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Genetic Mapping of Stem Rust Resistance in Durum Wheat Cultivar 'Arrivato'

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ABSTRACT

Genetic analysis of seedling stem rust resistance in the durum wheat cultivar 'Arrivato' indicated the presence of three independent genes. Replicated tests on F_3 families derived from 'Arrivato'/'Bansi Strain 168', putatively segregating at a single locus, were performed to confirm monogenic segregations. These families represented three distinct infection types, viz., IT;1, IT2= and ITX and the genes conditioning these different phenotypic expressions were temporarily named *SrAr1*, *SrAr2* and *SrAr3*, respectively. Up to 100 plants from at least one family representing segregation for each distinct infection type were grown and harvested individually. These monogenically segregating populations were progeny tested. Bulked segregant analyses were conducted and *SrAr1* was mapped 0.7 cM proximal to *Xgwm47* in chromosome 2BL. *SrAr2* mapped 5.7 cM distal to *Xwmc59* in the long arm of chromosome 6A, whereas *SrAr3* showed genetic association (4.6 cM) with *Xgwm334* in chromosome 6AS. Based on combinations of infection type with genomic locations and/or pathogenic specificities of previously characterized stem rust resistance genes *SrAr1*, *SrAr2* and *SrAr3* were concluded to be *Sr9e*, *Sr13* and *Sr8b*, respectively.

Keywords: genetic analysis, molecular mapping, *Puccinia graminis*, *Triticum turgidum* ssp. *durum*, Ug99

INTRODUCTION

Stem rust of wheat, caused by *Puccinia graminis* Pers. f. sp. *tritici* Eriks. & Henn. (Pgt), can infect tetraploid wheat including *Triticum turgidum* L., ssp. *durum* (Desf); durum wheat. Durum wheat is grown on over 20 million ha globally and Australian durum wheat production ranges between 300,000 to 700,000 tons annually, depending on climatic conditions. Stem rust can seriously affect durum wheat production and sustained control can be achieved through the deployment of diverse effective resistance gene combinations. A continuous effort to genetically characterise rust resistance in durum breeding materials and commercial cultivars is necessary to ensure the maintenance of host genetic diversity. Unlike hexaploid wheat (*Triticum aestivum* L.), few reports on the genetic bases of stem rust resistance in durum wheat genotypes are published (Gough and Williams 1963; Williams *et al*. 1978; Bechere *et al*. 1991; Singh *et al*. 1992; Klindworth *et al*. 2007). Consequently, very little effort has been expended on the molecular mapping of stem rust resistance at the tetraploid level. Availability of a large number of highly polymorphic and reproducible microsatellite (SSR) markers could facilitate identification of genomic regions controlling traits of economic importance such as resistance to rust diseases.

The durum cultivar 'Arrivato' (parentage; 'Tetraprelude'/'Waitohi') was released by the Crop and Food Research, New Zealand in 1987. It was released in Australia in 1995 by Heritage Seeds. Arrivato (AUS 33332, Australian Winter Cereals Collection accession number) possesses high levels of stem rust resistance in Australia and the genetic basis of resistance remained unclear. This study was conducted to assess the inheritance of stem rust resistance in 'Arrivato' and to determine the genomic locations of the components of stem rust resistance.

MATERIALS AND METHODS

Host materials

Stem rust resistant durum cultivar 'Arrivato' was crossed with the susceptible landrace 'Bansi Strain 168' (AUS 1866). F_1 plants were grown in the field and harvested individually. The field grown F_2 plants were harvested and threshed individually to produce F_3 families. Stem rust tests were performed on 198 F_3 families. Approximately 100 plants from selected F_3 families displaying monogenic segregations for distinct seedling stem rust reactions were grown individually, to develop monogenically segregating mapping populations (MSPs).

Greenhouse studies

F_3 families were tested for stem rust reaction in the seedling stage under temperature-controlled greenhouse conditions. Sixteen to 20 seeds of each family were sown in 9 cm pots and held in a rust-free microclimate room maintained at 20°C prior to inoculation. A rust testing procedure, described by Bariana and McIntosh (1993), including growing and inoculation of seedlings under greenhouse conditions, was followed. Urediniospores of Pgt pathotype (pt) 34-1,2,3,4,5,6,7 (PBI culture no. 103) suspended in light mineral oil (Shellsol T® 3 mg spores per 10 ml oil for 200 pots) were sprayed over 10-12 days old seedlings using a hydrocarbon propellant pressure pack. Stem rust inoculated seedlings were incubated under natural light at 18-20°C for 48 hrs on water filled trays covered with polythene hoods. Inoculated seedlings were then transferred to a temperature-controlled microclimate room maintained at 25°C. Stem rust seedling infection types were scored 14-16 days after inoculation according to Stakman *et al*. (1962) with slight modifications proposed by Luig (1983). The symbols '+' and '-' were added to describe variations from the typical expression of a given infection type. Symbols 'N' or 'C' were also used where more than usual necrosis and chlorosis, respectively, were associated with a particular infection type. The Pgt pts 40-1,2,3,4,5,6,7 (PBI culture

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no. 383) and 34-1,2,3,4,5,6,7,11 (PBI culture no. 171) were used to confirm identities of stem rust resistance genes *Sr9e* and *Sr8b*, respectively, in monogenically segregating populations.

Molecular mapping

DNA was extracted from 10 days old plants using the CTAB method (Doyle and Doyle 1990). PCR amplifications were performed in 20 µL volumes with final concentrations containing 50 ng of genomic DNA, 0.2 mM dNTPs, 0.5 µM of each primer, 1.5 mM $MgCl_2$, 1×PCR buffer and 1U Taq DNA polymerase. A standard touch down PCR profile (Don *et al*. 1991) was used for all PCR amplifications. PCR products were mixed with 20 µL of sequencing dye (98% formamide, 10 mM EDTA pH 8 and 0.025% bromophenol blue-xylene cyanole) and stored until further use. Amplified product was separated using 2% Agarose or 8% polyacrylamide gel electrophoreses (PAGE). Agarose gels were stained with ethidium bromide to view PCR products on the Gel Documentation System (Pathtech. Pty Ltd., Australia), whereas polyacrylamide gels were silver stained using the protocol developed by Basam *et al*. (1991).

Bulk segregant analysis (BSA) was used to scan the entire genome with microsatellite markers. DNA from 10 individual families each from non-segregating resistant (HR) and non-segregating susceptible (HS) classes, were pooled to constitute the resistant (R) and susceptible (S) bulks. Two hundred and thirteen microsatellite primers (Roder *et al*. 1998) uniformly spread over the A and B genomes were used. Markers that exhibited polymorphism among the resistant and susceptible bulks and parents were genotyped on the entire relevant segregating populations.

Statistical analyses

Chi-squared (χ^2) analyses were performed to check the goodness-of-fit of the observed segregation to the expected genetic ratios for different segregation models. Recombination fractions were calculated with the MAP MANAGER Version QTXb20 (Manly *et al*. 2001) using the Kosambi (1944) mapping function.

RESULTS

Inheritance studies

Parents 'Arrivato' and 'Bansi Strain 168' produced infection types IT0; and IT4, respectively, when tested against Pgt pt 34-1,2,3,4,5,6,7. Stem rust responses of 198 F_3 families were noted and families were classified as non-segregating resistant (HR), segregating (Seg) and non-segregating susceptible (HS). A genetic ratio of 45:12:6:1 (based on pooling families heterozygous at three loci with families homozygous for at least one locus; 45: families heterozygous at two loci; 12: families heterozygous at a single locus: 6: triple recessive families; 1) was used for analysis as only 16-20 seeds were tested. Chi-squared analysis of data presented in **Table 1** conformed to segregation at three genetically independent loci. The monogenically segregating families produced either of the three distinct infection types; IT;1, IT2= and ITX and the genes conditioning these responses were temporarily designated as *SrAr1*, *SrAr2* and *SrAr3*, respectively.

Table 2 Stem rust response frequency distribution of progenies of monogenically segregating F_3 families from the cross 'Arrivato'/'Bansi Strain 168' when tested with Pgt pt 34-1, 2, 3, 4, 5, 6, 7.

Gene/MSP	No. of progenies			Total	$\chi^2_{1:2:1}$
	HR	Seg	HS		
SrAr1 (IT)	;1	;1, 3+	3+		
MSP107	24	49	21	94	0.30
MSP165	13	24	11	48	0.16
Total	37	73	32	142	0.46
SrAr2 (IT)	2=	2=, 3+	3+		
MSP159	15	32	13	60	0.40
SrAr3 (IT)	X	X, 3+	3+		
MSP77	16	24	13	53	0.80

*Significant at P=0.05 and 2 d.f., ** Significant at P=0.01 and 2 d.f.

Development of monogenically segregating populations (MSPs)

Additional tests were performed on 12 F_3 families that showed monogenic segregation. Of the 12 families, eight showed segregation at a single locus and represented three distinct phenotypic groups. Stem rust reaction segregation for four families deviated significantly from monogenic segregation due to a low number of susceptible plants indicating that these lines were misclassified into the single gene category. Up to 100 seeds of families 77, 107, 159 and 165 were space planted in the field and were individually harvested to develop MSPs. The MSPs 107 and 165 represented *SrAr1*, whereas MSPs 159 and 77 segregated for *SrAr2* and *SrAr3*, respectively. Unfortunately, a significant proportion of plants from MSPs 159 and 77 got flooded and consequently numbers in these families were reduced. All MSPs were progeny tested and data are presented in **Table 2**. Chi-squared analyses of segregation data confirmed the monogenic inheritance of resistance conditioned by *SrAr1*, *SrAr2* and *SrAr3*. These families were used for molecular mapping.

Mapping of stem rust resistance genes

Of the 213 markers (Roder *et al*. 1998) used for screening parents, 106 markers were polymorphic between 'Arrivato' and 'Bansi Strain 168'. The percentage of observed polymorphism was 49.7%. Some primer pairs failed to amplify any product presumably due to the fact that hexaploid wheat derived microsatellite libraries may not have represented the total genotypic variation amongst durum cultivars. The BSA identified associations of genomic regions on chromosome 2BL, 6AL and 6AS with *SrAr1*, *SrAr2* and *SrAr3*, respectively. The chromosome 2BL located markers gwm47 and gwm191 showed close genetic association with *SrAr1* and markers wmc59 and gwm169 from chromosome 6AL exhibited linkage with *SrAr2*. A single chromosome 6AS located marker, gwm334, was linked with *SrAr3*. These linked markers were genotyped on the respective MSPs.

SrAr1

The MSP107 and MSP165 segregated at the *SrAr1* locus and the heterogeneity Chi-squared analysis indicated that the segregation data for MSP107 and MSP165 were homo-

Table 1 Stem rust response frequency distribution of 'Arrivato'/'Bansi Strain 168' F_3 families when tested against *Puccinia graminis* f. sp. *tritici* pathotype 34-1, 2, 3, 4, 5, 6, 7 under greenhouse conditions.

Stem rust response	Observed frequency	Expected proportion	Expected frequency	χ^2 (45:12:6:1)[a]
HR	148	45	139.05	0.58
Seg (15:1)	31	12	37.08	1.00
Seg (3:1)	18	6	18.54	0.01
HS	1	1	3.09	1.40
Total	198	64	197.76	2.99

Table value of χ^2 at P = 0.05 and 3 d.f. = 7.82; the calculated value of 2.99 is non-significant.

[a] Based on three gene segregation model, HR – included families showing no susceptible segregates, Seg – included monogenically and digenically segregating families, HS – included homozygous susceptible families.

Table 3 Joint segregation of *SrAr1* with *Xgwm47* and *Xgwm191* on pooled families from MSP107 and MSP 165.

Marker locus	Genotype/Frequency			Total
	SrAr1 SrAr1	***SrAr1 srAr1***	***srAr1 srAr1***	
Xgwm47				
Xgwm47$_{150bp}$	37	1	0	38
Xgwm47$_{150/125bp}$	0	71	0	71
Xgwm47$_{125bp}$	0	1	32	33
Total	37	73	32	142
Xgwm191				
Xgwm191$_{125bp}$	31	3	1	35
Xgwm191$_{125/115bp}$	5	68	1	74
Xgwm191$_{115bp}$	1	2	30	33
Total	37	73	32	142

*Significant at P=0.05, ** Significant at P=0.01
$\chi^2_{SrAr1vs.srAr1} = 0.46$, $\chi^2_{Xgwm47\text{-}150\ vs.\ Xgwm47\text{-}125} = 0.35$, $\chi^2_{1:2:1:2:4:2:1:2:1} = 269.7$**,
$\chi^2_{Xgwm191\text{-}125\ vs.\ Xgwm191\text{-}115} = 0.30$, $\chi^2_{1:2:1:2:4:2:1:2:1} = 200.3$**
Table value of χ^2 at P=0.05, 2 d. f. =5.99, χ^2 at P=0.01, 2 d. f. =9.21,
χ^2 at P=0.05, 8 d. f. =15.51, χ^2 at P=0.01, 8 d. f. =20.09.

Table 4 Joint segregation of *SrAr2* with *Xwmc59* and *Xgwm169* among MSP159.

Marker locus	Genotype/Frequency			Total
	SrAr2 SrAr2	***SrAr2 srAr2***	***srAr2 srAr2***	
Xwmc59				
Xwmc59$_{201bp}$	14	4	1	19
Xwmc59$_{198/201bp}$	0	25	0	25
Xwmc59$_{198bp}$	1	3	12	16
Total	15	32	13	60
Xgwm169				
Xgwm169$_{220bp}$	12	6	1	19
Xgwm169$_{195/220bp}$	1	23	4	28
Xgwm169$_{195bp}$	2	3	8	13
Total	15	32	13	60

*Significant at P=0.05, ** Significant at P=0.01.
$\chi^2_{SrAr2vs.srAr2} = 0.04$, $\chi^2_{Xwmc59\text{-}201\ vs.\ Xwmc\text{-}198} = 1.96$, $\chi^2_{1:2:1:2:4:2:1:2:1} = 76.2$**,
$\chi^2_{Xgwm169\text{-}195\ vs.\ Xgwm169\text{-}220} = 1.46$, $\chi^2_{1:2:1:2:4:2:1:2:1} = 40.33$**
Table value of χ^2 at P=0.05, 2 d. f. =5.99, χ^2 at P=0.01, 2 d. f. =9.21,
χ^2 at P=0.05, 8 d. f. =15.51, χ^2 at P=0.01, 8 d. f. =20.09.

geneous and can be pooled ($\chi^2_{heterogeneity} = 2.02$, non significant at P = 0.05 with 2 d.f.). The pooled segregation data also conformed well to the single gene model. 'Arrivato' and 'Bansi Strain 168' amplified 150bp and 125bp products when marker gwm47 was used. All HR families amplified the 'Arrivato' allele *Xgwm47*$_{150bp}$ and likewise all HS families carried the 'Bansi Strain 168' allele *Xgwm47*$_{125bp}$ (**Table 3**). Of 73 segregating families, 71 amplified both 'Arrivato' and 'Bansi Strain 168' alleles and of two recombinants, one each amplified the 'Arrivato' and 'Bansi Strain 168' alleles. The highly significant Chi-squared value for joint segregation of *SrAr1* and *Xgwm47* suggested a close genetic association between these loci (**Table 3**). 'Arrivato' and 'Bansi Strain 168' carried the *Xgwm191*$_{125bp}$ and *Xgwm191*$_{115bp}$ alleles, respectively. Markers gwm191 amplified the *Xgwm191*$_{125bp}$ allele in 31 of 37 HR families and the *Xgwm191*$_{115bp}$ allele in 30 of 32 HS families. Sixty eight of 73 segregating families amplified both alleles. A total of 13 recombinants were observed and a significant Chi-squared value indicated genetic association of *Xgwm191* with *SrAr1*. *SrAr1* was flanked by *Xgwm47* (0.7 ± 0.5 cM) and *Xgwm191* (6.2 ± 1.2 cM) distally and proximally, respectively, on the long arm of chromosome 2B (**Fig 1A**).

Table 5 Joint segregation of *SrAr3* and *Xgwm334* among MSP77

Marker locus	Genotype/Frequency			Total
	SrAr3 SrAr3	***SrAr3 srAr3***	***srAr3 srAr3***	
Xgwm334				
Xgwm334$_{125bp}$	14	2	0	16
Xgwm334$_{125/120bp}$	0	16	2	18
Xgwm334$_{120bp}$	0	2	10	12
Total	14	20	12	46

*Significant at P=0.05, ** Significant at P=0.01.
$\chi^2_{SrAr3vs.srAr3} = 1.08$, $\chi^2_{Xgwm334\text{-}125\ vs.\ Xgwm334\text{-}120} = 3.69$, $\chi^2_{1:2:1:2:4:2:1:2:1} = 88.36$**.
Table value of χ^2 at P=0.05, 2 d. f. =5.99, χ^2 at P=0.01, 2 d. f. =9.21,
χ^2 at P=0.05, 8 d. f. =15.51, χ^2 at P=0.01, 8 d. f. =20.09.

SrAr2

The chromosome 6AL located markers gwm169 and wmc59 showed polymorphism among parents and bulks. These markers were mapped on the entire MSP159 which segregated for *SrAr2*. The joint segregation analysis of markers and the *SrAr2* phenotypic data are presented in **Table 4**. The highly significant Chi-squared values for joint segregation analyses between *SrAr2* and marker loci *Xmwc59* and *Xgwm169* indicated genetic association among these loci. *SrAr2* was mapped on the long arm of chromosome 6A, 5.7 cM and 13.6 cM distal to *Xmwc59* and *Xgwm169*, respectively (**Fig. 1B**).

SrAr3

The MSP77 segregated for *SrAr3*, which produced ITX. The BSA showed close association between the marker gwm334 located in the short arm of chromosome 6A with *SrAr3*. 'Arrivato' and 'Bansi Strain 168' amplified 125bp and 120bp PCR products, respectively. The marker gwm334 was mapped on a population of 46 individuals. Joint segregation data for the *Xgwm334* and *SrAr3* loci are presented in **Table 5**. The highly significant Chi-squared value for joint segregation at these loci suggested genetic linkage. A genetic distance of 4.6 ± 1.01 cM was calculated between *Xgwm334* and *SrAr3* (**Fig. 1C**).

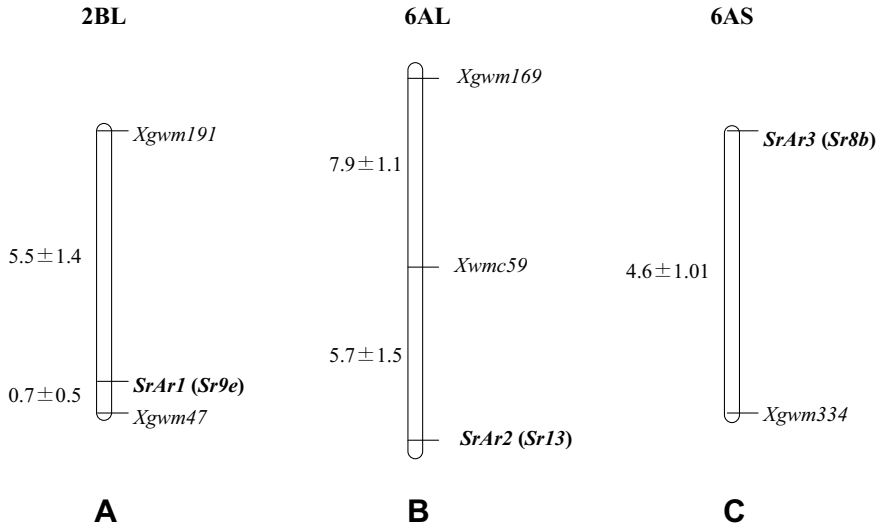

Fig. 1 Genetic map showing SSR markers linked with stem rust resistance genes (**A**) *SrAr1*, (**B**) *SrAr2* and (**C**) *SrAr3* in monogenically segregating progenies derived from 'Arrivato' / 'Bansi Strain 168'.

DISCUSSION

Genetic analysis of seedling stem rust resistance carried by the durum cultivar 'Arrivato' demonstrated the involvement of three independent genes. Three distinct infection types; IT;1, IT2= and ITX were observed among monogenically segregating families. The genes conditioning these infection types were temporarily designated as *SrAr1* (IT;1), *SrAr2* (IT2=) and *SrAr3* (ITX). *SrAr1* was flanked by *Xgwm47* (0.7 cM) and *Xgwm191* (5.5 cM) in the long arm of chromosome 2B. The marker locus *Xgwm47* was located distal to *SrAr1*. According to available genetic maps (http://www.graingenes.org/cgi-bin/ace/pic/graingenes), SSR marker *Xgwm47* was located 6.0 cM from *Xgwm191* and a similar genetic distance (6.2 cM) was observed in the present study. The chromosome 6AL located marker locus *Xwmc59* mapped 5.7 cM proximal to stem rust resistance gene *SrAr2*. *Xgwm334*, located distally in the chromosome 6AS, displayed close genetic association with the stem rust resistance gene *SrAr3* (4.6 cM). According to the consensus map (Somers *et al*. 2004) *Xgwm459* is the most distal marker on chromosome 6AS followed by *Xgwm334*. *Xgwm459* was monomorphic between 'Arrivato' and 'Bansi Strain 168'.

Luig (1983) reported the presence of stem rust resistance genes *Sr9e*, *Sr13* and *SrB* in North American durum wheat cultivars. Infection types reported to be produced by *Sr9e* and *Sr13* were IT;1 and IT2=, respectively (McIntosh *et al*. 1995). *Sr9e* is located in chromosome 2BL and *Sr13* in 6AL (McIntosh *et al*. 1995). Based on the infection type comparison and chromosome location, it appeared that *SrAr1* and *SrAr2* were *Sr9e* and *Sr13,* respectively. Susceptible reactions of homozygous resistant families from MSP107 against the *Sr9e*-virulent pathotype (40-1,2,3,4,5,6,7) confirmed the presence of *Sr9e* in 'Arrivato'. Virulence for *Sr13* does not exist in Australia to conduct a similar experiment.

There are only a few stem rust resistance genes that produce infection type ITX. These include *Sr8b* (previously *SrBB*), *Sr15*, *Sr17* and *Sr38* (McIntosh *et al*. 1995). The Pgt pt used in the present study was virulent on *Sr15* and *Sr17* located on chromosomes 7AL and 7BL, respectively, and therefore these genes were unlikely to be encountered in the present study. The third gene in 'Arrivato', *SrAr3*, cannot be *Sr38* (2AS) as it was originally derived from *Aegilops ventricosa* (Bariana and McIntosh 1993). The only gene with ITX located on chromosome 6AS was *Sr8b,* therefore we concluded *SrAr3* to be *Sr8b*. Susceptible responses of HR families from MSP77 against the *Sr8b*-virulent Pgt pathotype 34-1,2,3,4,5,6,7,11 confirmed this conclusion.

All three stem rust resistance genes are effective against the predominant Pgt pt 98-1,2,3,5,6 in Australia. The detection of a highly virulent pathotype, TTKS (Ug99) of Pgt (Stokstad 2007), has pointed the scientific community to the danger of the evolutionary potential of this devastating pathogen. 'Arrivato' was tested in Kenya against the Ugandan Pgt stem rust pathotype "Ug99"and was rated as moderately susceptible (Bariana and Park, unpublished). The pathotype "Ug99" was virulent on stem rust resistance genes *Sr9e* and *Sr8b*. Several durum cultivars carry these three genes for stem rust resistance (Bariana and Hare, unpublished). A moderately susceptible stem rust reaction on some of these cultivars against Pgt pt 'Ug99' in Kenya indicated that the durum industry would be at risk if 'Ug99' spreads across different countries. Virulence for *Sr13* has not yet been detected in Australia but it does not provide a high level of protection when present alone (Luig 1983, McIntosh *et al*. 1995). The presence of *Sr2* and *Sr13* together in Australian wheat cultivar 'Machete' provides a higher level of protection (H.S. Bariana, unpublished) suggesting that pyramiding of *Sr13* with other genes would be useful.

This study clearly demonstrated the genetic basis of stem rust resistance carried by 'Arrivato' and characterised identities of genes involved. The close genetic association of *Xgwm47* with *Sr9e* would be useful for marker-assisted selection of this gene in breeding populations. Although genetic associations of *Xwmc59* and *Xgwm334* with *Sr13* and *Sr8b*, respectively, were not very close, these markers could be used in conjunction with phenotypic screening. The future aim of our research group is to develop markers closely linked with *Sr13* using the functional genomic approach.

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