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Characterisation of *Triticum vavilovii*-derived stripe rust resistance using genetic, cytogenetic and molecular analyses and its marker-assisted selection

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Abstract Stripe rust resistance was identified in *Triticum vavilovii* (*T. vavilovii* Aus22498)-derived Russian wheat aphid (RWA)-resistant germplasm. Inheritance studies indicated monogenic control of resistance. The resistance gene was tentatively designated as *Yrvav* and was located on chromosome 1B by monosomic analysis. A close association (1.5±0.9% recombination) of *Yrvav* with a *T. vavilovii*-derived gliadin allele (*Gli-B1vav*) placed it in chromosome arm 1BS. *Yrvav* was allelic with *Yr10*. Tests with *Yr10* avirulent and virulent pathotypes showed that *Yrvav* and *Yr10* possess identical pathogenic specificity. *Yrvav* and *Yr10* showed close genetic associations with alternate alleles at the *Xpsp3000* (microsatellite marker), *Gli-B1* and *Rg1* loci. Based on these observations *Yrvav* was named as *Yr10vav*. The close association between *Xpsp3000* and *Gli-B1* was also confirmed. The *Yr10vav*-linked *Xpsp3000* allele (285 bp) was not present in 65 Australian cultivars, whereas seven Australian wheats lacking *Yr10* carried the same *Xpsp3000* allele (260 bp) as *Yr10* carrying wheat cultivar Moro. *Xpsp3000* and/or *Gli-B1* could be used in marker-assisted selection for pyramiding *Yr10vav* or *Yr10* with other stripe rust resistance genes. *Yr10vav* was inherited independently of the *T. vavilovii*-derived RWA resistance.

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Introduction

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici*, is an important disease of wheat in cooler climates. Seedling resistance to stripe rust has been short-lived because of single-step mutations in the pathogen (Wellings and McIntosh 1990) and hence a continued search for diverse sources of resistance is essential. A seedling resistance gene, temporarily designated, *Yrvav*, was identified in *Triticum vavilovii* (AABBDD)-derived Russian wheat aphid (RWA)-resistant wheat germplasm produced by the Leslie Research Centre, Toowoomba, Queensland, Australia. Australian multi-pathotype studies suggested that this gene may be different from those previously identified; thus, genetic and cytogenetic analyses were conducted to determine the inheritance, chromosome location and linkage with other genes.

Genetic linkages between rust resistance genes (*Sr24* and *Lr24*) and phenotypic markers [seedling chlorosis (*Sc*), pseudo black chaff (*Pbc*) and *Sr2*] are exploited for enabling germplasm enhancement by the National Cereal Rust Control Program in order to combine rust resistance genes. Genetically linked molecular markers have been reported for genes *Yr10* (Frick et al. 1998) and *Yr17* (Robert et al. 1999), and *Yr15* in tetraploid wheats (Sun et al. 1997). Closely linked DNA markers provide a powerful alternative tool for gene-pyramiding and marker assisted selection in breeding programs. Devos et al. (1995) and Manifesto et al. (1998) reported a close genetic association between the microsatellite marker *Xpsp3000* and *Gli-B1* located in chromosome 1BS.

The present study determined the genetic association of *Xpsp3000* with *Yrvav* and *Yr10*. The potential role of *Xpsp3000* in marker-assisted selection for *Yrvav* and *Yr10* was investigated. Since the germplasm was originally developed for Russian wheat aphid (RWA) resis-

tance, the genetic relationship between stripe rust resistance and RWA resistance was also evaluated.

Materials and methods

Host materials

Line QLD709, a backcrossed derivative of *T. vavilovii* in cultivar (cv) Janz (Janz*2/*T. vavilovii* accession AUS22498), was originally selected for resistance to RWA, subsequently it was found to carry resistance to stripe rust evidently also transferred from *T. vavilovii*. An F3 population was produced from a cross between QLD709 and selection Avocet S used at PBI Cobbitty as a standard susceptible line for stripe rust research. QLD709 was crossed with all 21 Chinese Spring (CS) monosomics and F2 populations were produced from monosomic individuals in each cross. QLD709 was also crossed with Moro/6*Avocet S and a F2 population was generated. Cultivar Moro carries *Yr10*, which is closely linked with *Gli-B1moro* (Payne et al. 1986) and *Rg1*, for brown glume colour (Metzger and Silbaugh 1970). An Iranian *Triticum spelta* accession 415 (*T. spelta* acc. 415) was also tested. The stripe rust resistance of line QLD709 was tentatively designated *Yrvav*.

Pathogen material

Puccinia striiformis f. sp. *tritici* (Pst) pathotype 110 E143A+ (PBI accession 861725) was used to screen F3 lines in the seedling stage. This pathotype is avirulent on seedlings with *Yr10*. North American Pst pathotypes CDL29 (*Yr10*-virulent) and CDL45 (*Yr10*-avirulent) were used to test selected F3 lines, parental and control genotypes.

Stripe rust response tests

Seedlings were raised, inoculated and evaluated for stripe rust resistance according to procedures described by Bariana and McIntosh (1993).

Gel electrophoresis

Unreduced grain-protein extracts were analysed using a 12% polyacrylamide gel. *Gli-B1* alleles were designated *Gli-B1vav* (*T. vavilovii* and a derivative QLD709), *Gli-B1avs* (Avocet S) and *Gli-B1moro* (Moro).

Primer sequences

Primer sequences described by Devos et al. (1995) were used to amplify the *Xpsp3000* microsatellite locus. This microsatellite was referred to as (CAA) and *Xpsp2(gli1)*, respectively, by Devos et al. (1995) and Manifesto et al. (1998). Devos and Gale (1997) subsequently gave the *Xpsp3000* designation to the locus amplified in these studies.

DNA isolation

DNA was isolated from 10–15 F3 seedlings grown in the greenhouse according to the method described by Dellaporta et al. (1983).

PCR amplification and electrophoretic separation of PCR products

PCR was carried out in a DNA thermal sequencer (Hybaid PCR Express) in a 10-µl reaction volume containing 50–75 ng of DNA, 1× reaction buffer (Advanced Biotechnologies Buffer 4), 1.5 mM $MgCl_2$, 500 nM of each primer, 200 µM of each dNTP and 1.0 units of *Taq* DNA polymerase. The amplification profile was an initial denaturation at 95°C for 3 min followed by 30 cycles of denaturation at 94°C for 1 min, annealing at 55°C for 1 min and extension at 72°C for 1 min (Devos et al. 1995), and a final extension at 72°C of 5 min. Five microliters of each PCR product was separated in a 0.4-mm-thick denaturing gel of 6% polyacrylamide (19:1 Acrylamide: Bis) and 7 M urea by electrophoresis at 60 W for 2.5 to 3 h. PCR products were visualised by silver staining (Bassam et al. 1991). PCR amplification with a *Yr10*-diagnostic marker (Frick et al. 1998) was performed on a small group of selected homozygous resistant and homozygous susceptible lines and the controls.

Russian wheat aphid (RWA) screening

Forty F3 lines showing monogenic segregation for stripe rust response were screened for RWA response at the Colorado State University, Fort Collins, USA. The RWA screening procedure is described in Nkongolo et al. (1989). The RWA resistance gene possessed by QLD709 was tentatively designated *Dnvav.*

Statistical analyses

Chi-square analyses were performed to determine the goodness of fit of observed phenotypic frequencies with expected ratios. The maximum-likelihood method of Allard (1956) was used to calculate recombination.

Results

Parental lines QLD709 and Avocet S produced infection types (IT) “0;” (resistant) and “4” (susceptible), respectively, when tested with Pst pathotype 110 E143A+ and F1 plants produced IT “0;”, similar to the resistant parent, indicating dominance of the resistance.

Inheritance and monosomic analysis of stripe rust resistance in QLD709

Stripe rust tests were conducted on F3 seedlings derived from Avocet S/QLD709 to determine the inheritance of resistance to stripe rust. Of 100 F3 lines, 24 were scored homozygous resistant, 51 segregating and 25 homozygous susceptible ($\chi^2_{1:2:1}$=0.06, P>0.9) indicating monogenic inheritance. Monosomic F2 analysis for a dominant gene depends on distinguishing a segregation pattern that deviates from monogenic inheritance in one cross compared to others (Sears 1953). Segregation in the F2 population derived from the cross Chinese Spring monosomic 1B/QLD709 clearly deviated from 3:1 with a deficiency in the number of susceptible (presumably nullisomic) seedlings (Table 1). Segregation in all other crosses, as well as the pooled data, conformed with monogenic inheritance. It was concluded that *Yrvav* was located in chromosome 1B.

Genetic association of *Yrvav*, *Gli-B1* and *Xpsp3000*

Chromosomes of homoeologous group 1 carry *Gli-1/Glu-3* genes on the short arms. Line QLD709 and Avo-

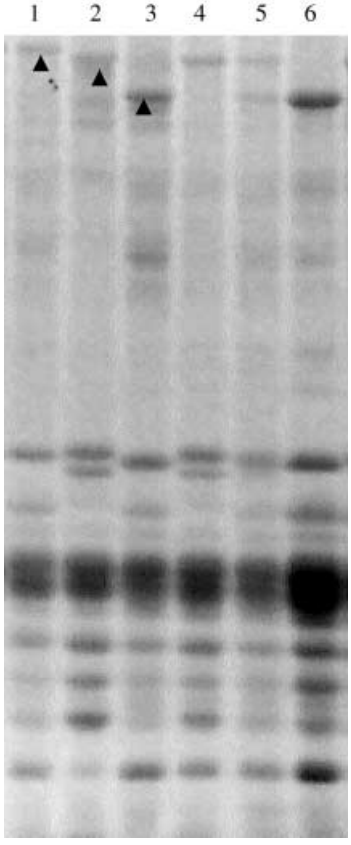

Fig. 1 *Gli-B1* patterns of *1* Moro (*Yr10*), *2* Avocet S, *3* QLD709 (*Yrvav*), *4–6* F3 lines *yrvavyrvav*, *Yrvavyrvav* and *YrvavYrvav*, respectively. *Arrows* indicate polymorphic bands

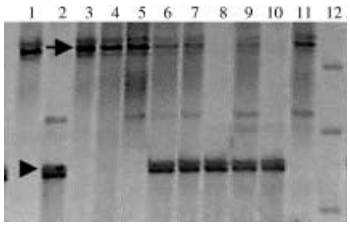

Fig. 2 Segregation of the *Xpsp3000* marker in F3 lines of Avocet S/QLD709 classified for stripe rust response. *Lanes 1 T. vavilovii*; *2* Avocet S; *3* QLD709; *4, 5, 11* homozygous resistant; *6, 7, 9* Segregating; *8, 10* homozygous susceptible F3 lines; *12* 25-bp DNA ladder. *Arrows* indicate polymorphic bands

cet S showed polymorphism at the *Gli-B1* locus (Fig. 1). The joint segregation in F3 lines for *Yrvav* and *Gli-B1* loci is presented in Table 2. Only three recombinant individuals were observed among 98 F3 lines. All recombinants were of the *Yrvavyrvav Gli-B1vavGli-B1vav* genotype. Genes *Yrvav* and *Gli-B1vav* showed coupling linkage with 1.5±0.9% recombination. This close genetic association placed *Yrvav* in chromosome arm1BS.

QLD709 and Avocet S showed polymorphism for the microsatellite locus *Xpsp3000* with the 285- and 240-bp alleles, respectively (Fig. 2). Like the *Gli-B1* locus the QLD709 and Avocet S *Xpsp3000* alleles were designated '*vav*' and '*avs*', respectively. Genotypic frequencies of F3 lines with respect to the *Gli-B1* and *Xpsp3000* loci conformed to single-gene segregation in each case (Table 3). Chi-square analysis of joint segregation indicated close genetic linkage between these loci (1.1±0.8% recombination).

Table 1 F2 segregation in crosses involving 21 Chinese Spring monosomics and QLD709

Cross	Resistant (IT "0;")	Susceptible (IT "4")	$\chi^2_{(3:1)}$
CSM1B/QLD709	148	8	32.8**
Pooled non-critical crosses[a]	522	162	0.63

** Significant at P=0.01
[a] $\chi^2_{\text{heterogeneity}}$ 18 *df*=7.86; P>0.9

Table 2 Genotypic frequencies for the *Yrvav* and *Gli-B1* loci in the F3 population derived from Avocet S/Line QLD709. $\chi^2_{1:2:1;\ Yrvav\ vs\ yrva}$=0.12, $\chi^2_{1:2:1;\ Gli\text{-}B1vav\ vs\ Gli\text{-}B1avs}$=0.18, $\chi^2_{1:2:1:2:4:2:1:2:1}$=181.58. Value for significance at P=0.05 and 2 *df* is 5.99, and P=0.05 and 8 *df* is 15.50

Genotype (IT)	Gli-B1vav vav	Gli-B1vav avs	*Gli-B1avs avs*	*Total*
Yrvav Yrvav (0;)	23	0	0	23
Yrvav yrvav (0;:3+)	3	47	0	50
yrvav yrvav (3+)	0	0	25	25
Total	26	47	25	98

Table 3 Genotypic frequencies for the *Gli-B1* and *Xpsp3000* loci in the F3 population derived from Avocet S/Line QLD709. $\chi^2_{1:2:1;\ Gli\text{-}B1\ vav\ vs\ avs}$=0.02, $\chi^2_{1:2:1;\ Xpsp3000\ vav\ vs\ avs}$=0.19, $\chi^2_{1:2:1:2:4:2:1:2:1}$=172.6. Value for significance at P=0.05 and 2 *df* is 5.99, and P=0.05 and 8 *df* is 15.50

Genotype	*Xpsp3000 vav vav*	*Xpsp3000 vav avs*	*Xpsp3000 avs avs*
Gli-B1vav vav	23	1	0
Gli-B1vav avs	0	47	0
Gli-B1avs avs	0	1	22

Table 4 F2 genotypic frequencies for the *Yrvav* and *Xpsp3000* loci based on tests of the F3 population derived from Avocet S/QLD709. $\chi^2_{1:2:1;\ Yrvav\ vs\ yrvav=0.18}$. $\chi^2_{1:2:1;\ Xpsp3000vav\ vs\ avs=0.03}$. $\chi^2_{1:2:1:2:4:2:1:2:1=154.4}$. Value for significance at P=0.05 and 2 *df* is 5.9, and P=0.05 and 8 *df* is 15.50

Genotype	*Xpsp3000* vav vav	*Xpsp3000 vav avs*	*Xpsp3000 avs avs*
Yrvav Yrvav	21	1	0
Yrvav yrvav	3	46	0
yrvav yrvav	0	1	22

Table 5 Comparative responses of *Yrvav* and *Yr10*, when tested with *Yr10*-avirulent and *Yr10*-virulent pathotypes and allelic variation at closely linked loci

Genotype	CDL-45 IT	CDL-29 IT	*Gli-B1 allele*	*Rg1*	*Xpsp3000*
Homozygous susceptible F3 lines (*yrvavyrvav*)	4	4	avs	–	240 bp
Avocet S (*yrvavyrvav*)	4	4	avs	–	240 bp
Homozygous resistant F3 lines (*YrvavYrvav*)	0;	4	vav	–	285 bp
QLD709 (*YrvavYrvav*)	0;	4	vav	–	285 bp
Moro/6*Avocet S (*Yr10Yr10*)	0;	4	moro	+	260 bp
T. spelta acc. 415 (*YrvavYrvav*)	0;	4	vav	–	285 bp

The genotypic frequencies for the *Yrvav* and *Xpsp3000* loci are given in Table 4. Segregation at both loci conformed to the expected 1:2:1 ratios, and the joint segregation ratio indicated a close genetic association. Recombination of 2.7±1.1% was estimated using the maximum-likelihood equation (Allard 1956).

Relationship of *Yrvav* and *Yr10*

Hybrid analysis

Moro (*Yr10*)/6*Avocet S was crossed with QLD709 in order to test for allelism or linkage. The absence of segregation among 398 F2 seedlings indicated genetic association or allelism between the resistance genes.

Stripe rust tests with Yr10-*avirulent and virulent pathotypes*

As Australian Pst pathotypes failed to differentiate lines with *Yrvav* and *Yr10*, tests were conducted in Canada using *Yr10* –avirulent (CDL-45) and *Yr10*-virulent (CDL-29) pathotypes. The infection-type data for two homozygous resistant lines and two homozygous susceptible lines from the F3 population of QLD709/Avocet S, the parents and selected controls are given in Table 5. Lines with both *Yr10* and *Yrvav* showed susceptible responses with Pst pathotype CDL-29 indicating that they were the same gene.

Comparison of alleles at linked loci Gli-B1, Rg1, Xpsp3000 *and the* Yr10-PCR *test*

Yr10 is distal to the *Gli-B1* locus. *Rg1*, for brown glume colour, is located between *Gli-B1* and *Yr10* (Payne et al. 1986), whereas *Yrvav* and *Yr10* may be allelic. Lines carrying *Yrvav* possessed alternate alleles at the *Rg1*, *Gli-B1* and *Xpsp3000* loci compared with those possessing *Yr10*. The *Yr10* and *Yrvav* stocks carry *Gli-B1moro* and *Gli-B1vav*, respectively (Fig. 1), and *Yrvav* lines do not carry *Rg1*. Lines with *Yr10* produced a 260-bp product when amplified with the psp3000 microsatellite, whereas *Yrvav* produced a 285-bp product. The resistance genes *Yrvav* and *Yr10* showed 2.7% and 3.5% (Bariana et al., unpublished) recombination with the *Xpsp3000* microsatellite locus, respectively. The *Yr10*-diagnostic PCR test (Frick et al. 1998) failed to amplify the 1,100-bp product in two homozygous *YrvavYrvav* F3 lines and the *Yrvav* parent QLD709. These results demonstrated that lines carrying *Yrvav* and *Yr10* possessed alternate alleles at the closely linked loci *Xpsp3000*, *Gli-B1* and *Rg1*.

Potential role of *Xpsp3000* in marker-assisted selection

Sixty five current Australian cultivars lacking *Yr10* and *Yrvav* were screened using the *Xpsp3000* microsatellite marker. None of these cultivars carried the *Yrvav*-linked 285-bp allele, whereas seven cultivars possessed the *Yr10*-linked 260-bp allele. These seven lines, however, possessed different *Gli-B1* alleles than the *Yr10* parent Moro. This implies that care should be taken in the selection of recurrent parents if *Xpsp3000* is to be used for marker-assisted selection of *Yr10*. The absence of the 285-bp allele in 65 cultivars demonstrated the unique association of this allele with *Yrvav*, indicating that *Xpsp3000* could be used in marker-assisted selection for *Yrvav*. Combined selection for the linked *Xpsp3000* and *Gli-B1* alleles would enhance the accuracy of marker-assisted selection.

Parents QLD709, Avocet S and 40 F3 lines showing monogenic segregation at the *Yrvav* locus were screened for RWA resistance. While Avocet S was uniformly susceptible, QLD709 segregated for RWA response. Due to the heterozygosity of QLD709, only 17 segregating (*Dnvavdnvav*) genotypes were available for comparison. These lines were scored 4 *YrvavYrvav*:8 *Yrvavyrvav*:5 *yrvavyrvav*, a good fit to a 1:2:1 ratio ($\chi^2_{1:2:1}$=0.16, *P*>0.8). These results suggested that the genes determining stripe rust resistance and RWA resistance were genetically independent.

Discussion

Results from inheritance studies and monosomic analysis indicated that *Yrvav* is a single dominant gene located in chromosome 1B. The close linkage of *Yrvav* and *Gli-B1vav* confirmed the results of monosomic analysis and placed *Yrvav* in chromosome arm 1BS. Stripe rust resistance genes *Yr10*, *Yr15*, *Yr24* (McIntosh et al.1998), *Yr26* (R.A. McIntosh, personal communication) and *YrH52* (Peng et al.1999) are also located in chromosome 1BS. Previous studies showed linkage of *Yr10* with *Gli-B1* (5.0±2.18 cM) in a cross between Moro and Lee (Payne et al. 1986). The high-molecular-weight gliadin encoded by *Gli-B1moro*, however, migrates more slowly than those encoded by *Gli-B1avs* and *Gli-B1vav* (Fig. 1). An analysis of backcross derivatives of Moro in five genetic backgrounds confirmed the close association of the *Gli-B1moro* allele with *Yr10* (Bariana and Ahmed, unpublished).

Payne et al. (1986) reported close association of *Rg1* with *Gli-B1* (1.8±0.8 cM). Earlier Metzger and Silbaugh (1970) reported a recombination value of 2.0% between *Rg1* and *Yr10*. While Moro (*Yr10*) has a brown glume colour, both *T. vavilovii* and Line QLD709 have a white glume colour.

Frick et al. (1998) developed a diagnostic SCAR marker for *Yr10*. The 1,100-bp *Yr10*-diagnostic product has significant homology at the amino-acid level to the nucleotide-binding site (NBS) regions of other plant disease resistance genes/gene analogues. This marker, however, did not amplify the 1,100-bp *Yr10*-diagnostic product in *Yrvav* lines, suggesting that *Yrvav* does not have sequences similar to *Yr10* at the target priming sites. Spielmeyer et al. (2000) detected RFLP differences between *Yr10* and *Yrvav* stocks when rga*Yr10* was used as a probe. Devos et al. (1995) and Manifesto et al. (1998) reported close linkage (1.5 cM and complete association, respectively) of *Xpsp3000*, a tri-nucleotide repeat (CAA)15 with a 1BS encoded γ-gliadin. Screening of F3 families from Avocet S/QLD709 and Moro/Avocet S using the primer set of Devos et al. (1995) revealed close linkages of *Gli-B1vav* (1.1%), *Yrvav* (2.7%) and *Yr10* (3.5%) with the *Xpsp3000* locus. *Gli-B1vav* and *Yrvav* were linked in coupling and showed 1.5±0.9% recombination. Comparisons of linkage estimates (Fig. 3) suggested that *Yrvav* is distal to *Gli-B1*, whereas *Xpsp3000* is proximal to *Gli-B1*. The absence of segregation in F2 population derived from Moro (*Yr10*)/6*Avocet S//QLD709 (*Yrvav*) and similar pathogenic specificity suggested that *Yrvav* and *Yr10* may be identical. Based on linkage with alternate alleles at closely linked loci, the white glumed source of *Yr10* is named as *Yr10vav*.

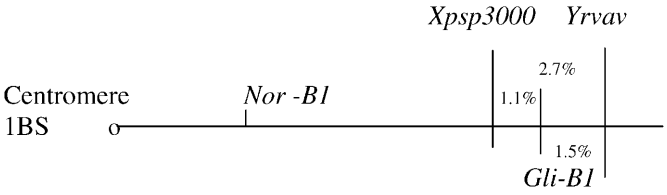

Fig. 3 Map of chromosome arm 1BS showing location of *Yrvav*, *Gli-B1*, and *Xpsp3000* in the Avocet S/QLD709 population and inferred location of the *Nor-B1* locus

Kema and Lange (1992) reported a source of *Yr10* with white glumes in the Iranian spelt accession 415. Accession 415 was found to have identical alleles to *T. vavilovii* AUS22498 at the *Gli-B1*, *Yrvav* and *Xpsp3000* loci (Table 5). *T. vavilovii*, spelt accession 415 and PI178383 (donor of the brown glumed *Yr10* source) originated from the former USSR, Iran and Turkey, respectively. These three countries are geographically close to each other.

The unique genetic associations of *Yr10vav* and *Yr10* with specific alleles of *Gli-B1* and *Xpsp3000* will be useful in marker-assisted selection and gene pyramiding. Certain Australian wheats, however, possessed the *Yr10*-linked *Xpsp3000* allele but not *Yr10*, indicating a necessity to conduct disease response tests and/or *Gli-B1* assays to confirm the presence of *Yr10*. Similarly a combination of *Xpsp3000* and *Gli-B1* assays would be useful for marker-assisted identification and pyramiding of *Yr10vav*.

Although *Yr10vav* was first identified in lines selected for RWA resistance, the resistances were found to be genetically independent. This agreed with the results of Dong et al. (1997). They reported allelism of RWA resistances in the line AUS-VA1-F3 (a line derived from the same cross as QLD709) and PI294994, which carries *Dn5* located in chromosome 7D.

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