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Characterization of Chinese wheat germplasm for resistance to Fusarium head blight at CIMMYT, Mexico

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Abstract Fusarium head blight (FHB) poses a challenge for wheat breeders worldwide; there are limited sources of resistance and the genetic basis for resistance is not well understood. In the mid-1980s, a shuttle breeding and germplasm exchange program launched between CIMMYT-Mexico and China, enabled the incorporation of FHB resistance from Chinese bread wheat germplasm into CIMMYT wheat. Most of the Chinese wheat materials conserved in the CIMMYT germplasm bank had not been fully characterized for FHB reaction under Mexican environments, until 2009, when 491 Chinese bread wheat lines were evaluated in a FHB screening nursery in Mexico, and 304 (61.9 %) showed FHB indices below 10 %. Subsequent testing occurred in 2010 for plant height (PH), days to heading (DH), and leaf rust response. In 2012, 140 elite lines with good agronomic types were further evaluated for field FHB reaction and deoxynivalenol (DON) accumulation. Most of the tested lines showed good resistance: 116 (82.9 %) entries displayed FHB indices lower than 10 %, while 89 (63.6 %) had DON contents lower than 1.0 ppm. Significant negative correlations were observed between FHB traits (FHB index, DON content, and Fusarium damaged kernels) and PH, DH, and anther extrusion. A subset of 102 elite entries was selected for haplotyping using markers linked to 10 well known FHB quantitative trait loci (QTL). 57 % of the lines possessed the same 2DL QTL marker alleles as Wuhan 1 or CJ 9306, and 26.5 % had the same 3BS QTL allele as Sumai 3. The remaining known QTL were of low frequency. These materials, especially those with none of the above tested resistance QTL (26.5 %), could be used in breeding programs as new resistance sources possessing novel genes for FHB resistance and DON tolerance.

Keywords Bread wheat · Germplasm · Scab · Resistance breeding · DON content · Anther extrusion

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Introduction

Fusarium head blight (FHB) in bread wheat (*Triticum aestivum* L.) is caused by more than 17 *Fusarium*

species, although *Fusarium graminearum* Schwabe (Teleomorph *Gibberella zeae* (Schwein) Petch) is the predominant species in many locations (Bai and Shaner 2004). FHB is a globally important wheat disease; in addition to yield reduction, it produces mycotoxins (such as deoxynivalenol, DON) that are toxic to humans and animals, thereby creating safety concerns for food and feed. Cultural practices and fungicide applications can reduce the disease to some extent, but host resistance has long been recognized as the most effective, environmentally safe, and cost-efficient approach of managing FHB. Evidence has shown that fungicide treatment alone cannot provide sufficient protection to susceptible cultivars under high disease pressure (Mesterhazy et al. 2003; Wegulo et al. 2011), highlighting the importance of developing cultivars with adequate levels of resistance.

Resistance to FHB is quantitative and non-specific to *Fusarium* species. Of the various resistance mechanisms, Type I (resistance to initial infection) and Type II (resistance to fungal spread within host tissues) have been widely investigated (Schroeder and Christensen 1963). Type III (resistance to toxin accumulation), Type IV (resistance to kernel infection), and Type V (resistance to yield loss) resistances have also been described (Mesterhazy et al. 1999). Several morphological and developmental traits, including days to heading (DH), plant height (PH), and anther extrusion (AE), were reported to be associated with FHB resistance (Buerstmayr et al. 2012).

FHB is endemic to major wheat areas in China. Chinese germplasm, notably Sumai 3 and its derivatives, has been known as a rich source of resistance worldwide (Bai and Shaner 2004). Quantitative trait loci (QTL) mapping indicated that the Sumai 3 resistance was controlled largely by three genes: *Fhb1* on chromosome 3BS (Liu et al. 2008), *Fhb2* on 6BS (Cuthbert et al. 2007), and *Fhb5* on 5AS (Buerstmayr et al. 2003; Xue et al. 2011). These genes have been fine mapped and closely linked markers are available for marker assisted selection (MAS).

Resistance QTL in other Chinese germplasm were also mapped and *Fhb1* was found to occur frequently. It is present in Sumai 3 derivatives, such as Ning 7840 (Bai et al. 1999), as well as cultivars with multiple parents or unknown pedigree, such as CJ 9306 (Jiang et al. 2007) and Huapei 57-2 (Bourdoncle and Ohm 2003), and also in cultivars and landraces that are not known to be related to Sumai 3, e.g. Ning 894037 (Shen et al. 2003), Wangshuibai (Lin et al. 2004), Huangfangzhu (Li et al. 2012), and Baishanyuehuang (Zhang et al. 2012). Other QTL found in more than one study, in addition to those from Sumai 3, are *Fhb4* on chromosome 4BL from Wuhan 1 (Somers et al. 2003) and Wangshuibai (Xue et al. 2010), and a QTL on 2DL from Wuhan 1 (Somers et al. 2003) and CJ 9306 (Jiang et al. 2007). Many other QTL have been found in Chinese germplasm, but they either exhibit small phenotypic effects, or have not yet been validated (Liu et al. 2009). Globally, FHB resistance breeding programs have depended heavily on a few major genes, mostly from Sumai 3 and its derivatives (Ruckenbauer et al. 2001; Yang et al. 2006). There is therefore a need to explore and utilize new sources of resistance, especially genotypes carrying new resistance genes, not only to prevent resistance breakdown but also to broaden the genetic basis for development of durable resistant cultivars.

It is rare to find wheat cultivars with high levels of resistance to FHB, and no sources of immunity have been identified. From 1974 to 1980, with the cooperation of 13 institutes in China, 34,571 wheat lines were screened, and only 1,765 (5.1 %) showed resistant (R) or moderately resistant (MR) reactions to FHB (All-China Cooperation of Research on Wheat Scab 1984). From the late-1970s to the mid-1980s, more than 20,000 wheat lines were evaluated by provincial agricultural academies in Shanghai, Nanjing, and Wuhan, but only around 3 % showed R or MR responses (Zhou 2003). Later, Wan et al. (1997) identified 30 genotypes with high FHB resistance from a collection of 886 bread wheat lines, mostly from China. In another study, Yu et al. (2008) screened 94 wheat cultivars and landraces, mainly from China and Japan, and found 26 resistant lines, from which a few new resistance QTL were identified, including a major QTL on chromosome 7D from Haiyanzhong, a Chinese landrace (Li et al. 2011).

Breeding for FHB resistance at the International Maize and Wheat Improvement Center (CIMMYT), Mexico, started in the early 1980s and benefited from Chinese germplasm introductions (Gilchrist et al. 1996; Duveiller et al. 2008). Before 1984, no R or MR materials had been identified in CIMMYT germplasm, and even moderately susceptible (MS) lines were rare (0.46 % of 4,361 lines tested; Liu et al. 1997). From 1981, CIMMYT began to utilize Chinese

sources in hybridization schemes, resulting in the development and release of resistant germplasm. From 1985 to 1993, the frequency of MS lines increased to 9.8 %, and R and MR lines became available, representing 2.8 % of the 2,173 lines tested (Liu et al. 1997).

In the mid-1980s, a shuttle breeding and germplasm exchange program was launched between CIMMYT and three Chinese institutes: Jiangsu Academy of Agricultural Sciences, Nanjing; Sichuan Academy of Agricultural Sciences, Chengdu; and Heilongjiang Academy of Agricultural Sciences, Harbin. Around 700 Chinese cultivars were sent to CIMMYT to generate crosses that combine high FHB resistance from Chinese germplasm and high yielding, semi-dwarf and rust resistance from the CIMMYT genepool (He et al. 2000). However, only a fraction of the Chinese resistance sources were explored and utilized, and most lines were uncharacterized for FHB resistance in Mexican environments.

This study aimed to identify new sources of resistance to FHB in Chinese germplasm that might be utilized in the CIMMYT global breeding program, by characterizing Chinese germplasm conserved in the CIMMYT wheat germplasm bank for FHB resistance traits such as FHB index, DON content, and Fusarium damaged kernels (FDK), and presence of known resistance QTL, as well as PH and DH trait information.

Materials and methods

Plant materials

The 583 accessions of bread wheat from the CIMMYT wheat germplasm bank were tested, including Chinese landraces, cultivars, and advanced lines, as well as a few derivatives of Chinese wheats generated at CIMMYT. These were from all 10 wheat production zones in China (He et al. 2001), with 81.9 % from the four major FHB epidemic regions, i.e. Zone III (Middle and Lower Yangtze Valley Autumn-sown Spring Wheat Zone), Zone IV (Southwestern Autumn-sown Spring Wheat Zone), Zone V (South China Autumn-sown Spring Wheat Zone), and Zone VI (Northeastern Spring-sown Spring Wheat Zone). The susceptible check cultivar Gamenya and the resistant check cultivar Sumai 3 were included in all field tests.

Experimental design and phenotyping approaches

Field FHB evaluations were performed in 2009 and 2012 at the CIMMYT research station at El Batán, Texcoco, Edo. de Mexico, Mexico; located at an altitude of 2,240 m above sea level (masl), latitude 19°31′N, longitude 98°50′W, with an annual rainfall of 625 mm. In 2009, materials were planted on May 30 in hill plots of 0.40 × 0.45 m, with one plot per line. At anthesis, 10 spikes of each line were tagged in the morning with a subsequent spray inoculation in the afternoon, using a precision CO_2 backpack sprayer with flat fan nozzles at a constant pressure of 40 psi. The spore-inoculum was composed of five highly virulent strains of DON-producing *F. graminearum*, that had been collected and characterized according to He et al. (2013), and spore concentration was adjusted to 50,000 spores/ml. The inoculation was repeated two days later. The nursery was subjected to a programmable misting system, activated for 10 min/h from 9:00 to 20:00. At 31 days post inoculation (dpi), FHB symptoms were evaluated on the 10 tagged spikes by counting the spikes infected (incidence) and infected spikelet numbers of each spike (severity). FHB index was calculated by multiplying disease incidence and severity (He et al. 2013). Lines with an FHB index lower than 10 % and those heading earlier than 90 days after planting were selected for more detailed evaluations.

The selected accessions were planted at the Centro Experimental de Norman E. Borlaug (CENEB) station on November 15, 2009, for seed multiplication, leaf rust tests, and PH and DH evaluation. CENEB is located in the State of Sonora, Mexico, near Cd. Obregón at 39 masl, latitude 27°22′N, longitude 109°55′W, with average annual rainfall of 330 mm. Wheat accessions were grown in 1 m double row plots spaced 20 cm apart, on 75 cm wide raised beds. The leaf rust susceptible cultivar Morocco was planted as spreader around the experimental block, and was inoculated on January 10 2010 using a hand-sprayer containing urediniospores of *Puccinia triticina* Erikss. & Henn., races MCJ/SP and MBJ/SP, suspended in mineral oil Soltrol®170. Disease scores were recorded on March 18, 2010 using four categories: R (percentage symptomatic leaf area <15 %), MR (15–30 %), MS (30–45 %), and S (>45 %). In addition, the FHB related traits DH and PH were scored and a further

selection was made by eliminating the late lines and those with plant heights greater than 120 cm.

The 2012 El Batán field experiment was similar to 2009, except that the materials were planted in 1 m double rows, arranged in randomized complete block design with three replications, and FHB was evaluated at 25 dpi. In addition to DH and PH, AE was visually scored based on a linear scale from 0 (no extrusion) to 9 (100 % extrusion), according to Skinnes et al. (2010). FDK was estimated by visually assessing grain samples in a petri dish; both symptomatic (pinkish or discolored) and shrived kernels were assessed as FDK. For DON analysis, samples of 20 g grain were ground from each accession, and a 2 g sub-sample was tested using the Ridascreen® Fast DON ELISA kit (R-Biopharm GmbH, Darmstadt, Germany).

Haplotyping

Wheat lines with an FHB index less than 16 % and DH less than 80 days in the 2012 field tests were further selected to test the presence of validated QTL. Genomic DNA was extracted from bulked young leaves from five individual plants, using the CTAB method described in the CIMMYT laboratory protocols (CIMMYT 2005). Seventeen molecular markers linked to 10 validated FHB resistance QTL (Tables 1 and S2) were used to genotype the selected lines at the GenServe Laboratories, Saskatchewan, Canada. The markers were fluorescently labeled (Schuelke 2000) and the PCR system and cycling program followed the recommended protocols for each marker. All PCR were performed in an Applied Biosystems Veriti 96 well thermal cycler. PCR products were analyzed using an ABI 3500xl Genetic Analyzer through capillary electrophoresis; allele-calling was conducted using GENEMAPPER version 4.0 (Applied Biosystems, Foster City, CA). The strategy for declaring a QTL followed He et al. (2013), whereby a resistance QTL was considered to be present only when both flanking markers showed the resistance alleles (marked as '+', in contrast to '−', indicating absence of the resistance allele, whereas '?' indicated one flanking marker showed resistance genotype (Table 1), except for the 3BS QTL from Sumai 3, the 3AS QTL from *T. dicoccoides*, and the 3AL QTL from Frontana, where only one closely linked marker was accepted as indicative of the resistance gene or QTL).

Statistical analyses

SAS program ver. 9.2 was employed to analyze the phenotypic data. Mean values were calculated using the LSMEANS statement in PROC GLM, and Pearson correlation coefficients were calculated using the PROC CORR function.

Results

El Batán 2009 field trial

Of the 583 accessions planted, only 491 were successfully phenotyped (the rest had germination problems or were very late due to strong winter habits). The resistant and susceptible checks, Sumai 3 and Gamenya, showed FHB indices of 1.5 and 76.9 %, respectively, indicating a satisfactory epidemic. Of the lines evaluated, 84 (17.1 %) showed resistance levels lower than that of Sumai 3. The distribution was skewed significantly towards resistance (Fig. 1a), indicating promising prospects for further screening. No significant correlation was found between DH and FHB index in the evaluated lines (data not shown). Finally, 304 accessions with a FHB index less than 10 % and DH less than 90 days were selected for the next round of evaluation.

CENEB 2009-2010 field trial

Lines in this trial generally showed good leaf rust resistance; the percentages of R, MR, MS, and S accessions were 22.8, 33.1, 30.1, and 13.9 %, respectively. However, 67 (22.0 %) lines were taller than 120 cm, and 19 (6.3 %) showed DH greater than 90 days; most of these lines were excluded from further evaluation. Leaf rust resistance was taken only as a reference and rust susceptible lines were only excluded when PH or DH values were high, or when relatively high FHB infection was observed in 2009. Finally, 140 lines were selected for further study (Table S1); most showed good FHB resistance and agronomic type. Among the selected lines, the percentages of leaf rust resistance categories R, MR, MS, S were 24.3, 32.9, 24.3, and 18.6 %, respectively.

Table 1 Haplotyping results of the 102 selected lines with their FHB parameters indicated

INTRID[a]	Entry name[b]	Phenotyping[c]				Haplotyping[d]									
		FHB 2009	FHB 2012	DON 2012	FDK 2012	WU 2D	CJ 2D	FR 3A	SU 3B	DI 3A	WU 4B	SU 5A	FR 5A	SU 6B	DI 7A
BW18604	80.25	1.48	2.13	0.52	5	?	+	–	–	–	–	?	?	–	–
BW28916	80456/Yangmai 5	1.07	5.82	1.90	17.5	+	?	–	–	–	–	?	?	–	–
CWI38229	8143	1.00	6.75	1.12	27.5	?	–	–	–	–	–	–	–	?	?
CWI38231	83072	4.19	2.51	0.41	15	+	+	–	–	–	–	–	–	–	?
CWI38280	8429.1.1.3	0.60	0.68	0.08	7.5	–	?	–	+	–	–	?	–	+	?
BW9464	Chang chun 14	6.00	6.54	1.92	30	–	?	–	–	–	–	–	–	?	–
BW11272	Chuanmai 18	13.59	15.84	3.25	42.5	+	?	–	–	–	–	?	?	–	?
BW19766	Chuanyu 10	1.36	4.79	1.50	20	+	?	–	–	–	–	–	?	–	?
BW17533	Chuanzhi 4331	5.12	5.35	1.01	7.5	?	–	–	–	–	–	?	?	–	?
CWI38298	CP881	0.00	4.32	0.68	2.5	?	?	–	–	–	–	+	?	–	+
CWI37772	CY8902	8.59	5.70	0.70	32.5	–	–	–	–	–	–	?	–	na	?
BW19888	DGB BV84.1406/ JIANGSU	0.31	2.35	0.20	7.5	?	?	–	+	–	–	–	?	?	–
CWI38227	ER63403	0.99	5.14	0.87	7.5	?	?	–	na	–	–	?	?	?	?
BW10289	Fufan 17	3.90	10.45	1.55	15	?	–	–	–	–	+	–	–	–	?
CWI1915	Fujing 538	1.49	3.16	0.03	10	+	+	–	–	–	–	?	–	–	?
CWI1917	Fujing 633	3.37	1.22	0.02	7.5	–	+	–	+	–	?	+	–	na	–
CWI38257	G823.4.1.3.1	2.20	4.35	2.25	5	–	–	–	+	–	–	?	–	–	–
CWI35995	Gang85-454	0.48	2.30	0.15	12.5	?	–	–	–	–	?	–	?	?	?
BW17538	HAAS3621-2	0.85	3.72	0.08	2.5	–	?	–	–	–	?	–	?	?	–
CWI36116	HAAS8193	2.13	0.81	0.15	7.5	–	?	–	–	–	?	–	?	?	?
BW17542	HAAS8676	0.57	1.75	0.79	7.5	–	?	–	–	–	?	–	?	?	?
BW17536	HAAS88-307-1	0.00	4.57	0.57	2.5	?	?	–	–	–	?	–	?	?	–
CWI36119	HAAS8855	6.35	1.81	0.60	5	+	–	–	–	–	na	?	–	?	–
CWI36003	HXL30646	0.43	4.28	0.89	10	?	+	–	–	–	?	–	?	?	–
CWI36005	HXL41547	0.00	1.49	0.30	7.5	?	+	–	–	–	?	–	?	?	?
BW17546	HXL7493	2.87	4.50	0.22	7.5	+	?	–	–	–	–	?	–	–	–
CWI36108	HXL7525	10.44	0.63	0.18	30	+	?	–	–	–	–	?	–	–	–
CWI36109	HXL7555	0.54	7.21	1.64	50	+	?	–	–	–	+	–	?	–	?
CWI36114	HXL8144	8.14	2.08	0.70	2.5	–	–	–	–	–	–	–	?	na	?
BW28928	Jian 85.11//Suzhou 7906/Ning 8249	1.01	2.78	0.06	5	+	–	–	+	–	+	–	?	–	–
CWI27139	Jinghong 7	0.71	5.20	7.05	92.5	?	–	+	–	–	–	?	?	?	?
CWI236	Kung Chiao	4.11	3.10	0.27	12.5	–	–	–	–	–	–	–	?	?	–
BW19504	Longmai 16	7.07	2.40	1.09	5	–	–	–	–	–	–	–	–	?	?
BW28935	Lu 95	1.50	5.90	0.32	5	+	+	–	–	–	–	?	–	–	?
BW12209	Nanjing 8176	4.84	2.81	0.51	7.5	+	?	–	+	–	–	–	?	?	?
BW13299	Nanjing 8180	0.66	0.87	0.59	20	+	?	–	+	–	–	?	–	?	?
BW13300	Nanjing 8308	2.58	6.45	2.15	37.5	+	+	–	–	–	–	+	–	–	–
BW15892	Nanjing 8508	2.15	0.22	0.07	15	+	+	–	–	–	–	+	–	–	–
BW15895	Nanjing 8609	3.39	3.40	0.27	17.5	?	?	–	+	–	–	?	–	+	–
BW15896	Nanjing 8611	0.87	2.68	0.22	17.5	–	?	–	–	–	–	?	–	?	–
BW15897	Nanjing 8615	5.58	3.82	1.30	15	–	+	–	+	–	–	–	?	–	–

Table 1 continued

INTRID[a]	Entry name[b]	Phenotyping[c]				Haplotyping[d]									
		FHB 2009	FHB 2012	DON 2012	FDK 2012	WU 2D	CJ 2D	FR 3A	SU 3B	DI 3A	WU 4B	SU 5A	FR 5A	SU 6B	DI 7A
BW15898	Nanjing 8618	0.59	4.41	1.20	5	?	–	–	–	–	–	?	–	?	–
BW15900	Nanjing 8634	3.55	0.78	2.10	27.5	–	+	–	+	–	–	–	–	?	–
BW15902	Nanjing 8647	4.69	1.69	0.83	12.5	–	+	–	na	–	–	–	–	–	–
CWI38278	Nannong 87.7053	1.41	6.22	0.45	37.5	–	?	–	+	–	–	+	?	–	–
BW28918	NG8675/Ning 8645	0.52	2.54	0.18	12.5	–	+	–	+	–	–	–	–	?	–
BW12212	Ning 8331	5.44	2.67	0.54	7.5	+	?	–	+	–	–	?	–	?	–
BW21798	Ning 8401	4.76	4.30	1.90	20	?	?	–	+	–	–	?	–	?	–
CWI36188	Ning 8611	2.93	2.65	0.40	22.5	+	?	–	–	–	–	?	–	?	–
BW17518	Ning 8675	3.78	1.99	0.44	12.5	–	+	–	+	–	–	–	–	?	–
CWI38232	Ning 8745	1.43	5.54	0.29	10	–	–	–	–	–	–	–	–	?	?
CWI38235	Ning 89.6812	1.73	2.78	0.18	20	–	+	–	–	–	–	–	?	–	–
CWI38234	Ning 8903	0.00	0.36	0.28	5	+	+	–	–	–	–	?	–	–	–
BW19873	Ning 91112	4.93	5.98	0.15	10	+	+	–	–	–	–	?	–	–	?
BW27588	Ning 9131 (X)	1.08	2.23	0.48	22.5	–	+	–	–	–	–	?	–	?	?
BW37892	Ningmai 50	6.51	2.19	1.45	5	+	?	+	+	–	?	?	–	–	–
BW37893	Ningmai 9558	5.78	3.61	0.07	10	+	+	–	–	–	?	?	?	?	–
CWI38223	Ningxia 88R3438	5.04	1.80	0.96	10	+	?	–	–	–	?	–	?	?	?
CWI35799	Qinmai 6	1.90	6.33	0.57	7.5	?	?	–	–	–	–	?	–	?	?
BW18353	SHA3/SERI	1.45	2.64	0.59	15	?	+	–	–	–	–	?	–	–	?
BW19889	Shaan 32109	1.03	1.08	0.06	7.5	+	+	–	+	–	–	?	–	?	?
BW39946	Shanghai	4.30	3.07	0.06	2.5	+	?	–	+	–	–	?	?	–	–
BW39984	Shanghai	1.59	1.18	0.18	7.5	–	?	–	–	–	–	?	–	–	?
BW43961	Shanghai	3.03	1.19	0.27	7.5	–	?	–	–	–	–	?	–	–	?
BW17415	Shanghai 15E235	5.28	4.94	0.20	7.5	+	+	–	–	–	–	?	–	?	–
BW37895	Shanghai 8	3.08	0.87	0.33	5	+	+	–	–	–	–	?	–	?	?
BW18863	Shanghai 8	3.33	4.43	0.79	12.5	+	+	–	–	–	–	?	–	?	?
BW15904	Shanghai 84114	4.95	5.40	0.41	15	+	?	–	+	–	–	?	–	na	?
CWI1704	Shaoxing Canhuamimai	2.07	5.06	0.34	12.5	+	+	–	–	–	–	?	–	–	–
CWI27279	Sumai 1	8.06	2.86	0.38	12.5	–	–	–	+	–	+	?	–	?	–
BW11783	Suzhou 3	0.00	2.78	0.30	22.5	?	–	–	–	–	–	+	–	?	?
BW11787	Suzhou 9	3.68	1.15	0.07	5	–	+	–	+	–	–	+	–	+	?
BW21870	Suzhou F3 #1 0M	3.61	4.34	0.46	10	?	?	–	+	–	–	+	–	–	?
BW17525	SW87-2323	6.58	0.15	0.25	5	?	–	–	–	–	–	–	–	–	–
CWI38082	SW89.2060	4.35	6.71	1.00	20	+	–	–	–	–	–	–	+	?	–
CWI38083	SW89.2068	4.52	6.38	1.55	60	+	–	–	–	–	–	–	+	?	–
CWI38084	SW89.2089	2.43	5.45	0.98	42.5	+	–	–	–	–	–	–	+	?	–
CWI38086	SW89.2814	2.22	4.76	0.45	20	+	?	–	na	–	–	–	+	?	–
CWI38096	SW89.4974	7.66	3.06	0.86	7.5	?	?	–	–	–	–	–	?	na	?
BW17523	SW89-13649	8.72	7.69	2.20	40	?	–	–	–	–	–	?	+	–	–
BW17530	SW89-3052	4.00	4.32	1.03	7.5	+	?	–	–	–	–	–	+	?	–
BW17529	SW89-3218	7.77	8.51	5.60	30	+	–	–	na	–	–	–	?	–	–

Table 1 continued

INTRID[a]	Entry name[b]	Phenotyping[c]				Haplotyping[d]									
		FHB 2009	FHB 2012	DON 2012	FDK 2012	WU 2D	CJ 2D	FR 3A	SU 3B	DI 3A	WU 4B	SU 5A	FR 5A	SU 6B	DI 7A
BW19887	Taigu wheat derivative	1.04	1.30	0.18	22.5	–	+	–	–	–	?	?	–	–	–
CWI35800	W226.16	6.25	2.28	1.01	7.5	+	–	–	–	–	?	?	?	?	?
CWI38220	Xifeng	5.79	4.06	0.59	52.5	–	–	–	+	–	+	–	–	–	–
BW17520	Yang 85-85	8.25	4.60	0.46	17.5	+	+	–	–	–	–	?	–	?	?
CWI1666	Yangmai 1	1.10	6.00	0.49	7.5	?	?	–	–	–	–	?	–	?	?
BW37896	Yangmai 158	3.17	3.19	0.30	15	–	?	–	–	–	–	?	–	?	–
CWI38213	Yangmai 4	4.75	9.28	4.25	17.5	?	–	–	–	–	–	–	–	–	?
BW19878	Yangmai 4	4.01	2.82	0.23	5	+	+	–	–	–	–	?	–	–	?
BW37897	Yangmai 5	5.89	2.08	0.31	7.5	+	+	–	–	–	–	?	–	–	?
CWI50575	Yangmai 6	1.44	3.49	0.02	5	+	+	–	–	–	–	?	–	?	–
BW16622	YIE83.5070	4.71	6.78	1.20	55	–	?	–	–	–	–	?	–	?	–
BW16623	YIE86.6074	1.20	6.20	0.64	32.5	–	?	–	–	–	–	–	–	–	–
BW15937	YIU 83.5070	4.12	3.82	1.45	42.5	–	+	–	–	–	–	?	–	?	–
BW16616	Zhejiang 2	0.58	5.68	0.30	60	–	+	–	+	–	–	+	–	?	?
BW16617	Zhejiang 3	8.37	6.58	0.74	22.5	?	–	–	+	–	–	?	–	–	?
BW19764	Zhejiang 4	3.13	3.24	2.45	20	?	–	–	–	–	+	+	?	?	?
BW18605	Zhejiang 84/Chuannong 83.2.2	1.01	6.49	0.89	17.5	+	–	–	+	–	?	–	–	?	–
CWI38299	Zhejiang 84/Chuannong 83.2.2	5.34	4.09	1.15	22.5	?	–	–	+	–	?	–	–	?	–
CWI38219	Zhengjian 8709	2.16	3.37	0.20	12.5	+	–	–	–	–	–	+	–	?	+
BW28913	Zuo 1330	1.44	4.46	0.52	7.5	+	?	–	–	–	–	*?*	?	–	*?*
BW10294	Sumai 3 (R-check)	1.50	1.09	0.08	3	–	+	–	+	–	–	+	–	+	+
CWI11851	Gamenya (S-check)	76.93	41.91	8.25	100	?	–	–	–	–	?	–	–	–	–

'+' denotes the presence of the QTL supported by both flanking markers (except for SU_3B, DI_3A, and FR_3A, where only one flanking marker was applied); '?', supported by only one marker; '–' putative absence of a QTL; *na* not analyzed. More detailed information on SSR allele sizes is available in Table S3

[a] CIMMYT germplasm bank accession number

[b] There are lines with the same name, e.g. Yangmai 4, which could be attributed to either redundancy or labeling error. Since the phenotypic values and genotypes are usually different between the lines, we did not eliminate the 'redundancy'

[c] FHB index (%) evaluated in 2009 and 2012; DON content (ppm) and FDK (Fusarium damaged kernels, %) measured in 2012

[d] Haplotyping results using 17 markers linked to 10 validated QTL, where WU stands for Wuhan 1, CJ for CJ 9306, FR for Frontana, SU for Sumai 3, and DI for *T. diccocoides*. The markers used were *WMC144* and *WMC245* for WU_2D (Somers et al. 2003), *GWM157* and *GWM539* for CJ_2D (Jiang et al. 2007), *DUPW227* for FR_3A (Steiner et al. 2004), *UMN10* for SU_3B (Liu et al. 2008), *GWM2* for DI_3A (Otto et al. 2002), *WMC238* and *GWM149* for WU_4B (Somers et al. 2003), *BARC186* and *BARC180* for SU_5A (Anderson 2007), *BARC197* and *GWM129* for FR_5A (Steiner et al. 2004), *GWM133* and *WMC179* for SU_6B (Cuthbert et al. 2007), and *BARC121* and *WMC488* for DI_7A (Kumar et al. 2007)

El Batán 2012 field trial

In 2012, 116 (82.9 %) lines showed FHB indices less than 10 % (the threshold for selection in 2009), and 16 (11.4 %) lines exhibited higher resistance than Sumai 3, which had an FHB index of 1.1 % (Fig. 1b). The FHB ranking differed across the 2 years and only a moderate correlation coefficient of 0.38 ($P < 0.0001$)

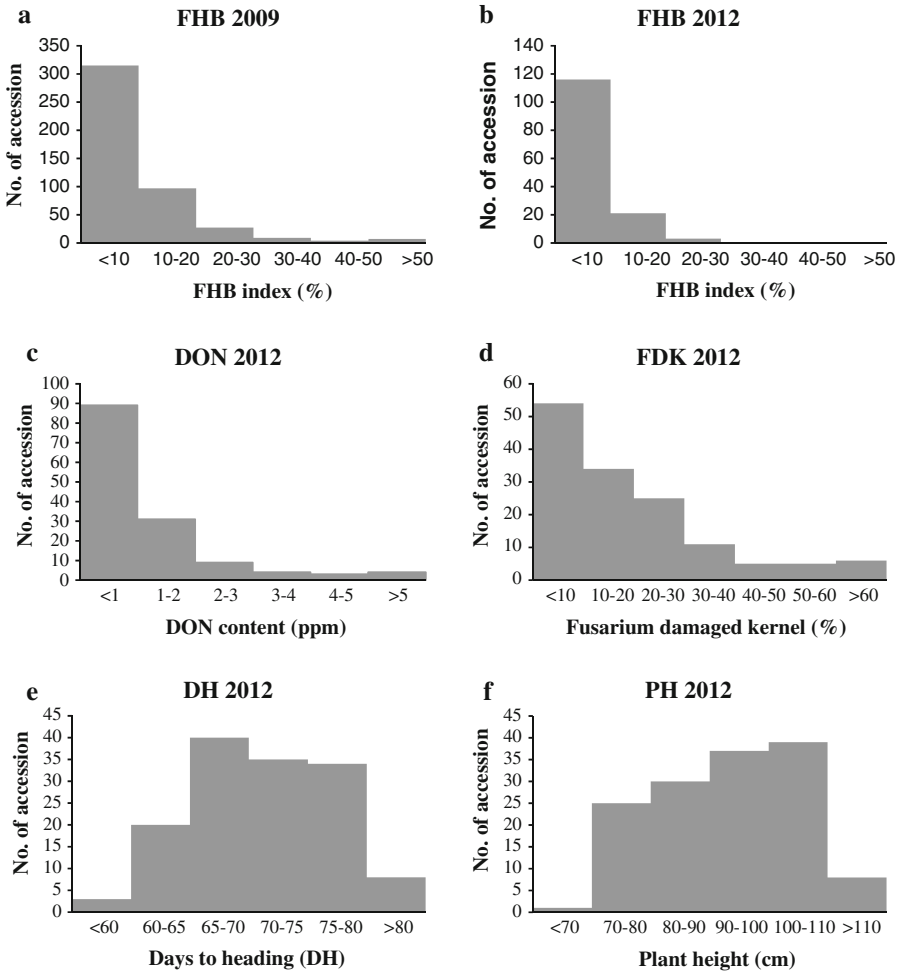

Fig. 1 Frequency distribution of FHB response in the 491 lines evaluated in 2009, and of FHB, DON, FDK, DH, and PH in the 140 lines tested in 2012

was observed. Fourteen (10 %) lines showed DON contents less than Sumai 3 (0.08 ppm), and 89 (63.6 %) lines had DON contents less than 1 ppm (Fig. 1c), with Gamenya exhibiting a very high concentration of 8.25 ppm. FDK had a wider range, from 2.5 to 92.5 % (Fig. 1d), with Sumai 3 and Gamenya recording 3 and 100 %, respectively. Compared to FHB traits, DH and PH were more evenly distributed (Fig. 1e, f). The distribution patterns of both AE versus FHB and PH versus FHB were typically 'fan-shaped', i.e. the lines showing high AE/PH tended to have low FHB indices, while those showing low AE/PH exhibited a wide range of FHB (Fig. 2).

In 2012, moderate correlations were found between FHB index, DON concentration, and FDK, ranging from 0.45 to 0.56, all highly significant (Table 2). PH, DH, and AE also showed significant associations with FHB. Although DH was not related to FHB index, it was correlated with DON concentration and FDK (Table 2). PH and AE were correlated with all three FHB traits, although PH had higher correlation coefficients (Table 2).

QTL haplotype prediction

The same QTL alleles on chromosome 2D as in Wuhan 1 or CJ 9306 were the most frequent among the 102 lines, with frequencies of 42.2 and 32.4 %, respectively, and 59 lines (57.8 %) had either or both of these alleles (Tables 1 and S3). The same 3BS QTL allele as in Sumai 3 (*Fhb1*) showed a frequency of 26.5 %, while the same 3AS QTL allele as in

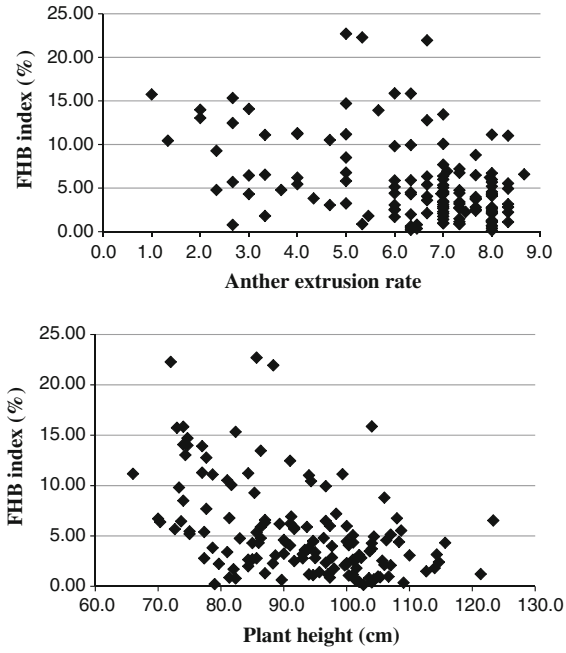

Fig. 2 Scatter plots for the FHB index against anther extrusion rate and plant height among 140 lines in 2012

T. diccocoides was absent. The same 3AL QTL allele as in Frontana was detected in only two lines (Tables 1 and S3). The other five QTL (4B as in Wuhan 1, 5A and 6B as in Sumai 3, 5A as in Frontana, and 7A as in *T. dicoccoides*) showed high proportions of '–' and '?' genotypes (Table 1), suggesting low frequencies in the Chinese germplasm tested in the present study. Finally, there were 27 (26.5 %) lines with none of the validated QTL being present, implying that they may be potential sources of new resistance genes (Table 1).

Discussion

Screening strategy

FHB resistance is a quantitative trait greatly influenced by environmental factors (Buerstmayr et al. 2012), which is the reason for re-evaluation of the Chinese materials in Mexican environments before their utilization in breeding programs, even though many of them had already shown resistance when tested in China.

Field FHB screening was done twice in El Batán. At CENEB, the dry climatic conditions are unfavorable for FHB development; therefore only DH, PH, and leaf rust reponses were scored. CENEB is, however, an ideal location for screening for leaf rust response and our evaluations of the Chinese germplasm for leaf rust response provided additional information to breeders. Based on our leaf rust evaluations in 2010, 57.2 % of the 140 elite lines were R or MR, and are therefore promising candidates for breeders using the germplasm to develop cultivars with resistance to both FHB and leaf rust.

The CIMMYT collection of lines and cultivars is widely adaptive, owing to its broad genetic base and the shuttle breeding program that exposes wheat materials to diverse photoperiod, temperature, and disease conditions (Ortiz et al. 2008). In this study, a 'shuttle screening' between El Batán and CENEB was carried out to select materials that can easily be incorporated into the CIMMYT breeding program. The materials used in this study came from diverse latitudes (from 25°N to 47°N), with the majority from 29°N to 32°N. In the current study, the germplasm was screened at 19°N (El Batán) and 27°N (CENEB) to

Table 2 Pearson correlation coefficients among traits assessed on 140 selected lines in 2012

	FHB	DON	FDK	DH	AE	PH
FHB	1					
DON	0.54***	1				
FDK	0.45***	0.56***	1			
DH	−0.07	−0.25**	−0.28***	1		
AE	−0.43***	−0.35***	−0.26**	0.14	1	
PH	−0.46***	−0.42***	−0.55***	0.13	0.35***	1

FHB Fusarium head blight index (%), *DON* deoxynivalenol concentration (ppm), *FDK* Fusarium damaged kernels (%), *DH* days to heading, *AE* anther extrusion rate, *PH* plant height (cm)

** and ***, significance at P levels < 0.01 and 0.001, respectively

eliminate late lines, so the remaining should all be photoperiod-insensitive and can be utilized in any photoperiod conditions.

Plant height has been reported as a passive mechanism of resistance to FHB in numerous studies, where taller plants tend to have less disease (Buerstmayr et al. 2012). Our study also revealed this trend (Table 2, Fig. 2), and it is noteworthy that of the 12 accessions showing zero infection in 2009, eight were taller than 120 cm and were not included in further evaluations. Admittedly, there may be new resistance genes or alleles in those tall accessions, but lack of FHB symptoms is often associated with tall stature and low yield, and breeding experience in China showed that it is difficult to utilize such materials in breeding (Zhou 2003; Bai and Shaner 2004).

Phenotyping

It was not unexpected that only a moderate correlation of FHB index was found between 2009 and 2012, considering that, as previously discussed, FHB is highly influenced by environmental factors (Buerstmayr et al. 2012). Although FHB severity is usually positively correlated with DON concentration and FDK, there have also been reports of zero or negative correlations (Paul et al. 2005), thus they are classified as different resistance mechanisms. In this study, moderate correlations were found among the three parameters and as expected, several lines with low FHB index but very high DON concentration and/or FDK (or vice versa) were found (Table 1). For example, Jinghong 7 had relatively low field FHB index in both 2009 (0.71 %) and 2012 (5.20 %), but showed surprisingly high DON concentration (7.05 ppm) and FDK (92.5 %) in 2012; and similar situation also occurred for the related line Jinghong 5(S). The reason may be strong Type I and/or Type II resistance, but very weak Type III and IV resistance in the cultivars, suggesting that these resistance mechanisms are controlled by independent genes. This emphasizes the importance of evaluating DON concentration and FDK to identify cultivars with durable and holistic resistance to FHB.

Numerous studies have indicated negative correlations between DH and FHB under spray or spawn inoculation (Emrich et al. 2008). Our results did not show such an association due to inoculation of each line at anthesis and scoring responses at a fixed time after inoculation, thereby ensuring that the scoring of lines with different heading dates was done at the same developmental stage. Nevertheless, the impact of DH was shown in DON concentration and FDK, as reflected by the significantly negative correlations between DH and DON/FDK (Table 2) because early lines were exposed to the epidemic environment for a longer time than late lines. However, selection on late lines with low infection levels is not advisable, considering this negative association was mainly caused by developmental or epidemiological conditions.

The association of AE and FHB was reported in Chinese germplasm in the early 1980s and was confirmed subsequently by numerous researchers, as reviewed by Lu et al. (2001). Recently, AE has attracted attention in Europe (Graham and Browne 2009; Skinnes et al. 2010; Lu et al. 2013), and the co-localizations of QTL for AE and FHB traits were reported, providing a genetic basis for the phenotypic association. AE provides Type I resistance through a FHB avoidance mechanism, i.e. pathogens colonizing on anthers extruded out from florets were prevented from further infection. AE can be used as a morphological marker for selecting lines with Type I resistance, which may be especially useful in places where the epidemic is sporadic and Type I resistance alone may provide sufficient protection.

Throughout the screening, outstanding lines with low FHB parameters, high leaf rust resistance, and good agronomic type were identified, e.g. China 8, Wuhan 3, Nanjing 4840, SW87-2323, and HAAS8193 (Table S1). A few of them (e.g. Wuhan 3) have already been used in the CIMMYT wheat breeding program, but most remain unutilized.

Haplotyping

Functional markers that are suitable for MAS (Liu et al. 2012) are now unavailable for selection of FHB resistance, due to the fact that no FHB resistance gene has been cloned. A major shortcoming of flanking markers is that the results could be difficult to interpret if when only one flanking marker is present resulting in wrong interpretation for the presence/absence of the flanked resistance gene. However, selection for both flanking markers is highly efficient in capturing resistance gene or QTL.

Jiang et al. (2007) suggested that the chromosome 2D QTL in CJ 9306 is allelic to that of Wuhan 1, but

our results did not validate this as no clear trend for either identical or complimentary haplotypes was observed between the two QTL (Tables 1 and S3). This may be due to loose linkages between the QTL and markers, or because the prevailing haplotypes in Chinese materials were different from the one on which the linkage relationship was established. Another QTL found frequently in our study was *Fhb1*, the most significant and stable QTL found in wheat. Although the global wheat FHB research community has been trying to find and utilize QTL other than, or in addition to, *Fhb1*, this study shows that a significant proportion of Chinese germplasm carries this QTL. Considering the ease and precision of utilizing the linked marker *UMN10* in MAS, reasonable employment of *Fhb1* in FHB resistance breeding is beneficial and may not lead to the breakdown of its resistance.

As for the remaining seven QTL, low frequencies of '+' genotypes were observed (Table 1), implying their low occurrence frequencies. However, there were many '?' genotypes found for the 4B QTL as in Wuhan 1 (*Fhb4*), the 5A QTL as in Sumai 3 and Frontana (two alleles of *Fhb5*), the 6B QTL as in Sumai 3 (*Fhb2*), and the 7A QTL as in *T. dicoccoides*, the actual frequencies of these QTL might be higher than estimated. Since the 3AS QTL as in *T. dicoccoides* and the 3AL QTL as in Frontana were either not detected or occurred at very low frequencies in the tested materials, their introduction and utilization in Chinese breeding programs might be beneficial. For the lines where no '+' genotypes were detected, new QTL or new favorable alleles from known QTL may be present and the lines could be used in breeding programs as novel resistance sources, e.g. HXL8144, SW89.4974, and Ning8745 (Table 1).

Accessions resistant to FHB identified in this study by two years of FHB field evaluations and haplotyping data provide new sources of resistance to FHB that could be utilized to broaden and develop durable resistant cultivars.

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