Mol Breeding (2016) 36:98
DOI 10.1007/s11032-016-0528-1

Adult plant stripe rust resistance gene *Yr71* maps close to *Lr24* in chromosome 3D of common wheat

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Received: 27 April 2016 / Accepted: 4 July 2016 / Published online: 11 July 2016

Abstract Australian cultivar Sunco carries three adult plant stripe rust resistance genes. One of these genes corresponded to *Yr18* in chromosome 7DS; the second, *YrCK*, was mapped on chromosome 2D. Here, we describe the characterization of the third adult plant resistance (APR) gene from Sunco. Sunco/2*Avocet S-derived lines SA65 (resistant) and SA67 (susceptible) were crossed and a recombinant inbred line F_6 population was generated. Monogenic segregation among SA65/SA67-derived RIL population was demonstrated and the resistance locus was designated *YrSA3*. Selective genotyping using an iSelect 90 K Infinium SNP array and SSR markers located *YrSA3* on chromosome 3D. Development of KASP markers for SNP loci showing association with *YrSA3* allowed construction of a genetic map harboring the resistance gene. Ten KASP markers (*KASP_8306*, *KASP_9142*, *KASP_10438*, *KASP_16434*, *KASP_17207*, *KASP_20836*, *KASP_23518*, *KASP_23615*, *KASP_57983* and *KASP_63653*), one SSR marker (*gwm114b*) and *Lr24/Sr24* were mapped 1.8 cM distal to *YrSA3*. Comparison of marker data indicated that the previously named seedling stripe rust resistance gene *Yr45* was located proximal to *YrSA3*, and therefore the latter was formally designated *Yr71*. Two recombinants carrying *Lr24/Sr24* and *Yr71* in combination were identified for use as donor sources in wheat breeding programs. The robustness of *gwm114b*, *KASP_16434*, *KASP_17207* and *KASP_20836* for marker-assisted selection of these genes was demonstrated through tests on 74 Australian wheat cultivars.

Keywords Adult plant resistance · Leaf rust · Molecular markers · Stem rust · Stripe rust · Wheat

Introduction

Stripe rust, caused by *Puccinia striiformis* f. sp. *tritici* (Pst), is the most important foliar disease of wheat worldwide. First reported by Gaddin in Europe in 1777 (Eriksson and Henning 1896), it has since been reported in 60 different countries (Stubbs 1985; Line 2002; Li and Zeng 2003). Stripe rust can cause up to 100 % yield losses on susceptible cultivars; however, in commercial production environments yield losses typically range from 10 to 70 % depending upon the cultivar, inoculum pressure and climatic conditions. Stripe rust was first detected in Australia in 1979 on

Electronic supplementary material The online version of this article (doi:10.1007/s11032-016-0528-1) contains supplementary material, which is available to authorized users.

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wheat cultivar Zenith (O'Brien et al. 1980). Following its introduction, devastating stripe rust epidemics occurred in southern New South Wales, Australia. These epidemics reduced grain yield up to 84 %, kernel mass 43 % and kernel number 72 % (Murray et al. 1995). Subsequent localized stripe rust epidemics have occurred in certain seasons and regions of eastern Australia. The wheat growing regions of western Australia remained free from stripe rust due to physical separation by the Nullabor Desert and predominant west to east air movement until the migration of another exotic Pst pathotype, 134 E16A+ (WA pathotype), in 2002 (Wellings et al. 2003). It reached eastern Australia in 2003, and unlike the pathotypes prevalent in eastern Australia prior to 2003, the WA pathotype appeared to have defeated at least a component of adult plant resistance in certain Australian wheat cultivars (Bariana et al. 2010).

Researchers across the world are engaged in the identification and characterization of new sources of resistance to combat the continuously evolving rust pathogens. Release of rust-resistant cultivars is the most economical and environmentally cautious strategy to control rust diseases. The concept of growing rust resistant cultivars dates back to the early twentieth century (Biffen 1905). Breeding for rust resistance in wheat has been a major objective in Australian breeding programs and involves identification and deployment of durable sources of resistance (McIntosh 1998). Resistance based on race-specific genes (major genes) has not been durable as the stripe rust pathogen can evolve to render such genes ineffective. On the contrary, resistance based on adult plant resistance (APR) genes is assumed to be durable (Johnson 1988). APR genes slow the rate of rust development and are often referred to as 'slow-rusting' genes. Deployment of combinations of two or more APR genes in commercial cultivars is essential to achieve acceptable levels of resistance (Singh and Rajaram 1994; Bariana and McIntosh 1995).

Australian wheat cultivar Sunco (SUN9E27*4/3Ag14//WW15/3/3*Cook) exhibits a moderately resistant response against the prevalent Pst pathotypes (Kaur and Bariana 2010). These workers tested Sunco/2*Avocet S-derived BC_1F_2 families and found the involvement of three APR genes. Resistant and susceptible sibs were selected from families showing monogenic segregation. Sunco is reported to carry *Yr18* (Kolmer et al. 2008) and *YrCK* (Bariana et al. 2001). Based on genotyping with the *Yr18*-linked marker and high-temperature rust screening, candidate lines carrying the third APR gene from Sunco/2*Avocet S-derived BC_1F_2 families were identified. In this study we report the molecular mapping and characterization of the third APR gene in one of the Sunco/2*Avocet S resistant derivatives that did not carry *Yr18* and/or *YrCK*.

Materials and methods

A Sunco/2*Avocet S-derived BC_1F_2 family (number 153) that showed monogenic segregation was used in this study. The resistant plant from 153.11 (SA65) was crossed with a susceptible sib 153.6 (SA67), and an F_6 recombinant inbred line (RIL) population (123 RILs) was developed. This RIL population was named SA65/SA67. The population development process is shown in Fig. 1.

The SA65/SA67 F_6 population was sown in the field during the cropping seasons 2013, 2014 and 2015 as 1-m rows at the Plant Breeding Institute, Cobbitty (PBIC) experimental site Lansdowne. After every five experimental rows, one row of susceptible cultivar Morocco was sown to get a uniform spread of stripe rust inoculum. Stripe rust epidemic was initiated by inoculating the susceptible spreader rows with Pst pathotype 134 E16A+Yr17+Yr27+ following the procedure described in Bariana et al. (2010). Stripe rust response was assessed on a 1–9 scale (Bariana et al. 2007), where 1 = very resistant, 2 = resistant, 3 = resistant to moderately resistant, 4 = moderately resistant, 5 = moderately resistant to moderately susceptible, 6 = moderately susceptible, 7 = moderately susceptible to susceptible, 8 = susceptible and 9 = very susceptible.

Seedling tests

SA65/SA67 F_6 population was tested at the two-leaf stage against *Puccinia triticina* pathotype 104-2,3,6,7 (culture no. 231) according to Bariana and McIntosh (1993) to record segregation for *Lr24*.

Molecular mapping

DNA from each RIL and both parents (SA65 and SA67) was extracted using a modified CTAB method

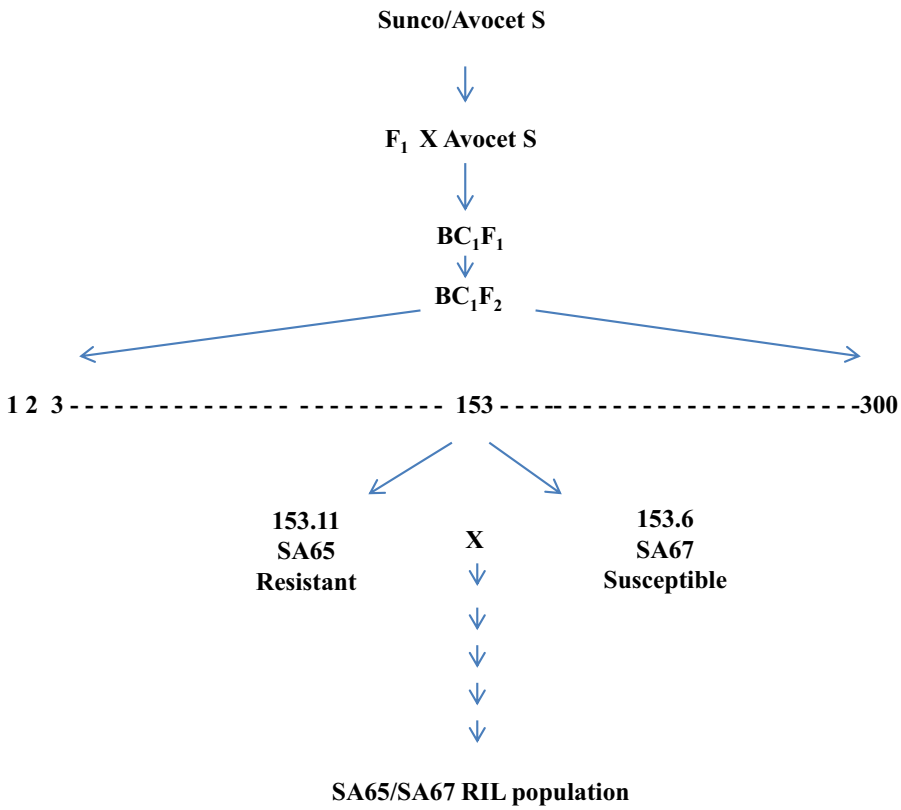

Fig. 1 Scheme for generating single gene line RIL population

(Bansal et al. 2014a). DNA from eight resistant and eight susceptible RILs were subjected to selective genotyping using an Illumina iSelect 90 K Infinium SNP genotyping array (Wang et al. 2014). SNPs showing linkage between the resistant and susceptible RILs were converted into Kompetitive Allele-Specific Primers (KASP) and genotyped on the parents using KASP technology (LGC genomics UK). KASP assays were performed following the protocol described by LGC Genomics using KASP mix, which contains universal FRET (fluorescence resonance energy transfer) cassettes (FAM and HEX), ROX™ passive reference dye, Taq polymerase, free nucleotide, and $MgCl_2$ in an optimized buffer. End-point fluorescent images were visualized using the CFX96 Touch™ real-time PCR detection system (BioRad, USA) and the data analyzed using Bio-rad CFX Manager Software (BioRad, USA).

Eighteen SSR markers representing the target region on chromosome 3D were also tested on parents using the touchdown (depending upon the annealing temperature of primers) profile according to Bansal et al. (2014b). The markers that showed polymorphism between parents were genotyped on the RIL population and included in the map. The *Lr24/Sr24* linked marker *Sr24#12* (Mago et al. 2005) was also used to confirm the presence of these genes in addition to seedling leaf rust tests.

Statistical analysis and genetic mapping

Chi-squared analysis was performed to assess deviations of observed segregations from the expected genetic ratios. MapManager QTXb20 (Manly et al. 2001) was used to construct the genetic linkage map. The Kosambi map function (Kosambi 1943) was used to convert recombination fractions to centi-Morgans. The linkage map was drawn using Map Chart version 2.2 (Voorrips 2002).

Results

Inheritance of resistance

Parental genotypes SA65 and SA67 were susceptible at the seedling stage (infection type 3^+) and exhibited adult plant stripe rust responses 6–7 and 8–9, respectively, in the field. The RIL population showed stripe rust response variation ranging from 6 to 9. RILs were grouped in two classes; homozygous resistant (scores 6–7) and homozygous susceptible (scores 8–9). Chi-squared analysis of adult plant stripe rust data conformed to monogenic segregation (66 homozygous resistant: 52 homozygous susceptible, $\chi^2_{1:1} = 1.66$, non-significant at $P = 0.05$ and *1d.f.*). The stripe rust resistance locus was temporarily named *YrSA3*.

Molecular mapping

One hundred and twelve SNP markers from chromosome 3D showed genetic association with *YrSA3* in a selective genotyping experiment. In the consensus 90 K SNP map (Wang et al. 2014), the linked SNPs spanned the chromosome 3D interval from 134.8 to 152.83 cM (total map length 166.16 cM). *IWB72555* was located at the 134.81 cM position, whereas all other SNPs were mapped in the 142.31 to 152.83 cM interval. The map locations of nine SNP loci were not known. As most of the SNPs represented the same consensus map position, KASP assays were designed for 60 SNPs (Supplementary Table S1). The KASP assays were performed on parents and controls to confirm their specificity before being genotyped on the entire RIL population.

In addition, 18 SSR markers previously mapped on chromosome 3D were genotyped on the parental lines. These included *cfd4*, *cfd141*, *cfd152*, *cfd201*, *cfd219*, *gdm8*, *gwm3*, *gwm66*, *gwm71*, *gwm114*, *gwm161*, *gwm183*, *gwm191*, *gwm314*, *gwm383*, *gwm497*, *gwm645*, and *wmc674* (http://wheat.pw.usda.gov/cgi-bin/westsql/map_locus.cgi). Markers *cfd152*, *gdm8*, *gwm114*, *gwm314*, and *gwm497* showed polymorphism between parents (SA65 and SA67) and were genotyped on the entire population. Markers *cfd152*, *gdm8*, *gwm314*, and *gwm497* segregated independently of stripe rust resistance, whereas *gwm114* revealed segregation at two loci: *gwm114a* and *gwm114b*. Allele *gwm114b* exhibited linkage with *YrSA3*. The *gwm114b* allele was previously mapped on the long arm of chromosome 3D in the Opata/Synthetic and Arina/Forno RIL populations (https://ccg.murdoch.edu.au/cmap/ccg-live/cgi-bin/cmap/feature?feature_acc=403114).

Screening for *Lr24*

Sunco is known to carry the linked rust resistance genes *Lr24* and *Sr24* (McIntosh et al. 1976) on chromosome 3DL. Parental lines SA65, SA67, and Sunco were tested in the seedling stage against Pt pathotype 104-2,3,6,7. SA67 produced infection type (IT) 0; similar to Sunco, whereas SA65 was scored susceptible ($IT3^+$). The entire SA65/SA67 RIL population was screened and monogenic segregation at the *Lr24* locus was observed (Table 1). These results were further confirmed using the *Sr24*-linked marker *Sr24#12* (Mago et al. 2005). *Sr24#12* is a dominant marker and produces a 500bp amplicon in lines carrying *Lr24/Sr24*. Joint frequency distribution analysis of seedling leaf rust and adult plant stripe rust data (Table 1) revealed linkage between *Lr24/Sr24* and *YrSA3*. Four recombinants between *Lr24/Sr24* and *YrSA3* were observed. Two recombinants carried *Lr24/Sr24* and *YrSA3* in combination and possessed $gwm114b_{134bp}$ allele. The other two recombinants lacked both loci and carried $gwm114b_{132bp}$ allele. *Lr24/Sr24* was incorporated into the map.

Map construction

The final linkage map comprising one SSR, 10 SNPs, and *Lr24/Sr24* is shown in Fig. 2. The stripe rust resistance gene *YrSA3* was located 1.8 cM proximal to all markers. These results confirmed the location of *YrSA3* in the long arm of chromosome 3D.

Genotyping of linked markers on Australian cultivars

A set of 74 Australian wheat cultivars (Table 2) was used for assessing the robustness of *gwm114b* and 10 SNP markers that co-segregated with linked rust resistance genes *Lr24* and *Sr24* and showed close association with *YrSA3*. Marker *gwm114b* amplified 134bp products in 57 cultivars that lacked *Lr24/Sr24*. A 132bp product was observed in 17 *Lr24/Sr24* carrying cultivars indicating the robustness of this marker in the detection of these linked genes. The

Table 1 Joint frequency distribution of *YrSA3* and *Lr24/Sr24* among SA65/SA67 F_6 RIL population

Genotype/frequency	*Lr24Lr24/Sr24Sr24*	*lr24lr24sr24sr24*	Total
YrSA3YrSA3	2	64	66
yrSA3yrSA3	50	2	52
Total	52	66	118

$\chi^2_{(YrSA3 \text{ vs. } yrSA3)} = 1.66$, $P = 0.1976$, d$f = 1$; $\chi^2_{(Lr24 \text{ vs. } lr24)} = 1.66$, $P = 0.1976$, d$f = 1$; $\chi^2_{(YrSA3 \text{ vs. } Lr24)} = 105.86$, $P \leq 0$, d$f = 3$

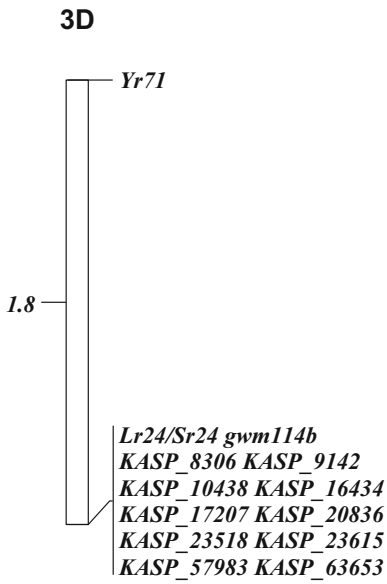

Fig. 2 Genetic linkage map of chromosome arm 3DL showing location of stripe rust resistance gene *Yr71* (*YrSA3*)

132bp amplicon of marker *gwm114b* appears either to be *Agropyron* specific or positioned very close to the translocation breakpoint. Seven KASP markers that co-segregated with *Lr24*/*Sr24* did not detect the presence/absence of these loci accurately and resulted in a high level of misclassification. Three KASP markers (*KASP_16434*, *KASP_17207* and *KASP_20836*), however, amplified alleles alternate to that linked with *Lr24*/*Sr24* in 57 cultivars lacking these genes. Of the 17 *Lr24*/*Sr24* carrying cultivars 12, 14, and 15 were accurately identified by *KASP_20836*, *KASP_17207*, and *KASP_16434*, respectively (Table 2).

Discussion

This study followed an earlier investigation by Kaur and Bariana (2010) in which they reported tri-genic inheritance of adult plant stripe rust resistance among Sunco/2*Avocet S-derived BC_1F_2 families. Here, we used the SA65/SA67 RIL population derived from a Sunco/2*Avocet S BC_1F_2 family 153 (Fig. 1), which was shown not to carry the previously known APR genes *Yr18* (Kolmer et al. 2008) and *YrCK* (Bariana et al. 2001) from Sunco, to genetically map the remaining APR gene. Adult plant stripe rust response assessments across three seasons on SA65/SA67 F_6 population showed monogenic segregation, and the resistance locus was temporarily designated *YrSA3*. Molecular mapping using a 90 K Infinium SNP genotyping array (Wang et al. 2014) located *YrSA3* in the long arm of chromosome 3D. Ten KASP markers, *Sr24#12*, and *gwm114b* clustered together at 1.8 cM distal to *YrSA3*. The *Agropyron elongatum* translocation carrying rust resistance gene *Lr24/Sr24* was responsible for clustering of these markers.

Sunco carries linked stem rust and leaf rust resistance genes *Lr24* and *Sr24*. The Sunco*2/Avocet-derived resistant line SA65 possessed Avocet S alleles for all markers and lacked *Sr24*/*Lr24*, whereas the susceptible line SA67 carried Sunco alleles and *Sr24*/*Lr24* (Table 3). This created confusion about the donor of *YrSA3*. The derivation of *YrSA3* in SA65 from Sunco can be explained based on double recombination between this gene and the flanking markers (*gwm114b* and 10 SNPs) or an allosyndetic event during the generation of BC_1F_2 population. Since *Sr24* and *Lr24* are located on an *Agropyron elongatum* wheat translocation T3DS.3DL-3Ae#1 (Smith et al. 1968) in which 1.25 µm of 3Ae#1 replaced 1.38 µm of 3DL (Jiang et al. 1994), allosyndesis can be expected. We tried additional markers located on both arms of chromosome 3D, but all markers were monomorphic due to derivation of SA65 and SA67 form the same BC_1F_2 family. The second scenario is that *YrSA3* was contributed by Avocet S. The contribution of *YrSA3* by Sunco through double recombination or an allosyndetic event seems more

Table 2 List of cultivars tested with linked markers and their genotypic status

Cultivars	*Lr24/Sr24*	*gwm114* (bp)	*KASP_16434*	*KASP_17207*	*KASP_20836*
AGT Katana	–	134	T	T	T
Axe	–	134	T	T	T
Baxter	–	134	T	T	T
Beaufort	–	134	T	T	T
Bolac	–	134	T	T	T
Calingiri	–	134	T	T	T
Carnamah	–	134	T	T	T
Catalina	–	134	T	T	T
Chara	–	134	T	T	T
Cobra	–	134	T	T	T
Correll	–	134	T	T	T
Crusader	–	134	T	T	T
Dart	–	134	T	T	T
Diamondbird	–	134	T	T	T
EGA Bonnie Rock	–	134	T	T	T
EGA Bounty	–	134	T	T	T
EGA Gregory	–	134	T	T	T
EGA Wedgetail	–	134	T	T	T
EGA Wylie	–	134	T	T	T
Emu Rock	–	134	T	T	T
Envoy	–	134	T	T	T
Estoc	–	134	T	–	T
Forrest	–	134	T	T	T
Fortune	–	134	T	T	T
Gauntlet	–	134	T	T	T
Grenade CL Plus	–	134	T	T	T
Impala	–	134	T	T	T
Justica CL Plus	–	134	T	T	T
King Rock	–	134	T	T	T
Kord CL Plus	–	134	T	T	T
Kunjin	–	134	T	T	T
Lincoln	–	134	T	T	T
Livingston	–	134	T	T	T
Mackellar	–	134	T	T	T
Merlin	–	134	T	T	T
Phantom	–	134	T	T	T
Preston	–	134	T	T	T
Scout	–	134	T	T	T
Sentinel	–	134	T	T	T
Spitfire	–	134	T	T	T
SQP Revenue	–	134	T	T	T
Strzelecki	–	134	T	T	T
Suntop	–	134	T	T	T
Sunvale	–	134	T	T	T
Sunzell	–	134	T	T	T

Table 2 continued

Cultivars	*Lr24/Sr24*	*gwm114* (bp)	*KASP_16434*	*KASP_17207*	*KASP_20836*
Ventura	–	134	T	T	T
Waagan	–	134	T	T	T
Wallup	–	134	T	T	T
Westonia	–	134	T	T	T
Wyalkatchem	–	134	T	T	T
Wylah	–	134	T	T	T
Yandanooka	–	134	T	T	T
Yitpi	–	134	T	T	T
Young	–	134	T	T	T
Harper	–	134	T	T	T
Mansfield	–	134	T	T	T
Trojan	–	134	T	T	T
Elmore CL PLus	+	132	G	C	C
Espada	+	132	T	T	T
Gazelle	+	132	G	C	C
GBA Sapphire	+	132	G	C	H
Giles	+	132	G	C	T
Gladius	+	132/134	H	T	T
Janz	+	132	G	C	C
Lang	+	132	G	C	C
Magenta	+	132	G	C	C
Merinda	+	132	T	T	T
Naparoo	+	132	G	C	C
Shield	+	132	G	C	C
Sunco	+	132	G	C	C
Sunguard	+	132	G	C	C
Sunvex	+	132	G	C	C
Wedin	+	132	G	C	C
Lancer	+	132	G	C	C

plausible as Avocet S showed susceptible stripe rust response score 9 in comparison to *YrSA3* score 6. Of the four recombinant RILs, two carried *Sr24/Lr24* and *YrSA3* and the other two lacked both genes (Table 3). This indicates that frequency of recombination is 1.75 %.

Stripe rust resistance genes *Yr45* (Li et al. 2011), *Yr49* (McIntosh et al. 2011) and *Yr66* (McIntosh et al. 2013) were mapped in chromosome 3D previously. *Yr45* was mapped in long arm, while other two genes were mapped in short arm of chromosome 3D. *Yr45* was flanked by RGAP markers *wgp118* and *wgp115* and two SSR markers *wmc656* and *barc6* were mapped 11.7 and 12.6 cM proximal to *Yr45*. We tried to compare the SSR markers *wmc656*, *barc6* and *gwm114b* reported by Li et al. (2011) and present study, however, none of the map carries all three markers together. Marker *wmc656* was mapped at 75 cM position (Somers et al. 2004) of the 110 cM of total map length, whereas *gwm114b* has been mapped at the distal region in Arina/Forno and Opata/Synthetic populations (https://ccg.murdoch.edu.au/cmap/ccg-live/cgi-bin/cmap/map_details?ref_map_set_acc=10;ref_map_accs=164;highlight=12503). These results reflect that *Yr45* and *YrSA3* were positioned at different locations. Comparison of location and resistance expression led us to conclude that these two genes are different. The genetic association with *Lr24* and 3DL

Table 3 Allelic comparisons of recombinant lines and parental genotype for linked markers and rust resistance genes

Genotype	*Yr71*	*Lr24/Sr24*	*gwm114b*	*KASP_57983*	*KASP_63653*	*KASP_10438*	*KASP_17207*	*KASP_23615*	*KASP_23518*	*KASP_8306*	*KASP_16434*	*KASP_9142*	*KASP_20836*	Mean rust response
RIL-23	+	+	134	C	G	C	C	C	G	G	G	C	C	6
RIL-67	+	+	134	C	G	C	C	C	G	G	G	C	C	6
RIL-85	–	–	132	A	A	T	T	T	A	A	T	A	T	9
RIL-112	–	–	132	A	A	T	T	T	A	A	T	A	T	9
Avocet	–	–	134	A	A	T	T	T	A	A	T	A	T	9
SA65	+	–	134	A	A	T	T	T	A	A	T	A	T	6
SA67	–	+	132	C	G	C	C	C	G	G	G	C	C	9
Sunco	+	+	132	C	G	C	C	C	G	G	G	C	C	4

markers clearly demonstrated the uniqueness of *YrSA3*, and based on these results it was permanently named *Yr71*.

All 10 KASP markers and *gwm114* were tested on a set of Australian cultivars differing for *Lr24/Sr24* (Table 2). All the lines carrying *Lr24/Sr24* produced Sunco allele (132bp) when tested with *gwm114* and those lacking these genes amplified the alternate allele (134bp). Seven KASP markers showed variable results indicating the non-robustness of these markers to detect *Lr24/Sr24*. Their segregation among SA65/SA67 population could be due to derivation of parental lines from the same BC_1F_2 family. The detection of large number of markers linked with the target gene takes place due to high level of linkage disequilibrium (owing to less numbers of recombination cycles) among bi-parental populations. That is why validation on independently developed cultivars is essential to identify robust trait–marker associations. *KASP_16434* was the most robust SNP marker to detect *Lr24/Sr24* and *YrSA3*, followed by *KASP_17207* and *KASP_20836.* The detection of non-*Lr24*/*Sr24*-linked haplotype of *KASP_16434, KASP_17207*, and *KASP_20836* in two, three, and five cultivars, respectively, carrying this *Agropyron*-derived gene combination suggested the location of these markers on the common wheat segment of chromosome 3DL. We suggest that recombinants (RIL-23 and RIL-67) should be used as a source of *Yr71* for simultaneous transfer of *Lr24*/*Sr24*. Although development of KASP markers for *Lr24*/*Sr24* was not an objective of this study, markers *KASP_16434, KASP_17207* and *KASP_20836* provide a co-dominant alternative to the 'breeder friendly' and robust dominant marker developed by Mago et al. (2005). Alternatively, the co-dominant SSR marker, *gwm114b*, demonstrated to be the most robust for the detection of *Lr24/Sr24,* can be used for the detection of this linked locus among diverse plant genetic resources and for marker-assisted selection in breeding programs.

Yr71 is an APR gene and can be combined with other major or minor stripe rust resistance genes to achieve low rust severity and durability. Molecular markers for numerous all stage resistance (listed in Bariana et al. 2007) and APR genes *Lr34/Yr18*, *Lr67/Yr46* and *Yr36* (Lagudah et al. 2006; Forrest et al. 2014; Uauy et al. 2005) are available and can be used for gene stacking.

Acknowledgments Financial support from the University of Sydney and the GRDC Australia is gratefully acknowledged.

Author's contribution H.B drafted the manuscript; H.M, H.B, and U.B developed segregating population; H.B and U.B did rust phenotyping; U.B and N.Q did marker work; K.F and M.H perform Illumina iSelect 90 K Infinium SNP genotyping Array; U.B, H.B, and M.H edited the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards Experiments were conducted following ethical standards.

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