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ORIGINAL PAPER

Marker-assisted characterization of Asian wheat lines for resistance to *Fusarium* head blight

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Abstract The major quantitative trait locus (QTL) on 3BS from Sumai 3 and its derivatives has been used as a major source of resistance to *Fusarium* head blight (FHB) worldwide, but resistance genes from other sources are necessary to avoid complete dependence on a single source of resistance. Fifty-nine Asian wheat landraces and cultivars differing in the levels of FHB resistance were evaluated for type II FHB resistance and for genetic diversity on the basis of amplified fragment length polymorphism (AFLP) and simple sequence repeats (SSRs). Genetic relationships among these wheat accessions estimated by cluster analysis of molecular marker data were consistent with their geographic distribution and pedigrees. Chinese resistant landraces had broader genetic diversity than that of accessions from southwestern Japan. The haplotype pattern of the SSR markers that linked to FHB resistance quantitative trait loci (QTLs) on chromosomes 3BS, 5AS and 6BS of Sumai 3 suggested that only a few lines derived from Sumai 3 may carry all the putative QTLs from Sumai 3. About half of the accessions might have one or two FHB resistance QTLs from Sumai 3. Some accessions with a high level of resistance, may carry different FHB resistance loci or alleles from those in Sumai 3, and are worth further investigation. SSR data also clearly suggested that FHB resistance QTLs on 3BS, 5AS, and 6BS of Sumai 3 were derived from Chinese landrace Taiwan Xiaomai.

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Introduction

Wheat *Fusarium* head blight (FHB), mainly caused by *Fusarium graminearum*, is an economically important wheat disease in humid and semi-humid wheat-growing areas worldwide (Parry et al. 1995; McMullen et al. 1997). The grain harvested from FHB-infected wheat spikes shows reduced test weight, poor baking quality, and low germination rate when used as seed (Bai and Shaner 2004). Grain contaminated with deoxnivalenol (DON) produced by the fungus is also a major concern for animal production and human health (Snijders 1990; Bai et al. 2001).

There is no single effective measure for complete control of wheat FHB. The use of resistant cultivars, together with proper crop management practices, is the most effective strategy for control of the disease (Bai and Shaner 1994; McMullen et al. 1997). Two types of FHB resistance have been extensively studied and well

documented: type I resistance against initial infection and type II resistance against spread within the infected spike (Schroeder and Christensen 1963). So far, a few FHB resistant germplasm have been reported in wheat, such as Sumai 3 (Anderson et al. 2001), Wangshuibai (Zhou et al. 2004; Lin et al. 2006), Renan (Gervais et al. 2003), Frontana (Steiner et al. 2004), Arina (Paillard et al. 2004), Goldfield (Gilsinger et al. 2005) and so forth. Type II resistance is more stable than type I in the majority of the resistant cultivars identified to date (Bai and Shaner 2004).

Fusarium head blight resistance is a complex trait (Bai and Shaner 1994; van Ginkel et al. 1996; Ban and Suenaga 2000). Two to five major genes, plus several minor genes, have been reported from various sources of FHB resistance (Buerstmayr et al. 1997; Yao et al. 1997; Grausgruber et al. 1998, 1999; Somers et al. 2003; Zhou et al. 2004). QTLs for FHB resistance have been mapped to almost all wheat chromosomes when different mapping populations were investigated (Bai and Shaner 2004). In Sumai 3, QTLs for FHB resistance have been identified on 3BS, 5AS, 6AS, 6BS, and 3BSc, a QTL region proximal to the centromere on 3BS (Anderson et al. 2001; Buerstmayer et al. 2002; Zhou et al. 2002; Yang et al. 2003). In Wuhan 1, the QTLs for FHB resistance were mapped to 2DL and 4B (Somers et al. 2003). QTLs on other chromosomes were also reported including those on chromosomes 2A, 2B, 3A, 3B, 5D, 6D, 5B, 4A, 1B, and 7A in wheat germplasm from Europe, Brazil, and Asia (Gervais et al. 2003; Paillard et al. 2004; Steiner et al. 2004; Zhou et al. 2004). But only the QTL on 3BS from the Chinese cultivar Sumai 3 consistently showed a major effect on Type II resistance across different genetic backgrounds and environments (Bai et al. 1999; Anderson et al. 2001; Buerstmayr et al. 2002, 2003; Zhou et al. 2002, 2004; Yang et al. 2003). Other QTLs for FHB resistance exhibited a minor effect, and their expression varied significantly with genetic backgrounds and the environments where the disease was evaluated (Bai and Shaner 2004). Therefore, Sumai 3 has been extensively used as a major source of resistance to FHB in breeding programs worldwide (Rudd et al. 2001; McCartney et al. 2004). However, heavy use of narrow FHB resistance sources may increase selection pressure on the pathogens to wear away the effectiveness of the resistance genes involved. New FHB resistance germplasm are desired to broaden the genetic diversity of FHB resistant sources and improve the level of wheat resistance to FHB (Ruckenbauer et al. 2001; Gervais et al. 2003). The objectives of this study were to identify new sources of FHB resistance from the Asian wheat gene pool, and elucidate the genetic relationship among these accessions using molecular markers.

Materials and methods

Plant materials

Fifty-nine wheat accessions originated from China (38 accessions), southwestern Japan (20 accessions), and Korea (one accession) (Table 1). The majority of the Asian accessions were believed to have some degrees of FHB resistances, including the well-known FHB resistant cultivars (Sumai 3, Wangshuibai, and Ning 7840) from China. Three U.S. cultivars (Ernie, Freedom and Clark) were also included as moderately resistant and susceptible controls, respectively. Funo from Italy and Avrora from Russia were also included because Funo is a parent of Sumai 3 and Avrora is a parent of Ning 7840. Both of them have been extensively used as parents in Chinese breeding programs from the 1950s to the 1970s (Bai et al. 2003).

Evaluation of FHB resistance

Type II resistance was measured by using a syringe to inject 1,000 conidia spores of *F. graminearum* into a basal floret of a central spikelet of a spike at anthesis. All wheat accessions were evaluated for FHB resistance in the greenhouse of Kansas State University in 2003 as described by Bai et al. (2003). The inoculum of *F. graminearum* was a field isolate (GZ 3639) that originated from Kansas. This isolate has been well characterized for its high aggressiveness and DON production (Desjardins et al. 1996). After vernalization at 4°C in a growth chamber for eight weeks, six plants were transplanted into a $5' \times 5'$ tora pot (Hummert Int., St. Louis, MO, USA) filled with Metro Mix 360 soil mix (Hummert Int.,), and were grown on a greenhouse bench with a 12-h daylight period. The FHB resistance evaluation experiment was repeated once, with three replications in each experiment. Four to six plants, one head per plant, were inoculated for each pot. Inoculated plants were incubated in a moist chamber for 3 days to initiate infection. Then the infected plants were moved to the original bench position and were grown at 25°C during day and 22°C during night. Infected and total spikelets in a spike were counted at the 21st day after inoculation, and the proportion of symptomatic spikelets (PSS) was calculated as a measure for disease severity.

Table 1 Origin, pedigree and *Fusarium* head blight severity for 64 wheat accessions

ID	Name	Origin	[a] Source	Pedigree	[b] PSS	[c] FHB reaction
1	Dabaipao	China	PI 462150	Landrace	78.5 ± 24.4	S
2	Nanda 2419	China	JAAS	Selection of Mentana	81.5 ± 21.0	S
3	Sanyuehuang	China	JAAS	Landrace	92.2 ± 12.3	S
4	Clark	USA	PI 512337	Beau//65256A1-8-1/67137B5-16/ Sullivan/Beau//5517B8-5-3-3/Logan	94.1 ± 9.0	S
5	Mazhamai	China	PI 382153	Landrace	–[d]	–
6	Funo	Italy	JAAS	Duecentodieci/Demiano	51.8 ± 11.6	MS
7	Shanghai Caizihuang	China	PI 435110	Landrace	53.5 ± 26.3	MS
8	Dafanliuzhu	China	PI 447402	Landrace	54.4 ± 28.0	MS
9	Zhen 7495	China	JAAS	Youyimai/Fusuihuang	54.5 ± 23.9	MS
10	Chile	Japan	ACC.26869	Chili	57.3 ± 24.6	MS
11	Shironankin	Japan	ACC.23277	Landrace	60.5 ± 27.4	MS
12	Zairai Yuubou	Japan	ACC.22130	Landrace	61.8 ± 27.9	MS
13	Heshangmai	China	JAAS	Landrace	66.2 ± 28.6	MS
14	NTDHP	China	JAAS	Landrace	66.6 ± 19.8	MS
15	Jingzhou1	China	JAAS	Nanda 2419/Sereal	69.1 ± 18.0	MS
16	Avrora	Russia	JAAS	Neuzucht/Bezostaja 4//Bezostaja 1	70.2 ± 35.9	MS
17	Chinese Spring	China	CItr 14108	Landrace	76.5 ± 10.0	MS
18	Shou Komugi II	Japan	ACC.23653	Landrace	26.3 ± 21.7	MR
19	WZHHS	China	JAAS	Landrace from China	26.9 ± 14.0	MR
20	Freedom	USA	PI 562382	GR876/OH217	27.8 ± 22.7	MR
21	Hongjianzi	China		Landrace	28.6 ± 17.5	MR
22	Chokwang	Korea	JAAS	unknown	28.7 ± 30.2	MR
23	Emai 6	China	JAAS	Selection from radiated Nanda 2419	29.0 ± 33.5	MR
24	Itou Komugi	Japan	ACC.23647	Landrace	30.1 ± 35.3	MR
25	Yangmai 158	China	JAAS	St1472/506//Yangmai 4	30.3 ± 27.6	MR
26	Kagoshima	Japan	ACC.23542	Landrace	31.2 ± 15.0	MR
27	FSW	China	JAAS	Landrace from China	32.2 ± 25.5	MR
28	Nobeokabouzu Komugi	Japan	PI 382153	Landrace	32.3 ± 24.1	MR
29	Soba Komugi 1B	Japan	ACC.23662	Landrace	32.4 ± 9.1	MR
30	Sotome A	Japan	ACC.23660	Landrace	32.5 ± 34.5	MR
31	Yangmai 4	China	JAAS	(Nanda 2419/Triumph)F5/Funo	34.6 ± 29.5	MR
32	Canlaomai	China	JAAS	Landrace	39.4 ± 28.5	MR
33	Shinchunaga	Japan	PI 197130	Selection from landrace Nakanaga	39.6 ± 18.4	MR
34	Nyubai	Japan	ACC. 22957	Landrace	40.2 ± 36.1	MR
35	Sotome	Japan	ACC.23595	Landrace	42.7 ± 32.8	MR
36	Dahongpao	China	JAAS	Landrace	43.3 ± 39.0	MR
37	Wangnian 2	China	JAAS	Selection of Mentana	44.1 ± 32.8	MR
38	Xueliqing	China	JAAS	Landrace	47.8 ± 18.5	MR
39	Abura Komugi	Japan	ACC.23516	Landrace	48.0 ± 18.5	MR
40	Sanshukomugi	Japan	PI 592001	Landrace	49.0 ± 13.8	MR
41	Fusuihuang	China	PI 213833	Landrace	49.3 ± 23.2	MR
42	Kikuchi	Japan	ACC.22952	Landrace	49.3 ± 21.5	MR
43	Ning 7840	China	JAAS	Avrova/Anhui 11/Sumai 3	6.6 ± 1.4	R
44	F60096	China	JAAS	Jingzhou 1/Sumai 2	6.9 ± 1.2	R
45	Fu 5114	China	JAAS	LongXi 18/(Avrora/Anhui11//Sumai 3)	7.4 ± 1.6	R
46	Sumai 49	China	PI 447405	N7922/(Avrova/Anhui 11/Sumai 3)	7.8 ± 1.5	R
47	Wangshuibai	China	PI 197129	Landrace	8.7 ± 3.8	R
48	Aso Zairai II	Japan	ACC.23524	Landrace	8.9 ± 3.7	R
49	Baisanyuehuang	China	JAAS	Landrace	12.5 ± 6.9	R
50	Aso Zairai (Yuubou Kappu)	Japan	ACC.23521	Landrace	12.7 ± 7.7	R
51	Taiwan Xiaomai	China	JAAS	Landrace	13.0 ± 3.2	R
52	Huangcandou	China	JAAS	Landrace	13.4 ± 7.6	R
53	Haiyanzhong	China	JAAS	Landrace	13.7 ± 6.3	R
54	Fumai 3	China	PI 447404	Orofen/Funo	18.6 ± 16.4	R
55	Sumai 3	China	PI 462149	Funo/Taiwan Xiaomai	18.8 ± 11.9	R
56	Huangfangzhu	China	JAAS	Landrace	20.2 ± 17.4	R
57	Ernie	USA	PI 584525	PI584525 PIKE/3/Stoddard/ Blueboy//Stoddard/D1707	20.5 ± 13.7	R
58	Huoshaomai	China	JAAS	Landrace	21.4 ± 13.7	R

Table 1 continued

ID	Name	Origin	[a] Source	Pedigree	[b] PSS	[c] FHB reaction
59	Caizihuang	China	JAAS	Landrace	22.0 ± 14.2	R
60	Huoshaobairimai	China	JAAS	Landrace	22.0 ± 22.3	R
61	Shirasaya No 1	Japan	PI 197128	Landrace	22.4 ± 14.5	R
62	Qiaomai Xiaomai	Japan	ACC.24142	Landrace	22.4 ± 18.4	R
63	Yangmai 1	China	PI 447403	Selection of Funo	22.5 ± 22.0	R
64	Nobeokabouzu	Japan	JAAS	Landrace	24.3 ± 19.3	R

[a] *JAAS* seeds were provided by Jiangsu Academy of Agricultural Science, Nanjing, P.R. China and all these accessions were selected based on their good resistance to FHB in China, *PI* seeds were provided by the National Small Grains Research Facility at Aberdeen, ID, USA and they were selected based on their diverse geographic distribution in China without knowing their FHB resistance, *ACC* accession number in Gene Bank of MAFF, JAPAN and all these accessions were selected based on FHB resistance tested in Japan

[b] Average of proportion of symptomatic spikelets in a spike (PSS) from replication means of two season greenhouse evaluations in 2003 ± standard deviation.

[c] *R* resistant (PSS < 25%), *S* susceptible (PSS >75%), *MR* moderately resistant (50%>PSS >25%), *MS* moderately susceptible (50% < PSS < 75%)

[d] Data are not available

Molecular marker analysis

DNA was isolated from seedling leaf tissue according to CTAB method (Saghai-Maroof et al. 1984). For AFLP analysis, DNA restriction digestion (with *Eco*RI and *Mse*I), adapter ligation, and PCR amplification were carried out as described by Bai et al. (2003). Pre-amplification was conducted with an *Eco*RI primer (5′-ACTGCGTACCAATTC) and an *Mse*I primer (5′-GATGAGTCCTGAGTAA). Selective PCR used 24 primer combinations between six IR-dye-labeled *Eco*RI primers with selective nucleotides of AGT, AAC, ACT, GCTG, CTCG, and CATG and five unlabeled *Mse*I primers with selective nucleotides of CAC, CAT, CAGT, TGC, and AGTG.

Twenty-five SSR markers (Table 2) associated with FHB-resistance QTLs on 3BS (Anderson et al. 2001; Buerstmayer et al. 2002; Zhou et al. 2002), 3BSc (Somers et al. 2003), 5AS (Buerstmayer et al. 2002), 6BS (Anderson et al. 2001; Yang et al. 2003), 4B, and 2DL (Somers et al. 2003) were screened for polymorphisms among these accessions. The FHB-resistance QTLs on 4B and 2DL were originally detected from Wuhan 1, a Chinese breeding line with unknown pedigree (Somers et al. 2003), and five SSR markers linked to the two QTLs (McCartney et al. 2004) were included in this study (Table 2). The SSR markers were amplified according to the protocol described by Bai et al. (2003). For PCR detection, an M13 tail sequence was added to the 5′-end of the forward SSR primers (5′-ACGACGTTGTAAAACGAC). A PCR with 10-μl reaction volume consisted of ~50 ng DNA, 1× PCR buffer, 0.2 mM dNTPs, 2 mM $MgCl_2$, 1 pmol each of tailed-forward and reverse primers, as well as IR-dye-labeled M13 primer (Li-Cor, Inc., Lincoln, NE, USA). The SSR markers on 3BS were directly labeled with IR-dye in the 5′-ends without adding the M13 primer in PCR reaction mixture. To amplify SSR, a touchdown PCR profile started at 95°C for 5 min, followed by 5 cycles of 45 s at 95°C, 5 min at 68°C, and 1 min at 72°C; the annealing temperature was lowered by 2°C in each following cycle. Then 5 more cycles in which the annealing time was 2 min and the temperature was lowered 2°C in each following cycles. For the last 25 additional cycles, the annealing temperature was held constantly at 50°C, with 5 min at 72°C for a final extension. The AFLP and SSR fragments were analyzed in a Li-Cor 4200 DNA Sequencer (Li-Cor, Inc., Lincoln, NE, USA).

Data analysis

Polymorphic DNA fragments were scored as either present (1) or absent (0) for each marker locus by using SAGA software (Li-Cor, Inc., Lincoln, NE, USA). The SAS software package was used for basic statistical analysis (SAS Institute Inc., Cary, NC, USA). Cluster analysis was performed using NTSYSpc version 2.11a (Rohlf 1998). The genetic diversity among accessions, on the basis of the AFLP and SSR data, was estimated according to Jaccard's similarity coefficient and was calculated as $1 - [a/(n - d)]$, where a is the number of bands in common between two wheat accessions, n is the number of bands in the matrix, and d is the number of bands absent in both wheat accessions. The SIMQUAL routine of NTSYSpc program was used to generate the Jaccard's similarity coefficient matrix. The unweighted pair-group method with arithmetic

Table 2 Allele sizes of the SSR markers that were reported to be tightly linked to QTLs for FHB resistance in Sumai 3 and Wuhan 1 for 64 wheat accessions

ID	Accession	2DL		3BSc		4B			5AS						6BS							3BS				
		Xwmc 144[a]	Xwmc 245	Xwmc 777	Xwmc 612	Xwmc 48	Xgwm 113	Xgwm 165	Xgwm 293	Xgwm 415	Xwmc 705	Xgwm 129	Xbarc 117	Xgwm 304	Xgwm 518	Xwmc 494	Xgwm 508	Xwmc 398	Xwmc 105	Xwmc 397	Xgwm 219	Xgwm 389	Xbarc 75	Xgwm 533	Xbarc 133	Xgwm 493
1	Dabaipao	[b] 159	165	156	274	216	166	274	218	150	188	241	239	231	185	231	200	159	353	177	208	158	128	156	140	212
2	Nanda 2419	161	166	133	296	209	168	279	214	152	160	239	235	217	201	241	200	159	377	177	206	134	ND	160	142	ND
3	Sanyuehuang	161	166	133	280	218	168	281	218	150	186	247	243	233	178	276	200	175	367	185	199	150	128	160	109	162
4	Clark	159	166	111	302	218	168	276	214	152	158	235	239	235	187	220	N	166	ND	179	199	134	128	132	134	180
5	Mazhamai	157	165	147	284	216	168	272	218	148	198	249	ND	229	185	226	200	159	349	175	194	150	ND	156	130	212
6	Funo	161	168	108	298	209	168	276	214	150	156	239	243	237	180	231	200	166	353	187	194	ND	ND	134	138	160
7	Shanghai Caizihuang	162	165	150	ND	ND	166	ND	ND	148	184	ND	239	231	209	235	N	ND	343	173	182	150	128	160	145	212
8	Dafanliuzhu	159	166	131	284	216	168	274	216	150	184	244	239	233	209	241	200	168	343	179	192	150	128	160	130	212
9	Zhen 7495	157	166	111	302	218	168	274	218	150	156	239	239	237	183	226	200	166	ND	173	208	134	ND	109	145	ND
10	Chile	159	165	144	268	216	168	264	218	150	184	241	239	233	185	226	200	176	ND	185	192	154	128	156	109	216
11	Shironankin	159	165	131	282	216	168	279	218	150	193	249	239	233	175	272	200	174	353	179	194	154	128	160	152	214
12	Zairai Yuubou	159	166	133	282	214	168	272	218	150	193	241	239	231	209	233	N	172	343	177	199	152	126	163	140	214
13	Heshangmai	159	166	131	280	216	168	276	216	148	195	244	243	233	187	230	N	168	343	179	199	152	128	162	109	200
14	NTDHP	157	166	133	282	216	168	274	216	150	184	247	239	231	209	239	200	172	343	177	192	150	128	157	130	212
15	Jingzhou 1	159	165	111	302	209	168	276	216	150	156	239	239	235	201	239	N	159	ND	173	204	137	128	157	138	182
16	Avrora	161	166	111	292	216	168	261	214	150	153	237	243	231	185	226	N	159	ND	182	189	ND	ND	132	145	162
17	Chinese Spring	157	165	150	300	214	168	264	216	150	193	241	239	235	181	235	200	176	336	179	194	152	126	171	109	214
18	Shou Komugi II	159	166	150	239	216	168	274	218	150	191	244	239	233	209	237	200	159	343	179	202	154	128	162	140	214
19	WZHHS	159	166	129	280	216	166	276	218	150	191	241	239	237	178	272	200	172	ND	179	199	152	128	160	ND	160
20	Freedom	155	166	144	302	214	168	270	212	152	156	237	239	233	164	223	200	159	ND	185	171	134	126	152	138	162
21	Hongjianzi	161	168	133	287	218	170	274	218	150	195	241	239	231	187	237	N	168	ND	177	209	152	126	157	142	218
22	Chokwang	162	166	163	307	216	168	274	216	150	153	249	243	231	183	230	N	159	353	182	206	150	128	157	140	214
23	Emai 6	159	166	131	298	209	168	279	216	150	156	244	239	237	185	229	200	159	377	173	204	134	ND	157	145	ND
24	Itou Komugi	155	166	144	276	209	168	ND	216	150	189	244	239	229	209	239	200	159	339	179	206	152	128	159	140	214
25	Yangmai 158	159	166	111	302	209	168	276	216	150	156	239	239	235	180	231	200	166	349	187	194	ND	ND	132	138	160
26	Kagoshima	155	166	133	282	216	168	270	216	152	191	244	239	233	175	272	200	174	343	182	208	152	128	157	140	210
27	FSW	157	165	153	307	212	168	272	220	150	178	247	239	237	175	272	200	172	341	177	199	152	128	160	140	214
28	Nobeokabouzu Komugi	157	166	147	284	212	168	272	218	150	188	244	239	233	209	239	200	159	341	179	206	150	128	157	140	214
29	Soba Komugi 1B	157	166	133	279	ND	168	281	220	150	195	249	239	235	183	272	N	172	343	177	199	154	128	160	109	210
30	Sotome A	159	166	133	282	216	168	272	207	150	198	241	239	233	178	270	N	172	346	179	204	150	126	157	140	212
31	Yangmai 4	161	168	108	300	209	168	276	216	150	156	239	239	235	178	230	200	159	ND	173	202	ND	ND	132	138	160
32	Canlaomai	161	166	131	284	216	170	274	218	150	193	244	239	233	183	243	200	175	ND	185	189	154	128	162	140	220
33	Shinchunaga	157	166	131	280	216	168	272	216	150	188	244	239	235	209	231	N	172	343	175	194	152	128	160	138	212
34	Nyubai	157	166	147	284	212	168	272	218	150	188	244	239	233	209	239	200	159	341	179	206	150	128	157	140	214
35	Sotome	159	166	133	282	218	168	274	218	150	195	244	239	233	178	270	N	159	ND	179	204	158	126	109	138	214
36	Dahongpao	159	165	131	279	218	168	276	216	150	193	241	239	231	189	241	200	176	ND	182	202	152	128	159	145	210
37	Wangnian 2	159	168	129	298	209	168	276	216	150	156	237	239	237	219	239	N	159	377	173	206	134	ND	160	140	214
38	Xueliqing	159	166	150	279	218	168	272	218	152	184	241	239	233	209	243	200	168	343	179	192	152	126	163	147	210
39	Abura Komugi	157	166	133	289	212	168	276	216	150	189	249	239	233	ND	233	200	168	339	179	199	137	128	159	140	212
40	Sanshukomugi	157	166	129	289	209	168	272	216	150	186	239	239	235	183	235	200	175	349	185	204	152	128	154	140	212
41	Fusuihuang	159	166	133	298	216	168	274	212	152	158	241	235	215	187	237	200	198	349	187	202	134	ND	157	142	ND
42	Kikuchi	157	ND	129	284	214	166	272	218	150	186	241	ND	233	180	266	N	172	339	179	204	154	128	160	140	214
43	Ning 7840	157	166	111	292	218	168	276	218	150	186	239	239	233	209	231	N	172	343	175	194	152	128	160	140	212

Table 2 continued

ID	Accession	2DL		3BSc		4B			5AS						6BS							3BS				
		Xwmc 144[a]	Xwmc 245	Xwmc 777	Xwmc 612	Xwmc 48	Xgwm 113	Xgwm 165	Xgwm 293	Xgwm 415	Xwmc 705	Xgwm 129	Xbarc 117	Xgwm 304	Xgwm 518	Xwmc 494	Xgwm 508	Xwmc 398	Xwmc 105	Xwmc 397	Xgwm 219	Xgwm 389	Xbarc 75	Xgwm 533	Xbarc 133	Xgwm 493
44	F60096	159	166	111	292	209	168	276	218	150	186	241	239	233	209	231	N	174	343	175	194	150	128	159	140	212
45	Fu 5114	157	166	108	287	209	168	276	ND	152	186	249	239	233	178	ND	N	166	ND	179	ND	152	128	160	142	214
46	Sumai 49	157	166	111	292	218	168	270	216	150	156	241	239	237	209	231	N	174	341	175	194	137	126	163	ND	212
47	Wangshuibai	157	166	156	311	214	168	274	220	150	176	244	239	235	180	272	200	172	343	175	199	150	128	159	136	212
48	Aso Zairai II	155	166	150	239	212	168	279	216	152	195	249	239	237	209	237	200	159	343	177	204	158	128	159	140	200
49	Baisanyuehuang	159	166	156	274	214	168	276	218	150	178	244	239	231	183	276	200	172	346	175	199	150	128	160	109	214
50	Aso Zairai (Yuubou Kappu)	157	166	150	239	214	168	276	216	150	195	244	239	237	209	237	200	159	343	177	209	154	128	159	140	214
51	Taiwan Xiaomai	157	166	129	282	216	168	274	218	148	186	241	239	233	209	231	N	172	ND	175	194	152	128	160	140	212
52	Huangcandou	161	166	133	287	218	168	274	218	150	184	244	239	233	175	239	200	172	346	177	206	150	128	162	142	214
53	Haiyanzhong	159	166	156	287	216	168	276	218	150	178	247	ND	231	183	276	200	172	346	177	199	150	128	159	109	214
54	Fumai 3	159	168	ND	298	209	168	ND	214	150	156	237	239	235	180	230	200	166	349	187	204	134	ND	132	138	160
55	Sumai 3	157	166	131	282	209	168	276	218	150	186	239	239	233	209	231	N	172	343	175	194	152	128	160	140	212
56	Huangfangzhu	161	166	131	284	216	170	276	216	150	193	241	239	235	209	237	N	168	ND	179	192	152	128	156	109	214
57	Ernie	155	166	147	302	216	168	272	212	152	156	239	239	237	185	229	N	166	349	179	204	134	128	109	142	160
58	Huoshaomai	161	168	147	272	218	168	274	218	150	186	244	239	229	175	243	200	159	346	182	192	152	126	157	142	210
59	Caizihuang	159	166	133	284	218	168	276	218	150	186	247	239	231	185	243	200	174	367	182	194	150	128	160	142	220
60	Huoshaobairimai	161	168	133	287	216	170	274	218	152	186	244	239	233	175	241	200	174	343	177	206	152	128	159	140	216
61	Shirasaya No.1	157	166	133	282	218	168	274	220	150	184	241	239	233	185	230	200	168	341	175	194	152	128	160	136	162
62	Qiaomai Xiaomai	159	166	133	280	212	168	276	214	150	156	239	239	235	180	231	200	166	349	187	206	150	128	160	109	210
63	Yangmai 1	159	168	113	298	209	168	276	216	150	156	237	239	237	180	231	200	166	349	187	206	ND	ND	132	138	160
64	Nobeoka Bozu	157	166	147	284	212	168	272	218	150	188	244	239	233	209	239	200	159	341	179	206	150	128	157	140	214
PIC		0.70	0.43	0.87	0.92	0.77	0.23	0.77	0.68	0.36	0.88	0.80	0.28	0.75	0.85	0.91	0.45	0.78	0.82	0.82	0.86	0.80	0.53	0.84	0.81	0.83
No. of alleles		5	3	12	18	5	3	8	6	3	14	7	3	7	12	16	2	8	9	7	11	6	2	12	10	11
Haplotypes[c]		ND		4		ND			24						23							21				

N Null allele, *ND* no data, *PIC* polymorphism information content

[a]Marker closes to the QTL for FHB resistance in Sumai 3 or Wuhan 1

[b]Numbers are amplicon sizes (in bp) for the respective marker in wheat lines. Amplicon sizes of the five 3BS SSR markers are the sizes from directly labeled primers plus the 18 bp M13 tailing nucleotides

[c]Haplotype based on Sumai 3/non-Sumai 3 alleles

mean (UPGMA) and SHAN routine of NTSYSpc program were used to construct a dendrogram. Bootstrapping ($n = 500$) was performed to evaluate the robustness of the branching points using Phyltools (Buntjer 2001). The neighboring and consensus modules from the Phylip program (Felsenstein 2005) were used to construct the consensus tree. Bootstrap values were percentages of number of runs showing a specific branch point in the consensus tree when the data were randomly re-sampled for 500 times. Haplotypes of the 64 wheat cultivars were determined on the basis of the allelic distribution pattern of SSR markers linked to 3BS, 5AS, 4B, and 6BS QTL in Sumai 3. The polymorphism information content (PIC) refers to the ability of a given marker to detect polymorphism within a population (Anderson et al. 1993). The PIC depends on the number of detectable alleles and their frequency. In this study, the simplified version (Lagercrantz et al. 1993) is used, which assumes that the wheat accessions are all homozygous.

$$\mathrm{PIC}_i = 1 - \sum_{j=1}^{n} p_{ij}^2,$$

where p_{ij} is the frequency of the jth pattern for marker i, and n is the total number of patterns.

Results

Type II FHB resistance of Asian wheat accessions

Asian wheat accessions differed significantly in FHB severity, as reflected by their PSS (Table 1). The correlation coefficient for PSS between the two experiments was highly significant ($r = 0.66$, $P < 0.0001$). Wheat responses to FHB infection ranged from highly resistant (PSS < 10%, F60096 and Fu5114) to highly susceptible (PSS > 85%, Sanyuehuang). Approximately 67% of the Asian wheat accessions tested showed a high or moderate level of FHB resistance, with a mean PSS of less than 50% under the favorable epidemic conditions. More than half of the highly resistant accessions originated from China. Ernie from the USA also showed a high level of FHB resistance. The remaining highly resistant lines originated from Japan, including Aso Zairai II, Aso Zairai (Yuubou Kappu), Itou Komugi, and Shirasaya No.1. Taiwan Xiaomai, one of the parents of Sumai 3, had a PSS of less than 15%, which was similar to Sumai 3. Another parent of Sumai 3, Funo, showed moderate susceptibility to FHB in two experiments.

Genetic relationships among the wheat accessions

A total of 25 SSR alleles and 483 AFLP polymorphic alleles were scored. The AFLP and SSR data illustrated that the resulted groups from cluster analysis of these accessions basically matched with their geographic distribution and/or available pedigrees, with only a few exceptions (Fig. 1). In general, the cluster analysis roughly separated the 64 accessions into three major clusters, a Chinese/Japanese landrace cluster, an Avrora-related cluster, and a Funo-related cluster. Avrora- and Funo-related clusters consisted of all improved cultivars from China, with Avrora and Funo, respectively, as one parent. Most of the southwestern Japanese landraces (17 out of 19) formed a closely related subgroup within the Chinese/Japanese landrace cluster (Fig. 1). The Japanese subgroup was separated from the Chinese landraces at a similarity coefficient about 0.82, whereas the most distant Chinese landrace, Chinese Spring, was separated from the other Chinese landraces at a similarity coefficient about 0.77. It was interesting that Japanese landraces Shironankin and Shinchunaga were closer to Chinese accessions than to Japanese landraces. Overall, the genetic distance between the Chinese and the Japanese landraces was closer than between some of the Chinese landraces.

The closest accessions in this study were Japanese accessions Nyubai, Nobeokabouzu and Nobeokabouzu Komugi, and they were separated at a similarity coefficient about 0.99. Two Chinese landraces, Huoshaobairimai and Huacandou, were also very close and were separated at a similarity coefficient about 0.96. The Avrora-related cluster and the Funo-related cluster were separated from the Chinese/Japanese landrace cluster at similarity coefficients of 0.71 and 0.73, respectively. No Japanese landraces were classified into the Avrora-related cluster or the Funo-related cluster. Accessions in the Avrora-related cluster (6 lines) and the Funo-related cluster (11 lines) were in good agreement to their pedigrees. As for FHB resistant sources, the genetic diversity within the Chinese landraces was broader than that of the Japanese landraces (Fig. 1).

Allelic variation in SSR marker loci linked to QTLs for FHB resistance

Twenty-five SSR markers linked to six putative QTLs on five chromosome arms of wheat were highly polymorphic among the wheat accessions evaluated (Table 2). The PIC values for these SSRs ranged from 0.23 (Xgwm113) to 0.92 (Xwmc612). Two (Xbarc75 and Xgwm508) to 18 (Xwmc612) alleles per SSR locus

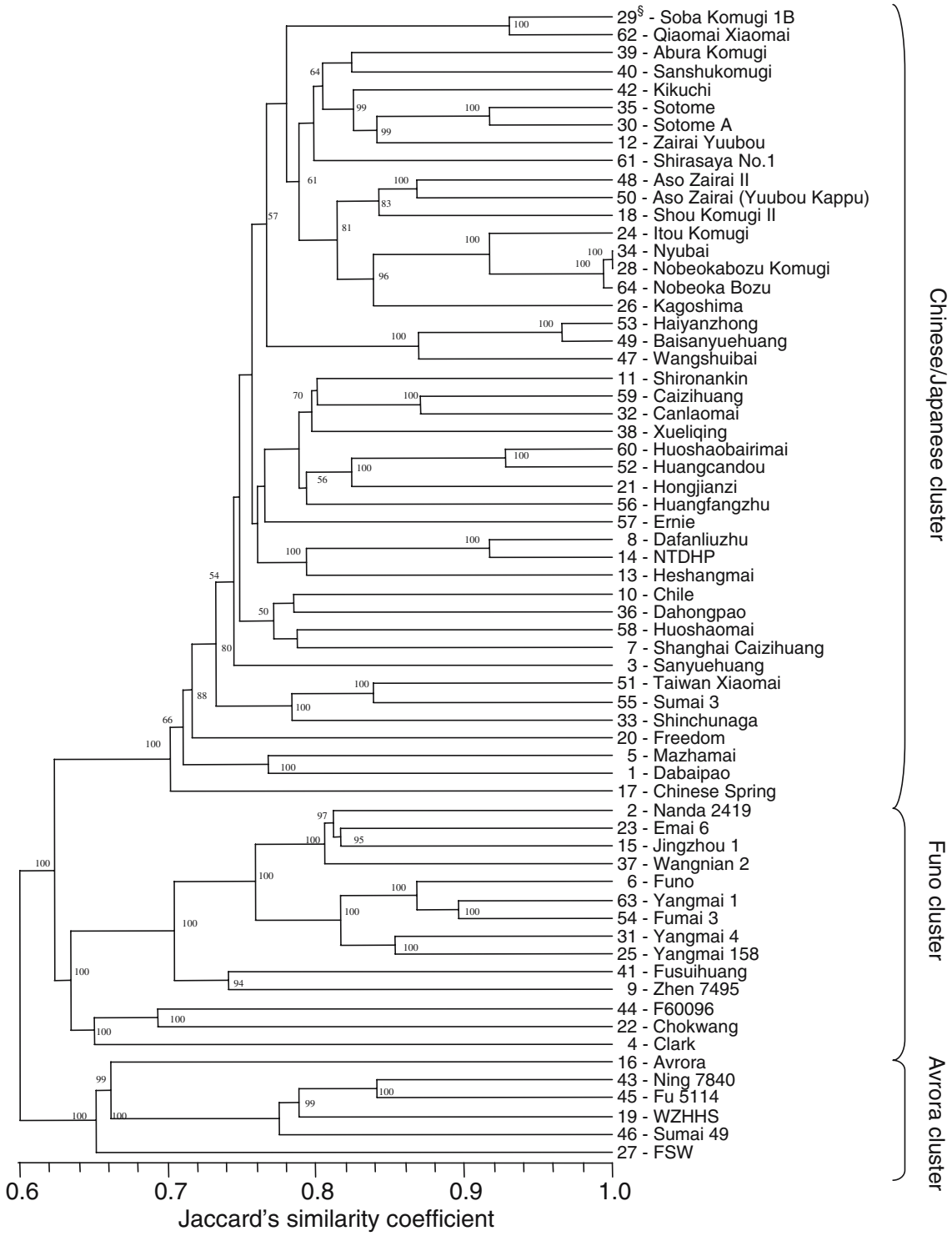

Fig. 1 UPGMA dendrogram based on Jaccard's similarity coefficient from AFLP and SSR marker data showing genetic relationships among the 64 wheat accessions used in this study. Bootstrap values (%) for each branch point are indicated if they are > 50%. § Accession ID

were detected across all 64 accessions (Table 2). Haplotypes based on Sumai 3/non-Sumai 3 alleles were identified—from 4 on 3BSc to 24 on 5AS (Table 2).

Twenty-one haplotypes were identified for the five SSR markers linked to the major QTL on 3BS among the 64 accessions when the marker alleles were ana-

lyzed as Sumai 3 and non-Sumai 3 alleles. Only two accessions, Ning 7840 and Taiwan Xiaomai, shared the identical haplotype with Sumai 3 (Table 2). Two Japanese accessions (Sanshukomugi and Shinchunaga) and one Chinese accession (FSW) had four of the five Sumai 3 SSR alleles; 34 accessions contained two to three Sumai 3 SSR alleles; 11 accessions carried only one Sumai 3 SSR allele; and the remaining 12 lines, including Funo (another parent of Sumai 3) and Avrora (one of Ning 7840's parents), didn't carry any of the five Sumai 3 SSR alleles for the major QTL on 3BS (Table 2). Among those 23 accessions with none or only one Sumai 3 allele, 7 lines expressed a similar level of FHB resistance as that of Sumai 3, and another 8 accessions demonstrated moderate FHB resistance, with less than 50% PSS under a high disease pressure. The 15 wheat lines are unlikely to carry the major QTL for FHB resistance and the resistance in those accessions may be controlled by different QTLs or alleles from that on 3BS of Sumai 3.

The QTLs on 2DL and 4B were only reported from Wuhan 1 and have not been reported in Sumai 3. Wuhan 1 was not included in this study, so it was difficult to determine the alleles of the FHB resistance related SSR markers among the accessions, but most Sumai 3 SSR alleles on the 2DL and 4B QTL regions seemed to be the same as those of susceptible controls (Tables 1, 2), indicating that these SSR are not polymorphic between Sumai 3 and FHB susceptible accessions. For SSR markers linked to QTLs on 3BS, 5AS, and 6BS, a high level of polymorphism was observed between Sumai 3 or its derivatives and susceptible controls. The overall results indicated a trend in which the more the putative Sumai 3 marker alleles for QTLs on 3BS, 5AS, and 6BS an accession had, the more likely the accession had a lower average PSS.

Discussion

Genetic relationships among Asian FHB resistant germplasm

In this study, a collection of FHB resistant germplasm was characterized on the basis of both FHB phenotypic and molecular marker data. In this collection, some are well-known FHB resistant cultivars, whereas most of them are landraces from China, Japan and Korea. Their FHB resistance has not been systematically characterized, and their genetic relationship to Sumai 3 is still unclear because their pedigrees are not available. Molecular-marker-based cluster analysis has been used as a highly reliable means for estimating the genetic relationships among cultivars, with or without known pedigrees (Barrett et al. 1998; Sun et al. 2003; Bai et al. 2003; McCartney et al. 2004). Both analysis methods were used in this study and provided consistent results that led to further understanding of genetic relationships among these Asian FHB resistant accessions. Some putative new sources of FHB resistance other than Sumai 3 were identified. This study also provided systematic pedigree information for many well-known FHB resistant wheat cultivars, and useful FHB data and molecular marker profiles for these accessions. Therefore, the information from this study will help breeders to select different sources of resistant materials for enlarging the genetic diversity of FHB resistance in their breeding programs.

Cluster analysis indicated that the genetic similarities for all pair-wise comparisons among the 64 wheat lines ranged from 0.71 to 0.99, which suggested relatively limited genetic diversity among the accessions in this collection. This result was not surprising because most of FHB resistant wheat landraces originated from the southeast China and from the Kyushu area of southwestern Japan, where FHB epidemics have been frequent and severe, and the improved cultivars were mainly related to Avrora from Russia, Mentana, and its relative Funo from Italy. The results on genetic similarities of Chinese/Japanese FHB resistance accessions from this study agreed with a previous study (Bai at al. 2003).

The genetic relationship based on cluster analysis matched well with their pedigree information and their geographic origins. The dendrogram clearly separated the Funo-related accessions and the Avrora-related accessions from the Chinese/Japanese landraces. This might be because the Russian cultivar Avrora and Italian cultivar Funo and Mentana were far from Asian landraces and were extensively used in early wheat breeding programs in China. Introduction of cultivars Funo and Avrora from Europe significantly broadened the genetic diversity of Chinese wheat. It was unexpected that the three accessions from the USA, Freedom, Ernie, and Clark, didn't form a separate group in the dendrogram. These three cultivars were in a completely different cluster from the Chinese landraces and cultivars in a previous study when more cultivars from the USA were used (Bai et al. 2003). This could be because the small number of accessions with diverse genetic backgrounds from the USA could not provide sufficient genetic information to form their own group. Therefore, interpretation of genetic relationships between Asian landraces and the cultivars from the USA should be cautious.

The Chinese landrace Taiwan Xiaomai and the Italian cultivar Funo are two parents of Sumai 3, and Sumai 3 locates between the Funo and Taiwan Xiaomai, although it is closer to Taiwan Xiaomai in the Chinese/Japanese landrace cluster (Fig. 1). On the other hand, Sumai 3 and Avrora are the parents of Ning 7840, and Ning 7840 is closer to Avrora than to Sumai 3 (Fig. 1). The Funo cluster is further separated into three subgroups. Cultivars Nanda 2419, Emai 6, Jingzhou 1, and Wannian 2 form a subgroup that share a common Italian ancestor Mentana (Fig. 1). Yangmai 1, Yangmai 4, Fumai 3, and Yangmai 158 form another subgroup in which Funo serves as a common ancestor. Fusuihuang and Zhen 7495 form the third subgroup because Zhen 7495 was derived from a cross between Fusuihang and Youyimai, a derivative of Funo. Therefore, the results clearly confirmed the pedigree relationships within each of the three subgroups. Results for the Avrora-related cluster were similar. In this cluster, Ning 7840, Sumai 49, and Fu 5114 shared the common ancestor Avrora. But the two Chinese landraces FSW and WZHHS were close to Ning 7840, and their pedigree information was not available to verify this relationship.

The landrace accessions collected from Japan Kyushu area were stored on the Gene Bank of MAFF, Japan. They were selected as the best FHB resistant germplasm on the basis of several years of field FHB evaluations conducted in Japan and CIMMYT-Mexico. These Japanese landraces form a sub-cluster within Chinese landrace cluster, indicating the genetic bases of FHB resistant landraces from southwestern Japan is narrower than that of the Chinese landraces. It is interesting that the Japanese landraces Shinchunaga and Shironankin are closer to Sumai 3 and Caizihuang, respectively, than to the other Japanese landraces (Fig. 1). Shironankin might directly originate from China because ''Shironankin'' means 'White Nanjing' in Japanese and Nanjing is a Chinese city where many FHB resistant Ning lines were developed. The same might also be true for Shinchunaga, which has been a major source of FHB resistance widely used in Japanese breeding programs for decades (Ban 2000). Shinchunaga had similar banding patterns to those in Sumai 3 at most SSR marker loci in the three QTL regions of Sumai 3 (Table 2). The results suggested that some of FHB resistant QTLs in Japanese germplasm might also originate from Chinese landraces.

Another Japanese landrace Nobeokabouzu Komugi was reported to have the best resistance in Japanese germplasm (Ban 2000). In our study, two other accessions, Nobeokabouzu and Nyubai, are very close to Nobeokabouzu Komugi, with 99% identity according to AFLP marker data and 100% identity according to the 25 SSR marker alleles scored in this study. In our collection, Nyubai and Nobeokabouzu Komugi were originally from the Gene Bank of Japan, and Nobeokabouzu was obtained from China. Therefore, it is possible that Nobeokabouzu Komugi and Nobeokabouzu are the same landrace with different identification because 'Komugi' means 'wheat' in Japanese and it can be omitted from its name. Nyubai may also be the same landrace as Nobeokabouzu. Therefore, any one of them should be able to represent the same accession in breeding programs.

Origin of QTLs for FHB resistance from Sumai 3

The major FHB resistance in Sumai 3 was once assumed to be from Funo, or from transgressive segregation of resistance genes from both parents (Liu and Wang 1990). More recent studies suggested that Taiwan Xiaomai might be the donor of 3BS major QTL from Sumai 3 by comparing haplotypes of 3BS markers from Sumai 3 and Funo (Bai et al. 2003; Liu and Anderson 2003). But, marker data for other QTLs and phenotypic data from Taiwan Xiaomai were not available in those studies. The FHB and SSR marker data from this study provided more solid evidence to support the recent assumption. Taiwan Xiaomai demonstrated the same high level of FHB resistance as Sumai 3, whereas Funo, the other parent of Sumai 3, was moderate susceptible to FHB. The five SSR marker alleles closely linked to the 3BS FHB resistant QTL in Taiwan Xiaomai were exactly the same as those of Sumai 3, whereas those from Funo were completely different. In addition, Taiwan Xiaomai had most of Sumai 3 SSR alleles at 5AS and 6BS loci, whereas Funo has only a few Sumai 3 SSR alleles in the two QTL regions. Therefore, Taiwan Xiaomai was also likely the donor of the QTLs on 5AS and 6BS in Sumai 3. This study reveals the origin of 5AS and 6BS QTLs for FHB resistance in Sumai 3.

Haplotype pattern and FHB resistance

The haplotype of SSR markers that flank QTL can help to predict whether an accession carries known or different QTL. The results from this study show a trend in which the more the putative Sumai 3 marker alleles an accession has for QTLs on 3BS, 5AS and 6BS, the more likely the accession has lower average PSS, suggesting that QTLs on 3BS, 5AS and 6BS are important in most of the resistant accessions. For example, the accessions with less than six Sumai 3 SSR alleles for the three QTLs had an average PSS of

43%, whereas those with more than 10 Sumai 3 alleles had an average PSS of 17%. This result also suggested that marker-assisted selection based on one marker per QTL might not be sufficient, and two or more flanking markers per QTL could provide better selection progress.

On the other hand, haplotype information could only roughly predict if an accession had one or more of the putative QTL(s) and predict its FHB-resistance performance in general. For instance, Fu 5114 was a descendant of Sumai 3 and carried three Sumai 3 SSR alleles at 3BS, three Sumai 3 SSR alleles at 5AS and one Sumai 3 SSR allele at 6BS. The haplotyping data suggested that Fu 5114 might inherit both the 3BS and the 5AS QTL (Table 2). Therefore, its good FHB resistance was consistent with the anticipation based on its haplotype information. But several factors may affect the accuracy of QTL predictions, including the genetic relationship between a target line and the line with known QTLs, the phenotypic effect of the target QTLs, non-precise locations of QTLs, and the genetic distance between the QTL and the markers used for the prediction. If an accession is not genetically related to the QTL donor, haplotype information may not provide a valid prediction for the presence of target QTL. If the markers are far from the target QTL, the prediction may also not be accurate. For example, the Chinese landrace Sanyuehuang carries two Sumai 3 3BS alleles, including Xgwm533, the most closely linked SSR maker for 3BS QTL in Sumai 3, and four Sumai 3 5AS alleles, but it showed high susceptibility to FHB. In contrast, Huoshaomai, which carries one 3BS marker allele (Xgwm389) of Sumai 3, and four 5AS marker alleles of Sumai 3, showed high FHB resistance. Although both had similar haplotypes, their reactions to FHB were completely different. These two landraces might not relate to Taiwan Xiaomai or Sumai 3 and the high susceptibility of Sanyuehuang is possibly due to epistasis or has several other QTLs that increase susceptibility. Excellent FHB resistance from Huoshaomai might be contributed by other QTLs than those on 3BS and 6BS or by different alleles of the QTLs on 3BS and 6BS.

Potential new QTL for FHB resistance

Haplotyping wheat accessions with SSR markers flanking FHB resistant QTLs may also provide useful information for predicting novel QTLs by comparison of haplotypes of target accessions with known cultivars. The underlying assumption is that if a wheat line has the same allelic pattern for marker loci flanking the QTL as that in the known resistant line, the two lines most likely have the same QTL (Bai et al. 2003; Sun et al. 2003; McCartney et al. 2004); on the other hand, if a wheat line has a different allelic pattern from that in the known resistant line, the two lines most likely have different alleles of the QTL.

In this study, 21 wheat lines expressed a similar level of FHB resistance as that of Sumai 3. Among them, Ning 7840, Fu 5114, and Sumai 49 were descendents of Sumai 3, and haplotyping data also supported a conclusion that they carry one to three of these QTLs on 3BS, 5AS, and 6BS. The other 18 accessions did not have clear genetic relationships with Sumai 3 or Taiwan Xiaomai. Among them, 12 accessions including F60096, Wangshuibai, Asozairai II, Huoshaobairimai, Shirasaya No 1, and Huangfangzhu had two to three Sumai 3 marker alleles at 3BS, one to four Sumai 3 marker alleles at 5AS, and one to six Sumai 3 marker alleles at 6BS. The haplotyping data indicated that the 12 accessions might carry at least one of the three Sumai 3 FHB resistant QTL, and the QTLs from the 12 lines were possibly either the same as, or allelic to, QTLs on 3BS, 5AS, or 6BS of Sumai 3. The remaining six accessions, Fumai 3, Yangmai 1, Haiyanzhong, Huoshaomai, Huangcandou, and Ernie, carried none or only one Sumai 3 SSR allele at 3BS and 6BS, and no more than four Sumai 3 SSR alleles at 5AS; therefore, these lines might not have the 3BS and 6BS QTL, and might have the 5AS QTL in a few accessions. Novel FHB resistant QTL might contribute to their high level of FHB resistance because the 5AS QTL only had a minor effect on Type II resistance (Somers et al. 2003). These accessions can be used to enlarge the wheat FHB resistance gene pool and enhance genetic diversity by incorporating different types of resistance in FHB resistant cultivars.

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