An adult plant stripe rust resistance gene maps on chromosome 7A of Australian wheat cultivar Axe

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Abstract
Key message An adult plant stripe rust resistance gene Yr75 was located on the long arm of chromosome 7A. Fine mapping of the region identified markers closely linked with Yr75.

Abstract Australian wheat cultivar Axe produced resistant to moderately resistant stripe rust responses under field conditions and was exhibiting seedling responses varying from 33C to 3+ under greenhouse conditions. Experiments covering tests at different growth stages (2nd, 3rd and 4th leaf stages) demonstrated the clear expression of resistance at the 4th leaf stage under controlled-environment greenhouse conditions. A recombinant inbred line (RIL) population was developed from the Axe/Nyabing-3 (Nyb) cross. Genetic analysis of Axe/Nyb RIL population in the greenhouse at the 4th leaf stage showed monogenic inheritance of stripe rust resistance. Selective genotyping using the iSelect 90 K Infinium SNP genotyping array was performed, and the resistance locus was mapped to the long arm of chromosome 7A and named Yr75. The Axe/Nyb RIL population was genotyped using a targeted genotype-by-sequencing assay, and the resistance-linked SNPs were converted into competitive allele-specific PCR (KASP) markers. These markers were tested on the entire Axe/Nyb RIL population, and markers sunKASP_430 and sunKASP_427 showed close association with Yr75 in the Axe/Nyb RIL population. A high-resolution mapping family of 1032 F2 plants from the Axe/Nyb cross was developed and genotyped with sunKASP_430 and sunKASP_427, and these markers flanked Yr75 at 0.3 cM and 0.4 cM, respectively. These markers cover 1.24 Mb of the physical map of Chinese Spring, and this information will be useful for map-based cloning of Yr75.

Introduction

Stripe rust or yellow rust, caused by Puccinia striiformis f. sp. tritici (Pst), ranks high among fungal diseases of wheat worldwide. This disease has the potential to cause almost 1 billion AUD of losses in Australia (Murray and Brennan 2009). Previously, this disease was endemic to cooler wheat-growing regions, but in the last two decades the pathogen has adapted to relatively warmer regions causing worldwide expansion and leading to many destructive pandemics (Ali et al. 2014).

The global progression and rapid evolution of the stripe rust pathogen have led to increased application of fungicides, effectively decreasing the economic losses in several epidemics (Carmona et al. 2020), but the use of fungicides is neither an environment-friendly nor cost-effective control measure. Experiments have also been conducted on the biological control of stripe rust, but no significant reduction in severity of disease has been noted. This approach is also not practically viable (Reiss and Jørgensen 2017; Fedorova-Fedotova et al. 2019). Both these control measures are resource-demanding and unprofitable for farmers with small land holdings in developing nations. In contrast, breeding for stripe rust resistance is considered a preferred method to effectively control this disease due to its eco-friendly and economic nature (Bariana et al. 2007a).

Resistance to stripe rust has been classified into two broad classes (Bariana 2003; Chen 2005) often referred to as...
overall resistance (also known as all stage resistance; ASR) and adult plant resistance (APR). Genes that condition ASR follow gene-for-gene model (Flor 1942) and exhibit high levels of resistance. Deployment of ASR genes individually in wheat cultivars makes them vulnerable to breakdown through acquisition of virulence in pathogen populations (Bariana et al. 2016). Genotypes carrying APR genes display slow disease development at the post-seeding stages. This type of resistance has also been referred to as partial or slow rusting or non-hypersensitive resistance and is considered more durable (Caldwell 1968). Some APR genes conferred pleiotropic resistance toward multiple diseases including stripe rust, leaf rust, stem rust and powdery mildew. These include Yr18/Lr34/Sr57/Pm38; Yr29/Lr46/Sr58/Pm39 and Yr46/Lr67/Sr55/Pm46 (https://wheat.pw.usda.gov/GG3/wgc). A third category of resistance expresses clearly at the 3rd to 4th leaf stages onward and behaves like ASR in expression. Such resistance can be referred to as mid-stage resistance (MSR) (Chhetri et al. 2016a), for example; Yr58 (Chhetri et al. 2016b), Lr48 (Nsabiyera et al. 2016) and Lr49 (Nsabiyera et al. 2020).

To date, 83 stripe rust resistance genes have been formally designated (https://wheat.pw.usda.gov/GG3/wgc) and most of these genes belong to the ASR category. The availability of various high-throughput genotyping platforms (e.g. DArT array, DArTseq, 40 K and 90 K SNP arrays, genotyping-by-sequencing) has accelerated the discovery of new disease resistance loci and the development of trait-linked molecular markers. Moreover, complete genome assembly of common wheat genotype Chinese Spring IWGSC RefSeq v1.0 (IWGSC RefSeq v2.0) has offered opportunities for fine mapping and map-based cloning of loci that control economic traits.

Stripe rust resistance genes Yr26 (Wu et al. 2018), Yr29 (Cobo et al. 2019) and Yr47 (Qureshi et al. 2017) have recently been fine mapped. Resistance genes Yr5, Yr7, Yr5p (Marchal et al. 2018), Yr15 (Klymiuk et al. 2018), Yr18/Lr34 (Krattinger et al. 2009), Yr36 (Fu et al. 2009), Yr10 (Wu et al. 2014) and Yr46/Lr67 (Moore et al. 2015) have been cloned using these new tools. Axe, an Australian cultivar released in 2015 by the Australian Grain Technologies, was susceptible at the seedling stage against Australian Pst pathotypes and showed a high level of resistance at the adult plant stage. A recombinant inbred line (RIL) population was developed for genetic analysis of stripe rust resistance in cultivar Axe and molecular mapping of underlying gene (s).

Materials and methods

Population development

Cultivar Axe (96W657-37/Kukri) was crossed with a susceptible genotype Nybing-3 (Nyb), a selection from cultivar Nybing [WT329/(W753.WD194)]. F1 seeds were grown and harvested separately for producing the F2 population. Individual F2 seeds were planted 10 cm apart in the field, and each plant was harvested separately. A single spike was harvested from each greenhouse grown F2 family to generate an F3 population. Similarly, single head harvest from F4 generation led to the production of an F5 population. Single seed from each F5 line was grown and the whole plant was harvested to raise an F6 generation. The final set of 151 lines is referred to as the Axe/Nyb RIL population. A large population of 1032 F2 plants (2064 gametes) from the Axe/Nyb cross was also developed for fine mapping.

Greenhouse screening

The Axe/Nyb RIL population was screened in the greenhouse against the most prevalent Pst pathotype 134E16A+Yr17+Yr27+ (Plant Breeding Institute culture no. 617). Eight to 10 seeds from each RIL (four RILs per pot) were sown in 9-cm diameter pots filled with a potting mixture comprising of composted pine bark and sand in a 2:1 ratio, followed by fertilizer treatment (25 g Aquasol®; Hortico Pty. Ltd., Revesby, NSW, Australia /10L of water for 100 pots). Seedlings were fertilized weekly with Urea at the same rate as Aquasol. Inoculations were carried out at the 4th leaf stage in a specialized inoculation chamber by atomisinguredini- spores of Pst pathotype 134E16 A+Yr17+Yr27+ suspended in light mineral oil (Isopar L, 5 mg spores 10 ml-1 of oil as solvent) using a hydrocarbon propellant pressure pack. After inoculation, plants were moved to lukewarm water-filled steel trays covered with polythene hoods in the incubation room set at 9–12 °C. Following 24 h of incubation, plants were transferred to microclimate rooms (automated temperature and irrigation control) set at 17 °C. Rust response assessments were performed 16–18 days after inoculation using a 0–4 scale described in McIntosh et al. (1995). The Axe/Nyb RILs were classified as homozygous resistant (HR), homozygous susceptible (HS) and segregating (this class can have very low frequency and sometime could represent a mixture).

Molecular mapping

DNA extraction

Axe/Nyb RIL population DNA from 10 to 12 day-old seedlings of each Axe/Nyb RIL and parents was extracted and
quantified following a modified CTAB method outlined in Bansal et al. (2014).

High-resolution F2 population A modified SDS (sodium dodecyl sulfate) DNA extraction protocol (M. Pourkheirandish personal communication) was used to extract DNA from Axe/Nyb F2 population of 1032 plants (2064 gametes). Leaf tissue from individual F2 plants was collected in 96 wells plate and two ball bearings, and 450 µl of extraction buffer (100 mM Tris–HCl pH 8.0, 50 mM EDTA pH 8.0, 500 mM NaCl and 10 mM 2-mercaptoethanol) was added in each well and samples were crushed in a tissue lyser (1600 MiniG™) for 3 min. After crushing, 60 µl of 10% SDS buffer was added, and samples were inverted vigorously for homogenous mixing. Samples were then incubated at 65 °C for 60 min, and the plate was centrifuged for 1 min at 3600 rpm. After centrifugation, 200 µl of 7.5 M ammonium acetate was added, and the plate was shaken vigorously, and incubated for 60 min at 4 °C. After centrifugation at 1000 rpm for 1 min, 300 µl of chloroform : isoamyl alcohol (24:1) was added and the plate was again shaken vigorously, followed by centrifugation for 10 min at 4800 rpm. One hundred µl of supernatant was added to 100 µl of chilled isopropanol in new plate and mixed gently. After centrifugation for 10 min at 4800 rpm, the isopropanol was removed, and the pellet was resuspended in 100 µl of 1 M Tris HCl (pH 8) containing 10 mM RNase and incubated at 37 °C for 1–2 h.

Chromosomal location of stripe rust resistance

Selective genotyping For identification of chromosomal location of the resistance locus, selective genotyping was carried out on eight resistant and eight susceptible RILs using the Illumina iSelect 90K Infinium SNP genotyping array (Wang et al. 2014).

Detailed mapping using a targeted genotyping-by-sequencing (tGBS) assay

Once the genomic region that controls stripe rust resistance was identified through selective genotyping, we used targeted genotyping-by-sequencing (tGBS) assay for saturation of the map. This service was provided by Agriculture Victoria, Agribio, Bundoora, Victoria. The purpose of the tGBS assay was to capture additional polymorphisms between parents by sequencing the genomic region of interest. The genetic map was constructed using the R package ASMap (Taylor and Butler 2017), and imputations for missing SNP data were performed using Impute v2.2 (Sargolzaei et al. 2014).

Marker design An automated bioinformatic pipeline Poly-Marker (Ramirez-Gonzalez et al. 2015) was used for designing KASP markers from the SNPs associated with stripe rust resistance identified through selective genotyping and tGBS mapping. Allele-specific primers A1 and A2 were tagged with diagnostic sequences for fluorescent dyes FAM (gaaggtcacaagttagctgcgt) and HEX (gaaggtcggagctcaacggtt) at their 5’, respectively. These markers were tested on parental lines (Axe and Nyb) using the protocol described by LGC (Laboratory of the Government Chemist) genomics, UK (www.biosearchtech.com/NGS). The KASP markers which gave clear clusters were genotyped on the entire RIL population for construction of a linkage map.

Statistical analysis and genetic mapping

Chi-squared ($\chi^2$) analysis was used to identify segregation distortion among markers located near the resistance locus. The KASP and SSR marker data were converted to ‘A’ for Axe allele and ‘B’ for Nyb allele and ‘H’ for heterozygotes for mapping. Genetic linkage maps were constructed using MapManager QTXb20 (Manly et al. 2001) with the Kosambi map function (Kosambi 1943) and then presented graphically using MapChart version 2.3 (Voorrips 2002). The physical position of markers that flanked the resistance locus and structural variation in the genomic region was investigated using the tool Pretzel (Keeble-Gagnère et al. 2019) which compares genetic and physical maps.

Results

Phenotypic assays

Wheat cultivar Axe displayed resistant to moderately resistant (RMR) responses at the adult plant stage and Nybing-3 (Nyb) was scored susceptible (S), when tested in the National Variety Trials across Australia. The Axe/Nyb RIL population was inoculated with the Pst pathotype 134 E16A+Yr17+Yr27+ under greenhouse conditions at the 2nd, 3rd and 4th leaf stages. Expression of resistance was not clear at the 2nd to 3rd leaf stages; however, a clear expression of resistance was observed at the 4th leaf stage. The resistant parent Axe produced infection type (IT);1°C, and the susceptible parent produced IT3+ (Fig. 1). Infection types among resistant RILs ranged from IT1C to IT23C. These results suggested that resistance carried by Axe does not typically belong to the either of the currently defined ASR or APR categories.

The Axe/Nyb RILs were classified as homozygous resistant (HR = IT1C–23C) and homozygous susceptible
Eighty-four lines were placed in the HR class, while 67 were categorized as HS. Chi-squared analysis of stripe rust response variation among RILs conformed to segregation at a single locus (Table 1). The underlying stripe rust resistance locus was named YrAxe.

Molecular mapping of YrAxe

Selective genotyping with the 90K SNP array was used to identify the chromosomal location of YrAxe. Of 306 linked SNPs, 140 SNPs were mapped in chromosome 7AL, 55 in 7BL and 7 in 7DL of the wheat consensus map (Wang et al. 2014). Among the 7AL SNPs, 128 SNPs spanned a region of 708,363,089–726,684,629 bp of the Chinese Spring physical map (IWGSC RefSeq v1.0) and showed strong linkage with YrAxe. One SNP from each representative LD block (28 SNPs in total) was converted into a KASP assay. Two KASP markers, KASP_34640 and KASP_38710, clearly differentiated the parents (Table 2), and Nyb was heterozygous/heterogeneous for KASP_39562.

YrAxe was mapped on the long arm of chromosome 7A and KASP_34640 showed close association. The SSR marker, cfa2040, previously mapped on chromosome 7A, was polymorphic between parents and was used to confirm the location of linked SNP markers and was genotyped on the entire Axe/Nyb RIL population. YrAxe was flanked by cfa2040 and KASP_34640.

Detailed mapping of Yr75

Low-resolution mapping

Seven SNPs from the tGBS assay that showed close association with Yr75 were converted into KASP markers (sunK-AS2_425, sunKAS_426, sunKASP_427, sunKASP_428, sunKASP_429, sunKASP_430 and sunKASP_431). Primer sequences of these markers are given in Table 3. These markers differentiated the parents clearly and were genotyped on the entire Axe/Nyb RIL population. A genetic map carrying Yr75 was developed including two 90K SNPs and cfa2040. Marker sunKASP_427 mapped at 0.3 cM proximal to Yr75 and sunKASP_430 co-segregated with the gene (Fig. 2a). The flanking markers were physically located at 719,076,651 (sunKASP_427) and 717,832,538 bp (sunKASP_430) in the Chinese Spring (IWGSC RefSeq v1.0) sequence (Fig. 3).

High-resolution mapping

Markers sunKASP_425, sunKASP_426, sunKASP_427, sunKASP_428, sunKASP_429, sunKASP_430 and sunKASP_431 from the Axe/Nyb low resolution map were genotyped on 1032 individual F2 plants (2064 gametes) to refine recombination in the region. KASP_34640 and KASP_38710 did not produce clear clusters for heterozygotes and therefore were not included in mapping. Marker cfa2040 is a multi-locus marker (amplify alleles on chromosome 7A, 7B and 7D), size difference was only 2 bp (7A) which can be assessed clearly in the RIL population, but it is very difficult to score in the F2 population; therefore, this marker was also genotyped.

Table 2 List of YrAxe-linked KASP markers developed from the iSelect 90K SNP genotyping

| Marker   | SNP     | Position in 90K map (cM)* | Primer sequence Allele 1a | Primer sequence Allele 2b | Common primer |
|----------|---------|---------------------------|---------------------------|---------------------------|---------------|
| KASP_34640 | [A/G]   | 216.36                     | Aagataaaatgtctcaagctt    | aagataaaatatgtctcaagctt   | atgaagagacgaacacagac |
| KASP_38710 | [T/C]   | 212.97                     | Ggagatgacagtgcaaatatat   | ggaagatgacagtgcaaatatat   | tatactcatcatctçaçãttaçaçá       |
| KASP_39562 | [T/C]   | Not known                  | Caggataagctctgtt         | caggataagctctgtt          | tggagagatagctgtt          |

*aMarker position in 90K SNP consensus map (Wang et al. 2014), aA1 primer labeled with FAM, GAAGGTCGAGTCAAACGGATT, aA2 primer labeled with HEX, GAAGGTCGAGTCAAACGGATT*
not used for genotyping. Thirty recombinants were identified between the sunKASP_427 and sunKASP_431 interval and were grown for progeny testing. These progenies were scored at the 4th leaf stage, and a high-resolution map was constructed. Markers sunKASP_427 and sunKASP_430 flanked Yr75 at 0.4 cM and 0.3 cM proximally and distally, respectively (Fig. 2b).

Discussion

This study demonstrated the clear expression of stripe rust resistance in wheat cultivar Axe at the 4th leaf stage (IT;1C), and the flag leaf also exhibited a similar response under greenhouse conditions. The underlying locus was mapped on the long arm of chromosome 7A. Rosewarne et al. (2013) listed five QTL on chromosome 7A (QRy7A.1, QRy7A.2, QRy7A.3, QRy7A.4 and QRy7A.5), and all these QTL were located in the short arm of chromosome 7A. As none of the formally named stripe rust resistance genes previously mapped in this region (https://shigen.nig.ac.jp/wheat/komugi/genes/symbolDetailAction.do?geneId=12217), the resistance locus was permanently named Yr75. The expression of stripe rust resistance at post-seedling stages was previously described by Chhetri et al. (2016a, b) in a landrace W195 from India and in an Australian cultivar Sentinel by Chemayek (2016). This type of genes does not belong to the typical slow rusting APR class Yr18 and Yr29 (Lagudah et al. 2006; McIntosh 1992; Singh 1992) and ideally fit into the MSR category.

This investigation used the state-of-the-art technologies and sequence information for detailed mapping of the
chromosome 7A region that carried \textit{Yr75}. Several studies have used an integrated approach for development of molecular markers for rust resistance, and these include \textit{Lr49} (Nsabiyera et al. 2020), \textit{Yr47} (Qureshi et al. 2017) and \textit{Yr26} (Wu et al. 2018).

The Axe/Nyb map was saturated through a targeted genotyping-by-sequencing (tGBS) assay that generates sequence data for genomic regions surrounding known exome-derived SNPs. SNPs identified from the tGBS analysis, 90K Infinium array and SSR marker \textit{cfa2040} led to the development of a low-resolution map with 0.7 cM interval (\textit{sunKASP\_427} and \textit{Yr75-sunKASP\_430}). Markers \textit{cfa2040} and \textit{KASP\_34640} were located in the tGBS scaffolds scaffold43271-1 and scaffold96044, respectively, from which \textit{Yr75}-flanking markers were developed. Due to the lack of good clustering and similar positioning in the scaffolds, these markers were not genotyped on the high resolution population. Markers developed from tGBS SNPs were genotyped on a high-resolution Axe/Nyb F\textsubscript{2} population, and genetic distances of 0.4 cM for \textit{sunKASP\_427} (11 recombinants) and 0.3 cM for \textit{sunKASP\_430} (10 recombinants) from \textit{Yr75} were observed. These markers were developed from two scaffolds (scaffold96044 and scaffold43271-1) and were represented in the superscaffold 32 of the IWGSC v1.0 genome assembly (IWGSC 2018). The tGBS approach has been used for mapping and development of molecular markers for only a few genes including \textit{Yr82} (Pakeerathan et al. 2019) \textit{Sr26} (Qureshi et al. 2018) and \textit{Yr26} (Wu et al. 2018) in wheat.

Despite the low genetic distance (1.24 Mb physical distance; IWGSC RefSeq v1.0 genome assembly) between closely linked markers \textit{sunKASP\_427} and \textit{sunKASP\_430} and \textit{Yr75}, we were unable to validate these markers on a diverse set of wheat genotypes, which suggested either chromosomal rearrangement or the suppressed recombination in this region. Markers \textit{sunKASP\_427} and \textit{sunKASP\_430} can, however, be used for marker-assisted selection of \textit{Yr75} following confirmation of parental polymorphism among the recurrent parents and the donor source. \textit{Yr75} is located near the telomere of the 7A chromosome, where frequent recombination should be expected. The existence of suppressed recombination is also supported by previous studies on pleiotropic locus \textit{Sr15/Lr20/Pm1} (Sears and Briggle 1969; Watson and Luig 1966) on chromosome 7AL, which

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{Fig3.png}
\caption{Position of \textit{Yr75}-linked markers on chromosome 7AL in the IWGSC v1.0 Chinese Spring genome assembly. The figure was constructed using Pretzel (Keeble-Gagnère et al. 2019)}
\end{figure}
showed a total genetic distance of 9.6 cM flanked by markers psr148 and psr687 (Gale 1995). The fine mapping of chromosome 7AL later revealed that the markers edo347, psr121 and ksu9 covered a region of 30 cM (Peña et al. 1997). Genetic mapping of the Lr20-Pm1 locus in three different F₂ populations also revealed that markers at the distal end were completely linked with Lr20-Pm1 locus, but at the proximal end there was a discrepancy compared to previous map for this locus (Neu et al. 2002). These results also suggested reduced recombination in this region and/or chromosomal rearrangements. Suppressed recombination was also reported in another study for root lesion nematode gene Rhn1 which is tightly linked with the Sr15/Lr20 locus (Jayatilake et al. 2013). These results supported the hypothesis that terminal region of chromosome 7A is one of the complex region resulted due to several chromosomal aberrations (Badaeva et al. 2007). To move forward, different approaches such as flow sorting of chromosome of the line carrying the target locus could be helpful in saturating the region and finding close marker-gene associations. Further study of this region using advanced genomic techniques including sequence capture and CRISPR-mediated genetic manipulation will facilitate the unexplained reason for complexity of this region.

In conclusion, this study provided a new adult plant stripe rust resistance gene Yr75 and tightly linked markers for marker-assisted selection of this gene in breeding programs following parental polymorphism checks. These results will also be useful in map based cloning of Yr75.

Author contribution statement UB and HB planned the study; MK, MG and HB developed segregating populations and performed phenotyping; KF and NQ performed genotyping and iGBS analysis; UB and MK designed KASP primers; MK and PB performed KASP genotyping; MK drafted the manuscript; UB, HB, KF and NQ edited the manuscript.

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Data availability All data are given in the manuscript.

Code availability Publicly available software are used in this study.

Declarations

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

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