Theor Appl Genet (2005) 110: 1138–1144
DOI 10.1007/s00122-005-1945-4

ORIGINAL PAPER

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Genetics of resistance to septoria tritici blotch in the Portuguese wheat breeding line TE 9111

Received: 14 June 2004 / Accepted: 26 January 2005 / Published online: 10 March 2005

Abstract We report the genetics of resistance of the Portuguese wheat breeding line TE 9111 to septoria tritici blotch (STB), which is caused by *Mycosphaerella graminicola*. TE 9111 is the most resistant line known in Europe and combines isolate-non-specific, partial resistance with several isolate-specific resistances. We show that, in addition to high levels of partial resistance to STB, TE 9111 has a new gene for resistance to *M. graminicola* isolate IPO90012, named *Stb11*, that maps on chromosome 1BS, the *Stb6* gene for resistance to isolate IPO323 and, probably, the *Stb7* gene for resistance to isolate IPO87019. All of these genes are closely linked to microsatellite markers, which can be used for marker-assisted selection. TE 9111 may therefore be a valuable source of resistance to STB for wheat breeding, especially in Mediterranean environments.

Communicated by P. Langridge

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Introduction

Septoria tritici blotch (STB), caused by the ascomycete fungus *Mycospaerella graminicola*, is now the most important foliar disease of wheat in many regions of the world, including Europe, the Mediterranean, South America, the USA and parts of Australia (Eyal et al. 1973; Eyal et al. 1987; Hardwick et al. 2001; Loughman and Thomas 1992; Polley and Thomas 1991; Schlüter and Janati 1976). Resistant cultivars provide an effective and economical way of controlling STB, but until recently little was known about the genetics of resistance to STB in wheat and breeders had to rely on unknown genes.

Recent work has focused on the genetics of resistance to STB in northern European varieties, but little is known about the genetics of resistance in the southern Europe and Mediterranean regions where the disease is often more severe than in colder regions. STB can be particularly severe when early sowing is followed by rainfall in late winter or spring (Catedra et al. 2003; Nasraoui et al. 2003; Schlüter and Janati 1976), which is typical of the conditions found in Mediterranean-type environments.

The Portuguese breeding line TE 9111 is the most resistant line to STB known in Europe. In tests on adult plants with single-pycnidium isolates of *M. graminicola*, TE 9111 was the second most resistant line of all those tested after the Brazilian cultivar Veranopolis, which has long been known to be an important source of resistance (Brown et al. 2001).

As in other diseases of wheat such as powdery mildew and rusts, resistance to STB may be specific or partial. Specific resistance is near complete, oligogenic and follows a gene-for-gene relationship (Arraiano et al. 2001b; Brading et al. 2002; McCartney et al. 2002; Somasco et al. 1996), whereas partial resistance is incomplete, polygenetic and isolate-non-specific (Chartrain et al. 2004b; Jlibene et al. 1994; Simon and Cordo 1998; Zhang et al. 2001). Eleven genes (*Stb1–10* and *Stb12*) for

resistance to STB have been identified to date (*Stb1*, Adhikari et al. 2004a; *Stb2* and *Stb3*, Adhikari et al. 2004b; *Stb4*, Somasco et al. 1996; *Stb5*, Arraiano et al. 2001b; *Stb6*, Brading et al. 2002; *Stb7*, McCartney et al. 2003; *Stb8*, Adhikari et al. 2003; *Stb9*, Chartrain 2004; *Stb10* and *Stb12*, Chartrain et al. 2005b).

In tests using seedlings, TE 9111 was found to have specific resistance to isolates IPO323, IPO90012, IPO87019 and ISR398 of STB as well as high levels of partial resistance to all 12 isolates tested (Chartrain et al. 2004a). Genes for resistance to three of these isolates have been identified. The *Stb6* gene for resistance to IPO323 was mapped on chromosome 3A in Flame and is present in many other lines, including many sources of resistance to STB (Chartrain et al. 2005a). Genes for resistance to ISR398 and IPO87019 were identified in Kavkaz-K4500 (KK) (Chartrain et al. 2005b) and mapped to the same region on the distal end of chromosome 4A. The gene for resistance to IPO87019 may be the *Stb7* gene identified in ST6 by McCartney et al. (2003).

The aims of the investigation reported here were to identify and map the gene or genes conferring isolate-specific resistance to IPO90012 and test whether or not TE 9111 also has *Stb6* and *Stb7*.

Materials and methods

Isolates

Four *Mycospaerella graminicola* isolates were used in this study. IPO323, IPO90012 and IPO87019 were chosen for their avirulence on wheat breeding line TE 9111, and IPO90004 was used as a virulent control (Chartrain et al. 2004a). All isolates were grown on potato dextrose agar (PDA) for 7–10 days before being used for inoculation. The inoculum concentration was adjusted to 10^7 conidia ml^{-1} .

Plant material

Experiments were conducted on several populations for practical reasons. For resistance to IPO323, F_2 populations of TE 9111 × Flame and TE 9111 × Longbow were used. Flame is the cultivar in which *Stb6* has been identified, while Longbow is susceptible to STB. Resistance to IPO90012 was studied in 94 lines of an F_4 single-seed descent (SSD) population of TE 9111 crossed with the susceptible Dutch cultivar Baldus (Brown et al. 2001). The virulent control isolate IPO90004 was also tested on this population. Finally, resistance to IPO87019 was tested later on 94 lines of the F_5 SSD generation because not enough F_4 seed was available.

Pathology tests

Pathology tests were carried out on whole seedlings or on detached leaves. Whole seedling tests allow a greater number of plants to be tested simultaneously than the detached leaf method does but has the disadvantage that the environmental conditions are less strictly controlled. For specific resistance, tests on whole seedlings and detached leaves give similar results (Arraiano et al. 2001a). IPO90012 and IPO323 are both aggressive isolates (Chartrain et al. 2004a) so they were tested on whole seedlings in the glasshouse, whereas IPO87019 and IPO90004, which are not aggressive enough to be tested on whole seedlings (Chartrain et al. 2004a), were tested on detached leaves only.

Seedling tests were conducted using the method of Brading et al. (2002). For tests with IPO90012, 18 seedlings per F_4 SSD line were tested. For IPO323, 100 F_2 plants of TE 9111 × Flame and 98 F_2 plants of TE 9111 × Longbow were tested as seedlings. Detached leaf tests were carried out using the method of Arraiano et al. (2001a). For IPO87019, 12 replicate leaves were tested in order to identify possible segregants in the F_5 SSD population. Four replicate plants of each F_4 SSD line were tested with IPO90004 to verify that the line was susceptible. In all tests, both of the parents and the susceptible cultivar Longbow were used as controls.

Disease scoring

In all tests, disease was scored as the percentage leaf area covered with lesions bearing pycnidia. In whole-seedling tests, disease was scored only once, when several leaves were severely diseased (90% or more of lesions bearing pycnidia). Disease scores were logit-transformed in order to make the residual variance normally distributed and the mean logit-scores and the standard deviation of the logit-scores calculated for each line.

In detached-leaf tests, the leaves were scored four to five times between 1 week and 4 weeks after inoculation and the area under the disease progress curve calculated (AUDPC) (Shaner and Finney 1977). The variate analysed was the AUDPC as a proportion of the maximum AUDPC (MAXAUDPC, calculated assuming a score of 100% on every date the test was scored). The mean AUDPC was calculated for each line by generalized linear mixed modelling (GLMM) using the statistics program GENSTAT 5 for windows, 6th edition (Payne 2000).

Molecular mapping

DNA was extracted from three to four 15-day-old seedlings. The leaves were freeze-dried and DNA extracted following the method of Dellaporta (1983). Two bulks, each of eight lines resistant or susceptible to IPO90012, were tested, along with wheat breeding lines TE 9111 and Baldus with 627 SSR markers chosen for their ease of amplification, high polymorphism and coverage of the genome. The markers were provided by

Table 1 Summary of microsatellite markers used on TE9111 × Baldus F_4 and F_5 SSD populations to map genes for resistance to septoria tritici blotch

	Total	Public	Proprietary
Polymorphic	211	123	88
Monomorphic	227	152	75
Not scorable	77	29	48
Not amplified	112	79	33
Total tested	627	383	344

Syngenta, including both public and non-public markers developed by WMC (Wheat Microsatellite Consortium, http://wheat.pw.usda.gov/ggpages/SSR/WMC), the Institute of Plant Genetics and Crop Plant Research (IPK), Gatersleben (Röder et al. 1998), the John Innes Centre (Stephenson et al. 1998) and Beltsville Agricultural Research Centre (http://www.scabusa.org) (Table 1). The PCR cycling conditions consisted of 32 cycles of a 30-s denaturation at 94°C, a 30-s annealing at 60°C and a 30-s extension at 72°C. The samples were initially denatured for 5 min at 94°C. The PCR mix contained 1.65 m *M* $MgCl_2$, 250 μM of each deoxynucleotide, 1 × *Taq* buffer, 0.2 U *Taq* polymerase (Invitrogen, Carlsbad, Calif.), 100 ng template DNA and 400 n *M* of each non-fluorescent primer or 200 n *M* of each fluorescently labelled primer. Fluorescent primers were labelled with 6-FAM, NED or HEX. Non-fluorescent PCR products were separated by electrophoresis on 3% agarose gels (Resophor, Eurobio) at 360 V with a cooling system. Gels were stained with ethidium bromide. Fluorescent PCR products were separated on an ABI 3700 capillary sequencer and their sizes measured using Applied Biosystem's GENESCAN and GENOTYPER fragment analysis software (Applied Biosystems, Foster City, Calif.). Fluorescently labelled primers were used in genetic mapping only, whereas non-fluorescent primers were used for bulk segregant analysis (BSA) and marker validation.

For resistance to IPO90012, we used BSA was used to identify the chromosome of interest. Selected public markers of interest, *Xbarc008* and *Xbarc137* were then screened against the 94 F_4 SSD lines. For resistance to IPO87019, five microsatellite markers—*Xwmc500*, *Xgwm160*, *Xwmc497, Xwmc219 and Xwmc313*—linked to resistance to this isolate in KK (Chartrain 2004) were tested with the 94 F_5 SSD lines.

Linkage analysis was done using JOINMAP 2.0 (Stam and van Ooijen 1995). Recombination fractions were converted into map distances by the Kosambi function (Kosambi 1944). The output from JOINMAP was converted to a graphical format using the programme MAPCHART (Voorrips 2001). Quantitative trait locus (QTL) analysis was done using interval mapping and the Kruskall-Wallis test (Jansen 1993) using MAPQTL VER. 4.0 (van Ooijen and Maliepaard 1996). Levels of significance of each QTL were calculated using the permutation test in MAPQTL.

Results

Pathology tests

Ninety-four F_4-SSD lines were tested with the control virulent isolate IPO90004, which was chosen for its virulence on both TE 9111 and Baldus (Chartrain et al. 2004a). Baldus was very susceptible, with a 90% mean AUDPC, but TE 9111 had only 20% AUDPC. Twenty-one lines were more resistant than TE 9111 with a mean AUDPC between 2% and 18% (Fig. 1), which is consistent with TE 9111 having high levels of partial resistance (Chartrain et al. 2004a).

The 94 F_4-SSD lines segregated for resistance to IPO90012. The distribution of scores was continuous so that no clear segregation ratio could be determined (Fig. 2a,b), but it was possible to identify clearly resistant and clearly susceptible lines (i.e. lines for which all 18 replicate leaves had consistent scores). The 16 most clearly resistant and susceptible lines were used for BSA.

The 94 F_5-SSD lines segregated for resistance to IPO87019 but as with IPO90012, the distribution of the mean AUPDC was continuous, so once again no clear segregation ratio could be determined (Fig. 3).

Tests on 100 F_2 plants from TE 9111 × Flame showed that all the lines were resistant to IPO323. The lack of segregation indicated that TE 9111 and Flame both have the same gene for resistance to IPO323, *Stb6*, or two genes that are allelic or closely linked.

Tests on 98 F_2 plants of TE 9111 × Longbow showed that the F_2 population segregated for resistance to IPO323 (Fig. 4a–c). For most plants, pycnidium coverage was low with a maximum of 25% of the leaf area covered by lesions bearing pycnidia, but many plants were highly necrotic. The correlation between necrosis and pycnidia coverage was moderate ($r = 0.5$).

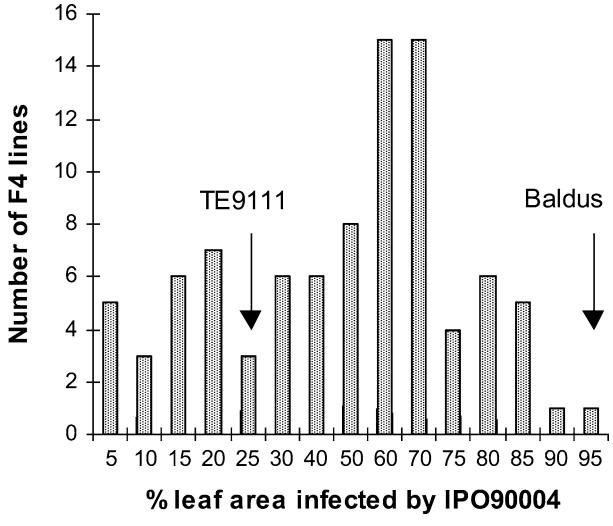
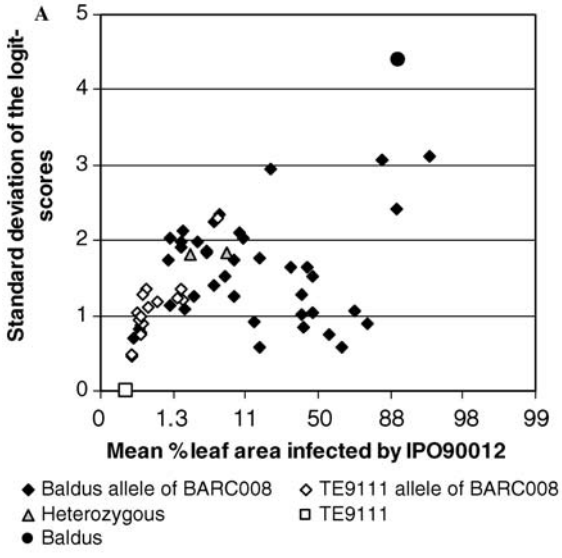


Fig. 1 Segregation of responses to *Mycosphaerella graminicola* isolate IPO90004 in F_4-SSD lines of a cross between TE 9111 and Baldus. The number of F_4-SSD lines is plotted against the percentage of leaf area covered by lesions bearing pycnidia



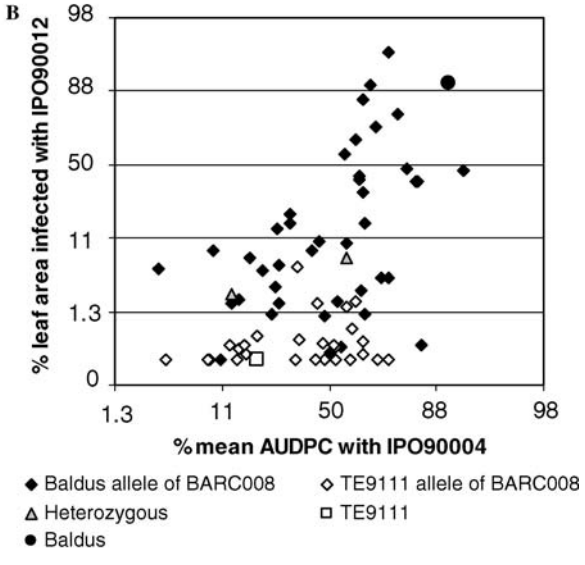


Fig. 2 **a** Segregation of responses of TE 9111 × Baldus F_4-SSD lines to *M. graminicola* isolate IPO90012. Standard deviations of the logit disease scores are plotted against mean disease scores for each line. Lines are marked by their allele at *Xbarc008* on chromosome 1B. The axis showing the mean disease scores is logit-scaled. **b** Segregation of TE 9111 × Baldus F_4-SSD lines for specific resistance to *M. graminicola* isolates. Mean AUDPC for each line inoculated with IPO90012 is plotted against mean AUDPC with the virulent control isolate IPO90004. Lines are marked by their allele at *Xbarc008* on chromosome 1B. The axes are logit-scaled

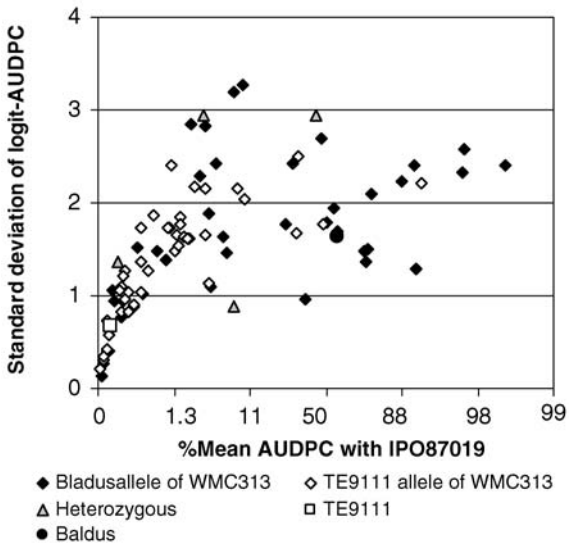


Fig. 3 Segregation of responses of TE 9111 × Baldus F_5-SSD lines to *M. graminicola* isolate IPO87019. Standard deviations of logit disease scores are plotted against mean disease scores for each line. Lines are marked by their allele of *Xwmc313* on chromosome 4AL. The axis showing the mean disease scores is logit-scaled

Necrosis was therefore scored as well as pycnidia coverage. There was a continuous distribution of the scores for pycnidia coverage and necrosis so that no segregation ratio could be determined.

Mapping

Resistance to IPO90012

Two markers mapping on chromosome 1B close to the centromere, *Xbarc008* and *Xbarc137*, were identified by BSA as being associated with the response to the isolate IPO90012. Each of these markers was tested on the 94 F_4-SSD lines, and a Student's *t*-test compared the mean logit-scores for the lines with the TE 9111 allele to those with the Baldus allele. Both markers were closely linked to resistance to IPO90012 ($P < 0.001$). Seven more markers which mapped to chromosome 1B and were polymorphic between TE 9111 and Baldus were tested with the 94 SSD lines to generate a map of chromosome 1B suitable for QTL analysis. Seven of the nine markers tested mapped in the same linkage group, giving a map length of 40 cM (Fig. 5a).

QTL analysis by interval mapping showed that one gene for resistance to IPO90012 mapped on chromosome 1B. The log-likelihood of this gene was 13.3 (critical LOD = 1.4), and it explained 50% of the phenotypic variance in means of the logit-scores. This new gene is named *Stb11*, and the closest marker was *Xbarc008*, which maps to chromosome 1BS (Somers et al. 2004). The TE 9111 allele of *Xbarc008* was 275 bp, while the Baldus allele was 250 bp. No marker distal to *Stb11* on chromosome 1BS could be identified as polymorphic between TE 9111 and Baldus (Fig. 5a). No QTL for resistance to IPO90004 was identified in this region, which was as expected, because IPO90004 was used as a virulent control. Therefore, *Stb11* is a gene for isolate-specific resistance to IPO90012.

Resistance to IPO87019

Resistance to IPO87019 was mapped by QTL analysis using the map of chromosome 4A comprising the five

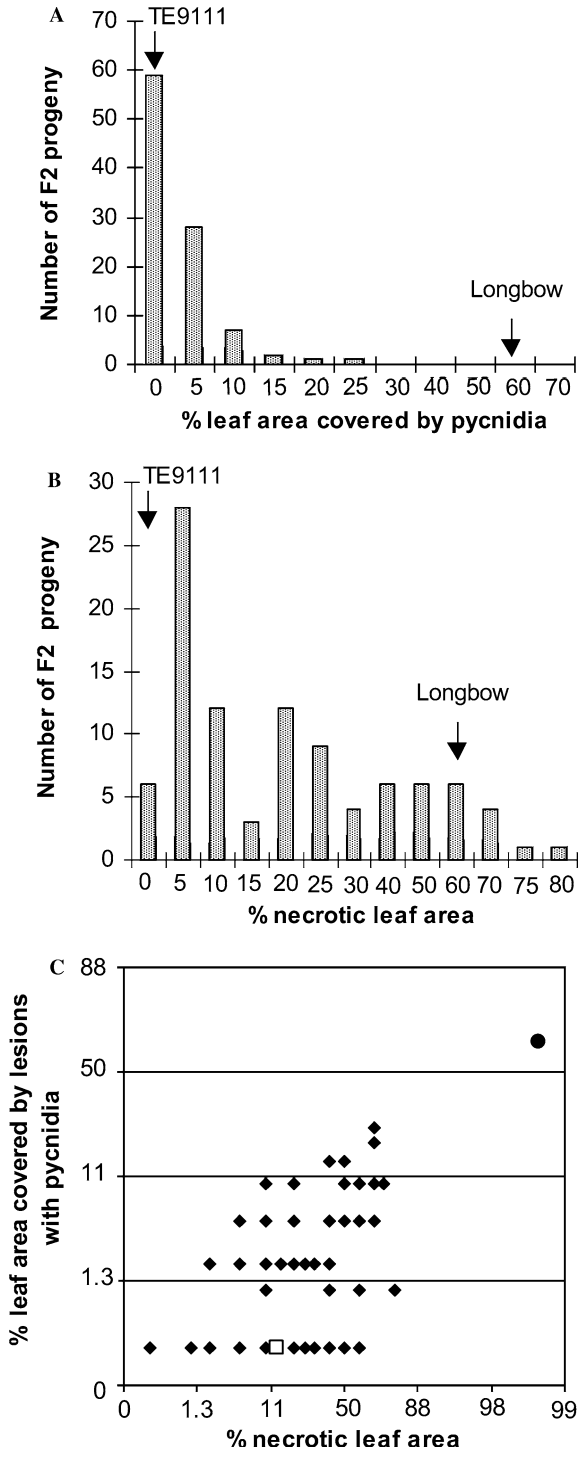


Fig. 4 Segregation of responses to *M. graminicola* isolate IPO323 in F_2 progeny of a cross between TE 9111 and Longbow. **a** The number of F_2 plants is plotted against the percentage of leaf area covered by lesions bearing pycnidia. **b** The number of F_2 plants is plotted against the percentage of leaf area covered by necrosis. **c** Correlation between pycnidia coverage and necrosis. The percentage leaf area covered by lesions bearing pycnidia is plotted against the percentage necrotic leaf area

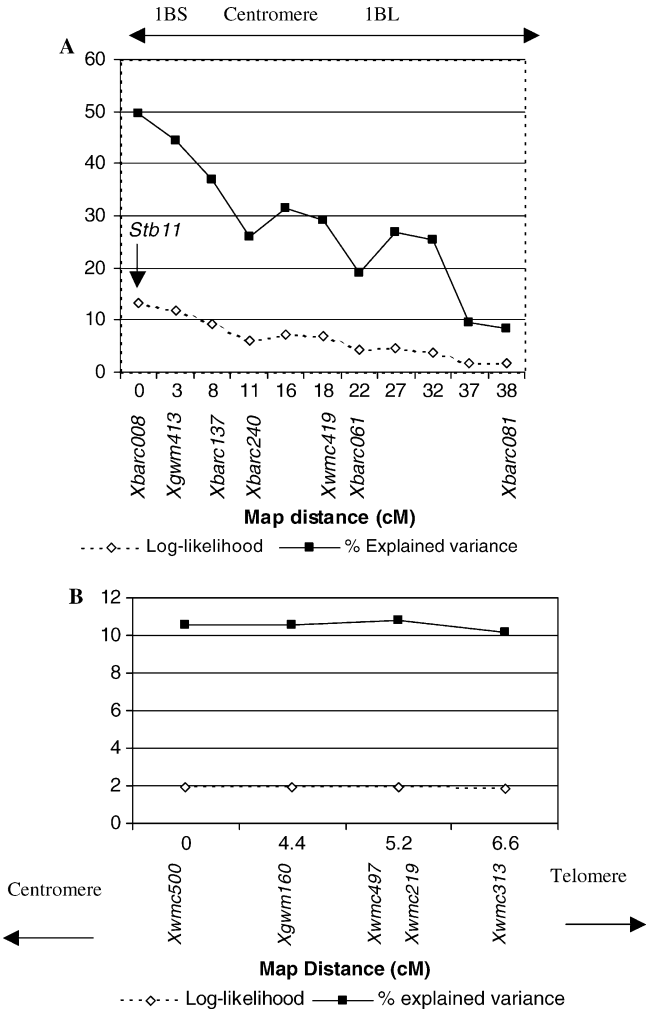


Fig. 5 **a** Location of the *Stb11* gene for specific resistance to *M. graminicola* isolate IPO90012. The *arrows* indicate the position of the QTLs. The log-likelihood is plotted against map distance. **b** QTL analysis for specific resistance to *M. graminicola* isolate IPO87019 on chromosome 4A

microsatellite markers tested. Kruskal-Wallis analysis and interval mapping were used because high levels of partial resistance in TE 9111 might have masked the effects of isolate-specific resistance. The Kruskal-Wallis analysis showed that each of the five markers was closely linked to resistance to IPO87019 ($P < 0.0001$). Interval mapping confirmed that a QTL for resistance to IPO87019 mapped on chromosome 4A; the log-likelihood of the QTL score was 1.96 (critical LOD = 0.7), and it explained 11% of phenotypic variation in means of the AUDPC (Fig. 5b). The TE 9111 allele of *Xwmc313*, the closest marker to the gene for resistance to IPO87019 in KK, was 194 bp in size, while that of Baldus was 312 bp.

Discussion

TE 9111 is the first variety from the Mediterranean area in which the genetics of resistance to STB has been analysed. This variety may be a major source of

resistance for breeding spring wheat for Mediterranean environments where STB can be severe, causing substantial foliar damage and therefore yield losses (Catedra et al. 2003; Nasraoui et al. 2003; Schlüter and Janati 1976).

This study identified and mapped a new gene for resistance to STB, *Stb11*, in TE 9111. This gene, located on chromosome 1BS, is isolate-specific and confers resistance to the Mexican *M. graminicola* isolate IPO90012 but not to the Mexican isolate IPO90004. The closest marker is *Xbarc008*, and the high log-likelihood of the gene at the *Xbarc008* locus suggests that *Stb11* is a gene very tightly linked to *Xbarc008*. No marker flanking *Stb11* on the short arm of chromosome 1BS could be identified. The effect of *Stb11* on resistance to STB in the field is not yet known, but if it does confer field resistance to STB, *Xbarc008* will be valuable for use in marker-assisted selection (MAS).

The results of this study also show that resistance of TE 9111 to IPO323 is conferred either by *Stb6* or by a different allele or another gene closely linked to *Stb6*. Previous work showed that the *Stb6* gene is widely distributed among major sources of resistance to STB, suggesting that it might have an effect on general resistance to STB in the field (Brading et al. 2002; Chartrain et al. 2005a). The results of tests carried out on F_2 plants of TE 9111 × Longbow did not indicate just how many genes were involved in the resistance to IPO323 since the disease levels of the F_2 plants were generally low. The lack of a clear segregation of responses to IPO323, unlike what was observed in crosses tested previously (Chartrain et al. 2005a), is probably the result of TE 9111 having a high partial resistance to STB (Brown et al. 2001; Chartrain et al. 2004a). If this partial resistance is polygenic, as in cv. Arina (Chartrain et al. 2004b), it would segregate in the progeny, all of which would have some partial resistance genes. The segregation of partial resistance makes it difficult to identify specific resistance genes (i.e. to test if there is a single gene for resistance to IPO323) and explains the low and moderate log-likelihoods of *Stb7* and *Stb11*, respectively. Previous work has shown that in most of the lines tested with *Stb6*, isolate-specific resistance to IPO323 is controlled by *Stb6* only, although in KK, two genes probably control resistance (Chartrain et al. 2005b).

In KK, two genes mapped at the distal end of chromosome 4A (Chartrain et al. 2005b) near the locus of *Stb7* (McCartney et al. 2003). One of these is probably *Stb7* itself, for resistance to IPO87019 and possibly ISR398, and the other is a new gene, *Stb12*, for resistance to ISR398 only. Kruskal-Wallis tests on five markers located on chromosome 4A in the *Stb7* and *Stb12* region showed that TE 9111 has a gene for resistance to IPO87019 mapping in this region. This gene may therefore be the same as the gene in KK for resistance to IPO87019, probably *Stb7*, or a gene which is allelic or closely linked to it.

Although the F_4- or F_5-SSD lines segregated for responses to both IPO90012 and IPO87019, no clear segregation ratio could be identified so that resistance to each of these isolates may be conferred by more than one gene. Resistance to STB can be assessed quantitatively by measuring the percentage leaf area covered by lesions bearing pycnidia. Since the expression of symptoms vary according to the cultivar, the isolate and the environment (Eyal 1999), the establishment of a threshold differentiating resistant from susceptible reactions is often difficult to establish (Chartrain et al. 2004a). In previous work, we showed that TE 9111 had high partial resistance to STB (Chartrain et al. 2004a). Genes for isolate-non-specific, partial resistance to STB may modify the expression or mask the effects of isolate-specific resistance genes such as *Stb6*, *Stb7* and *Stb11*. The fact that *Stb11* explained 50% of the phenotypic variance for resistance to IPO90012 suggests that other genes, including isolate-non-specific partial resistance genes, are involved in resistance to IPO90012.

Markers closely linked to *Stb6*, *Stb7* and *Stb11* are now available (Brading et al. 2002; McCartney et al. 2003) so that these major resistance genes in TE 9111 can be selected by MAS in breeding. Results from previous investigations suggested that 'pyramiding' genes for resistance may be useful in breeding to develop varieties with excellent resistance to STB (Chartrain et al. 2004a). Along with having three isolate-specific resistance genes, TE 9111 also has good levels of isolate-non-specific, partial resistance, which can be selected by field screening. TE 9111 will therefore be useful in breeding for resistance to STB in Mediterranean climates. An effective strategy might be to select for both isolate-specific resistance genes such as *Stb6*, *Stb7* or *Stb11*, as well as partial resistance to STB.

Acknowledgements We thank Gert Kema for the gift of the *M. graminicola* isolates. This research was supported by DEFRA and a consortium of six wheat breeding companies: Advanta Seeds UK, Cebeco Seed Innovations, Elsoms Seeds, Nickerson UK, SW Seeds and Syngenta Seeds, through the Sustainable Arable LINK programme.

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