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ORIGINAL PAPER

Characterisation of a new stripe rust resistance gene *Yr47* and its genetic association with the leaf rust resistance gene *Lr52*

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Abstract Two Iranian common wheat landraces AUS28183 and AUS28187 from the Watkins collection showed high levels of seedling resistance against Australian pathotypes of leaf rust and stripe rust pathogens. Chi-squared analyses of rust response segregation among F_3 populations derived from crosses of AUS28183 and AUS28187 with a susceptible genotype AUS27229 revealed monogenic inheritance of leaf rust and stripe rust resistance. As both genotypes produced similar leaf rust and stripe rust infection types, they were assumed to carry the same genes. The genes were temporarily named as *LrW1* and *YrW1*. Molecular mapping placed *LrW1* and *YrW1* in the short arm of chromosome 5B, about 10 and 15 cM proximal to the SSR marker *gwm234*, respectively, and the marker *cfb309* mapped 8–12 cM proximal to *YrW1*. *LrW1* mapped 3–6 cM distal to *YrW1* in two F_3 populations. AUS28183 corresponded to the accession V336 of the Watkins collection which was the original source of *Lr52*. Based on the genomic location and accession records, *LrW1* was concluded to be *Lr52*. Because no other seedling stripe rust resistance gene has previously been mapped in chromosome 5BS, *YrW1* was permanently named as *Yr47*. A combination of flanking markers *gwm234* and *cfb309* with phenotypic assays could be used to ascertain the presence of *Lr52* and *Yr47* in segregating populations. This investigation characterised a valuable source of dual leaf rust and stripe rust resistance for deployment in new wheat cultivars. Transfer of *Lr52* and *Yr47* into current Australian wheat backgrounds is in progress.

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Introduction

Global wheat production is hampered by several biotic stresses including three rust diseases. Stem rust, leaf rust and stripe rust of wheat are caused by *Puccinia graminis* f. sp. *tritici* (Pgt), *Puccinia triticina* (Pt) and *Puccinia striiformis* f. sp. *tritici* (Pst), respectively. The release of rust resistant cultivars is considered to be the best option to control rust diseases. Characterisation of genetically diverse sources of rust resistance and their strategic deployment in commercial cultivars determines the success of resistance breeding. More than 45 genes for resistance to each of the three rust pathogens have been formally named (McIntosh et al. 2008). The demise of a high proportion of these resistance genes due to the detection of virulent pathotypes of the respective pathogens necessitates identification of new sources of resistance to achieve sustained rust control.

Stripe rust causes significant economic losses in terms of reduced production and/or high costs for chemical control of the disease (http://www.globalrust.org; Wellings 2007). Although leaf rust is considered to be the least important of the three rust pathogens, it has been recognised as the most prevalent disease in the Southern Cone (German et al. 2007), the USA (Kolmer et al. 2007) and Canada (McCallum et al. 2007). A majority of leading Australian

wheat cultivars carry moderate to high levels of leaf rust resistance (Bariana et al. 2004, 2007). Donor sources that carry linked resistance to more than one disease are favoured by wheat breeders. Linked rust resistance genes *Sr24/Lr24*, *Sr31/Lr26/Yr9* and *Sr38/Lr37/Yr17* have been extensively used worldwide. Although these genes have been individually defeated in some parts of the world, these can be used in combinations. Pathotypes virulent on genotypes carrying *Lr24* and *Lr37* individually have been detected in Australia; however, a combination of these genes provides effective protection against all current Australian Pt pathotypes.

Two Iranian common wheat landraces AUS28183 and AUS28187 showed low responses against Australian Pt and Pst pathotypes both under field and greenhouse conditions. This study investigated the inheritance of leaf rust and stripe rust resistance in AUS28183 and AUS28187 and identified the genomic locations of the resistance genes involved.

Materials and methods

Host materials

Common wheat landraces AUS28183 and AUS28187, collected from the Caspian Sea area of Iran by AE Watkins in the 1920s to 1930s, were crossed with a stripe rust and leaf rust susceptible landrace AUS27229. One hundred and thirty-eight F_3 families each, generated from AU28183/AUS27729 and AUS28187/AUS27229 crosses, were used for inheritance and molecular mapping studies.

Greenhouse studies

AUS28183, AUS28187 and AUS27229 were tested at the seedling stage against the Pst pathotypes: 134 E16A+ (PBI culture no 572), 134 E16A+Yr17+ (599) and 150 E16A+ (598); and Pt pathotypes: 104-1,2,3,6,7,9,11 (521), 104-1,2,3,(6),(7),11,13 (547) and 10-1,3,9,10,11,12 (592). Experimental materials were sown in 9 cm pots filled with a 2:1 mixture of pine bark and river sand. An initial dose of the water soluble fertiliser Aquasol® (10 g/10 l of tap water) was applied before sowing. Seven-day-old seedlings were fertilised with urea at the same rate as Aquasol®. Urediniospores of Pst and Pt pathotypes were suspended in light mineral oil Isopar-L®. These suspensions were atomized on 10–12-day (two leaf stage) old seedlings using a hydrocarbon pressure pack. Stripe rust inoculated seedlings were humidified at 9°C on water filled steel trays covered with plastic hoods. Leaf rust inoculated seedlings were humidified at ambient temperature regime (15–20°C) in a room fitted with ultrasonic humidifier. Inoculated seedlings were moved to microclimate rooms maintained at 17°C (stripe rust) and 25°C (leaf rust) 24 h after inoculation. Infection types (ITs) were scored 12 and 14 days after inoculation for leaf rust and stripe rust, respectively, using the 0–4 scales described in McIntosh et al. (1995) for both diseases. More than usual necrosis or chlorosis was denoted by letters 'N' and 'C', respectively. Similarly '−' and '+', respectively, explained slight variations in the expression of an IT. The AUS28183/AUS27229 and AUS28187/AUS27229 F_3 families were tested against the Pt pathotype 104-1,2,3,(6),(7),11,13 and the Pst pathotype 134 E16A+.

Molecular mapping

DNA was extracted from the AUS28183/AUS27229 and AUS28187/AUS27229 F_3 families and parents according to Bansal et al. (2010). Bulked segregant analysis (BSA) was used to determine the chromosomal location of leaf rust and stripe rust resistance. Resistant and susceptible bulks were comprised of equal amounts of pooled DNA from 10 homozygous leaf rust and stripe rust resistant and 10 homozygous susceptible F_3 families from both crosses. BSA was performed using multiplex-ready PCR (Hayden et al. 2008). A set of 488 published microsatellite (SSR) markers selected for high genome coverage was used. PCR products were separated on an ABI3730xl DNA fragment analyser (Applied Biosystems) using the procedure described by Hayden et al. (2008). SSR scoring was performed using Gene Mapper v4.0 software (Applied Biosystems). SSR markers showing associations with the resistance bulks in BSA were genotyped on 138 F_3 families from each population to confirm the marker–trait associations. In addition, chromosome 5BS markers *cfb306, cfb309, cfb331, cfb341, gbr233, gpw1072*, *gpw4098* (Alfares et al. 2009), *cfb322* and *cfb400* (map information and primer sequences were provided by C. Feuillet) were also genotyped on parents.

Statistical analyses and genetic mapping

F_3 families were classified as homozygous resistant (*LrW1LrW1* or *YrW1YrW1*), homozygous susceptible (*lrw1lrw1* or *yrw1yrw1*) and segregating (*LrW1lrw1* or *YrW1yrw1*). Chi-squared (χ^2) analyses were performed to determine the number of genes involved in controlling leaf rust and stripe rust resistance. Genetic mapping was conducted using the Map Manager QTXv20b software (Manly et al. 2001) and the Kosambi mapping function (Kosambi 1944). An LOD score of 3.0 was used to determine genetic linkages.

Table 1 Infection types produced by AUS28183, AUS28187 and AUS27229 against different Pst and Pt pathotypes

Pst pathotypes	Genotype/infection type[a]			Pt pathotypes	Genotype/infection type[b]		
	AUS28183	AUS28187	AUS27229		AUS28183	AUS28187	AUS27229
150 E16A+	1CN	1CN	3+	10-1,3,9,10,11,12	0;	;	3+
134 E16+	1CN	1CN	3+	104-1,2,3,6,7,9,11	;	;	3+
134 E16A+Yr17+	1CN	1CN	3+	104-1,2,3,(6),(7),11,13	;1-	;1-	3+

[a] 1 = necrotic and chlorotic areas with restricted sporulation, 3+ = abundant sporulation without chlorosis

[b] 0 = no visible uredinia, ; = hypersensitive flecks, 1 = small uredinia with necrosis, 3+ = large sporulating uredinia without chlorosis, ;1- = presence of slightly higher response than ; and slightly lower response than 1

Results

Parental responses

Seedling rust response scores for genotypes AUS28183, AUS28187 and AUS27729 against three pathotypes each of Pst and Pt are presented in Table 1. AUS28183 and AUS28187 exhibited infection type 1CN against three Pst pathotypes and leaf rust responses of these genotypes ranged from infection types 0; to ;1- (Table 1). AUS27729 was susceptible (infection type 3+) to both leaf rust and stripe rust. Figure 1 shows the stripe rust and leaf rust infection types produced by AUS28183 and AUS27729. Genotypes AUS28183 and AUS28187 produced resistant to moderately resistant (R-MR) stripe rust responses and moderately resistant (MR) leaf rust responses under field conditions.

Genetic analyses

One hundred and thirty-eight F_3 families each from AUS28183/AUS27229 and AUS28187/AUS27229 crosses were phenotyped for leaf rust and stripe rust responses at the seedling stage. The leaf rust response segregation among AUS28183/AUS27229 F_3 population against the Pt pathotype 104-1,2,3,(6),(7),11,13 indicated the presence of a single gene (34HR: 64SEG: 40HS; $\chi^2_{1:2:1} = 1.24$, $P = 0.538$ at 2 *df*) for resistance in AUS28183 (Table 2). This population also showed monogenic inheritance of stripe rust resistance, when tested with the Pst pathotype 134 E16A+ (26HR: 73SEG: 39HS; $\chi^2_{1:2:1} = 2.91$, $P = 0.233$ at 2 *df*). Monogenic segregations for leaf rust and stripe rust resistance were also observed among the AUS28187/AUS27229 F_3 population (33HR:69SEG: 36HS; $\chi^2_{1:2:1} = 0.13$, $P = 0.937$ at 2 *df* and 26HR: 74SEG: 38HS; $\chi^2_{1:2:1} = 2.81$, $P = 0.245$ at 2 *df*). Chi-squared analyses of segregation data for both diseases in two F_3 populations indicated genetic linkage between leaf rust and stripe rust resistance (Table 2). Similar results for both populations suggested presence of the same genes for stripe rust and leaf rust resistance in AUS28183 and AUS28187. Based on this assumption, leaf rust and stripe rust resistance genes carried by these genotypes were temporarily named as *LrW1* and *YrW1*, respectively.

Fig. 1 Seedling stripe rust and leaf rust responses of parental genotypes against Pst pathotype 134 E16A+ (*1* AUS27229 and *2* AUS28183) and Pt pathotype (104-1,2,3,(6),(7),11,13 (*3* AUS28183 and *4* AUS27229)

Molecular mapping of *LrW1* and *YrW1*

Bulked segregant analysis, using 488 SSR markers selected for genome coverage, was performed to identify the genomic regions controlling leaf rust and stripe rust resistance in genotypes AUS28183 and AUS28187. Microsatellite marker *gwm234* from chromosome 5BS (Somers et al. 2004; Alfares et al. 2009) showed polymorphism between the parental lines and linkage with the resistant and susceptible DNA bulks. These results indicated the location of *YrW1* and *LrW1* in chromosome 5BS. This

Table 2 Chi-squared analyses of stripe rust and leaf rust response segregation among F_3 families from two crosses

Cross/genotype	Number of families			Total
	YrW1YrW1	*YrW1yrw1*	*yrw1yrw1*	
AUS28183/AUS27229[a]				
LrW1LrW1	26	8	–	34
Lrw1lrw1	–	64	–	64
lrw1lrw1	–	1	39	40
Total	26	73	39	138
AUS28187/AUS27229[b]				
LrW1LrW1	26	5	2	33
LrW1lrw1	–	68	1	69
lrw1lrw1	–	1	35	36
Total	26	74	38	138

[a] $\chi^2_{1:2:1}$ (*LrW1* vs. *lrw1*) = 1.24; $\chi^2_{1:2:1}$ at $P = 0.538$; (*YrW1* vs. *yrw1*) = 2.91 at $P = 0.233$; $\chi^2_{1:2:1:2:4:2:1:2:1}$ (*LrW1* vs. *Yrw1*) = 239.21** at $P \leq 0.0001$

[b] $\chi^2_{1:2:1}$ (*LrW1* vs. *lrw1*) = 0.13 at $P = 0.937$; $\chi^2_{1:2:1}$ (*YrW1* vs. *yrw1*) = 2.81 at $P = 0.245$; $\chi^2_{1:2:1:2:4:2:1:2:1}$ (*LrW1* vs. *YrW1*) = 218.46** at $P \leq 0.0001$

putatively linked marker was genotyped on all 138 lines from both AUS28183/AUS27229 and AUS28187/AUS27229 F_3 populations. Marker *gwm234* (LOD 29.3 and 25.5 in AUS28183/AUS27229 and AUS28187/AUS27229, respectively) showed genetic association with leaf rust resistance in both crosses. The LOD values for linkage between *LrW1* and *YrW1* in both populations were more than 42. Multiple bands were amplified by *gwm234* and, therefore, to confirm which amplicon corresponds to the chromosome 5B, this marker was genotyped on a set of nulli-tetrasomics. The results from this experiment confirmed the association of 275 bp product with chromosome 5B. The marker *gwm234* amplified two SSR loci; a monomorphic locus characterised by a 135 bp PCR product and a polymorphic locus characterised by 265, 271 and 273 bp products from AUS28187, AUS28183 and AUS27229, respectively, was assumed to be homologous to the 275 bp band from Chinese Spring assigned to chromosome 5B.

To determine map orientation, several markers that are mapped proximal to *gwm234* (Alfares et al. 2009), were genotyped on parents. All markers, except *cfb309*, were monomorphic. Marker *cfb309* amplified a 360 bp product when DNA from AUS27229 was used, whereas it failed to amplify any product in resistant parents AUS28183 and AUS28187. The marker *cfb309* mapped 9.6 cM (LOD = 16.0) and 8.2 cM (LOD = 16.0) proximal to *YrW1* in AUS28183/AU27229 and AUS28187/AU27229 crosses, respectively (Fig. 2). The final map order of *gwm234-LrW1-YrW1-cfb309* was consistent in both populations.

Discussion

This study demonstrated the presence of linked leaf rust and stripe rust resistance genes in Iranian landraces AUS28183 and AUS28187. Similar rust responses (Table 1) and genomic locations in chromosome 5BS (Fig. 2) indicated that both landraces carry the same leaf rust and stripe rust resistance genes and these genes were tentatively designated as *LrW1* and *YrW1*, respectively. The map order comprised *gwm234-LrW1-YrW1-cfb309* with *gwm234* being the most distal and *cfb309* the most proximal loci (Fig. 2). Marker *cfb309* was mapped 0.2 cM distal to *gwm234* (Alfares et al. 2009); however, the subsequent work mapped it about 5 cM proximal to *gwm234* (C. Feuillet personal communication).

Dyck and Jedel (1989) backcrossed *LrW* from V336 into Thatcher to produce a near iso-genic line (Thatcher*6/V336) that was later named RL6107. The chromosomal location of *LrW* using a RL6107/AC Foremost F_3 population led to its permanent designation as *Lr52* (Hiebert et al. 2005). *Lr52* was mapped distal to the SSR marker *gwm443* (16 cM) in chromosome 5BS (Hiebert et al. 2005). This marker was monomorphic among the parents used in the present study. Although Hiebert et al. (2005) either did not genotype *gwm234* in their study or it would have been

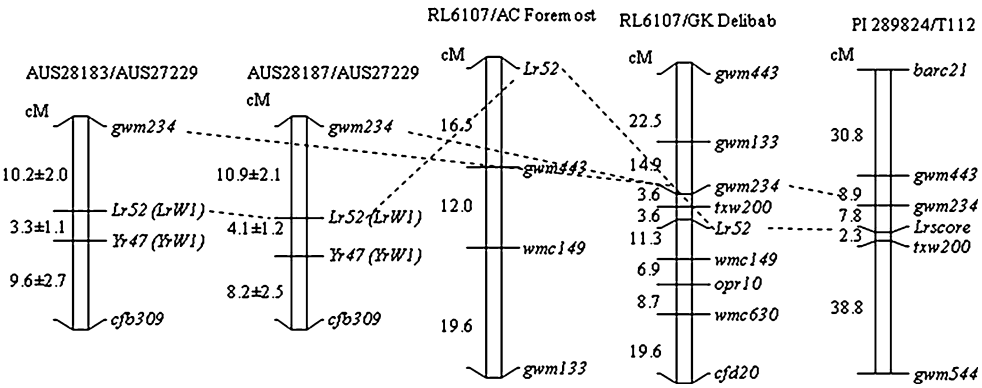

Fig. 2 Genetic association between *Lr52* and *Yr47* in chromosome 5BS and with markers *gwm234* and *cfb309* in AUS28183/AUS27229 and AUS28187/AUS27229 F_3 populations and other maps of this region involving leaf rust resistance; RL6107/AC Foremost (Hiebert et al. 2005), RL6107/GK Delibab (Tar et al. 2008) and PI 289824/T112 (Obert et al. 2005)

monomorphic, Tar et al. (2008) who used the same genotype RL6107 (Fig. 2) mapped this marker at a similar genetic distance to that in the current investigation. The location of *gwm443* is conflicting in Hiebert et al. (2005) and Tar et al. (2008), although both investigations were based on RL6107. It is likely that Tar et al. (2008) has misplaced *gwm443* as it has been mapped 5–10 cM proximal to *gwm234* by Paillard et al. (2003), Peleg et al. (2008) and Alfares et al. (2009).

AUS28183 corresponds to the accession V336 of the Watkins collection (G. Grimes, personal communication), the donor of *LrW* in Canadian studies. The AUS28187 equivalent of the Watkins collection is V731 and it was reported to carry *Lr33* and *LrW* by Dyck (1994). *Lr33* is ineffective against Australian Pt pathotypes in the seedling stage (McIntosh et al. 1995) and therefore AUS28187/AUS27229 F_3 population segregated only for *LrW1* in this study. Based on these results *LrW1* was concluded to be *Lr52*.

In another study, Obert et al. (2005) located a leaf rust resistance gene (temporarily designated as *Lrscore*) in the Iranian landrace PI 289824 in chromosome 5BS. *Lrscore* was also associated with the SSR marker *gwm234* on the distal side and the STS marker tmx_{200} on the proximal end. This accession was also collected from the Caspian Sea region of Iran and it showed resistance to Pst pathotypes PST17, PST20, PST27 and PST29 (http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1219372). Marker tmx_{200} was monomorphic among the parents used in the present study; however, Tar et al. (2008) validated association of tmx_{200} with *Lr52*. These workers placed tmx_{200} between *gwm234* and *Lr52* (Fig. 2), whereas Obert et al. (2005) mapped tmx_{200} at a similar distance but proximal to *Lrscore*. The genetic distances reported by Obert et al. (2005) between *Lrscore* and *gwm234* and by Tar et al. (2008) between *Lr52* and *gwm234* were 7.2 and 10.1 cM, respectively. These values are within the range of standard error which was not presented by either of these workers. As both V336 and PI 289824 originated from the Caspian Sea region of Iran and the relative positions *Lrscore* and *Lr52* to *gwm234* (Fig. 2), the gene in PI 289824 is likely to be *Lr52*. The presence of stripe rust resistance in PI 289824 in the USA (http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1219372) lends further support to this conclusion.

Lr52 produced low leaf rust responses against 29 Canadian (Hiebert et al. 2005), nine American (Obert et al. 2005) and three Australian Pt pathotypes (this study). Dyck and Jedel (1989), Dyck (1994), Hiebert et al. (2005) and Obert et al. (2005) did not screen their populations against stripe rust. In the present study linkage between leaf rust and stripe rust resistance was identified (Table 2). As no other seedling stripe rust resistance gene has been previously located in chromosome 5BS, *YrW1* was permanently named as *Yr47*. Although the genetic linkage between *Lr52* and *Yr47* is not complete (<5 cM), both genes would inherit together in a majority of segregates in breeding populations.

The monomorphic nature of several chromosome 5BS molecular markers prevented in this study the identification of a more closely linked DNA marker that could be used for selection of these rust resistance genes. Nevertheless, it was not the aim of this investigation. *Lr52* and *Yr47* are flanked by markers *gwm234* and *cfb309*, respectively. Although the recombination values are higher than those suggested for effective marker-assisted selection, these flanking markers could be used in combination with phenotypic assays to verify the presence of *Lr52* and *Yr47* in breeding populations. Highly diagnostic gene-based markers have been reported for the pleiotropic adult plant resistance (APR) gene *Lr34/Yr18* in different genetic backgrounds (Lugudah et al. 2006; Krattinger et al. 2009; Dakouri et al. 2010; Cao et al. 2010). The combined genotypic and phenotypic assays for *Yr47* and *Lr52* and marker-assisted selection of *Lr34/Yr18* would enable selection of combinations of seedling and APR genes in new cultivars. Double or triple resistance gene combinations are preferred by breeders due to the ease of selection for multiple resistance simultaneously in segregating populations. Some of the linked resistance genes derived from wild relatives of wheat have been reported to carry deleterious linkages. AUS28183 and AUS28187 are common wheat genotypes and therefore, are less likely to carry deleterious linkages. *Yr47* and *Lr52* are currently being backcrossed into stem rust resistant cultivars that require improvement in stripe rust and leaf rust resistance to increase diversity of resistance in new Australian wheat cultivars. Care is, however, taken not to transfer these genes singly in susceptible backgrounds to curtail the rate of evolution of virulence in leaf rust and stripe rust pathogens.

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