL effects were estimated as the proportion of phenotypic variance explained (PVE) by the QTL. Normally, there are minor differences in the peaks of LOD contours for a single QTL across different environments. The QTL within one-log support confidence interval (14 cM) were considered to be the same.

STARP marker design

The STARP marker designed from an SNP tightly linked with the 3B QTL included five primers: two AMAS-primers (asymmetrically modified allele-specific primers) for specifically amplifying two alleles from genomic DNA to provide priming sites for PEA-primers by six touchdown cycles, two universal PEA-primers (priming element-adjustable primers) amplifying with the AMAS amplification products to distinguish two alleles by gel-free fluorescence signals, and their common reverse primer designed from information in the GSP website (http://probes.pw.usda.gov/GSP/index.php). PCR procedures and conditions followed Long et al. (2017). Gel-free fluorescence signals scanning and allele separation were conducted by microplate reader (Multiscan Spectrum BioTek, Synegy/H1) with the Klustercaller 2.24.0.11 software (LGC, Hoddesdon, UK).

Results

Seedling reactions to powdery mildew in the greenhouse

Seedlings of control cultivar Jingshuang 16 were susceptible (IT 3–4) to powdery mildew. Zhou8425B and Chinese Spring were also susceptible to E09 and E20 (IT 3–4). Among the 244 RILs, 243 exhibited susceptible infection types (IT 3–4), whereas one was highly resistant. This line was considered to be a contaminant and was excluded from subsequent analysis.

Powdery mildew scores in the field

The MDS of the 243 RILs ranged from 0 to 77% across four environments, indicating significant differences among genotypes. Zhou8425B and Chinese Spring exhibited averaged MDS scores of 5 and 7%, respectively. Pearson's correlation coefficients for the population ranged from 0.53 to 0.73 among four environments ($P < 0.01$) (Table S1). The frequency distribution of powdery mildew MDS in each environment with a coefficient of variation of 63.6% showed a continuous distribution skewed toward resistance (Figure S1), indicating polygenic inheritance and transgressive segregation. Broad-sense heritability of MDS across the four environments was 0.80. ANOVA confirmed significant variation among genotypes, environments, and genotype × environment interactions (Table S2), demonstrating both genotypic and environmental influences on these traits.

The MDS of 103 derivatives of Zhou8425B were 0–70, 0–50, and 1–70% in Beijing, Xingyang, and Zhengzhou, respectively, with correlation coefficients ranging from 0.45 to 0.58 among three environments.

QTL for powdery mildew resistance

QPm.caas-1BL.1 in marker interval *IWB72835-IWB18787* identified at Beijing 2016, Zhengzhou 2016, and the averaged value of four environments explained 5.44, 5.69, and 7.20% of the phenotypic variances, respectively (Fig. 1; Table 1). The additive effects were − 2.33, − 3.22, and − 2.38, respectively. The resistance allele was derived from Zhou8425B.

QPm.caas-3BS in marker interval *IWB21064-IWB64002* was stably detected in all environments and averaged values, explaining 4.36–9.05% of the phenotypic variances, with additive effects ranging between − 1.51 and − 3.80. The resistance allele was from Zhou8425B.

QPm.caas-4BL.2 located in the region *IWB35851-IWB60096* explained 6.43 and 8.77% of the phenotypic variance in Zhengzhou 2016 and the average for four environments, with additive effects of − 3.43 and − 2.63, respectively. The resistance allele was from Zhou8425B.

QPm.caas-7DS in marker interval *IWB41108–IWB53819* was identified in Beijing 2015, Zhengzhou 2015, Beijing 2016, and the average of four environments, explaining 10.37, 5.20, 4.10, and 4.21% of the phenotypic variances, respectively. The additive effects were 4.60, 1.15, 2.05, and 1.84, respectively. The resistance allele was contributed by Chinese Spring.

Validation of *QPm.caas-3BS* in Zhou8425B derivatives

QPm.caas-3BS with the resistance allele from Zhou8425B was an important APR QTL for powdery mildew resistance, exhibiting a stable effect in all environments. We transferred SNP *IWB41105* that was closely linked to *QPm.caas-3BS* into an STARP marker named *Str-IWB41105* (Table 2), and tested 103 Zhou8425B derivatives (Table S3). Student's *t* tests indicated that varieties with the resistance allele significantly ($P < 0.05$) reduced the average MDS of all environments by 5.3% (Table 3).

Discussion

Comparisons with previous reports

QPm.caas-1BL.1

There are several reports of QTL for APR to powdery mildew mapped on chromosome 1BL. These include *QPmvt-1BL* and *QPm.vt-1B* detected in the North American winter wheat cultivar Massey and derived line USG 3209, respectively (Liu et al. 2001; Tucker et al. 2007). The pleiotropic APR gene *Lr46*/*Yr29*/*Pm39* in CIMMYT bread wheat line Saar was at a similar position to the above two QTL (Lillemo et al. 2008), and they all shared the closely linked simple sequence repeat (SSR) locus *Xbarc80* (Tucker et al. 2007; Lillemo et al. 2008). Nevertheless, our experiment indicated that parents Zhou8425B and Chinese Spring did not have *Lr46*/*Yr29*/*Pm39* as tested by the cleaved amplified polymorphic sequences (CAPS) marker *csLV46G22* (Figure S2), and this pleiotropic QTL was also not previously detected in the population for leaf rust resistance (Zhang et al. 2017). One of the parents, Zhou8425B (donor of *QPm.caas-1BL.1*), has winter growth habit which is different from Saar (donor of *Pm39*) having spring growth habit. Therefore, it is likely that *QPm.caas-1BL.1* is different from *Pm39*.

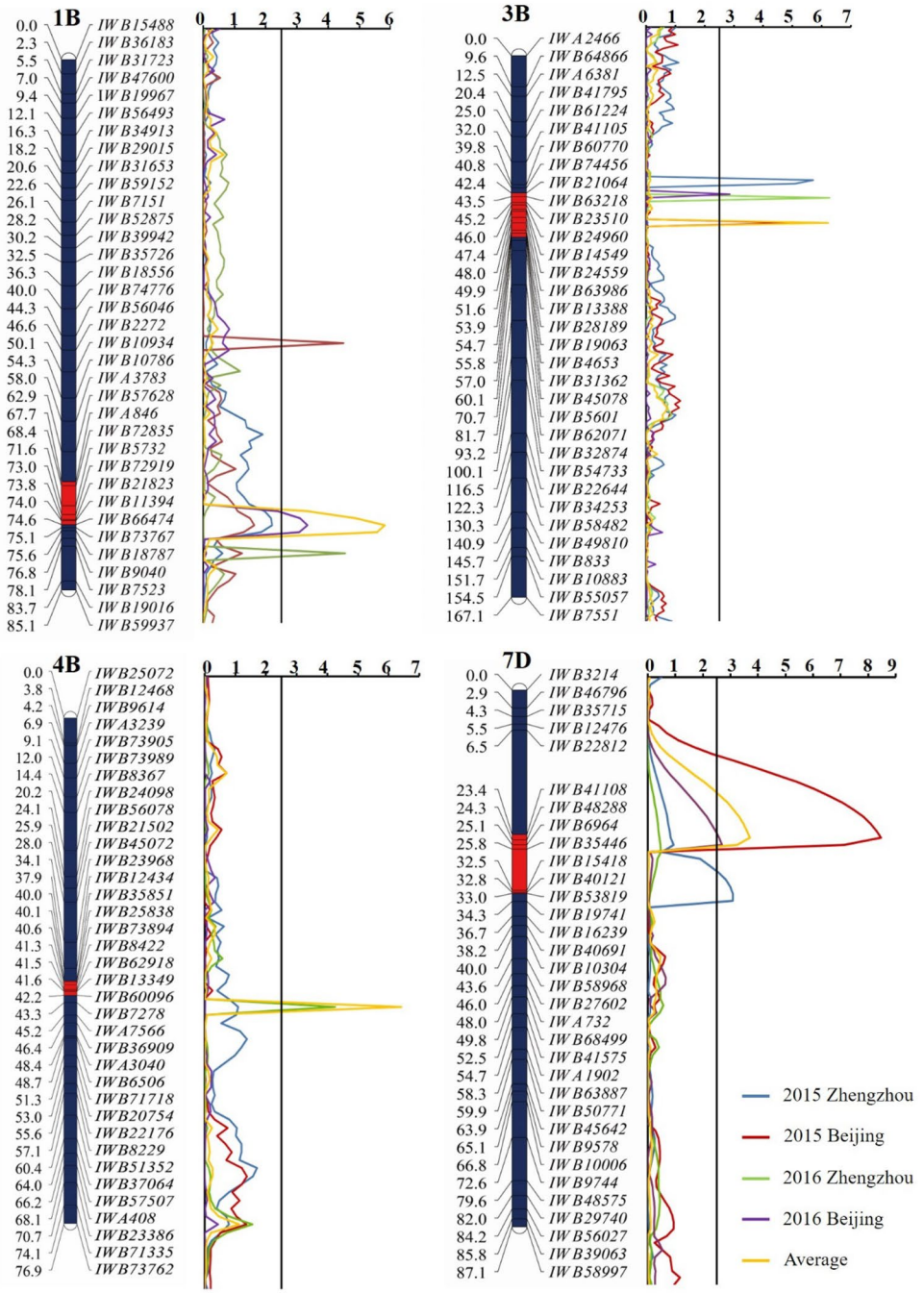

Fig. 1 QTL mapping of powdery mildew response in the Zhou8425B/Chinese Spring RIL population grown in four environments

QPm.caas-3BS

Powdery mildew APR QTL *QPm.inra-3B* linked with *Xgwm389* and *Xbarc133* and derived from French semi-dwarf cv. Courtot was identified in one environment (Bougot et al. 2006). One major pleiotropic gene *Sr2* on chromosome 3BS was tightly linked with pseudoblack chaff (Kota et al. 2006), *Lr27* (Singh and McIntosh 1984) and a powdery mildew resistance gene (Mago et al. 2011b). *QPm.caas-3BS* is different from the powdery mildew gene co-segregating with *Sr2,* because neither the RILs nor parents have pseudoblack chaff and tests with the CAPS marker *csSr2* that co-segregates with *Sr2* also indicated the absence of *Sr2* (Figure S3) (Mago et al. 2011a). Moreover, there were no evidence that the Hope or H-44 derivatives of Yaroslaw emmer (*T. dicoccoides*) (McFadden 1930) or a derivative was involved in the pedigree of Zhou8425B. The proximal SNP markers *BobWhite_c9711_71* (ID: *IWB4653*) and *Excalibur_c6330_1158* (ID: *IWB28189*) of *QLr.hebau-3BS* (Zhang et al. 2017) were located at 53–55 cM (Zhang et al. 2017) in the same region

Table 1 QTL for maximum disease severities of powdery mildew by inclusive composite interval mapping in F_8 lines from Zhou8425B/Chinese Spring

QTL[a]	Environment	Position[b]	Marker interval	LOD[c]	PVE (%)[d]	Add[e]
QPm.caas-1BL.1	2016 Beijing	71	*IWB72835–IWB18787*	3.34	5.44	– 2.33
	2016 Zhengzhou	75	*IWB72835–IWB18787*	4.55	5.69	– 3.22
	Average[f]	71	*IWB72835–IWB18787*	5.82	7.20	– 2.38
QPm.caas-3BS	2015 Beijing	55	*IWB21064–IWB64002*	5.18	6.03	– 3.49
	2015 Zhengzhou	43	*IWB21064–IWB64002*	5.71	9.05	– 1.51
	2016 Beijing	47	*IWB21064–IWB64002*	2.86	4.36	– 2.09
	2016 Zhengzhou	48	*IWB21064–IWB64002*	6.28	7.87	– 3.80
	Average	55	*IWB21064–IWB64002*	6.23	7.10	– 2.38
QPm.caas-4BL.2	2016 Zhengzhou	41	*IWB35851–IWB60096*	4.26	6.43	– 3.43
	Average	41	*IWB35851–IWB60096*	6.42	8.77	– 2.63
QPm.caas-7DS	2015 Beijing	23	*IWB41108–IWB53819*	8.47	10.37	4.60
	2015 Zhengzhou	31	*IWB41108–IWB53819*	3.08	5.20	1.15
	2016 Beijing	24	*IWB41108–IWB53819*	2.70	4.10	2.05
	Average	23	*IWB41108–IWB53819*	3.71	4.21	1.84

[a]QTL overlapping within a one-log support confidence interval was assigned with the same symbol

[b]Position of QTL on chromosome: cM distance from the top of each map

[c]Logarithm of odds (LOD) score

[d]Percentages of phenotypic variance explained by individual QTL

[e]Additive effect of QTL; positive values indicate that resistance alleles were contributed by Chinese Spring, whereas negative values indicate that resistance alleles were contributed by Zhou8425B

[f]Average of four environments was estimated BLUEs value by in R package lme4

Table 2 Primer sequences and annotation of STARP marker *Str-IWB41105* linked to *QPm.caas-3BS*

Primer name	Sequence
PEA-1[a]	(5′Fam)AGCTGGTT(Spacer(C9))GCA ACAGGAACCAGCT(Dabcyl)ATGAC
PEA-2	(5′Hex)ACTGCTCAAGAG(Spacer(C9)) GACGCAAGTGAGCAGT(Dabcyl) ATGAC
AMAS-1	[Tail 1][b] ACTGTGCTCTTCCGTTCG
AMAS-2	[Tail 2][c] ACTGTGCTCTTCCGCCCA
Reverse	CCAACCAACTTCACTGATATGAAAA

[a]PEA primers can be universally used for any STRAP markers

[b][Tail 1], GCAACAGGAACCAGCTATGAC-3′ (Long et al. 2017)

[c][Tail 2], GACGCAAGTGAGCAGTATGAC-3′ (Long et al. 2017)

as *QPm.caas-3BS*. Moreover, *QLr.hebau-3BS* (in a 14.4 cM interval *Xbarc147–Xgwm493*) and *QPm.inra-3B* (16.9 cM from *Xgwm389*) are in different chromosomal bins (Sourdille et al. 2004). It is thus concluded that *QPm.caas-3BS* is likely a new APR QTL that is pleiotropic with a QTL for leaf rust resistance (Zhang et al. 2017).

QPm.caas-4BL.2

Five QTL for APR to powdery mildew were identified near the chromosome 4B centromere in previous studies. *QPm.ipk-4B* and *QPm.sfr-4B* in the synthetic hexaploid line W7984 and Swiss spelt cv. Oberkulmer were detected in RFLP (restriction fragment length polymorphism) marker intervals *Xcdo795–Xbcd1262* and *Xpsr593b–Xpsr1112* (Keller et al.1999; Börner et al. 2002). *QPm.caas-4BL* in Israeli wheat Oligoculm was mapped in SSR interval *Xgwm375–Xgwm251* (Liang et al. 2006). *QPm.nuls-4BL* in wheat line Avocet was between DArT (Diversity arrays technology) marker *XwPt1505* and SSR marker *Xgwm149* (Lillemo et al. 2008). *QPm.caas-4BL.1* located in interval *Xgwm149–Xgwm495* in Italian cv. Libellula explained an average PVE of 14.7% (Asad et al. 2012). *Xgwm149*, *Xgwm375,* and the SNP marker *BS00109813_51* (ID: *IWB12434*) were adjacent according to the wheat map in Zhang et al. (2017). In the present genetic map, *QPm.caas-4BL.2* was flanked by markers *IWB35851* and *IWB60096* located at 39.97–42.20 cM and closely linked with *IWB12434* at position 37.89 cM. Because *QPm.ipk-4B* and *QPm.sfr-4B* were mapped only with RFLP markers, it is difficult to compare the locations with our QTL. *QPm.caas-4BL.2* was mapped in a similar location to the latter three QTL and, hence, represents a same gene.

QPm.caas-7DS

Chromosome 7DS harbors the multi-pathogen resistance gene *Lr34/Yr18/Pm38* that has shown durable resistance for more than 80 years (Krattinger et al. 2009); this gene stimulates senescence-like processes in the flag leaf tips and

Table 3 *t* tests of powdery mildew MDS for 103 wheat varieties derived from Zhou8425B

Environment	Genotype[a]	Number	Mean (%)[b]	95% CL mean[c]	*df*	*t* value
2017 Beijing	A	46	27.2	22.3–32.0	101	2.26*
	B	57	20.4	16.7–24.1		
2017 Zhengzhou	A	46	27.3	22.3–32.4	101	2.13*
	B	57	20.7	16.8–24.6		
2017 Xingyang	A	46	9.5	7.3–11.7	101	2.15*
	B	57	6.6	5.0–8.3		
Average[d]	A	46	21.3	17.5–25.1	101	2.34*
	B	57	16.0	13.1–18.8		

[a]Genotype tested by the STARP marker *Str-IWB41105* closely linked to *QPm.caas-3BS*. Absence and presence of resistance allele at *QPm.caas-3BS* locus are signified by A and B, respectively

[b]Mean maximum disease severity

[c]95% confidence limits for the mean values

[d]Average of three environments was estimated BLUEs value by in R package lme4

*Significant at $P = 0.05$

edges, leading to tip necrosis and functioning resistance in the adult plant (Singh 1992; Kolmer et al. 2008). Six other QTL were also detected in the position of *Pm38*, including *QPm.ipk-7D*, *QPm.inra-7D.1*, *Qaprpm.cgb-7D*, *QPm.caas-7D,* and *QPm.caas-7DS* in Opata 85, Courtot, Hanxuan 10, Opata 85, Fukuho-komugi, and Libellula, respectively (Börner et al. 2002; Huo et al. 2005; Bougot et al. 2006; Liang et al. 2006; Asad et al. 2012). Many previous reports indicated that Chinese Spring had *Lr34/Yr18/Pm38* (Dyck 1977; Bossolini et al. 2006; Lagudah et al. 2006, 2009; Krattinger et al. 2009; Wu et al. 2015a, b; Zhang et al. 2017). Thus, *QPm.caas-7DS* should be *Pm38* in Chinese Spring.

Implications of *QPm.caas-3BS* and *QPm.caas-7DS* for wheat breeding

The pleiotropic QTL *QPm.caas-3BS*, significantly reducing MDS to powdery mildew and leaf rust, could be used to develop new cultivars for disease resistance. Aikang 58, containing the resistance allele of *QPm.caas-3BS* and manifesting prominent resistance, is an excellent powdery mildew resistance source. Zhoumai 22, the most widely grown cultivar in Henan province (Xu et al. 2010; Zou et al. 2017), has resistance to stripe rust, leaf rust, and powdery mildew. Cultivars Zhoumai 26, Zhoumai 28, Zhoumai 36, Xinmai 32, Xinmai 36, and Yude 1, all derived from Zhoumai 22, carry the 3BS resistance allele and can be used as breeding parents.

The pleiotropic APR gene *Lr34/Yr18/Pm38* has been successfully used in CIMMYT wheat breeding programs (Singh 1993; Bahl et al. 1997; Singh et al. 2005; Kolmer et al. 2008; Liang et al. 2009; Wu et al. 2010, 2015a, b) and in Canada. It is present at high frequency in Chinese wheat landraces (85.1% of 422 landraces, Yang et al. 2008), and the resistance gene probably originated from Chinese landraces (Dakouri et al. 2014). Nevertheless, due to ease of selection for major resistance genes in Chinese wheat breeding programs, *Lr34/Yr18/Pm38* is present in relatively few current wheat cultivars (Yang et al. 2008), and was not found in any of the 103 Zhou8425B derivatives included in the present study. The accumulation of 4–5 slow rusting or slow mildewing resistance genes can achieve high levels of resistance in wheat cultivars (Singh et al. 2000, 2005; Lu et al. 2009). Therefore, it is important to combine genes such as *QPm.caas-3BS* and *Pm38* with other APR genes in the future especially given that at least some of these genes protect against multiple diseases.

Author contribution statement ALJ performed the experiment and data analysis, and wrote the paper. FMG contributed to construction of the genetic map. YR, JDL, LG, and JZZ participated in the field trials. GHY developed the RIL population and collected 103 Zhou8425B derivative wheat cultivars. ZHH and XCX designed the experiment and wrote the paper. All authors read and approved the final manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no competing interests.

Ethical standards We declare that these experiments complied with the ethical standards in China.

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