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Documentation of multi-pathotype durable resistance in exotic wheat genotypes to deadly stripe and leaf rust diseases

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Abstract

Leaf and yellow rusts are considered as one of the most serious biotic constraints of wheat inflicting massive economic losses globally. Host resistance is the only efficient, economical, ecofriendly way of controlling the rust diseases. Characterization of diverse wheat materials is always of a paramount importance for identifying potential varietal material to effectively control rusts and insignificant yield losses. With this background, the present experiments were designed and carried out at Wheat Rusts Multiplication and Phenotyping Facility, Wheat Pathology Experiment Farm and National Phytotron Facility of ICAR-IARI, New Delhi, and ICAR-IIWBR, Regional Station, Flowerdale, Shimla, for two consecutive years 2018–2019 and 2019–2020. Multi-environment phenotyping and characterization of stripe and leaf rust resistance were performed at both seedling stage in temperature-controlled growth chamber/greenhouse and adult plant stage in field conditions. By applying the gene-matching technique using multi-pathotypes data, five *Yr* (*Yr*A, *Yr*2, *Yr*9, *Yr*18 and *Yr*27) and eight *Lr* (*Lr*1, *Lr*3, *Lr*10, *Lr*13, *Lr*19, *Lr*23, *Lr*26 and *Lr*34) genes in 98 exotic wheat genotypes (PG-Parent genetic pool, GS-Genomic selection genotype of CIMMYT-BISA, CIMCOG-CIMMYT Mexico core germplasm panel) were characterized singly or combinations with other vital genes. Adult plant slow rusting resistance was assessed through host response and different epidemiological parameters. All these promising rust-resistant genotypes at adult plant stage were susceptible at seedling stage to one or more pathotype(s), which indicated the presence of non-race-specific resistance gene(s). The lines identified could play pivotal role in the hybridization programs to enhance the resistance.

Keywords Wheat · Yellow rust · Brown rust · Durable resistance · Epidemiological parameters

Introduction

Several biotic stresses limit the yield of wheat crop from attaining desired levels of its production. Stripe or yellow rust (*Puccinia striiformis* f.sp. *tritici*) and leaf or brown rust (*Puccinia triticina*) is indeed a potential biotic restraint, damaging the crop and causing substantial economic losses worldwide (Ali et al. 2017; Kumar et al. 2020; Meyer et al. 2021). The stripe rust is continuing to be a serious threat and dominant factor limiting yield potential in wheat globally (Chen et al. 2014, 2020). Severe and extensive epidemics occur about once in every 10 years, and yield losses due to stripe rust have been estimated from 10–70%, while in severe epidemic losses can be as great as 100% (Chen 2005; Chen et al. 2020; Aggarwal et al. 2018; Bhardwaj et al. 2022).

A global yield loss of about 5.5 million tons per year was assessed due to wheat stripe rust (Beddow et al. 2015). In recent past, localized stripe rust epidemics with significant

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crop losses were reported from different major wheat-growing areas of the world, in addition to African and Central Asian regions (Ezzahiri et al. 2009; Rahmatov et al. 2012; Singh et al. 2016). In the past few years, increased incidences of stripe rust have been reported with greater reoccurrence (Wellings 2007; Hovmøller et al. 2008, 2016), which was mainly due to the higher and faster growth rates in the population of rust pathogens (Hovmøller and Justesen 2007), long-distance spore spreading (Zadoks 1961; Brown and Hovmøller 2002) and development of novel pathotypes (Rodriguez-Algaba et al. 2014).

Through the emergence of newer and more virulent rust races, the prevalent pathotypes are being substituted, which resulted in extensive and widespread epidemics in the current years (Rahmatov et al. 2017). Stripe rust remains a major biotic constraint for wheat production in Asia, menacing 43 million hectares of wheat area (Singh et al. 2004a). In India, stripe rust has gained importance in recent past especially in cooler parts and is a threat in 10 mha area under Northern parts (Prashar et al. 2015; Bhardwaj et al. 2019).

The leaf rust of wheat is also considered the most prevalent and widely distributed of the three rusts and has major economic importance worldwide causing significant losses (Huerta-Espino et al. 2011; Singh et al. 2014; Yan et al. 2021). The crop losses due to leaf rust are mainly because of their infection at flag leaf stage, which plays a significant role in the physiological process of grain formation and grain filling. In case of severe leaf rust infection on vulnerable wheat cultivars, the overall yield losses may be up to 30–70% (Ordonez et al. 2010). In India, leaf rust prevails more in all wheat-growing areas when temperature rises (15–25 °C) and its capability to spread in Indian conditions is duly documented, while stripe rust is favored by lower temperatures less than or around 15 °C and dominates in cooler parts (Bhardwaj et al. 2006, 2019).

Recently, five new *P. striiformis tritici* pathotypes, 46S117, 110S119, 238S119, 110S247 and 110S84, and three leaf rust pathotypes, 77–9 (121R60-1), 77–5 (121R63-1) and 104–2 (21R55), have been identified in India, which showed virulence on *Yr*11, *Yr*12 and *Yr*24 genes (Gangwar et al. 2016). Race 110S119 is considered the most dominant, aggressive and rapid population which builds ability (Gangwar et al. 2016; McIntosh et al. 1995; Yang et al. 2003; Bhardwaj et al. 2019).

Race-specific resistance is lost very rapidly due to development of new rust virulences especially, when a single *R*-gene-based cultivars are grown over large area (Wan and Chen 2012). Conversely, non-race-specific is mainly polygenic and effective at adult plant stage, and this type of resistance has often been described as slow rusting or partial resistance and typically is longer lasting and more durable than specific single-gene resistance (Singh et al. 2004b; Herrera-Foessel et al. 2011).

Of the 70 yellow rust resistance genes designated so far, only nine genes, *Yr*18, *Yr*29, *Yr*30, *Yr*36, *Yr*39, *Yr*46, *Yr*48, *Yr*49 and *Yr*52 are associated with non-race-specific/adult plant resistance (McIntosh et al. 2012). More than 100 genes and alleles of leaf rust resistance genes have been described (McIntosh et al. 2017). Majority of the designated *Lr* genes are effective at seedling stage (race-specific) and remain effective through the adult plant stage (race-specific APR). Among the race-specific genes, some genes, *Lr*12, *Lr*13, *Lr*21, *Lr*22, *Lr*35, *Lr*37, *Lr*48, *Lr*49, *Lr*74, *Lr*75 and *Lr*77, are race-specific APR genes. Only four *Lr* genes, *Lr*34, *Lr*46, *Lr*67 and *Lr*68, are reported to confer non-race-specific/adult plant resistance. Development of rust resistance in wheat has mostly been based on the use of race-specific resistance. However, short-lived nature of race-specific hypersensitive resistance has twisted the necessity to search for the more durable type of resistance.

Genetic resistance is the most effectual, dominant, economical and environmentally affable method to control wheat rusts and besides eliminate the uses of fungicides (Van der Plank 1963; Singh et al. 2005). Finding those new genes that provide durable resistance (adult plant/slow rusting) to rusts has been important to wheat scientist around the world. More emphasis is also given on deployment of resistance by combining both race-specific (major) and non-race-specific (minor) resistance as a more efficient and durable control strategy of wheat rusts (Singh et al. 2004b). Hence, to control rusts effectively, wheat genetic resources with diverse resistance are needed to explore. For that matter, characterization of wheat genotypes/germplasm lines for identification of such diverse resistances is of paramount importance. Considering the facts, present experiment was conducted with the aim to phenotype and characterize some of the exotic wheat genotypes/germplasm lines to find out potential new resistance sources to stripe and leaf rusts.

Materials and methods

The present experiments were designed and carried out at three multiple locations, Wheat Rusts Multiplication and Phenotyping Facility, Wheat Pathology Experiment Farm and National Phytotron Facility of ICAR-IARI, New Delhi, and ICAR-IIWBR, Regional Station, Flowerdale, Shimla, for two consecutive *rabi* seasons, 2018–2019 and 2019–2020. Geographically, the experimental farms at ICAR-IARI, New Delhi, are located at 28°40′23″North latitude and 77°13′27″East longitude with an altitude of 228.61 m above the mean sea level (MSL). The soil type is alluvial with clay loam texture and falls under semiarid, subtropical climatic conditions. This region is categorized under the Northern Western Plain Zone (NWPZ) of wheat-growing areas of the country. The weather details (maximum and minimum temperature, maximum and minimum relative humidity, rainfall, sunshine hours, evaporation and average wind speed) at both the experimental farm for the period of investigations are given in Supplementary Table 1.

Plant materials

The seeds of 98 different exotic wheat genotypes/germplasm lines (PG-Parent genetic pool, GS-Genomic selection genotypes and CIMCOG-CIMMYT Mexico core germplasm panel) were obtained from Borlaug Institute for South Asia (BISA), Ludhiana, Punjab, India. The cross/pedigree details of these exotic wheat materials are given in Supplementary Table 2. All these exotic wheat genotypes/germplasm lines were evaluated for resistance to stripe and leaf rusts at both seedling and adult plant stage to identify promising new sources of rust resistance.

Rust Pathotypes

Seven different pathotypes of *Puccinia striiformis tritici* (*Pst*) and 19 different pathotypes of *Puccinia triticina* (*Ptr*) representing all group of both rusts were used for seedling resistance tests (Table 1). The urediospores inoculum of the above pathotypes of *Pst* and *Ptr* was received from ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Regional Station, Flowerdale, Shimla, Himachal Pradesh, India. The urediospores inoculum of each pathotype of *Pst* and *Ptr* was increased separately on highly susceptible wheat cvs. A-9-30-1 (for *Pst*) and Agra Local (for *Ptr*) following standard protocols (Joshi et al. 1988).

Seedling rust resistance tests and characterization of rust resistance gene(s)

All the 98 exotic wheat genotypes/germplasm lines were evaluated for rust resistance at seedling stage against different pathotypes of *Pst* and *Ptr* in temperature-controlled growth chamber/greenhouse at Division of Plant Pathology, ICAR-Indian Agricultural Research Institute (IARI), New Delhi, India, and ICAR-IIWBR, Regional Station, Flowerdale, Shimla, Himachal Pradesh, India. The seedlings of each genotype were raised in aluminum trays (11 × 4 × 3 inch) containing a mixture of fine loam soil and farm yard manure (3:1 ratio) and 5gm NPK (12:32:16 ratio) that had been autoclaved at 60 °C temperature for 1 h. About 4–5 seeds were grown for each genotype. Together with the tested genotypes, proper checks including two highly susceptible cultivars and line with known rust resistance genes/NILs/differentials with adult plant (APR) effect and known rust resistance genes were also grown and tested. The spore-proof greenhouse chambers maintained at 25–30 °C temperature, 50–70% relative humidity and 12 h daylight were used to raise the seedlings. A one-week-old seedlings with wholly expanded primary leaves were inoculated uniformly by using a hand glass atomizer that contained 10–15 mg uredospores of specific pathotypes of *Pst* and *Ptr* duly suspended in 2 ml light grade mineral oil (Soltrol 170)® (Chevron Phillips Chemicals Asia Pvt. Ltd., Singapore). Suspension containing uredospores in mineral oil was permitted to disperse for 30 min. Seedlings were then sprayed with a fine mist of water and placed for in dew chamber 48 h for incubation maintained at 15 ± 2 °C temperature for stripe rust and 20 ± 2 °C temperature for leaf rust, 100% relative humidity and 12 h daylight (Bhardwaj et al. 2010b). Afterward, seedlings were transferred to greenhouse and kept grown at 16 ± 2 °C temperature for stripe rust and 22 ± 2 °C temperature for leaf rust in relative humidity of 80–90%, and illumination at about 15,000 lx for 12 h. Seedling infection types (ITs) on the tested genotypes were scored 14 days after inoculation according to scale based on Stakman et al. (1962), with suitable modifications (Nayar et al. 1997; Bhardwaj et al. 2010b). Where needed, tests were repeated twice to clarify ambiguous results.

The presence of stripe and leaf rust resistance genes (*Yr* and *Lr* genes) was assumed by applying gene-matching technique using multi-pathotype data (Browder 1973). A high IT on test line showed that the genotype did not possess a resistance gene(s) for which existing pathotype was avirulent. Additional information, such as the genetic linkage between the different resistance genes, characteristic infection types, pedigree/cross of the wheat genotypes and morphological marker were also taken into consideration to infer the presence of some of the resistance genes. The presence of *Yr*9 gene was postulated through susceptibility to *Pst* pathotype 46S119 and 78S84, which are virulent on *Yr*9, resistance to

Table 1 Pathotypes, susceptible check and host differentials used for leaf and yellow rusts against exotic wheat genotypes

S. No	Disease type	Pathotypes	Host differentials	Susceptible check
1	Leaf rust	12–3, 12–512-7, 77, 77–1, 77–2, 77–5, 77–7, 77–8, 77–9, 77–10, 77A-1, 104–2, 106, 107–1, 108–1, 162–1, 162–2, 162A	Malakoff *Lr*1, Democrat *Lr*3, Tc* *Lr*10, Tc* *Lr*13, *Lr*19, IWP 94 *Lr*23 +, Tc* *Lr*23, *Lr*24, Benno *Lr*26, *Lr*34	Local Red, Agra Local
2	Yellow rust	14S64, K(47S102), P(46S102), T(47S103), 46S119, 110S119, 78S84, 7S0, 79S68, 110S84, 238S119	Tc* *Yr*9, Tc* *Yr*18, Sonalika (*Yr*2 + *Yr*A +), Kalyansona (*Yr*2 +)	Local Red, A-9–30-1

other pathotypes confirmed by linkage with *Lr*26/*Sr*31. The presence of *Yr*18/*Lr*34, APR genes, was inferred on the basis of their genetic association with the morphological marker (leaf tip necrosis and broken stripes in case of yellow rust) (Singh 1992; Rubiales and Niks 1995; Nayar et al. 1999). *Yr*2 gene was assumed through infection type matrices. This gene is susceptible to all these pathotypes except 13(67S8). The existence of leaf rust resistance genes *Lr*1*, Lr*10*, Lr*13*, Lr*23*, Lr*26 and *Lr*34 was assumed through infection type matrices by gene-matching techniques using multi-pathotype data (Browder 1973), and by morphological marker, leaf tip necrosis. *Lr*34 was postulated through morphological marker, leaf tip necrosis. The presence of gene *Lr*1 was postulated through avirulence of 12 groups of pathotypes on this gene. *Lr*10 gene is effective against the pathotypes 12–5, 16–1 and 77 and susceptible with other pathotype tested. *Lr*13 gene expresses resistance to pathotypes 12–2, 16–1 and 77. *Lr*23 produces resistance infection type with the pathotypes 16–1 and 77, while susceptible with the other pathotypes tested. Likewise, pathotypes 12–2, 16–1, 77 and 77–2 produce immune response on *Lr*26 gene, while other pathotypes tested are virulent to this gene (Bhardwaj et al. 2010b).

Adult plant resistance evaluation in field conditions

The field experiment was conducted for rust resistance evaluation at adult plant stage against stripe and leaf rust separately in the field under artificial epiphytotic conditions at Wheat Rusts Pathology Experiment Farm belonging to ICAR-Indian Agricultural Research Institute (IARI), New Delhi, India (Latitude 28°40′23″N; Longitude 77°13′27″E; MSL 228.61 M), for two consecutive *rabi* seasons (in Indian condition, winter season is also called as *rabi* season, starting from October to March end) during 2018–2019 and 2019–2020. The same set of 98 exotic genotypes including 2 susceptible checks was sown in randomized block design (RBD) with 3 replications. Each genotype was sown in strips of small adjacent plots consisted of 2 rows, with a row length of 1 m spaced at 25 cm and plot to plot distance at 50 cm apart. The irrigation channels were made on the space given between two replicates. The sowing of each genotype took place separately for stripe and leaf rust on November 22, 2018, and November 24, 2019, in each *rabi* season 2018–2019 and 2019–2020, respectively. The recommended agronomic package and practices were stringently followed to maintain the uniform stand of crop. The experimental material was surrounded by 2 rows of the mixture of highly susceptible wheat cvs. A-9–30-1, Agra Local and Local Red to provide high and uniform disease pressure in field. The urediospores inoculum having a mixture of 6 virulent and most predominant *Pst* pathotypes, viz. 47S103, 46S119, 110S119, 78S84, 110S84 and 238S119*,* and 4 virulent and most prevalent *Ptr* pathotypes, viz. 12–5(29R45), 77–5(121R63-1), 77–9(121R60-1) and 104–2(21R55), representing all groups of both stripe and leaf rust pathotypes was used for creating artificial epiphytotic in field conditions. Inoculation to susceptible infector rows was carried out with urediospores suspension (10–15 mg/ml) prepared by mixing spore dust in water with the help of few drops of tween-20 and sprayed on infector rows through hand sprayer during evening time in last week of December each year. After some time, leaf canopy was saturated with fine droplets of water till evening.

Adult plant/slow rusting resistance was assessed through host response and different epidemiological parameters estimates, *i.e.,* final disease severity (FDS), area under the disease progress curve (AUDPC), relative area under the disease progress curve (rAUDPC), coefficient of infection (CI) and apparent infection rate (*r*). The disease severity and infection type were recorded at weekly intervals, and final disease severity (FDS) was taken for stripe rust on March 8 and 4 and for leaf rust on March 30 and 27 during *rabi* seasons 2018–2019 and 2019–2020, respectively. Recording of the disease severity was started when susceptible checks showed 25–30% severity from individual genotype/plot in all the replications according to the modified Cobb's scale (Peterson et al. 1948), and the response of individual genotype referred to the adult plant infection types (ITs) was categorized as resistant (R), moderately resistant (MR), moderately susceptible (MS) and susceptible (S) reaction based on Roelfs et al. (1992). CI value was calculated by multiplying disease severity with constant values of infection type (Stubbs 1985). AUDPC and rAUDPC value for rust development on each genotype was calculated from multiple disease severity readings using formula given by Milus and Line (1986). Apparent infection rate (*r*) was also estimated in terms of disease severity recorded on genotypes at different times (Van der Plank 1963). Based on the values of different APR parameters recorded, the 98 exotic wheat genotypes and two susceptible checks were classified into four different categories of adult plant slow rusting resistance levels, viz. high, moderate and low (Singh et al. 2020). The data were statistically analyzed to determine the significance of the differences among the genotypes for APR parameters, and Pearson correlation coefficient matrices were calculated using SPSS software (version 16.0).

Results

Seedling resistance and rust resistance genes characterized

The differential infection types data of the tested genotypes obtained from SRT (seedling resistance test) were compared with those of the differentials and near isogenic lines with known *Yr* and *Lr* genes. The evaluated genotypes mainly inferred the presence of 5 important yellow rust resistance genes, viz. *Yr*A, *Yr*2, *Yr*9, *Yr*18 and *Yr*27, singly or in combination with other genes (Table 2). Among these genes, the presence of *Yr*2 gene was characterized in 31 genotypes. The presence of *Yr*A gene was inferred in 21 genotypes. *Yr*9 gene was characterized individually in 14 genotypes, whereas gene combination *Yr*9 + *Yr*18 + and *Yr*9 + *Yr*27 + was characterized in 5 and 4 genotypes, respectively. Adult plant resistance gene *Yr*18 was postulated singly in 14 genotypes and in combination with other genes in 5 genotypes (Fig. 1). Among the *Yr* gene characterized, *Yr*18 is conferred adult plant resistance gene, while *Yr*9 and *Yr*27 are race-specific/seedling resistance. APR gene *Yr*18/*Lr*34 had an interactive action and was found to be more effective in combination with other resistance genes (McIntosh et al. 1995; Bhardwaj et al. 2010a).

The gene-matching data revealed that these 98 genotypes possess 8 different leaf rust resistance genes, viz. *Lr*1, *Lr*3, *Lr*10, *Lr*13, *Lr*19, *Lr*23, *Lr*26 and *Lr*34, either present individually or in combination with other genes. The different gene combinations postulated in these genotypes are given in Table 2. Gene *Lr*13 was postulated in 17 genotypes, whereas gene combination *Lr*13 + *Lr*1 + , *Lr*13 + *Lr*10 + and *Lr*13 + *Lr*10 + *Lr*1 + was inferred in 10, 8 and 2 genotypes, respectively. APR gene *Lr*34, based on morphological marker and leaf tip necrosis, was postulated singly in 13 genotypes while in combination with *Lr*26 gene in one genotype, while *Lr*3, *Lr*10 and *Lr*19 gene was postulated in 8, 7 and 1 genotype, respectively. *Lr*23 was characterized singly in 2 genotypes, whereas gene combination *Lr*23 + *Lr*1 + , *Lr*23 + *Lr*3 + , *Lr*23 + *Lr*10 + and *Lr*23 + *Lr*10 + *Lr*1 + was postulated in 5, 1, 14 and 1 genotypes, respectively. *Lr*26 was characterized alone in 2 genotypes, whereas the gene combination *Lr*26 + *Lr*1 + , *Lr*26 + *Lr*3 + , *Lr*26 + *Lr*10 + , *Lr*26 + *Lr*34 + and *Lr*26 + *Lr*23 + *Lr*1 + was characterized in 2, 2, 1, 1 and 2 genotypes, respectively. Among the *Lr* gene characterized (Fig. 2), *Lr*34 is conferred adult plant resistance gene, *Lr*13 is race-specific APR gene, and *Lr*10 is temperature-sensitive gene, while remaining *Lr*1, *Lr*3, *Lr*19, *Lr*23, *Lr*24 and *Lr*26 are race-specific resistance genes. *Lr*13 is known to confer added resistance in combination with many other resistance genes (Kolmer 1996).

In our current study, majority of the tested wheat genotypes were susceptible to one or more virulent and most predominant pathotype(s) of *Pst* and *Ptr* and some genotypes were susceptible against all the pathotypes of both rusts tested, while none of the genotypes were resistant to all the pathotypes of both rusts tested at seedling stage and were further assessed for characterization of promising adult plant slow rusting resistance in field conditions.

Field-based rust resistance evaluation (Adult plant/slow rusting resistance)

Adult plant slow rusting resistance evaluation and phenotyping of the same set of 98 exotic genotypes were carried out against virulent and most predominant pathotypes of stripe and leaf rusts separately under artificial field epiphytotic conditions. Adult plant slow rusting resistance was assessed based on the host response, and different epidemiological parameters estimates (FDS, CI, rAUDPC and *r*) are given in Supplementary Tables 3 and 4. The analysis of variance revealed that there was highly significant difference ($p < 0.01$) among 98 exotic wheat genotypes and 2 susceptible checks for all these APR parameters studied against stripe and leaf rusts during both *rabi* seasons 2018–2019 and 2019–2020 (Supplementary Tables 5 and 6).

Based on the host response and values of different APR parameters recorded (FDS, CI, rAUDPC and *r*), we were characterized the 98 exotic wheat genotypes/germplasm lines into different categories/levels of adult plant slow rusting resistance (high, moderate and low) against stripe rust, leaf rust and both rusts. Data on disease severity and infection type for both rusts were recorded. Six genotypes with 'TR' infection type, 20 genotypes with 'MR' infection type and 28 genotypes having 'MS' infection type were observed against stripe rust, while 19 genotypes with 'R-TR' infection type, 41 genotypes with 'TMR-MR' infection type and 22 genotypes having 'MS' infection type were observed against leaf rust. Genotypes which had 'MS' or 'MR' infection type at adult plant stage may carry APR genes (Singh et al. 2005). Against stripe rust, 68, 23 and 9 genotypes were characterized with high, moderate and low levels of APR, respectively (Table 3). In case of leaf rust, 77, 17 and 2 genotypes were identified to have high, moderate and low levels of adult plant slow rusting resistance, respectively (Table 4). Against both stripe and leaf rusts, promising adult plant slow rusting resistance was observed on genotypes PG-1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12, 13, 14, 15, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 35, 36, 39, 41, 42, 43, 44, 45, 48, 49, 50, 52, 54, 55, 56, 57, 58, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69, 70, 71, 72, 73, 74, 75, 76, 77, 78, 79, 82, 85, 86, 87, GS-2037, 3009, 3011, 4042, 4051, 5047, 5049, 6016, 6058, 7015, 9001, 9008, 9010, 9030, 9031, 9055, 10,027, 10,032, 10,057, CIMCOG-10, 20, 30, CHEWINK, KINGBIRD, PAVON-76 and BOBWHITE consistently during *rabi* seasons 2018–2021.

Association between adult plant slow rusting resistance parameters

In this study, we have also attempted to elucidate the association between different adult plant resistance parameters across the 98 wheat materials and 2 susceptible checks for

Table 2 Inferred presence of *Yr* and *Lr* gene(s) in exotic wheat genotypes

S. No	Exotic genotype	*Yr* gene(s)	*Lr* gene(s)	S. No	Germplasm accessions	*Yr* gene(s)	*Lr* gene(s)
1	PG-1	*Yr*A+	*Lr*23+10+	50	PG-63	*Yr*9+	*Lr*26+1+
2	PG-2	*Yr*2+	*Lr*23+1+	51	PG-64	*Yr*9+	*Lr*26+3+
3	PG-3	*Yr*18+	*Lr*34+	52	PG-65	*Yr*A+	*Lr*3+
4	PG-4	*Yr*A+	*Lr*23+10+	53	PG-66	*Yr*A+	*Lr*3+1+
5	PG-5	*Yr*2+	*Lr*13+10+	54	PG-67	S	*Lr*23+10+
6	PG-6	*Yr*2+	S	55	PG-68	*Yr*9+	*Lr*26+23+1+
7	PG-7	*Yr*2+	*Lr*10+	56	PG-69	*Yr*2+	*Lr*13+10+
8	PG-9	S	*Lr*3+	57	PG-70	S	*Lr*3+1+
9	PG-10	*Yr*18+	*Lr*34+	58	PG-71	S	*Lr*23+1+
10	PG-11	*Yr*2+	*Lr*13+	59	PG-72	S	*Lr*23+10+
11	PG-12	*Yr*2+	*Lr*13+	60	PG-73	S	*Lr*13+1+
12	PG-13	*Yr*2+	*Lr*13+10+	61	PG-74	*Yr*A+	*Lr*10+1+
13	PG-14	S	*Lr*23+3+	62	PG-75	S	*Lr*13+
14	PG-15	*Yr*9+	*Lr*26+10+	63	PG-76	S	*Lr*13+1+
15	PG-17	*Yr*2+	*Lr*23+10+	64	PG-77	S	*Lr*13+
16	PG-18	*Yr*9+27+	*Lr*13+10+	65	PG-78	S	*Lr*13+
17	PG-19	*Yr*2+	*Lr*13+10+	66	PG-79	*Yr*A+	*Lr*13+
18	PG-20	*Yr*9+	*Lr*26+3+	67	PG-82	S	S
19	PG-21	*Yr*2+	*Lr*13+	68	PG-85	*Yr*A+	S
20	PG-22	*Yr*A+	*Lr*10+3+	69	PG-86	S	*Lr*23+10+
21	PG-23	S	*Lr*3+1+	70	PG-87	S	S
22	PG-24	*Yr*A+	*Lr*23+10+	71	GS-2037	*Yr*A+	*Lr*10+1+
23	PG-25	*Yr*A+	*Lr*23+1+	72	GS-3009	*Yr*A+	S
24	PG-26	S	*Lr*10+1+	73	GS-3011	*Yr*A+	*Lr*13+1+
25	PG-27	S	*Lr*10+3+	74	GS-4042	*Yr*A+	*Lr*13+
26	PG-28	S	*Lr*13+	75	GS-4051	*Yr*A+	*Lr*13+10+
27	PG-29	S	*Lr*13+10+	76	GS-5047	S	*Lr*13+1+
28	PG-30	S	S	77	GS-5049	*Yr*2+	*Lr*13+1+
29	PG-35	S	*Lr*13+	78	GS-6016	S	*Lr*13+
30	PG-36	*Yr*9+18+	*Lr*26+34+	79	GS-6058	S	*Lr*13+1+
31	PG-39	*Yr*A+	*Lr* 3+	80	GS-7015	*Yr*2+	*Lr*13+
32	PG-41	*Yr*A+	*Lr*10+3+	81	GS-9001	S	*Lr*23+10+
33	PG-42	*Yr*9+	*Lr*26+1+	82	GS-9008	S	*Lr*23+10+
34	PG-43	*Yr*2+	*Lr*13+1+	83	GS-9010	*Yr*9+	*Lr*23+10+
35	PG-44	*Yr*2+	S	84	GS-9019	*Yr*A+	*Lr*23+10+
36	PG-45	S	S	85	GS-9030	*Yr*2+	*Lr*13+
37	PG-46	S	S	86	GS-9031	*Yr*2+	*Lr*13+
38	PG-48	S	S	87	GS-9055	*Yr*2+	*Lr*13+10+
39	PG-49	*Yr*A+	S	88	GS-10027	S	*Lr*13+1+
40	PG-50	*Yr*2+	*Lr*13+10+1+	89	GS-10032	*Yr*2+	*Lr*13+1+
41	PG-52	*Yr*A+	*Lr*23+10+	90	GS-10057	S	*Lr*23+10+1+
42	PG-54	S	*Lr*13+1+	91	CIMCOG-10	*Yr*9+	*Lr*26+
43	PG-55	S	*Lr*13+	92	CIMCOG-20	S	*Lr*13+
44	PG-56	S	*Lr*13+10+	93	CIMCOG-22	*Yr*9+	*Lr*26+
45	PG-57	*Yr*2+	*Lr*3+1+	94	CIMCOG-30	S	*Lr*23+
46	PG-58	*Yr*A+	*Lr*23+10+	95	CHEWINK	S	*Lr*19+
47	PG-60	S	*Lr*13+	96	KINGBIRD	*Yr*2+	*Lr*23+1+
48	PG-61	*Yr*2+	*Lr*23+1+	97	PAVON-76	*Yr*2+	*Lr*13+10+1+
49	PG-62	*Yr*2+	*Lr*3+1+	98	BOBWHITE	*Yr*9+	*Lr*26+23+1+

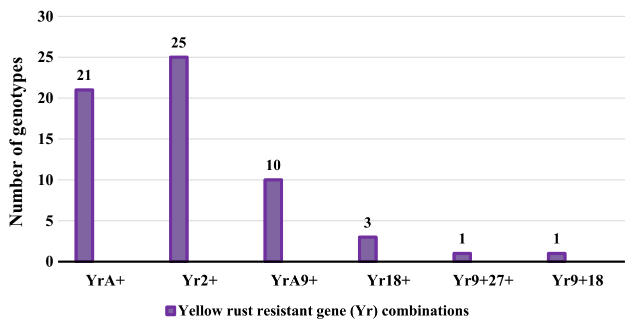

Fig. 1 Seedling resistance genes characterized in exotic wheat genotypes to stripe rust

stripe and leaf rusts. Coefficient of infection (CI) is the mostly used parameter for this purpose (Ali et al. 2009). We have observed a positive relation of CI with FDS, rAUDPC and *r* with a strong R^2 value of 0.9864, 0.9752 and 0.9621 in case of stripe rust (Fig. 3) and R^2 value of 0.9874, 0.9763 and 0.9654 in case of leaf rust (Fig. 4), respectively.

Discussion

More than 100 genes and alleles of leaf rust resistance genes have been described (McIntosh et al. 2017). More than 70 stripe rust resistance genes designated so far, only nine genes *Yr*18, *Yr*29, *Yr*30, *Yr*36, *Yr*39, *Yr*46, *Yr*48, *Yr*49 and *Yr*52 are associated with non-race-specific/adult plant resistance (McIntosh et al. 2012). The different combinations of five yellow rust resistance genes, viz. *Yr*A, *Yr*2, *Yr*9, *Yr*18 and *Yr*27, and nine leaf rust resistance genes, viz. *Lr*1, *Lr*3, *Lr*10, *Lr*13, *Lr*19, *Lr*23, *Lr*24, *Lr*26 and *Lr*34, were characterized in Indian wheat materials by applying gene-matching technique using multi-pathotype data.

These results compliment previous study on characterization of stripe and leaf rust resistance gene(s), such as postulation of gene *Yr*A, *Yr*2, *Yr*9 and *Yr*18 in promising Indian wheat genotypes/germplasm accessions (Kumar et al. 2014) and characterization of different combinations of three important yellow rust resistance genes *Yr*2, *Yr*9 and *Yr*18 in Indian wheat genotypes by applying gene-matching technique using multi-pathotypes data (Singh et al. 2015),

Fig. 2 Seedling resistance genes characterized in exotic wheat genotypes to leaf rust

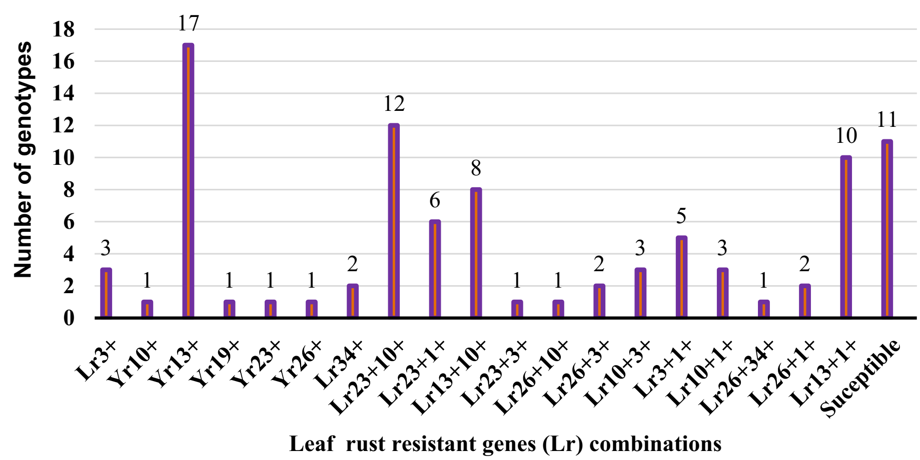

Table 3 Promising levels of adult plant resistance characterized against stripe rust

APR level	Number	Exotic wheat genotype/germplasm lines
High	68	PG-3, PG-6, PG-9, PG-10, PG-11, PG-14, PG-15, PG-17, PG-18, PG-21, PG-23, PG-24, PG-25, PG-26, PG-27, PG-28, PG-29, PG-35, PG-41, PG-44, PG-45, PG-48, PG-49, PG-52, PG-54, PG-57, PG-60, PG-62, PG-63, PG-64, PG-65, PG-66, PG-67, PG-68, PG-70, PG-71, PG-72, PG-73, PG-74, PG-75, PG-76, PG-77, PG-78, PG-79, PG-82, PG-85, PG-86, PG-87, GS-2037, GS-3009, GS-3011, GS-4042, GS-4051, GS-5047, GS-5049, GS-6016, GS-6058, GS-7015, GS-9001, GS-9008, GS-9010, GS-9019, GS-9030, GS-9031, GS-9055, GS-10027, GS-10032 and GS-10057
Moderate	23	PG-1, PG-4, PG-7, PG-12, PG-13, PG-19, PG-22, PG-36, PG-39, PG-42, PG-50, PG-55, PG-58, PG-61, PG-69, CIMCOG-10, CIMCOG-20, CIMCOG-22, CIMCOG-30, CHEWINK and KINGBIRD
Low	09	PG-2, PG-5, PG-20, PG-30, PG-43, PG-46, PG-56, PAVON-76 and BOBWHITE
Susceptible	02	Local Red and A-9–30-1

Table 4 Promising levels of adult plant resistance characterized against leaf rust

APR level	Number	Exotic wheat genotype/germplasm lines
High	77	PG-1, PG-2, PG-3, PG-4, PG-5, PG-6, PG-7, PG-9, PG-10, PG-11, PG-12, PG-13, PG-14, PG-15, PG-17, PG-18, PG-19, PG-20, PG-21, PG-22, PG-23, PG-24, PG-25, PG-26, PG-27, PG-28, PG-29, PG-35, PG-39, PG-41, PG-42, PG-43, PG-48, PG-50, PG-52, PG-54, PG-55, PG-56, PG-57, PG-58, PG-60, PG-61, PG-62, PG-63, PG-64, PG-65, PG-66, PG-67, PG-68, PG-70, PG-71, PG-72, PG-73, PG-74, PG-75, PG-76, PG-77, PG-78, PG-79, PG-82, PG-85, PG-86, GS-2037, GS-3009, GS-3011, GS-4042, GS-4051, GS-5047, GS-5049, GS-6016, GS-6058, GS-7015, GS-9001, GS-9008, GS-9010, GS-9030 and GS-9031
Moderate	17	PG-36, PG-44, PG-45, PG-49, PG-69, PG-87, GS-9055, GS-10027, GS-10032, GS-10057, CIMCOG-10, CIMCOG-20, CIMCOG-30, CHEWINK, KINGBIRD, PAVON-76 and BOBWHITE
Low	02	PG-30 and PG-46
Susceptible	02	Local Red and A-9–30-1

and also, the different combinations of seven leaf rust resistance genes, viz. *Lr*1, *Lr*3, *Lr*10, *Lr*13, *Lr*23, *Lr*26 and *Lr*34, were characterized by applying the gene-matching technique in 39 advance wheat lines that showed race-specific adult plant resistance to one and/or the other pathotypes (Bhardwaj et al. 2010b; Mathuria et al. 2016). Kumar et al. (2020) evaluated exotic wheat accessions and characterized the presence of *Lr*13 singly in 38 accessions and in combination with *Lr*10, *Lr*1 and *Lr*2 gene in 16, 11 and 1 accessions, respectively. They also postulated *Lr*23 in 12 genotypes, whereas gene combination *Lr*23 + *Lr*1 and *Lr*23 + *Lr*10 was inferred in 5 and 3 genotypes, respectively. The gene combination *Lr*26 + *Lr*23 + *Lr*1 was characterized in 19 accessions. Dakouri et al. (2013) reported that *Lr*1, *Lr*3, *Lr*10 and *Lr*20 were the most prevalent genes around the world, while *Lr*9, *Lr*14b, *Lr*3ka and/or *Lr*30 and *Lr*26 were rare.

All these promising rust-resistant genotypes/germplasm lines at adult plant stage were susceptible at seedling stage to one or more pathotype(s) including most prevalent and virulent of both stripe and leaf rust, which indicated the presence of effective adult plant slow rusting resistance among the exotic genotypes studied. Many wheat researchers have used these APR parameters to assess the adult plant slow rusting resistance of wheat genotypes/lines (Pathan and Park 2006; Herrera-Foessel et al. 2007; Ali et al. 2009; Safavi et al. 2013; Shah et al. 2014; Singh et al. 2015, 17; Mishra et al. 2021; Bhardwaj et al. 2022).

FDS is assumed to represent the cumulative result of all resistance factors during the progress of epidemic (Parlevliet 1988). Many researchers used FDS as a parameter to assess slow rusting behavior of wheat lines (Kumar et al. 2014; Singh et al. 2015, 17). They observed lower values for wheat cultivars exhibiting adult plant slow rusting, as compared to the susceptible checks. Similarly, Singh et al. (2017) also conducted field-based experiments to assess the levels of slow rusting/adult plant resistance in exotic wheat germplasm. As per the APR levels based on FDS along with other parameters (CI, rAUDPC and *r*), they observed that resistance level was ranged from very low to very high among the tested genotypes. Cultivars with a low level of CI and other quantitative resistance parameters will most probably have adult plant resistance genes, and their resistance cannot last for a long time (Dehghani and Moghaddam 2004). Earlier, Pathan and Park (2006) evaluated APR to leaf rust in European wheat based on CI value and reported the presence of different partial resistance conferring genes in these lines effective against all the virulences tested. Similarly, many researchers reported the presence of varying levels of slow rusting in wheat breeding lines (Shah et al. 2014; Singh et al. 2015, 17). Pathan and Park (2006) appraised adult plant resistance, a kind of slow rusting resistance, to leaf rust in European wheat lines by calculating CI value and reported the presence of different partial resistance conferring genes in these lines.

Similarly, many researchers reported the presence of varying levels of slow rusting in wheat breeding lines (Shah et al. 2014; Singh et al. 2015, 2017). Based on the rAUDPC values, the genotypes were categorized into two distinct groups according to Ali et al. (2007). One group included the genotypes exhibiting rAUDPC values up to 30% of the susceptible check, and the other included the genotypes showing rAUDPC values up to 60% of the susceptible checks. The genotypes in group-1 were marked as having high level of APR, and those of group-2 were marked as having moderate level of APR. The reasons for the markings were because they also developed epiphytotic of very low potential as indicated by their rAUDPC values, despite the ultimate expression of high infection type. Genotypes with such characters are expected to possess genes that confer slow rusting/partial/adult plant resistance (Parlevliet 1988). The genotypes that exhibited rAUDPC value less than 30% of susceptible checks were considered as having better level of partial resistance. This group was composed of cultivars with varying degrees of adult plant resistance, which has been advocated to be more durable (Singh et al. 2004b, 2015; Safavi et al. 2013, 17). Moreover, cultivars with acceptable levels of slow rusting restrict the evolution of new virulent races of the pathogen because multiple point mutations are extremely rare in nature (Ali et al. 2007).

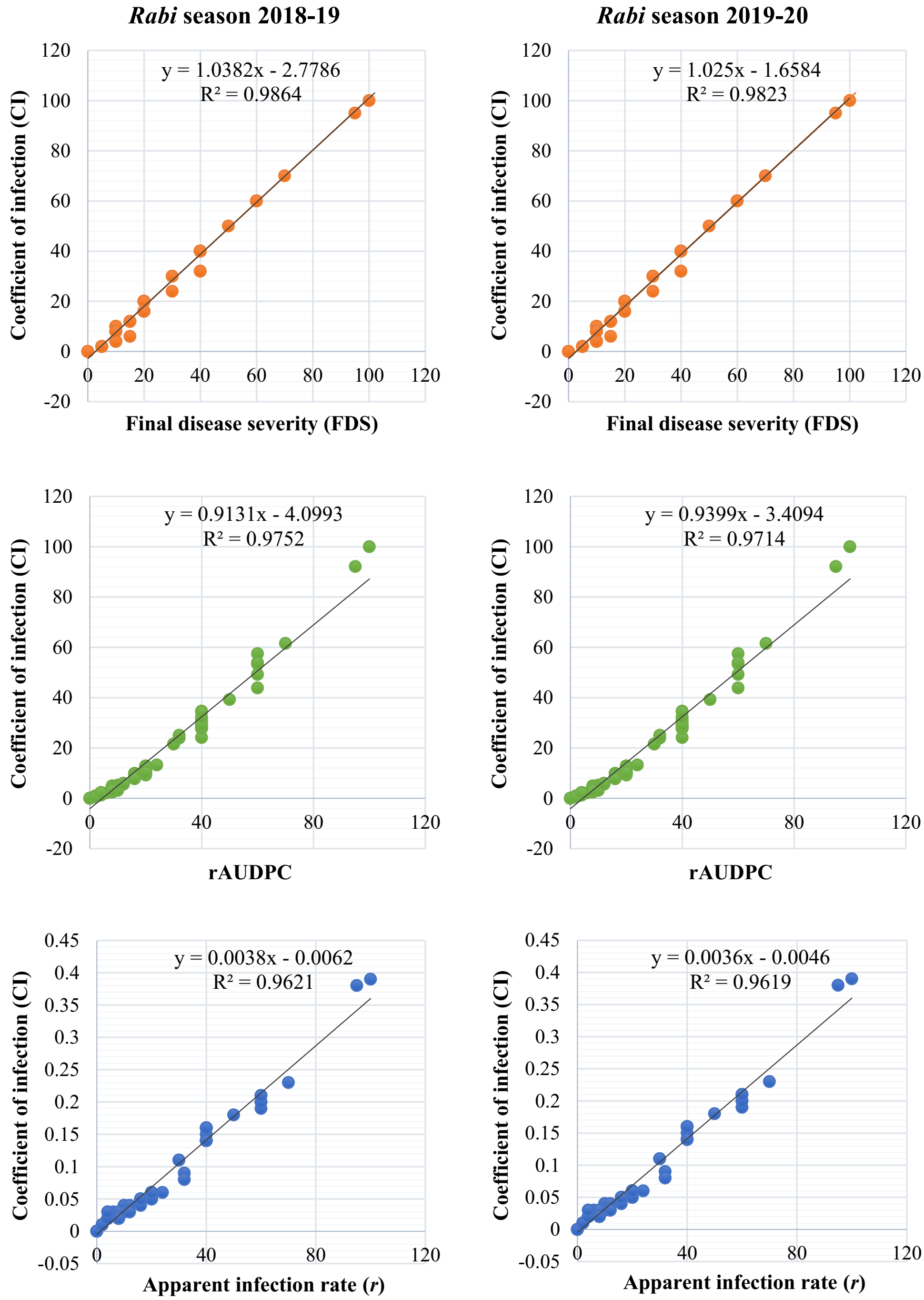

Fig. 3 Association between slow rusting/adult plant resistance parameters to stripe rust across ninety-eight exotic wheat genotypes/cultivars and two susceptible checks during *rabi* seasons 2018–2019 and 2019–2020

This positive correlation was in agreement with the results of other researchers on cereals-rust pathosystems (Sandoval-Islas et al. 2007; Safavi 2012; Safavi et al. 2013; Singh et al. 2015, 17). Sandoval-Islas et al. (2007) found good correlation of rAUDPC with quantitative resistance components, *i.e.*, latent period and infection frequency. Field selection of the slow rusting trait preferably by low rAUDPC and FDS along with CI was feasible where greenhouse facilities were inadequate (Singh et al. 2007).

Since all these APR parameters were strongly and positively correlated in our present study, we can strongly conclude that the FDS, CI and rAUDPC followed by infection rate (*r*) are the most appropriate parameters/components to assess the levels of adult plant slow rusting resistance in genotypes/lines. Genotypes with a different level of adult plant slow rusting resistance are advocated to be more durable and long lasting (Singh et al. 2004b). With an acceptable level of slow rusting resistance, these genotypes reduce the

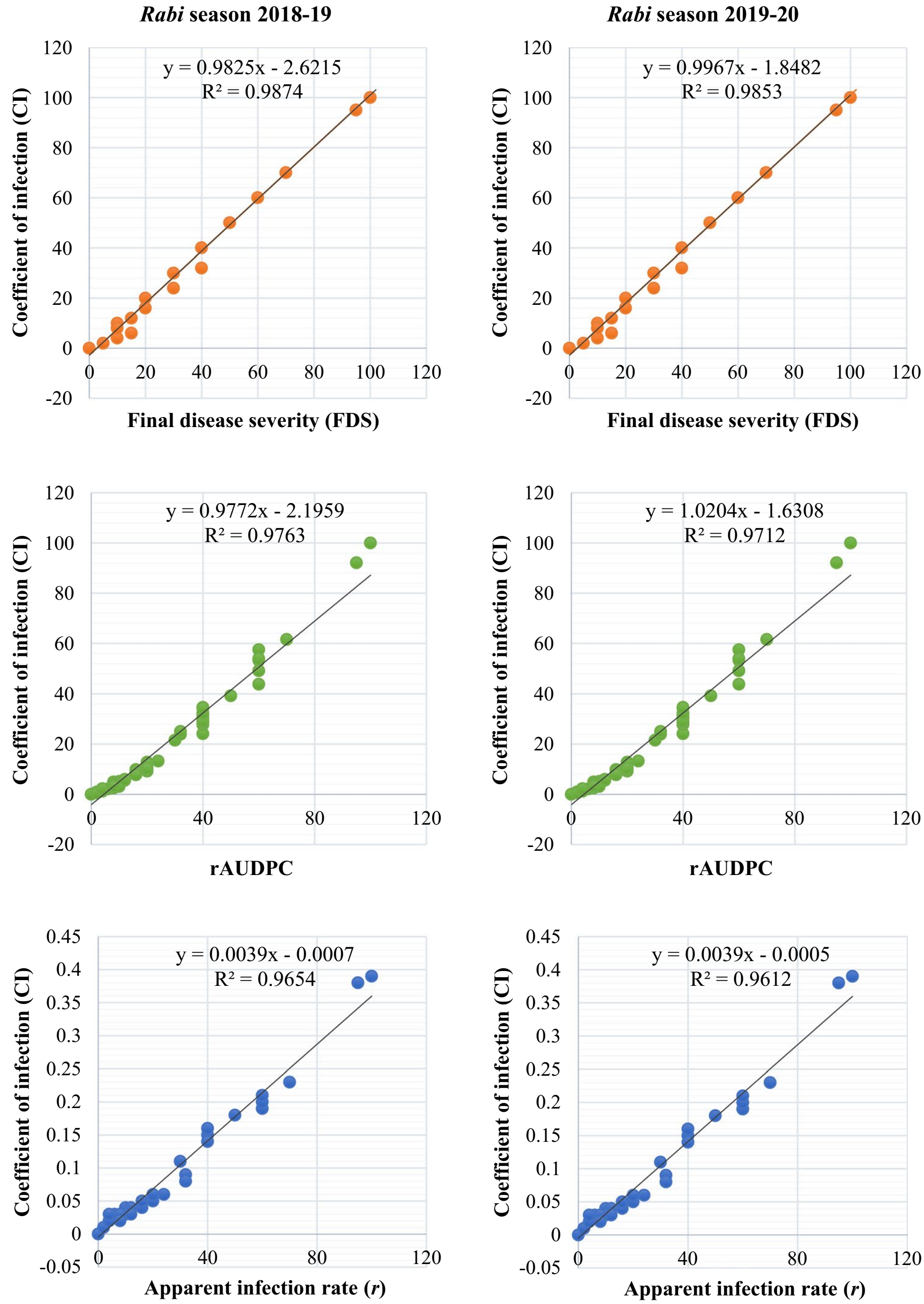

Fig. 4 Association between adult plant slow rusting resistance parameters to leaf rust pathogen across ninety-eight exotic wheat genotypes and two susceptible checks during *rabi* seasons 2018–2019 and 2019–2020

epidemic progress/disease development rate and also do not influence the evolution of races of the pathogens (excluding when considering demography). These genotypes are, however, operated by many minor genes to overcome them in the field which will take longer time. There are rusts fungi which have more potential to change by different events such as mutation, migration in long-distances and selection pressure of cultivars on pathogen genotypes (Hovmøller, 2001; Ben Yehuda et al. 2004). In view of these potentials to change, researchers should deploy non-race-specific/seedling resistance or a combination of non-race-specific/adult plant/slow rusting resistance with race-specific resistance instead of using only race-specific resistance.

The overall results demonstrate that the exotic wheat materials have significant diversity regarding resistance reaction, ranging from complete resistance to susceptible ones. Majority of the tested genotypes/germplasm lines exhibited moderate (MR/MS) or moderately susceptible to susceptible (MSS) reactions under high stripe and leaf rust disease pressure shown by susceptible checks under field conditions. Resistance of all categories of adult plant slow rusting resistance to both stripe and leaf rusts was observed. Genotypes susceptible at seedling stage exhibited MR-MS types reaction at adult plant stage may probably carry major gene or combination of major and minor gene-based resistance against all the virulences used in the study, which can be used further used in wheat improvement program after confirmatory studies to develop more durable varieties as a control strategy against both stripe and leaf rust. Also, in view of frequent breakdown of single *R*-gene-based race-specific resistant cultivars due to rapid evolution of new races of rust pathogens, varietal improvement program should focus on deployment of non-race-specific or combination of race-specific/seedling and non-race-specific/adult plant resistance sources instead of using only single R-gene-based race-specific resistance. In this study, cultivars having adult plant slow rusting resistance with low values of epidemiological parameters were identified. Such cultivars can be further used in varietal development program to get improved varieties with high levels of resistance against new pathotypes of rusts and also insignificant yield losses.

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Declarations

Conflict of interest No potential conflict of interest relevant to this article was reported.

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