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Mapping quantitative resistance to septoria tritici blotch in spelt wheat

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Abstract The foliar wheat disease septoria tritici blotch can cause significant yield losses. A source of resistance has been mapped on chromosome 7D of spelt wheat, *Triticum aestivum* L. subsp. *spelta* (L.) Thell. The microsatellite-based genetic map was constructed from a set of 87 single-chromosome recombinant doubled-haploid lines bred from the cross between the landrace 'Chinese Spring' and a 'Chinese Spring'-based line carrying chromosome 7D from spelt wheat. Two regions of the chromosome were associated with isolate-specific QTL expressed one at the seedling and another at the adult plant stage. The seedling resistance locus *QStb.ipk-7D1* was found in the centromeric region of chromosome 7D, which corresponds to the location of the major resistance genes *Stb4* originating from bread wheat cultivar 'Tadinia' and *Stb5* originating from *Triticum tauschii*. The adult resistance locus *QStb.ipk-7D2* was found on the short arm of chromosome 7D in a similar position to the locus *Lr34/Yr18* known to be effective against multiple pathogens. Composite interval mapping confirmed *QStb.ipk-7D1* and *QStb.ipk-7D2* to be two distinct loci.

Keywords *Mycosphaerella graminicola* · QTL mapping · *Septoria tritici* · *Triticum aestivum* L. subsp. *spelta* (L.) Thell

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Introduction

The foliar wheat disease septoria tritici blotch is caused by *Mycosphaerella graminicola* (Fückel) Schröter in Cohn (anamorph *Septoria tritici* Rob ex Desm.). Severe levels of infection can lead to significant yield losses (Hardwick et al. 2001). Resistant cultivars provide an effective, economical and environmentally friendly approach to control septoria tritici blotch epidemics, but until recently

little was known about the genetics of resistance to the disease.

Both qualitative and quantitative resistance have been identified in wheat germplasm. The former typically gives near complete resistance, is isolate specific and is simply inherited (Brading et al. 2002). In contrast, while the latter gives only partial, although often more durable protection, it is not generally isolate specific and is mainly under polygenic control (Jlibene et al. 1994; Simón and Cordo 1998). The 13 major resistance genes mapped to date in bread wheat (*Triticum aestivum* L.) are *Stb1-Stb12* and *Stb15* (McIntosh et al. 2008). A number of quantitative trait loci (QTL) has also been identified (McIntosh et al. 2008). Raman et al. (2009) have identified recently a major gene conferring seedling resistance on wheat chromosome arm 1BS, which is, probably, allelic to *Stb11*.

Some other *Triticum* species have also been identified carrying resistance. *Triticum monococcum*, *T. piramidale*, *T. dicoccoides*, *T. dicoccum*, *T. polonicum*, *T. carthlicum* and *T. macha* have been reported to carry resistance (Arraiano et al. 2001a; Simón et al. 2005b; Singh et al. 2008). Arraiano et al. (2001b) identified the *Stb5* gene on the short arm of chromosome 7D of a synthetic hexaploid wheat. In addition resistance was found in 24 *T. monoccocum* accessions and a single genetic locus, *TmStb1*, was linked to the microsatellite locus *Xbarc174* on chromosome $7A^m$ (Jing et al. 2008). Spelt wheat (*Triticum aestivum* L. subsp. *spelta* (L.) Thell) represents a source of genetic resistance to various diseases, including stem rust (McVey and Leonard 1990), yellow rust (Kema 1992), septoria tritici blotch (Simón et al. 2005b; Singh et al. 2008), and head blight (Wiwart et al. 2004). Simón et al. (2005b) identified substitution lines of chromosome 7D of *T. aestivum* subsp. *spelta* that carried resistance to *Mycosphaerella graminicola*. However, the resistance factor has not been identified. Chromosomes 7B and 7D also carry factors on their short arms which interact to influence resistance to *Puccinia striiformis* (Pink and Law 2009)

A complication in identifying genetic resistance to septoria tritici blotch is a possible interaction between resistance and flowering time, with increased disease severity being associated with earlier flowering cultivars (Van Beuningen and Kohli 1990). Although those traits may not be genetically associated and the association instead may be due to epidemiological factors (Simón et al. 2005a), information is lacking about the position of resistance genes and late-flowering genes in the same germplasm using molecular marker-based approaches to confirm the absence of genetic associations. Association of resistance to *S. tritici* with chromosome 7D of *T. aestivum* subsp. *spelta* (Simón et al. 2005b) may suggest a possible linkage to some locus controlling this trait, because homoeologous group 7 chromosomes are known to carry several loci controlling this trait (McIntosh et al. 2008).

The aim of this research was to genetically map the position of the resistance against septoria tritici blotch on chromosome 7D using a cross between 'Chinese Spring' ('CS') and the chromosome substitution line 'CS' (*T. aestivum* subsp. *spelta* 7D) and to test whether this effect was associated with variation for flowering time.

Materials and methods

Parental screening with several isolates

The landrace 'Chinese Spring' ('CS') and the single-chromosome substitution line 'CS' (*T. aestivum* subsp. *spelta* 7D) (in which 'CS' chromosome 7D has been replaced by *T. aestivum* subsp. *spelta* 7D in the genetic background of 'CS') ('CS' (*T.a.s*.7D)) differed in their reaction to *M. graminicola* infection with one isolate (Simón et al. 2005b). The two lines were tested with a set of Argentinean pathogen isolates in two environments (one in the field and the other in pots outside) in 2004 using a factorial randomized block design with three replications. The field experiment was performed at the Estación Experimental J. Hirschhorn, and the pot experiment at the Universidad Nacional de La Plata. Eight to ten seeds per line were sown into 10-l pots or in each row in the field. The plants were watered regularly (every 2–3 days), and provided at sowing with 50 kg ha^{-1} of N as urea and 50 kg ha^{-1} of ammonium diphosphate, and at tillering with 50 kg ha^{-1} of urea.

The ten fungal isolates (FALP 6792, 1493, 0103, 0203, 0303, 0403, 0503, 0603, 0703 and 0803) were selected according to their different origins in the Argentinean wheat region. The isolates were kept in silica gel and were transferred to malt extract agar for 5–6 days before carrying out the experiments. Inoculum was prepared by suspending conidia scraped from sporulating colonies in deionized water at a concentra-

tion of 5×10^6 spores ml^{-1}. Tween 20 (0.5 ml per litre) was added as a surfactant. Plants were inoculated at both the seedling (two-leaf stage, GS 12, Zadoks et al. 1974) and adult stages (at tillering, GS 23, Zadoks et al. 1974). For the experiment in pots, plants were covered with a transparent plastic wrap for 48 h immediately after inoculation to maintain the level of humidity. For the experiment in the field, plants were kept moist by spraying with water for 15 min every 2 h during three days.

To estimate seedling resistance, the first leaf of each plant was visually assessed for necrosis and pycnidial coverage at 28 to 30 days after inoculation . For the evaluation of adult-stage resistance, plants were scored for necrosis and pycnidial coverage at 30 days after flag leaf emergence (GS 82). Analysis of variance was performed on necrosis and pycnidial coverage on the first leaf of seedlings and on the flag leaf of plants at GS 82. Factors were the environments (years), the isolates and the lines.

Mapping population and resistance analysis

A random set of 87 single-chromosome recombinant doubled-haploid (SCRDH) lines was derived by crossing the F_1 'CS' (*T. a.e.*7D) / 'CS' with maize, and treating the progeny with colchicine, following established methods (Laurie and Bennett 1988). The SCRDH lines were sown in pots placed outside along with both parental lines at the La Plata National University in 2005, 2006 and 2007.

Inoculation and evaluation were performed at both seedling and adult stages, using the same procedures as in the screening experiment. On the basis of a differential reaction between the parental lines, pathogen isolate FALP 0103 was selected to inoculate the mapping population at the seedling stage, using the same spore concentration as for the screening experiment. During the period between the inoculation and the evaluation of disease reaction, the mean temperature in each of the growing seasons was 11.7°C, 12.7°C and 7.3°C, and the relative humidity was 90.0%, 78.0% and 74.4%. To estimate adult-plant resistance, percentage necrosis and pycnidial coverage on the flag leaf was recorded 30–35 days after flowering (GS 82), except in 2005 when only necrosis was scored. The mean temperature and relative humidity between inoculation and evaluation were 15.3°C, 16.5°C and 13.3°C and 66%, 67.0% and 70.3% for 2005, 2006 and 2007 respectively. The flowering dates of all lines were recorded when 50% of plants within a line reached anthesis. The amount of rainfall in the three years was

Table 1 Means of necrosis and pycnidial coverage (%) in seedlings of Chinese Spring (CS) and CS (*T. aestivum* subsp. *spelta* 7D) tested with 10 isolates of *Mycosphaerella graminicola*

Isolates	CS[a]		CS (7D)[b]	
	Necrosis	Pycnidia	Necrosis	Pycnidia
6792	40.6	10.0	28.6	8.9
1493	40.0	12.5	32.1	13.5
0103	58.3	33.3	20.7	13.2
0203	57.5	35.0	67.9	37.5
0303	70.8	42.5	67.5	43.6
0403	62.9	47.1	37.5	20.0
0503	25.0	24.2	19.0	19.2
0603	35.0	25.0	40.0	30.0
0703	51.2	36.2	61.2	40.0
0803	77.5	35.0	78.0	40.0

[a] Chinese Spring

[b] Chinese Spring (*T. aestivum* susbsp. *spelta* 7D)

LSD for the interaction isolate by line necrosis=10.1; LSD for the interaction isolate by line pycnidial coverage=8.3

Table 2 Means of necrosis and pycnidial coverage (%) in adult stage (GS 82) for Chinese Spring (CS) and CS (T. *aestivum* subsp. *spelta* 7D) tested with 10 isolates of *Mycosphaerella graminicola*

Isolates	CS[a]		CS (7D)[b]	
	Necrosis	Pycnidia	Necrosis	Pycnidia
6792	38.6	25.1	27.5	22.1
1493	40.2	31.0	35.1	23.7
0103	35.7	30.2	15.0	10.2
0203	54.8	35.3	45.4	29.9
0303	48.6	37.8	50.5	31.8
0403	62.0	46.6	55.1	40.9
0503	46.2	36.4	51.6	35.0
0603	38.3	32.3	36.0	27.6
0703	57.7	40.8	52.4	34.5
0803	52.5	39.6	60.2	34.2

[a] Chinese Spring

[b] Chinese Spring (*T. aestivum* susbsp. *spelta* 7D)

LSD for the interaction isolate by line necrosis=12.2; LSD for the interaction isolate by line pycnidial coverage=7.5

153, 247 and 272 mm, respectively, for the whole growing period. A linear regression of the number of days to flowering against percentage necrosis or pycnidial coverage was not significant, so no correction to the data was applied.

Analysis of variance was performed on necrosis and pycnidial coverage on the first leaf of seedlings and on the flag leaf of plants at GS 82. Factors were the environments (years) and the lines. Means were compared by LSD test (P=0.05). Correlation between necrosis and pycnidial coverage for each trait was also tested. Significant correlation between percentage necrosis and pycnidial coverage was observed, therefore only one of the two subsets of the scoring data (percentage necrosis) was used for QTL analysis. The results obtained during different years and replicates were combined into one residual mean percentage necrosis score per line. This was performed separately for seedling and adult-plant resistance scores. Then the two datasets were subjected to QTL analysis.

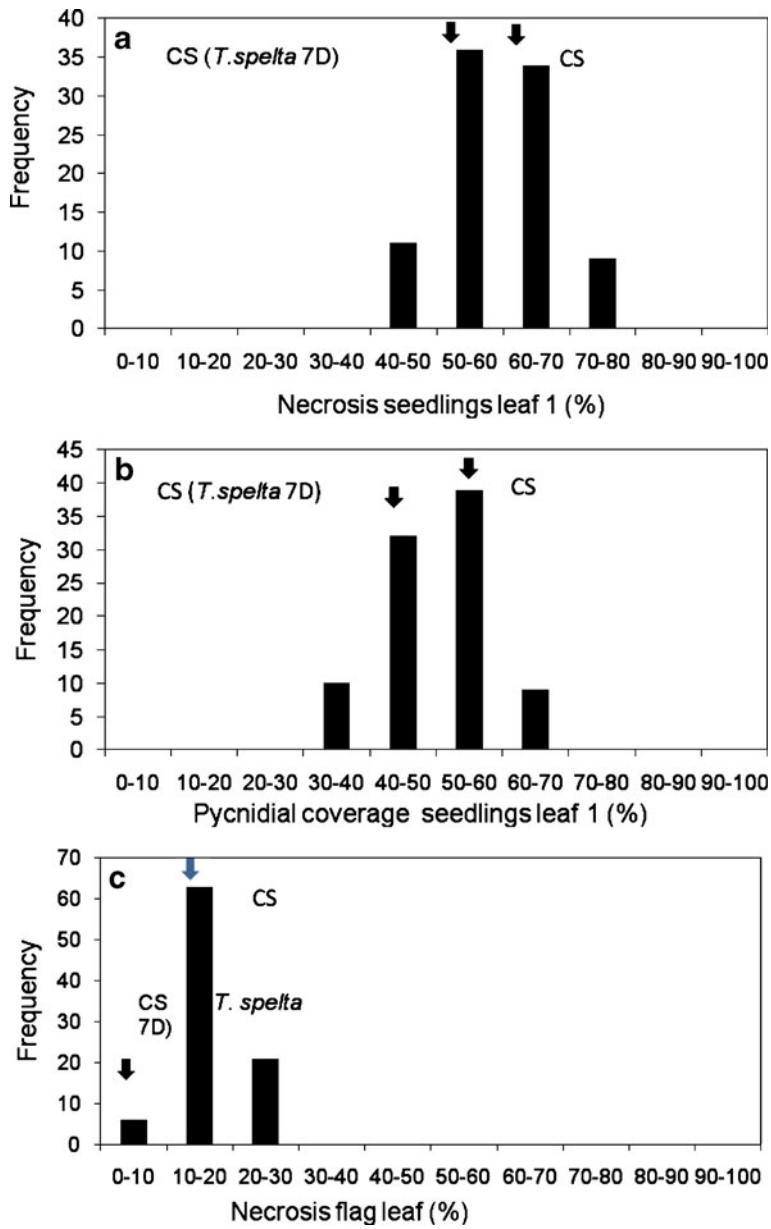

Fig. 1 Histograms of disease severity means over three years of 87 double-haploid lines derived from the cross of 'CS' (*T. aestivum* subsp. *spelta* 7D) by 'CS' inoculated with *Mycosphaerella graminicola* isolate **a**. Necrosis in seedlings. **b**. Pycnidial coverage in seedlings. **c**. Necrosis in flag leaves

Microsatellite genotyping and QTL analysis

Genomic DNA was extracted following the procedure of Plaschke et al. (1995), and used to assign allelic status at a set of 49 GWM (Gatersleben wheat microsatellite) loci mapped to chromosome 7D. Genotyping methodologies are described elsewhere (Röder et al. 1998). A genetic map of chromosome 7D was constructed with MAPMAKER v2.0 software (Lander et al. 1987). The QTL analysis was carried out using QTX (Manly et al. 2001). QTX expresses the quality of a QTL assignment in the form of a likelihood ratio statistic (LRS). Experiment-wise threshold values were calculated by performing 1000 permutations of the phenotypic data. To control for linked QTL, composite interval mapping was performed using the option provided by QTX, which reduces effects of background QTL.

Results

Parental screening with several isolates

There were significant differences for necrosis and pycnidial coverage between isolates, lines and for the interaction isolates by lines. Isolate FALP 0103 was selected on the basis of the greatest differential reaction severity between the parental lines in seedlings and the adult stage. *T .aestivum* subsp. *spelta 7D* also showed some level of resistance in seedlings to isolate FALP 6792 and FALP 0403, whereas both parents showed similar resistance scores to the other isolates (Tables 1 and 2). Thus, on the basis of a differential reaction between the parental lines, pathogen isolate FALP 0103 was selected to inoculate the lines.

Mapping population: resistance test

The ANOVA showed significant differences between environments and SCRDH lines for necrosis and pycnidial coverage at the seedling and adult plant stage. The interaction environment by line was not significant in any case (data not shown). Average data distribution over the three years is shown in Fig. 1. In seedlings there was a resistant:susceptible segregation ratio of 1:1. For necrosis at the flag-leaf stage most of the lines were susceptible and there was a transgressive segregation; 22 were more susceptible than the susceptible parent (Fig. 1).

Mapping population: genotyping and QTL analysis

Of the 49 microsatellite loci tested, 16 were informative for the contrast between 'CS' and 'CS' (*T.a.s.*7D), and the allelic status of the SCRDH lines at these loci provided the basis for the genetic map of chromosome 7D (Fig. 2). The interval mapping analysis performed using seedling and adult-plant percentage necrosis

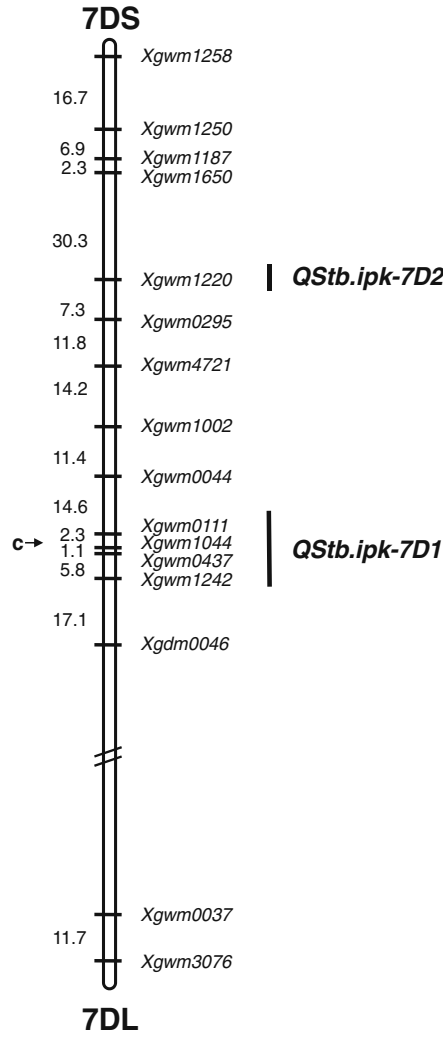

Fig. 2 The genetic map of chromosome 7D constructed from a set of single-chromosome recombinant doubled-haploid lines bred from the cross 'CS' (*T. aestivum* subsp. *spelta* 7D) by 'CS'. Genetic distances are given in centimorgans (cM); 7DS = short arm; 7DL = long arm; c = centromeric region. Locations of septoria tritici blotch QTL are indicated to the right. *QStb. ipk-7D1* is a locus for the seedling and *QStb.ipk-7D2* for the adult-plant stages of resistance. The centromere is indicated according Khlestkina et al. (2009). Double diagonal slashes indicate missing linkage

scores (Fig. 3) suggested the presence of the seedling disease-resistance locus in the centromeric region linked to *Xgwm0111* (Figs. 2 and 3a), while the adult-plant resistance locus was detected on the short arm in the region of *Xgwm1220* (Figs. 2 and 3b). These loci were designated *QStb.ipk-7D1* and *QStb.ipk-7D2*, respectively. Although the two parental lines of the mapping population 'CS' (*T.a.s.*7D) displayed higher resistance in comparison with 'CS' in both seedling and adult-plant stages, the additive regression coefficient suggested that 'CS' (*T.a.s.*7D) conferred the susceptible allele of the seedling resistance locus *QStb.ipk-7D1* (Fig. 3a) and the resistant allele of the locus *QStb.ipk-7D2* detected using adult-plant resistance scores (Fig. 3b).

Because two linked QTL had been detected, we applied composite interval mapping to reduce effects of such QTL to each other. We performed composite mapping for the seedling resistance trait using adult-plant resistance for the trait variances (Supplementary Fig. 1a) and did the same for the adult-plant resistance trait using *vice versa* the seedling resistance background (Supplementary Fig. 1b). The results obtained for composite interval mapping (Supplementary Fig. 1) were very similar to those derived from interval mapping analysis, confirming existence of two linked resistance QTL on chromosome 7D. Thus, the two distinct loci *QStb.ipk-7D1* and *QStb.ipk-7D2* confer the resistance in seedlings and adult plants.

Interval mapping analysis of flowering time did not reveal significant LRS values and no measurable correlation between flowering time and seedling or adult-plant resistance was observed, suggesting that the QTL observed for resistance are not associated with variation for flowering time. This was also confirmed by composite interval mapping of the seedling and adult-plant resistances, performed using flowering time for trait variances (Supplementary Fig. 2).

Discussion

In this paper, we describe two loci on wheat chromosome 7D conferring resistance to septoria tritici blotch. Interestingly, the locus conferring adult-plant resistance, *QStb.ipk-7D2*, maps in the region of microsatellite locus *Xgwm1220* where known adult-plant disease resistance locus *Lr34/Yr18*, effective against multiple pathogens such as leaf rust, stripe rust, and powdery mildew, is located (Krattinger et al. 2009; Spielmeyer et al. 2008,). It has been shown that the LR34 protein

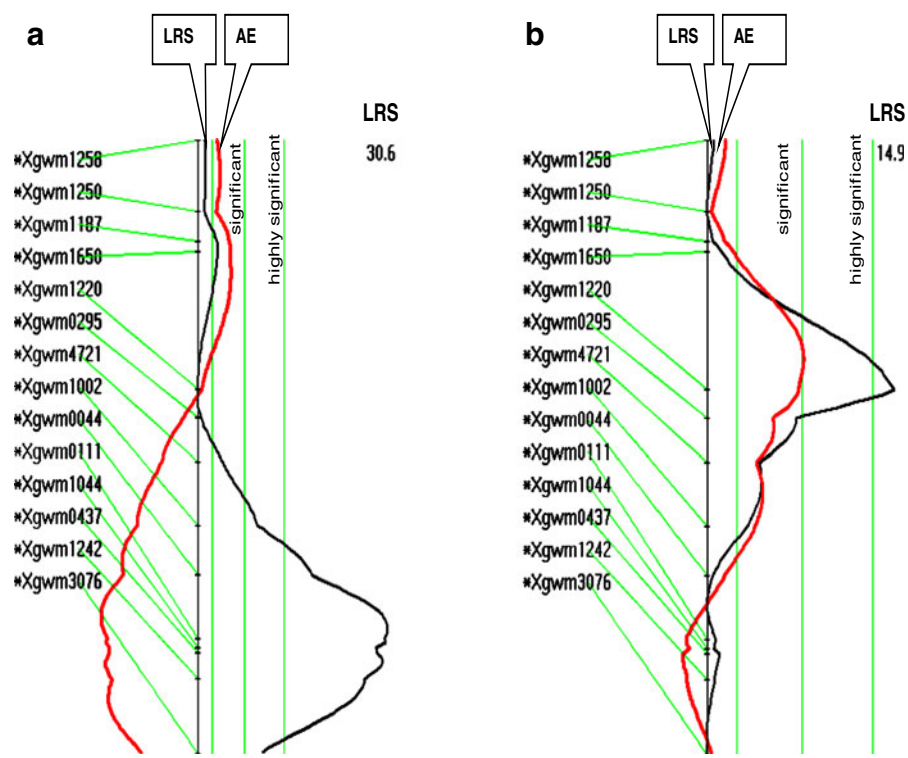

Fig. 3 Interval mapping of the seedling (**a**) and adult plant stage (**b**) resistances. LRS: likelihood ratio statistic; AE: additive effect. "Significant" and "highly significant": LRS threshold lines

resembles adenosine triphosphate-binding cassette transporters of the pleiotropic drug resistance subfamily (Krattinger et al. 2009). 'CS' carries the *Lr34* resistance allele (Dyck 1991). Nevertheless, in our study, the 'CS' parent conferred an allele for susceptibility to septoria tritici blotch in the adult stage. A similar observation was made for *Lr34* and stem rust; *Lr34* in 'CS' does not confer resistance to stem rust, while in 'Thatcher' it does (McIntosh et al. 2008). Spielmeyer et al. (2008) proposed that *Lr34* interacts with unlinked gene(s) in the 'Thatcher' background resulting in enhanced stem rust resistance in adult plants. Probably, the *Lr34* allele of spelt wheat interacts with one or more unlinked genes in the 'CS' background, to enhance septoria tritici blotch resistance in comparison with the combination of the genes in 'CS'. To elucidate this, it will be of interest to investigate in the future how adult-plant septoria tritici blotch resistance in 'CS' (*T.a.s.*7D) and the 'CS'/'CS' (*T.a.s.*7D) population correlates with resistance/susceptibility to leaf rust, stripe rust and powdery mildew.

The map position of the locus conferring seedling resistance, *QStb.ipk-7D1*, also coincides with locations of the known genes: *Stb4* (Adhikari et al. 2004), *Stb5* (Arraiano et al. 2001b), *Dn1*, *Dn2*, *Dn5*, *Dn6*, and *Dnx* (the *Dn* genes confer resistance to Russian wheat aphid; Liu et al. 2001, 2002). This may be either a resistance gene cluster or a locus similar to *Lr34*/*Yr18* conferring resistance to multiple pathogens. Whether *QStb.ipk-7D1* is allelic to the major genes *Stb4* and/or *Stb5* remains unclear.

The unexpected result of the QTL analysis that 'CS' (*T.a.s.*7D) confers the susceptible allele of the locus *QStb.ipk-7D1* suggests occurrence of a background effect. A similar effect was observed during QTL analysis performed for other traits (Pshenichnikova et al. 2008). Although a single-chromosome substitution line usually receives up to eight backcrosses in the course of its development, this may not be sufficient to fully reconstitute the recipient genetic background (Khlestkina et al. 2010). Thus, the use of the single-chromosome substitution line in the current analysis cannot completely rule out the possibility of a background effect from other chromosomes originating from the donor parent (*T. aestivum* subsp. *spelta*). Further chromosomes contributing to resistance of *T. aestivum* subsp. *spelta* are 2D, 5A, 5D, 6B and 6D (Simón et al. 2005b). Thus, use of the *T. aestivum* subsp. *spelta QStb.ipk-7D1* allele as a new source of seedling resistance may be limited to combinations with other *T. aestivum* subsp. *spelta* resistance loci. Unlike this, the resistance allele at locus *QStb.ipk-7D2* is conferred by the 'CS' (*T.a.s.*7D) parent, suggesting that it can be used as a new source of adult-plant resistance to septoria tritici blotch.

The septoria tritici blotch resistance mapped in the current study appears to be isolate specific since the *T. aestivum* subsp. *spelta* accession used to create the 'CS' (*T.a.s.* 7D) line has a good level of resistance to *M. graminicola* isolate FALP 0103 in seedling and adult stages, some resistance to FALP 9267 in seedlings, but no resistance to the other eight isolates tested here. *Stb5*, originating from *Triticum tauschii*, is known to be resistant to IPO 94269 (Arraiano et al. 2001b) and to two Argentinean isolates (Simón et al. 2007). *Stb4*, originating from bread wheat cultivar 'Tadinia' and conferring resistance at both seedling and adult stages, was effective in California for more than 15 years up to the end of the 1990s (Jackson et al. 2000) but then broke down rapidly.

Overall, resistance to *M. graminicola* can be expressed at either or both the seedling and adult stages. Although there are cultivars with specific resistance available to individual isolates at both stages, others only carry resistance at one stage (Kema and van Silfhout 1997). Cultivars with a reasonable level of quantitative resistance at both stages are available, while others showed resistance in seedlings but were fully susceptible at the adult stage, or *vice versa* (Simón et al. 2005a). Similarly, some resistance QTL which are growth-stage specific have been identified (McIntosh et al. 2008).

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