ISSN 1479-2621
Plant Genetic Resources: Characterization and Utilization (2020) **18**(1); 11–18
doi:10.1017/S147926211900039X

Characterization of seedling and adult plant resistance to stripe rust in recombinant inbred lines derived from wheat landrace PI388222 × Avocet cross

Yesrab Aman[1]*, Fatima Khalid[1], Muzaffar Shaukat[1], Tariq Mahmood[1], Syed Wasim Hasan[2] and Javed Iqbal Mirza[3]

[1]*Department of Plant Sciences, Faculty of Biological Sciences, Quaid-i-Azam University, Islamabad- 45320, Pakistan,* [2]*Department of Plant Breeding and Genetics, College of Agriculture, University of Sargodha, Sargodha, Pakistan and* [3]*Crop Disease Research Institute (CDRI), Pakistan Agriculture Research Council, Murree, Pakistan*

Received 2 September 2019; Accepted 10 December 2019 – First published online 10 January 2020

Abstract

Stripe rust caused by *Puccinia striiformis* f. sp. *tritici* (*Pst*), is a devastating fungal disease of wheat (*Triticum aestivum* L.). The best economical technique for disease control is breeding for genetic resistance to stripe rust. To find resistance genes in landrace PI388222 from Pakistan, a segregating population was developed by a cross between PI388222 and susceptible Australian spring wheat line Avocet 'S'. The F2:4 seeds were harvested and seeds were planted in the greenhouse of Washington State University Pullman, to grow F4:5 recombinant inbred lines (RIL). A variable set of seedling reactions were noted when a set of 136 F5 and parental lines were screened with four *Puccinia striiformis f.* sp. *tritici* races (PSTv-37, PSTv-40, PSTv-4 and PSTv-51). The great proportion of RILs showed resistant reaction displayed by the RILs was against PSTv-40, for which 85% of the RILs showed resistant reaction, while less resistance to the race PSTv-37 was detected against which the resistance was for only 49% of the RILs. The RIL population was further evaluated at two locations; Palouse Conservation Field Station (PCFS) and Mount Vernon (MV). In MV field, 76% of RILs displayed resistant reaction while 15% of RILs exhibited moderate reaction. About 53% of RILs exhibited resistant reaction to four *P. tritici* races that were used in glasshouse screening and they were also resistant in field environments at PCFS and MV. This study demonstrates that landrace comprises partial resistance in the range of resistant to moderately resistant lines.

Keywords: disease pressure, genetic resistance, landrace, races, susceptible

Introduction

In various developing countries, wheat is an essential crop equally in consumption and production. On more than 200 million hectares of area, the wheat is cultivated and the total production of wheat is about 733 million tons every year (FAO, 2015). Since the world population is increasing fast and predictable to touch over 9 billion in 2050 (Edmeades *et al.*, 2010), the production of more wheat is likely to become a great urgency (Wise, 2013).

Wheat production is influenced by the stripe, stem and leaf rusts. Among these, stripe rust (caused by *Puccinia striiformis* Westend f. sp. *tritici* Erikss) is specified by high frequency, a wide area of incidence and large economic damages is one of the most predominant wheat diseases, responsible for great production losses globally (Chen *et al.*, 2014). Presently, about 88% of the worldwide wheat production is prone to wheat stripe rust, responsible for worldwide damages

*Corresponding author. E-mail: yesrabqau07@gmail.com

of more than 5 million tons of wheat (Beddow *et al.*, 2015).

Stripe rust resistance is generally characterized as all-stage resistance (ASR) and adult-plant resistance (APR) (Chen, 2005). Among these two, ASR is shown in all plant growth steps and might be identified in seedlings. ASR resistance is usually ideal in breeding for the reason that the specific genes give high levels of resistance. This type of resistance is exposed more to the evolution of pathogen when used individually in cultivars (Chen *et al.*, 2010). On the other hand, APR normally gives defence against a wider range of races and inclines to be durable (Niks *et al.*, 2015). Until now in wheat, more than 80 yellow rust (also known as stripe rust) resistance (*Yr*) genes have been designated, together with the newly mapped *Yr79* (Feng *et al.*, 2018) and *Yr80* (Nsabiyera *et al.*, 2018). Though these *Yr* genes have been found in various wheat accessions, the seedling resistance gene's race specificity confines their effectiveness against pathotypes. In contrast, APR is commonly regarded to be durable, but APR genes denote a smaller number of known resistance genes (Kankwatsa *et al.*, 2017). Bux *et al.* (2012) found Pakistan landraces with high-temperature adult plant resistance (HTAP) resistance. The accessions having HTAP resistance worked as new germplasm for breeding resistant cultivars for wheat-growing areas of Pakistan such as southern Sindh and Punjab, where high-temperature climates are appropriate for the presence of such kind of resistance against stripe rust.

The use of cultivars using single-gene resistance (race-specific resistance) allows selection of mutations on a single locus. Because of selection pressure, novel virulent races of fungus arise, therefore, the utilization of mixtures of resistance genes has been proposed as the finest way for genetic control of stripe as well as other rusts. Slow rusting provides more durable resistance against stripe rust (Venkata *et al.*, 2008). The current study was carried out to characterize the recombinant inbred line (RIL) population developed from a landrace originated from Pakistan for rust resistance. The slow rusting or APR mechanism in the landrace was characterized at the phenotypic level to demonstrate the usefulness and inheritance of putatively new rust resistance gene.

Materials and methods

Plant material

A total of 25 landraces was selected randomly on the basis of field reactions 2014–2015, the details of 25 landraces showing the collected sites from different areas of Pakistan is shown in Table 1. Under glasshouse conditions, a set of 25 landraces was screened against stripe rust races 574730, 574212, 574232, 574216, 410202, 430220 and 476232 at seedling stage (Table 2). A mapping population was developed by a cross between landrace PI388222 and susceptible Australian spring wheat line, Avocet 'S'. Landrace PI388222 showed moderately resistant to resistant reaction to stripe rust in field conditions, so it was taken as a resistant parent (female) and Avocet 'S' was selected as a susceptible parent (male). The seed of both parents was kindly provided by USDA small grain collection Aberdeen, Idaho, USA and conserved at CDRI Murree seed collection. A total of 136 lines were used for greenhouse and field stripe rust phenotyping.

The F1 produced were sown separately in small pots under glasshouse conditions at Crop Disease Research Institute (CDRI) Murree. The F2:4 families were developed in the field of National Agricultural Research Centre (NARC), Pakistan, from single seed descent from F1plants. The F2:4 families were sown and assessed for stripe rust resistance to natural inoculum in 2016 at NARC (Pakistan). From the F2:4 seeds collected from the field, single seeds were planted in the greenhouse of Washington State University Pullman, WA to develop F4:5 RIL. The F4:5 lines were used for additional phenotyping.

Phenotyping in the greenhouse

Seedling test

The F2 and F3 of the population (PI388222 × Avocet 'S') were screened for stripe rust resistance at the seedling stage. The seedling screening was conducted in greenhouse conditions in CDRI Murree. Murree is a hilly resort town, situated in the Galyat region of the Pir Panjal Range, in the District Rawalpindi of Punjab, Pakistan. It makes the borders of the Islamabad-Rawalpindi metropolitan zone and is nearly 30 km (19 mi) northeast of Islamabad. Nearly five seeds of each line were sown in pots (7×7 cm^2). The inoculums which are conserved at −80°C temperature were taken from the freezer and rapidly dipped in water bath, the temperature of which was fixed at 65°C for 15 min for breaking the dormancy of spores. The inoculums suspension was made in the mixture of petroleum ether and paraffin oil (80:20 v/v) and sprayed on 14 d old plants with the help of fine atomizer at two leaf period (Rizwan *et al.*, 2010). Prior to shifting the plants to growth room whose temperature was fixed at 10°C, the plants were exposed in air for 2 hours and at comparative moisture of 100. A 12-hour period was provided to plants in a growth room, after this period they were moved to glasshouse at 18–20°C temperature. Three weeks after inoculation, infection types (ITs) were noted by the help of 0–9 scale (Line and Qayoum, 1992) when higher infection was exhibited by Morocco (susceptible check). Plants displaying

https://doi.org/10.1017/S147926211900039X Published online by Cambridge University Press

Table 1. List of 25 landraces collected from different areas of Pakistan and evaluated for stripe rust resistance in this study. PI refers to plant identification number at National Small Grain Genebank, Aberdeen, Idaho, USA

PI No.	ACP	Country	Province
388082	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388092	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388093	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388094	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388095	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388096	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388097	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388102	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388105	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388106	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388108	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388122	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388123	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388124	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388151	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388158	*Triticum aestivum* subsp. aestivum	Pakistan	Punjab
388172	*Triticum aestivum* subsp. aestivum	Pakistan	North-West Frontier (KPK)
388194	*Triticum aestivum* subsp. aestivum	Pakistan	North-West Frontier (KPK)
388213	*Triticum aestivum* subsp. aestivum	Pakistan	Sind
388221	*Triticum aestivum* subsp. aestivum	Pakistan	Sind
388222	*Triticum aestivum* subsp. aestivum	Pakistan	Sind
388224	*Triticum aestivum* subsp. aestivum	Pakistan	Sind
478129	*Triticum aestivum* subsp. aestivum	Pakistan	Baluchistan
478135	*Triticum aestivum* subsp. aestivum	Pakistan	Baluchistan
572784	*Triticum aestivum* subsp. aestivum	Pakistan	Northern Areas

infection type of 0–4 were measured as resistant, whereas plants revealing ITs 5–6 were categorized as intermediate resistance, and plants displaying infection type of 7–9 were measured as susceptible. The seedling test was done on F2 stage for the race (574212) and at F3 the races used were 574212, 476232, 430220 and 574232. The seedling test done on F5 stage was against races (PSTv-37, PSTv-40, PSTv-4, PSTv-51) in the glasshouse of Washington State University, Pullman USA. Seedling screening process in WSU, Pullman USA was dissimilar. It comprised the following steps: On the leaves of Avocet 'S' (susceptible spring wheat line), fresh urediniospores were produced as specified by Chen *et al.* (1995). After about 16 d of inoculation, the collection of fresh urediniospores was done three to five times for enough quantity. Collected urediniospores were desiccated in a desiccator at 4°C and utilized for inoculation for 1-month period. Sowing of RIL (F5:6) and parental seeds was done in 72-well trays having five seeds/ line and developed in the greenhouse. Separate inoculation was done for seedlings at two-leaf stage (14 d after planting) and adult-plants at booting stage with urediniospores of every single race mixed with talc nearly 1:20 ratio (Line and Qayoum, 1992). The seedling incubation was done in a dark dew chamber, inoculated seedlings were incubated at a temperature of 10°C for around 24 h and shifted to a growth chamber having a diurnal temperature cycle gradually varying between 4°C at 2:00 am and 20°C at 2:00 pm and 8 h dark/16 h light as designated by Chen and Line. On inoculated seedlings, ITs were noted at 18–21 d after inoculation depending on the 0–9 IT scale for stripe rust.

Field screening for populations (PI 388222 × Avocet 'S') on F5 stage

Field screening of the population was conducted in USA at two locations i.e. Palouse Conservation Field Station (PCFS) field and Mount Vernon (MV) during the wheat growing season of the year 2017. Inoculations of border rows at

https://doi.org/10.1017/S147926211900039X Published online by Cambridge University Press

Table 2. Disease score of 25 wheat landraces against stripe rust resistance at seedling stage against seven *P. striiformis* races

PI No.	574730	574212	574232	574216	410202	430220	476232
388082	4	3	4	4	6	4	3
388092	4	4	7	6	5	4	5
388093	6	5	6	6	6	4	5
388094	4	3	4	6	5	3	3
388095	6	5	3	4	4	4	4
388096	7	5	3	6	6	5	5
388097	4	5	6	6	6	5	3
388102	5	5	5	6	6	3	3
388105	6	4	6	5	5	4	5
388106	6	4	7	5	6	3	4
388108	6	4	4	4	4	3	4
388122	5	4	5	5	4	3	4
388123	6	5	3	5	4	6	4
388124	7	5	3	6	5	5	4
388151	7	5	5	6	6	4	4
388158	5	4	5	7	3	4	5
388172	6	6	5	7	6	6	6
388194	4	3	6	7	6	4	3
388213	4	4	6	7	6	4	5
388221	4	4	6	7	6	3	3
388222	4	4	5	7	4	3	4
388224	4	5	6	7	5	5	6
478129	5	5	9	6	6	4	3
478135	5	5	6	6	6	3	3
572784	6	5	3	7	3	5	3

Pullman were done on 15 June 2017 with the race PSTv-37. Border rows were planted with Avocet 'Susceptible' (Avocet 'S'). All spring wheat plots were planted in PCFS on 10 May 2017. The following day (11 May), 100-pounds/acre fertilizer (urea, 46-0-0) was applied. In MV, the populations were exposed to natural infection. For stripe rust resistance, RILs and parental lines were screened in the year 2017. Seed sowing was carried out in rows of 0.5 m set apart at 30 cm. In 2017, three replications were sown in randomized complete block design (RCBD) at both locations. The Avocet 'S' was planted around the plots as spreader rows and was planted after each 20th row to improve even rust development all over the field. For the F5 RIL population, DS was changed to AUDPC values according to Chen *et al.* (1995). For the parents and every RIL of population, AUDPC was measured $'\text{AUDPC} = \sum_i [(x_i + x_i + 1)/2]t_i'$. For each RIL and parent, relative AUDPC (rAUDPC) values were calculated as a % of mean AUDPC value of the susceptible parent, Avocet 'S' (Lin and Chen, 2007).

Statistical analysis

For the assessment of the goodness of fit of 'observed to expected segregation ratios', χ^2 tests were used to assess the number of resistance genes adapting resistance.

Results

Glasshouse results of PI388222 × Avocet 'S' at F5 stage

The response of the 25 landraces against Pakistani PSTv races is shown in Fig. 1 and the avirulence/virulence formula of the races is shown in Table 3. Landrace PI388222 gave infection type 4 with race 574212, infection type 5 with 574232, infection type 3 with race 430220 and infection type 4 with 476232. The response of Landrace PI388222 and near-isogenic lines to selected *Pst* races is shown in Table 4. Among the 7 PSTv races, the maximum

https://doi.org/10.1017/S147926211900039X Published online by Cambridge University Press

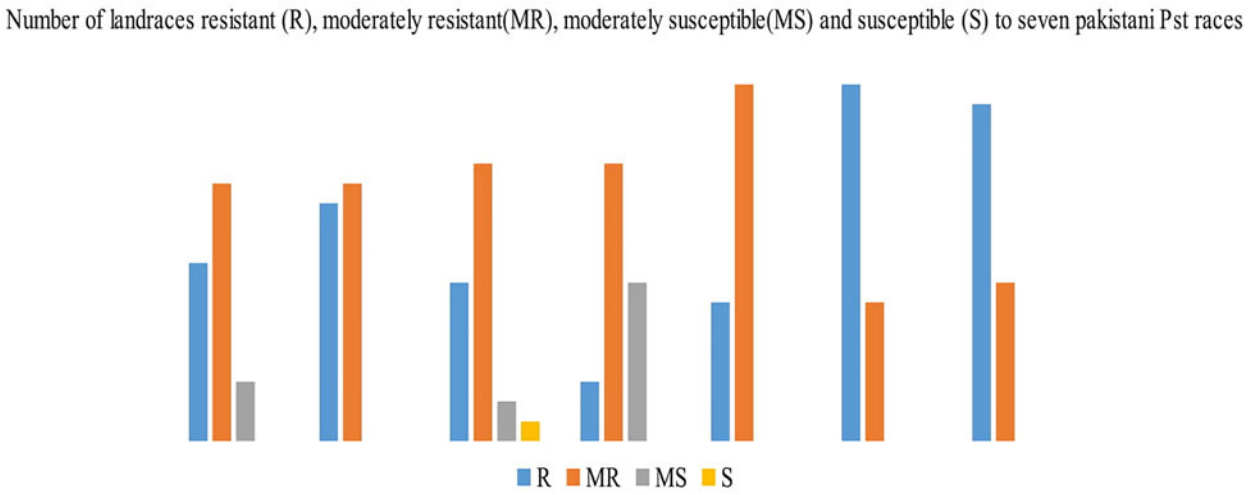

Fig. 1. Reaction of landraces to Pakistani *Pst* races 574730, 574212, 574232, 574216, 410202, 430220 and 476232.

Table 3. Avirulence/virulence formula for stripe rust

PSTv races	Avirulence/Virulence
574730	5/,10,15,SP,Tr1,EXP2,Tye/1,6,7,8,9,17,24,27,32,4344
574212	5,10,15,24, 32, 44, SP,Tr1, Tye/ 1,6, 7,8,9,17,27,43, EXP2
574232	5,10,15,24,32,SP,Tr1,Tye2/1,6,7,8,9,17,27,43,44,EXP2
574216	5,10,15,24,32,44,SP,EXP2,Tye/1,6,7,8,9,17,27,43,Tr1
410202	1,5,8,9,10,15,17,24,32,43,44,SP,Tr1,Tye/6,7,27,EXP2
430220	1,5,9,10,15,17,24,32,43,SP,Tr1,EXP2,Tye/6,7,8,2744
476232	1,5,10,24,32,SP,Tr1,Tye/6,7,8,9,15,17,27,43,44,EXP2

Table 4. Response of Landrace PI388222 and near-isogenic lines to selected Pst races

Line	LIT[a]	Race 574212	Race 574232	Race 430220	Race 476232
PI388222	–	4	5	3	4
Yr10	0–1	0	0	0	0
Yr15	0–1	0	0	0	9
Yr24	2–4	3	2	0	0
Yr44	2	8	8–9	7	6

LIT[a], Low Infection Type.

resistant response shown by the landraces was against the race 430220 (18R and 7MR and none of the landrace exhibited MS-S reaction), whereas the minimum resistant response of the landraces was shown against the PSTv race 574216 (3R, 14MR and 8MS) as shown in online Supplementary Table S1. A variable set of seedling reactions were detected when a set of 136 RILs together with parental lines were screened with *Puccinia striiformis f.* sp. *tritici* races PSTv-37, PSTv-40, PSTv-4 and PSTv-51 for identification of the putative major gene. The virulence/avirulence formulae for PSTv races is shown in online Supplementary Table S2. The seedling response of RIL population to the PSTv-37 identified 67 (49%) RILs were resistant, 57 (42%) were moderately resistant and 12 RILs (9%) were susceptible and the response of parents was 3 and 8 for PI38822 and Avocet 'S', respectively (Fig. 2). The seedling response of RIL population to the PSTv-40 revealed that out of 136 RILs, 116 (85%) were resistant, 19

https://doi.org/10.1017/S147926211900039X Published online by Cambridge University Press

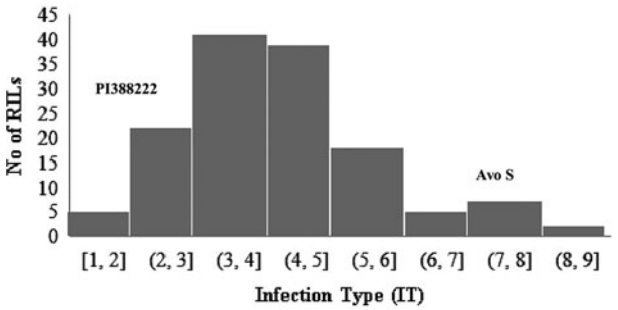

Fig. 2. Frequency distribution of infection types in F5 population of the cross PI388222 × Avocet 'S' when screened with PSTv-37 at F5.

(14%) were moderately resistant, and only one (1%) RIL was susceptible (online Supplementary Fig. S1). The PI38822 response was 3 and scored as moderately resistant, while Avocet 'S' response 8 and scored as susceptible. The score of all RILs against PSTv-40 was R/MR or less than 5 because the selections were made on the basis of their reaction to *Pst* race 574212 and were raised to F5. Then the material was tested in Pullman, USA, where it was screened against different stripe rust race. The selection process would have skipped lines susceptible to US stripe rust race (PSTv-40), as the race was not available during the selection process. The seedling response of RILs population to the PSTv-4 showed that 102 (75%) RILs were resistant, 26 (19%) were moderately resistant and 8 (6%) were susceptible (PI388222 response was 3 and response shown by Avocet 'S' was 9) (online Supplementary Fig. S2). The seedling response of RIL population (PI38822 response was 3 and Avocet 'S' was 9) at F5 to the PSTv-51 revealed that out of 136 RILs 114 were resistant, 18 RILs were moderately resistant and 4 RILs were susceptible (online Supplementary Fig. S3). The maximum resistant response shown by the RILs was against PSTv-40 against which 85% of the RILs were resistant while the low resistance to the race PSTv-37 was noticed against which 49% of the RILs were resistant.

Adult plant resistance in PI388222 × Avocet 'S' RILs

Frequency distribution of mean IT and DS in PCFS and MV are shown in online Supplementary Figs S4–S7. Higher disease pressure was observed at both sites and maximum rust severity up to 100% was observed in susceptible check 'Morocco'. The FRS of the RIL population and the parents (PI388222 and Avocet 'S') is described in online Supplementary Table S3. In RILs population, 80% of the RILs were resistant in PCFS, 12% showed moderate reaction and 8% showed susceptible reaction. The disease severity was higher in MV, where 76% of RILs were resistant, 15% were moderately resistant, 9% were susceptible. Out of 136 RILs, 53% of the RILs revealed resistant reaction towards four *Pst* races that are used in glasshouse screening and were also resistant in field environments at PCFS and MV.

The rAUDPC was used for identification of slow rusting or durable resistance germplasm. At PCFS, 42 (31%) RILs were resistant with rAUDPC 0-10, while 70 (51%) RILs had rAUDPC values of >30 and were intermediately resistant, whereas 24 (18%) RILs had rAUDPC of 30-90 and were susceptible. The MV field results showed that only 1 RIL was resistant, 12 RILs (11.5%) were intermediately resistant, and 91 RILs were (87.5%) were susceptible based on rAUDPC (online Supplementary Table S3).

Discussion

The genetic resistance is a cost-effective technique for the development of resistant varieties. One of the best strategies for finding new resistant sources and the discovery of durable rust-resistant genes is the characterization of the primary gene pool of wheat (Mujeeb-Kazi *et al.*, 2013). Primary gene pool includes landraces, wild and primarily domesticated wheat relatives. Landraces are normally considered to have good diversity for biotic and abiotic stress tolerances (Zeven, 1998). Wheat landraces are favourable source of new genes of rust resistance for developing novel and diverse resistant germplasm (Sthapit *et al.*, 2014).

The set of 25 wheat landraces showed a high resistant reaction in the field which indicated that these landraces may have some important resistant genes. The response of a selected wheat landrace PI38822 against stripe rust was moderately resistant to resistant in the field, which indicated the presence of slow rusting genes, and was selected for further study.

Previously, a wheat landrace collected in Pakistan, AUS27858, from the Watkins collection showed high levels of resistance against Australian pathotypes of Pst. An analysis was carried out on AUS27858/Westonia F3 population showed that AUS27858 possessed two stripe rust resistance genes that were temporarily designated as YrAW1 and YrAW2 (Randhawa *et al.*, 2014). Randhawa *et al.* (2014) further developed an F6 RIL population and identified that YrAW1 is located on the long arm of chromosome 4A, and officially designated as Yr51 (https://maswheat.ucdavis.edu/protocols/Yr51/index.htm). Segregation of resistance identified in segregating population of PI388222 × Avocet 'S' in F2s and F3s revealed a good fit to the expected segregation ratio (15:1) for two genes, except PSTv-51 which indicated the presence of an extra gene against this race. Previously, Chhuneja *et al.* (2008) carried out an experiment on RIL population produced from the cross of *T. monococcum* (acc, PAU 14087) and *T. boeoticum* (acc, pau5088) and identified the presence of two genes for stripe rust resistance.

https://doi.org/10.1017/S147926211900039X Published online by Cambridge University Press

A variable set of seedling reactions were observed when a set of 136 F2:F5 RILs of the cross PI388222 × Avocet 'S' were screened with races PSTv -37, PSTv -40, PSTv -4 and PSTv -51 for the presence of major genes. The *Yr6*, *Yr9 and Yr27* were virulence genes against all the races mentioned above, excluding the chance of the existence in the landrace (Wan *et al*., 2016). Depending on avirulence pattern of pathotype, it is likely that one or combination of the stripe rust-resistant genes *Yr10*, *Yr15, Yr24/Yr26*, *Yr44* could be present in PI388222. The *Yr10* gene which normally gives low infection type with most of the races was identified in *T. spelta* (Bariana *et al*., 2002). Therefore, its presence in PI388222 could be ruled out. Similarly, *Yr15* was identified in *T. dicoccoides* (Gerechter-Amital and Grama, 1974), therefore it is likely to be absent in the landrace PI388222. *Yr24* also known as *Yr26* is identified in the synthetic hexaploid wheat contributed by the wild accessions of *Ae. tauschii* (McIntosh and Lagudah, 2000). Therefore, it is likely that landraces, PI388222, does not contain *Yr24/Yr26* gene. *Yr44* is identified in cultivar Zak (released by Washington State University in 2000) (Cheng and Chen, 2010). Hence, the landrace PI388222 most likely does not contain *Yr44*, and genes present in this landrace could be new.

In earlier studies, field assessment of quantitative stripe rust resistance was used to classify RIL populations for adult plant resistance (Safavi, 2012). According to the results for field assessment, RILs showed the possibility of APR in the contender landrace together with the chance of major genes. Ali *et al*. (2009) and Safavi (2012) did field assessment for grouping of lines, which are used for quantitative resistance to stripe rust. Lines that displayed resistance reaction at both stages might more possibly have the major gene or mixture of major genes-based resistance effective for all utilized virulences. Because slow rusting resistance is durable, the study of the genetic nature of such type and its introduction to breeding material is striking for breeders (Zhang *et al*., 2003). On the basis of rAUDPC values, accessions were classified to two diverse groups: accessions showing slow rusting behaviours are likely to have genes that give partial resistance which is durable compared to the other resistance types (Parlevliet, 1988). The 31% of the RIL population at PCFS and 1% of RIL population at MV field showed lower rAUDPC and could have slow rusting genes.

Previously, cloning of the wheat multipathogen APR genes Lr34/Yr18/Sr57/Pm38 and Lr67/Yr46/Sr55/Pm46 shown that a single gene can give resistance to multiple pathogens (Moore *et al*., 2015). It is shown that these genes are involved in slow rusting at the adult plant stage and provide durable resistance against multiple fungal pathogens. Similarly, another gene Yr71 provides APR gene and can be combined with other major or minor stripe rust resistance genes to achieve low rust severity and durability (Bariana *et al*., 2016). Durable resistance should be measured by investigators because the rust pathogens are capable of changing their genotypes without complications through migration, selection consequence of resistant cultivars on pathogens and mutation (Hovmøller, 2001). Several researchers similarly verified the presence of variable slow rusting levels in wheat breeding resources (Shah *et al*., 2014). Formerly, Ali *et al*. (2007) assessed wheat breeding material from Pakistan to evaluate their partial resistance regarding slow rusting behaviour. Many investigators employed FRS as a feature to measure slow rusting behaviour of wheat lines (Shah *et al*., 2014).

Conclusion

The partial resistance identified in landrace PI388222 is due to the two genes or interaction between two genes (except for PSTv-51 which shows segregation of three genes). Based on the virulence pattern of *Pst* races, this landrace could have putatively new slow rusting genes. Further characterization of stripe rust resistance and mapping of resistance loci in this landrace will be valuable for developing new wheat cultivars for sustainable control of stripe rust.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S147926211900039X.

Acknowledgements

The authors are thankful to Dr Awais Rasheed for comments on the manuscript. The authors are grateful to Crop Disease Research Institute (CDRI) Murree and National Agricultural Research Centre (NARC) Islamabad, Pakistan for support of the studies embodied in the paper.

References

Ali S, Shah SJA and Ibrahim M (2007) Assessment of wheat breeding lines for slow yellow rusting (*Puccinia striiformis* West. tritici). *Pakistan Journal of Biological Sciences* 10: 3440–3444.

Ali S, Shah SJA, Raman IKH, Maqbool K and Ullah W (2009) Partial resistance to yellow rust in introduced winter wheat germplasm at the north of Pakistan. *Australian Journal of Crop Science* 3: 37.

Bariana HS, Brown GN, Ahmed NU, Khatkar S, Conner RL, Wellings CR, Haley S, Sharpe PJ and Laroche A (2002) Characterisation of *Triticum vavilovii*-derived stripe rust resistance using genetic, cytogenetic and molecular analyses and its marker-assisted selection. *Theoretical and Applied Genetics* 104: 315–320.

Bariana HS, Forrest K, Qureshi N, Miah H, Hayden M and Bansal U (2016) Adult plant stripe rust resistance gene Yr71 maps close to Lr24 in chromosome 3D of common wheat. *Molecular Breeding* 36: 98.

Beddow JM, Pardey PG, Chai Y, Hurley TM, Kriticos DJ, Braun HJ, Park RF, Cuddy WS and Yonow T (2015) Research investment implications of shifts in the global geography of wheat stripe rust. *Nature Plants* 1: 15132.

Bux H, Ashraf M and Chen X (2012) Expression of high-temperature adult-plant (HTAP) resistance against stripe rust (*Puccinia striiformis f.* sp. *tritici*) in Pakistan wheat landraces. *Canadian Journal of Plant Pathology* 34: 68–74.

Chen XM (2005) Epidemiology and control of stripe rust [*Puccinia striiformis f. sp. tritici*] on wheat. *Canadian Journal of Plant Pathology* 27: 314–337.

Chen XM, Line RF and Jones SS (1995) Chromosomal location of genes for resistance to *Puccinia striiformis* in winter wheat cultivars Heines VII, Clement, Moro, Tyee, Tres, and Daws. *Phytopathology* 85: 1362–1367.

Chen X, Penman L, Wan A and Cheng P (2010) Virulence races of *Puccinia striiformis f.* sp. *tritici* in 2006 and 2007 and development of wheat stripe rust and distributions, dynamics, and evolutionary relationships of races from 2000 to 2007 in the United States. *Canadian Journal of Plant Pathology* 32: 315–333.

Chen W, Wellings C, Chen X, Kang Z and Liu T (2014) Wheat stripe (yellow) rust caused by *Puccinia striiformis f.* sp. *tritici*. *Molecular Plant Pathology* 15: 433–446.

Cheng P and Chen XM (2010) Molecular mapping of a gene for stripe rust resistance in spring wheat cultivar IDO377s. *Theoretical and Applied Genetics* 121: 195–204.

Chhuneja P, Kaur S, Garg T, Ghai M, Kaur S, Prashar M, Bains NS, Goel RK, Keller B, Dhaliwal HS and Singh K (2008) Mapping of adult plant stripe rust resistance genes in diploid A genome wheat species and their transfer to bread wheat. *Theoretical and Applied Genetics* 116: 313–324.

Edmeades G, Fischer RA and Byerlee D (2010) Can we feed the world in 2050. In: Proceedings of the New Zealand Grassland Association, November 2010, Vol. 72, pp. 35–42.

FAO (2015) FAO Statistical Pocketbook: World Food and Agriculture. Rome, Italy: FAO

Feng J, Wang M, See DR, Chao S, Zheng Y and Chen X (2018) Characterization of novel gene Yr79 and four additional quantitative trait loci for all-stage and high-temperature adult-plant resistance to stripe rust in spring wheat PI 182103. *Phytopathology* 108: 737–747.

Gerechter-Amital ZK and Grama A (1974) Inheritance of resistance to stripe rust (*Puccinia striformis*) in crosses between wild emmer (*Triticum dicoccoides*) and cultivated tetraploid and hexaploid wheats. I. *Triticum durum*. *Euphytica* 23: 387–392.

Hovmøller MS (2001) Disease severity and pathotype dynamics of *Puccinia striiformis f.* sp. *tritici* in Denmark. *Plant Pathology* 50: 181–189. https://maswheat.ucdavis.edu/protocols/Yr51/index.htm.

Kankwatsa P, Singh D, Thomson PC, Babiker EM, Bonman JM, Newcomb M and Park RF (2017) Characterization and genome-wide association mapping of resistance to leaf rust, stem rust and stripe rust in a geographically diverse collection of spring wheat landraces. *Molecular Breeding* 37: 113.

Lin F and Chen XM (2007) Genetics and molecular mapping of genes for race-specific all-stage resistance and non-race-specific high-temperature adult-plant resistance to stripe rust in spring wheat cultivar Alpowa. *Theoretical and Applied Genetics* 114: 1277–1287.

Line RF and Qayoum A (1992) Virulence, aggressiveness, evolution and distribution of races of *Puccinia striiformis* (the cause of stripe rust of wheat) in North America, 1968–87. *Technical Bulletin (USA)*.

McIntosh RA and Lagudah ES (2000) Cytogenetical studies in wheat. XVIII. Gene Yr24 for resistance to stripe rust. *Plant Breeding* 119: 81–93.

Moore JW, Herrera-Foessel S, Lan C, Schnippenkoetter W, Ayliffe M, Huerta-Espino J, Lilemmo M, Viccars L, Milne R, Peiryannan S, Spielmeyer W, Talbot M, Bariana H, Patrick JW, Dodds P, Singh R and Lagudah E (2015) A recently evolved hexose transporter variant confers resistance to multiple pathogens in wheat. *Nature Genetics* 47: 1494.

Mujeeb-Kazi A, Kazi AG, Dundas I, Rasheed A, Ogbonnaya F, Kishii M, Bonnet D, Wang RRC, Xu S, Chen P, Mahmood T, Bux H and Farrakh S (2013) Genetic diversity for wheat improvement as a conduit to food security. *Advances in Agronomy* 122: 179–257.

Niks RE, Qi X and Marcel TC (2015) Quantitative resistance to biotrophic filamentous plant pathogens: concepts, misconceptions, and mechanisms. *Annual Review of Phytopathology* 53: 445–470.

Nsabiyera V, Bariana HS, Qureshi N, Wong D, Hayden MJ and Bansal UK (2018) Characterisation and mapping of adult plant stripe rust resistance in wheat accession Aus27284. *Theoretical and Applied Genetics* 131: 1459–1467.

Parlevliet JE (1988) Strategies for the utilization of partial resistance for the control of cereal rusts. In: Breeding Strategies for Resistance to the Rusts of Wheat, El Batan, Mexico (Mexico), 29 June–1 July 1987. CIMMYT.

Randhawa M, Bansal U, Valárik M, Klocová B, Doležel J and Bariana H (2014) Molecular mapping of stripe rust resistance gene Yr51 in chromosome 4AL of wheat. *Theoretical and Applied Genetics* 127: 317–324.

Rizwan S, Iftikhar A, Kazi AM, Sahi GM, Mirza JI, Attiq-ur-Rehman and Ashraf M (2010) Virulence variation of *Puccinia Striiformis Westend*. *F.* sp. *tritici* In Pakistan. *Archives of Phytopathology and Plant Protection* 43: 875–882

Safavi SA (2012) Evaluation of slow rusting parameters in thirty-seven promising wheat lines to yellow rust. *Technical Journal of Engineering and Applied Sciences* 2: 324–329.

Shah SJA, Hussain S, Ahmad M and Ibrahim M (2014) Characterization of slow rusting resistance against *Puccinia Striiformis f.* sp. *tritici* in candidate and released bread wheat cultivars of Pakistan. *Journal of Plant Pathology & Microbiology* 5: 1.

Sthapit J, Newcomb M, Bonman JM, Chen X and See DR (2014) Genetic diversity for stripe rust resistance in wheat landraces and identification of accessions with resistance to stem rust and stripe rust. *Crop Science* 54: 2131–2139.

Venkata BP, Bansal UK, Singh RP, Park RF and Bariana HS (2008) Genetic analyses of durable adult plant resistance to stripe rust and leaf rust in CIMMYT wheat genotype 11IBWSN50. *International Journal of Plant Breeding* 2: 64–68.

Wan A, Chen X and Yuen J (2016) Races *of Puccinia Striiformis* f. sp. tritici in the United States in 2011 and 2012 and comparison with races in 2010. *Plant Disease* 100: 966–975.

Wise TA (2013) Can we feed the world in 2050. *A scoping paper to assess the evidence. Global Development and Environment Institute Working Paper (13-04)*.

Zeven AC (1998) Landraces: a review of definitions and classifications. *Euphytica* 104: 127–139.

Zhang YM, Jun-Yi G and Yong-Hua Y (2003) The EIM algorithm in the joint segregation analysis of quantitative traits. *Genetics Research* 81: 157–163.