

Review

QTL mapping and marker-assisted selection for *Fusarium* head blight resistance in wheat: a review

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With 1 figure and 3 tables

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Abstract

During the past decade, numerous studies have been published on molecular mapping of *Fusarium* head blight (FHB) resistance in wheat. We summarize the relevant findings from 52 quantitative trait loci (QTL) mapping studies, nine research articles on marker-assisted selection and seven on marker-assisted germplasm evaluation. QTL for FHB resistance were found on all wheat chromosomes except chromosome 7D. Some QTL were found in several independent mapping studies indicating that such QTL are stable and therefore useful in breeding programmes. We summarize and update current knowledge on the genetics of FHB resistance in wheat resulting from QTL mapping investigations and review and suggest FHB breeding strategies based on the available information and DNA markers.

Key words: *Triticum aestivum* — *Triticum durum* — *Fusarium* head blight — quantitative trait loci — marker-assisted selection — resistance breeding

Among the many diseases of wheat, *Fusarium* head blight (FHB), also known as *Fusarium* ear blight (FEB), has received much attention, especially during the past decades. Severe FHB epidemics in some important wheat growing areas and improved technology for detecting mycotoxins that pose food safety threats, have contributed to this research emphasis.

A range of different *Fusarium* species has been associated with the disease but *Fusarium graminearum* (teleomorph *Gibberella zeae*), *Fusarium culmorum* and *Fusarium avenaceum* (teleomorph *Gibberella avenaceae*) appear to predominate depending on climatic conditions (Parry et al. 1995). Apart from losses in grain yield and reductions in baking and seed quality, the major peril due to FHB is the contamination of the crop with toxic fungal secondary metabolites known as mycotoxins. To protect consumers from mycotoxicosis many countries, including the European Union Member States have established maximum allowed levels for the most prevalent *Fusarium* mycotoxins in cereals and cereal products (Van Egmond 2004, Anonymous 2005). For example, the EU regulation allows a maximum deoxynivalenol (DON) content in unprocessed bread wheat of 1.25 ppm, in bread and bakeries of 0.5 ppm and in baby food of 0.2 ppm (Anonymous 2005). In 1993 the Food and Drug Administration of the USA published advisory levels of 1 ppm DON on finished wheat products

(<http://www.cfsan.fda.gov/~dms/graingui.html>). Health Canada has established guidelines for DON in soft wheat of 2 and 1 ppm for non-staple foods and baby foods, respectively (http://www.hc-sc.gc.ca/fn-an/securit/chem-chim/contaminants-guidelines-directives_e.html). Crop management and agrochemical measures are only partly effective to control the disease. Therefore, the cultivation of *Fusarium* resistant varieties plays a key role in integrated *Fusarium* control and the prevention of mycotoxin contaminations. Breeding for improved FHB resistance has thus become an important breeding goal for numerous cereal breeders. Fortunately, large genetic variation for FHB resistance is available in the wheat gene pool, but often the best regionally adapted and highly productive cultivars are susceptible to FHB. The difficult task for the wheat breeder is to create regionally adapted cultivars that combine high and stable yield and quality performance with resistance to the relevant diseases and pests including resistance to FHB. Considerable improvements in genetic resistance have been achieved by conventional selection, resulting from repeated testing of breeding lines under induced and natural epidemic conditions. DNA-based markers are a relatively recent tool that can be applied to augment conventional breeding, especially for traits such as FHB that are difficult or cost intensive to select using conventional methods. Numerous studies have shown that inheritance of resistance of wheat to FHB is of a quantitative nature. Therefore, the method of choice to investigate FHB resistance is to apply a QTL (quantitative trait locus/loci) mapping approach.

During the past years, several review articles have been published on *Fusarium* diseases of cereals covering different aspects. Parry et al. (1995) reviewed the significance of the disease with an emphasis on phytopathological aspects. Reviews of conventional breeding for FHB resistance were published by Mesterhazy (1995), Miedaner (1997) and Mesterhazy et al. (1999). Placinta et al. (1999) documented the worldwide occurrence and significance of *Fusarium* mycotoxins. The first review on molecular markers for FHB resistance in wheat by Kolb et al. (2001) summarized the early findings in this field and later Anderson (2007) listed some of the more stable FHB QTL. A comprehensive monograph edited by Leonard and Bushnell (2003) reports in 18 book chapters a range of aspects on

Fusarium diseases of small grain cereals, including the pathogen, the associated mycotoxins, resistance breeding and other control options as well as the social and economic impact of the disease. Bai and Shaner (2004) reviewed the management and resistance to FHB in wheat and barley including the knowledge on FHB resistance QTL mainly from a North American perspective. The objectives of this article are (i) to summarize and update current knowledge on the genetics of FHB resistance in wheat resulting from QTL mapping investigations and (ii) review and suggest FHB breeding strategies based on the available information and DNA markers.

Before reviewing the literature on genetic mapping of FHB resistance, several terms have to be clarified and discussed. The intention of this review is to give a comprehensive review of FHB QTL publications that appeared in peer-reviewed journals only, focussing on the most significant findings in these papers. Stability of QTL is an important issue. If a QTL was found in a similar genomic region in different studies using related resistant sources but different susceptible parents, we concluded that this QTL was stable in terms of expression in different genetic backgrounds. If a QTL was found significant using varying phenotyping methods, especially inoculation techniques and/or in independent biological experiments, we considered it stable across environments and epidemic conditions. We are aware that the opinions and conclusions of the authors of this review may not necessarily agree in all aspects with the original publications.

We first give a brief introduction on QTL mapping in general with some specific considerations relevant for mapping *Fusarium* resistance. Then the actual review of FHB resistance QTL follows.

Plant Material

In classical mapping approaches, segregating populations, derived from a cross of contrasting genotypes are used. In this case, the relationship of the lines in a mapping population is clearly defined and the segregation of loci can be predicted and tested based on marker segregation. Frequently used population types are recombinant inbred lines (RIL) in more or less advanced selfing generations, fully homozygous doubled haploid (DH) populations or populations derived from backcrosses. Backcross-derived populations are of advantage in cases where the resistance donor is an 'exotic' or 'wild' line and the recipient line a regionally adapted genotype (Tanksley and Nelson 1996). A further option is the establishment and use of introgression lines or intervarietal substitution lines that can be developed by a backcrossing strategy. The aim is to establish a series of near isogenic lines (NIL) with small chromosomal segments of a donor line in a specific genetic background, usually a highly productive cultivar (Eshed and Zamir 1995). Alternatively, sets of genotypes, which may be cultivars, breeding lines or introduced germplasm, with or without pedigree and kinship information can be used. In this case, methods of association mapping have to be applied, in which one attempts to associate the occurrence of certain marker haplotypes with trait expression. The basic principle is to detect correlations between genotypes and phenotypes in a sample of individuals on the basis of linkage disequilibrium (Gupta et al. 2005, Breseghello and Sorrells 2006, Rostoks et al. 2006). The concept of association analysis has been known for many years. The increased availability of molecular markers, and the refinement of statistical tools, has rekindled interest in this

approach. Although several reports on DNA marker evaluation of FHB resistant and susceptible germplasm have been published (Table 3), no study applying in depth association mapping to detect FHB resistance QTL has been published yet.

Phenotyping

The goal is to determine the level of genetically determined resistance on every line of the analysed population as precisely as possible. One of the main problems in testing for *Fusarium* resistance is reproducibility (Groth et al. 1999, Dill-Macky 2003). The severity of FHB is a quantitative trait that is modulated by (i) genetic factors of the host (resistance factors in the plant) and of the pathogen (aggressiveness of the fungus) and (ii) environmental influence on disease establishment and development leading to significant genotype-by-environment (GxE) interactions (Campbell and Lipps 1998, Fuentes et al. 2005), which can significantly bias QTL estimates (Ma et al. 2006b). Therefore, in most FHB resistance studies, measures are taken to provoke *Fusarium* infections and apply uniform inoculum pressure over time (flowering period) and space (e.g. experimental field or greenhouse bench). FHB resistance is a complex trait and not one single, simple way of measuring FHB resistance is practiced. For a more detailed review on inoculation and evaluation methods see Dill-Macky (2003). The concept of resistance to initial infection (type 1) and resistance to fungal spread from an infected floret along the rachis (type 2) first described by Schroeder and Christensen (1963) is now widely accepted. Type 1 and type 2 resistance may vary independently between genotypes. This differentiation is based on symptom development only and does not imply a certain physiological resistance reaction. In addition, further types or components of resistance to FHB have been described (Mesterhazy 1995, Mesterhazy et al. 1999). The ultimate goal in FHB resistance breeding is the development of productive cultivars with low disease symptoms and low mycotoxin contamination despite high infection pressure. Therefore, in some studies, mycotoxin contamination was measured and the relationship of toxin content with FHB symptoms was investigated. In a few mapping experiments toxin content, in most cases DON content, was used as a measure for FHB severity. Because of the considerable cost of toxin analysis, most mapping projects were content with other observations of FHB symptoms. Type 2 resistance is typically measured following, single-floret or single-spikelet inoculation, conidial spray or grain-spawn inoculation. Usually, the amount and/or speed of spread of the typical *Fusarium* symptoms from the inoculation site along the ear is used as a measure for type 2 disease severity. Type 1 resistance is considered more difficult to assess and therefore fewer reports have been published on type 1 resistance QTL. As a measure for type 1 resistance, disease incidence (percentage of ears with disease symptoms) in spray or naturally inoculated plots or pots are commonly used. Several authors applied spray inoculations and scored disease severity (percentage of diseased spikelets per unit area) as a measure for FHB resistance. It is believed that using such an approach mimics the situation as it may occur under natural infections. The disease reaction should thus reflect all possible mechanisms, which may contribute to the resistant phenotype under epidemic conditions. Alternatively to spray inoculations, the grain-spawn method (scattering *Fusarium*-infected corn or barley grains), sowing in fields with maize stubble on the soil surface or

sowing trials in natural hot spots for *Fusarium* infection, has been applied to provoke infections. Measures for FHB disease severity may be visual scoring of disease symptoms on the heads, visual scoring of percentage of diseased grains in harvested samples, measurement of yield or yield components relative to non-inoculated controls or mycotoxin (mostly DON) content. Morphological and developmental characteristics such as plant height (e.g. Mesterhazy 1995, Paillard et al. 2004, Schmolke et al. 2005, Draeger et al. 2007, Klahr et al. 2007), ear compactness (Schmolke et al. 2005), flower opening (Gilsinger et al. 2005), or heading date (Miedaner et al. 2006, Klahr et al. 2007, Wilde et al. 2007) may also influence the response to pathogen inoculation under field conditions. The difficulty in QTL mapping is to separate pleiotropic effects on FHB response of genes involved in morphological or developmental traits from effects of true resistance genes which may be tightly linked to such morphological or developmental genes. Including resistant and susceptible checks with a broad range of flowering dates helps to separate and interpret effects due to flowering date, but positive correlations between plant height and disease resistance are more difficult to separate, especially under field conditions. The choice of the pathogen species or pathogen strains for inoculation has also been subject to discussions. Although a range of species may be implicated in the disease, *F. graminearum*, *F. culmorum* and *F. avenaceum* have been described as the dominating species involved in FHB of cereals (Parry et al. 1995, Dill-Macky 2003). Different *Fusarium* strains (isolates) may differ widely in aggressiveness, but until now no biological races with a specific host-pathogen interaction have been detected. Therefore, resistance to FHB is of horizontal or non-specific nature (Snijders and Van Eeuwijk 1991, Van Eeuwijk et al. 1995, Mesterhazy et al. 1999) at least for the most prevalent species like *F. culmorum* and *F. graminearum*. However, given the large genetic variability known to exist in *Fusarium* spp. (Bowden and Leslie 1999), the reliance on at least a few different resistance genes would be a wise approach.

Genotyping

The goal is to determine the genotype of each line in the mapping population relative to the parental genotypes. The type and number of markers applied depends on the equipment and resources available. During the 1990s, RFLP (restriction fragment length polymorphism) markers dominated the scene, but PCR (polymerase chain reaction)-based markers have become increasingly popular in recent years. Locus specific simple sequence repeat (SSR) markers, sometimes in combination with higher throughput PCR markers, like AFLP (amplified fragment length polymorphism) or TRAP (target region amplified polymorphism) markers were frequently applied. In the near future, markers based on SNPs (single nucleotide polymorphisms) may become more popular. Array-based medium to high throughput markers, like DArT (diversity array technology) markers (Akbari et al. 2006) or other high throughput SNP detection systems (Shen et al. 2005, Rostoks et al. 2006) will complement electrophoresis-based PCR markers in the coming years.

Dimension of Mapping Projects

The question of how many lines are needed for an informative segregating population, how many markers and replications of

the resistance evaluation needs careful consideration. It has been shown that using more lines is always better than using few lines (Beavis 1998). If QTL of moderate to small individual effects contribute to trait expression, a large number of lines are needed for meaningful QTL estimation (Vales et al. 2005). Usually, the effects of the detected QTL are over-estimated because of a limited number of recombinant lines in the population. Because of practical limitations more than 300 lines are rarely used in QTL mapping in plants, although over 300 lines would be desirable at least for quantitative traits controlled by multiple loci (Melchinger et al. 2004, Schön et al. 2004). Most studies to date have used 100–200 lines. We consider <100 recombinant lines too low to detect anything other than large effect QTL for FHB resistance. The number and choice of markers should allow full coverage (e.g. no gaps >20 cM) of the genome and should include suspected QTL regions based on previous work. Although more than a thousand SSR markers are now available in the public domain and can be chosen to map almost any part of the wheat genome, the development of a dense map in hexaploid wheat is still resource demanding and not trivial.

The number and design of the phenotyping experiments is crucial for successful QTL mapping. At least two independent biological experiments (locations or years) are necessary to estimate the repeatability of the resistance evaluation (e.g. calculation of broad sense heritability and/or correlation between experiments) and determine the stability of QTL estimates across environments (QTL-by-environment interactions).

QTL for FHB Resistance

The results of 52 peer-reviewed studies reporting QTL for FHB resistance in wheat are summarized in three tables and one figure. Of the 52 studies, 46 were carried out with hexaploid wheat, four with tetraploids and two with related species. A detailed list including information on the mapping population, the phenotyping methods and the association of the detected FHB resistance QTL with other traits is given in Table 1. The approximate position of most of the QTL listed in Table 1 is illustrated in Fig. 1. Table 2 lists peer-reviewed reports on QTL validation and marker-assisted selection (MAS) and Table 3 lists marker-assisted germplasm evaluations. The linkage maps of the wheat chromosomes 1A–7B (no QTL have been identified on 7D yet) in Fig. 1 were drawn in Mapchart (Voorrips 2002) using the wheat consensus map data published by Somers et al. (2004) which were downloaded from the graingenes database (<http://wheat.pw.usda.gov/>). The map for chromosome 7el is based on the publication by Shen and Ohm (2007). For readability, only selected markers mapped and published by Somers et al. (2004) are displayed in Fig. 1, numerous additional markers can be found in the graingenes database. To locate the positions of the FHB resistance QTL reported in 52 mapping studies relative to the wheat consensus map, we used primarily SSR markers as anchor points. For many QTL, this was quite easy to achieve especially in cases where more than one SSR marker was in common between the consensus map and the specific QTL mapping study. For other QTL, finding the corresponding chromosome regions in the consensus map was more difficult to achieve. In cases where no direct alignment between the consensus map and a specific QTL map was possible, further genetic or physical maps published in graingenes, like the

Table 1: QTL detected for components of *Fusarium* head blight resistance in wheat

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
Sumai 3	3BS	15.4	<i>Xcdo981</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[1] Waldron et al. (1999)
Sumai 3	6BS	3.9–6	<i>Xbcd331</i> , <i>Xcdo524</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[1] Waldron et al. (1999)
Stoa	2AL	14.3	<i>XksuH16</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[1] Waldron et al. (1999)
Stoa	4B	7.2	<i>Xwg909</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.	Unclear map position	No	[1] Waldron et al. (1999)
Sumai 3	3BS	41.6	<i>Xgwm493</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[2] Anderson et al. (2001)
Sumai 3	6BS	9.2	<i>Xbarc101</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[2] Anderson et al. (2001)
Stoa	2AL	14.3	<i>XksuH16</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[2] Anderson et al. (2001)
Stoa	4BS	7.2	<i>Xwg909</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.	Unclear map position	No	[2] Anderson et al. (2001)
ND2603	3BS	24.8	<i>Xgwm493</i>	FHB spread		ND2603 × Butte86, 139 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[2] Anderson et al. (2001)
ND2603	6AS	11.6	<i>XksuH4</i>	FHB spread		ND2603 × Butte86, 139 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[2] Anderson et al. (2001)
ND2603	3AL	9.1	<i>Xbcd941</i>	FHB spread		ND2603 × Butte86, 139 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.	Unclear map position	No	[2] Anderson et al. (2001)
Sumai 3	3BS	55	<i>Xsts3B-138</i>	FHB spread		Sumai 3 × Stoa, 112 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.	STS markers from ESTs		[3] Liu and Anderson (2003a)
Ning 7840	3BS	60	AFLP markers	FHB spread		Ning 7840 × Clark, 133 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.	Map position determined in ref. [5] Zhou et al. (2002)		[4] Bai et al. (1999)
Ning 7840	3BS	18–52	<i>Xgwm533- Xbarc147</i>	FHB spread		Ning 7840 × Clark, 133 RIL	<i>Fusarium graminearum</i> , SFI: 4 greenhouse exp.			[5] Zhou et al. (2002)
Ning 7840	2BL	4–7	<i>Xgwm120</i>	FHB spread		Ning 7840 × Clark, 133 RIL	<i>Fusarium graminearum</i> , SFI: 4 greenhouse exp.			[5] Zhou et al. (2002)
Ning 7840	2AS	3–5	<i>Xgwm614</i>	FHB spread		Ning 7840 × Clark, 133 RIL	<i>Fusarium graminearum</i> , SFI: 4 greenhouse exp.			[5] Zhou et al. (2002)
Ning 7840	3BS	25–56	<i>Xsrst.3B1</i>	FHB spread		Ning 7840 × Clark, 132 RIL	<i>Fusarium graminearum</i> , SFI: 4 greenhouse exp.	Conversion of AFLP in STS		[6] Guo et al. (2003)
Fukuhokomugi	n.d.	–	<i>Xopz10.680- Xopaf06.345</i>	FHB spread		Fukuhokomugi × Oligo Culm, 110 DH	<i>Fusarium graminearum</i> , sprinkler inoculation, field exp.	RAPD	No	[7] Ban (2000)
Fukuhokomugi	n.d.	–	<i>Xopw13.435</i>	FHB spread		Fukuhokomugi × Oligo Culm, 110 DH	<i>Fusarium graminearum</i> , sprinkler inoculation, field exp.	RAPD	No	[7] Ban (2000)
CM-82036	3BS	57	<i>Xgwm533- Xgwm493</i>	FHB spread		CM-82036 × Remus, 239 DH	<i>Fusarium graminearum</i> , SFI: 4 field exp.			[8] Buerstmayr et al. (2002)
CM-82036	5A	11	<i>Xgwm293- Xgwm304</i>	FHB spread		CM-82036 × Remus, 239 DH	<i>Fusarium graminearum</i> , <i>Fusarium culmorum</i> , SFI: 4 field exp.			[8] Buerstmayr et al. (2002)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
CM-82036	1B	10	<i>GluB1</i>	FHB spread		Remus × CM-82036, 239 DH	<i>Fusarium graminearum</i> , <i>Fusarium culmorum</i> , SFI: 4 field exp.			[8] Buerstmayr et al. (2002)
CM-82036	3BS	29.1	<i>Xgwm533</i> – <i>Xgwm493</i>	FHB severity		CM-82036 × Remus, 239 DH	<i>Fusarium graminearum</i> , <i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[9] Buerstmayr et al. (2003a,b)
CM-82036	5A	20.5	<i>Xgwm293</i> – <i>Xgwm156</i>	FHB severity		CM-82036 × Remus, 239 DH	<i>Fusarium graminearum</i> , <i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[9] Buerstmayr et al. (2003a,b)
CM-82036	3BS	92.6	<i>Xgwm533</i> – <i>Xgwm493</i>	DON resistance		CM-82036 × Remus, 94 DH	DON infiltration, SFI: 2 greenhouse exp.			[10] Lemmens et al. (2005)
Ning 894037	3BS	42.5	<i>Xbarc133</i> – <i>Xgwm493</i>	FHB spread		Ning 894037 × Alondra, 218 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse & 1 field exp.	BSA, bulks 12 + 12 lines		[11] Shen et al. (2003a)
Alondra	2DS	12.1	<i>Xgwm296</i> – <i>Xgwm261</i>	FHB spread		Ning 894037 × Alondra, 218 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse & 1 field exp.	BSA, bulks 12 + 12 lines		[11] Shen et al. (2003a)
Ning 894037	6BS	4.4	<i>Xgwm88</i> – <i>Xgwm644</i>	FHB spread		Ning 894037 × Alondra, 218 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse & 1 field exp.	BSA, bulks 12 + 12 lines		[11] Shen et al. (2003a)
Huapei 57-2	3BS	23.6	<i>Xbarc133</i>	FHB spread		Huapei 57-2 × Patterson, 163 RIL	<i>Fusarium graminearum</i> , SFI: 1 field & 2 greenhouse exp.	BSA, bulks 8 + 8 lines		[12] Bourdoncle and Ohm (2003)
Huapei 57-2	3BL	10.7	<i>Xgwm247</i>	FHB spread		Huapei 57-2 × Patterson, 163 RIL	<i>Fusarium graminearum</i> , SFI: 1 field & 2 greenhouse exp.	BSA, bulks 8 + 8 lines		[12] Bourdoncle and Ohm (2003)
Huapei 57-2	3AS	8.1	<i>Xgwm5</i>	FHB spread		Huapei 57-2 × Patterson, 163 RIL	<i>Fusarium graminearum</i> , SFI: 1 field & 2 greenhouse exp.	BSA, bulks 8 + 8 lines		[12] Bourdoncle and Ohm (2003)
Patterson	5BL	7.1	<i>Xbarc59</i>	FHB spread		Huapei 57-2 × Patterson, 163 RIL	<i>Fusarium graminearum</i> , SFI: 1 field & 2 greenhouse exp.	BSA, bulks 8 + 8 lines		[12] Bourdoncle and Ohm (2003)
Wuhan 1	2DL	9	<i>Xgwm539</i>	FHB spread		Wuhan 1 × Nyu Bai, 110 DH ²	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 2 field exp.			[13] Somers et al. (2003)
Nyu Bai ²	3BS	11–13	<i>Xgwm533</i>	FHB spread, DON content		Wuhan 1 × Nyu Bai, 110 DH ²	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 2 field exp.			[13] Somers et al. (2003)
Nyu Bai ²	3BSc	4	<i>Xgwm566</i>	FHB severity		Wuhan 1 × Nyu Bai, 110 DH ²	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 2 field exp.			[13] Somers et al. (2003)
Wuhan 1	4BS	12	<i>Xwmc238</i>	FHB severity		Wuhan 1 × Nyu Bai, 110 DH ²	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 2 field exp.			[13] Somers et al. (2003)
Nyu Bai ²	5AS	6	<i>Xgwm96</i>	DON content		Wuhan 1 × Nyu Bai, 110 DH ²	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 2 field exp.			[13] Somers et al. (2003)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
Nyu Bai ²	2D	–	<i>Xwmc25</i>	DON content	Plant height	Wuhan 1 × Nyu Bai, 110 DH ²	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 2 field exp.			[13] Somers et al. (2003)
DH181	2DS	11.1–12.8	<i>Xwmc144–Xgwm539</i>	FHB incidence, FHB spread, kernel infection		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
DH181	3BS	6–11	<i>Xgwm533</i>	FHB incidence, FHB spread, kernel infection		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
DH181	6BS	5.8–24	<i>Xwmc397</i>	FHB incidence, FHB spread, kernel infection		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
DH181	7BL	8.4	<i>Xwmc526</i>	FHB spread		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
DH181	3BC	5.6–7.9	<i>Xwmc612</i>	FHB incidence, kernel infection		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
DH181	4DL	12.5–13.3	<i>Xwmc331</i>	FHB incidence, kernel infection		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
DH181	5AS	6.2	<i>Xgwm293</i>	FHB incidence		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
DH181	IDL	16.6	<i>Xgdm126</i>	Kernel infection		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.			[14] Yang et al. (2005a)
AC Foremost	3A	11.8	<i>Xwmc264–Xwmc428</i>	FHB incidence		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.; SPRAY: 2 field exp.	Unclear map position	No	[14] Yang et al. (2005a)
W14	3BS	33	<i>Xgwm493–Xgwm533</i>	FHB spread		W14 × Pion2684, 96 DH lines	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 1 field exp.			[15] Chen et al. (2006a)
W14	3BS	10	<i>Xbarc133–Xgwm493</i>	FHB incidence		W14 × Pion2684, 96 DH lines	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 1 field exp.			[15] Chen et al. (2006a)
W14	5A	24	<i>Xbarc117–Xbarc186</i>	FHB incidence		W14 × Pion2684, 96 DH lines	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp., SPRAY: 1 field exp.			[15] Chen et al. (2006a)
CS-SM3-7ADS	3BS	30.2	<i>Xgwm533–Xgwm493</i>	FHB spread		CS-SM3-7ADS × Annong8455, 92 RIL	<i>Fusarium graminearum</i> , SFI: 1 field exp.			[16] Ma et al. (2006b)
CS-SM3-7ADS	2D	11.8	<i>XmCGAcTGC.102–XmCGTApACT.236</i>	FHB spread		CS-SM3-7ADS × Annong8455, 92 RIL	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp., 1 field exp.			[16] Ma et al. (2006b)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
CS-SM3-7ADS	4D	10.8	<i>Xcfd84-Xwmc331</i>	FHB spread		CS-SM3-7ADS × Annong8455, 92 RIL	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp., 1 field exp.		[16]	Ma et al. (2006b)
CJ 9306	3BS	22.8–30.7	<i>Xgwm533b-Xgwm493</i>	FHB spread, DON content		Veery × CJ 9306, 152 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.		[17,18]	Jiang et al. (2007a,b)
CJ 9306	2DL	15.5–19.9	<i>Xgwm157-Xwmc041</i>	FHB spread, DON content		Veery × CJ 9306, 152 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.		[17,18]	Jiang et al. (2007a,b)
CJ 9306	1AS	5.9–9.5	<i>Xbarc148</i>	FHB spread, DON content		Veery × CJ 9306, 152 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.		[17,18]	Jiang et al. (2007a,b)
CJ 9306	7BS	7.3	<i>Xgwm400</i>	FHB spread		Veery × CJ 9306, 152 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.		[17,18]	Jiang et al. (2007a,b)
CJ 9306	5AS	5.2	<i>Xgwm425-Xbarc186</i>	DON content		Veery × CJ 9306, 152 RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.		[17,18]	Jiang et al. (2007a,b)
Sumai 3	3BS	–	<i>Xsis3B.189-Xsis3B.206</i>	FHB spread		F7 heterozygous plant, 382 recombinants	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.	3BS fine mapping	[19]	Liu et al. (2006)
Sumai 3	3BS	–	<i>Xsis3B.80-Xsis3B.142</i>	FHB spread		Thatcher × 5*Sumai 3, 51 BC4F2 (from 467)	<i>Fusarium graminearum</i> , SFI: one greenhouse exp.	3BS fine mapping	[20]	Cuthbert et al. (2006)
Nyu Bai	3BS	–	<i>Xsis3B.80-Xsis3B.66</i>	FHB spread		HC374 × 3*98B69-L47, 66 BC2F3 (from 420)	<i>Fusarium graminearum</i> , SFI: one greenhouse exp.	3BS fine mapping	[20]	Cuthbert et al. (2006)
Sumai 3	6BS	–	<i>Xgwm133-Xgwm644</i>	FHB spread, FHB severity, FDK		BW278 × AC Foremost, 89 RIL (from 1440)	<i>Fusarium graminearum</i> , SPRAY: 2 field exp.	6BS fine mapping	[21]	Cuthbert et al. (2007)
Gamenya	2DS	14–25	<i>Xgwm261-MRP</i>	FHB spread, FHB severity, DON content	plant height (<i>rht8/Rht8</i>)	Sumai 3 × Gamenya, 118 DH	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp.		[22]	Handa et al. (2008)
Wangshuibai	3BS	13.3–13.6	<i>Xgwm533.1-Xbarc147.1</i>	FHB spread		Nanda2419 × Wangshuibai, 154 RIL	<i>Fusarium graminearum</i> , SFI: 2 field exp.		[23]	Lin et al. (2004)
Wangshuibai	6B	17.8	<i>Xwmc539-Xbarc024</i>	FHB spread		Nanda2419 × Wangshuibai, 154 RIL	<i>Fusarium graminearum</i> , SFI: 2 field exp.	*In 1 of 2 exp.	[23]	Lin et al. (2004)
Wangshuibai	3BS	13.7–23.8	<i>Xbarc147-Xgwm493</i>	FHB spread		Wangshuibai × Alondra, 104 RILS	<i>Fusarium graminearum</i> , SFI: 3 field exp. & 2 greenhouse exp.		[24]	Zhang et al. (2004)
Alondra	1B	15.6	<i>XeTCG-mAGC.7-Xe-ACCGmCT-C.7</i>	FHB spread		Wangshuibai × Alondra, 104 RILS	<i>Fusarium graminearum</i> , SFI: 3 field exp. & 2 greenhouse exp.	*In 1 exp., T1BL, IRS translocation	[24]	Zhang et al. (2004)
Wangshuibai	3BS	30.5–37.3	<i>Xbarc147</i>	FHB spread		Wangshuibai × Wheaton, 139 RIL	<i>Fusarium graminearum</i> , SFI: 2 experiments		[25]	Zhou et al. (2004)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
Wangshuibai	1B	6.4–11.9	<i>Xgwm759</i>	FHB spread		Wangshuibai × Wheaton, 139 RIL	<i>Fusarium graminearum</i> , SFI: 2 experiments			[25] Zhou et al. (2004)
Wangshuibai	7A	3–6.8	<i>Xgwm1083</i>	FHB spread		Wangshuibai × Wheaton, 139 RIL	<i>Fusarium graminearum</i> , SFI: 2 experiments			[25] Zhou et al. (2004)
Wangshuibai	3BS	3.4–7.4	<i>Xbarc344</i>	FHB spread		Wangshuibai × Wheaton, 139 RIL	<i>Fusarium graminearum</i> , SFI: 2 experiments			[25] Zhou et al. (2004)
Wangshuibai	2D	10.6	<i>Xgwm261–Xgwm484</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	3BS	11	<i>Xgwm533–Xgwm493</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	4B	9.9	<i>Xgwm368–Xgwm149</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	5B	13.3	<i>Xgwm443–Xbarc32</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	5B	10.8	<i>Xgwm335–Xgwm371</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	7A	12.6	<i>Xgwm276–Xgwm282</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	3BS	16.7	<i>Xgwm533–Xgwm493</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	2DL	8.14	<i>Xgwm539–Xs15/m24</i>	FHB severity		Wangshuibai × Alondra, 134 DH	Natural infection: 3 field exp.			[26] Jia et al. (2005)
Wangshuibai	5A	16.6–20.3	<i>Xwmc96–Xgwm304</i>	FHB incidence		Nanda2419 × Wangshuibai, 154 RIL	SPRAY: 3 field exp., grain spawn: 1 field exp.			[28] Lin et al. (2006)
Wangshuibai	4B	12.1–17.5	<i>Xwmx349–Xgwm149</i>	FHB incidence		Nanda2419 × Wangshuibai, 154 RIL	SPRAY: 3 field exp., grain spawn: 1 field exp.			[28] Lin et al. (2006)
Wangshuibai	2D	10.1–12.3	<i>Xgwm539–Xwmc181</i>	FHB incidence		Nanda2419 × Wangshuibai, 154 RIL	SPRAY: 3 field exp., grain spawn: 1 field exp.			[28] Lin et al. (2006)
Wangshuibai	3BS	6–17	<i>Xgwm533.1–Xbarc133</i>	FHB spread, DON content		Wangshuibai × Anong8455, 118 RIL	<i>Fusarium graminearum</i> , SFI: 2 field exp.			[29] Ma et al. (2006a)
Wangshuibai	2A	8.5–11.5	<i>Xgwm425–XmCCTeAAG.2</i>	FHB spread, DON content		Wangshuibai × Anong8455, 118 RIL	<i>Fusarium graminearum</i> , SFI: 2 field exp.			[29] Ma et al. (2006a)
Wangshuibai	5A	12.4	<i>XmCCTeAAG.2–Xgwm156</i>	DON content		Wangshuibai × Anong8455, 118 RIL	<i>Fusarium graminearum</i> , SFI: 2 field exp.			[29] Ma et al. (2006a)
Wangshuibai	3BS	13–34	<i>Xbarc147</i>	FHB spread, FHB Incidence, DON content		Wangshuibai × Wheaton, 139 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 greenhouse exp, SFI: 3 greenhouse exp.			[30] Yu et al. (2008)
Wangshuibai	3BS	8.1	<i>Xgwm376</i>	FHB spread, DON content		Wangshuibai × Wheaton, 139 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 greenhouse exp, SFI: 3 greenhouse exp.			[30] Yu et al. (2008)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
Wangshuibai 3DL		7.3	<i>XpCATmTGCG.188</i>	FHB spread		Wangshuibai × Wheat, 139 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 greenhouse exp, SFI: 3 greenhouse exp.			[30] Yu et al. (2008)
Wangshuibai 3AS		8.1	<i>XpCGAmGTG.352</i>	FHB incidence		Wangshuibai × Wheat, 139 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 greenhouse exp, SFI: 3 greenhouse exp.			[30] Yu et al. (2008)
Wangshuibai 5DL		6.8	<i>Xgwm292</i>	FHB incidence, DON content		Wangshuibai × Wheat, 139 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 greenhouse exp, SFI: 3 greenhouse exp.			[30] Yu et al. (2008)
Frontana 3A		16.2	<i>Xdupw227-Xgwm720</i>	FHB severity, FHB incidence		Remus × Frontana, 180 DH	<i>Fusarium graminearum</i> , SPRAY: 2 greenhouse exp, SFI: 3 greenhouse exp.			[31] Steiner et al. (2004)
Frontana 5A		8.8	<i>Xgwm129-Xbarc197</i>	FHB severity		Remus × Frontana, 180 DH	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[31] Steiner et al. (2004)
Frontana 2B		6.1	<i>Xs13m25.8-Xs24m15.6</i>	FHB severity, FHB incidence		Remus × Frontana, 180 DH	<i>Fusarium graminearum</i> , SPRAY: 3 field exp.		No	[31] Steiner et al. (2004)
Frontana 6B		6.7	<i>Xs23m14.4</i>	FHB severity, FHB incidence		Remus × Frontana, 180 DH	<i>Fusarium graminearum</i> , SPRAY: 3 field exp.		No	[31] Steiner et al. (2004)
Remus 1B		5.5	<i>Xs12m25.14-Xs24m17.2</i>	FHB severity, FHB incidence		Remus × Frontana, 180 DH	<i>Fusarium graminearum</i> , SPRAY: 3 field exp.		No	[31] Steiner et al. (2004)
Remus 2A		7.9	<i>Xs13m26.4</i>	FHB severity		Remus × Frontana, 180 DH	<i>Fusarium graminearum</i> , SPRAY: 3 field exp.		No	[31] Steiner et al. (2004)
Seri82 1BL		7.9	<i>Xe38m50.10-Xe32m65.10</i>	FHB severity		Seri82 × Frontana; 171 F3 plants, 120 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 field exp.			[32] Mardi et al. (2006)
Frontana 3AL		7.7	<i>Xgwm720-Xgwm1121</i>	FHB severity		Seri82 × Frontana; 171 F3 plants, 120 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 field exp.			[32] Mardi et al. (2006)
Frontana 7AS		7.6	<i>Xe77m47.22-Xgwm233</i>	FHB severity		Seri82 × Frontana; 171 F3 plants, 120 RIL	<i>Fusarium graminearum</i> , SPRAY: 2 field exp.			[32] Mardi et al. (2006)
Chokwang 5DL		10.5	<i>Xbarc239</i>	FHB spread		Chokwang × Clark, 79 RIL (mapping), 240 RIL (validation)	<i>Fusarium graminearum</i> , SFI: 4 + 1 greenhouse exp.			[33] Yang et al. (2005b)
Chokwang 4BL		4.7	<i>Xbarc1096</i>	FHB spread		Chokwang × Clark, 79 RIL (mapping), 240 RIL (validation)	<i>Fusarium graminearum</i> , SFI: 4 + 1 greenhouse exp.			[33] Yang et al. (2005b)
Chokwang 3BS		6	<i>Xgwm533</i>	FHB spread		Chokwang × Clark, 79 RIL (mapping), 240 RIL (validation)	<i>Fusarium graminearum</i> , SFI: 4 + 1 greenhouse exp.			[33] Yang et al. (2005b)
Sincron 1BL1RS		–	<i>Gli-R1</i>	FHB spread		Sincron × F1054W, 108 RIL	<i>Fusarium graminearum</i> ; SFI: 3 field exp.	T1BL.1R-S translocation		[34] Ittu et al. (2000)
Sincron 1DS		–	<i>Gli-D1b</i>	FHB spread		Sincron × F1054W, 108 RIL	<i>Fusarium graminearum</i> ; SFI: 3 field exp.			[34] Ittu et al. (2000)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
Renan	2BS	8.5–12	<i>Xgwm374</i>	FHB severity	Flowering date, plant height	Renan × Réctal, 194 RIL	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[35] Gervais et al. (2003)
Renan	5AL	14–19.2	<i>Xgwm639b</i>	FHB severity	Plant height	Renan × Réctal, 194 RIL	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[35] Gervais et al. (2003)
Renan	5AL	7.1–8.5	<i>B1</i>	FHB severity		Renan × Réctal, 194 RIL	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[35] Gervais et al. (2003)
Renan	2A	6.4–14.4	<i>Xgwm311–Xgwm382</i>	FHB severity		Renan × Réctal, 194 RIL	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[35] Gervais et al. (2003)
F201R	1B	12.4	<i>Xharc8</i>	FHB spread		Patter-son × F201R, 318 (118) RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.	BSA, 11 + 12 lines		[36] Shen et al. (2003b)
F201R	3A	13.4	<i>Xharc76, Xgwm674</i>	FHB spread		Patter-son × F201R, 318 (118) RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.	BSA, 11 + 12 lines		[36] Shen et al. (2003b)
Patterson	3D	3.8	<i>Xgwm341</i>	FHB spread		Patter-son × F201R, 318 (118) RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.	BSA, 11 + 12 lines		[36] Shen et al. (2003b)
F201R	5A	3.6	<i>Xgwm304</i>	FHB spread		Patter-son × F201R, 318 (118) RIL	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.	BSA, 11 + 12 lines		[36] Shen et al. (2003b)
Goldfield	2BS	29	<i>Xharc200–Xgwm210</i>	FHB incidence	Narrow flower opening	son × Goldfield, 100 RIL	<i>Fusarium graminearum</i> , grain spawn, 5 field exp.	BSA, bulks 8 + 8 lines		[37] Gilsinger et al. (2005)
Goldfield	2B	12	<i>Xwmc149</i>	FHB incidence	Narrow flower opening	Patter-son × Goldfield, 100 RIL	<i>Fusarium graminearum</i> , grain spawn: 5 field exp.	BSA, bulks 8 + 8 lines		[37] Gilsinger et al. (2005)
Goldfield	7B	7	<i>Xgwm344</i>	FHB incidence		Patter-son × Goldfield, 100 RIL	<i>Fusarium graminearum</i> , grain spawn: 5 field exp.	BSA, bulks 8 + 8 lines		[37] Gilsinger et al. (2005)
Arina	4AL	10.1	<i>Xcd6545–Xgwm160</i>	FHB severity		Arina × Formo, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*In 4 exp.		[38] Paillard et al. (2004)
Forno	5BL	14.3	<i>Xgwm371–Xgwm639a</i>	FHB severity	Heading date	Arina × Formo, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*In 4 exp.		[38] Paillard et al. (2004)
Arina	6DL	22.1	<i>Xcfa19a–Xcfa47</i>	FHB severity	Plant height, heading date	Arina × Formo, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*In 4 exp.		[38] Paillard et al. (2004)
Forno	3AL	10	<i>Xwmc264–Xgwm155</i>	FHB severity		Arina × Formo, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*In 2 exp.	No	[38] Paillard et al. (2004)
Arina	3BL	6.3	<i>Xcfa2134b–Xgwm131b</i>	FHB severity		Arina × Formo, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*In 2 exp.	No	[38] Paillard et al. (2004)
Forno	3DS	8.1	<i>Xbcd907c–Xgwm161</i>	FHB severity		Arina × Formo, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*In 1 exp.	No	[38] Paillard et al. (2004)
Arina	5AL	7	<i>Xgwm291–Xglk348c</i>	FHB severity	Plant height	Arina × Formo, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*In 1 exp.	No	[38] Paillard et al. (2004)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
Arina	2AL	6.8	<i>Xcfa2086-Xgwm311</i>	FHB severity	Plant height, heading date	Arina × Forno, 240 RIL	<i>Fusarium culmorum</i> , SPRAY: 6 field exp.	*For means only	No	[38] Paillard et al. (2004)
Arina	1BL	19.6	<i>Xp43m62.400-wPr3475</i>	FHB severity		Ari-na × NK93604, 93 DH	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[39] Semagn et al. (2007)
Arina	6BS	7.8	<i>xp46m62.107-xp45m60.265</i>	FHB severity		Ari-na × NK93604, 93 DH	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.	*In 2 exp.		[39] Semagn et al. (2007)
NK93604	1AL	27.9	<i>wPr-5577-Xbarc213</i>	FHB severity and DON		Ari-na × NK93604, 93 DH	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[39] Semagn et al. (2007)
NK93604	7AL	14.8	<i>Xgwm276-Xdupw226</i>	FHB severity		Ari-na × NK93604, 93 DH	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[39] Semagn et al. (2007)
NK93604	2AS	26.7	<i>wPr184-Xbarc124.1</i>	DON content		Ari-na × NK93604, 93 DH	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[39] Semagn et al. (2007)
Arina	4DS	12.9–23.9	<i>Rht-D1</i>	FHB severity, and associated traits	Plant height (<i>Rht-D1a/Rht-D1b</i>)	Arina × Riband, 116 DH	<i>Fusarium culmorum</i> , SPRAY: 2 field exp., 3 polytunnel exp.	*In 4 exp.		[40] Draeger et al. (2007)
Arina	6BL	9.9–14.8	<i>Xp3131</i>	FHB severity, and associated traits		Arina × Riband, 116 DH	<i>Fusarium culmorum</i> , SPRAY: 2 field exp., 3 polytunnel exp.	*In 2 exp.		[40] Draeger et al. (2007)
Spark	4DS	50.9	<i>Rht-D1</i>	FHB severity	Plant height (<i>Rht-D1a/Rht-D1b</i>)	Spark × Rialto, 129 DH	<i>Fusarium culmorum</i> , SPRAY: 3 field exp.			[41] Srinivasachary et al. (2008)
Dream	6AL	19	<i>Xp77m51.430-Xp66m55.242; Xgwm82-Xarc107</i>	FHB severity	Plant height, ear compactness	Dream × Lynx, 145 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[42] Schmolke et al. (2005), [43] Häberle et al. (2007)
Lynx	1B	12	<i>Xp78m51.237-Xs26m23.365 (Xgwm18, tag95)</i>	FHB severity		Dream × Lynx, 145 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.	T1BL.1RS translocation		[42] Schmolke et al. (2005)
Dream	2BL	11	<i>Xp74m53.272-Xs25m12.206</i>	FHB severity		Dream × Lynx, 145 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[42] Schmolke et al. (2005)
Dream	7BS	21	<i>Xs25m15.187-Xs23m21.497; Xgwm46-Xp70m56.237</i>	FHB severity	Heading date	Dream × Lynx, 145 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[42] Schmolke et al. (2005), [43] Häberle et al. (2007)
Cansas	1BS	16.5	<i>Xe38m52.378-Xgwm131</i>	FHB severity		Cansas × Ritmo, 94 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[44] Klahr et al. (2007)
Ritmo	1DS	8.2	<i>Xs16m22.162-Xwls2001-1D</i>	FHB severity		Cansas × Ritmo, 94 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[44] Klahr et al. (2007)
Ritmo	3B	11.1	<i>Xe35m59.107-Xe38m52.441</i>	FHB severity		Cansas × Ritmo, 94 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.	Unclear map position	No	[44] Klahr et al. (2007)
Cansas	3DL	11.2	<i>Xe33m57.457-Xgwm645</i>	FHB severity		Cansas × Ritmo, 94 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[44] Klahr et al. (2007)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
Cansas	5BL	20	<i>Xe35m52.331–Xs25m20.245</i> <i>Xs23m21.271–Xs18m22.369</i> <i>Xgwm46–Xc42m58.394</i> <i>Xgwm276b</i>	FHB severity	Plant height	Cansas × Ritmo, 94 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[44] Klahr et al. (2007)
Ritmo	7AL	9.9	<i>Xs23m21.271–Xs18m22.369</i> <i>Xgwm46–Xc42m58.394</i> <i>Xgwm276b</i>	FHB severity	Plant height, heading date	Cansas × Ritmo, 94 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[44] Klahr et al. (2007)
Cansas	7BS	11	<i>Xgwm46–Xc42m58.394</i> <i>Xgwm276b</i>	FHB severity		Cansas × Ritmo, 94 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[44] Klahr et al. (2007)
Ernie	2B	4.2	<i>Xgwm276b</i>	FHB spread		Ernie × - MO94-317, 243 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[45] Liu et al. (2007)
Ernie	3B	12.9	<i>Xgwm285</i>	FHB spread		Ernie × - MO94-317, 243 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[44] Liu et al. (2007)
Ernie	4BL	8.8	<i>Xgwm495</i>	FHB spread		Ernie × - MO94-317, 243 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[45] Liu et al. (2007)
Ernie	5A	17.4	<i>Xbarc165</i>	FHB spread		Ernie × - MO94-317, 243 RIL	<i>Fusarium graminearum</i> , SFI: 2 greenhouse exp.			[45] Liu et al. (2007)
Hussar	1A	9.7	<i>Xs26m12.188</i>	FHB severity	plant height	G16-92 × Hussar, 136 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.		No	[46] Schmolke et al. (2008)
G16-92	2BL	14.1	<i>Xgwm501–Xgwm47</i>	FHB severity		G16-92 × Hussar, 136 RIL	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.			[46] Schmolke et al. (2008)
<i>Triticum macha</i>	4AS	n.d.	<i>Xgwm165</i>	FHB incidence		HsTm4A × - Hobbit-sib, 43 DH	<i>Fusarium culmorum</i> , SPRAY: Type 1 only			[47] Steed et al. (2005)
<i>Thinopyrum ponticum</i> , 7el2	7el	15–30	<i>Xpsr121–Xc/a2240</i>	FHB spread		K2620 × - K11463, 283 RILs	SFI: 1 polytunnel exp. <i>Fusarium graminearum</i> , SFI: 4 greenhouse exp.			[48] Shen and Ohm (2007)
<i>Triticum dicoccoides</i> : FA-15-3	3AS	37	<i>Xgwm2</i>	FHB spread		Langdon(Dicc-3A) × Langdon, 83 RILs	<i>Fusarium graminearum</i> , SFI, 2 greenhouse exp.			[49] Otto et al. (2002)
<i>Triticum dicoccoides</i> : FA-15-3	3AS	–	<i>Xgwm2</i>	FHB spread		Langdon(Dicc-3A) × Langdon, 83 RILs	<i>Fusarium graminearum</i> ; SFI, 2 greenhouse exp.	Refined map from ref. [49] Otto et al. (2002)		[50] Chen et al. (2007)
<i>Triticum durum</i> cv. 'Strongfield'	2BS	26	<i>Xwmc474–Xwmc175</i>	FHB spread		Black-bird × Strongfield, 85 DH	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp.			[51] Somers et al. (2006)

Table 1: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	Shown in Fig. 1	References ¹
<i>Triticum carthlicum</i> cv. 'Blackbird'	6BS	23	<i>Xgwm518-Xbarc125</i>	FHB spread		Black-bird × Strongfield, 85 DH	<i>Fusarium graminearum</i> , SFI, 1 greenhouse exp.			[51] Somers et al. (2006)
<i>Triticum dicoccoides</i> : PI478742	7AL	19	<i>Xksun176-Xbarc121</i>	FHB spread		Langdon × Langdon(Dicc-7A), 118 RIL	<i>Fusarium graminearum</i> , SFI, 3 greenhouse exp.			[52] Kumar et al. (2007)

*Indicates the significant values.

SPRAY, spray inoculation; SFI, single floret inoculation.

¹Numbers in square brackets for cross reference with Fig. 1.

²Published as Wuhan 1 × Maringa (Somers et al. 2003) but corrected to Wuhan 1 × Nyu Bai (McCartney et al. 2007).

'Synthetic' × 'Opata maps', were used as a bridge to identify the QTL regions. The graingenes comparative map viewer (CMap) was used in these cases (<http://rye.pw.usda.gov/cmap/>). QTL positions in Fig. 1 are indicated by vertical bars and named with the genotype that contributed the resistant allele and a number referring to the respective reference. The only exceptions are the resistance loci *Fhb1* (syn: *Qfhs.ndsu-3BS*), and *Fhb2*, both derived from the highly resistant cultivar 'Sumai 3' or its close relatives, which are indicated by their proposed gene names and numbers for the references. The sizes of the bars in Fig. 1 indicating the QTL positions do not reflect the magnitude of a QTL effect, but only the estimated location of the respective QTL. A small bar indicates that this QTL could be located relatively precisely on the map, a long bar indicated that locating this QTL was more uncertain.

Resistance Sources from Asia

Some wheat growing regions in Asia have suffered from regular FHB epidemics (Liu 1985, Bai and Shaner 1994). Breeding for resistance to FHB has therefore a long tradition, with remarkable successes like the cultivars 'Sumai 3', 'Ning 7840', 'Ning 8331', and other lines developed by Chinese wheat breeders. This material has been distributed to other parts of the world and used in resistance breeding programmes worldwide. These lines have also been the basis of the earlier projects to determine the genetic basis of *Fusarium* resistance.

The first two published QTL mapping studies by Waldron et al. (1999) and Bai et al. (1999) were based on populations derived from Chinese cultivars, which showed remarkably high type 2 FHB resistance. Waldron et al. (1999) reported RFLP mapping of type 2 FHB resistance QTL in a 'Sumai 3' × 'Stoa' population. They detected five QTL for type 2 resistance. The QTL with the largest effect was derived from 'Sumai 3', mapped to chromosome 3BS, and was designated *Qfhs.ndsu-3BS*. Two smaller effect QTL descending from 'Sumai 3' mapped to separate regions on 6BS. In addition, two 'Stoa' derived QTL mapped to 2A and 4BL, respectively. At about the same time, Bai et al. (1999) reported one major QTL in a 'Ning 7840' × 'Clark' population based on AFLP genotyping. 'Ning 7840' has the pedigree 'Aurora'/'Anhui11'/'Sumai 3'. This major QTL could not be assigned to a wheat chromosome unambiguously. By integrating SSR markers and the analysis of a further 'Sumai 3' derived population, Anderson et al. (2001) confirmed the major QTL for resistance to fungal spread on chromosome 3BS (*Qfhs.ndsu-3BS*). This finding was verified by another independent mapping report using a large DH population of CM-82036 × 'Remus', where CM-82036 is a selection from the cross 'Sumai 3' × 'Thornbird' from the CIMMYT wheat programme (Buerstmayr et al. 2002). The integration of SSR markers in the 'Ning 7840' × 'Clark' population revealed that the major QTL derived from 'Ning 7840' was also in the same region on chromosome 3BS. In addition, two smaller effect QTL derived from 'Ning 7840' were mapped to 2BL and 2AS (Zhou et al. 2002). Because of its high breeding potential the chromosomal segment covering *Qfhs.ndsu-3BS* was further characterized with SSR, STS (sequence tagged sites) and AFLP markers (Guo et al. 2003, Liu and Anderson 2003a,b). A first clue to decipher the function of this QTL was proposed by Lemmens et al. (2005) who found that wheat lines carrying *Qfhs.ndsu-3BS* were able to convert DON into the less phytotoxic DON-3-O-glycoside and hypothesized that *Qfhs.ndsu-3BS* either encodes a

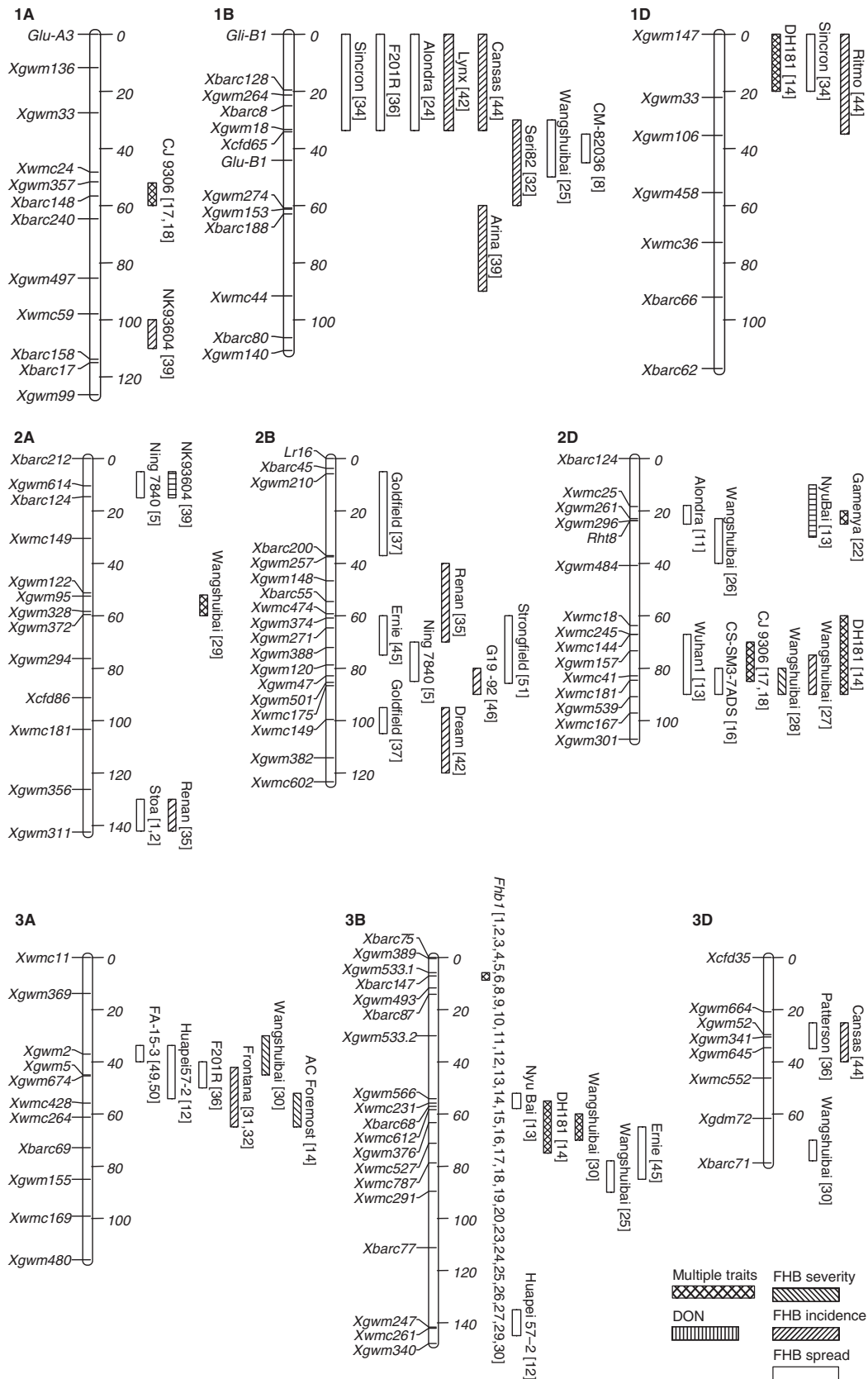


Fig. 1: Location of FHB resistance QTL on wheat chromosomes 1A–7B and the *Thinopyrum ponticum* chromosome 7e1. The QTL *Fhb1* (3B) and *Fhb2* (6B) are named with their gene names. All other QTL are identified with the name of the cultivar contributing the resistant allele and numbers in brackets referring to the specific publications in which the QTL were reported (see column references in Table 1). The length of bars representing each QTL is meant to designate the QTL location, with shorter bars indicating more precise QTL locations. Patterns of bars indicate the FHB-associated trait(s) – see figure legend

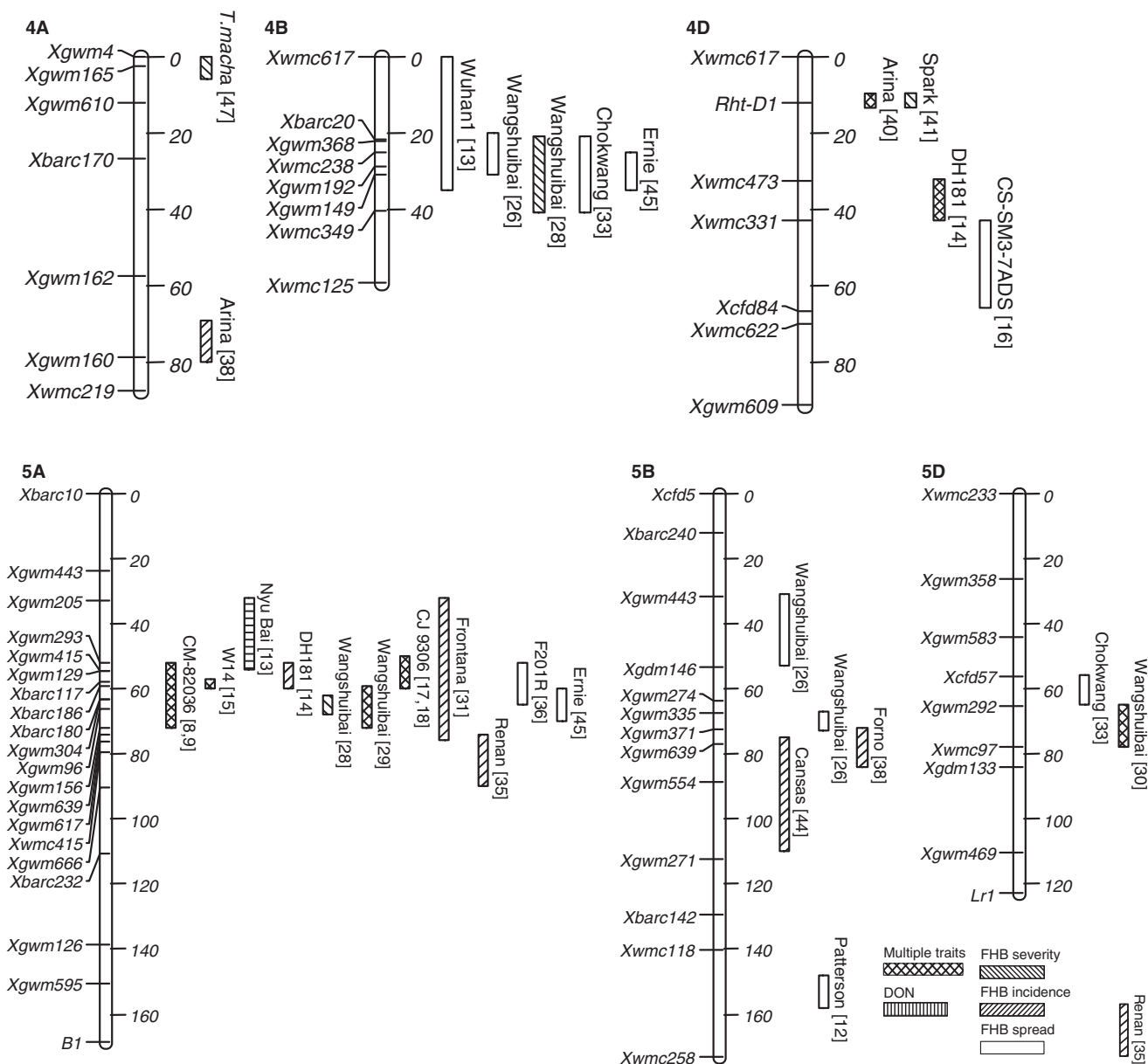


Fig. 1: Continued

DON-glucosyltransferase or modulates the expression or activity of such an enzyme. The QTL *Qfhs.ndsu-3BS* was recently re-designated as *Fhb1* (Liu et al. 2006). In high resolution mapping populations segregating for *Fhb1*, this locus could be mapped as a single Mendelian gene with high precision. Flanking STS markers bracketing *Fhb1* within a 1.2-cM interval are now available (Cuthbert et al. 2006, Liu et al. 2006). A large scale project on map-based isolation of *Fhb1* is well underway and should result in the first cloned FHB resistance gene with known function in the near future (J. A. Anderson and S. Liu, personal communications).

In populations derived from other Asian resistance sources, the largest effect on type 2 resistance appeared regularly at *Fhb1*: ‘W14’ (Chen et al. 2006a), ‘Huapei 57-2’ (Bourdoncle and Ohm 2003), ‘Ning 894037’ (Shen et al. 2003a), ‘CJ 9306’ (Jiang et al. 2007a). ‘W14’ and ‘CJ 9306’ are both highly FHB resistant lines derived from a complex cross involving ‘Sumai 3’ and other resistant lines (Chen et al. 2006a, Jiang et al. 2007a).

The pedigree of ‘Huapei 57-2’ was not reported, and ‘Ning 894037’ was described as a somaclonal variant from the FHB susceptible cultivar ‘Yangmai 3’ (Shen et al. 2003a) but has the same marker haplotype as ‘Sumai 3’ at five SSR markers around *Fhb1* (Liu and Anderson 2003b). It is therefore very likely that ‘W14’, ‘CJ 9306’, ‘Huapei 57-2’, and ‘Ning 894037’ possess the same FHB resistance allele by descent as ‘Sumai 3’ at *Fhb1*.

Buerstmayr et al. (2003a) evaluated their CM-82036 × ‘Remus’ DH population for FHB severity using spray inoculations in mist irrigated field nurseries to detect field resistance and found two significant QTL mapping to chromosomes 3BS and 5A, respectively. Using spray inoculations, the effects of the two QTL *Fhb1* and *Qfhs.ifa-5A* were in a comparable range. In contrast, after single floret inoculation, *Fhb1* showed a much larger effect than *Qfhs.ifa-5A* (Buerstmayr et al. 2002, 2003a). The authors interpreted this as an indication that *Qfhs.ifa-5A* may contribute more towards type 1 resistance

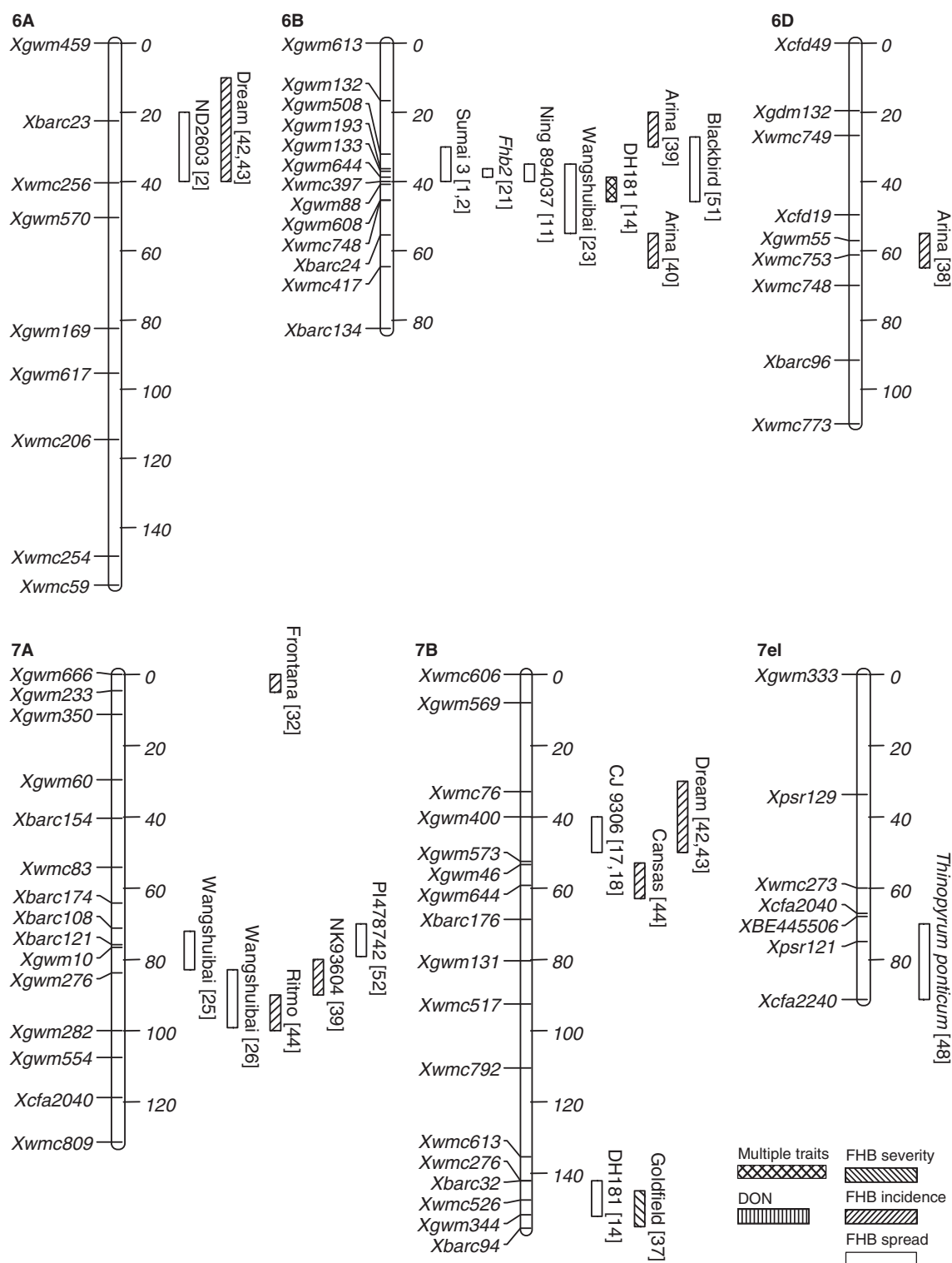


Fig. 1: Continued

and to a lesser extent to type 2 resistance, whereas *Fhb1* appears to play a role primarily in type 2 resistance. Similar conclusions were drawn by Chen et al. (2006a) who evaluated a 'W14' × 'Pioneer Brand-2684' DH population and found a QTL for type 2 resistance in single-floret inoculated greenhouse tests at 3BS, and for FHB incidence and FHB severity in a spray inoculated field experiment on 3BS and 5AS. Again, the effect of the 5A QTL was stronger after spray inoculation

than after single floret inoculation. No high resolution maps around the 5A QTL are available yet, because the QTL resides in an area of low recombination most likely near the centromere of the 5A chromosome (Buerstmayr et al. 2003a).

In several mapping populations derived from Chinese wheat lines, a significant type 2 FHB resistance QTL was found on chromosome 6BS deriving from 'Sumai 3' or related lines (Waldron et al. 1999, Shen et al. 2003a, Lin et al. 2004, Yang

Table 2: QTL validation and marker-assisted selection studies for *Fusarium* head blight resistance in wheat

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	References
Sumai 3	3BS	30–31	Xgwm533–Xgwm274	FHB spread		36 HRSW lines	<i>Fusarium graminearum</i> , SFI: several exp.	QTL validation in breeding lines	Del Blanco et al. (2003)
Ning 7840	3BS	–	Xgwm389, Xgwm533, Xbarc147	FHB spread		Ning 7840 × Wheaton and Ning 7840 × IL89–7978	<i>Fusarium graminearum</i> , SFI: greenhouse exp.	MAS with 6 markers on 3B	Zhou et al. (2003)
DH181	3BS	17	Xgwm533–Xgwm493	FHB spread		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.	MAS with 8 markers	Yang et al. (2003)
DH181	6B	21	Xgwm644	FHB spread		DH181 × AC Foremost, 174 DH	<i>Fusarium graminearum</i> , SFI: 3 greenhouse exp.	MAS with 8 markers	Yang et al. (2003)
93FHB21	3BS	48	Xgwm389–Xgwm493	FHB spread		AC Foremost × 93FH-B21, 76 DH	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp.	MAS with 8 markers	Yang et al. (2003)
93FHB21	5A	5	Xgwm291	FHB spread		AC Foremost × 93FH-B21, 76 DH	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp.	MAS with 8 markers	Yang et al. (2003)
93FHB21	6B	6	Xgwm644	FHB spread		AC Foremost × 93FH-B21, 76 DH	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp.	MAS with 8 markers	Yang et al. (2003)
Sumai 3	3BS	–	Xgwm493–Xgwm533	FHB spread		Sumai 3 × Australian wheat, four crosses	<i>Fusarium graminearum</i> , SFI: 1 controlled exp.	MAS with 2 markers	Xie et al. (2007)
Wuhan 1	4B	–	Xwmc238, Xgwm149	FHB severity, DON content	Plant height	3 backcross populations involving: Nyu Bai, Wuhan 1 and Sumai 3	<i>Fusarium graminearum</i> , SPRAY: 2 field exp..	MAS with 15 SSR markers	McCartney et al. (2007)
Wuhan 1	4B	–	Xwmc245, Xgwm608	FHB severity, DON content		3 backcross populations involving: Nyu Bai, Wuhan 1 and Sumai 3	<i>Fusarium graminearum</i> , SPRAY: 2 field exp..	MAS with 15 SSR markers	McCartney et al. (2007)
Nyu Bai or Sumai 3	3BS	–	Xgwm566, Xwmc231, Xwmc625, Xwmc693, Xwmc307, Xwmc418	FHB severity, DON content	Plant height	3 backcross populations involving: Nyu Bai, Wuhan 1 and Sumai 3	<i>Fusarium graminearum</i> , SPRAY: 2 field exp..	MAS with 15 SSR markers	McCartney et al. (2007)
Nyu Bai or Sumai 3	5AS	–	Xwmc705, Xgwm304, Xgwm154	FHB severity, DON content		3 backcross populations involving: Nyu Bai, Wuhan 1 and Sumai 3	<i>Fusarium graminearum</i> , SPRAY: 2 field exp..	MAS with 15 SSR markers	McCartney et al. (2007)

Table 2: Continued

Source of resistance allele	Chromosome	% variation explained	Markers	FHB trait	Association with	Plant material	Phenotyping	Comment	References
Sumai 3	3BS	—	<i>Xgwm533</i> , <i>Xgwm493</i>	FHB severity, DON content	3 backcross populations involving: Nyu Bai, Wuhan 1 and Sumai 3	<i>Fusarium graminearum</i> , SPRAY: 2 field exp..	MAS with 15 SSR markers	McCartney et al. (2007)	
CM-82036	3BS	—	<i>Xgwm389</i> , <i>Xgwm533</i> , <i>Xbarc133</i>	FHB severity, DON content	DH[CM-82036/Remus]/ Nandu/2/DH[Frontana/ Remus]/Munk	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.	MAS with 6 markers	Miedaner et al. (2006), Wilde et al. (2007)	
CM-82036	5A	—	<i>Xgwm156</i> , <i>Xgwm304a</i>	FHB severity, DON content	DH[CM-82036/ Remus]/Nandu/2/ DH[Frontana/Remus]/Munk	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.	MAS with 6 markers	Miedaner et al. (2006), Wilde et al. (2007)	
Frontana	3A	—	<i>Xgwm720</i>	FHB severity, DON content	DH[CM-82036/Remus]/Nandu/2/ DH[Frontana/Remus]/Munk	<i>Fusarium culmorum</i> , SPRAY: 4 field exp.	MAS with 6 markers	Miedaner et al. (2006), Wilde et al. (2007)	
Sumai 3	3BS	—	<i>Xgwm493</i> , <i>Xbarc133</i> , <i>Xgwm533</i>	FHB severity, kernel infection	19 QTL F4:5 NIL pairs from 13 crosses	<i>Fusarium graminearum</i> , SPRAY: 2 field exp., grain spawn: 2 field exp., SFI: 3 controlled environment exp.	QTL validation in breeding lines	Pumphrey et al. (2007)	
Dream	6AL	—	<i>Xgwm82</i>	FHB severity	Plant height	Dream/4* Lynx, 127 BC2F4 lines	QTL validation in BC lines	Häberle et al. (2007)	
Dream	7BS	—	<i>Xgwm46</i>	FHB severity	Plant height	Dream/4* Lynx, 127 BC2F4 lines	QTL validation in BC lines	Häberle et al. (2007)	

SPRAY, spray inoculation; SFI, single floret inoculation.

et al. 2005a) indicating that this chromosome carries another stable QTL for resistance to fungal spread. Recently, the 6B QTL was named *Fhb2* and mapped as a single Mendelian factor in a fine mapping population 2 cM from the SSR locus *Xgwm644* (Cuthbert et al. 2007).

In a DH population that was originally described as 'Wuhan 1' × 'Maringa' (Somers et al. 2003), but later corrected to 'Wuhan 1' × 'Nyu Bai' (McCartney et al. 2007), several QTL were detected for different components of resistance depending on the phenotyping methods applied. Two type 2 resistance QTL were found, one on 2DL (resistant allele from 'Wuhan 1') and one on 3BS (resistant allele from 'Nyu Bai'). For disease severity after spray inoculation, two QTL were detected on 3BSc (resistant allele from 'Nyu Bai') and 4BS (resistant allele from 'Wuhan 1'). Two QTL for DON content after spray inoculation were detected on 3BS and 5AS (both resistant alleles derived from 'Nyu Bai'). In a population DH181 (a line selected from the cross 'Sumai 3' × 'HY368') crossed with 'AC Foremost', Yang et al. (2005a) reported seven QTL for type 1 resistance, four QTL for type 2 resistance and six QTL for resistance to kernel infection. QTL on 2DS, 3BS and 6BS were associated with all three traits. Recently, also in a 'Chinese Spring' 'Sumai 3' chromosome 7A substitution line (CS-SM3-7ADS), a major QTL for type 2 resistance was found on 3BS and smaller effect QTL on 2D and 4D (Ma et al. 2006b).

Marker haplotypes have been used to compare QTL regions of FHB resistant and susceptible lines (Bai et al. 2003, Liu and Anderson 2003b, McCartney et al. 2004, Yang et al. 2006, Yu et al. 2006). Using five SSR markers around *Fhb1*, Liu and Anderson (2003a) detected eight haplotypes on 54 FHB-resistant wheat lines. Bai et al. (2003) showed that several FHB-resistant lines related to 'Sumai 3' have similar SSR and AFLP marker alleles at *Fhb1*. The largest set of genotypes and markers was analysed by McCartney et al. (2004) who reported allele sizes of 41 SSR markers on 79 wheat lines. The same marker haplotype as 'Sumai 3' for the SSR markers *Xgwm493*, *Xbarc147* and *Xgwm533* (spanning *Fhb1*), was found in seven genotypes, including the highly resistant varieties 'Ning 7840', 'Ning 984037', ND2710, and CM-82036. In a similar approach, Yu et al. (2006) analysed 59 Asian wheat landraces using SSR and AFLP markers. Chinese resistant landraces displayed broader genetic diversity than accessions from Japan and several highly resistant Asian landraces differed for some of the known QTL regions (3BS, 5A, 6BS) in their SSR marker haplotypes from that of 'Sumai 3', suggesting that several Asian landraces carry some different QTL than 'Sumai 3'.

Although 'Sumai 3' has been shown to possess the alleles contributing to enhance FHB resistance at several QTL, it also possesses negative alleles at some loci. For example, in the 'Sumai 3' × 'Stoa' population, 'Sumai 3' contributed the negative alleles for the QTL on chromosomes 2AL and 4B (Waldron et al. 1999, Anderson et al. 2001). In two populations: 'Sumai-3' × 'Nobeokabozu komugi' and 'Sumai 3' × 'Gamenya', a significant QTL was detected on chromosome 2DS near the *rht8/Rht8* semi dwarfing gene locus. Interestingly, both alleles from the FHB susceptible variety 'Gamenya' and from the resistant variety 'Nobeokabozu komugi' enhanced FHB resistance and reduced DON accumulation compared to the 'Sumai 3' allele (Handa et al. 2008). The 'Sumai 3' allele at this QTL decreased plant height by about 10 cm indicating that 'Sumai 3' possesses a semi-dwarf allele at the *Rht8* locus. The authors identified and mapped a

Table 3: Marker-assisted germplasm evaluation studies for *Fusarium* head blight resistance in wheat

Markers	Plant material	Phenotyping	Comment	References
2 SSR markers and 16 AFLP primer combinations	65 cultivars with varying head blight resistance (type 2)	<i>Fusarium graminearum</i> , SFI: 1 greenhouse and 1 field exp.	Genetic diversity for AFLP and SSR at <i>Fhb1</i>	Bai et al. (2003)
5 SSR markers	74 wheat lines	–	SSR haplotyping for <i>Fhb1</i>	Liu and Anderson (2003b)
17 RAPD primers	35 wheat lines	<i>Fusarium graminearum</i> , SPRAY: 1 field exp.	Genetic diversity using RAPDs	Sun et al. (2003)
41 SSR markers	79 wheat lines	<i>Fusarium graminearum</i> , SPRAY: 2 field exp.	SSR haplotyping for 6 QTL regions	McCartney et al. (2004)
5 SSR markers	36 Asian wheat lines	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp., SPRAY: 2 field exp.	SSR markers for <i>Fhb1</i> and <i>Fhb2</i>	Yang et al. (2006)
25 SSR markers and 24 AFLP primer combinations	58 Asian wheat accessions	<i>Fusarium graminearum</i> , SFI: 1 greenhouse exp.	SSR and AFLP haplotyping for 6 QTL regions	Yu et al. (2006)
282 DNA markers (SSR, STS)	WSY and its parents: Sumai 3, Wangshuibai, Nobeokabouzu	<i>Fusarium graminearum</i> , grain spawn: field exp., SFI: 1 exp.	Haplotype analysis of a selection from three resistant parents	Shi et al. (2008)

SPRAY, spray inoculation; SFI, single floret inoculation.

multidrug resistance-associated protein (*MRP*) gene at the QTL closely linked to the SSR locus *Xgwm261* and suggested that *MRP* may be associated with type 2 resistance and reduced DON accumulation. In conclusion, Handa et al. (2008) hypothesized that the QTL on chromosome 2DS is a gene complex consisting of morphological traits modulated by *rht8/Rht8* associated with type 1 resistance and specific gene(s) controlling type 2 resistance by detoxification of DON, like *MRP*. In a similar chromosomal region on 2DS, QTL were detected deriving from the susceptible cultivar ‘Alondra’ (Shen et al. 2003a), and from the resistant cultivars ‘Wangshuibai’ (Jia et al. 2005) and ‘Nyu Bai’ (Somers et al. 2003).

The Chinese landrace ‘Wangshuibai’, which possesses high and stable resistance, has received considerable attention as an alternative source for improving FHB resistance. Because ‘Sumai 3’ and ‘Wangshuibai’ were considered not related by descent, the expectation was to find novel QTL in ‘Wangshuibai’. This was supported by the finding that for several SSR and AFLP markers around the 3BS QTL ‘Wangshuibai’ showed the same marker alleles as ‘Nyu Bai’ (McCartney et al. 2004) but slightly different allele sizes than ‘Sumai 3’ (Bai et al. 2003, Liu and Anderson 2003b, McCartney et al. 2004). Several groups have been working on mapping ‘Wangshuibai’s’ *Fusarium* resistance using different mapping populations. In all mapping studies for type 2 resistance, the largest effect was found on 3BS with maximum R^2 values of 17–37.3% as shown in Table 1 (Lin et al. 2004, Zhang et al. 2004, Zhou et al. 2004, Ma et al. 2006a, Yu et al. 2008). Similarly, Mardi et al. (2005) found a significant QTL on 3BS for field resistance evaluated in spray inoculated field tests. Jia et al. (2005) reported six QTL, including the 3BS QTL in naturally infected experiments. Lin et al. (2006) analysed their ‘Wangshuibai’-derived population for FHB incidence as a measure for type 1 resistance and found QTL effects on 2D, 4B and 5A, but not 3B. In conclusion, ‘Wangshuibai’ possesses either the same QTL or a functionally similar allele at *Fhb1* as its major component of type 2 resistance. Recently, unpublished data have indicated that several FHB resistance sources of Asian origin, including ‘Sumai 3’, ‘Nyu Bai’ and ‘Wangshuibai’ share the same sequence for candidate genes in the *Fhb1* region (Liu et al. 2006, S. Liu, personal communications).

For field resistance, a range of further QTL have been described (see Table 1 for details). As an example in the

‘Wangshuibai’ × ‘Alondra’s’ DH population, QTL for FHB severity measured in naturally infected field experiments were detected on chromosomes 2B, 3BS, 4B, 5B and 7A by Jia et al. (2005). In spray inoculated trials, Lin et al. (2006) found significant QTL effects for FHB incidence on 2D, 4B and 5A.

The Korean cultivar ‘Chokwang’ was found to carry significant type 2 FHB resistance QTL on chromosomes 4BL and 5DL, but not on 3BS (Yang et al. 2005b). This cultivar, despite originating from the Asian gene pool, seems to carry QTL different from those in ‘Sumai 3’ and its relatives and therefore has high potential in breeding, as a source of alternative or complementary resistance genes.

Resistance Sources from Latin America

The Brazilian cultivar ‘Frontana’ was described as a source of FHB resistance by Schroeder and Christensen (1963). An extensive mapping study using 180 DH lines derived from a ‘Frontana’ × ‘Remus’ cross was evaluated by Steiner et al. (2004) for resistance using single floret inoculations and spray inoculations in replicated field tests. Stable QTL for field resistance were detected on chromosomes 3A and 5A, and less stable QTL on 2B and 6B. A QTL with a minor effect on resistance to fungal spread in ‘Frontana’ was detected on chromosome 2B. In a population of ‘Frontana’ × ‘Falat’, Mardi et al. (2006) confirmed the 3AL QTL of ‘Frontana’ and detected an additional effect on chromosome 7AS. In summary, ‘Frontana’ appears as a source of moderate type 1 FHB resistance which is possibly partly based on morphological or developmental traits, such as hard glumes and narrow flower opening, although no specific results to support this hypothesis have been published so far. To date, no large-effect QTL has been detected in any ‘Frontana’ derived population.

Winter Wheat Resistance Sources

While large investments went into mapping spring wheat resistance sources, less emphasis was put into molecular genetic analysis of winter wheat varieties for FHB resistance. This probably reflects that the most FHB resistant lines were found in spring wheat and that severe FHB epidemics since 1993 hit particularly the huge spring wheat areas of the northern USA and southern Canada (McMullen et al. 1997).

So a very urgent need to speed up breeding for FHB resistance was evident in the spring wheat growing areas of the northern Great Plains in North America. Variation for resistance to FHB is significant in different native winter wheat gene pools, for example in Europe (Snijders 1990, Buerstmayr et al. 1996) and in Japan (Nishio et al. 2004). Genotypes with quantitative resistance have been found by chance or by targeted screening of breeding lines or germplasm collections for the trait. Even in breeding programmes where no specific FHB testing was performed, variation for resistance could be detected (Snijders 1990, Buerstmayr et al. 1996, Groth et al. 1999). In some wheat growing areas, such as the UK, the majority of the current cultivars were highly susceptible (Gosman et al. 2007), possibly because *Fusarium* diseases of cereals were not prevalent in Britain in the past. However, the incidence of FHB has increased in recent years also in the UK (Gosman et al. 2007). In other parts of Europe, like in Germany, FHB resistance became an important trait for cultivar registration. Screening and selection for improved FHB resistance has therefore been implemented in practical breeding by a range of breeders since more than a decade (Spanakakis 2003).

The first winter wheat population that was analysed for FHB resistance and with several storage protein markers was 'Sincron' × F1054W from Romania (Ittu et al. 2000). Storage protein markers on the T1BL.1RS translocation chromosome and on chromosome 1D were associated with enhanced type 2 FHB resistance derived from 'Sincron'. However, only a few markers were available for QTL detection in this population. Gervais et al. (2003) performed the first full scale QTL analysis in winter wheat using the mapping population 'Renan' × 'Recital'. Several QTL were detected, with the largest effect QTL being mapped to 2A, 2BS and 5AL. Overlap of FHB resistance QTL with plant height QTL (2BS, 5A) and flowering date QTL (2BS) was observed. The type 2 resistance of F201R, a FHB resistant breeding line from Romania, was analysed in RILs from a cross with 'Patterson' (Shen et al. 2003b). They used bulked segregant analysis to detect promising markers first and screened only those markers on the entire population. Using this approach, they found three QTL derived from the resistant line F201R on chromosomes 1B, 3A and 5A and one QTL derived from susceptible 'Patterson' on chromosome 3D. Gilsinger et al. (2005) evaluated 100 RILs from the cross 'Patterson' × 'Goldfield' for FHB incidence in six field experiments. In addition, data for flower opening width and flower opening duration were collected from five experiments. Bulked segregant analysis was used to map QTL for FHB incidence. The region *Xbarc200-Xgwm210* on chromosome 2BS was associated with FHB incidence and narrow flower opening. Another unlinked marker on 2B was also associated with both traits, but at lower significance. The marker *Xgwm344* mapped to chromosome 7B and was associated with FHB incidence, but not with flower opening.

The Swiss cultivar 'Arina' has long been known for its moderate FHB resistance (Snijders 1990, Buerstmayr et al. 1996) and has been used in three independent QTL mapping studies to date: 240 RILs from the cross 'Arina' × 'Forno' (Paillard et al. 2004), 93 DHs from the cross 'Arina' × NK93604 (Semagn et al. 2007) and 116 DHs from the cross 'Arina' × 'Riband' (Draeger et al. 2007). In the 'Arina' × 'Forno' cross, both stable and unstable QTL for FHB severity assessed in spray-inoculated field experiments were reported. Among the eight listed QTL, the more constant QTL effects were found on chromosomes 4AL and 6DL of 'Arina'

and 5BL of 'Forno'. The QTL on 5BL and 6DL overlapped with plant height and/or heading, indicating either linkage or pleiotropy between morphological/developmental traits and FHB severity (Paillard et al. 2004). In the 'Arina' × NK93604 population, QTL derived from 'Arina' were detected on 1BL and 6BS, while QTL on 1AL and 7AL were detected from NK93604 (Semagn et al. 2007). In the 'Arina' × 'Riband' cross, 10 QTL were detected for different traits associated with FHB, but only the QTL at the *Rht-D1* locus on chromosome 4DS was significant in four of five independent phenotyping experiments. The semi-dwarf allele (*Rht-D1b*) inherited by 'Riband' contributed to significantly increased susceptibility. The authors presented evidence that this association could be due to pleiotropy or linkage of deleterious genes to the *Rht-D1b* semi-dwarfing allele rather than differences in height *per se*. The association of *Rht-D1b* with increased susceptibility to FHB was verified in an independent mapping study based on the population 'Rialto' × 'Spark' (Srinivasachary et al. 2008). Additional evidence that presence of *Rht-D1b* impairs FHB resistance significantly was provided by Gosman et al. (2007) and Buerstmayr et al. (2008). Further research is needed to determine whether the association of *Rht-D1b* with susceptibility to FHB is due to tight linkage or to pleiotropy and to further investigate the relationship of other widely used dwarfing genes like *Rht-B1b* and *Rht8* with FHB response. Surprisingly, there is close to no overlap in the results of QTL positions and effects among the three independent studies using 'Arina'. The QTL detected in the different 'Arina' populations depended largely on the susceptible parent, indicating that 'Arina's' resistance appears not to be amenable to MAS.

Another winter wheat mapping project used a RIL population derived from the cross 'Dream' × 'Lynx' (Schmolke et al. 2005). Of four QTL detected, three were derived from FHB resistant 'Dream' (6AL, 2AL, 7BS). The fourth QTL was associated with the T1BL.1RS translocation chromosome present in the susceptible parent 'Lynx'. A winter wheat RIL population derived from the cross 'Ritmo' × 'Cansas' was tested in four spray-inoculated field experiments (Klahr et al. 2007). QTL for field resistance were detected on seven chromosome segments (1BS, 1DS, 3B, 3DL, 5BL, 7BS and 7AL), two of which strongly overlapped with plant height and/or heading date QTL (5BL, 7AL) indicating disease escape effects rather than physiological resistance at these two QTL. Schmolke et al. (2008) reported two QTL for field resistance in the population G16-92 × 'Hussar' mapping to chromosomes 1A (resistant allele from the susceptible parent 'Hussar') and 2BL (resistant allele from resistant G16-92). While the QTL on 1A was associated with plant height, the 2BL QTL was independently inherited from morphological traits.

Liu et al. (2007) used 248 RILs from the cross of the moderately FHB resistant Missouri winter wheat 'Ernie' with the susceptible breeding line MO94-317 to map QTL for resistance to fungal spread. Stable QTL were detected on chromosomes 2B, 3B, 4BL and 5A and none of these FHB resistance QTL was associated with presence or absence of awns, earliness, or the number of spikelets per spike.

Resistance in Tetraploid Wheat

In tetraploid durum wheat, the need for improving FHB resistance is certainly at least as urgent as for hexaploid wheat. Current durum wheat cultivars are generally highly susceptible

to FHB (Stack et al. 2002). Durum wheat is almost exclusively used for human consumption, leading to a high risk that toxin-contaminated grain may enter the food chain. Introgressing FHB resistance from hexaploid into tetraploid wheat has had only limited success so far (H. Buerstmayr, unpublished results). Because of the limited variation for FHB resistance available in *T. durum* its cultivated or wild relatives like *Triticum dicoccum* and *Triticum dicoccoides* may provide alternative sources for resistance genes (Buerstmayr et al. 2003b, Oliver et al. 2007). So far the published reports on mapping FHB resistance in tetraploid wheat were indeed based on resistance derived from related species of tetraploid wheat. Ban and Watanabe (2001) found that the 3A chromosome from the *T. dicoccoides* accession 'FA-15-3' (syn. 'Israel A') provided resistance to head bleaching after *Fusarium* inoculation. Stack et al. (2002) and Otto et al. (2002) developed a single chromosome recombinant population for the 3A chromosome of 'FA-15-3' based on the cross of 'Langdon' × 'Langdon' (*T. dicoccoides*-3A). A QTL for resistance to fungal spread was located near *Xgwm2* on 3AS. Recently, this QTL region was saturated with additional markers. The QTL region of about 10 cM is flanked by two TRAP markers and peaks near two SSRs (*Xgwm2*, *Xbarc45*), a region not homoeologous to *Fhb1* (Chen et al. 2007). In a similar approach, Kumar et al. (2007) mapped a significant QTL to chromosome 7AL derived from the *T. dicoccoides* accession PI478742, in a chromosomal region where several QTL in hexaploid wheat also have been found (Fig. 1). In a mapping population derived from the cross of the *T. durum* cultivar 'Strongfield' with the *Triticum cartholicum* cultivar 'Blackbird', two significant QTL for FHB spread were found, one from each of the two parents (Somers et al. 2006). At the QTL on 2BS, 'Strongfield' carried the resistant allele and at 6BS 'Blackbird'. In both regions, QTL also have been found in different hexaploid wheat populations. Notably, the 6BS QTL in 'Blackbird' appears coincident with *Fhb2*.

FHB Resistance in Related Species of Wheat

Based on previous evaluations of the intervarietal substitution series of *Triticum macha* in 'Hobbit-sib' (Mentewab et al. 2000), a single chromosome recombinant population for chromosome 4A derived from 'Hobbit-sib' × 'Hobbit-sib' (*T. macha*-4A) was generated. This DH population proved useful to map a *T. macha* derived QTL for type 1 resistance on the short arm of chromosome 4A co-segregating with *Xgwm165* (Steed et al. 2005).

Shen et al. (2004) evaluated several wheat substitution and translocation lines with *Thinopyrum ponticum* (syn. *Lophopyrum ponticum*). They found that wheat lines possessing chromosome 7el from two different *Thinopyrum ponticum* sources expressed different FHB response. While chromosome segment 7el₂ showed enhanced FHB resistance, 7el₁ did not (Shen et al. 2004). For mapping, they developed a recombinant population derived from two chromosome 7el(7D) disomic substitution lines with different origins and different reactions to FHB. A single QTL contributing resistance to fungal spread was thus mapped to the distal region on the long arm of the 7el chromosome. Further work is underway to generate translocations possessing only a short piece of the alien chromosome around the resistance QTL (Shen and Ohm 2007).

Several further alien species that have potential as donors of FHB resistance genes have not been genetically mapped so far,

like *Elymus humidus*, *Elymus racemiflorus*, *Roegneria kamoji* and *Leymus racemosus* (Ban 1997, Chen et al. 2005, Oliver et al. 2005). To incorporate *L. racemosus* FHB resistance in wheat several addition, substitution and translocation lines were generated by Chen et al. (2005). FHB resistance in lines with a single chromosome or a chromosome segment from the wild species was lower than that of the alien parent indicating FHB resistance in *L. racemosus* is oligogenic and quantitative like in wheat. Some alien species probably possess highly effective FHB resistance genes leading to an almost immune phenotype. No such resistance genes for FHB have yet been detected in cultivated wheat. Mapping and tagging of such types of 'complete' resistance would be of great potential for wheat breeding. In case, a single gene alone would be sufficient to ensure a high level of FHB resistance, breeding of resistant cultivars may be feasible much easier and faster than now. On the other hand, reliance on major gene resistance, if ever available, bears a high risk of sudden resistance breakdown, as the experience with other wheat diseases like the rusts and powdery mildew shows.

Validation of FHB Resistance QTL and MAS

Marker-assisted selection for FHB resistance has been a goal for breeders for more than a decade (Van Sanford et al. 2001). The best validated gene for FHB resistance is *Fhb1* on chromosome 3BS, which was found in numerous independent mapping studies based on Chinese FHB resistant sources. Using linked SSR markers or phenotypic selection *Fhb1* has been introduced into many breeding populations worldwide, including the USA (Del Blanco et al. 2003, Zhou et al. 2003, Pumphrey et al. 2007), Canada (Yang et al. 2003, McCartney et al. 2007), Australia (Xie et al. 2007) and Germany (Miedaner et al. 2006). As an example, Pumphrey et al. (2007) used 19 pairs of NIL for *Fhb1* derived from an ongoing breeding programme. The average reduction in disease severity between NIL pairs was 23% for disease severity and 27% for kernel infection, but with large variation. The presence of *Fhb1* did not result in a significant improvement in FHB resistance in all NIL pairs, but this group later demonstrated successful implementation of MAS for this QTL (Anderson et al. 2007). Miedaner et al. (2006) showed that MAS for three FHB resistance QTL simultaneously (3B and 5A from CM-82036, and 3A from 'Frontana') was highly effective in enhancing FHB resistance in German spring wheat backgrounds. The QTL on 3BS and 5A contributed more to FHB resistance than the 3A QTL from 'Frontana'. FHB resistance was the highest in recombinant lines with multiple QTL, especially 3B plus 5A, combined. Derived from the same progeny, Wilde et al. (2007) compared phenotypic selection with marker-based selection in a four-way cross-combination segregating for resistance derived from CM-82036 and 'Frontana'. Selection gain for FHB resistance and reduced DON content was larger when phenotypic selection was applied compared to marker-based selection. However, selection gain per unit time was larger with marker-based selection. The authors concluded that marker-based selection for major QTL (3BS, 5A) is an efficient tool for quickly improving the FHB resistance level in adapted, high-yielding wheat germplasm. Wilde et al. (2007) further stated that to exploit the full range of quantitative variation for resistance, phenotypic selection should follow marker-based selection to incorporate positive alleles that have gone undetected in QTL-mapping studies. The

Chinese breeding line 'WSY' was phenotypically selected from the cross 'Sumai 3'/'Wangshuibai'/'Nobeokabouzu komugi', it showed a higher resistance to FHB than any of its parents (Shi et al. 2008). SSR marker haplotyping revealed that 'WSY' possessed the marker alleles on 1BL, 2BL, 5AS and 7AL from 'Sumai 3', on 2AS, 2DS, 3AS and 6BS from 'Wangshuibai', and on 3BS from 'Nobeokabouzu-komugi' (Shi et al. 2008).

FHB resistance QTL alleles from 'Nyu Bai', 'Sumai 3' and 'Wuhan 1' were evaluated for their effect on FHB-associated traits including DON content as well as plant height, heading date and grain quality traits in Canadian spring wheat backgrounds by McCartney et al. (2007). The 'Wuhan 1' 4B FHB resistance QTL was the most effective QTL enhancing FHB resistance but was associated with a significant increase in plant height. The 'Wuhan 1' 2D, 'Nyu Bai' 3BSc, 'Sumai 3' 3BSc, 'Nyu Bai' 5AS and 'Sumai 3' 5AS alleles also enhanced FHB resistance. Notably, the 'Nyu Bai' and 'Sumai 3' 3BS alleles were the least effective of the FHB resistance alleles in this experimental series. Again, FHB resistance tended to increase with more FHB resistance alleles introgressed into the elite genetic background.

In European winter wheat, Häberle et al. (2007) evaluated the effect of two QTL on 6AL and 7BS derived from the cultivar 'Dream' (Schmolke et al. 2005). Each QTL alone resulted in an average reduction on FHB severity of 27% compared to the lines without the resistant allele and lines with both QTL combined showed 36% reduced FHB severity. Thus, MAS also proved successful for moderately strong QTL derived from winter wheat.

Chromosome View of Repeatable QTL Regions

More than 100 QTL for FHB resistance have been reported in wheat and reviewed herein. Given the relatively small population sizes used in some mapping experiments, a significant portion of these are certainly false positives. However, many QTL regions have been detected in more than one mapping population, thus greatly increasing the chances that the QTL is a real effect. We count 22 such regions after reviewing the 52 papers published to date. These are on chromosomes 1B (two regions), 1D, 2A (2), 2B (2), 2D (2), 3A, 3B (2), 3D, 4B, 4D, 5A, 5B, 6A, 6B, 7A and 7B (2). Flowering date and plant height are morphological characteristics known to have dramatic effect on FHB symptoms, especially when the inoculation methods mimic the natural conditions (e.g. grain spawn instead of spraying conidia at flowering time for each entry). It is unfortunate that only a few of the field-based FHB evaluations included an analysis of these traits. Even without complete analysis of these important morphological traits, 10 of the 22 QTL regions listed above were also associated with increased plant height and four were associated with flowering date. QTL on 2D, 4B and 4D overlapping with plant height are possibly pleiotropic or linked effects of *Rht* genes. Further investigations are needed to clarify this association. The B genome has the most repeatable QTL regions (11), more than the A (5) and D (4) genome combined. This may be at least partially an artefact of the generally higher rates of polymorphism observed with the B genome. The D genome maps are particularly lacking full marker coverage. The following is a brief synopsis of each of the 22 QTL regions:

1B: The region associated with FHB resistance in 'Sincron', F201R, 'Alondra's', 'Lynx', and 'Cansas' had R^2 ranging from

12% to 16%. In these lines, resistance is associated with the T1BL.1RS translocation chromosome. It remains currently unclear whether the resistance locus resides on the rye segment or is linked to it. The region centred on *Glu-B1* was found in the CIMMYT wheat 'Seri82' and two cultivars with Chinese heritage with R^2 ranging from 8% to 10%.

1D: QTL with moderate effects were reported in two European winter wheat varieties and one spring wheat.

2A: The region on 2AS is derived from Chinese sources, but R^2 varied from 3% to 27%. The QTL region on 2AL, R^2 10–14%, was associated with greater resistance deriving from the susceptible parent 'Stoa' analysed in the cross with 'Sumai 3'.

2B: Almost the entire length of this chromosome is covered by QTL intervals, ranging in R^2 from 4% to 29%. Resistance sources contributing QTL to this chromosome include Chinese, native sources from European and US winter wheat, and durum wheat. The 'Renan' QTL was associated with flowering date and height and the 'Goldfield' QTL was associated with narrow flower opening.

2D: The QTL region near *Rht8* is associated with plant height. The other QTL region was found exclusively in materials of Chinese origin and has shown consistent effects of 9–17% and has been associated with multiple FHB traits, including reduced incidence.

3A: The QTL near *Xgwm2* was detected in *T. dicoccoides*, Chinese, South American, and European winter wheat backgrounds with R^2 ranging from 8% to 37%. One study showed a clear association with lower incidence.

3B: *Fhb1*, near *Xbarc133* has been detected in at least 26 different studies. Another QTL region, designated 3BSc has a moderate effect from Chinese materials (4–8%) and was also found in 'Ernie', a US winter wheat with an R^2 of 13%.

3D: A region centred near *Xgwm341* with moderate effects (R^2 4–11%) was found in the susceptible US winter wheat 'Patterson' and the moderately resistant European winter wheat 'Cansas'.

4B: This QTL region has been found in Asian resistance sources and 'Ernie', with one report of lower incidence. R^2 range from 5% to 14%, but the study using 'Wuhan 1' reported an association with plant height, possibly correlated with *Rht-B1*.

4D: The QTL at *Rht-D1* was reported in two independent studies so far. The association of the semi-dwarfing allele (*Rht-D1b*) with significantly increased FHB susceptibility appears a common phenomenon, because *Rht-D1b* cultivars are generally quite susceptible. Whether or not increased susceptibility of *Rht-D1b* lines is a pleiotropic effect or due to linked susceptibility genes warrants further research.

5A: *Qfhs.ifa-5A* has long been known as a consistent QTL associated primarily with reduced incidence (type 1 resistance). Interestingly, QTL in this region have been found in materials with Asian, South and North American, and European origins.

5B: QTL were mapped to different parts of this chromosome. Possibly, the European winter wheat varieties 'Cansas' and 'Forno' share a common QTL.

6A: This QTL has been identified in two studies, but was associated with plant height in one.

6B: *Fhb2* has been identified in numerous studies using Chinese resistance sources with R^2 ranging from 4% to 24%. A region overlapping *Fhb2* was found in the *T. carthlicum* cultivar 'Blackbird' that explained 23% of the variation.

7A: A region near *Xgwm276* was found in several wheat varieties of Chinese origin. A QTL with moderate effect in the susceptible winter wheat 'Ritmo' was associated with flowering date and plant height.

7B: The QTL from 'Dream' was associated with both flowering date and height effects in a validation population. A second QTL of moderate effect, R^2 7–8%, was found in a line with Chinese origin and a US winter wheat.

Conclusions

Clearly, the most repeatable QTL are those on chromosomes 3BS (*Fhb1*), 5AS (*Qfhs.ifa-5A*) and 6BS (*Fhb2*). For the purposes of MAS, diagnostic markers are available for only *Fhb1*. Other FHB QTL have also been used in MAS programmes, especially in cases where breeders are familiar with marker allele types of the QTL donors and the recipient germplasm. More diagnostic markers should be developed for QTL to be easily adopted by breeders. Therefore, the emphasis of future research activities should be to discover and/or develop more diagnostic markers for the most repeatable QTL reported. Fine mapping populations that examine several hundred to several thousand gametes can be used both for QTL validation and finding diagnostic markers with close linkage to the QTL. While in hexaploid wheat both conventional and marker-assisted breeding for improving FHB resistance have made significant progress, in tetraploid durum wheat good sources of resistance are still sparse and more work is needed to identify resistant germplasm and to decipher its FHB resistance.

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