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Chromosomal location of an uncharacterised stripe rust resistance gene in wheat

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Abstract A recent introduction of *Puccinia striiformis* f. sp. *tritici* (Pst) pathotype 134 E16A+ in Western Australia differed from existing pathotypes in its virulence for stripe rust resistance genes *Yr8* and *Yr9*, and avirulence for *Yr3*, *Yr4*, *Yr34* and some uncharacterized sources of resistance. The Australian wheat cultivar Rubric exhibited a very low seedling stripe rust response when tested against the Pst pathotype 134 E16A+. Genetic analysis of a Rubric/Avocet 'S' F_3 population indicated monogenic inheritance of resistance. The resistance gene was tentatively designated *YrRub*. Bulked segregant analysis using multiplex-ready PCR technology placed *YrRub* distal to the microsatellite marker *barc75* in chromosome 3BS. Follow up studies mapped SSR marker *cfb3530* between *YrRub* (2.9 ± 1.3 cM) and *barc75* (2.4 ± 1.2 cM). Genotypes Bolac, EMU 'S', Nesser, Hybrid 46 (*Yr4*) and Avalon (*Yr4*) amplified the *YrRub*-linked *barc75* and *cfb3530* alleles. The amplification of PCR products similar to that of Rubric in *Yr4*-carrying cultivars Hybrid 46 and Avalon suggested that *YrRub* was most likely to be *Yr4*. Due to unavailability of genotypes carrying *Yr4* singly, test of allelism was not possible. Thirty-eight Australian wheat cultivars known to lack *YrRub*, an advanced breeding line WAWHT2046 (*Yr34*) and Vilmorin 23 (*Yr3*) amplified PCR products different from that of Rubric at the *barc75* and *cfb3530* marker loci. The amplification of non-Rubric alleles at the marker *barc75* and *cfb3530* loci among a set of diverse wheat genotypes demonstrated that these markers could be used for marker assisted selection of *YrRub* in combination with other molecularly tagged seedling and adult plant stripe rust resistance genes in wheat breeding programs.

Keywords Stripe rust resistance · *Puccinia striiformis* f. sp. *tritici* · Multiplex-ready PCR · SSR markers

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Introduction

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (Pst), was first reported in Australia in 1979 and resulted in an epidemic rendering several wheat cultivars susceptible (O'Brien et al. 1980; Wellings 2007). A committed breeding effort of deploying seedling and adult plant resistance gene combinations in eastern Australia resulted in improved levels of

resistance in Australian cultivars (Bariana et al. 2001). No significant evolution in the stripe rust pathogen was detected for over a decade after the identification of Pst pathotype 110 E143A+ in 1986 (Wellings and McIntosh 1990). The *Yr17* virulent pathotype 104 E137A− Yr17+ was detected in 1999 (Wellings 2007). This pathotype was avirulent on genotypes carrying stripe rust resistance genes *Yr6*, *Yr7* and *YrA* and therefore a combination of these genes with *Yr17* provided protection against predominant pathotypes in Australia (Bariana et al. 2004).

The wheat growing area in Western Australia is geographically separated from the eastern Australian wheat belt and remained free from stripe rust until the detection of Pst pathotype 134 E16A+ in 2002 (Wellings et al. 2003). This pathotype differed from eastern Australian Pst pathotypes in its virulence on seedling resistance genes *Yr8* and *Yr9* and its avirulence on *Yr3*, *Yr4* and *Yr34* and some other uncharacterised resistance sources. It also produced a significantly higher level of infection on many Australian cultivars previously reported to have moderate levels of adult plant resistance.

The Australian wheat cultivar Rubric (AUS33333), a selection from the CIMMYT genotype EMU 'S' (AUS17224), was released in 2002. It exhibited a high level of stripe rust resistance when tested under field conditions in 2003. Rubric showed susceptible seedling responses to the pre-2002 Pst pathotypes, whereas it showed a low seedling response against the Pst pathotype 134 E16A+. The seedling infection type (IT) of Rubric (IT;;C) was considerably lower than that expressed by WAWHT2046 (IT23C), which carries *Yr34*, another gene that confers seedling resistance to this pathotype. Genetic analysis was undertaken to study the mode of inheritance of seedling stripe rust resistance in cultivar Rubric. Bulked segregant analysis, using multiplex PCR technology, was performed to determine the genomic location of gene(s) involved.

Materials and methods

Generation of a segregating population

Cultivar Rubric was crossed with the susceptible line Avocet 'S'. The F_1 plants were grown during summer and F_2 plants were space planted under rust free field conditions. A total of 89 F_2 plants were successfully harvested and the F_3 families were used for inheritance and genomic location studies.

Pathogen material

The Pst pathotypes used for seedling studies included: 110 E143A+ (444) and 134 E16A+ (572). The avirulence and virulence details of these pathotypes are described in Wellings (2007). The initial introduction of Pst pathotype, 104 E137A−, to Australia evolved to acquire virulence for *Yr6* and *YrA* (108 E141A+), another single step mutation for virulence on *Yr7* produced pathotype 110 E143A+ (Wellings 2007). The addition of A+ indicates virulence for the gene *YrA*. The post-2002 pathotype 134 E16A+ carries additional virulence for *Yr8* and *Yr9* when compared to the most virulent pre-2002 pathotype 110 E143A+. Pathotype 134 E16A+ also differs from 110 E143A+ for avirulence on *Yr3*, *Yr4*, *Yr34* and some other uncharacterized sources of resistance.

Greenhouse screening

Twenty seeds of each F_3 family were sown in 9 cm pots filled with a mixture of pinebark and sand. The parents Rubric and Avocet 'S' were included as controls. Ten grams of the water soluble fertiliser Aquasol® was dissolved in 10 l of tap water and applied to 100 pots. A single application of nitrogenous fertilizer urea was applied at the same rate as Aquasol to seven days old seedlings. Genotypes (with known resistance genes) Vilmorin 23 (*Yr3*), Hybrid 46 (*Yr4*), Avalon (*Yr4*) and WAWHT2046 (*Yr6*, *Yr34*) together-with Rubric and Avocet 'S' were sown in duplicate for evaluation against two pathotypes. Cultivars Bolac and Nesser showing response patterns similar to Rubric, were also included in this experiment. Seedlings were grown under rust free conditions in a temperature-controlled greenhouse maintained at 20°C before inoculation.

Twelve-day old Rubric/Avocet 'S'-derived $F_{2:3}$ seedlings (two leaf stage) were inoculated with urediniospores of the Pst pathotype 134 E16A+, whereas all other genotypes were inoculated with two pathotypes. Inoculated seedlings were incubated at 9–12°C for 24 h, under 100% relative humidity, and then moved to the greenhouse room maintained at 17 ± 2°C. Seedling responses were scored on a 0–4

scale as described in Bariana and McIntosh (1993). The F_3 families were classified as non-segregating resistant (families showing uniform resistant response), segregating (families with both resistant and susceptible responses) and non-segregating susceptible (families with uniform susceptible response).

Molecular mapping

Genomic DNA was extracted from silica gel dried leaf tissue of each F_3 family. Leaf sample for DNA isolation represented tissue from at least eight plants. Dried leaves were crushed using a stainless steel ball bearing in a Retsch MM300 Mixer Mill (Retsch, Germany) in 2 ml tubes. Seven hundred µl of pre-warmed (65°C) extraction buffer (50 mM Tris–HCl, 10 mM EDTA, 100 mM NaCl, 1% (w/v) SDS, 10 mM ß-mercaptoethanol, pH 8.0) was added to each tube. Samples were incubated at 65°C for 10 min and cooled at room temperature for 3 min. One hundred and fifty microliters of 3 M potassium acetate pH 5.2, was added and the tubes were shaken vigorously before cooling at −20°C for 20 min. The tubes were centrifuged at 13,000 rpm for 10 min and 700 µl of supernatant was transferred to fresh tubes. An equal volume of isopropanol was added and the tubes were inverted several times to mix supernatant with isopropanol. The tubes were then centrifuged at 10,000 rpm for 10 min to precipitate the DNA. The pellet was washed with 500 µl of 70% ethanol and air dried before re-suspension overnight in 200 µl of 10 mM Tris–HCl, pH 8.0. The tubes were centrifuged at 10,000 rpm for 5 min and 180 µl of supernatant containing the DNA was transferred to fresh tubes for storage at −20°C. The DNA samples were quantified using a Nanodrop ND-1000 Spectrophotometer (Nanodrop Technologies).

Bulk segregant analysis (BSA), as described by Michelmore et al. (1991), was used to determine the chromosomal location of the resistance gene(s) associated with low stripe rust response in the Rubric/Avocet 'S' cross. The resistant and susceptible bulks contained equal amounts of pooled DNA from nine resistant and nine susceptible F_3 families, respectively. BSA was performed using a multiplex-ready PCR (Hayden et al. 2008) whole genome scan kit consisting of 488 published microsatellite (SSR) markers selected for high polymorphism in Australian wheat germplasm and genome coverage. Multiplex-ready PCR assays for BSA and genetic mapping were performed as described in Hayden et al. (2008). Electrophoresis and visualisation of the PCR products was performed on a GelScan2000 (Corbett Research) and ABI3730 DNA fragment analyser (Applied Biosystems). For analysis on the GelScan2000, the PCR products were mixed with an equal volume of gel loading dye (98% formamide, 10 mM EDTA, and 0.5% basic fuchsin as tracking dye), heated for 3 min at 95°C, chilled quickly on ice and separated on a 5% sequencing gel (Sambrook and Russell 2001). The 80 bp fluorescent DNA ladder was used to calculate allele sizes. For ABI3730 analysis, the procedure described by Hayden et al. (2008) was followed. SSR allele scoring was performed using GeneMapper v4.0 (Applied Biosystems). Four new primers mapped in the most distal deletion bin on 3BS (3BS3-0.87-1.00) from the physical map developed by Paux et al. (2008) were used to refine genomic location of the resistance gene. All these primers were distal to *barc75*.

Data analyses and genetic mapping

Chi-squared tests were used to determine the goodness-of-fit of observed segregation with expected genetic ratios. Recombination fractions were calculated with the MAP MANAGER version QTXb20 (Manly et al. 2001) using the Kosambi (1944) mapping function.

Results

Inheritance studies

Cultivar Rubric displayed a susceptible stripe rust response (IT3) when tested against pre-2002 Australian Pst pathotypes, and produced a resistant response (IT;;C) against the Pst pathotype 134 E16A+ (Table 1). The susceptible parent Avocet 'S' exhibited IT3+ against all pathotypes used. The Rubric/Avocet 'S' F_3 families showed monogenic segregation ($\chi^2_{1:2:1} = 0.06$ non-significant at $P = 0.05$ and 1 *df*), when tested against the Pst pathotype 134 E16A+ (Table 2). The resistance gene conferring the low stripe rust response was tentatively designated *YrRub*.

Table 1 Seedling infection types produced by different genotypes against two *Puccinia striiformis* f. sp. *tritici* pathotypes

Genotype	Gene(s)	Pathotype/infection type	
		110 E143A+	134 E16A+
Rubric	*YrRub*	3	;;C
Vilmorin 23	*Yr3*	3C	;1N
Hybrid 46	*Yr4*	23−	;
WAWHT2046	*Yr6*, *Yr34*	3+	23C
Avalon	*Yr4*	3+	0;
Bolac	*YrRub*	3+	0;
Nesser	*YrRub*	3+	0;
Avocet 'S'	–	3+	3+

Table 2 Frequency distribution of F_3 lines derived from Rubric/Avocet 'S' when tested against the *Puccinia striiformis* f. sp. *tritici* pathotype 134 E16A+ at the seedling stage

Genotype	No. of F_3 lines		$\chi^2_{(1:2:1)}$
	Observed	Expected	
YrRubYrRub	22	22	0.00
YrRubyrRub	45	44	0.02
yrRubyrRub	21	22	0.04
Total	88	88	0.06

Table value of χ^2 at $P = 0.05$ at 2 $df = 5.99$

Chromosome location and genetic mapping

A whole genome scan kit consisting of 488 SSR markers was used to screen the parental lines and contrasting DNA bulks for loci associated with stripe rust response in the Rubric/Avocet 'S' cross. Nine markers revealed polymorphism between the parental lines and showed linkage with the resistant and susceptible DNA bulks. The entire F_3 population was genotyped for the linked microsatellite markers. Four markers located on the short arm of chromosome 3B, namely *barc75*, *gwm533*, *gwm493* and *barc102* showed strong genetic association with resistance. Marker *barc75* mapped closest to *YrRub*. In order to refine the location of *YrRub* in chromosome 3BS, four SSR markers (*cpf3132*, *cfp140*, *cfb3530* and *cfb3296*) that mapped distal to *barc75* were tested on parents and bulks. Marker *cpf3132* was monomorphic, whereas markers *cfp140*, *cfb3530* and *cfb3296* were polymorphic and linked. Markers *cfp140* and *cfb3296* failed to amplify any product, when DNA from parent Avocet S was used, indicating the dominant inheritance of these markers. These markers were not mapped on the entire population as they were expected to be non-informative on 50% of heterozygous individuals of the F_3 population. The co-dominant marker *cfb3530* amplified 150 and 155 bp products, respectively, when DNA from Rubric and Avocet S were used. This marker was genotyped on the entire population. The marker *cfb3530* mapped between *YrRub* and *barc75* (Fig. 1). All markers conformed to the expected 1:2:1 segregation ratio. The LOD values for all of the linked markers were more than 30.0.

Tests on selected genotypes

Genotypes carrying known resistance genes Vilmorin 23 (*Yr3*), Hybrid 46 (*Yr4*) and WAWHT2046 (*Yr6*, *Yr34*) produced high infection types against the pre-2002 Pst pathotype 110 E143A+, whereas these genotypes produced infection types IT;1N, IT; and IT23C, respectively, against the Pst pathotype 134 E16A+ (Table 1). Cultivars Avalon, Bolac and Nesser produced infection types similar to that of Rubric. These genotypes and a set of current Australian wheat cultivars were genotyped using the SSR markers *barc75* and *cfb3530*, and results are presented in Table 3. Rubric, Bolac, Nesser and EMU 'S' amplified the *YrRub*-linked $barc75_{132bp}$ and $cfb3530_{150bp}$ alleles. Stripe rust differential Hybrid 46 and the English wheat cultivar Avalon, both known to carry *Yr4*, amplified the *YrRub*-linked alleles at the *barc75* and *cfb3530* loci indicating that *YrRub* could be *Yr4*. Genotypes carrying *Yr3*, *Yr34*

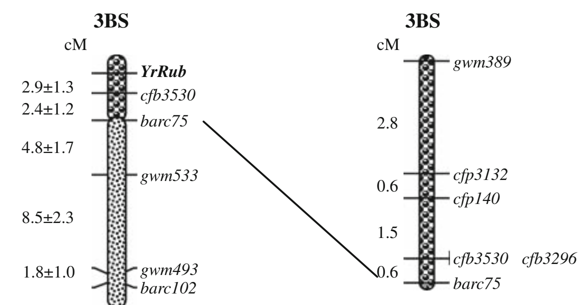

Fig. 1 Genetic linkage map showing location of *YrRub* at the distal end of the chromosome 3BS (Kosambi map distances cM shown on the left side) and comparison of map from this study with that of the distal deletion bin 3BS3-0.87-1.00 of chromosome 3BS (Paux et al. 2008)

Table 3 Genotypic status of wheat cultivars with respect to closely linked microsatellite markers

Gene/cultivars	Allele size (bp)	
	barc75	*cfb3530*
YrRub		
Rubric, Bolac, Nesser, EMU 'S'	132	150
Yr4		
Avalon, Hybrid 46	132	150
Neither *YrRub* nor *Yr4* in all groups below		
Carinya, Datatine	135	155
Aroona, Barham, Baxter, Binnu, Bullaring, Frame, Giles, Gladius, Halberd, Janz, QAL 2000, Schomburgk, Sunco, Sunlin, Tasman, Tatiara, Westonia	136	155
Breawood, Calingri, Camm, Carnamah, Derrimut, Diamondbird, Ellison, Goldmark, EGA Gregory, H45, Kellalac, Kukri, Lang, Sunstate, Sunvale, Sunzell, Ventura, Vilmorin 23 (*Yr3*), WAWHT2046 (*Yr6*, *Yr34*), Wyalkatchem, Yitpi	139	155

and a set of current Australian wheat cultivars amplified PCR products different to that of Rubric (Table 3).

Discussion

Genetic analysis of stripe rust resistance in the Australian cultivar Rubric indicated the presence of a single gene tentatively designated as *YrRub*. Bulked segregant analysis indicated close genetic association of *YrRub* with the chromosome 3BS located marker *barc75* (Fig. 1). Paux et al. (2008) published a physical map of chromosome 3BS and reported some additional markers that mapped distal to *barc75* in the most distal deletion bin (3BS3-0.87-1.00). Marker *gwm389* is the most distal marker (Fig. 1) and it segregated independently of *YrRub*. In contrast, marker *cfb3530* mapped 2.9 ± 1.3 cM proximal to *YrRub* and 2.4 ± 1.2 cM distal to *barc75* (Fig. 1). These results confirmed the location of *YrRub* in the most distal deletion bin of chromosome 3BS.

The possibility of *YrRub* being identical to one of the stripe rust resistance genes *Yr3* and *Yr4* and *Yr34* that showed high and low responses against the pre- and post-2002 Australian Pst pathotypes, respectively, was considered. *YrRub* cannot be *Yr34* as the latter was located in the chromosome arm 5AL (Bariana et al. 2006) and produces an infection type higher than that produced by *YrRub* (Table 1). Although location of *Yr3* was listed in chromosome 5BL (McIntosh et al. 1995), Chen et al. (1996) located it in chromosome 2B. Similarly McIntosh et al. (1995) listed the location of *Yr4* in chromosome 3B based on the 1987 Annual Report of the Plant Breeding Institute Cambridge, UK. Again Chen et al. (1996) located a gene thought to be *Yr4* on chromosome 6B. These locations were never validated. Based on the amplification of the Rubric-specific PCR products at the *cfb3530* and *barc75* loci in genotypes known to carry *Yr4* (Hybrid 46 and Avalon), we concluded that *YrRub* could be *Yr4*. Allelism test was not possible due to the absence of *Yr4* carrying single gene stocks.

Chromosome 3BS carries durable stem rust resistance gene *Sr2* (Hare and McIntosh 1979) and resistance to *Fusarium* head blight (Somers et al. 2003). The microsatellite marker *gwm533* amplifies a 120 bp PCR product in *Sr2* carrying genotypes (Spielmeyer et al. 2003). The absence of *Sr2*-linked physiological marker, pseudo black chaff, in Rubric and the amplification of a 143 bp allele at the *gwm533* locus, suggested the absence of *Sr2* in this cultivar. The amplification of non *Sr2*-linked alleles at marker loci (data not presented) *stm559tcac*, *stm598tgag*, *stm560.3tgag* and *stm560tgag* (Hayden et al. 2004, 2006) also indicated the absence of *Sr2* in Rubric. *YrRub* may be linked closely in repulsion with *Sr2*. The location of the *Sr2*-linked marker *gwm533* in the second deletion bin (Paux et al. 2008) and estimation of a genetic distance of approximately 10 cM between *YrRub* and *gwm533* suggested that *YrRub* and *Sr2* can be combined in a single genotype.

Validation of markers closely linked with commercially important traits such as disease resistance across diverse genetic backgrounds is essential to

assure their robustness in marker assisted selection. Often, positive validation is performed on genotypes known to carry the target gene, however, negative validation is also necessary to show the absence of the gene-linked marker allele among commercial cultivars that are potential parents for marker assisted selection of the gene in question. A set of Australian cultivars and some additional genotypes were screened with markers *barc75* and *cfb3530*. The $barc75_{132bp}$ and $cfb3530_{150bp}$ alleles were amplified in Rubric, Bolac, EMU S, Nesser and *Yr4* carrying genotype Hybrid 46 and Avalon (Table 3). Australian wheat genotypes lacking *YrRub* and/or *Yr4* carried allele(s) different from Rubric at the *barc75* and *cfb3530* loci (Table 3). These results demonstrated that *barc75* and *cfb3530* could be used for marker assisted selection of *YrRub* in breeding programs.

Although *YrRub* is not effective against the pre-2002 Pst pathotypes, it could still play an important role in gene combinations in Australia and elsewhere. It is effective against all five post-2002 pathotypes that are present in the eastern Australian wheatbelt (H·S. Bariana unpublished results). Redeployment of previously defeated rust resistance genes in gene combinations is not uncommon. Following the detection of virulence in stem rust pathogen for a widely deployed gene, *Sr31*, a previously defeated gene *Sr36* did serve as a transient source of resistance against Ug99 in some cultivars. Virulence for *Sr36* was detected in Australia in 1984 (Zwer et al. 1985), however, the current predominant pathotypes in Australia are avirulent on *Sr36* (Park 2007). Similarly, the effectiveness of *YrRub* against post-2002 pathotypes supports the deployment of *YrRub* in strategically chosen gene combinations in new wheat cultivars.

This study clearly demonstrated the genomic location of *YrRub* in the short arm of chromosome 3BS. The presence of *YrRub* in CIMMYT (EMU S) and ICARDA (Nesser) germplasm was also demonstrated through marker genotyping. *YrRub* may have been transferred into CIMMYT and ICARDA germplasm through crosses involving winter wheats. Molecular markers linked with several stripe rust resistance genes (*Yr10*, *Yr15*, *Yr24*, *Yr36* and *Yr18*) have been listed in Bariana et al. (2007). Although the use of combinations of APR genes for rust proofing the wheat industry globally will be desirable, strategic deployment of molecularly tagged seedling and adult plant resistance genes would ensure durability of stripe rust resistance in new wheat cultivars.

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