

Advanced backcross QTL mapping of resistance to Fusarium head blight and plant morphological traits in a *Triticum macha* × *T. aestivum* population

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Abstract While many reports on genetic analysis of Fusarium head blight (FHB) resistance in bread wheat have been published during the past decade, only limited information is available on FHB resistance derived from wheat relatives. In this contribution, we report on the genetic analysis of FHB resistance derived from *Triticum macha* (Georgian spelt wheat). As the origin of *T. macha* is in the Caucasian region, it is supposed that its FHB resistance differs from other well-investigated resistance sources. To introduce valuable alleles from the landrace *T. macha* into a modern genetic background, we adopted an advanced backcross QTL mapping scheme. A backcross-derived recombinant-inbred line population of 321 BC₂F₃ lines was developed from a cross of *T. macha* with the Austrian winter wheat cultivar Furore. The population was evaluated for Fusarium resistance in seven field experiments during four seasons using artificial inoculations. A total of 300 lines of the population were genetically fingerprinted using SSR and AFLP markers. The resulting linkage map covered 33 linkage groups with 560 markers. Five novel FHB-resistance QTL, all descending from *T. macha*, were found on four chromosomes (2A, 2B, 5A, 5B). Several QTL for morphological and developmental traits were mapped in the same population, which partly overlapped with FHB-resistance QTL. Only the 2BL FHB-resistance QTL co-located with a plant height QTL. The largest-effect FHB-resistance QTL in this population

mapped at the spelt-type locus on chromosome 5A and was associated with the wild-type allele *q*, but it is unclear whether *q* has a pleiotropic effect on FHB resistance or is closely linked to a nearby resistance QTL.

Introduction

Resistance to Fusarium head blight (FHB) is one of the most important traits for modern wheat varieties in many wheat growing areas worldwide. Resistance to FHB is a quantitative trait, governed by polygenes, and quantitative trait loci have been detected on all wheat chromosomes (Buerstmayr et al. 2009; Liu et al. 2009; Löffler et al. 2009). Apart from active physiological resistance plant developmental and morphological characters, especially plant height, flowering time, spike morphology and environmental conditions modulate disease development. The complex nature of the resistance and the important role of genotype-by-environment interactions render breeding for improved FHB resistance difficult. Large genetic variation for FHB resistance is available in the wheat gene pool, but often the regionally best adapted and most highly productive cultivars are susceptible to FHB (Buerstmayr et al. 2009).

Considering the resistance sources used for genetic analysis thus far, two main approaches can be distinguished. One is to evaluate and map populations based on agronomically adapted cultivars, with moderate to good FHB resistance. The other is to employ and genetically characterize more or less exotic resistance sources, such as introduced cultivars, landraces or alien species. Unadapted or exotic genotypes are usually agronomically inferior to modern varieties. In populations from bi-parental crosses between an adapted parent and an exotic parent, the desired

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resistance traits may be confounded with ‘wild’ plant traits such as excessive height or spike morphology. To allow target traits from exotic parents to be evaluated in a more adapted genetic background, the advanced backcross quantitative trait locus (AB-QTL) scheme was proposed by Tanksley and Nelson (1996) for combining QTL detection with variety development. Populations are generated by repeated backcrossing to an adapted elite parent. In such backcross-derived lines, donor chromosome fragments are distributed throughout the genome in a standardized genetic background close to the elite parent. Repeated backcrossing increases recombination events between the remaining donor genome and elite genome, which leads to smaller donor fragments and enhances chances of separating linked genes. Molecular marker techniques and QTL mapping routines adjusted to this specific population design will reveal favourable alleles. Several AB-QTL analyses of different wheat populations identified valuable QTL alleles derived from exotic donor lines (Huang et al. 2004; Kunert et al. 2007; Leonova et al. 2007; Liu et al. 2006; Narasimhamoorthy et al. 2006; Naz et al. 2008).

In the present work, an advanced backcross population derived from a cross between a well-adapted Austrian bread wheat cultivar and *Triticum macha* as donor was screened for FHB-resistance QTL. *T. macha*, a hulled hexaploid wheat, is endemic to the Caucasus area where it was discovered in 1929. In Georgia, a popular local variety ‘Makha’ that had stable yields in different climatic conditions and high resistance to various diseases was grown until the 1930s (Barisashvili and Gorgidze 1979). Previous work identified a line of *T. macha* with remarkably high level of quantitative FHB resistance almost comparable to that of Sumai-3 (Buerstmayr et al. 1996; Grausgruber et al. 1998; Mentewab et al. 2000). This resistant line was used as donor parent. Investigations of Cao et al. (2000) confirm the phylogenetic difference between *T. macha* and common wheat as well as between *T. macha* and *T. spelta*. Because of the distinct origin of *T. macha*, we considered it likely that *T. macha* harbours novel resistance QTL.

Plant morphology, especially spike-related traits, differs considerably between the parents of the investigated population. Gross morphology of wheat spike is substantially influenced by the three major genes: *Q* (speltoid ear, Faris et al. 2005; Mac Key 1954), *C* (compact ear, Rao 1972) and *SI* (sphaerococcum grains, Rao 1977; Salina et al. 2000). *T. aestivum* wheats carry the alleles *QQ cc SISI*, and *T. macha* possesses *qq CC SISI* (Morris and Sears 1967; Swaminathan and Rao 1961). A population from *T. aestivum* × *T. macha* is therefore expected to segregate at *Q/q* (square-headed and free threshing/speltoid and non-free threshing, chromosome 5A) and *C/c* (compact spike/non-compact spike, chromosome 2D), but should be fixed

at *SI* (non-sphaerococcum grains, chromosome 3D). Plant height (Buerstmayr et al. 2000; Gervais et al. 2003; Hilton et al. 1999; Mesterhazy 1995; Steiner et al. 2004), compactness of the spikes (Steiner et al. 2004; Zhu et al. 1999), flowering time (Gervais et al. 2003; Holzapfel et al. 2008; Paillard et al. 2004; Schmolke et al. 2005; Steiner et al. 2004) and flower opening (Gilsinger et al. 2005) have been reported as associated with FHB infection and development. Therefore, in this study, special attention was given to morphological traits and their association with FHB resistance.

A previous study with *T. macha* showed that its FHB resistance is located on several wheat chromosomes (Grausgruber et al. 1998; Mentewab et al. 2000). To date, only one *T. macha*-derived FHB-resistance QTL at chromosome 4A was mapped, in a single chromosome recombinant population (Steed et al. 2005).

We report here about an AB-QTL analysis where a BC₂-derived population was used for simultaneous map calculation and genome-wide QTL detection. The aim of this study was to genetically characterize novel QTL for FHB resistance derived from *T. macha* and for morphological traits and to investigate their associations.

Materials and methods

Plant material and population development

A single homozygous line of *T. macha* was crossed to *T. aestivum* cultivar Furore, and F₁ plants were backcrossed as maternal plants to Furore. A total of 321 independent BC₁F₁ plants were backcrossed as female to Furore. From each of the 321 individually obtained BC₂F₁ plants, one BC₂F₃ plant was derived by single-seed descent. Bulk seed from each BC₂F₃ plant was propagated in 0.5 m² BC₂F_{3;4} plots. The resulting seed was used for multi-environment resistance evaluations as BC₂F_{3;5} lines. The recurrent parent Furore is an Austrian winter wheat cultivar with pedigree POKAL//HP35719/EXTREM/3/CAROLUS/P9094. Furore is moderately susceptible to *Fusarium* head blight. The donor parent *T. macha* is a Transcaucasian landrace. It is a hexaploid hulled wheat with brittle rachis, has a dense but non-compact spike phenotype and pubescent and glaucous glumes. The *T. macha* line used in this project was originally obtained from JIC Norwich, UK (JIC accession 1240001), which was the same accession used for the generation of the *T. macha*—Hobbit-‘sib’ single chromosome substitution lines described by Law and Worland (1996) and analysed for FHB resistance by Grausgruber et al. (1998) and Mentewab et al. (2000). It showed excellent resistance to FHB in previous investigations (Buerstmayr et al. 1996).

Fusarium head blight resistance evaluation

Field design

The 321 BC₂F_{3:5} lines, their parental lines and several control lines were evaluated in seven field experiments from 2005 to 2008 at the IFA-Tulln experiment farm, 30 km west of Vienna (16°04'E, 48°19'N, 177 m above sea level).

Each experiment was defined by a *Fusarium* isolate: *F. culmorum* (FC) or *F. graminearum* (FG) and a specific year encoded by the unit and the decade. For example, the experiment FC06 was the *F. culmorum*-inoculated experiment conducted in 2006. Each experiment had a randomized complete block design with two replications. The plot size was a double row of 0.8 m length with 17 cm row spacing. Sowing time was late autumn (October to November) in all years. The two blocks in each experiment were sown 2–3 weeks apart depending on the specific weather conditions, which delayed anthesis by 1–3 days for the later-sown blocks. Seed treatment, sowing density and crop management were essentially as described by Buerstmayr et al. (2002).

Disease inoculation

For six experiments, spray inoculation and for one experiment (FG08) grain spawn inoculation methods were applied. For spray inoculation, two different *Fusarium* isolates were used, either macroconidia of the *F. culmorum* single-spore isolate 'IFA-106' prepared as described by Buerstmayr et al. (2000) or the *F. graminearum* single-spore isolate 'IFA-65' prepared as described by Buerstmayr et al. (2002). We used a highly aggressive *F. culmorum* isolate and a moderately aggressive *F. graminearum* isolate. Conidia stock solutions in distilled water (500×) were aliquoted into plastic vials and stored at –30°C until use. At each inoculation day, the needed number of inoculum aliquots were thawed and diluted in deionized water to the desired concentration of 2.5×10^4 for the *F. culmorum* isolate and to 5×10^4 for *F. graminearum* isolate. Each plot was individually inoculated twice, first when 50% of the plants had reached anthesis and again 2 days later. Using a battery-driven backpack sprayer, inoculum was sprayed onto the heads until runoff. Inoculations were carried out in the evenings, usually from 4 to 6 p.m. An automated mist-irrigation system, triggered by leaf wetness measurement, maintained humidity and kept the plants wet for 20 h after inoculation. For grain spawn inoculation, 15 g m⁻² *Gibberella zeae*-infected scabby maize grains were spread throughout the experiment 5 weeks before anthesis. The infested grains were taken from a maize field experiment, which was inoculated with a mix of three

F. graminearum (teleomorph: *Gibberella zeae*) isolates in the previous season. Also, this trial was mist irrigated using the same time schedule as described above during the flowering period to provide optimal infection conditions.

Assessment of disease severity

FHB severity was recorded on days 10, 14, 18, 22 and 26 after the first inoculation or after 50% anthesis for the spray and the grain spawn-inoculated experiments, respectively. Severity was estimated as the percentage of infected spikelets per plot by visually averaging whole plots.

Evaluation of other traits

All lines were evaluated for date of anthesis, plant height, spike length, number of spikelets per spike, spike density, threshability, spike glaucousness, hairiness of glumes and severity of leaf chlorosis. As an index of earliness, the date of 50% anthesis was recorded for each plot and converted into the number of days after May 1. Plant height was measured as the distance in centimetre from the soil surface to the top of the ears excluding awns in the experiments FG05, FG06, FG07, FC07 and FG08. Spike length in centimetre and number of spikelets per spike were determined on six randomly chosen ears per plot from a non-inoculated field experiment in 2009. The average number of spikelets per centimetre was calculated and used as measurement for spike density. Plots from this non-inoculated trial were harvested and threshed with a combine harvester (Nursery Master, Wintersteiger, Ried, Austria). Percent threshability was calculated as the weight proportion of free threshed seeds in all seeds harvested. In the experiments, FC07, FG07, FC08 and FG08 verdant spikes were assessed visually for glaucousness based on a 0 (non-glaucous) to 9 (intensely glaucous) scale. Similarly, the severity of physiological leaf chlorosis was scored on a 0 (non-chlorotic) to 9 (severely chlorotic) scale in experiments FG05, FG06, FC06, FG07, FC07 and FG08 at the heading stage. In addition, every line was classified for possessing hairy glumes, non-hairy glumes or heterogeneity for this trait. This trait was treated as a morphological marker.

Molecular marker analysis

Of 321 lines, 300 were randomly chosen for marker analysis. Genomic DNA was extracted from young leaves based on the CTAB method (Saghai Maroof et al. 1984) from ten pooled plants of each BC₂F_{3:4} line and the parental lines. For molecular genotyping, microsatellite (simple sequence repeat, SSR) and amplified fragment length polymorphism (AFLP) markers were applied.

SSR marker analysis

SSR marker analysis was done as described by Steiner et al. (2004) by fluorescent detection of PCR fragments on an LI-COR 4200 dual-dye DNA analyser (LI-COR Biosciences, Lincoln, Nebraska USA). The parents were checked for polymorphism with 282 SSR primer pairs, of which 128 polymorphic pairs were chosen for genotyping 300 lines of the mapping population, composed of 89 GWM markers (Roeder et al. 1998), 27 BARC markers (Song et al. 2005), 9 WMC markers (Somers et al. 2004), 1 GDM marker (Pestsova et al. 2000) and 2 markers within the *Q* locus. For these, we compared the reported genome sequence of *T. aestivum*, GenBank no AY702956 (*Q* allele), and *T. macha*, GenBank no AY714342 (*q* allele), and designed two primer pairs flanking the variable microsatellites CCT repeat within the intron 9 (Simons et al. 2006). The first pair has forward primer 5′GCA-GTA-GCA-CCT-CAG-CAG-AGT and reverse primer 5′TTC-AGT-AAG-CTG-GTG-GAG-CA; the second pair has forward primer 5′AG-CTC-ATC-TTC-GTC-CCA-GTG and reverse primer 5′TTC-AGT-AAG-CTG-GT G-GAG-CA.

AFLP marker analysis

For the AFLP marker analysis (Vos et al. 1995), restriction digestion using *Mse*I and *Sse*8387I restriction enzymes, adapter ligation, PCR amplification and gel electrophoresis were carried out as described by Hartl et al. (1999) and Buerstmayr et al. (2002). Altogether, 64 AFLP primer combinations with two or three selective nucleotides on the 3′ end of either primer were performed for selective amplification. The 5′ end of the selective *Sse*8387I-primer was labelled with *IRD700* or *IRD800* when detected on an LI-COR 4200 dual-dye DNA analyser (LI-COR Biosciences, Lincoln, Nebraska USA), or was labelled with *Cy5*, *Cy3* or *FAM* when scanned on a Typhoon-TRIO fluorescence scanner (GE Healthcare). AFLP markers were named according to the standard list for AFLP primer nomenclature (<http://wheat.pw.usda.gov/ggpages/keygene/AFLPs.html>) followed by a number allocated to each polymorphic AFLP locus in this population within each primer combination, from smaller to larger fragments.

Statistical analysis

Field data

As a measure of FHB severity, the field scores were used to calculate the area under disease progress curve (AUDPC) as described by Buerstmayr et al. (2000). Analysis of variance (ANOVA) was calculated using the general linear

model (GLM) procedure to estimate the effects of replications within experiments, experiments, genotypes and genotype-by-experiment interactions, with all effects treated as fixed. For the estimation of variance components, all effects were considered random. Broad-sense heritability was estimated from variance components with the equation $H^2 = \sigma_G^2 / (\sigma_G^2 + \sigma_{G \times E}^2 / e + \sigma_e^2 / en)$, where σ_G^2 = genotypic variance, $\sigma_{G \times E}^2$ = genotype-by-experiment interaction variance, σ_e^2 = error variance, e = number of experiments, and n = number of replications (Nyquist 1991). Pearson correlation coefficients were calculated for each experiment and trait combination. Statistical analyses were calculated in SAS/STAT version 9.2 (SAS Institute Inc 2008).

Marker data

Maps were calculated using CarthaGène version 0.999-LKH for Linux (de Givry et al. 2005). We used a modified version of CarthaGène (provided by Dr. Clare Nelson, Kansas State University, USA) that allows map calculation in advanced backcross designs. For grouping a maximum distance of 30 centimorgan (cM) and a logarithm of odds (LOD) threshold of 3 were set. Linkage groups composed of many markers and those containing SSR markers with known map location on different chromosomes were grouped at higher LOD values. Cosegregating markers were merged into single markers. The most likely positions of the markers along the linkage groups were determined with the commands *nicemapl*, *nicemapd*, *mfmapl*, *mfmapped*, *flips*, *build* and *annealing*. The obtained maps were compared to the wheat consensus SSR map (Somers et al. 2004) available in the GrainGenes database (<http://wheat.pw.usda.gov/ggpages/maps.shtml>).

QTL analysis

QTL analysis was done with QGene (version 4.2.3) (Nelson 1997). The association between trait data and marker data was calculated by single-marker regression (SMR) and the locations of the detected QTL were estimated using simple interval mapping (SIM) (Haley and Knott 1992). The percentage of phenotypic variance (%PV) explained by a QTL and its additive effect (add) were calculated. The critical LOD values at a type I error rate of $\alpha < 0.05$ and $\alpha < 0.01$ were determined by 1,000 permutations for each trait. Possible segregation distortion was tested using a Chi-square test for each marker. To estimate the total percentage of phenotypic variance explained by QTL, we fitted a linear model of all significant QTL simultaneously using the GLM procedure of SAS/STAT (SAS Institute Inc 2008). Linkage groups and LOD profiles were drawn with MapChart 2.2 (Voorrips 2002).

Results

Trait variation and trait correlations

Means of the parents and the population, population range, least significant differences and broad-sense heritability for FHB severity and for several morphological traits are presented in Table 1. The population displayed significant variation for FHB severity, date of anthesis, plant height, spike length, number of spikelets per spike, density of the spikes, percent free threshing grains, glaucousness of spikes and leaf chlorosis. The population showed continuous variation for AUDPC means across all experiments. *T. macha* was the most resistant line on average over all experiments, Furore was susceptible, but several lines showed higher disease severity than Furore (Fig. 1).

Table 1 Means of parents and population, minimum and maximum scores of the population, least significant difference at $\alpha < 0.05$ (LSD) and broad-sense heritability (H^2) for FHB severity (AUDPC) and further plant traits

	Parents		Population			LSD	H^2
	Furore	<i>T. macha</i>	Mean	Min.	Max.		
FHB severity (AUDPC)							
Mean over all experiments	558	70	390	78	847	98	0.88
Mean <i>F. culm.</i>	946	114	639	163	1143	126	0.84
Mean <i>F. gram.</i>	267	32	207	32	639	71	0.83
FG05	210	12	118	14	519	48	
FG06	392	– ^f	332	38	919	82	
FC06	1224	– ^f	829	172	1395	131	
FG07	261	6	153	3	582	52	
FC07	860	96	535	64	1313	115	
FG08	206	64	216	33	771	88	
FC08	755	133	563	91	1272	132	
Date of anthesis ^a	32.4	34.2	32.2	29.0	35.9	0.8	0.93
Plant height (cm)	96.0	123.0	99.8	77.5	120.0	3.7	0.93
Spike length (cm)	8.3	8.9	8.0	5.8	12.5	0.6	
Spikelets per spike	15.2	18.6	15.7	12.6	20.4	1.1	
Spike density ^b	1.8	2.1	2.0	1.4	2.7	0.2	
Threshability (%) ^c	100	19.0	96.1	56.0	100	2.3	
Glaucousness of spikes ^d	5.0	9.0	6.0	3.1	9.0	0.6	0.97
Leaf chlorosis ^e	0	0.15	1.4	0.2	8.0	0.5	0.97

^a Number of days from 1 May to mid-anthesis

^b Number of spikelets per cm

^c Percent free threshing seeds

^d Visually scored 0 = non-glaucous to 9 = extremely glaucous

^e Visually scored 0 = non-chlorotic to 9 = extremely chlorotic

^f Missing values due to frost damage

Analysis of variance for AUDPC resulted in highly significant effects for all sources of variance (Table 2). The mean squares for genotypes were much larger than those for the genotype-by-experiment interaction, resulting in high broad-sense heritability of $H^2 = 0.88$ for AUDPC.

Pearson correlation coefficients for AUDPC between experiments were all positive and highly significant ($P < 0.001$) and ranged from $r = 0.54$ to $r = 0.76$. Inoculation with *F. culmorum* led to significantly higher average FHB severity than inoculation with *F. graminearum* (Table 1). The correlation between the average AUDPC obtained after inoculation with *F. graminearum* and *F. culmorum* was high ($r = 0.82$, $P < 0.001$) and the correlations for the grain spawn-inoculated experiment (FG08) with *F. graminearum* and *F. culmorum* spray inoculated experiments ranged from $r = 0.54$ to $r = 0.62$.

Date of anthesis, spike density and threshability were positively correlated with FHB severity (AUDPC) and there was a negative correlation between FHB severity and plant height, spike length and glaucousness of the spikes (Table 3). Increased plant height, early flowering, long and lax spikes, and more intense spike glaucousness were associated with increased resistance to FHB. Plant height was associated with spike length, spike density,

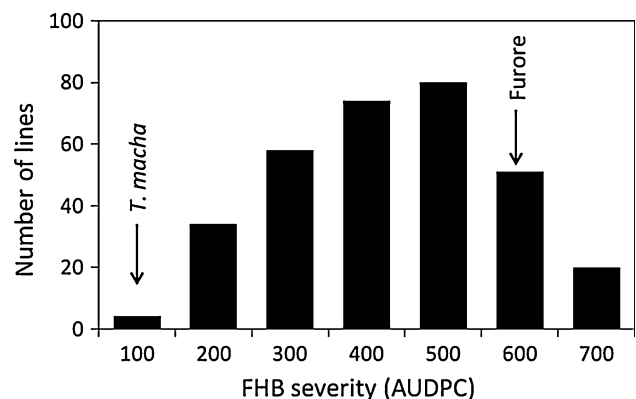


Fig. 1 Frequency distribution of 321 BC₂F₃ lines for FHB severity (AUDPC) means over all experiments. Arrows indicate the values of the parental lines

Table 2 Analysis of variance for FHB severity measured by AUDPC across seven experiments

Source	DF	Mean square	F value	P value
Replication within experiment	7	308,875.5	24.5	<0.0001
Experiment	6	41,005,134.6	3257.5	<0.0001
Genotype	322	273,034.1	21.7	<0.0001
Genotype x experiment	1916	34,100.3	2.7	<0.0001
Error	2178	12,587.8		

Table 3 Pearson correlation coefficients among line mean values for AUDPC, date of anthesis, plant height, spike length, spikelet per spike, spike density, threshability and glaucousness of spikes

Trait	Date of anthesis	Plant height	Spike length	Spikelets per spike	Spike density	Threshability	Glaucousness
AUDPC	0.30***	−0.53***	−0.27***	0.04	0.28***	0.44***	−0.19***
Date of anthesis		−0.07	0.06	0.11*	0.00	0.23***	0.03
Plant height			0.29***	−0.05	−0.32***	−0.28***	0.21***
Spike length				0.39***	−0.75***	−0.35***	0.23***
Spikelets per spike					0.29***	0.10	−0.17***
Spike density						0.38***	−0.36***
Threshability							−0.30***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

glaucousness and threshability. Taller plants tended towards elongated, lax and more glaucous spikes, and had reduced threshability. The number of spikelets per spike was positively correlated with both spike length and density of the spikes. More compact types were non-glaucous and had free threshing seeds. Severity of leaf chlorosis was weakly correlated with plant height and not correlated with any other trait (results not shown).

Marker segregation and polymorphism

Among 282 SSR markers tested on the parents, 202 (=72%) were polymorphic. Marker data generated on 300 lines with 128 SSR primer and 64 selective AFLP primer combinations and one morphological marker (hairy glumes) were used for map construction, with the SSR markers contributing 163 polymorphic loci and the AFLP analysis 533 clearly informative AFLP markers. After merging co-segregating markers into single markers, the remaining 560 unique markers were composed of 117 codominant and 443 dominant markers, among which *T. macha* carried the dominant allele for 230 and Furore for 213. The observed segregation in the population fitted the expected segregation ratio for a BC₂F₃ RIL population. Only 33 cM on parts of chromosomes 1D, 3A, 3D, 5A and one unassigned linkage group, and 62 cM on parts of chromosomes 3A, 5A, 5B and three unlinked groups exhibited segregation distortion towards *T. macha* and Furore, respectively.

Linkage map

Of the 560 markers, 554 could be placed in 33 different linkage groups. The groups were assigned to individual wheat chromosomes using previously mapped SSR markers and their map information from GrainGenes as anchor points. Ten groups were assigned to the A genome, nine to the B genome and six to the D genome, while eight linkage groups that contained only AFLP markers remained

unassigned. At least partial maps were obtained for all wheat chromosomes except 4D. The total length of the map was 2,226 cM, with 803, 830 and 455 cM assigned, respectively, to the A, B and D genomes and 138 cM unassigned to specific chromosomes. The average distance between markers was 4 cM. The arrangement of common SSR markers were in most cases consistent with those in published maps in GrainGenes.

QTL analysis

Quantitative trait loci mapping of FHB resistance

Simple interval mapping identified five significant QTL on four different chromosomes associated with FHB severity measured by overall mean AUDPC across all experiments (Table 4). Permutation analysis resulted in LOD thresholds for AUDPC means of 3.8 and 4.2 at $\alpha < 0.05$ and $\alpha < 0.01$, respectively. For all of these five QTL, the allele improving resistance was derived from *T. macha*. The linkage groups and the LOD profiles for AUDPC means are shown in Fig. 2.

The QTL with the largest effect, explaining 23% of the phenotypic variance (PV) for AUDPC means mapped to chromosome 5AL at the interval between *Xs20m18_11* and *Xbarc319* and peaked at the *Q* locus; 11.5% of PV was explained by a QTL at the position of *Xs11m24_10* on chromosome 2A. A QTL on the distal end of chromosome 2BL mapped close to *Xwmc317* and accounted for 9.7% of the PV. The QTL on 2A was consistently found in all experiments with LOD values >3, while QTL on 5AL and 2BL were significant in six experiments. A second QTL on 2B and one on 5B were found in three and four experiments accounting for 7.1 and 9.3% of PV, respectively. On chromosome 2D, a QTL with LOD >3 was found in the *F. graminearum*-inoculated experiments only. The LOD value for means over all experiments was below significance. For this putative 2D QTL, the favourable allele was derived from Furore (Table 4; Fig. 2). The five significant

Table 4 Associated chromosome, closest marker and flanking markers of QTL for AUDPC

Chromosome	Closest marker	Flanking markers	Overall mean		<i>Fusarium graminearum</i>																		
			Fusarium culmorum		Mean		FC08		FG05		FG06		FG07		FG08								
			Add ^a	LOD ^b	%PV	LOD	PV%	LOD	PV%	LOD	PV%	LOD	PV%	LOD	PV%	LOD	PV%						
2A	Xs11m24_I0	Xgwm296a-Xs12m14_5	71	7.9	11.5	6.8	9.9	6.3	9.5	5.2	7.7	5.0	7.4	7.3	10.6	3.3	5.0	6.1	8.9	5.3	7.9	5.0	7.3
2BS	Xs20m13_4	Xwmc25a-Xbarc200	58	4.8	7.1	4.9	7.3	2.6	4.0	4.9	7.2	4.6	6.9	3.9	5.7	4.8	7.1	1.5	2.3	3.9	5.9	2.7	4.1
2BL	Xs24m19_6	Xwmc317-Xs24m19_6	71	6.7	9.7	8.0	11.6	4.0	6.1	8.2	11.8	6.7	9.9	4.4	6.5	4.0	6.0	3.0	4.5	2.7	4.1	3.0	4.4
5AL	q	Xs20m18_11-Xbarc319	89.7	16.7	22.7	17.4	23.4	23.0	30.4	7.7	11.2	8.2	11.8	11.1	15.7	2.6	4.0	17.2	23.2	5.5	8.0	6.0	8.8
5B	Xgwm497e	Xs22m75_1-Xs13m87_1	63	6.4	9.3	7.2	10.4	6.6	9.9	5.1	7.6	5.4	8.0	4.3	6.4	3.2	4.8	3.5	5.3	2.8	4.2	2.6	3.9
2D	Xgwm261	Xgwm296b-Xs11m75_2	-45	2.1	3.2	1.1	1.7	0.8	1.3	1.9	2.9	1.2	1.8	4.7	7.0	3.0	4.5	4.5	6.6	2.9	4.3	2.8	4.3

LOD values, % of phenotypic variance (%PV) and additive effects (add) are calculated for overall means using SIM (simple interval mapping). LOD and %PV are estimated by SIM for means over isolates as well as individual experiments. LOD values >3 are printed in bold

^a Positive values for the additive effects indicate that the *T. macha* allele reduces the average trait values relative to the Furoro allele

^b Permutation test for AUDPC over all means, 1,000 iterations: α 0.05 = 3.8, α 0.01 = 4.2

QTL together explained 48% of the phenotypic variance for mean AUDPC across all experiments.

Quantitative trait loci of other traits

The QTL identified for the date of anthesis, plant height, spike length, number of spikelets per spike, density of the spike, threshability, glaucousness of the spikes and leaf chlorosis are summarized in Table 5. Date of anthesis was modulated by QTL on 1B, 4A, 5AS, 5AL, 7B and 7D. The alleles from *T. macha* on chromosome 1B, 4A, 5AS, 5AL and 7B accelerated flowering, and on 7D retarded flowering. Plant height was affected by QTL on chromosomes 2BL, 2D, 4A, 4B, 5AS, 5AL and 6A where the *T. macha* allele increased plant height, except for 2D. A QTL for spike length was found on 5AL, with the *T. macha* allele favouring longer spikes. QTL affecting number of spikelets per spike were identified on 2A, 3B and 7A. QTL on 2D, 3B, 3D and 5AL influenced spike density. The *T. macha* allele at the 2D, 3B and 3D QTL increased density and at the 5AL QTL, laxness. Threshability was strongly associated with the *Q* locus on 5AL. Glaucousness of the spike was influenced by QTL on chromosomes 1A, 2B and 5AL. Leaf chlorosis was influenced by one QTL detected on an unassigned group, with the *T. macha* allele conferring increased severity.

FHB QTL and their association with QTL for other traits

The large-effect QTL for AUDPC on 5AL was associated with several further traits: plant height, spike length, spike density, threshability and glaucousness of the spikes. Plants carrying the *T. macha* allele at this location were more resistant to FHB, taller and showed elongated lax, and more glaucous spikes and strongly reduced threshability. Co-localization of QTL for AUDPC and plant height was found on chromosome 2BL near *Xwmc317*, with the *T. macha* allele increasing FHB resistance and plant height. On chromosome 2D, QTL associated with plant height and spike density mapped to the same region, with the *T. macha* allele reducing plant height and favoring a dense spike. In terms of FHB, only *F. graminearum*-inoculated experiments with general low infection levels revealed a QTL with LOD as high as 3 at this locus.

Discussion

Precise phenotyping combined with a dense and reliable linkage map are essential for effective QTL detection. To ensure a complete and unbiased coverage of the donor genome, each of the 321 BC₂F_{3,4} lines was derived from a different BC₁ plant. In other studies on wheat with the

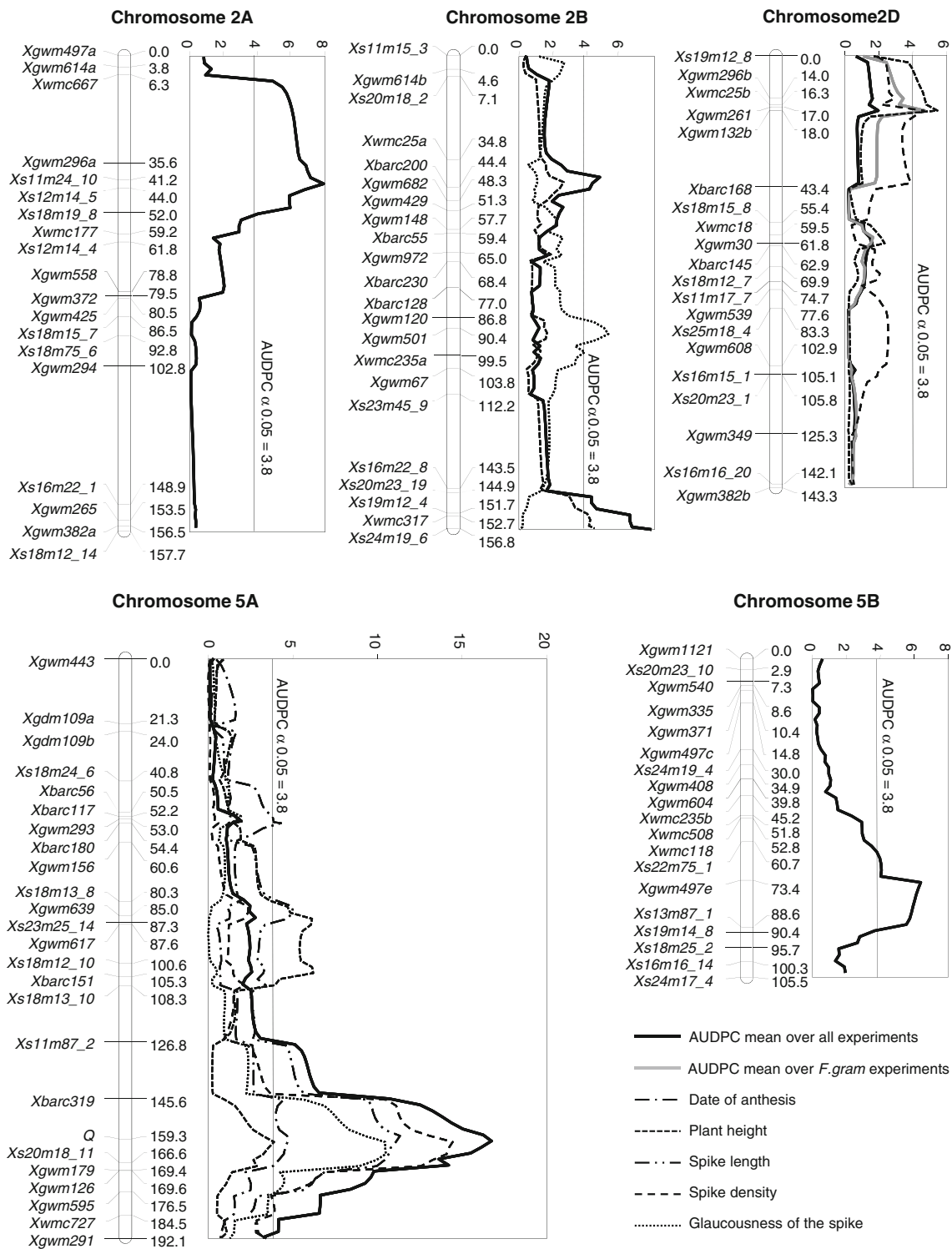


Fig. 2 Linkage maps and LOD profiles by SIM (simple interval mapping) for AUDPC means over all experiments on chromosome 2A, 2B, 2D, 5A, 5B and coinciding QTL for other traits

AB-QTL strategy, the populations were based on only few BC₁ parents. Huang et al. (2004), Narasimhamoorthy et al. (2006), Liu et al. (2006), Leonova et al. (2007), Kunert et al. (2007), and Naz et al. (2008) produced populations

descending from 42, 29, 15, 20, 42 and 22 BC₁ plants, which led to small recombination abilities resulting in low position resolution and spurious linkages (Narasimhamoorthy et al. 2006). By descending many BC₂ lines each

Table 5 Summary of QTL for morphological and developmental plant traits detected with SIM (simple interval mapping) and SMR (single-marker regression). Significance thresholds are shown as footnotes

Trait	Chromosome	Closest marker	Flanking markers	SIM			SMR		
				Add ⁱ	LOD	%PV	Add ⁱ	LOD	%PV
Date of anthesis ^a	1B	<i>Xs23m13_8a</i>	<i>Xs23m13_8a-Xs20m13_1</i>	0.4	5.6	8	0.4	5.6	8
	4A	<i>Xs14m22_6</i>	<i>Xs14m22_6-Xs14m87_5</i>	0.5	12.0	17	0.6	11.1	16
	5AS	<i>Xbarc180</i>	<i>Xbarc117-Xgwm156</i>	0.2	3.9	6	0.3	4.3	6
	5AL	<i>q</i>	<i>Xbarc319-Xs20m18_11</i>	0.4	4.7	7	0.5	5.8	9
	7B	<i>Xs19m19_11</i>	<i>Xgwm611-Xs11m14_7</i>	0.4	4.3	6	0.4	4.5	7
	7D	<i>Xgwm44</i>	<i>Xs13m15_1-Xgwm111a</i>	-0.4	3.6	5	-0.5	5.4	8
Plant height ^b	2BL	<i>Xs24m19_6</i>	<i>Xs19m12_4-Xs24m19_6</i>	-2.8	4.2	6	-2.9	4.5	7
	2D	<i>Xgwm132b</i>	<i>Xgwm296b-Xs11m75_2</i>	3.6	5.3	8	3.6	5.3	8
	4A	<i>Xs14m13_9</i>	<i>Xs18m24_2-Xgwm610</i>	-2.4	4.1	6	-2.4	4.4	7
	4B	<i>Xs18m12_6</i>	<i>Xs23m45_12-Xs19m12_17</i>	-2.7	4.0	6	-2.7	4.3	6
	5AS	<i>Xgwm617</i>	<i>Xgwm639-Xbarc151</i>	-2.9	6.1	9	-3.0	6.3	9
	5AL	<i>q</i>	<i>Xbarc319-Xs20m18_11</i>	-2.0	3.9	6	-2.4	5.0	7
Spike length ^c	6A	<i>Xs19m19_3</i>	<i>Xs18m24_8-Xbarc3</i>	-2.0	3.7	6	-2.4	3.9	6
	5AL	<i>q</i>	<i>Xbarc319-Xs20m18_11</i>	-0.6	11.3	16	-0.6	12.4	17
Spikelets per spike ^d	2A	<i>Xgwm425</i>	<i>Xgwm588-Xs18m15_7</i>	-0.5	5.1	8	-0.5	5.6	8
	3B	<i>Xs20m23_8</i>	<i>Xs20m23_8-Xs22m12_1</i>	-0.4	4.7	7	-0.6	5.6	8
	7A	<i>Xs13m17_6</i>	<i>Xs11m75_6-Xs13m17_6</i>	0.5	5.4	8	0.5	5.6	8
Spike density ^e	2D	<i>Xgwm132b</i>	<i>Xgwm296b-Xbarc168</i>	-0.1	4.5	7	-0.1	4.5	7
	3B	<i>Xs11m19_9</i>	<i>Xs14m12_4-Xbarc858</i>	-0.1	7.8	11	-0.1	8.1	12
	3D	<i>Xgwm341</i>	<i>Xs11m87_5-Xgwm341</i>	-0.1	5.6	8	-0.1	5.7	8
	5AL	<i>q</i>	<i>Xbarc319-Xs20m18_11</i>	0.1	14.4	20	0.2	15.8	22
Threshability ^f	5AL	<i>q</i>	<i>Xbarc319-Xs20m18_11</i>	10.0	64.8	63	10.8	81.2	71
Glauconsness ^g	1A	<i>hairy glume</i>	<i>hairy glume-Xs20m15_8</i>	-0.7	12.1	17	-0.7	12.1	17
	2B	<i>Xgwm501</i>	<i>Xs13m15_2-Xs19m19_14</i>	-0.5	5.3	8	-0.6	5.7	8
	5AL	<i>q</i>	<i>Xbarc319-Xs20m18_11</i>	-0.7	10.5	15	-0.8	12.9	18
Leaf chlorosis ^h	ni ^j	<i>Xs20m18_15</i>	<i>Xbarc57b-Xs11m87_10</i>	-1.7	27.7	36	-1.0	25.6	33

^a α 0.05 = 4, α 0.01 = 5.2

^b α 0.05 = 3.8, α 0.01 = 4.6

^c α 0.05 = 5.6, α 0.01 = 7.5

^d α 0.05 = 4.4, α 0.01 = 5.4

^e α 0.05 = 4.1, α 0.01 = 5.1

^f α 0.05 = 6.6, α 0.01 = 9

^g α 0.05 = 3.9, α 0.01 = 4.9

^h α 0.05 = 5.9, α 0.01 = 7.3

ⁱ Positive values for the additive effects indicate that the *T. macha* allele reduces the average trait values relative to the Furore allele

^j Linkage group not assigned to a chromosome

from a different BC₁ plant, a possible loss of parts of the donor genome was avoided. By using a large and unbiased population of 300 BC₂-derived lines, it was feasible to perform genetic mapping in the same population that was used for phenotyping and QTL mapping and the obtained maps appeared accurate in relation to other published maps.

We used spray inoculation and grain spawn inoculation methods for our experiments. As both methods provide information on overall FHB resistance, including type I

(resistance to initial infection) and type II (resistance to the fungal spread) (Schroeder and Christensen 1963), the different types of resistance could not be separated. The significant and positive correlation coefficients among experiments and the high broad-sense heritability coefficient ($H^2 = 0.88$) for FHB severity show that a large proportion of the observed variation among the tested lines was due to genetic effects and support the meaningful localization and estimation of QTL effects.

QTL detection

Essentially the same QTL were found for experiments inoculated with *F. graminearum* as for those with *F. culmorum*, but for *F. culmorum*-inoculated experiments QTL were estimated more precisely and at higher probability values. This indicates that QTL detection is more effective under high infection pressure.

The detection of five putative QTL for FHB resistance underlines the complex and polygenic inheritance of this trait already shown in numerous other QTL projects for FHB in wheat. While Steed et al. (2005) reported a significant type 1 FHB-resistance QTL derived from *T. macha*, no 4A QTL was found in our study. Possibly, this 4A QTL was specific to their population based on a Hobbit ‘sib’ (*T. macha* 4A) single chromosome recombinant doubled haploid (DH) population.

The largest-effect QTL in our study was found on chromosome 5AL at the *Q* locus, where no QTL for FHB was reported previously. We consider it a major QTL for FHB resistance. It coincided with QTL associated with spike-related traits as for threshability, spike length, spike density, glaucousness of the spikes, date of anthesis and with plant height. Grausgruber et al. (1998) reported similar findings for morphological characters of the ear and found positive effects on resistance to FHB on 5A in a Hobbit ‘sib’ (*T. macha*) intervarietal substitution line. *T. macha* carries the *q* allele (Faris et al. 2005; Kuckuck 1964; Mac Key 1966; Simons et al. 2006) and the detected QTL very likely corresponds to *q*. The *Q* locus with the alleles *Q* (free threshing) and *q* (speltoid, non-free threshing) is a major regulatory gene. It pleiotropically influences many other domestication-related traits such as glume shape and tenacity, rachis fragility, spike length, plant height and spike emergence time (Faris and Gill 2002; Simons et al. 2006), which is in accordance with our findings. Whether the association with FHB resistance is due to a pleiotropic effect of the *q* allele or close linkage between *q* and a FHB-resistance QTL cannot be determined with current results. A much larger high-resolution mapping population would be needed to search for potential recombinants. Goral et al. (2008) tested several spelt wheat cultivars and found highly resistant as well as highly susceptible spelt varieties, and among 151 *T. dicoccoides* accessions tested by Buerstmayr et al. (2003) most were susceptible to FHB. Thus, the presence of the allele *q* does not always confer high FHB resistance, supporting the hypothesis that FHB resistance is rather linked to *q* than pleiotropic. In our population, it is possible that part of the increased FHB resistance associated with the *q* allele may be due to morphological and developmental traits such as spike structure and flowering behaviour.

The QTL on 2BL close to *Xwmc317* was repeatedly detected in six experiments. This QTL coincided with a QTL for plant height, with the *Furore* allele reducing height. The *Rht4* gene is located on chromosome 2BL close to *Xwmc317* (Ellis et al. 2005). Whether or not the QTL for reduced height from *Furore* is caused by *Rht4* is currently not known. Schmolke et al. (2005) reported a resistance QTL for FHB in the Dream/Lynx population after spray inoculation in a similar position, but found no association with plant height. In our study, a second QTL on 2BS close to *Xbarc200* was revealed in four experiments. Gilsinger et al. (2005) detected a resistance QTL linked with *Xbarc200* on 2BS in the cultivar Goldfield and found a relation to narrow flower opening associated with resistance at this QTL. The flower opening trait was not investigated in our population. In the review of FHB-related QTL by Buerstmayr et al. (2009), QTL for FHB resistance are reported at several positions along chromosome 2B. Since *T. macha* is related neither to Dream nor to Goldfield, we suggest that both *T. macha*-derived QTL on 2B are novel.

In the 2AS region containing a FHB-resistance QTL significant in all experiments, no overlapping QTL for other traits were found. Three QTL related to FHB resistance were published on 2AS. The Asian wheat variety Ning7840 expressed a minor QTL for FHB spread associated with *Xgwm614* (Zhou et al. 2002). Variety NK93604 had a QTL for low DON (deoxynivalenol) accumulation at *Xbarc124*, although no association to FHB symptom severity was found (Semagn et al. 2007), and a resistance QTL derived from Wangshuibai mapped close to *Xgwm425* near the centromere. In the present population, *Xgwm614a* mapped 38 cM distal and *Xgwm425* 40 cM proximal to our QTL peak at the AFLP marker *Xs11m24_10*. We therefore assume that the *T. macha* QTL differs from these previously reported QTL at chromosome 2A. Based on our map and the maps of Xue et al. (2008) and Song et al. (2005), it appears likely that QTL for FHB severity on 2AS, 2BS and 2D reside at homoeologous genomic regions.

Bourdoncle and Ohm (2003) reported a QTL for FHB spread derived from Patterson with minor effects towards resistance in approximately the same location as our 5BL QTL observed in five experiments.

Morphological traits and their association with FHB resistance

Q locus

A *T. macha* line with good resistance to FHB served as donor parent. This line was 27 cm taller and 2 days later in anthesis compared to the recurrent parent *Furore*, a common hexaploid wheat. Ear morphology of *T. macha* differs

markedly from the bread wheat parent. *T. macha* is a hulled wheat, has a dense square-headed, but non-compact spike phenotype, has a fragile rachis, is only partly free threshing and has hairy and waxy glumes. Compared to *T. spelta* it does not show the speltoid ear shape, which is described as a spear-shaped spike with elongated rachis. The European spelt and *T. macha* carry the *q* allele, while the Iranian spelt carries *Q* (Simons et al. 2006). The *q* allele plays a key role in the present study. In accordance with the known modifications associated with the *q* allele, we identified QTL for plant height, date of anthesis, spike density, spike length and threshability at the location of *q*. In addition, we found QTL for glaucousness of the glumes and for FHB severity. Lines carrying the *q* allele showed typically speltoid ear-shape, which was not visible in *T. macha*, but appeared in the genetic background of Furore.

Compactness

T. macha has a compacting gene that appears to be allelic to *C* (Swaminathan and Rao 1961). *C* determines whether a spike is lax or compacted and it affects spike morphology, grain size, shape, spikelet number and perhaps other aspects of plant development (Gul and Allan 1972). In our study, QTL for plant height and dense spike co-located on chromosome 2D near *Xgwm261*. The *T. macha* allele changed lines towards smaller plants with dense square-headed spikes. Additionally, a minor but not significant QTL for FHB resistance coincided. Lines carrying *T. macha* allele were more highly infected. Johnson et al. (2008) mapped *C* to *Xgwm358* close to the centromere of 2D, which is in disagreement with our findings. Sourdille et al. (2000) and Ma et al. (2007) found a QTL for compactness on 2D at *Xgwm261*, consistent with our results. *Rht8* (Worland et al. 1998) is closely linked to *Xgwm261*, consistent with the QTL for plant height in our study. Nalam et al. (2007) and Ma et al. (2007) reported a QTL for glume tenacity and threshability at *Xgwm261*. The basically non-free threshing character of *T. macha* in combination with its long and dense but non-compact spike arises therefore from the specific allele combination of *q* and *C*.

A QTL for density of spikes was found at *Xgwm341* on 3D. *Xgwm341* maps about 0.2 cM from *Xgwm456* (Somers et al. 2004). The *SI* locus was mapped close to the centromeric marker *Xgwm456* of the long arm of 3D by Salina et al. (2000). Rao (1977) and Koba and Tsunewaki (1978) also reported that the *sphaerococcum* gene *SI* is near the centromere of chromosome 3D. Besides other characteristics, *SI* also influences spike density. Swaminathan and Rao (1961) confirmed that the *qq CC SIS1* alleles were present in *T. macha*. Even though the genotype of both *T. macha* and Furore are assumed to be *SIS1*, the *T. macha* allele conferred a denser spike than Furore. This indicates

that *T. macha* and Furore carry different alleles at this locus. Interestingly, no QTL for number of spikelets per spike coincided with the previously discussed loci on 5AL, 2D and 3D.

Glaucousness (waxiness/glossiness) of the spike

QTL for spike glaucousness coincided with QTL for FHB resistance on chromosome 5AL and the morphological marker *Hg* (hairy glumes) on 1AS. The QTL for glaucousness on 2B had no association with other traits. Glaucousness could possibly be a passive resistance factor, as a more waxy cuticle can potentially impede the entry of fungi. The positive phenotypic correlation between glaucousness and resistance may be accounted for by coinciding QTL for glaucousness and QTL for FHB resistance on 5AL rather than by glaucousness per se.

Plant height

Although seven QTL with significant influence on plant height were revealed, only QTL on 5AL and 2BL coincided with QTL for FHB resistance. Repeated observations of associations between FHB severity and plant height (Buerstmayr et al. 2000; Gervais et al. 2003; Hilton et al. 1999; Mesterhazy 1995; Steiner et al. 2004) as well as compactness of the spikes (Steiner et al. 2004; Zhu et al. 1999) may be partly explained by passive resistance. Tall plants are more exposed to wind and sun and therefore dry off earlier, whereby short plants, especially in combination with dense spikes, are exposed to a more humid microclimate, which favours FHB infections.

Date of flowering

Although *T. macha* was the later-flowering parent, the *T. macha* allele at QTL for date of anthesis favoured earlier flowering on chromosomes 1B, 4A, 5AS, 5AL and 7B and delayed flowering only on 7D. The chromosome 4A QTL showed the highest influence on the date of anthesis. Though FHB resistance was positively correlated with date of anthesis, no coinciding QTL except the 5AL one was revealed. Several different publications mention a positive effect of early flowering on FHB resistance (Gervais et al. 2003; Holzapfel et al. 2008; Paillard et al. 2004; Schmolke et al. 2005; Steiner et al. 2004) in agreement with our findings.

Chlorosis

A single major QTL for leaf chlorosis was found on an unassigned linkage group. This is in agreement with Tsunewaki (1971) and Naskidashvili et al. (2010) who

reported the occurrence of several chlorosis and necrosis alleles in *T. macha*. Leaf chlorosis was not associated with other traits evaluated in this study.

Summary and conclusions

In this AB-QTL analysis, several novel QTL deriving from the landrace *T. macha* were mapped. These novel *T. macha*-derived QTL appear valuable for broadening the genetic basis and diversity of FHB resistance in wheat. Some of the FHB-resistance QTL from Georgian spelt wheat coincide with those for spelt wheat traits. The major FHB-resistance QTL at chromosome 5A was closely associated with the wild-type allele *q*, and it is unclear whether *q* has a pleiotropic effect on FHB resistance or is closely linked to a nearby resistance QTL. Only the 2BL FHB-resistance QTL co-located with a plant height QTL; the allele *q* had only a moderate effect on height and none of the other plant height QTL corresponded to FHB-resistance QTL. Selected lines from this study appear useful for practical resistance breeding, because they carry QTL from the landrace *T. macha* in an already agronomically adapted background. In addition, selected lines carrying *q* (spelt wheat ear type) could be useful as crossing partners for spelt wheat breeding.

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