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Molecular mapping of stem and leaf rust resistance in wheat

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Abstract Stem rust caused by *Puccinia graminis* f. sp. *tritici* Eriks and Henn and leaf rust caused by *Puccinia triticina* Rob. ex Desm. are major constraints to wheat production worldwide. In the present study, F_4-derived SSD population, developed from a cross between Australian cultivars 'Schomburgk' and 'Yarralinka', was used to identify molecular markers linked to rust resistance genes *Lr3a* and *Sr22*. A total of 1,330 RAPD and 100 ISSR primers and 33 SSR primer pairs selected on the basis of chromosomal locations of these genes were used. The ISSR marker UBC 840_{540} was found to be linked with *Lr3a* in repulsion at a distance of 6.0 cM. Markers cfa2019 and cfa2123 flanked *Sr22* at a distance of 5.9 cM (distal) and 6.0 cM (proximal), respectively. The use of these markers in combination would predict the presence or absence of *Sr22* in breeding populations. A previously identified PCR-based diagnostic marker STS638 linked to *Lr20* was validated in this population. This marker showed a recombination value of 7.1 cM with *Lr20*.

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Introduction

Wheat is one of the most important cereal food crops in the world and rust diseases pose a great threat to its production globally. Stem rust has the potential to cause losses up to 100%, whereas upto 40% losses due to leaf rust have been reported (Singh et al. 2002). Forty-nine stem rust resistance (*Sr*) and 51 leaf rust resistance (*Lr*) genes, conferring specific resistance to these diseases, have been identified and assigned to specific chromosomes (McIntosh et al. 2003). Introgression of resistance genes from related wild or cultivated species has provided genetic diversity for rust resistance in wheat. Deployment of genetic resistance in a new cultivar contributes to the reduction in economic losses, production costs and risk of environmental pollution due to fungicide usage. Since cultivars with single resistance genes have promoted emergence of virulent pathotypes, pyramiding of rust resistance genes has been advocated to increase commercial life of a cultivar (Watson and Singh 1952; Messmer et al. 2000). Pyramiding of rust resistance genes through traditional phenotypic-based technology is difficult when different resistance genes produce similar infection types. Identification of molecular markers linked to disease resistance genes facilitates marker-assisted selection (MAS) for achieving gene combinations in breeding programs (Sharp et al. 2001; Babu et al. 2004).

Various molecular marker systems such as RFLP, RAPD, ISSR, AFLP and microsatellites (SSRs) have been widely used to tag resistance genes in wheat. A few recent reports include markers linked to *Sr2* (Hayden et al. 2004), *Sr39* (Gold et al.1999), *Lr19* (Prins et al. 2001) and *Lr39* (Raupp et al. 2001). Furthermore, there have been efforts to isolate and characterize leaf rust resistance genes by high resolution mapping for *Lr1* (Ling et al. 2003) and map-based cloning for *Lr10* (Feuillet et al. 2003), and *Lr21* (Huang et al. 2003).

This study was undertaken to identify markers linked to rust resistance genes *Lr3a* and *Sr22*. We also vali-

dated the *Lr20*/*Sr15*/*Pm1*-linked marker STS638 on a single seed descent (SSD) population derived from 'Schomburgk'/'Yarralinka'.

Materials and methods

Plant material

Mapping population was developed at the University of Adelaide, Australia and consisted of 150 F_4-derived SSD lines from a cross between 'Schomburgk' and 'Yarralinka'. Owing to relatively higher levels of heterozygosity at the three loci studied in this population, lines homozygous for the presence or absence of the target locus were used.

Rust response tests

Rust response tests were performed at the University of Sydney, Plant Breeding Institute, Cobbitty. *Puccinia graminis* f. sp. *tritici* pathotypes 40-1,2,3,4,5,6,7,8,9,11 (*Sr9e* and *Sr36*-virulent and *Sr22*-avirulent) were used to score the presence/absence of stem rust resistance gene *Sr22*. *Puccinia triticina* pathotypes 104-2,3,6,7 (*Lr3a*-virulent and *Lr20*-avirulent) and 53-1,(6),7,10,11(*Lr3a*-avirulent and *Lr20*-virulent) were used to score rust responses conferred by leaf rust resistance genes *Lr20* and *Lr3a*, respectively. Details of disease screening and scoring procedures were described in Bariana and McIntosh (1993).

DNA extraction

Genomic DNA was extracted from young leaf tissue of cultivars 'Schomburgk', 'Yarralinka' and the entire SSD population, using a protocol described by Anderson et al. (1993). DNAs from susceptible variety Chinese Spring and other wheat genotypes lacking *Sr22* were also extracted.

PCR analysis and electrophoresis

A total of 1,330 random primers (780 from Operon Technologies, USA and 550 from University of British Columbia, Canada) and 100 ISSR primers (University of British Columbia, Canada, set#9) were used for parental screening as described by Ammiraju et al. (2002). Thirty-three SSR (Litt and Luty 1989) primer pairs located on chromosomes 6B and 7A as per the maps (Röder et al.1998; Pestsova et al. 2000; Somers et al. 2004) were used for PCR analysis according to Röder et al. (1998).

RAPD and ISSR PCR products were resolved on 2% agarose gels stained with ethidium bromide. PCR products of SSR analysis were resolved on 3% metaphor agarose gels or on 10% polyacrylamide gels stained with ethidium bromide or on 6% denaturing polyacrylamide gels with autoradiography based upon product size and desired resolution.

Bulk segregant analysis (BSA)

Bulk segregant analysis (Michelmore et al. 1991) was employed to identify putative RAPD and ISSR markers linked to the target rust resistance genes. For every gene, two DNA bulks were prepared using equal amounts of genomic DNA from eight resistant and eight susceptible lines. Markers exhibiting polymorphism between the parents and the resistant and susceptible bulks were used to screen the entire population.

Aneuploid analysis

Analysis of nulli-tetrasomic (NT) lines was performed to verify the chromosomal location of the linked random markers. Genomic DNA from hexaploid Chinese Spring wheat and NT lines, N7A-T7D, N7A-T7B, N7B-T7A, N7D-T7A, N6B-T6A, N6B-T6D, N6A-T6B and N6D-T6B, were used to confirm the genomic location of markers linked to *Sr22* and *Lr3a* according to Liu et al. (2001).

Linkage analysis

Genetic linkage analysis was performed using software MAPMAKER v.3.0 (Lander et al. 1987). The marker order was established using multipoint analysis at LOD 3.0 and above. Kosambi mapping function was used to determine the distance in centimorgans (cM) between the two markers (Kosambi 1944).

Results

Validation of *Lr20*-linked marker STS638

The leaf rust resistance gene *Lr20* is completely linked with the powdery mildew resistance gene *Pm1* and the stem rust resistance gene *Sr15* in the distal region of the chromosome arm 7AL. *Lr20* is ineffective both in Australia and India, whereas *Sr15* is effective against the predominant *P. graminis* f. sp. tritici pathotype 98-1,2,3,5,6 in Australia. Monogenic inheritance of resistance conferred by *Lr20* was observed amongst 109 SSD lines (50 *Lr20Lr20*: 59 *lr20lr20*; $\chi^2_{1:1} = 0.74$, nonsignificant at 1 df and $P = 0.05$) in the present rust response testing.

A PCR-based diagnostic STS marker, STS638, was developed for the detection of the *Lr20*/*Pm1* locus by Neu et al. (2002). A high specificity and reliability of this marker was also demonstrated by its presence in 12

resistant wheat lines carrying *Lr20*/*Pm1* locus and its absence in susceptible lines. In this study, the STS638 amplified a 542-bp fragment in cultivar 'Schomburgk', whereas this band was absent in cultivar 'Yarralinka'. Mapping of STS638 on SSD population derived from 'Schomburgk'/'Yarralinka' showed a recombination value of 7.1 cM at a LOD score of 14.0 between the marker and the leaf rust resistance gene *Lr20*. These results demonstrated that the marker STS638 reported by Neu et al. (2002) was not precisely diagnostic for *Lr20* in this population.

Molecular mapping of rust resistance genes

Identification of markers polymorphic for target regions

A total of 1,330 RAPD, 100 ISSR and 33 selective SSR primers were used to screen the two parents 'Schomburgk' and 'Yarralinka'. The presence of polymorphism was confirmed by at least three replications to ensure reproducibility of the results. Markers that showed polymorphism between the parents were initially screened on the bulks followed by mapping on the whole SSD population.

Mapping of rust resistance genes

Lr3a: *Lr3a* is commonly referred to as *Lr3* and is distally located on the chromosome arm 6BL (McIntosh et al. 2003). Three different alleles have been described near *Lr3* locus viz. *Lr3a*, *Lr3bg* and *Lr3ka*. Although pathotypes virulent on *Lr3a* have been reported worldwide, it may still be useful in combination with other genes. The cultivar 'Yarralinka' carries *Lr3a*, whereas the cultivar 'Schomburgk' lacks it. The rust response testing in the present study observed monogenic segregation at the *Lr3a* locus (43 *Lr3aLr3a*: 60 *lr3alr3a*; $\chi^2_{1:1} = 2.8$, non-significant at 1 df and $P = 0.05$).

Eight SSR primer pairs specific to chromosome 6B (gwm193, gwm191, gwm70, gwm361, gwm508, gwm132, gwm88 and gwm613) were analyzed in the present study. Of these gwm508, gwm132 and gwm361 were polymorphic; however, these SSR markers failed to show association with *Lr3a* when tested on the mapping population. Only one ISSR marker, $UBC840_{540}$, showed repulsion linkage with *Lr3a* at a distance of 6.0 cM (LOD score = 14.0).

Sr22: The stem rust resistance gene *Sr22* originally introgressed into chromosome 7AL from *T. boeoticum*, a diploid relative of wheat (Gerechter-Amitai et al. 1971), confers resistance to all *P. graminis* f. sp *tritici* pathotypes in Australia. Cultivar 'Schomburgk' (Rathjen 1987) and its boron-tolerant derivative BT-Schomburgk are the only commercial cultivars carrying this gene. *Sr22* is located 30 cM from the centromere and more than 50 cM proximal to *Pm1*/*Lr20*/*Sr15* resistance gene cluster (The 1973; The and McIntosh 1975). A total of 115 homozygous lines chosen for this study exhibited monogenic inheritance of resistance conferred by *Sr22* (54 *Sr22Sr22*: 61 *sr22sr22*; $\chi^2_{1:1} = 0.42$, nonsignificant at 1 df and $P = 0.05$).

Twenty-five SSR primer pairs specific to chromosome 7A were screened for polymorphism between the parents. Of these gwm573, gwm890, gwm1065, barc153, barc154, cfa2019 and cfa2123 showed polymorphism. Two RAPD markers, $UBC239_{686}$ and $UBC322_{1445}$, were also polymorphic between the parents and the corresponding bulks. All these polymorphic markers were used for population screening. Linkage map around the locus *Sr22* is presented in Fig.1. The markers cfa2019 and cfa2123 flanked *Sr22* at distances 5.9 cM and 6.0 cM, respectively, at a LOD score of 14.0. The entire interval mapped with nine markers around *Sr22* was 45.9 cM in length. The markers $UBC239_{686}$ and $UBC322_{1445}$ showed loose coupling and repulsion linkage with *Sr22*, respectively.

The *Sr22* carrying cultivar 'Schomburgk' and eight genotypes including 'Yarralinka' lacking *Sr22* were used to investigate the usefulness of markers cfa2019 and cfa2123 in MAS of *Sr22* (Table 1). The marker cfa2019 amplified a 234 bp band in 'Schomburgk' and a 200-bp band was amplified when genomic DNAs from *Sr22*-lacking genotypes were used. Similarly, marker cfa2123

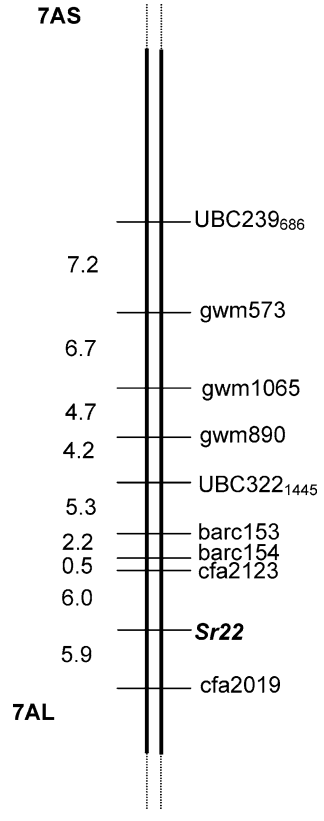

Fig. 1 Genetic linkage map of markers linked with *Sr22* on chromosome 7A in the cross Schomburgk/Yarralinka. Marker loci are indicated on the *right side of the map* and the genetic distances (cM) on the *left side*

Table 1 Amplification of markers cfa2019 and cfa2123 on genomic DNA from *Sr22*-carrying cultivar Schomburgk and some *Sr22*-lacking genotypes

Cultivar/Line	*Sr22* status[a]	cfa2019 (bp)	cfa2123 (bp)
Yarralinka	–	200	260
Schomburgk	+	234	245
Chinese Spring	–	200	260
Thatcher (Tc)	–	200	260
Tc + *Lr24*	–	200	260
Tc + *Lr28*	–	200	260
Tc + *Lr37*	–	200	260
CDM2D	–	200	260
Cappelle Deprez (CD)	–	200	260

[a]Plus denotes presence and minus denotes absence

amplified a 245-bp band when genomic DNA from 'Schomburgk' was used, whereas a 260-bp band was amplified from genomic DNA from *Sr22*-lacking genotypes including 'Yarralinka'.

Chromosomal location of random markers

To confirm the chromosomal location of rust response-linked RAPD and ISSR markers, PCRs were carried out with parents, a set of NT lines and Chinese Spring. As expected, $UBC322_{1445}$ was located on chromosome 7AL. However, a 686-bp band amplified by UBC239 (loosely linked to *Sr22* in coupling) and a 540-bp band amplified by UBC840 (Linked to *Lr3a*) could not be localized using NT lines, as these bands were absent in Chinese Spring.

Discussion

The marker STS638, reported to be closely linked with resistance gene cluster *Lr20*/*Sr15*/*Pm1* by Neu et al. (2002), showed a recombination value of 7.1 cM with *Lr20*/*Sr15*/*Pm1*cluster. It was concluded that the association was not close enough to detect the presence of *Lr20*/*Sr15*/*Pm1* accurately in breeding populations. Rust resistance genes *Sr22* and *Lr20* showed a recombination value of 42 cM similar to that reported by The and McIntosh (1975).

Among the three marker techniques used in our analysis, SSR markers were more polymorphic and informative than the RAPD and ISSR systems. These results are in accordance with previous observation that SSRs detect high levels of polymorphism in wheat (Pestsova et al. 2000).

This investigation identified markers linked with leaf rust resistance gene *Lr3a* and stem rust resistance gene *Sr22*. The co-segregation of the *Lr3* with the RFLP marker mwg 798 located on the chromosome arm 6BL was reported in two crosses involving wheat cultivar Sinvalocha M (Sacco et al. 1998). While Danna et al. (2002) reported complete linkage between a cDNA clone TaRr16 and *Lr3a* in the cross Sinvalocha M/Gamma-6. The *Lr3a*-linked ISSR marker, $UBC840_{540}$, from the present study is the first PCR-based marker. The genetic association, however, is not very close.

Identification of markers flanking genomic region carrying *Sr22* in the chromosome arm 7AL of wheat was achieved. Although the linkage of either cfa2019 or cfa2123 was not very close, these two markers flank *Sr22* distally and proximally (Fig.1), and therefore, would be useful in the detection of *Sr22* in segregating populations. Paull et al. (1994) reported linkage of RFLP markers with *Sr22*. On the basis of the RFLP distribution, they showed that at least 50% of the chromosome arm 7AS and 80% of the chromosome arm 7AL in 'Schomburgk' were of *Triticum boeoticum* origin. They reported a very low level of recombination among backcross-derivatives carrying *Sr22*; however, they identified several recombinants carrying *Sr22* on a highly reduced segment of *T. boeoticum*. In a mapping population derived from Courtot/Chinese Spring cross, markers cfa2123 and cfa2019 were mapped approximately 30 cM apart by French workers (Sourdille et al. 2005, http://wheat.pw.usda.gov/GG2/index.shtml). The lower genetic distance (11.2 cM) observed between these markers in this study may be due to the reduced rate absence of recombination between the *Sr22*-carrying chromosome 7A in 'Schomburgk' and normal chromosome 7A from 'Yarralinka'.

Markers reported in this study are PCR-based robust markers that are user-friendly and amenable for high throughput assays. The amplification of different-sized bands in eight *Sr22*-lacking genotypes to that amplified from 'Schomburgk' (Table 1) indicated the location of linked markers cfa2019 and cfa2123 on the *Sr22*-carrying *T. boeoticum* segment. The genotypes used for validation included *Agropyron*-derived genes *Sr24*/*Lr24*, *Triticum ventricosum*-derived genes *Lr37*/*Sr38*/*Yr17* and *Triticum speltoides*-derived gene *Lr28*. The markers gwm295 and gwm130 flanking leaf rust resistance gene *Lr34* at a distance same as reported in this study, could detect the presence of *Lr34* in a set of 28 Australian wheat genotypes (Rahman, Shariflou, Bariana and Sharp, unpublished). The concurrent use of markers cfa2019 and cfa2123 would predict the presence or absence of *Sr22* in breeding populations and hence would have a role in pyramiding stem rust resistance genes in new wheat cultivars.

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