Genetic Determinants of Wheat Resistance to Common Root Rot (Spot Blotch), *Fusarium* Crown Rot, and Sharp Eyespot

Jun Su [1,†], Jiaojie Zhao [1,†], Shuqing Zhao [1,†], Mengyu Li [1], Xiaofeng Shang [1], Shuyong Pang [1,4], Shisheng Chen [4], Feng Chen [5], Wenchao Zhen [3,*], Zhensheng Kang [2,*], Xiaodong Wang [1,*]

[1] State Key Laboratory of North China Crop Improvement and Regulation / College of Plant Protection, Hebei Agricultural University, Baoding, Hebei 071000, P. R. China; sujun20200801@163.com (J.S.); zhaojiaoj918@163.com (J.Z.); 18233283771@163.com (S.Z.); alimengyuuuu@163.com (M.L.); sxf1787796738@163.com (X.S.); shuyong150506@163.com (S.P.)
[2] State Key Laboratory of Crop Stress Biology for Arid Areas / College of Plant Protection, Northwest A&F University, Yangling, Shaanxi 712100, P. R. China;
[3] College of Agronomy, Hebei Agricultural University, Baoding, Hebei 071000, P. R. China;
[4] Institute of Advanced Agricultural Sciences, Peking University, Weifang, Shandong 261000, P. R. China; shisheng.chen@pku-iaas.edu.cn (S.C.)
[5] National Key Laboratory of Wheat and Maize Crop Science / Agronomy College, Henan Agricultural University, Zhengzhou 450046, P. R. China; chf0088@163.com (F.C.)
* Correspondence: zhbwxd@hebau.edu.cn (X.W.), kangzs@nwsuaf.edu.cn (Z.K.), and wenchao@hebau.edu.cn (W.Z.)
† These authors contributed equally to this work.

Abstract: Due to the field soil changes, high density planting, and straw-returning methods, wheat common root rot (spot blotch), *Fusarium* crown rot (FCR), and sharp eyespot (sheath blight) have become severe threatens to global wheat productions. Only a few wheat genotypes show moderate resistance to these root and crown rot fungal diseases, and the genetic determinants of wheat resistance to these devastating diseases have been poorly understood. This review summarizes the recent progress of genetic studies on wheat resistance to common root rot, *Fusarium* crown rot, and sharp eyespot. Wheat germplasms with relative higher resistance are highlighted and genetic loci controlling the resistance to each of the disease are summarized.

Keywords: wheat; resistance; QTLs; common rot root; spot blotch; *Fusarium* crown rot; sharp eyespot

1. Introduction

Various long-term environmental changes have greatly shaped the epidemics of different crop diseases. For instance, the higher temperatures associated with the trends of global warming may increase the severity of many plant diseases [1]. The bursts of wheat stem base rot diseases, including common root rot, *Fusarium* crown rot, and sharp eyespot are highly correlated with the crop rotations. The large-scale application of wheat-maize rotation in the North China wheat cultivation area has dramatically changed the organic carbon, fertilization state, and nitrogen balance of the soil [2,3]. The disease suppressive capacity of the soil microbiome is also largely dependent on crop rotational diversity [4].

41 **2. Pathogenic profiles**

42 Wheat common root rot is caused by *Bipolaris sorokiniana* infection (**Figure 1a**, teleomorph
43 *Cochliobolus sativus*) in the root and stem base of wheat plants. Severe infections of this fungal
44 pathogen in the root and crown of seedlings may lead to fatal damage of plants. The same pathogen
45 can also induce phenotypes of leaf spot (spot blotch, *Helminthosporium* leaf blight, or foliar blight,
46 **Figure 1b**), seedling wilt, head blight, and black point in *Triticeae* crops [5]. The average yield loss
47 caused by *B. sorokiniana* ranges from 15% to 20%, but under favorable heat and drought conditions
48 this disease can decrease wheat production by 70% and reduce seed quality [6]. This fungal
49 pathogen accumulates several toxins including prehelminthosporol, helminthosporol,
50 helminthosporic acid, sorokinianin, and bipolaroxin to kill or weaken plant cells [5,7]. However, the
51 potential negative impact of *B. sorokiniana*-infected wheat grains (black point) on food safety has not
52 been investigated in detail. The fungus *B. sorokiniana* has a very wide host range, and can infect
53 wheat, barley, maize, rice, and many other grass species [7]. Earlier studies suggested that
54 multiple-year *Triticeae* crop rotations of wheat and barley greatly promote the severity of common
55 root rot caused by *B. sorokiniana* [8]. Maize crops and returned straws may also serve as infection
56 hosts of this fungus, so common root rot and spot blotch have been more frequently observed in
57 wheat cultivation areas in North China, where large-scale wheat-maize rotation and the use of straw
58 returning have been applied.

59 *Fusarium* crown rot (FCR) is caused by infection of *Fusarium pseudograminearum* (**Figure 1c**), or
60 several other *Fusarium* pathogens including *F. culmorum*, *F. avenaceum*, and *F. graminearum.* These
61 fungal species infect the coleoptile, leaf sheath, and stem base of wheat seedlings, generating
62 browning and decay phenotypes (**Figure 1d**). *Fusarium* pathogens are globally wide-spread in arid
63 and semi-arid wheat planting areas [9]. The estimated yield loss of winter wheat due to FCR
64 infections in the Northwest Pacific region of the United States reached 35% [10]. Moreover, when
65 FCR-infected plants are co-infected with *Fusarium* Head Blight (FHB), wheat seeds are likely to be
66 contaminated by fungal toxins such as deoxynivalenol (DON) and nivalenol (NIV), which greatly
67 threaten the health of human and livestock [11,12]. Maize also can sever as host to various *Fusarium*
68 pathogens, and the fungi from infected plants can remain active in returned straw debris as long as

five years [13]. For these reasons, FCR is a growing threat to wheat cultivation in wheat-maize rotation regions in North China.

Wheat sharp eyespot (sheath blight) is caused by infection of *Rhizoctonia cerealis* (**Figure 1e**) in the root and stem base of wheat plants, generating disease phenotypes of stem eyespot (**Figure 1f**), crown rot, seedling fatal damage, and head blight. Wheat sharp eyespot is a typical soil-borne fungal disease that has been widely spread around the world [14]. *R. cerealis* also has a broad host range including many cereals. This fungal pathogen can be survived in soil or on infected crop residues for a long time. Consequently, wheat-maize rotation and straw-returning method have greatly facilitate the burst of this disease in China during the last two decades [15]. In 2005, the infected wheat field of sharp eyespot in China was approximately 8 million ha and the estimated yield loss was about 530,000 tons [16]. Moreover, infection of sharp eyespot also significantly decreases the grain quality of wheat [17].

These three diseases share several similar phenotypes such as stem base rot and head blight, but they can be distinguished by their phenotypic features. For common root rot caused by *B. sorokiniana*, the infected wheat plants can be easily pulled out, the stem base and root system feel wet, and black and brown striped spots can be observed in both the stem base and lower leaves (**Figure 1b**). For FCR caused by *F. pseudograminearum*, the stem base of the infected wheat plant is dry and fragile, and dark brown rot can be observed in the stem base (**Figure 1d**). For sharp eyespot caused by *R. cerealis*, the typical lesions on wheat stem are elliptical or in “eye” shape with sharply dark brown borders (**Figure 1f**).

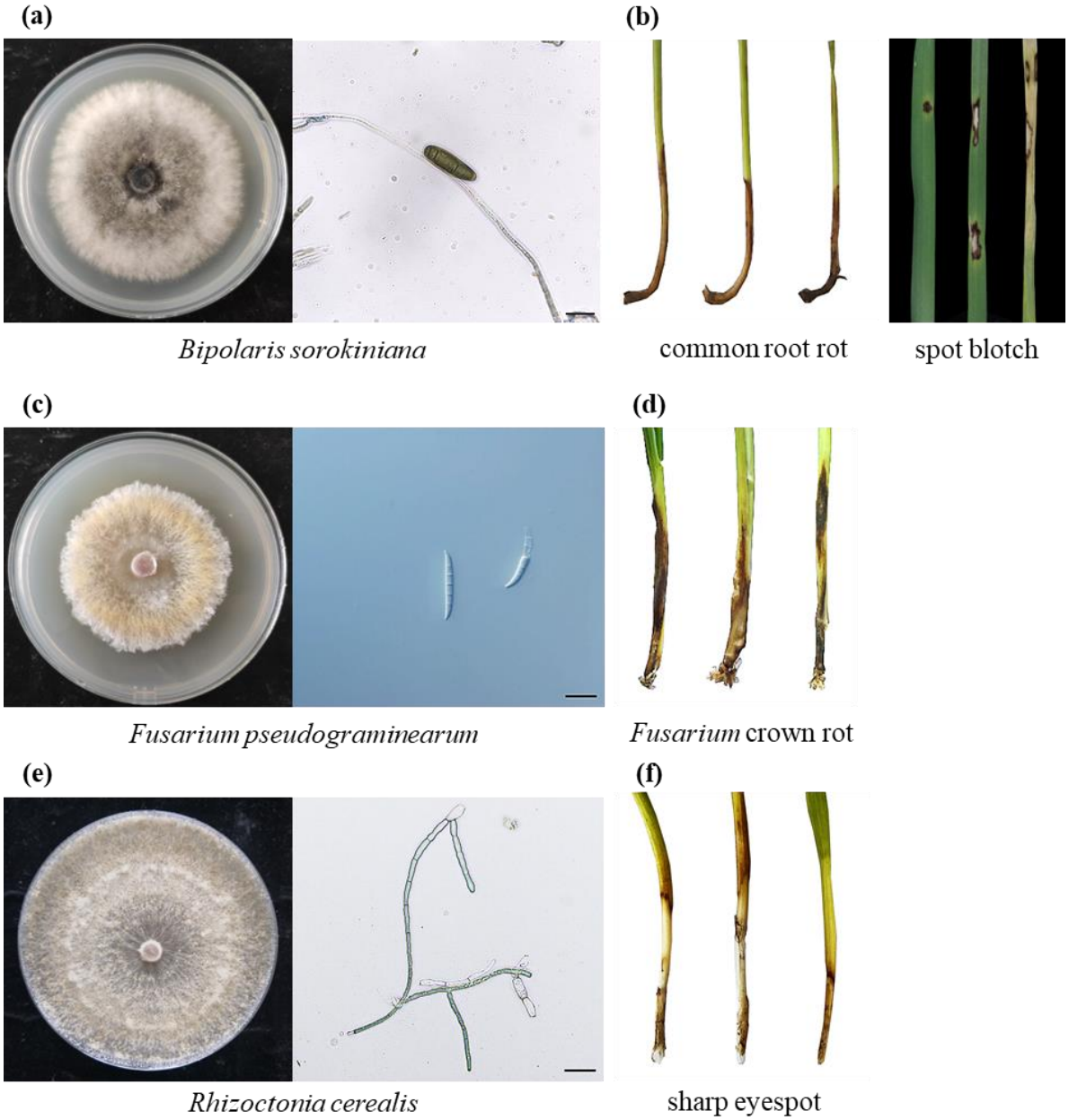

Figure 1. Pathogenic profiles of *Bipolaris sorokiniana*, *Fusarium pseudograminearum*, and *Rhizoctonia cerealis*. **(a)** *B. sorokiniana* cultivated on potato dextrose agar (PDA) medium. Spores were directly collected from cultures of *B. sorokiniana* on PDA medium. **(b)** Common root rot and spot blotch caused by *B. sorokiniana*. Infected wheat plants can be easily pulled out, the stem base and root system feel wet, and black and brown striped spots can be observed in both the stem base and lower leaves. **(c)** *F. pseudograminearum* cultivated on PDA medium. Spores of *F. pseudograminearum* can be induced on carboxymethyl cellulose sodium (CMC) medium. **(d)** *Fusarium* crown rot caused by *F. pseudograminearum*. The stem base of infected wheat plant is dry and fragile, so can be easily broken apart. Additionally, dark and red brown rot can be observed in the stem base. **(e)** *R. cerealis* cultivated on PDA medium. **(f)** Sharp eyespot caused by *R. cerealis*. The typical lesions on wheat stem are elliptical or in "eye" shape with sharply dark brown borders. Scale bar = 20 μm.

3. Genetic studies

3.1. Progress in Dissecting the Genetic Determinants of Wheat Resistance to Common Root Rot (Spot Blotch)

Breeding of wheat resistant cultivars remains the most efficient and economical way to control common root rot (spot blotch). However, there are insufficient germplasm resources with resistance to common root rot to meet the needs for global wheat breeding applications and there have been few studies to identify the genetic loci that control resistance to common root rot [7]. Early effort focused on the introgression of common root rot resistant loci from wheat relative *Thinopyrum ponticum* species [18]. Requiring complex quantitative trait loci (QTL), wheat breeding programs for common root rot resistance have faced many obstacles [19]. Using bi-parental populations and linkage mapping, four genetic loci with major resistant effect were identified and designated as *Sb* genes. *Sb1* was discovered in the bread wheat line "Saar", was mapped to chromosome 7DS, and is associated with the wheat leaf rust resistance gene *Lr34* [20]. The *Lr34*/*Yr18*/*Pm38* gene encodes a ATP-binding cassette (ABC) transporter that confers broad-spectrum resistance to multiple foliar fungal diseases, including leaf rust, stripe rust, and powdery mildew [21]. Another minor QTL that corresponded with *Lr46* on chromosome 1BL was also identified from "Saar". The *Lr46* gene is associated with adult plant slow rusting resistance toward leaf rust and is also associated with stripe rust resistance gene *Yr29* [22]. The *Sb2* gene was identified in bread wheat cultivar "Yangmai 6" and was mapped to chromosome 5BL between simple sequence repeat (SSR) markers of *Xgwm639* and *Xgwm1043* [23]. The *Sb2* gene was later reported to be linked with the *Tsn1* gene, which confers host-selective sensitivity to the fungal toxin ToxA produced by *Pyrenophora tritici-repentis* [24]. The *Sb3* gene was discovered in the winter wheat line "621-7-1" as providing immune response to *B. sorokiniana*. Using bulked segregant analysis (BSA), *Sb3* was mapped to chromosome 3BS, flanking SSR markers of *Xbarc133* and *Xbarc147* [25]. The *Sb4* gene was recently identified from two highly resistant wheat lines "Zhongyu1211" and "GY17". Using RNA-based BSA and single-nucleotide polymorphism (SNP) mapping, *Sb4* was delimitated in a 1.19 cM genetic interval region of chromosome 4BL, which contains 21 predicted genes in the corresponding "Chinese Spring" genome [26]. Future efforts to clone these designated *Sb* genes with major resistant effect may help elucidate the mechanism of wheat resistance toward this devastating fungal pathogen.

130 Several other major QTLs have been discovered and preliminarily mapped using bi-parental
131 populations. For instance, in an earlier investigation, two resistant QTLs derived from "Yangmai 6"
132 were mapped to chromosomes 5B and 7D using microsatellite markers [27]. Three QTLs on
133 chromosomes 5B, 6A, and 6D were designated based on analysis of SSR markers from resistant
134 genotype "G162" [28]. Four QTLs controlling resistance of wheat cultivar "Yangmai 6" to *B.*
135 *sorokiniana* were mapped to chromosomes 2AL, 2BS, 5BL, and 6DL [29]. A total of seven QTLs
136 providing resistance to *B. sorokiniana* infections were designated in wheat lines "Ning 8201" and
137 "Chirya 3" [30]. Three QTLs on chromosomes 1BS, 3BS, and 5AS explained 8.5%, 17.6%, and 12.3%,
138 respectively of resistant effect in "SYN1", a CIMMYT (International Maize and Wheat Improvement
139 Center) synthetic-derived bread wheat line [31]. From a Brazilian resistant cultivar "BH 1146", two
140 QTLs on chromosomes 7BL and 7DL were mapped using microsatellite markers [32]. A prominent
141 resistant QTL near the *Vrn-A1* locus on chromosome 5AL was found in "BARTAI" and "WUYA"
142 CIMMYT breeding lines [33]. QTLs in *Vrn-A1* and *Sb2/Tsn1* loci were also detected in two other
143 CIMMYT breeding lines, "CASCABEL" and "KATH" [34].
144 Genome-wide association study (GWAS) has been widely used to identify QTLs. Using 832
145 polymorphic Diversity Arrays Technology (DArT) markers, four QTLs resistant to spot blotch were
146 mapped to chromosomes 1A, 3B, 7B, and 7D after analysis of 566 spring wheat germplasms [35]. A
147 phenotypic screening of 11 parental genotypes and 55 F_2 lines identified "19HRWSN6" as a resistant
148 source. Subsequent simple linear regression analysis revealed SSR markers on chromosomes 5B, 6A,
149 and 7D associated with the resistance to *B. sorokiniana* [36]. With recent progress in drafting the
150 physical genome of hexaploid wheat [37], high-throughput SNP toolkits are now available for
151 GWAS on various complex traits of wheat [38]. A total of 528 spring wheat genotypes from different
152 geographic regions were tested for spot blotch resistance and eleven associated SNP markers were
153 found by 9K SNP assay [39]. Another study evaluated the responses of 294 hard winter wheat
154 genotypes to *B. sorokiniana* and performed GWAS by 15K SNP assay. A total of ten wheat genotypes
155 with relatively high resistance were identified and six major resistant QTLs were designated to
156 collectively explain 30% of the phenotypic variation [40]. A total of 159 spring wheat genotypes were
157 screened for common root rot resistance and twenty-four QTLs were identified, with a major one on
158 chromosome 7B that explained 14% of the phenotypic variation of spot blotch severity [41]. Another

159 study profiled the resistant phenotype of 287 spring wheat germplasms and performed GWAS using
160 90K SNP array. A total of eight genetic loci associated with incubation period, lesion number, and
161 disease score of *B. sorokiniana* infection were detected [42]. A recent study phenotyped 301 Afghan
162 wheat germplasms and found that approximately 15% of them exhibited lower disease scores than
163 the resistant control. A subsequent GWAS approach identified twenty-five marker-trait associations
164 on more than twelve chromosomes, including previously identified *Vrn-A1* and *Sb2*/*Tsn1* loci [43].
165 Another 141 spring wheat lines were collected for GWAS on spot blotch resistance. A total of 23
166 genomic regions were identified, including several stable regions on chromosomes 2B, 5B and 7D,
167 and a novel region on chromosome 3D [44].

168 We have summarized the previously reported wheat germplasms with relatively higher
169 resistance to *B. sorokiniana* **(Table 1)**. These wheat materials may serve as valuable resources for the
170 genetic improvement of wheat resistance to common root rot (spot blotch). We have also
171 summarized detailed information of previously designated resistant QTLs **(Table 1)** and drafted
172 their genomic distributions using the released genome of hexaploid wheat **(Figure 2)**.

173 **Table 1.** Genetic bases of wheat resistance to common root rot (spot blotch).

QTL name	Associated markers or SNPs	Resistant wheat germplasms	Reference
Sb1/Lr34* *Qsb* ***Qsb/Lr46/Yr29****	7DS: ***Xgwm295***, csLV34 7DS: *wPt-7654*, ***gdm88*** 1BL: ***wmc719***, *hbe248*, *ncw1-V*	Saar	[20]
Sb2/Tsn1*	5BL: ***Xgwm499***, *Xgwm639*, *Xgwm1043*	YS116, CASCABEL	[23,24,34,43]
Sb3*	3BS: ***Xbarc147***, *XWGGC3957*, *XWGGC4320*	621-7-1	[25]
Sb4*	4B: ***TraesCS4B01G295400.1***	Zhongyu1211, GY17	[26]
Qsb	5B: ***Xgwm544*** 7D: ***Xgwm437***	Yangmai 6	[27]
Qsb	5B: ***Xgwm67***	G162	[28]
QSb.bhu-2A *QSb.bhu-2B* *QSb.bhu-5B* *QSb.bhu-6D*	2AL: *Xbarc353*, ***Xgwm445*** 2BS: ***Xgwm148***, *Xgwm374* 5BL: *Xgwm067*, ***Xgwm371*** 6DL: ***Xbarc175***, *Xgwm732*	Yangmai 6	[29]
QSb.bhu-2A *QSb.bhu-2B* *QSb.bhu-5B* *QSb.bhu-7D*	2AS: ***Xgwm425***, *Xbarc159* 2BS: ***Xgwm148***, *Xbarc91* 5BL: ***Xgwm067***, *Xgwm213* 7DS:***Xgwm111***, *Xgwm1168*	Ning 8201	[30]
QSb.bhu-2B *QSb.bhu-2D* *QSb.bhu-3B* *QSb.bhu-7B* *QSb.bhu-7D*	2BS: ***Xgwm148***, *Xgwm129* 2DS: ***Xgwm455***, *Xgwm815* 3BS: *Xgwm533*, *Xgwm1037* 7BS: *Xgwm263*, *Xgwm255* 7DS: ***Xgwm111***, *Xswm008*	Chirya 3	[30]
QSb.cim-1B *QSb.cim-3B* *QSb.cim-5A*	1B: ***Xwmc128***, *Xgwm374* 3B: ***990937|F|0***, *1123330|F|0* 5A: ***1086218|F|0***, *982608|F|0*	SYN1, Mayoor, Tksn1081/Ae. squarrosa (222)	[31]
QSb.iiwbr-7B *QSb.iiwbr-7D*	7BL: *wmc758*, ***wmc335*** 7DL: *wmc653*, ***barc121***	BH 1146	[32]
Qsb/Vrn-A1*	5AL: ***Vrn-A1***	BARTAI, WUYA, CASCABEL, KATH	[33,34,43]
Qsb	1A: *wPt-730148*, ***wPt-668214*** 3B: ***wPt-1159, wPt-5769*** 7B: *wPt-2838* 7D: *wPt-664459*	Chirya 7, Forma Vinda de Varmland (PI 192569), IWA8600074 (PI 623098), Trigo (PI 477878), Soprimo (PI 479890), CI 10112 (PI 78814), Florentino (PI 565255), AW 6635A/86 (PI 572693), IWA8611737 (PI 625572), NW56A (PI 429667)	[35]
Qsb	1B: ***wsnp_Ex_c24700_33953160*** 5A: ***wsnp_Ex_c15342_23592740, wsnp_Ku_c17951_27138894*** 5B: ***wsnp_Ex_rep_c70120_69069789, wsnp_Ku_c20701_30355248*** 6B: ***wsnp_Ex_c15785_24157360***	PI25989, PI384237, PI384239, PI479802, PI479890, PI576639, PI245377, PI366685, PI481715, PI624517, PI481574, PI91235, PI350795, PI565213	[39]

	7B: ***wsnp_Ex_c52527_56097039***		
Qsb	5B: ***Xgwm544*** 6A: ***Xwgm570*** 7D: ***Xgwm437***	19HRWSN6, 30SAWSN5	[36]
QSb.sdsu-2D.1 *QSb.sdsu-3A.1* *QSb.sdsu-4A.1* *QSb.sdsu-4B.1* *QSb.sdsu-5A.1* *QSb.sdsu-7B.1*	2D: ***Kukri_c31121_1460*** 3A: ***Excalibur_c46082_440*** 4A: *IWA8475* 4B: ***Excalibur_rep_c79414_306*** 5A: ***Kukri_rep_c104877_2166*** 7B: *TA005844-0160*	Duster, Colt, Custer, Intrada, MT0495, NE99495, OK04525, OK05122, OK05723W, Venango	[40]
Qsb	1A: ***S1A_582293281*** 2A: ***S2A_16824871*** 3A: ***S3A_378506623*** 4B: ***S4B_554842477*** 5A: ***S5A_50162259*** 5B: ***S5B_513590441, S5B_504309131, S5B_528990456*** 6B: ***S6B_9296088, S6B_673978653*** 7A: ***S7A_483878120*** 7B: ***S7B_749474154***	Chirya.3, Aust-53, Pak-13, SB12-6704, 7HTWSN-4516, 7HTWSN-4513, Aust-8, SB12-6703, Aust-66, SB12-6720, Aust-12, 7HTWSN-4522, 7HTWSN-4526, 7HTWSN-4412, 7HTWSN-4405, 7HTWSN-4517, H.Sat-8, Aust-59, Aust-29, 7HTWSN-4406, 7HTWSN-4510	[41]
Qsb	1B: ***BobWhite_c17559_105*** 4A: ***BobWhite_c20322_153, BobWhite_c17524_242*** 5B: ***Tdurum_contig25513_123***, *tplb0027f13_1493* 6A: ***wsnp_Ra_c2270_4383252*** 6B: ***BS00092845_51*** 7A: ***Ku_c15750_761***	N. A.	[42]
Qsb	1B: ***TraesCS1B01G416200*** 5A: ***TraesCS5A01G391400, TraesCS5A01G369700***	0KATIA, DE9, OK82282//BOW/NKT/3/F4105, PSN/BOW//ROEK/3/MILAN, KAUZ 2*/OPATA//KAUZ, ALTAR84/AE.SQ//2*, CNDO/R143//ENTE/MEXI-2/3/…, PAMIR-94 x, NING9415, RENESANSA, VORONA/CUPE	[43]
Qsb	1A: ***TraesCS1A01G018700*** 1B: ***TraesCS1B01G424000, TraesCS1B01G423900*** 1D: ***TraesCS1D01G012500, TraesCS1D01G012900*** 2B: ***TraesCS2B01G505200, TraesCS2B01G552700, TraesCS2B01G12400, TraesCS2B01G30100*** 3A: ***TraesCS3A01G107400, TraesCS3A01G103000*** 3B: ***TraesCS3B01G520100*** 3D: ***TraesCS3D01G537500*** 5A: ***TraesCS5A01G402700, TraesCS5A01G457100*** 5B: ***TraesCS5B01G066200, TraesCS5B01G224500,***	N. A.	[44]

	TraesCS5B01G521500 6A: ***TraesCS6A01G061900*** 7A: ***TraesCS7A01G504700, TraesCS7A01G530700*** 7B: ***TraesCS7B01G002400, TraesCS7B01G003000, TraesCS7B01G169400*** 7D: ***TraesCS7D01G067000, TraesCS7D01G081100, TraesCS7D01G221000***

Genomic distribution of all these summarized resistant loci were drafted using associated markers and SNPs (bold labeled) that can be found in "Chinese Spring" wheat genome database. QTLs with major effect or linked with designated genes were labeled with asterisk (*) and highlighted in **Figure 2**.

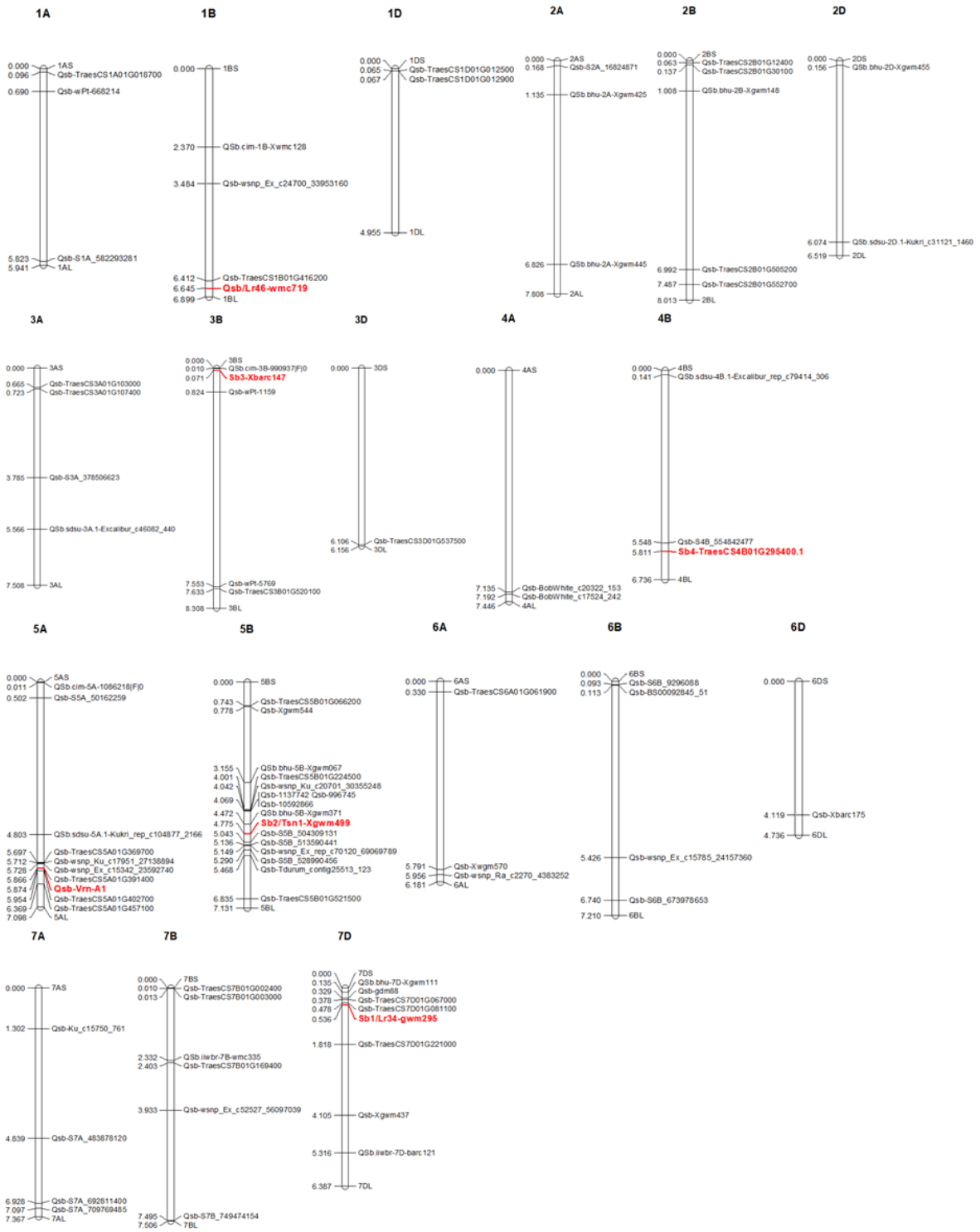

Figure 2. Genetic determinants of wheat resistance to common root rot (spot blotch). Molecular markers, SNPs, and genes associated with common root rot or spot blotch resistant QTLs were collected from previous publications and searched against the JBrowse-1.12.3-release of common wheat "Chinese Spring" genome available from the "*Triticeae* Multi-omics Center (http://202.194.139.32/)". Physical positions (numbers labelled on the left side of each chromosome) were used to generate a distribution map of all the collected QTLs using Mapchart v2.32 software. QTLs with major effect or linked with designated genes are highlighted in red. Detailed information for these QTLs can be found in **Table 1**.

186 *3.2. Genetic Loci Controlling Wheat Resistance to Fusarium Crown Rot*

187 Since the causal agent of *Fusarim* head blight (FHB), *Fusarium graminearum*, can also induce the
188 phenotype of *Fusarium* crown rot in certain regions [45,46], it is likely that FHB-resistant germplasms
189 and genetic loci can be exploited to improve FCR resistance. For instance, the recently cloned FHB
190 resistance gene *Fhb7* encodes a glutathione S-transferase (GST) and provides broad resistance to
191 *Fusarium* diseases, including FCR induced by *F. pseudograminearum*, by detoxifying trichothecenes
192 through de-epoxidation [47]. However, an earlier investigation found no significant correlation of
193 resistant phenotype or genetic loci conferring resistance to FHB and FCR in the same wheat
194 genotypes [48]. A recent large-scale phenotyping of 205 Chinese wheat cultivars for resistance to
195 both FHB and FCR also found no correlation [49]. Great efforts have also been towards identification
196 of FCR-resistant barley germplasms and genetic loci that control the FCR-resistance in barley [50].
197 Since recent review papers have already summarized QTLs conferring FHB resistance and
198 susceptibility in wheat in detail [51,52], here we have mainly focused on studies reporting wheat
199 resistance to FCR induced by *F. pseudograminearum* and *F. culmorum*.

200 A series of genetic studies revealed a major FCR-resistant QTL on chromosome 3BL (*Qcrs.cpi-3B*).
201 This resistant locus, *Qcrs.cpi-3B*, was derived from wheat genotype "CSCR6" belonging to the taxon
202 *Triticum spelta* [53]. In a wheat recombinant inbred line population of "Lang/CSCR6", a QTL on
203 chromosome 4B derived from "Lang" was responsible for the soil-free FCR resistance [54]. Another
204 significant QTL on chromosome 6B, but not *Qcrs.cpi-3B*, was identified and responsible for the FCR
205 resistance during an introgression process for durum wheat using "CSCR6" as the donor parent [55].
206 Near-isogenic lines for the *Qcrs.cpi-3B* locus were developed for both genetic research and breeding
207 practice [56]. Subsequent transcriptome and allele specificity analysis revealed differentially
208 expressed genes associated with the *Qcrs.cpi-3B* locus [57]. Fine mapping of this QTL shortened the
209 genetic interval to 0.7 cM, containing a total of 63 coding genes in the reference wheat genome [58].
210 Future map-based cloning and validation of the functional gene in this large-effect QTL may provide
211 valuable clues for us to understand the molecular bases of wheat resistance to FCR.

212 Other resistant QTLs have been identified using bi-parental populations. Early investigation
213 discovered a resistant locus near the dwarfing gene *Rht1* on chromosome 4B from the wheat cultivar
214 "Kukri" [59]. Inherited from a wheat line "W21MMT70" with partial resistance to FCR, two QTLs

215 were mapped to chromosomes 2D and 5D [60]. A major QTL on chromosome 1DL (*QCr.usq-1D1*)
216 and several minor QTLs were identified in wheat line "2-49 (Gluyas Early/Gala)" using SSR markers
217 [61,62]. An initial FCR resistance screening of 32 wheat genotypes revealed "2-49", "Aso zairai 11",
218 and "Ernie" as resistant sources. A QTL derived from "Ernie" was mapped to chromosome 3BL
219 close to markers *wPt-1151* and *wPt-1834* [48]. An Australian spring wheat cultivar "Sunco" showed
220 partial resistance to FCR induced by *F. pseudograminearum*. Using bi-parental QTL mapping, a major
221 QTL was identified on chromosome 3BL, between SSR markers *Xgwm247* and *Xgwm299* [63]. These
222 resistant sources of "W21MMT70", "2-49", and "Sunto" were then employed for QTL pyramiding
223 [64]. Four FCR-resistant QTLs were discovered and their resistant alleles were derived from the
224 bread wheat commercial variety "EGA Wylie". Major QTLs on chromosomes 5DS and 2DL were
225 consistently detected in all three populations and two minor QTLs were mapped to chromosome
226 4BS [65]. QTL mapping was also performed to find genetic loci controlling partial resistance to FCR
227 in the four wheat germplasms "2-49", "Sunco", "IRN497", and "CPI133817". FCR resistance was
228 evaluated in both seedlings and adult plants. A total of six QTLs among these resistant wheat
229 genotypes were detected [66].
230 A GWAS approach was used to screen 2,514 wheat genotypes for FCR resistance and identified
231 two major QTLs on chromosome 3BL explaining between 35% and 49% of the phenotypic variation
232 using DArT and SSR markers [67]. A set of 126 spring bread wheat lines from CIMMYT were
233 phenotyped against FCR induced by *F. culmorum* and further genotyped using DArT markers, which
234 resulted in the identification of three major QTLs on chromosomes 3B and 2D [68]. The use of GWAS
235 for FCR resistance has greatly benefited from advanced high-throughput sequencing techniques and
236 the released hexaploid wheat genome. A total of 234 Chinese wheat cultivars were evaluated for
237 FCR resistance in four greenhouse experiments, with GWAS conducted using a high-density 660K
238 SNP assay. This revealed a major QTL on chromosome 6A, which was subsequently validated using
239 a bi-parental population of "UC1110/PI610750" [69]. A recent GWAS approach phenotyped 358
240 Chinese germplasms for FCR resistance and less than 10% of germplasms showed a lower disease
241 index. The wheat 55K SNP assay was applied for the association analysis, resulting in detection of
242 significant QTLs on chromosomes 1BS, 1DS, 5DS, 5DL, and 7BL [70]. Another GWAS was performed
243 to evaluate FCR resistance of 161 wheat accessions under growth room and greenhouse conditions

using *F. culmorum* as the pathogen. Using a 90K SNP array, a total of fifteen QTLs for FCR resistance were detected with one major QTL on chromosome 3BS near the FHB resistance *Fhb1* locus [71]. A marker-assisted recurrent selection approach was performed on two populations to pyramid minor FCR-resistant QTLs. Using 9K SNP array, a total of 23 marker-trait associations were identified by GWAS [72].

In **Table 2**, we have summarized wheat germplasms resistant to FCR induced by either *F. pseudograminearum* or *F. culmorum*. Identified QTLs controlling FCR resistance are also highlighted (**Table 2**), with their genomic distributions annotated using the wheat genome database (**Figure 3**).

Table 2. Genetic loci controlling wheat resistance to *Fusarium* crown rot.

QTL name	Associated markers or SNPs	Resistant wheat germplasms	Reference
Qcrs.cpi-3B*	3BL: ***Xgwm0181***, *wPt-10505*, *wPt-2277*	CSCR6 (*T. spelta*), Lang, Kennedy	[53-58]
Qcsr.cpi-4B	4BS: ***wPt-5334***, *wPt-4918*, ***Xbarc199***		
Qcr	5A: ***Xwmc110***		
Qcr	6B: ***Xwmc494, Xgwm193, Xwmc397, Xbarc198, Xbarc178***		
Qcr	2BS: *Xgdm086*, ***Xbarc200***	W21MMT70, Mendos	[60]
	2D: *Xwmc018*, *Xwmc190*		
	5D: ***Xbarc205***, *barc143*		
Qcr	1AL: ***Xwmc120***, *Xwmc312*	Kukri, 2-49 (Gluyas Early/Gala), Janz	[59,61,62]
QCr.usq-1D.1	1DS: *Xcfd19*		
QCr.usq-2B.1	2BS: *Xbarc349.1*, ***Xgwm388***		
Qcr/Rht1*	4BL: *Xgwm165*, ***Xgwm251***		
Qcr	7BS: ***Xgwm400***, *Xwmc476*		
QCr.usq-1D.1	1DS: ***wPt-3738***, *Xcfd19*, *wPt-9380*	2-49, W21MMT70, Sunto	[64]
QCr.usq-2B.2	2B: *wPt-5374*, ***wPt-0434***		
QCr.usq-3B.1	3BL: ***wPt-7301***, *wPt-0365*		
QCr.usq-4B.1	4BS: ***wPt-4535***, *Xgwm251*		
Qcr	7AS: ***wPt-4748***, *wPt-8418*		
Qcr	3B: ***wPt-1834***, *wPt-1151*	2-49, Aso zairai 11, Ernie	[48]
Qcrs.wsu-3BL	3BL: *Xgwm247*, ***Xgwm299***	Sunco, Macon, Otis	[63]
Qcr	3BS: ***wPt-5390***, *Xwmc777*		
Qcr	7AS: ***wPt-3702***		
Qcrs.cpi-2D	2DL: ***1131013|F|0***, *1246993|F|0*	EGA Wylie	[65]
Qcrs.cpi-4B.1	4BS: ***100004319|F|0***, *2324159|F|0*		
Qcrs.cpi-4B.2	4BS: ***1108472|F|0***, *1093616|F|0*		
Qcrs.cpi-5D	5DS: ***1215315|F|0***, *1237596|F|0*		
Qcr	1AS: ***Xbarc148***, *Xgwm164*	2-49, Sunco, IRN497, CPI133817	[66]
	1BS: *Xcfd65*, ***Xgwm11***		
	1DL: *Xcfd19*, ***Xwmc216***		
	2A: ***Xgwm95,*** *Xcfa2043*		
	2B: ***Xgwm630***, *Xcfa2278*		
	2DS: ***Xgwm484***, *Xgwm102*		
	3AL: ***Xcfa2134,*** *Xcfa2262*		
	3BL: ***Xgwm299,*** *wPt-0021*, ***Xwmc236***, *wPt-0365*		
	4BS: *Xwmc467*, *Xgwm165*		
	4BS: ***Xbarc193***, *Xwmc349*		
	6DL: *Xcfd188*, ***Xcfd47***		

	6DL: *Xbarc196*, ***Xbarc273***		
Qcr	2DS: ***wPt-669517*** 3BS: *wPt-2193*, *wPt-22988*, *wPt-732330*, ***wPt-2766***	2-49, Sunco, Altay-2000	[68]
QFCR.heau-2A *QFCR.heau-2D* ***Qcr-6AL**** *QFCR.heau-6A* *Qcr-6B* *Qcr-6D*	2AS: *Xwms382*, *wPt-7462*, *wPt-3757* 2DS: ***Xcfd53*** 6AL: ***AX-111106634***, *AX-94534539* 6AS: ***Xbarc3***, *Xwmc754* 6B: ***SNP position 534,514,143*** 6D: ***SNP position 354,819,336***	Xunmai 118, Kaimai 26, Yanke 316, Xuke 732, Zhonglemai 9, Jinmai 1, Shenzhou 209, Fannong 1, Jiyanmai 7, UC1110, PI610750	[69]
Qcr *Qcr* *Qcr* *Qcr* *Qcr* ***Qcr-5DL**** *Qcr* *Qcr*	1BS: ***Affx-88612017, Affx-109495423*** 1DS: ***Affx-92108178, Affx-109205872*** 2AL: ***Affx-111557509*** 5DS: ***Affx-88597504, Affx-110248324*** 5AL: ***Affx-109253960*** 5DL: ***Affx-110484766, Affx-110079634*** 6BS: ***Affx-110282972*** 7BL: ***Affx-109846651, Affx-109540847***	Henong 982, Shiyou 17, Bao 6818, Quanmai 890, 04 Zhong 36, Junda 129, Xu 10054, Fanmai 5, Lian 0809, Shixin 733, Shi05-6678, Han 06-5170, Luomai 8, Zhongyuanzhixing, Yangao 21, Xumai 33	[70]
Qcr *Qcr* ***Qcr/Fhb1**** *Qcr* *Qcr* *Qcr* *Qcr* *Qcr* *Qcr* *Qcr* *Qcr* *Qcr*	2AL: *Kukri_c57491_156* 3AS: ***wsnp_Ra_c16278_24893033, CAP8_c1393_327*** 3BS: ***CAP12_rep_c3868_270*** 3DL: ***wsnp_Ex_c14027_21925404*** 4BS: ***wsnp_Ku_c12399_20037334*** 4BL: ***RAC875_rep_c72961_977*** 5BS: ***wsnp_Ku_c17875_27051169, Excalibur_c23304_353*** 5DS: ***RAC875_rep_c111521_246*** 5DL: ***Excalibur_c2795_1518*** 6BS: *RAC875_c17297_341* 6BL: ***BobWhite_c19298_97*** 6DS: *BS00021881_51*	VICTORYA, Katea, KOLLEGA, DORADE-5/3/BOW"S"/GEN//SHAHI, 2180*K/2163//?/3/W1062A*HVA114/W3416, L 4224 K 12, NE04424, TX69A509.2//BBY/FOX/3/GRK//NO64/PEX/4/CER/5/KAUZ//ALTAR 84/AOS, ID800994.W/MO88	[71]
Qcr	1A: ***BobWhite_c1027_1127, wsnp_Ku_c183_358844*** 1B: ***BS00070139_51, Tdurum_contig13117_1316*** 1D: ***wsnp_Ex_c3372_6195001*** 2D: ***BS00062567_51*** 3B: ***BS00072994_51, BS00079029_51, IACX11310*** 4A: ***BS00035307_51*** 4B: ***Ku_c3385_521*** 5B: ***BS00032003_51, BobWhite_c6094_447*** 6B: ***RAC875_c60007_199*** 7A: ***BobWhite_c33300_159, wsnp_JD_c1219_1766041***	AUS29529/2/2.49/Cunningham//Kennedy/3/Sunco, CSCR16/2/2.49/Cunningham//Kennedy/3/Sunco/2*Pastor	[72]

	7B: ***wsnp_be352570B_Ta_2_1***		
N. A.	N. A.	Cunmai633, LS4607, Pubing01, Hongyun2, Jimai216, Fengyunmai5, Huaihe15076, Luofeng2419, Yanfeng168, Zhengmai22, Zhoumai38, Zhoumai37, Lemai185, Xinmai38, Xinong733, Xinmai45, Guohemai12, Xinong625, Zhengmai162	[49]

Genomic distribution of all these summarized resistant loci were drafted using associated markers and SNPs (bold labeled) that can be found in "Chinese Spring" wheat genome database. QTLs with major effect or linked with designated genes were labeled with asterisk (*) and highlighted in **Figure 3**.

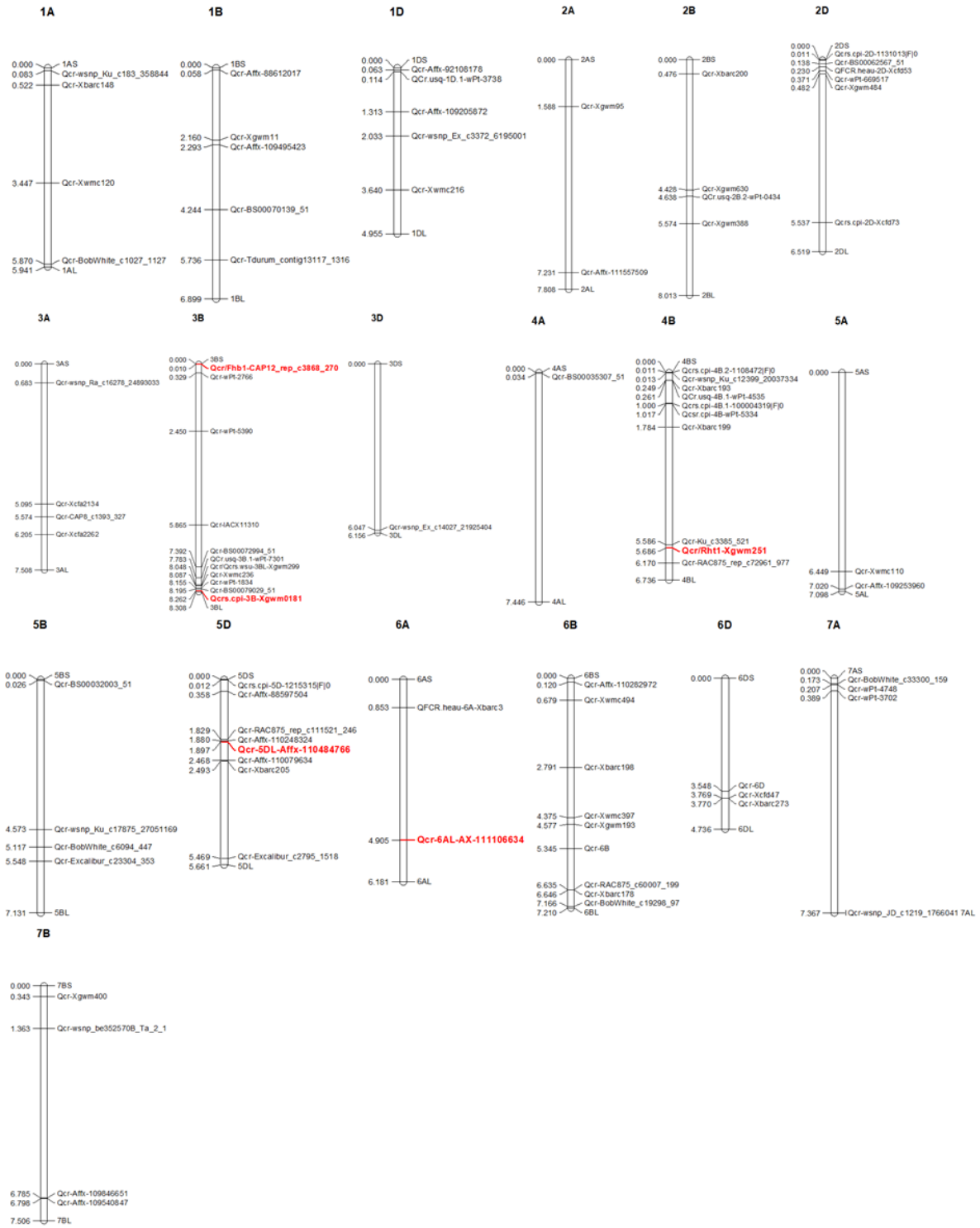

Figure 3. Genetic loci controlling wheat resistance to *Fusarium* crown rot. Molecular markers, SNPs, and genes associated with FCR-resistant QTLs were collected from previous publications and searched against the JBrowse-1.12.3-release of common wheat "Chinese Spring" genome available from the "*Triticeae* Multi-omics Center (http://202.194.139.32/)". Physical positions (numbers labelled on the left side of each chromosome) were used to generate a distribution map of all the collected QTLs using Mapchart v2.32 software. QTLs with major effect or linked with designated genes are highlighted in red. Detailed information for these QTLs can be found in **Table 2**.

3.3. Genetic Determinants of Wheat Resistance to Sharp Eyespot

Wheat resistance to sharp eyespot is controlled by QTLs. However, more efforts should be put in identification of resistant germplasms and genetic loci conferring resistance to this fungal disease. A recent large-scale screening of sharp eyespot resistant germplasms in Chinese wheat cultivars revealed no immune or highly resistant germplasms, but only 4% wheat germplasms showed moderate resistance to *R. cerealis* [15]. Introgression of exogenous chromosome segment from wheat relative species might be a solution to generate novel resistant germplasms. For instance, a wheat-rye 4R chromosome disomic addition line gained high resistance to sharp eyespot [73]. Wheat cultivars "Luke" and "AQ24788-83" showed high resistance to *R. cerealis*. Subsequent genetic investigations revealed seven sharp eyespot resistant QTLs on chromosomes 1A, 2B, 3B, 4A, 5D, 6B, and 7B [74,75]. Using 90 K SNP and SSR markers, five QTLs on chromosomes 2BS, 4BS, 5AL, and 5BS controlling the resistance to *R. cerealis* were identified from wheat cultivar "CI12633" [76]. Three QTLs controlling resistance of wheat cultivars "Niavt 14" and "Xuzhou 25" to *R. cerealis* were mapped to chromosomes 2B and 7D [77].

In **Table 3**, we have summarized wheat germplasms resistant to *R. cerealis*. Reported QTLs controlling sharp eyespot resistance are highlighted (**Table 3**), with their genomic distributions annotated using the wheat genome database (**Figure 4**).

Table 3. Genetic determinants of wheat resistance to sharp eyespot.

QTL name	Associated markers or SNPs	Resistant wheat germplasms	Reference
QSe.cau-1AS	1AS: ***barc148***, *wmc120*		
QSe.cau-2BS	2BS: *wmc154*, *barc200*		
QSe.cau-3BS	3BS: *wmc777*, ***barc73***		
QSe.cau-4AL	4AL: ***barc327***, *wmc776*	Luke, AQ24788-83	[74,75]
QSe.cau-5DL	5DL: ***gwm292***, *cfd29*, *gwm212*		
QSe.cau-6BL	6BL: *gwm626*, *barc187*, ***wmc397***		
QSe.cau-7BL	7BL: ***gwm611***, *wmc166*, ***wmc581***		
QSe.jaas-2BS	2BS: *RAC875_c730_234*, *RAC875_c16697_1502*		
QSe.jaas-4BS	4BS: *RAC875_c49792_228*, *Kukri_c34353_821*		
QSe.jaas-5AL.1	5AL: ***GENE-3601_145***, *Ku_c21002_908*	CI12633	[76]
QSe.jaas-5AL.2	5AL: ***IAAV3043***, *wsnp_Ex_c55777_58153636*		
QSe.jaas-5BS	5BS: ***wsnp_Ku_c11721_19085513***, *BS00068710_51*		
Qses.jaas-2b1	2B: *Xbarc101-2*, *Xbarc183*		
Qses.jaas-2b2	2B: ***Xbarc55***, *Xwmc149*	Niavt 14, Xuzhou 25	[77]
Qses.jaas-7d	7D: ***Xbarc126***, *Xwmc702*		
N. A.	N. A.	**Seedling resistance:** CI12633, Banmangmai, Banjiemang, Ibis, Hongyouzi, Shaanhe6, Chinese Spring, Hongxingmai, Pingyuan 50, Linfen139, Chuanyu12, Yongfengnong2, Yunong202, Xinmai68, Huabei187, Jinmai50, Neixiang184 **Adult plant resistance:** Shaanhe6, CI12633, Banmangmai, Chinese Spring, Huomai, Banjiemang, Pingyuan50, Pingyang181, Yumai8, Qingfeng1, Hongyouzi, Hongxingmai, Libellula, Zhengmai8998	[15]

Genomic distribution of all these summarized resistant loci were drafted using associated markers (bold labeled) that can be found in "Chinese Spring" wheat genome database. QTLs were annotated in **Figure 4**.

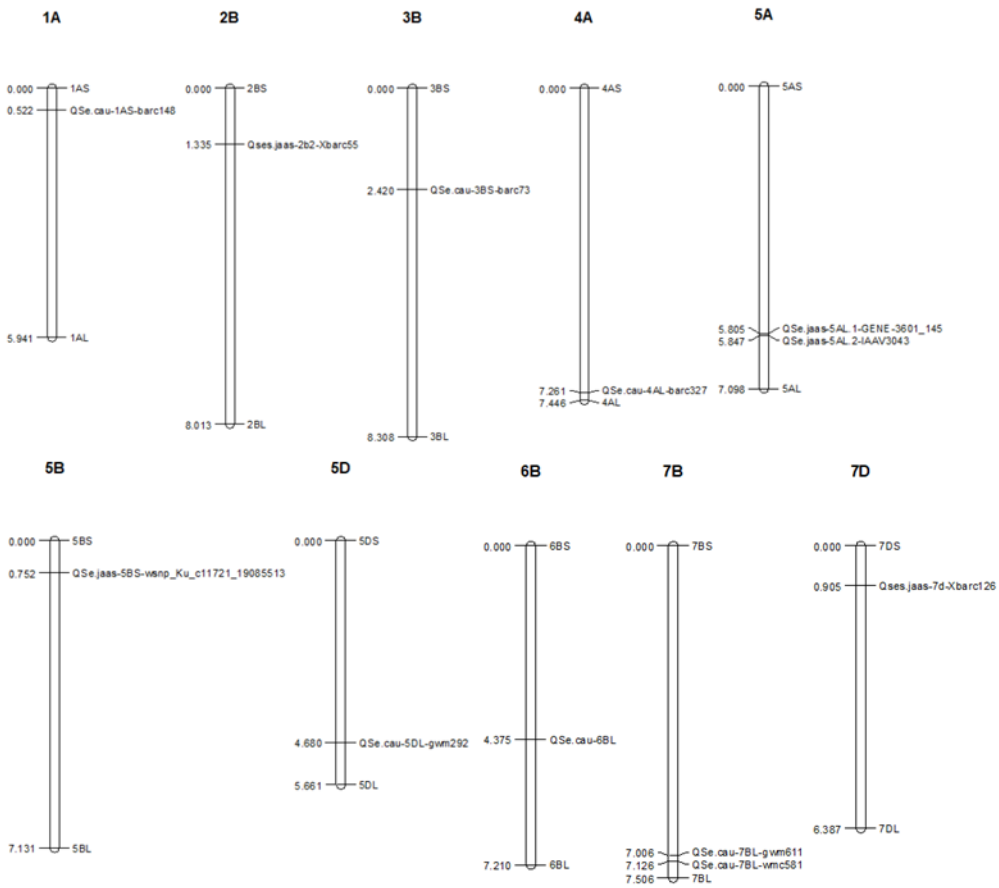

Figure 4. Identified QTLs controlling wheat resistance to sharp eyespot. Molecular markers associated with Rc-resistant QTLs were collected from previous publications and searched against the JBrowse-1.12.3-release of common wheat "Chinese Spring" genome available from the "Triticeae Multi-omics Center (http://202.194.139.32/)". Physical positions (numbers labelled on the left side of each chromosome) were used to generate a distribution map of all the collected QTLs using Mapchart v2.32 software. Detailed information for these QTLs can be found in **Table 3**.

4. Conclusion and future perspectives

We have briefly introduced three rot diseases that are commonly observed in the stem base of wheat plants (**Figure 1**). These diseases have become major threats to wheat productions in wheat-maize rotation areas with large-scale application of straw returning. Wheat breeding is still the most efficient way to control these devastating fungal diseases. However, as summarized in this review (**Tables 1, 2, and 3**), there are few wheat germplasms with relative high resistance to either *B. sorokiniana*, *F. pseudograminearum*, or *R. cerealis*. Large-scale screenings of resistant wheat germplasms are still urgently needed for effective wheat breeding applications.

Genetic improvement of wheat resistance to these diseases will be facilitated by exploring novel QTLs that control resistance and dissecting functional genes within these QTLs. In this review, we list previously reported resistant QTLs (**Tables 1, 2, and 3**) and present their genomic distributions

303 based on the released wheat genome (**Figures 2, 3, and 4**). Some of the identified QTLs conferring
304 resistance to *B. sorokiniana* are associated with certain resistant loci responsible for wheat resistance
305 to other foliar fungal diseases, such as *Lr34/Yr18/Pm38*, *Lr46/Yr29*, and *Tsn1*. Wheat leaves might
306 restrain the infection of different foliar fungal diseases by utilization of similar molecular
307 approaches mediated by these resistant genes. More wheat germplasms with broad-spectrum
308 resistant loci should be evaluated for their potential resistance to spot blotch or common root rot
309 induced by *B. sorokiniana.* For QTLs controlling resistance to *Fusarium* crown rot, ones that also have
310 resistance to FHB may be more valuable, since the major causal agents of these diseases (*F.*
311 *pseudograminearum*, *F. culmorum*, and *F. graminearum*) are very likely to co-exist in the same
312 cultivation environment. For genetic studies on QTLs controlling resistance to sharp eyespot, more
313 large-scale screenings of resistant wheat germplasms would greatly accelerate the identification of
314 novel sharp eyespot resistant QTLs. There is also an urgent need to employ GWAS technique to
315 explore more sharp eyespot resistant QTLs in a genome-wide level.
316 Great efforts should also be made to convert traditional markers (microsatellite, SSR, and DrAT
317 *etc.*) associated with previously identified resistant QTLs to SNP markers, the latter which may
318 serve as valuable tools for high-throughput marker-assisted selection in wheat breeding. Progress
319 in wheat genome research and increased availability of high-density SNP toolkits will facilitate the
320 use of GWAS on collected wheat germplasms to efficiently identify novel resistant sources and
321 genetic loci.
322
323 **Author Contributions:** Conceptualization, X.W., Z.K., and W.Z; Data collection, J.S., J.Z., S.Z., M.L.,
324 X.S., S.P.; Original draft preparation, X.W.; Review and editing, S.C. and F.C.; Supervision, X.W.,
325 Z.K., and W.Z. All authors have read and agreed to the published version of the manuscript.
326
327 **Funding:** This work was supported by Open Project Program of National Key Laboratory of Wheat
328 and Maize Crop Science, Provincial Supporting Program of Hebei for the Returned Oversea Scholars
329 (C20190180), Open Project Program of State Key Laboratory of North China Crop Improvement and
330 Regulation (NCCIR2020KF-4), and National Key R&D Program of China (2017YFD0300906).
331
332 **Conflicts of Interest:** The authors declare no conflict of interest.
333
334 **Reference**
335 1. Cohen, S.P.; Leach, J.E. High temperature-induced plant disease susceptibility: more than the sum of

its parts. *Curr. Opin. Plant Biol.* **2020**, *56*, 235-241.

2. Wang, J.; Wang, X.; Xu, M.; Feng, G.; Zhang, W.; Yang, X.; Huang, S. Contributions of wheat and maize residues to soil organic carbon under long-term rotation in north China. *Sci. Rep.* **2015**, *5*, 11409.
3. Zhao, R.; Chen, X.; Zhang, F.; Zhang, H.; Schroder, J.L.; Romheld, V. Fertilization and nitrogen balance in a wheat–maize rotation system in North China. *Agron. J.* **2006**, *98*, 938-945.
4. Peralta, A.L.; Sun, Y.; McDaniel, M.D.; Lennon, J.T. Crop rotational diversity increases disease suppressive capacity of soil microbiomes. *Ecosphere* **2018**, *9*, e02235.
5. Kumar, J.; Schafer, P.; Huckelhoven, R.; Langen, G.; Baltruschat, H.; Stein, E.; Nagarajan, S.; Kogel, K. *Bipolaris sorokiniana*, a cereal pathogen of global concern: cytological and molecular approaches towards better control. *Mol. Plant Pathol.* **2002**, *3*, 185-195.
6. Sharma, R.C.; Duveiller, E. Advancement toward new spot blotch resistant wheats in South Asia. *Crop Sci.* **2007**, *47*, 961-968.
7. Gupta, P.K.; Chand, R.; Vasistha, N.K.; Pandey, S.P.; Kumar, U.; Mishra, V.K.; Joshi, A.K. Spot blotch disease of wheat: the current status of research on genetics and breeding. *Plant Pathol.* **2018**, *67*, 508-531.
8. Conner, R.L.; Duczek, L.J.; Kozub, G.C.; Kuzyk, A.D. Influence of crop rotation on common root rot of wheat and barley. *Can. J. Plant Pathol.* **1996**, *18*, 247-254.
9. Kazan, K.; Gardiner, D.M. *Fusarium* crown rot caused by *Fusarium psudograminearum* in cereal crops: recent progress and future prospects. *Mol. Plant Pathol.* **2018**, *19*, 1547-1562.
10. Smiley, R.W.; Gourlie, J.A.; Easley, S.A.; Patterson, L. Pathogenicity of fungi associated with the wheat crown rot complex in Oregon and Washington. *Plant Dis.* **2005**, *89*, 949-957.
11. Obanor, F.; Chakraborty, S. Aetiology and toxigenicity of *Fusarium graminearum* and *F. pseudograminearum* causing crown rot and head blight in Australia under natural and artificial infection. *Plant Pathol.* **2014**, *63*, 1218-1229.
12. Monds, R.D.; Cromey, M.G.; Lauren, D.R.; Menna, M.E.D.; Marshall, J.W. *Fusarium graminearum*, *F. cortaderiae* and *F. pseudograminearum* in New Zealand: molecular phylogenetic analysis, mycotoxin chemotypes and co-existence of species. *Fungal Biol.* **2005**, *109*, 410-420.
13. Burgess, L.W.; Backhouse, D.; Summerell, B.A.; Swan, L.J. Crown rot in wheat----Chapter 20. In *Fusarium-Paul E Nelson Memorial Symposium*, Summerell, B.A., Leslie, J.F., Backhouse, D., Bryden, W.L., Burgess, L.W., Eds. APS Press: The American Phytopathological Society, St Paul, 2001.
14. Hamada, M.S.; Yin, Y.; Chen, H.; Ma, Z. The escalating threat of *Rhizoctonia cerealis*, the causal agent of sharp eyespot in wheat. *Pest Manag. Sci.* **2011**, *67*, 1411-1419.
15. Ren, Y.; Yu, P.-B.; Wang, Y.; Hou, W.-X.; Yang, X.; Fan, J.-L.; Wu, X.-H.; Lv, X.-L.; Zhang, N.; Zhao, L. Development of a Rapid Approach for Detecting Sharp Eyespot Resistance in Seedling-Stage Wheat and Its Application in Chinese Wheat Cultivars. *Plant Dis.* **2020**, PDIS-12-19-2718-RE.
16. McBeath, J.H.; McBeath, J. Plant diseases, pests and food security. In *Environmental Change and Food Security in China*, Springer, Dordrecht: Advances in Global Change Research, 2010; Vol. 35, pp. 117-156.
17. Lemańczyk, G.; Kwaśna, H. Effects of sharp eyespot (*Rhizoctonia cerealis*) on yield and grain quality of winter wheat. *Eur. J. Plant Pathol.* **2013**, *135*, 187-200.
18. Li, H.; Conner, R.L.; Chen, Q.; Li, H.; Laroche, A.; Graf, R.J.; Kuzyk, A.D. The transfer and characterization of resistance to common root rot from *Thinopyrum ponticum* to wheat. *Genome* **2004**, *47*, 215-223.

19. Joshi, A.K.; Kumar, S.; Chand, R.; Ortizferrara, G. Inheritance of resistance to spot blotch caused by *Bipolaris sorokiniana* in spring wheat. *Plant Breed.* **2004**, *123*, 213-219.
20. Lillemo, M.; Joshi, A.K.; Prasad, R.; Chand, R.; Singh, R.P. QTL for spot blotch resistance in bread wheat line Saar co-locate to the biotrophic disease resistance loci *Lr34* and *Lr46*. *Theor. Appl. Genet.* **2013**, *126*, 711-719.
21. Krattinger, S.G.; Lagudah, E.S.; Spielmeyer, W.; Singh, R.P.; Huerta-Espino, J.; McFadden, H.; Bossolini, E.; Selter, L.L.; Keller, B. A putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. *Science* **2009**, *323*, 1360-1363.
22. William, M.; Singh, R.P.; Huertaespino, J.; Islas, S.O.; Hoisington, D.A. Molecular marker mapping of leaf rust resistance gene *Lr46* and its association with stripe rust resistance gene *Yr29* in wheat. *Phytopathol.* **2003**, *93*, 153-159.
23. Kumar, S.; Roder, M.S.; Tripathi, S.B.; Kumar, S.; Chand, R.; Joshi, A.K.; Kumar, U. Mendelization and fine mapping of a bread wheat spot blotch disease resistance QTL. *Mol. Breed.* **2015**, *35*, 218.
24. Kumar, S.; Roder, M.S.; Singh, R.P.; Kumar, S.; Chand, R.; Joshi, A.K.; Kumar, U. Mapping of spot blotch disease resistance using NDVI as a substitute to visual observation in wheat (*Triticum aestivum* L.). *Mol. Breed.* **2016**, *36*, 95.
25. Lu, P.; Liang, Y.; Li, D.F.; Wang, Z.; Li, W.; Wang, G.; Wang, Y.; Zhou, S.; Wu, Q.; Xie, J. Fine genetic mapping of spot blotch resistance gene *Sb3* in wheat (*Triticum aestivum*). *Theor. Appl. Genet.* **2016**, *129*, 577-589.
26. Zhang, P.; Guo, G.; Wu, Q.; Chen, Y.; Xie, J.; Lu, P.; Li, B.; Dong, L.; Li, M.; Wang, R., et al. Identification and fine mapping of spot blotch (*Bipolaris sorokiniana*) resistance gene *Sb4* in wheat. *Theor. Appl. Genet.* **2020**, *133*.
27. Kumar, U.; Kumar, S.; Tyagi, K.; Chand, R.; Joshi, A.K. Microsatellite markers for resistance to spot blotch in spring wheat. *Commun. Agri. Appl. Biol. Sci.* **2005**, *70*, 59.
28. Sharma, R.C.; Duveiller, E.; Jacquemin, J.M. Microsatellite Markers Associated with Spot Blotch Resistance in Spring Wheat. *J. Phytopathol.* **2007**, *155*, 316-319.
29. Kumar, U.; Joshi, A.K.; Kumar, S.; Chand, R.; Roder, M.S. Mapping of resistance to spot blotch disease caused by *Bipolaris sorokiniana* in spring wheat. *Theor. Appl. Genet.* **2009**, *118*, 783-792.
30. Kumar, U.; Joshi, A.K.; Kumar, S.; Chand, R.; Roder, M.S. Quantitative trait loci for resistance to spot blotch caused by *Bipolaris sorokiniana* in wheat (*T. aestivum* L.) lines 'Ning 8201' and 'Chirya 3'. *Mol. Breed.* **2010**, *26*, 477-491.
31. Zhu, Z.; Bonnett, D.; Ellis, M.; Singh, P.K.; Heslot, N.; Dreisigacker, S.; Gao, C.; Mujeebkazi, A. Mapping resistance to spot blotch in a CIMMYT synthetic-derived bread wheat. *Mol. Breed.* **2014**, *34*, 1215-1228.
32. Singh, V.; Singh, G.; Chaudhury, A.; Ojha, A.; Tyagi, B.S.; Chowdhary, A.K.; Sheoran, S. Phenotyping at hot spots and tagging of QTLs conferring spot blotch resistance in bread wheat. *Mol. Biol. Rep.* **2016**, *43*, 1293-1303.
33. Singh, P.K.; He, X.; Sansaloni, C.; Juliana, P.; Dreisigacker, S.; Duveiller, E.; Kumar, U.; Joshi, A.K.; Singh, R.P. Resistance to Spot Blotch in Two Mapping Populations of Common Wheat Is Controlled by Multiple QTL of Minor Effects. *Inter. J. Mol. Sci.* **2018**, *19*, 4054.
34. He, X.; DREISIGACKER, s.; Sansaloni, C.; Duveiller, E.; Singh, R.P.; Singh, P.K. QTL mapping for spot blotch resistance in two bi-parental mapping populations of bread wheat. *Phytopathol.* **2020**.
35. Adhikari, T.B.; Gurung, S.; Hansen, J.M.; Jackson, E.W.; Bonman, J.M. Association mapping of quantitative trait loci in spring wheat landraces conferring resistance to bacterial leaf streak and

spot blotch. *Plant Genome* **2012**, *5*, 1-16.

36. Tembo, B.; Sibiya, J.; Tongoona, P.; Tembo, L. Validation of microsatellite molecular markers linked with resistance to *Bipolaris sorokiniana* in wheat (*Triticum aestivum* L.). *J. Agri. Sci.* **2017**, *155*, 1061-1068.

37. Appels, R.; Eversole, K.; Stein, N.; Feuillet, C.; Keller, B.; Rogers, J.; Pozniak, C.J.; Choulet, F.; Distelfeld, A.; Poland, J., et al. Shifting the limits in wheat research and breeding using a fully annotated reference genome. *Science* **2018**, *361*, eaar7191.

38. Sun, C.; Dong, Z.; Zhao, L.; Ren, Y.; Zhang, N.; Chen, F. The Wheat 660K SNP array demonstrates great potential for marker‐assisted selection in polyploid wheat. *Plant Biotechnol. J.* **2020**.

39. Gurung, S.; Mamidi, S.; Bonman, J.M.; Xiong, M.; Brownguedira, G.; Adhikari, T.B. Genome-wide association study reveals novel quantitative trait loci associated with resistance to multiple leaf spot diseases of spring wheat. *PLoS ONE* **2014**, *9*, e108179.

40. Ayana, G.T.; Ali, S.; Sidhu, J.S.; Hernandez, J.L.G.; Turnipseed, B.; Sehgal, S.K. Genome-wide association study for spot blotch resistance in hard winter wheat. *Front. Plant Sci.* **2018**, *9*, 926.

41. Jamil, M.; Ali, A.; Gul, A.; Ghafoor, A.; Ibrahim, A.M.H.; Mujeeb-Kazi, A. Genome-wide association studies for spot blotch (*Cochliobolus sativus*) resistance in bread wheat using genotyping-by-sequencing. *Phytopathol.* **2018**, *108*, 1307-1314.

42. Ahirwar, R.N.; Mishra, V.K.; Chand, R.; Budhlakoti, N.; Mishra, D.C.; Kumar, S.; Singh, S.; Joshi, A.K. Genome-wide association mapping of spot blotch resistance in wheat association mapping initiative (WAMI) panel of spring wheat (*Triticum aestivum* L.). *PLoS ONE* **2018**, *13*, e0208196.

43. Bainsla, N.K.; Phuke, R.M.; He, X.; Gupta, V.; Bishnoi, S.K.; Sharma, R.K.; Ataei, N.; Dreisigacker, S.; Juliana, P.; Singh, P.K. Genome-wide association study for spot blotch resistance in Afghan wheat germplasm. *Plant Pathol.* **2020**.

44. Tomar, V.; Singh, R.P.; Poland, J.; Singh, D.; Joshi, A.K.; Singh, P.K.; Bhati, P.K.; Kumar, S.; Rahman, M.; Dhillon, G.S., et al. Genome-wide association study and genomic prediction of spot blotch disease in wheat (*Triticum aestivum* L.) using genotyping by sequencing. *Res. Square* **2020**, *Preprint*.

45. Zhou, H.; He, X.; Wang, S.; Ma, Q.; Sun, B.; Ding, S.; Chen, L.; Zhang, M.; Li, H. Diversity of the *Fusarium* pathogens associated with crown rot in the Huanghuai wheat‐growing region of China. *Environ. Microbiol.* **2019**, *21*, 2740-2754.

46. Akinsanmi, O.A.; Backhouse, D.; Simpfendorfer, S.; Chakraborty, S. Genetic diversity of Australian *Fusarium graminearum* and *F. pseudograminearum*. *Plant Pathol.* **2006**, *55*, 494-504.

47. Wang, H.; Sun, S.; Ge, W.; Zhao, L.; Hou, B.; Wang, K.; Lyu, Z.; Chen, L.; Xu, S.; Guo, J., et al. Horizontal gene transfer of *Fhb7* from fungus underlies *Fusarium* head blight resistance in wheat. *Science* **2020**, *368*, eaba5435.

48. Li, H.B.; Xie, G.Q.; Ma, J.; Liu, G.R.; Wen, S.M.; Ban, T.; Chakraborty, S.; Liu, C.J. Genetic relationships between resistances to *Fusarium* head blight and crown rot in bread wheat (*Triticum aestivum* L.). *Theor. Appl. Genet.* **2010**, *121*, 941-950.

49. Shi, S.; Zhao, J.; Pu, L.; Sun, D.; Han, D.; Li, C.; Feng, X.; Fan, D.; Hu, X. Identification of new sources of resistance to crown rot and *Fusarium* head blight in Wheat. *Plant Dis.* **2020**, *104*, 1979-1985.

50. Liu, C.; Ogbonnaya, F.C. Resistance to *Fusarium* crown rot in wheat and barley: a review. *Plant Breed.* **2015**, *134*, 365-372.

51. Buerstmayr, M.; Steiner, B.; Buerstmayr, H. Breeding for *Fusarium* head blight resistance in wheat—progress and challenges. *Plant Breed.* **2020**, *139*, 429-454.

52. Fabre, F.; Rocher, F.; Alouane, T.; Langin, T.; Bonhomme, L. Searching for FHB resistances in bread

wheat: susceptibility at the crossroad. *Front. Plant Sci.* **2020**, *11*.

53. Ma, J.; Li, H.B.; Zhang, C.; Yang, X.M.; Liu, Y.; Yan, G.; Liu, C. Identification and validation of a major QTL conferring crown rot resistance in hexaploid wheat. *Theor. Appl. Genet.* **2010**, *120*, 1119-1128.
54. Yang, X.; Ma, J.; Li, H.; Ma, H.; Yao, J.; Liu, C. Different genes can be responsible for crown rot resistance at different developmental stages of wheat and barley. *Eur. J. Plant Pathol.* **2010**, *128*, 495-502.
55. Ma, J.; Zhang, C.Y.; Liu, Y.X.; Yan, G.J.; Liu, C.J. Enhancing *Fusarium* crown rot resistance of durum wheat by introgressing chromosome segments from hexaploid wheat. *Euphytica* **2012**, *186*, 67-73.
56. Ma, J.; Yan, G.; Liu, C. Development of near-isogenic lines for a major QTL on 3BL conferring *Fusarium* crown rot resistance in hexaploid wheat. *Euphytica* **2012**, *183*, 147-152.
57. Ma, J.; Stiller, J.; Zhao, Q.; Feng, Q.; Cavanagh, C.R.; Wang, P.; Gardiner, D.M.; Choulet, F.; Feuillet, C.; Zheng, Y. Transcriptome and allele specificity associated with a 3BL locus for *Fusarium* crown rot resistance in bread wheat. *PLoS ONE* **2014**, *9*, e113309.
58. Zheng, Z.; Ma, J.; Stiller, J.; Zhao, Q.; Feng, Q.; Choulet, F.; Feuillet, C.; Zheng, Y.; Wei, Y.; Han, B. Fine mapping of a large-effect QTL conferring *Fusarium* crown rot resistance on the long arm of chromosome 3B in hexaploid wheat. *BMC Genomics* **2015**, *16*, 850-850.
59. Wallwork, H.; Butt, M.; Cheong, J.; Williams, K.J. Resistance to crown rot in wheat identified through an improved method for screening adult plants. *Australas. Plant Path.* **2004**, *33*, 1-7.
60. Bovill, W.D.; Ma, W.; Ritter, K.; Collard, B.C.Y.; Davis, M.; Wildermuth, G.B.; Sutherland, M.W. Identification of novel QTL for resistance to crown rot in the doubled haploid wheat population 'W21MMT70'×'Mendos'. *Plant Breed.* **2006**, *125*, 538-543.
61. Collard, B.C.Y.; Jolley, R.; Bovill, W.D.; Grams, R.A.; Wildermuth, G.B.; Sutherland, M.W. Confirmation of QTL mapping and marker validation for partial seedling resistance to crown rot in wheat line '2-49'. *Crop Pasture Sci.* **2006**, *57*, 967-973.
62. Collard, B.C.Y.; Grams, R.A.; Bovill, W.D.; Percy, C.D.; Jolley, R.; Lehmensiek, A.; Wildermuth, G.; Sutherland, M.W. Development of molecular markers for crown rot resistance in wheat: mapping of QTLs for seedling resistance in a '2-49'×'Janz' population. *Plant Breed.* **2005**, *124*, 532-537, doi:10.1111/j.1439-0523.2005.01163.x.
63. Poole, G.J.; Smiley, R.W.; Paulitz, T.C.; Walker, C.; Carter, A.H.; See, D.R.; Garlandcampbell, K. Identification of quantitative trait loci (QTL) for resistance to *Fusarium* crown rot (*Fusarium pseudograminearum*) in multiple assay environments in the Pacific Northwestern US. *Theor. Appl. Genet.* **2012**, *125*, 91-107.
64. Bovill, W.D.; Horne, M.; Herde, D.J.; Davis, M.; Wildermuth, G.B.; Sutherland, M.W. Pyramiding QTL increases seedling resistance to crown rot (*Fusarium pseudograminearum*) of wheat (*Triticum aestivum*). *Theor. Appl. Genet.* **2010**, *121*, 127-136.
65. Zheng, Z.; Kilian, A.; Yan, G.; Liu, C. QTL conferring fusarium crown rot resistance in the elite bread wheat variety EGA Wylie. *PLoS ONE* **2014**, *9*, e96011.
66. Martin, A.; Bovill, W.D.; Percy, C.D.; Herde, D.J.; Fletcher, S.; Kelly, A.; Neate, S.M.; Sutherland, M.W. Markers for seedling and adult plant crown rot resistance in four partially resistant bread wheat sources. *Theor. Appl. Genet.* **2015**, *128*, 377-385.
67. Liu, C.; Ma, J.; Li, H.B.; Liu, Y.X.; Liu, G.R.; Wen, S.M.; Zhou, M.; Yan, G.; Chakraborty, S. The homoeologous regions on long arms of group 3 chromosomes in wheat and barley harbour major crown rot resistance loci. *Czech J. Genet. Plant Breed.* **2018**, *47*, 109-114.
68. Erginbasorakci, G.; Sehgal, D.; Sohail, Q.; Ogbonnaya, F.C.; Dreisigacker, S.; Pariyar, S.R.; Dababat, A.A.

Identification of novel quantitative trait loci linked to crown rot resistance in spring wheat. *Inter. J. Mol. Sci.* **2018**, *19*, 2666.

69. Yang, X.; Pan, Y.; Singh, P.K.; He, X.; Ren, Y.; Zhao, L.; Zhang, N.; Cheng, S.; Chen, F. Investigation and genome-wide association study for *Fusarium* crown rot resistance in Chinese common wheat. *BMC Plant Biol.* **2019**, *19*, 153.

70. Jin, J.; Duan, S.; Qi, Y.; Yan, S.; Li, W.; Li, B.; Xie, C.; Zhen, W.; Ma, J. Identification of a novel genomic region associated with resistance to *Fusarium* crown rot in wheat. *Theor. Appl. Genet.* **2020**, *133*, 2063-2073.

71. Pariyar, S.R.; Erginbasorakci, G.; Dadshani, S.; Chijioke, O.B.; Leon, J.; Dababat, A.A.; Grundler, F.M.W. Dissecting the genetic complexity of *Fusarium* crown rot resistance in wheat. *Sci. Rep.* **2020**, *10*, 1-13.

72. Rahman, M.; Davies, P.; Bansal, U.; Pasam, R.; Hayden, M.; Trethowan, R. Marker-assisted recurrent selection improves the crown rot resistance of bread wheat. *Mol. Breed.* **2020**, *40*, 28.

73. An, D.; Ma, P.; Zheng, Q.; Fu, S.; Li, L.; Han, F.; Han, G.; Wang, J.; Xu, Y.; Jin, Y., et al. Development and molecular cytogenetic identification of a new wheat-rye 4R chromosome disomic addition line with resistances to powdery mildew, stripe rust and sharp eyespot. *Theor. Appl. Genet.* **2019**, *132*, 257-272.

74. Chen, J.; Li, G.H.; Du, Z.Y.; Quan, W.; Zhang, H.Y.; Che, M.Z.; Wang, Z.; Zhang, Z.J. Mapping of QTL conferring resistance to sharp eyespot (*Rhizoctonia cerealis*) in bread wheat at the adult plant growth stage. *Theor. Appl. Genet*. **2013**, *126*, 2865-2878.

75. Guo, Y.; Du, Z.; Chen, J.; Zhang, Z. QTL mapping of wheat plant architectural characteristics and their genetic relationship with seven QTLs conferring resistance to sheath blight. *PLoS ONE* **2017**, *12*, e0174939.

76. Wu, X.; Cheng, K.; Zhao, R.; Zang, S.; Bie, T.; Jiang, Z.; Wu, R.; Gao, D.; Zhang, B. Quantitative trait loci responsible for sharp eyespot resistance in common wheat CI12633. *Sci. Rep.* **2017**, *7*, 1-7.

77. Jiang, Y.; Zhu, F.; Cai, S.; Wu, J.; Zhang, Q. Quantitative trait loci for resistance to Sharp Eyespot (*Rhizoctonia cerealis*) in recombinant inbred wheat lines from the cross Niavt 14× Xuzhou 25. *Czech J. Genet. Plant Breed.* **2016**, *52*, 139-144.