

Genome distribution of QTL for Fusarium head blight resistance in European wheat germplasm

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INTRODUCTION

Fusarium head blight (FHB) is a wheat disease of global significance. Breeding and cultivation of resistant varieties are very efficient means to cut the risk of FHB infection. However, FHB resistance shows polygenic inheritance and is significantly affected by environment (Buerstmayr et al. 2002). A limited genetic diversity in the Central European gene pool gives reason to suppose that FHB resistance depends—at least partially—in different cultivars on the same loci. Therefore, genetic analyses with the aid of molecular markers may shed some light on the relationship of resistances from different genotypes. The objective of the present study was to compare the locations of FHB resistance QTL (quantitative trait locus/loci) from four different winter wheat populations among each other and with published resistance QTL from further European winter wheats.

MATERIALS AND METHODS

Populations were derived from crosses of the FHB resistant *Rht-D1a* cultivars Apache, History, Romanus and Solitär with the susceptible *Rht-D1b* semi-dwarfs Biscay, Rubens, Pirat and Travix, respectively. Phenotypic data assessment and QTL analysis for FHB severity, plant height and ear emergence time in Apache/Biscay, History/Rubens and Romanus/Pirat were described in Voss et al. (2008) and Holzappel et al. (2008), respectively. Mapping population Solitär/Travix consisting of 180 F_{4,6} recombinant inbred lines was analysed in a similar way in four environments during 2005 and 2006 using spray inoculation technique with a *F. culmorum* conidia suspension.

Comparability of our QTL maps was achieved by common simple sequence repeats (SSRs) and co-migrating amplified fragment length polymorphisms (AFLPs). Regarding our populations, confidence intervals of QTL were compared. In the case of a clear overlap, QTL were considered as coincident. In some cases, a direct comparison of published QTL maps with our maps was not possible due to the lack of corresponding markers in QTL regions. For that, reference maps (e.g. Somers et al. 2004; Sourdille et al. 2004) were used for comparison with the cMap software (Fang et al. 2003). Marker order and linkage distances of those reference maps also composed the backbone of the integrated QTL map which was drawn using MapChart software version 2.1 (Voorrips 2002). In this schematic map, QTL for FHB severity which were coincident

among our mapping populations were plotted. Further, all QTL of published European winter wheat mapping populations, whose most likely position (marker interval, LOD curve) overlapped with QTL confidence intervals in our study, were included. Regarding the published studies, QTL for several FHB related traits (e.g. type I resistance, type II resistance, DON accumulation, FHB severity, fusarium damaged kernels) were considered.

RESULTS

QTL analysis revealed 13, 8 and 14 QTL for FHB severity in Apache/Biscay, History/Rubens and Romanus/Pirat, respectively (Holzappel et al. 2008). In the population Solitär/Travix, 18 significant ($P < 0.001$) QTL were detected of which nine showed significant ($P < 0.05$) QTL \times environment interactions. The QTL with the highest substitution effect, reducing FHB severity by 14.2% relative to lines without resistance allele, was detected at the *Rht-D1* locus on chromosome 4DS. The donor of the resistance allele was Solitär carrying the wild-type allele *Rht-D1a*. This QTL coincided with a major QTL for plant height which shortened the plants on average by 8.0 cm. Another two major QTL ($R^2 > 10\%$ in at least one environment) were located on the wheat-rye translocated chromosome 1BL.1RS and chromosome 7A. The resistance allele donors were the susceptible cultivar Travix (1BL.1RS) and the resistant cultivar Solitär (7A). Both QTL were not associated with QTL for plant height or ear emergence time.

Comparison of QTL positions among the four populations showed that the QTL at *Rht-D1* was common to all populations (Fig. 1). Three QTL overlaps were counted for chromosome 1BL. The donors of the resistance alleles were History, Biscay and Pirat (Fig. 1). QTL in six genome regions (1AS, 1Dc, 2Bc, 4BL, 4DL and 5AL) were detected that coincided between two populations.

An extension of the comparison considering already published results from European winter wheat identified a total of 27 genome regions repeatedly associated with FHB resistance and distributed over 18 chromosomes (Table 1). For 10, 4, 10 and 14 FHB QTL from Apache/Biscay, History/Rubens, Romanus/Pirat and Solitär/Travix, respectively, corresponding overlaps were found. The most frequent coincidences of QTL positions were observed on chromosomes 4DS (9 at *Rht-D1*) and 1RS (6) (Fig. 1), three overlaps each were

counted on chromosomes 1AS, 1Bc 1BL, 1DS, 2Bc, 3Bc, 4DL, 5AS, 5AL, and 6Ac (Table 1).

Table 1: Genome regions with FHB resistance QTL overlapping between European winter wheats

Genome region	Chr. ¹	Marker locus	No. of overlaps
1	1AS	<i>Xwmc818</i>	3
2	1AL	<i>Xwmc59</i>	2
3	1RS	<i>Xiag95</i>	6
4	1Bc	<i>Xgwm18</i>	3
5	1BL	<i>Xbarc80</i>	3
6	1DS	<i>Xbarc149</i>	3
7	1Dc	<i>Xbarc148</i>	2
8	2Ac	<i>Xgwm425</i>	2
9	2Bc	<i>Xgwm374</i>	3
10	3AS	<i>Xgwm2</i>	2
11	3Bc	<i>Xcfa2134</i>	3
12	3Dc	<i>Xgwm52</i>	2
13	4AL	<i>Xgwm160</i>	2
14	4BL	<i>Xgwm375</i>	2
15	4DS	<i>Rht-D1</i>	9
16	4DL	<i>Xgwm265</i>	3
17	5AS	<i>Xgwm154</i>	3
18	5AL	<i>Xwmc410</i>	3
19	5AL	<i>Xgwm410</i>	2
20	6Ac	<i>Xgwm82</i>	3
21	6AL	<i>Xwmc773</i>	2
22	6Bc	<i>Xgwm608</i>	2
23	6BL	<i>Xgwm219</i>	2
24	7Ac	<i>Xbarc121</i>	2
25	7BS	<i>Xgwm43</i>	2
26	7BL	<i>Xwmc276</i>	2
27	7DL	<i>Xbarc172</i>	2

¹ Chr., chromosome; S, short arm; L, long arm; c, centromere-near region

DISCUSSION

In the population Solitär/Travix, 18 significant QTL for FHB severity were found of which nine interacted significantly with the environments. A high number of QTL and QTL × environment interactions was observed in many studies (Gervais et al. 2003; Paillard et al. 2004; Draeger et al. 2007; Klahr et al. 2007; Srinivasachary et al. 2008) and thus seems to be characteristic for European winter wheat. The QTL which explained most of the variance for FHB severity in Solitär/Travix was located at the *Rht-D1* locus, as was also observed for Apache/Biscay, History/Rubens and Romanus/Pirat (Holzapfel et al. 2008). In a companion study, Voss et al. (2008) already reported that the semi-dwarfing allele *Rht-D1b* enhanced FHB susceptibility by 22 to 53%. This is in agreement with two studies from the UK,

where the same observations were made in different winter wheat populations (Draeger et al. 2007; Srinivasachary et al. 2008).

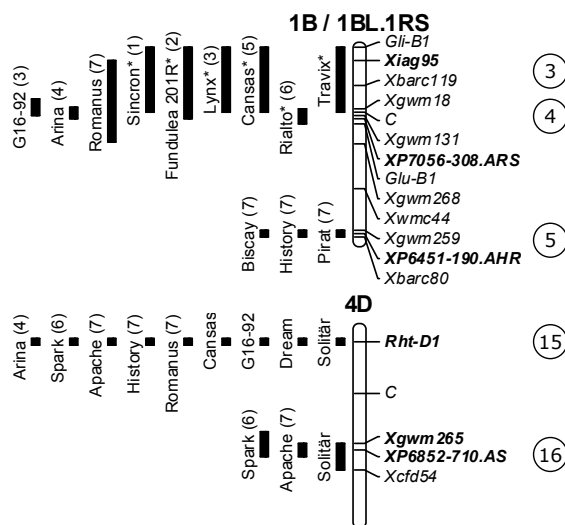


Fig. 1: Genome regions (indicated as numbers in circles referring to Table 1) on chromosomes 1B and 4D repeatedly associated with FHB resistance QTL in European wheat germplasm. Bars represent most likely QTL positions. QTL are identified by their resistance allele donors. Asterisks mark wheats carrying the 1BL.1RS wheat-rye translocation. (1) Ittu et al. 2000; (2) Shen et al. 2003; (3) Schmolke 2004; (4) Draeger et al. 2007; (5) Klahr et al. 2007; (6) Srinivasachary et al. 2008; (7) Holzapfel et al. 2008

Further investigations of our working group confirmed that *Rht-D1* also had major QTL effects in the winter wheat populations Dream (*Rht-D1a*)/Lynx (*Rht-D1b*), Canas (*Rht-D1a*)/Ritmo (*Rht-D1b*) and G16-92 (*Rht-D1a*)/Hussar (*Rht-D1b*) (Fig. 1). Taken together all these studies and the observations made by Gosman et al. (2007) about semi-dwarf UK winter wheats, it appears that the *Rht-D1* genome region is the major source of variation for FHB reaction in European winter wheat. The fact that *Rht-D1b* used in wheat breeding programmes originated from one common genotype (Norin 10) gives evidence that either the same deleterious genes are inherited as linkage drag or that *Rht-D1b* has negative pleiotropic effects on FHB. The characteristics of the protein encoded by *Rht-D1*, an orthologue of the *A. thaliana* GAI (Gibberellin Acid Insensitive) with a so-called DELLA region (Hedden 2003), give strong evidence for pleiotropic effects of the semi-dwarfing gene on FHB reaction. However, as shown in several studies (Draeger et al. 2007; Klahr et al. 2007; Holzapfel et al. 2008; Srinivasachary et al. 2008) semi-dwarf cultivars carry effective resistance loci to counteract the strong negative effect of *Rht-D1b* on FHB reaction.

Analysis of the genome distribution of FHB QTL revealed, in addition to *Rht-D1*, 26 genome regions which were repeatedly associated with FHB resistance in European winter wheat (Table 1). A major resistance allele in or at the wheat-rye translocated chromosome

1BL.1RS in Travix and five other carriers of the translocation (Fig. 1) suggests a meaningful influence of this genome region on FHB resistance. But this association could not be observed in every mapping population: In the populations G16-92/Hussar (Schmolke 2004) and Romanus/Pirat (Holzapfel et al. 2008), which segregated for 1BL.1RS, QTL with smaller effects were found proximal to 1RS on the wheat chromatin. In these populations the FHB-reducing allele was not inherited from the carriers of the translocation, but from G16-92 and Romanus. This suggests two different QTL regions on 1RS and 1Bc (Table 1; Fig. 1). Further, QTL originating from Arina and Rialto collocated with the QTL from G16-92 and Romanus on chromosome 1Bc (Fig. 1).

Although in many cases the effects of QTL varied strongly in different environments and populations and, moreover, different FHB resistance-related traits were measured in some of the studies, coincidences in map position were found for a large number of QTL. This shows that, in spite of the major effect of *Rht-D1*, even minor QTL were identified reliably. QTL originating from resistance sources other than European winter wheat also mapped into those genomic regions (data not shown). All this suggests that FHB resistance is inherited in a complex manner, at least partially by similar genes or genomic regions with varying effects.

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