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REVIEW

Breeding for the resistance to *Fusarium* head blight of wheat in China

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Abstract With the changes of climate and cultivation systems, the *Fusarium* head blight (FHB) epidemic area in China has extended since 2000 from the reaches of the Yangtze River to the north and west winter wheat region. Breeding for FHB resistance in wheat is an effective way to control the disease. Chinese wheat breeders commenced research on FHB in the 1950s. Sumai 3, Ning 7840, Yangmai 158, Ningmai 9 and other cultivars with improved FHB resistance were developed through standard breeding methods and widely applied in production or breeding programs. In addition to intervarietal crosses, alien germplasm was used to improve FHB resistance of wheat. Addition, substitution and translocation lines with alien chromosomes or chromosome fragments were created to enhance FHB resistance. Somaclonal variation was also used to develop a FHB resistant cv. Shengxuan 3 and other cultivars with moderate resistance to FHB were released by such methods. QTL (quantitative trait loci) for FHB resistance were characterized in cultivars originating from China. The major QTL, *Fhb1*, was identified on chromosome 3BS in Sumai 3, Ning 894037, Wangshuibai and other Chinese resistant sources. Diagnostic molecular markers for *Fhb1* have been applied in wheat breeding and breeding lines with improved FHB resistance and desirable agronomic traits have been obtained. However, breeding for FHB resistance is a long-term task, new technologies are likely to increase the efficiency of this process and better FHB resistance of new cultivars is expected to be achieved within the next decade.

Keywords breeding, *Fusarium* head blight, wheat

1 Introduction

Fusarium head blight (FHB) caused by *Fusarium graminearum* (teleomorph: *Gibberella zeae)* is a devastating disease of wheat in China as well as in other wheat-growing regions of the world where rainfall frequently occurs during flowering through to early grain-fill[1,2]. Previously, the FHB epidemics occurred mainly in the middle to lower reaches of the Yangtze River, including Zhejiang, Shanghai, south of Jiangsu, Anhui and Henan, north of Hubei in winter wheat, and north-eastern China in spring wheat. There were 7 years of severe epidemics and 10 years of moderately severe epidemics of FHB in 1951–1990[3]. Since 1990, the frequency of severe FHB epidemics has been lower in the reaches of Yangtze River due to the cultivation of wheat cultivars with moderate resistance to FHB. There were only two severe epidemics and seven moderately severe epidemics during 1991–2007[4]. However, since 1985, FHB has often occurred in other wheat production area, especially in the reaches of the Huai and Yellow Rivers. An outbreak of FHB occurred in 1985 with an area of about 3.3 Mha in Henan Province[5]. Also Gansu, Hebei, Ningxia, Qinghai, Shaanxi, Shandong and Sichuan regions have had epidemics of the disease since then[6,7].

Since 2000, the wheat FHB epidemic area has rapidly increased in China, and expanded from its previous epidemic area in the north and west winter wheat region. The epidemics of varying intensity have occurred, more frequently in the reaches of the Huai and Yellow Rivers, the largest region of wheat production in China. The largest epidemic area in Henan was 3.4 Mha in 2012[8]. On average, more than 5.4 Mha which accounts for about 23% of the total wheat production area of China are affected by the disease each year according to the data from the National Agro-Tech and Service Center of China (Fig. 1). There have been severe epidemics during five of the past

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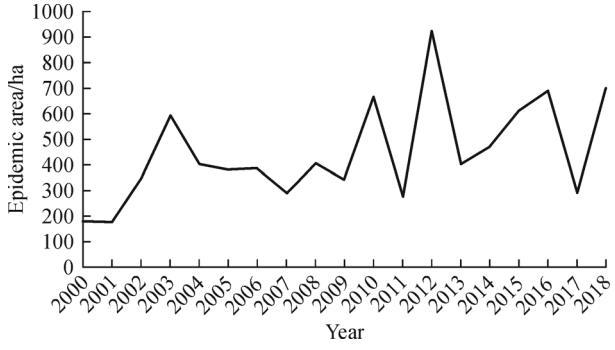

Fig. 1 Epidemic area of *Fusarium* head blight of wheat in China since 2000

10 years, 2012, 2014, 2015, 2016 and 2018[9,10], which suggests that the frequency of severe epidemics of FHB is significantly higher than in the last century.

FHB causes sterility, poor grain-fill and reduced test weight, thus resulting in significant yield loss. For example, the most severe FHB outbreak on record was in 2012 with an epidemic area of 9.95 Mha, causing direct yield losses of 2.08 Mt[10]. In addition to yield loss, the deteriorated quality of scabbed grain has become an even more critical issue of public concern because FHB infected grains contain mycotoxins such as trichothecenes and zearalenone (ZEN)[11,12], and significantly lower protein content. Trichothecenes are toxic to humans and animals, and cause dizziness, headaches, nausea, vomiting, abdominal pain, diarrhea, fever and sleepiness in humans, and cause food refusal and diarrhea in animals[13,14]. ZEN causes infertility and abortion in pregnant female animals, especially in pigs[15]. Recently, an analysis of mycotoxins in 158 wheat flour samples from markets in five regions including Anhui, Beijing, Henan, Jilin and Shandong revealed that the wheat flour was often contaminated by type B trichothecenes and ZEN. Deoxynivalenol (DON) was the most seriously contaminated type B trichothecenes with average concentration of 4.08 $mg \cdot kg^{-1}$ and 68% of samples were over 1 $mg \cdot kg^{-1}$, the upper limit for wheat flour contamination in China and other countries. ZEN was also detected with an average concentration of 86 $\mu g \cdot kg^{-1}$, and 24% of investigated samples were over the limit value of 60 $\mu g \cdot kg^{-1}$[16].

The frequency of severe epidemics of FHB has been increasing for the last decade in China and has been attributed in part to a combination of favorable weather conditions, increased area of corn-wheat and rice-wheat rotations, decreased fungicide effectiveness and lack of resistant cultivars.

FHB is a typical climatic disease in wheat. The germination of ascospores of *F. graminearum* is determined by temperature and humidity. Fungal cultures have shown that at 100% RH, 90% of ascospores germinated in 6–8 h when temperatures ranged from 25 to 30°C. The rate of ascospores germination also reached 90% in 12–24 h at 15°C. However, when RH was 90%, the germination rate of ascospores decreased significantly[17]. Thus, high humidity and warm weather will induce epidemics of FHB. A weather based model established using data in central China suggested climate change had direct impacts on the epidemics and severity of FHB[18]. El Nino indices coincided significantly with the epidemics of FHB in the reaches of the Yangtze River[19]. El Nino resulted in subtropical high pressure, cool summer, damp winter and warm wet conditions, which favor the development of epidemics of FHB. Sea surface temperature is a measure of El Nino and Southern Oscillation, known to strongly influence rainfall and air temperature, similar to the epidemics of FHB in the vicinity of Taihu Lake[20].

F. graminearum survives intercrop periods as mycelium, perithecium initials or chlamydospores in host crop residues. Corn, rice and wheat residues are especially suitable for survival and reproduction of *F. graminearum*[21,22]. To ensure food security in China, corn-wheat and rice-wheat rotations have over the last decades become major crop rotation systems in the reaches of the Yangtze and Yellow Rivers, respectively. In recent years, crop residue incorporation was fully applied in China. *F. graminearum* fungi propagate in large amounts on the soil surface and the undecayed residues provide an adequate source for outbreak of FHB[23]. Ding Kejian from Anhui Agricultural University determined that the rate of diseased spikes in incorporated corn residues was 2.78 times higher than in the control (personal communication). Thus, corn and rice-wheat rotations and residue incorporation caused the accumulation of *Fusarium* spp. and significantly increased the inoculum source for initial infection of FHB[24].

The application of fungicide is one of the effective ways to control FHB in wheat, with carbendazim being the main fungicide used in China since the 1970s[25]. Among 255 fungicides registered for FHB control, 226 include carbendazim as the main ingredient combined with other chemicals. However, more and more carbendazim-resistant isolates of *Fusarium* spp. have been found in the established FHB epidemic areas after 40 years of continuous application of such fungicide, which has resulted in lack of consistency in carbendazim efficacy[26,27]. The China Agriculture Research System monitored the carbendazim-resistant isolates in the reaches of the Yangtze and Yellow Rivers and found carbendazim-resistant isolates in all FHB epidemic areasbut they were most prevalent in the reaches of the Yangtze River. The average proportion of carbendazim-resistant isolates increased from 4.8% in 2008 to 40% in 2016 in Jiangsu Province, whereas the proportion of resistant isolates increased from 0.2% in 2009 to 13% in Anhui Province[10]. The rapid development of carbendazim-resistant isolates of *Fusarium* spp. has increased the difficulty of FHB

prevention and control, which has consequently increased the amount of fungicide used and exacerbated the problem of environmental pollution[28].

There is large variation in the FHB resistance of wheat cultivars. Dozens of cultivars with moderate resistance to FHB and desirable agronomic traits have been released and adopted for wheat production in the reaches of Yangtze River during recent decades[3,29,30]. Nevertheless, most cultivars released in China are susceptible to FHB. Among the 302 cultivars released from the national cultivar trials from 2005 to 2016, only 12 cultivars bred in Jiangsu Province have moderate resistance to FHB (Table 1). Almost all moderately resistant cultivars are limited to the reaches of the Yangtze River with the exception of Huaimai 21, as their vernalization requirements are different from that in the reaches of Huai and Yellow Rivers.

Among the factors increasing the frequency and severity of FHB epidemics, climate, crop rotation and residue incorporation system are difficult to change. Other agronomic practices, such as reducing plant density and nitrogen use, are not able to be used for controlling the disease. Fungicide application is the predominant method used to control FHB, however, this practice inevitably leads to higher investment and environmental contamination, and its effectiveness can be unpredictable due to the development of fungicide resistance and the timing of fungicide application in consistently raining weather[31]. There is also a growing body of evidence that suggests complex interactions between the environment, the pathogens and some fungicides can result in elevated mycotoxin levels[32,33]. Therefore, developing FHB resistant cultivars is the best choice for controlling the disease, and would reduce the need for fungicide application and promote sustainable development of agriculture.

Table 1 Number of cultivars with moderate resistance to FHB released from national trials

Year	Cultivars released	Cultivars with MR or R to FHB
2005	22	Yangmai 17 (MR)
2006	32	Ningmai 13 (MR)
2007	30	Zhenmai 168 (MR)
2008	20	Ningmai 15 (MR), Huaimai 21 (MR)
2009	33	Ningmai 16 (MR), Shengxuan 6 (R)
2010	22	Nannong 0686 (MR)
2011	18	–
2012	16	Ningmai 18 (MR), Sumai 188 (MR)
2013	25	Ningmai 23 (MR)
2014	21	–
2015	34	Huamai 6 (MR)
2016	26	–
Total	302	

Note: MR, moderate resistance; R, resistance.

2 Methods for evaluation of FHB resistance in wheat

The establishment of a resistance screening method is fundamental to the breeding of wheat with resistance to FHB. However, there are still conceptual gaps between resistance types and current methodology for FHB resistance screening. Schroeder and Christensen[34] proposed early in 1963 to divide FHB resistance into two types: type I resistance that prevents initial infection and type II resistance that prevents spread of symptoms within the spike. Miller et al.[35], Snijders and Perkowski[36] suggested a type of resistance that provides the ability to degrade trichothecene mycotoxins in kernels. Mesterhazy[37] included two additional types of resistance: resistance to kernel infection and tolerance (i.e., reduced yield loss).

The concept of types I and II resistance has been generally accepted and widely used by breeders[38]. To distinguish the two types of resistance, different inoculation methods are used in wheat. It is clear that type II resistance can be convincingly identified by point inoculation (i.e., the inoculation via injection of spore suspension into the single floret) and using severity or percentage of diseased spikelets as its rating criterion[39,40]. In a susceptible genotype, all of the spikelets will become blighted in as few as 10 days. But the situation with type I resistance appears not so clear, although there are some arguments that inoculation made by spawn inoculation (i.e., scattering infected kernels in the field) or spray inoculation (i.e., spraying spore suspension onto the wheat spikes) and recording disease incidence (i.e., percentage of scabbed spikes or spikelets) as rating criterion can be used as a suitable method for identification of this resistance type[41]. However, there are still a few unresolved questions in this approach for identification of type-Iresistance. Timing of inoculation may be critical for evaluation of type I resistance and inoculation should be performed at anthesis. If a plant is inoculated earlier or later than that, the proportion of scabbed spikes or spikelets could significantly decrease, which might result in false positives. Disease pressure is also responsible for the evaluation of type I resistance. Bai and Shaner[38] compared the resistance in five genotypes ranging from highly resistant to highly susceptible using different concentration of conidia as inoculum. When 10000 spores were sprayed over a spike, all inoculated spikes were infected, and there was no significant difference in incidence. Zhang et al.[42] compared the severity in genotypes with different FHB resistance using point and spray inoculations, and found that the correlation coefficients of the proportion of scabbed spikelets 21 d after inoculation between two inoculation methods were 0.85–0.93. It may be difficult to separate types I and II resistance when data are recorded at late grain-fill stage.

For other resistance types, resistance to kernel infection

can be measured as the percentage of infected kernels, and tolerance can be assessed by relative yield reduction when diseased and healthy plants of the same genotype are compared. These two resistance types have not been widely accepted because of some conceptual or operational weaknesses[41]. Resistance to trichothecene mycotoxins can be assessed as low DON content in kernels. Given that DON in the grain is toxic to humans and other animals, this adds additional economic losses to wheat and processing products. *F. graminearum* infected grain will usually contain DON regardless of the level of FHB resistance of the genotype. However, DON concentrations differ among genotypes[43]. Generally, DON accumulation is closely related to other resistant mechanisms. Low DON concentration in a bulk sample of grain may result from fewer infected kernels. Fewer infected kernels and lower yield reduction may be due to a high level of type I or II resistance, or due to loss of the severely affected kernels[44]. In general, DON concentration has a significant positive correlation with FHB severity, using both point and spray inoculations[41]. However, sometimes the resistance to DON accumulation appears inconsistent with type I or II resistance. If infection occurs during flowering, the infected ovary may not develop into a mature kernel, or the kernel may be so small and light that it is blown away during harvesting and threshing[41]. These lost kernels may have the highest levels of DON, and thus the DON content in the harvested grain may be lower than expected based on severity of head blight symptoms. For some moderately resistant genotypes, although infection occurs early, infected kernels may grow to normal size because of the faster grain-fill in these genotypes or the slower rate of fungal invasion of the spike. These genotypes can have an unacceptably high level of DON in harvested grain, whereas, if infection occurs later in the grain-filling stage, and weather favors fungal growth after infection, DON may also accumulate to a high concentration in harvested grain. In both cases, the harvested grain has a high DON concentration because these infected kernels are not light enough to be blown out of the combine with the chaff during harvest[45].

To breeders, the yield achieved under disease pressure is always of great concern irrespective of the kind of resistance involved. Therefore, the inoculation techniques and disease measurement parameters should be standardized for assaying FHB resistance in wheat cultivars. Based on the measurement of FHB resistance over many years, the Ministry of Agriculture in China established and issued two national industry standards: Rules for Resistance Evaluation of Wheat to *Fusarium* Head Blight (NY/T 1443.4-2007), and Technical Regulations for Resistance Evaluation of Wheat for Trials to *Fusarium* Head Blight Caused by *F. graminearum* (NY/T 2954-2016).

Two inoculation techniques and related measurement parameters are suggested in both regulations. For point inoculation, severity is divided into five levels ranging from zero to four according to the symptom of spikelets (Table 2). The average severity of inoculated spikes are counted to determine FHB resistance (Table 3). For spawn inoculation, the severity is also attributed to five levels from one to four, but the proportion of scabbed spikelets to determine severity level is different from that for point inoculation. The value given to FHB resistance of genotypes is called the disease index and is used for comparisons with resistant or susceptible controls. Sumai 3, Yangmai 158, Huaimai 20 and Annong 8455 are usually used as resistant, moderately resistant, moderately susceptible and susceptible controls, respectively. For consumers,

Table 2 Severity rating and its symptom with two inoculation methods

Severity	Symptom categories for point inoculation	Symptom categories for spawn inoculation
0	No symptoms	No symptoms
1	Symptom limited on inoculated spikelets	Proportion of scabbed spikelets less than 0.25
2	Proportion of scabbed spikelets less than 0.25	Proportion of scabbed spikelets from 0.25 to 0.5
3	Proportion of scabbed spikelets from 0.25 to 0.5	Proportion of scabbed spikelets from 0.5 to 0.75
4	Proportion of scabbed spikelets more than 0.5	Proportion of scabbed spikelets more than 0.75

Table 3 Criteria for evaluating the resistance to FHB in two inoculation methods

Resistance level	Average severity	Disease index (DI)
Immune	0	0
Resistant	0–2.0	Greater than 0 up to the DI of the resistant control
Moderately resistant	2.0–3.0	Greater than the DI of the resistant control up to the DI of the moderately resistant control
Moderately susceptible	3.0–3.5	Greater than the DI moderately resistant control up to the DI of the susceptible control
Susceptible	3.5	Greater than the DI of the susceptible control

the mycotoxins of grain needs more attention. However, the content of mycotoxin in grains is usually less than the safe limit in the genotypes with moderate resistance to FHB. Experience has shown that the national technical regulations are effective for evaluating FHB in wheat breeding programs.

3 Standard breeding methods

A nationwide collaborative network for studies on the resistance to wheat FHB was established in China in the mid 1970s. As a result, cultivars with improved FHB resistance were developed by different breeding programs especially using standard breeding strategies.

3.1 Systematic selection

Back in the 1950s, long before the nationwide network was established, Chinese wheat breeders had already began to select plants or spikes with resistance to FHB from the fields where FHB occurred frequently[3]. Some moderately resistant cultivars were developed from susceptible cultivars by using systematic selection. For instance, the moderately resistant Wannian 2 and Wangmai 15 were selected from Nanda 2419 in 1958, Yangmai 1 and Wumai 1 were selected from Funo in 1968[46]. The area sown to these cultivars was more than 400000 ha in the 1960s[47]. Furthermore, Yangmai 3, with better FHB resistance than Yangmai 1, was developed by systematic selection in 1983[48]. While systematic selection has a long history in wheat breeding, some breeders continued to use this approach to select lines with improved resistance to FHB in the 2000s. Ningmai 13, Ningmai 14 and Ningmai 24 with moderate resistance to FHB was selected from Ningmai 9[49,50].

3.2 Intervarietal crosses

The intervarietal cross is a main method of genetic improvement for resistance to FHB in wheat. Among the resistant cultivars developed by this method, Sumai 3 is the best resistant source and has been widely used in genetic research and breeding in China and abroad[51,52]. Sumai 3 was bred from a cross between Funo, an Italian cultivar susceptible to FHB, and Taiwan wheat, a moderately susceptible land race from China[53]. The segregation lines were planted in the field scattered with scabbed kernels for FHB severity measurement and the lines with lowest severity of FHB were selected in every generation. After the release of Sumai 3 in 1974, it was extensively used as a resistant parent to improve FHB resistance of commercial cultivars. In the 1980s, many resistant lines derived from Sumai 3 were developed through intervarietal crosses. Such lines usually had stable type II resistance, similar to that of Sumai 3. Bai et al.[54] evaluated FHB resistance of 803 wheat cultivars and breeding lines from the southern part of China and found 27 had resistance to FHB. From these 27 resistant genotypes, 20 accessions were derived from Sumai 3 or its derivatives. Sumai 3 has high general combining ability for FHB resistance and can be effectively used to enhance FHB resistance of its progeny. Ning 7840, Yang 89-110 and Yang 92-617 were derived from Sumai 3. Ning 7840 (a cross of Avrora/Anhui 11/ Sumai 3) not only has similar FHB resistance to Sumai 3, but also carries additional genes for resistance to other diseases, such as rusts and powdery mildew, and has better agronomic characteristics than Sumai 3[55]. More than 120 cultivars with FHB resistance developed in China are derived from Sumai 3[3]. However, most of them were not widely used for commercial wheat production because of other undesirable agronomic traits, such as excessive plant height, low spikelet density and low 1000-kernel weight[56].

Facing the difficulty of breaking the linkage between useful FHB resistance and undesirable agronomic traits during progeny selection, Cheng et al.[57]suggested that it is better to select progeny with improved FHB resistance from crosses between commercial cultivars with desirable agronomic traits and moderate susceptibility to FHB rather than using Sumai 3 as the parent. Yangmai 158, which has moderate resistance to FHB and desirable agronomic traits, was developed by using this strategy. Although parents including ND2419, Triumph, Funo and St1473/506 were susceptible or moderately susceptible to FHB, Yangmai 158 was obtained from transgressive segregation and has stable moderate resistance to FHB (Fig. 2). The greatest area sown to Yangmai 158 was about 200 ha in 1990s.

Ningmai 9 is another cultivar selected from transgressive segregation using the same approach. The parents of Ningmai 9 are ND2419, Jiangdongmen, E-rou, Zao 5 and Norin 129[58]. Ningmai 9 is also a major commercial cultivar and was widely used for wheat production and breeding in the reaches of the Yangtze River in 2000s (Fig. 3).

3.3 Recurrent selection

It is difficult to improve multiple traits including agronomic characters and disease resistance simultaniously by crossing two genotypes. Wu et al.[59] proposed a modified recurrent selection method to develop new cultivars with multiple improved characters including FHB resistance and desirable agronomic traits. Using a dominant male-sterile gene, *Ta1* (*Ms2*) on chromosome 4DS from Taigu male sterile wheat, gene pools were developed by crossing multiple parents followed by recurrent selection. In each cycle, new sources are incorporated into the improved population to permit continued improvement, and superior breeding lines will be selected from the population to develop new cultivars by selfing. Researchers[60,61] created a dwarf male-sterile

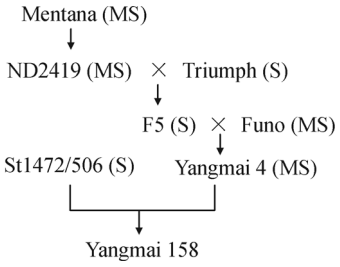

Fig. 2 The pedigree of Yangmai 158

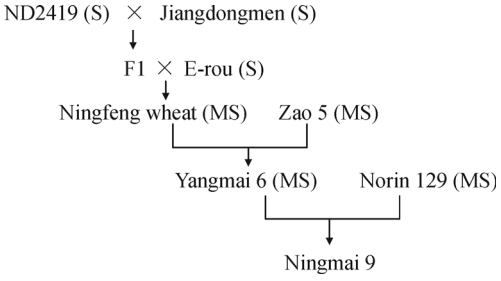

Fig. 3 The pedigree of Ningmai 9

wheat, in which the dwarf gene *Rht-D1c* and *Ms2* were closely linked on chromosome 4DS. It is easy to identify male-sterile and male-fertile progeny when using recurrent selection. Significant achievements using this approach have been made in wheat breeding in China. Nine lines with FHB resistance were developed, with the resistance of T154 being higher than that of Sumai 3[62]. Seven resistant lines, including Futai 8711, 8829 were also developed by Fujian Academy of Agricultural Sciences[63]. Emai 11 is a cultivar with moderate resistance to FHB and some improved agronomic traits developed by recurrent selection[64]. Huaihe 12013, released in 2017, is a cultivar with moderate resistance to FHB developed using this approach with an improved population from the parents of 276 cultivars.

4 Utilization of alien genes

Over 300 species in the tribe Triticeae carry homeologous wheat genomes A, B and D, and have different disease resistance which can be used in genetic improvement of wheat. A large number of wild species related to wheat have been evaluated for FHB resistance in China since the 1980s[65]. Wan et al.[66,67] evaluated 1507 accessions from 93 species in 18 genera and found that 31 accessions had resistance to initial infection and 151 accessions had resistance to spread. These resistant accessions were mostly from *Agropyron*, *Elymus*, *Hystrix* and *Kengyilia*. Most of the resistant accessions came from warm and subtropical areas with humid climates that would favor the growth and development of the FHB pathogen. However, such accessions inevitably had undesirable agronomic traits.

To avoid introduction of whole genome from wild species, individual chromosomes or chromosome fragments can be introduced into wheat. FHB resistance from wild species has been transferred to wheat by producing wheat-alien chromosome addition, substitution and translocation lines. Scientists from Nanjing Agricultural University have developed a number of wheat-alien chromosome lines and successfully transferred FHB resistant from wild species into wheat[68]. Evaluation of FHB resistance in the addition and substitution lines showed that chromosomes 7Lr and 5Lr from *Leymus racemosus*, chromosome $1S^c$, $1Y^c$, $2Y^c$, $3S^c$, $4S^c$, $5Y^c$ and $6S^c$ from *Elymus ciliare*, and chromosome $1E^{ts}$ from *Elymus tsukushiensis* might carry *FHB* resistant genes[69,70]. FHB resistant gene from a translocation line of T4BS.4BL-7Lr#1S was introduced into two commercial cultivars, Nannong 0686 and Yangmai 15, by backcross. Six lines in Nannong 0686 background and three lines in Yangmai 15 background significantly reduced the proportion of scabbed spikelets compared to the relative recurrent parent. Qi et al.[71] developed three PCR markers to identify the QTL associated with FHB resistance on chromosome 7Lr#1S and named the QTL as *Fhb3*.

Five translocation lines of chromosome 1Y and three translocation lines of chromosome 6S from *Roegneria cilliars* were developed and had high resistance to FHB. For *Elymus tsukushiensis*, Wang et al.[70] produced wheat-*E. tsukushiensis* chromosome lines and found that the disomic addition having the group 1E. *tsukushiensis* chromosome 1Ets#1S added to the wheat genome conferred resistance to FHB. Cainong et al.[72] replaced corresponding homeologous region of chromosome 1AS of wheat with the FHB resistance-associated chromatin derived from 1Ets#1S of *E. tsukushiensis*. Plant progenies homozygous for such chromosome fragment had a disease severity rating of 7% compared to 35% for the null progenies. The FHB resistant QTL originated from chromosome 1E in *E. tsukushiensis* was designated *Fhb6*.

Another relative of wheat that has been intensively surveyed for FHB resistance is *Elymus elongates*[73]. A set of wheat-*E. elongatus* substitution lines in Chinese Spring genetic background have been developed. Among them, the substitution lines 7E(7A), 7E(7B) and 7E(7D) has the most resistance to FHB[74]. The QTL associated with FHB resistance was located on the long arm of chromosome 7el2 and designated *Fhblop*. Guo et al.[75] redesignated this QTL as *Fhb7* and developed a recombinant inbred population for molecular mapping. *Fhb7* was mapped to the chromosome between markers XsdauK66 and Xcfa2240 with the genetic distance of 1.7 cM. Recently, Kong Lingrang from Shangdong Agricultural University created two translocation lines, SDAU2002 and SDAU2004, which had the most resistance to FHB. Four lines with moderate resistance to FHB and desirable

agronomic traits were bred by introducing an FHB resistance gene from *E. elongatus* into the commercial cv. Jimai 22 (personal communication).

In addition, wheat cvs Jingzhou 1 and Jingzhou 47 with moderate FHB resistance, were selected from the hybrid progenies of Nanda 2419 and indigenous rye accessions (Institute of Jingzhou Agricultural Sciences, Hubei Province, China). The moderately resistant Jingzhou 66 was selected from synthetic wheat material of Funo/durum and Nanda 2419/rye. The FHB resistant lines of Zhonghua series created by Jiangsu Academy of Agricultural Sciences originated from *Psathyrostachys huashanica*[29].

5 Somaclonal variation

Genetic variation in plants can be induced through tissue dedifferentiation and redifferentiation *in vitro* culture. Different tissues including immature embryo, immature spike, embryo, stem or node have been cultured *in vitro* to induce somaclonal variation. Among the cultured tissues, immature embryos were the best for inducing callus and forming plantlets[76]. Differences between many characters, such as stem height, spike shape, color and shape of grain were identified between wild type and variants[77]. The variations were validated by cytogenetics and DNA analysis[78]. Yu[79] demonstrated that *in vitro* culture could induce FHB resistant variants, and their resistance to FHB could be stably inherited. Such variants had high general combining ability for FHB resistance when they were used as parents. Among their progeny, 20%–30% lines had FHB resistance. Ningmai 3, a cultivar with high-yield potential but susceptible to FHB, was selected as material for inducing somaclonal variation. After *in vitro* culture of immature embryos, regenerated plants were evaluated for agronomic traits in the field and FHB resistance by artificial inoculation. Shengkang No. 1, a cultivar with moderate resistance to FHB, was obtained from the somaclonal variation of Ningmai 3 and released in Jiangsu in 1996 and Shanghai in 1999[76]. The area sown to this cultivar was up to 280000 ha in Anhui, Hubei, Jiangsu and Shanghai. Using the same approach, Shengxuan 3 was developed from Yangmai 158 somaclonal variants and released in 2003[80]. Shengxuan 3 has similar agronomic traits and the high-yield potential of Yangmai 158, but higher resistance to FHB (Table 4).

The rates of *in vitro* callus induction and plantlet formation for embryos were positively related to the resistance to FHB in cultivars when DON was added to the medium. Therefore, DON was added to medium for *in vitro* cultures to increase the efficiency of selection of somatic mutants. Immature embryo and young inflorescences of susceptible cultivar Alondra were used as explants to induce callus. The callus were cultured on MS differential medium with the addition of DON at 0.6×10^{-4}–0.8×10^{-4} mol·L^{-1}. About 20% callus cultures that tolerated DON were regenerated. FHB resistance evaluation in the field demonstrated that 40% to 50% of regenerated plants had better resistance than that of Alondra[29,78].

6 Molecular marker-assisted selection

Evaluation for the FHB resistance phenotype is time and resource-intensive, and results are often confounded by environmental factors, and therefore needs to be repeated in different environments. Molecular markers may provide an effective way for identifying FHB resistant genes/QTL in breeding populations. Marker-assisted selection (MAS) will reduce the need for phenotypic assays and increase the selection efficiency in wheat breeding for FHB resistance. Over the past 20 years, considerable research on molecular mapping of FHB resistance in wheat has been published. QTLs have been mapped on all 21 wheat chromosomes[81,82]. Chinese cultivars including Baisanyuehuang, CJ 9306, Haiyanzhong, Huangchandou, Huangfangzhu, Huapei 57-2, Ning 7840, Ning 894037, Sumai 3, Wangshuibai, and Wuhan 1 have been used as resistant or moderate resistant resources to identify QTLs associated with FHB resistance[83–97]. At least 13 chromosomes possessing QTL associated with FHB resistance were found in these cultivars (Table 5). Among the detected FHB resistant QTL, QTL on chromosomes 3BS, 6BS and 5AS were the most reproducible QTL in wheat cultivars especially in those cultivars originating from China and were designated as *Fhb1*, *Fhb2* and *Fhb5*, respectively. Another designated QTL, *Fhb4*, was identified on chromosome 4B in Wangshuibai[95], whereas three other designated QTL, *Fhb3*, *Fhb6*, and *Fhb7*, were identified in species related to wheat, *Leymus racemosus*, *Elymus tsukushiensis* and *E. elongatus*, respectively[71,72,75].

Table 4 Comparison of characters in Shengxuan 3 and Yangmai 158

Cultivar	Plant height/cm	Spike length/cm	Number of spikelets	Number of kernels per spike	Thousand kernel weight/g	Yield/(t·ha^{-1})	Test weight/(g·L^{-1})	Protein content/%	Gluten content/%	Proportion of scabbed spikelets/%
Shengxuan 3	78.9	9.3	19.1	45.1	38.9	6.25	767	13.4	30.1	14.5–16.0
Yangmai 158	78.6	8.8	18.6	43.8	38.8	6.24	772	13.1	29.0	30.1–34.0

Table 5 Chromosomes possessing QTL associated with FHB resistance in Chinese cultivars

Cultivar	1A	1B	2A	2B	2D	3A	3B	4B	5A	6B	6D	7A	7D	Reference
Baisanyuehuang						+	+		+					Zhang et al., 2012[83]
CJ 9306					+		+		+					Jiang et al., 2007[84]
Haiyanzhong									+	+			+	Li et al., 2011[85]
Huangcandou	+				+	+	+				+			Cai et al., 2014[86]
Huangfangzhu	+	+					+		+			+		Li et al., 2012[87]
Huapei 57-2						+	+							Bourdoncle & Ohm, 2003[88]
Ning 7840				+			+							Bai et al., 1999[89]; Zhou et al., 2002[90]
Ning 894037							+			+				Shen & Ohm, 2003[91]
Sumai 3			+				+	+	+	+				Waldron et al., 1999[92]; Anderson et al., 2001[93]
Wangshuibai		+	+		+	+	+	+	+	+			+	Zhang et al., 2004[94]; Ma et al., 2006[95]; Yu et al., 2008[96]
Wuhan 1					+			+						Somers et al., 2003[97]

Fhb1 was the first QTL associated with the resistance to FHB spread within a spike published. It was found in Sumai 3 and its derivate Ning 7840 by Waldron et al.[92] and Bai et al.[89], respectively. This is a major QTL and explained up to 53% of phenotypic variation in their studies. Thereafter, *Fhb1* was identified as a major QTL and explained 30%–43% of phenotypic variation in different Chinese cultivars including Wangshuibai, Ning 894037 and Chinese Spring using different linkage mapping populations, although there is no definite relationship in the pedigree between these two FHB resistant cultivars[95–98]. Three SSR markers, *Xgwm 389*, *Xgwm 493* and *Xgwm 533*, were always linked to *Fhb1* in mapping studies. Based on physical mapping of such SSR markers on 3BS deletion lines in Chinese Spring, the major QTL was located between the breakage point 3BS-3 and 3BS-8 with the fraction length of 0.78–0.87[90].

As *Fhb1* is a major QTL for FHB resistance, the linkage SSR markers were used for introducing the QTL from resistant cultivars to improve FHB resistance of susceptible cultivars. The results of marker-assisted selection suggest that *Fhb1* is a more effective QTL than other QTL for improving FHB resistance. Ning 7840 as an *Fhb1* donor was backcrossed with a susceptible cv. Clark. A series of isogenic lines of BC_5F_4 were created using *Xgwm 389*, *Xgwm 493* and *Xgwm 533* as selectable markers for *Fhb1*, and 71 combination primers as background selection markers. The evaluation of FHB resistance in isogenic lines and controls indicated that the proportion of scabbed spikelets was reduced by up to 40% and the marker *Xgwm 533* is more efficient than *Xgwm 493* and *Xgwm 389* (Table 6).

Fhb1 could be utilized to improve the resistance in susceptible cultivars, however, the banding patterns of SSR marker allele in this chromosome region show variation in different resistant sources (Table 7), which makes it difficult for breeders to use such SSR markers in cases where they are not familiar with marker allele types of QTL donors and the recipient germplasm. To improve the efficiency of marker-assisted selection for FHB resistance, diagnostic markers linked to the *Fhb1* should be developed. Sequence tagged site markers from wheat ESTs were developed and added to this region for saturating the *Fhb1* QTL region[99]. However, most of them have no polymorphisms when they are used in other breeding populations and some of them only amplify PCR fragments in susceptible cultivars[100]. Based on a physical map spanning the *Fhb1* region constructed using new DNA markers from BAC sequences, a high diagnostic marker, *UMN10*, was developed to separate resistant and susceptible cultivars. This marker consistently worked well with the Applied Biosystems 3130x1 Genetic Analyzer, and was used for large-scale marker-assisted selection for *Fhb1* in breeding programs in the USA[101]. However, PCR products of *UMN10* could not be clearly separated between resistant and susceptible cultivars on agarose gels[102] There is no facility similar to Genetic Analyzer in normal breeding programs in China. Therefore, two single nucleotide amplified polymorphism (SNAP) markers were developed by comparing the single nucleotide polymorphisms of PCR products between resistant and susceptible cultivars. These two markers are dominant and only amplified in resistant cultivars[103,104].

The two SNAP markers have been used for *Fhb1* selection in breeding programs in different wheat production areas. One was used to improve FHB resistance in susceptible commercial cv. Yangmai 15 by using marker-assisted selection. After the marker was used to screen each generation, lines with SNAP marker were selected for backcrossing for the next generation. The evaluation of

Table 6 Evaluation of FHB resistance in isogenic lines of *Fhb1* in cv. Clark background

Line	*Xgwm 389*	*Xgwm 493*	*Xgwm 533*	Proportion of scabbed spikelets/%
Ning 7840	+	+	+	19.0
Isogenic line 1	+	+	+	40.1
Isogenic line 2	–	+	+	48.4
Isogenic line 3	+	–	+	57.6
Isogenic line 4	–	+	–	67.3
Isogenic line 5	+	–	–	82.1
Isogenic line 6	–	–	–	88.1
Clark	–	–	–	88.7

Table 7 SSR marker alleles (bp) for the *Fhb1* region in different cultivars

Cultivars	BARC075	GWM389	GWM533	BARC147	GWM493	WMC754
Sumai 3	129	153	160	123	213	198, 154
Wangshuibai	129	151	158	125	215	194, 146
Ning 894037	129	153	160	123	213	198, 154
Fanshan wheat	139	153	131	123	215	202, 147
Wenzhouhongheshang	129	151	131	125	159	194, 148

FHB resistance showed that the proportion of scabbed spikelets ranged from 17% to 40% in the BC_5F_4 lines with *Fhb1* marker and 49% in Yangmai 15 (Table 8). This indicated that all selected lines have more FHB resistance than that of Yangmai 15 but have considerable variation in FHB resistance. These results suggest that marker-assisted selection is a useful tool for improving FHB resistance, but phenotypic evaluation remains an important method for wheat breeding.

With the development of molecular marker technology, KASP (kompetitive allele specific PCR) has been used as a high throughput system to detect SNP in wheat breeding. The best markers are functional markers that have been developed from SNP of functional genes. Rawat et al.[105] reported a pore-forming, toxin-like domain conferring FHB resistance for *Fhb1*. However, markers based on the SNP of this gene do not readily allow the distinction of FHB resistance or susceptible lines when hundreds of lines are assessed[106]. Based on sequencing of the *Fhb1* region of near-isogenic lines, fragment deletions and SNP variations of *His* (histidine-rich calcium binding protein) gene have been identified, and most of the materials lacking 752 bp fragments were scab resistant materials. Su et al.[107] designated the *His* gene as *TaHRC*, and developed PCR molecular markers and KASP markers. These markers are more effective than *UMN10* and other SSR markers developed earlier for the *Fhb1*. Zhu et al.[108] analyzed the distribution and putative donor of *Fhb1* in Chinese wheat cultivars and found that Nimgmai 9 was the major donor for *Fhb1* in Chinese cultivars. Actually, 23 cultivars derived from Ningmai 9 with moderate FHB resistance were released from national and provincial cultivar trials (Table 9).

Other QTL, such as *Fhb2*, *Fhb4* and *Fhb5* in landrace Wangshuibai, have been evaluated for improving FHB resistance in wheat cultivars in China[109]. However, such QTL have not been widely applied in marker-assisted selection in breeding for commercial cultivars, as the markers related to QTL for FHB resistance are not sufficiently diagnostic and effective[81].

7 Conclusions and prospects

Substantial progress in wheat breeding for FHB resistance has been made in China since the late of 1950s. Wheat cultivars with improved FHB resistance have been released mainly by standard breeding in China, especially in

Table 8 FHB resistance in BC_5F_4 lines with *Fhb1* marker

Genotype	Proportion of scabbed spikelets/%		
	Min	Max	Mean
BC_5F_4 lines with *Fhb1*	16.72	40.08	30.24±9.6
Yangmai 15	–	–	48.75±11.8
Sumai 3	–	–	6.20±0.9

Table 9 Cultivars derived from Ningmai 9

Cultivar	Release code	Pedigree	Breeder
Ningmai 13	National2006004	Ningmai 9 system selection	JAAS
Zhenmai 8	National2006008	Yangmai 158/Ningmai 9	LXH
Shengan 6	National2009004	Ningmai 8/Ningmai 9 DH	JAAS
Ningmai 16	National2009003	Ningmai 8/Ningmai 9	JAAS
Nannong 0686	National2010003	MV964091/Ningmai 9	NJAU
Ningmai 18	National2012003	Ningmai 9*3/Yang 93-111	JAAS
Zhenmai 5	Jiangsu200406	Yangmai 158/Ningmai 9	Zhenjiang
Ningmai 14	Jiangsu200601	Ningmai 9 system selection	JAAS
Shengxuan 4	Jiangsu200606	Ningmai 8/Ningmai 9 DH	JAAS
Yangfumai 4	Jiangsu200801	Ningmai 8/Ningmai 9 variant	LXH
Yangmai 18	Jiangsu200901	4 × Ningmai 9/3/6 × Yangmai 158//88-128/NNP045	LXH
Yangmai 21	Jiangsu201102	Ningmai 9/HJM	LXH
Ningmai 20	Jiangsu201202	Y18//Ningmai 8/Ningmai 9 DH	JAAS
Sumai 8	Jiangsu201302	Ningmai 9/Yangmai 11	Fengqing Seed Co. Ltd.
Ningmai 21	Jiangsu201303	Ningmai 9/Yangmai 158//Ningmai 9	JAAS
Ningmai 26	Jiangsu2016004	Ning 9351/Ningmai 9	JAAS
Sumai 9	Anhui201303	Ningmai 9/Yangmai 11	Fengqing Seed Co. Ltd.
Ningmai 24	Anhui201509	Ningmai 9 system selection	JAAS
Sumai 10	Anhui2016014	Ningmai 9/Yangmai 11	Fengqing Seed Co. Ltd.
Huimai 202	Anhui2016024	Ningmai 9/Yangmai 158	Tianqing Agri Co. Ltd.
Sunong 128	Anhui2016007	5E007/Ningmai 9	Chuzhou College
Guangmingmai 1311	National20180005	3E158/Ningmai 9	Guangming Seed Co. Ltd.
Nongmai 126	National20180008	Yangmai 16/Ningmai 9	Shengnong Seed Co. Ltd.

Note: JAAS, Jiangsu Academy of Agricultural Sciences; LXH, Lixiahe Regional Institute of Agricultural Sciences, Jiangsu; NJAU, Nanjing Agricultural University; Zhenjiang, Zhenjiang Regional Institute of Agricultural Sciences, Jiangsu.

Jiangsu Province, based on the standardized evaluation technology of FHB resistance. Several important cultivars including Sumai 3, Ning 7840, Yangmai 158 and Ningmai 9 have been widely used in wheat production and breeding programs. Chromosome engineering has been used to introduce FHB resistant genes from species related to wheat. Also, somaclonal variation has likewise been used to improve FHB resistance in wheat. Significant achievements in molecular mapping and marker-assisted selection have been made over the past 20 years. *Fhb1*, the major QTL on chromosome 3BS, is a consistent QTL for FHB resistance in Sumai 3, Wangshuibai, and other Chinese cultivars, and has been effectively applied in marker-assisted selection for improving FHB resistance. The efficiency of marker selection for *Fhb1* is increasing along with progress of molecular biology more widely. Ningmai 9 is now the major donor for *Fhb1* in Chinese breeding programs.

In 2006, Chinese wheat breeders reached a consensus that increasing FHB resistance will be one of the most important targets for wheat breeding over the next two decades. By 2030, 20% of cultivars released in the middle to lower reaches of the the Yangtze River will possess FHB resistance similar to Sumai 3, and 10% of cultivars in the reaches of the Haui and Yellow Rivers will have moderate resistance to FHB similar to Yangmai 158. However, there is still a great gap between this target and the status quo. To achieve such aims, considerably more research and breeding activity need to be undertaken. Firstly, it will be necessary to establish national nurseries with stable environmental conditions, and a rapid, efficient and accurate standard technique to evaluate FHB resistance in breeding materials with desirable agronomic traits provided by different breeding regions and institutions. Moderately susceptible or moderately resistant accessions will need to be tested with yield potential and quality in cultivar trials. Secondly, resistant sources from Chinese landraces and breeding lines need to be further evaluated and assayed for novel genes or QTL. Thirdly, a set of high throughput DNA extraction and KASP marker screening technologies should be established for introducing *Fhb1* from Ningmai 9 and other *Fhb1* related cultivars into major commercial cultivars suited to the reaches of the Haui and Yellow Rivers to increase FHB resistance by using marker-

assisted selection. Fourthly, effective diagnostic molecular markers for FHB resistant QTL, *Fhb2*, *Fhb4* and *Fhb5,* should be developed based on new progress in wheat genomics and used in combination with *Fhb1* to increase FHB resistance of cultivars. Finally, resistant genes or QTL, such as *Fhb3*, *Fhb6*, *Fhb7*, from species related to wheat need to be introduced to commercial cultivars backgrounds for improving FHB resistance thorough additive effects.

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