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Mapping resistance to leaf and stripe rusts in bread *Triticum aestivum* L. germplasm through GWAS and field phenotyping

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Abstract This study aims to evaluate the phenotypic and molecular levels of resistance of *Triticum aestivum* L. (bread wheat) genotypes to leaf rust (*Puccinia triticina*) and stripe rust (*Puccinia striiformis*). Increasing climate pressures and the rapid evolution of pathogens threaten wheat production, underscoring the critical role of understanding genetic resistance mechanisms for sustainable solutions. The study evaluated 175 wheat lines sourced from CIMMYT for disease severity and infection type under natural field conditions; subsequently, genome-wide association analysis was used to correlate these phenotypic data with existing molecular markers. The analyses identified four lines resistant to stripe rust, 33 lines resistant to leaf rust, and two lines (no. 69 and 164) resistant to both diseases. One hundred seventy-six marker-trait associations were identified on 19 of 21 chromosomes, particularly on chromosomes 3B, 5B, 7A, and the D genome, with significant *p*-values ($p < 0.001$). These QTL regions explain 6.8–27.0% of phenotypic variation in disease severity. The resistant lines obtained are suitable as genetic resources for classical breeding programs and can be effectively evaluated in marker-assisted selection studies. Thus, the study produces fundamental scientific knowledge and offers concrete solutions to increase wheat productivity in regions such as Pakistan, where rust epidemics are prevalent.

Keywords Bread wheat · Leaf rust · *Puccinia striiformis* · *Puccinia triticina* · QTL analysis

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Introduction

Wheat (*Triticum aestivum* L.) is one of the most important cereal crops, grown on approximately 237 million hectares worldwide each year, with a total production of 420 million tons, playing a fundamental role in human nutrition (Singh et al.,

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2023b). Bread wheat belongs to the Poaceae family, containing six chromosomes (2n = 6x = 42) comprising the A, B, and D genomes (Serrem et al., 2011). Wheat is not only a strategic crop due to its role as a staple food but also because it is the most important source of plant protein, particularly in developing countries (Arif et al., 2025).

The rapid growth of the world population and environmental stress factors such as climate change are driving an increase in demand for wheat, making the development of productive and resilient wheat varieties imperative (Sharma et al., 2015; Yanagi, 2024). Despite a record wheat production of 777 million metric tons (MMT) in 2019–2020, this amount is still far from meeting global demand (Kumar, 2022).

Wheat production is negatively affected by biotic (living organisms) and abiotic (environmental) stress factors. Among these biotic factors, rust diseases, particularly stripe rust (*P. striiformis*) and leaf rust (*P. triticina*), can cause yield losses of up to 70% (Tomar et al., 2021). The rapid evolution of rust pathogens can render even previously resistant varieties susceptible, necessitating continuously updating current breeding strategies (Hayit et al., 2021).

One of the primary goals of wheat breeding programs is to develop high-yielding, environmentally resilient, and disease-resistant varieties. In line with this objective, advanced genomic approaches such as molecular marker-assisted selection (MAS) and the identification of quantitative trait loci (QTL) are gaining increasing importance (Azizinia et al., 2020; Hayat et al., 2025).

Wheat yields in Pakistan remain below their potential. The reasons for this include using varieties with low genetic potential, poor soil health, late planting, climate change, and disease pressure (Nawaz et al., 2019). Wheat is susceptible to many diseases, such as rust, powdery mildew, smut, and root rot, and multiple diseases can occur in the same season (Kayim et al., 2022; Singh et al., 2023a).

Leaf rust disease poses a significant threat, particularly in critical wheat-producing regions such as Asia and the Middle East. The pathogen's wide distribution, high mutation rate, and ability to be carried long distances by wind make the development of resistant varieties even more urgent (Azizinia et al., 2020; Hayit et al., 2021; McDonald, 2025; Tomar et al., 2021).

The primary objective of this study is to determine the phenotypic responses of wheat genotypes to leaf and stripe rust diseases under natural field conditions and to correlate these phenotypic data with existing molecular marker data to identify resistant lines and their associated genetic regions. This is a critical step toward mapping resistance genes that can be used in future breeding programs and developing new resistant varieties.

Materials and methods

Derivation and collection of wheat germplasm

A massive amount of germplasm of the wheat crop is available in CIMMYT. That was characterized genomically and phenotypically, after which a core subset was selected. This core subset is composed of 25 elite lines, which are also available at the Nuclear Institute for Agriculture and Biology (NIAB), Pakistan. Each entry of the core subset was crossed with a chosen exotic accession carrying a desirable trait to produce an F1 hybrid. This was crossed with another elite entry to combine the characteristics of two elites and chosen exotic lines to produce TCF1 seeds. This TCF1 generation was subjected to a repeated cycle of selection to produce TCF7 seeds. This resulted in the availability of ~ 1000 accessions imported from CIMMYT in 2016 at NIAB. A set of 175 lines, randomly selected from this germplasm, was used in these recent studies. This germplasm's pedigree is provided in Supplementary Table A.

Experimental design

The experiment was conducted at NIAB in three replicates, whose latitude and longitude are 31.4504° N and 73.1350° E, respectively. Seeds were sown on the 8th Nov, 2018 with a dibbler. Single rows of 1.3 m length with 9 and 3 inches row to row (rxr) and plant to plant (pxp) distances, respectively, with a row of susceptible check (Morocco) after every 10 genotypes. The experiment was watered 4—5 times, beginning 4 weeks after sowing.

Genetic marker data

A group of 7180 genetic markers was available from CIMMYT for genetic examination and future analysis. These marker data covered the complete genome data of wheat, and the total map length of these marker data was 5664.89 cM. The maximum covered group of this genetic data was seven, where 1276 markers were mapped. Similarly, the minimum covered group was four, where only 575 markers were mapped.

Marker filtering and GWAS analysis

Prior to the genome-wide association analysis, quality control filtering was applied to the marker dataset to ensure reliability of the association signals. A total of 7,180 genetic markers were initially available. Markers with a minor allele frequency (MAF) lower than 0.05, a missing data rate greater than 10%, or excessive heterozygosity were excluded from the dataset. These filtering steps were implemented to remove low-frequency alleles and poorly genotyped markers that could lead to spurious associations.

After quality filtering, the remaining high-quality markers were used for the GWAS analysis. Population structure and kinship relationships among the wheat lines were incorporated into the model to reduce false-positive associations. Genome-wide association analysis was conducted using a mixed linear model (MLM) that accounts for both population structure (Q matrix) and kinship (K matrix). Statistical significance of marker–trait associations was determined using a threshold of $p < 0.001$, and the proportion of phenotypic variance explained by each significant locus was calculated.

Phenotypic data for leaf rust and stripe rust were obtained under natural infection conditions in the field.

Phenotypic measurements

The phenotype of wheat genotypes was recorded based on visual assessment of disease severity and host reaction against leaf and stripe rust (yellow rust). The modified Cobb scale was used to assess leaf and yellow rust disease severity as a percentage of the affected area (Peterson et al., 1948). The total area of the leaf infected by rust spores was measured on the Cobb scale. Details of the disease classification groups (0–100%) are listed as described in Roelfs et al. (1992).

Disease severity (DS) was assessed at four time points, with approximately 50% of the crop exhibiting visible symptoms. At each interval, the proportion of leaf area affected by rust was recorded. Plant responses were classified into five categories: Immune (0), Resistant (R), Moderately Resistant (MR), Moderately Susceptible (MS), and Susceptible (S) (Fig. 1). Rust incidence was quantified using the modified Cobb scale, which estimates the percentage of leaf surface covered by rust pustules (Peterson et al., 1948).

Seedling reactions were evaluated two weeks after inoculation based on infection types (IT) observed for each genotype. Infection categories (0, 0;, 1, 2, 3, 4, and X) were scored following the classification described by Johnston and Browder (1966). Infection types 0, 0;, 1, and 2 were classified as resistant (R), whereas types 3, 4, and X were classified as susceptible (S).

Association analysis

STRUCTURE 2.3.4 was used to find the number of subpopulations in the germplasm. For that purpose, 213 (~10 markers per chromosome) unlinked, randomly selected markers were chosen to classify the structure of the plant material under study. The admixture design with a burn of over 25.000 iterations and an approach time of 25.000 MCMC to the K over a range of 1—15 was used. The results from STRUCTURE 2.3.4 were incorporated into TASSEL5.2.43, and the MLM command was used to identify markers associated with the measured traits.

Results

Disease response of wheat rust

The response of wheat to rust diseases depends on host–pathogen interactions, environmental conditions, plant growth stage, and the expression of resistance genes. Wheat varieties relying on race-specific resistance often lose effectiveness within a few years due to the emergence of new virulent rust races. Moreover, the cultivation of large areas with

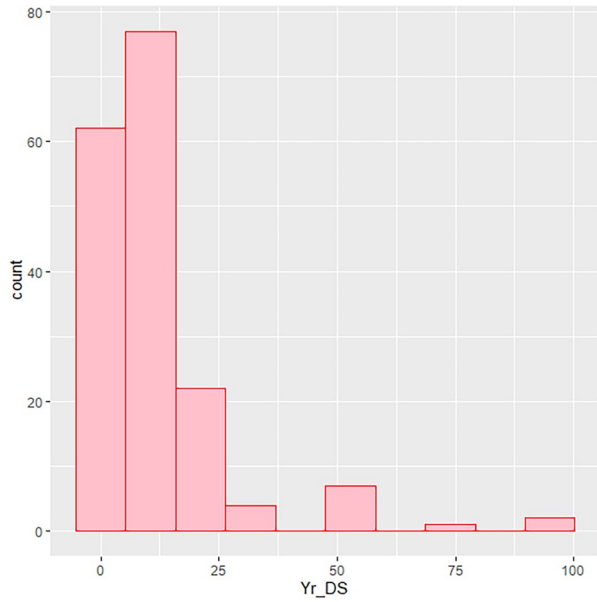

Fig. 1 Disease Severity (DS) in yellow rust. [counts = scoring against leaf area infected by disease, R = upto 25 counts, MR = 25—50 counts, MS = 50—70 counts, S = counts > 70]

Table 1 Descriptive statistics of disease parameters (DS & IT) recorded during the experiment

	Yr_DS	Yr_IT	Lr_DS	Lr_IT
Mean	13.57	4.92	13.66	3.66
Standard Error	1.11	0.14	1.29	0.16
Minimum	5	0	0	0
Maximum	100	10	100	10

susceptible wheat genotypes facilitates the proliferation and evolution of rust pathogens, increasing the risk of epidemics (Draz et al., 2015). Therefore, genetic resistance remains the most efficient and sustainable approach to reducing yield losses caused by rust diseases. In this study, the responses of 175 wheat lines to leaf rust and stripe rust were evaluated under natural field conditions, and their phenotypic responses were associated with molecular markers.

Descriptive statistics of the recorded disease parameters are presented in Table 1. Yr_DS ranged between 5 and 100 with a mean value of 13.57 ± 1.11, whereas Lr_DS ranged between 0 and 100 with a mean value of 13.66 ± 1.29. The mean infection type scores were 4.92 ± 0.14 for Yr_IT and 3.66 ± 0.16 for Lr_IT. Statistical analysis revealed significant variation among genotypes for both disease severity and infection type variables ($p < 0.001$), indicating substantial phenotypic diversity in rust resistance within the studied germplasm.

Disease severity

For stripe rust, 79.4% of genotypes exhibited a resistant (R) response, 14.8% were moderately resistant (MR), and 5.7% were moderately susceptible or susceptible (MS/S). This distribution indicates that a large proportion of the evaluated wheat lines carry effective resistance against stripe rust under natural field conditions.

For leaf rust, 4.6% of the lines showed highly resistant (HR) reactions, 74.3% were resistant (R), 13.7% were moderately resistant (MR), 4% were moderately susceptible (MS), and 2.9% were susceptible (S). These results suggest that although a large proportion of genotypes exhibit resistance, relatively few lines display very high levels of resistance. Most resistant lines showed relatively low disease severity scores, indicating their potential value as breeding material (Fig. 2).

Infection type

For stripe rust infection type (Yr_IT), less than 1% (0.5%) of the lines showed an immune response, while 8% were moderately resistant (MR), 28.6% moderately susceptible (MS), and 0.5% highly susceptible (HS). Notably, 62.3% of the lines showed heterogeneous responses (H) (Fig. 3).

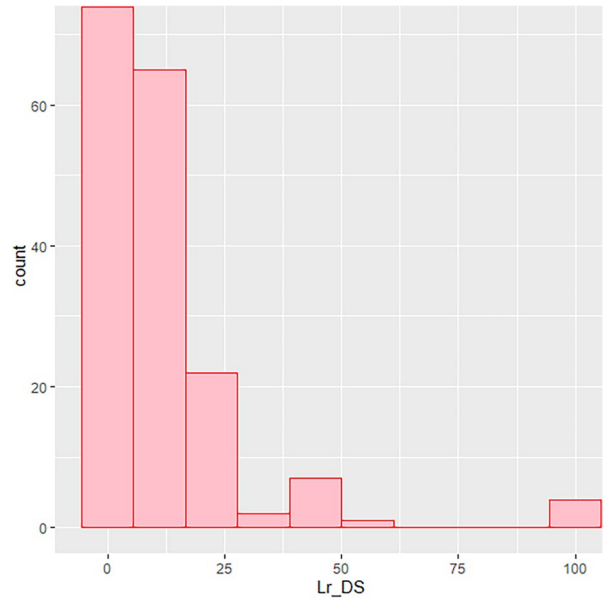

Fig. 2 Disease Severity (DS) of wheat leaf rust. [counts = scoring against leaf area infected by disease, R = upto 25 counts, MR = 25—50 counts, MS = 50—70 counts, S = counts > 70]

For leaf rust infection type (Lr_IT), 4.6% of the lines showed immune responses, 1.1% were resistant, 30.3% were moderately resistant, 30.3% were moderately susceptible, and 1.1% were highly susceptible. Additionally, 32.6% of the lines displayed heterogeneous reactions (Fig. 4). The relatively high frequencies of MR and MS responses suggest the presence of partial resistance mechanisms in several wheat lines.

Population structure of wheat germplasm

Population structure analysis divided the wheat germplasm into five subgroups (Q groups). The first group (Q1) contained 20 lines, the second group (Q2) contained 16 lines, the third group (Q3) contained 26 lines, while the fourth (Q4) and fifth (Q5) groups contained 101 and 12 lines, respectively. Pedigree information and subgroup assignments are presented in Table A,

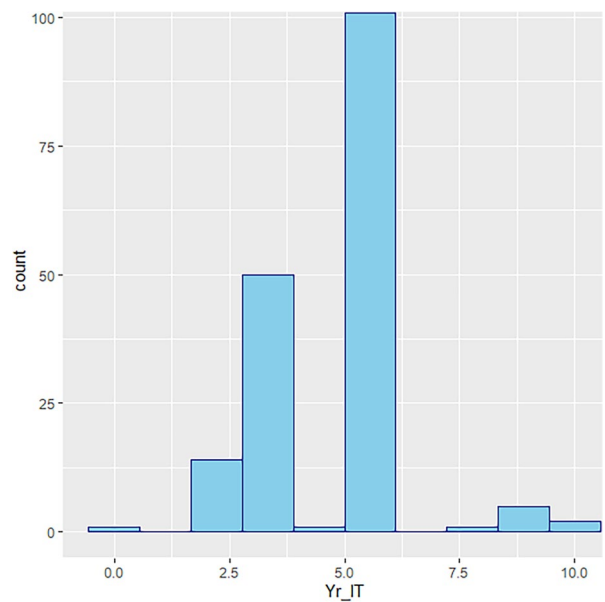

Fig. 3 Infection type of wheat yellow rust

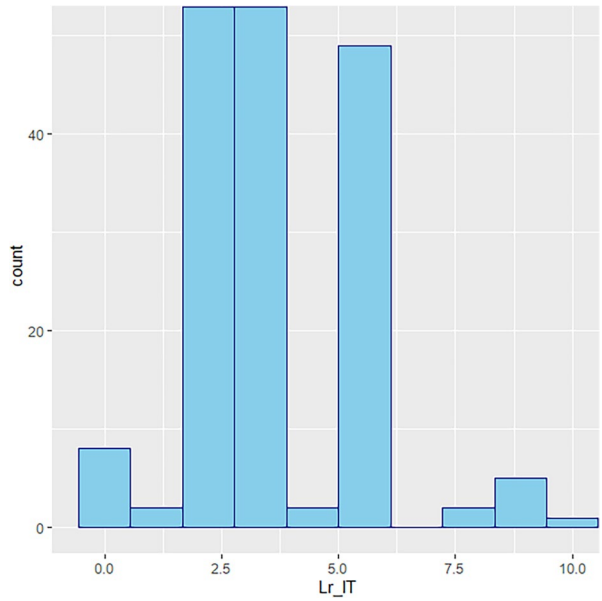

Fig. 4 Infection types of wheat leaf rust

and the STRUCTURE results were largely consistent with the pedigree relationships among the wheat lines.

This population structure indicates that genetic diversity within the germplasm is organized at the population level and that phenotypic variation in rust resistance corresponds to underlying genetic structure. These subgroups were considered during subsequent QTL analyses (Fig. 5).

Genome-wide association studies (GWAS) analysis

GWAS analysis was conducted to identify associations between molecular markers and rust resistance traits.

Leaf rust disease (Lr_DS)

Huge phenotypic variation enabled us to detect marker trait associations (MTAs) within our data. 65 MTAs were discovered for Lr_DS in our germplasm on 14 of 21 wheat chromosomes. In particular, the density on chromosomes 3B (10 MTA) and 5B (10 MTA) indicates that these regions are "hot spots" for leaf rust resistance.

The 16 MTA on chromosome 7 A was statistically significant ($p < 0.001$), explaining up to 24.4% of phenotypic variation. The MTAs in these regions can be validated as resistance genes in future functional validation studies (Fig. 6).

These MTAs were discovered on chromosomes 1 A (1), 1D (1), 2 A (2), 2B (3), 3B (10), 3D (2), 4 A (3), 5 A (6), 5B (10), 5D (1), 6B (4), 6D (1), 7 A (16) and 7D (5) explaining from 6.8—24.4% phenotypic variation (Supplementary Table B).

Leaf rust infection type (Lr_IT)

For the Lr_IT trait, four MTAs were detected across three wheat chromosomes (Fig. 7). These associations were located on chromosomes 2B (2 MTAs), 2D (1 MTA), and 7B (1 MTA), explaining approximately 9–10% of phenotypic variation.

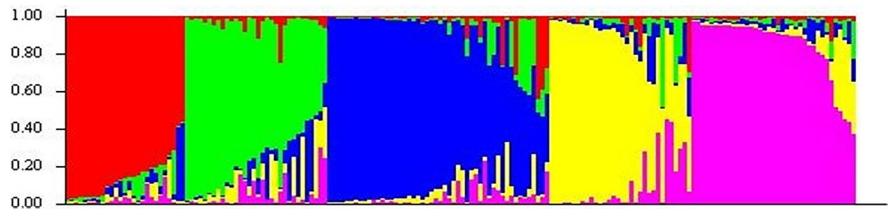

Fig. 5 Population structure of the wheat germplasm in five Q-groups

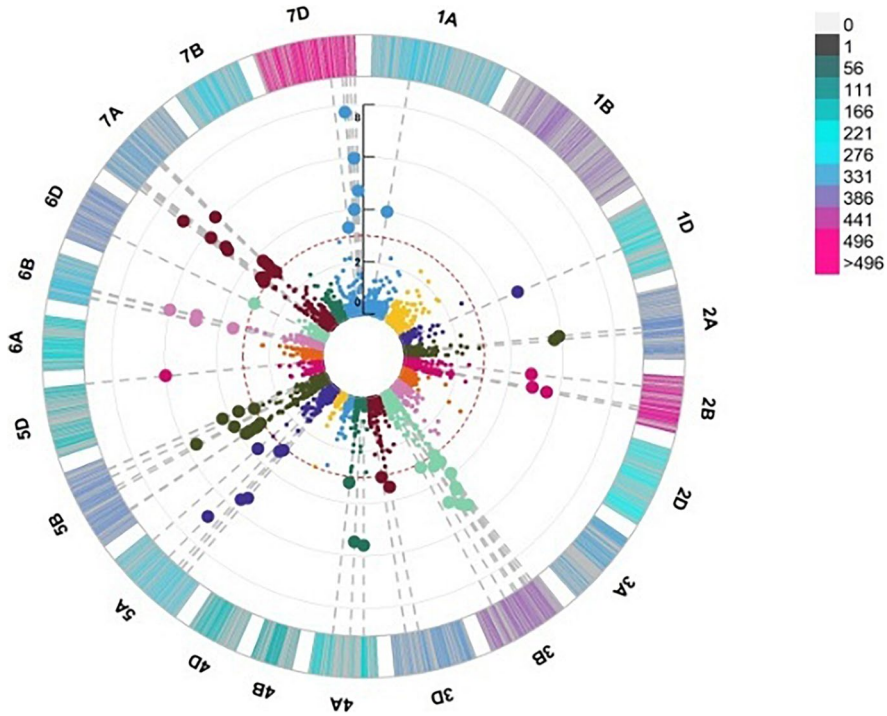

Fig. 6 Genome-wide scan of Lr_DS (inner circle) in circular form. Circular Manhattan plots display the chromosomes along the outermost ring. A thin, dotted red line marks the statistical significance threshold ($p < 0.001$, corresponding to $-\log10 \geq 3$), beyond which black-highlighted dots represent true marker-trait associations. The scale between chromosomes 7D and 1A denotes the LOD threshold. Additionally, the colored bar located at the upper right side of the plot reflects SNP density across the genome, ranging from white (low density) to pink (high density)

Yellow rust disease severity (Yr_DS)

GWAS analysis for stripe rust disease severity identified 104 MTAs distributed across 19 of the 21 wheat chromosomes (Fig. 8). These associations were located on chromosomes 1A, 1B, 1D, 2A, 2B, 2D, 3A, 3B, 3D, 4A, 4B, 4D, 5A, 5B, 5D, 6A, 7A, 7B, and 7D, explaining 6–27% of phenotypic variation.

The highest SNP density was observed on chromosomes 2B, 2D, 3A, and 5B, suggesting these regions

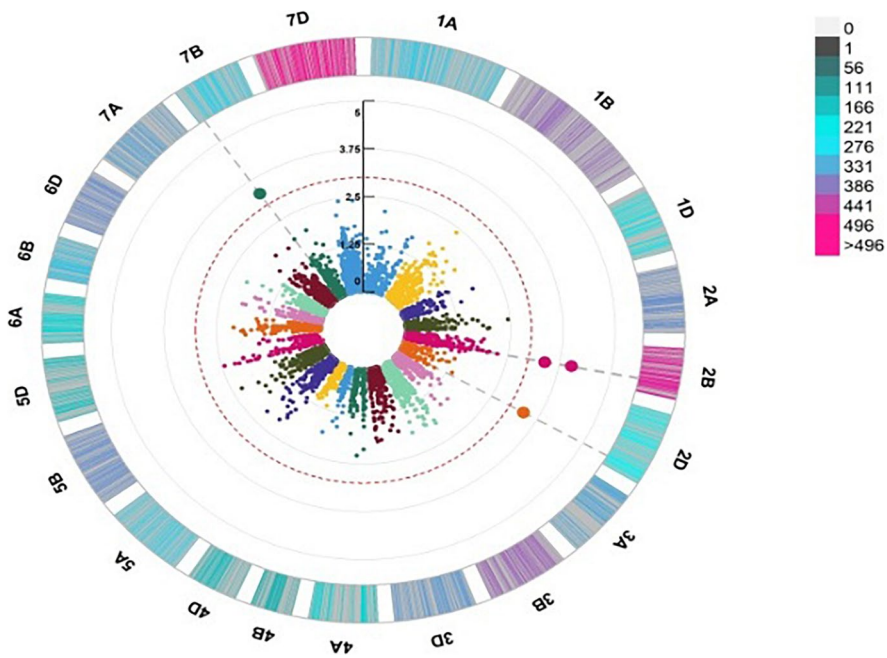

Fig. 7 Genome-wide scan of Lr_IT (inner circle) in circular form. Circular Manhattan plots display the chromosomes along the outermost ring. A thin, dotted red line marks the statistical significance threshold ($p < 0.001$, corresponding to $-\log10 \geq 3$), beyond which black-highlighted dots represent true marker-trait associations. The scale between chromosomes 7D and 1A denotes the LOD threshold. Additionally, the colored bar located at the upper right side of the plot reflects SNP density across the genome, ranging from white (low density) to pink (high density)

represent major QTL clusters involved in stripe rust resistance.

Yellow rust infection type (Yr_IT)

For stripe rust infection type, three MTAs were detected across two chromosomes (Fig. 9). These MTAs were located on chromosome 5D (1 MTA) and chromosome 7 A (2 MTAs), explaining approximately 9–10% of phenotypic variation.

In conclusion, the markers and resistant lines identified in this study are significant for molecular breeding strategies and marker-assisted selection (MAS). In particular, lines 69 and 164, which show resistance to both diseases, have great potential as genetic resources for developing next-generation wheat varieties.

Discussion

The Pakistani economy is primarily based on agriculture, and wheat production is strategically essential. However, average wheat yields lag behind those of many developed countries (Mahmood et al., 2019; Shahzad et al., 2022). Wheat accounts for more than 40% of the country's total cultivated area; therefore, even slight declines in yield can have significant economic and social consequences (Shah et al., 2024).

This study evaluated the resistance levels of 175 wheat lines to leaf and stripe rust under natural conditions for the first time in this scope using phenotypic and genotypic data. The high variation obtained indicates that these lines are based on a broad genetic foundation and that different genetic mechanisms may be effective in rust resistance.

Wheat rust diseases pose a serious threat, particularly due to rapidly evolving strains. Therefore, genetic resistance is considered the most effective solution in terms of environmental sustainability (Gao et al., 2017; Singh et al., 2016; Wang & Chen, 2017). In this study, four wheat lines (3, 27, 108 and 146) were identified as resistant to stripe rust, while 33 lines were resistant to leaf rust based on the resistance criteria of producing a disease severity of less than 5% (DS < 5), and a a resistant infection type (IT < 2) (Table 2). Additionally, two lines (69 and 164) exhibited resistance to both diseases, highlighting their potential importance for resistance gene pyramiding in advanced wheat breeding programs.

The existence of lines that show resistance to both diseases simultaneously (e.g., lines 69 and 164) is

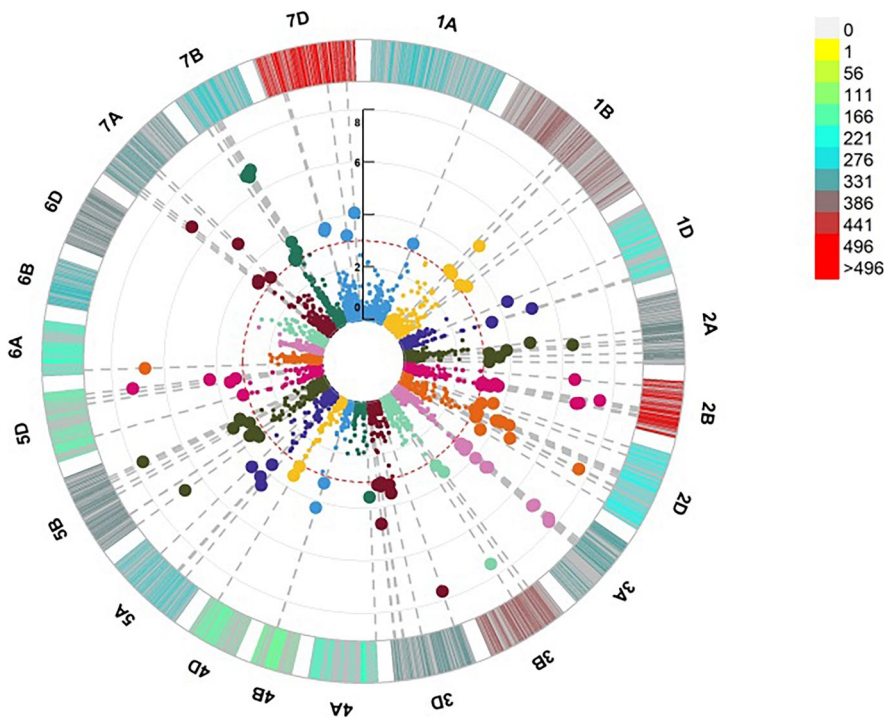

Fig. 8 Genome-wide scan of Yr_DS (inner circle) in circular form. Circular Manhattan plots display the chromosomes along the outermost ring. A thin, dotted red line marks the statistical significance threshold ($p < 0.001$, corresponding to $-\log10 \geq 3$), beyond which black-highlighted dots represent true marker-trait associations. The scale between chromosomes 7D and 1 A denotes the LOD threshold. Additionally, the colored bar located at the upper right side of the plot reflects SNP density across the genome, ranging from white (low density) to pink (high density)

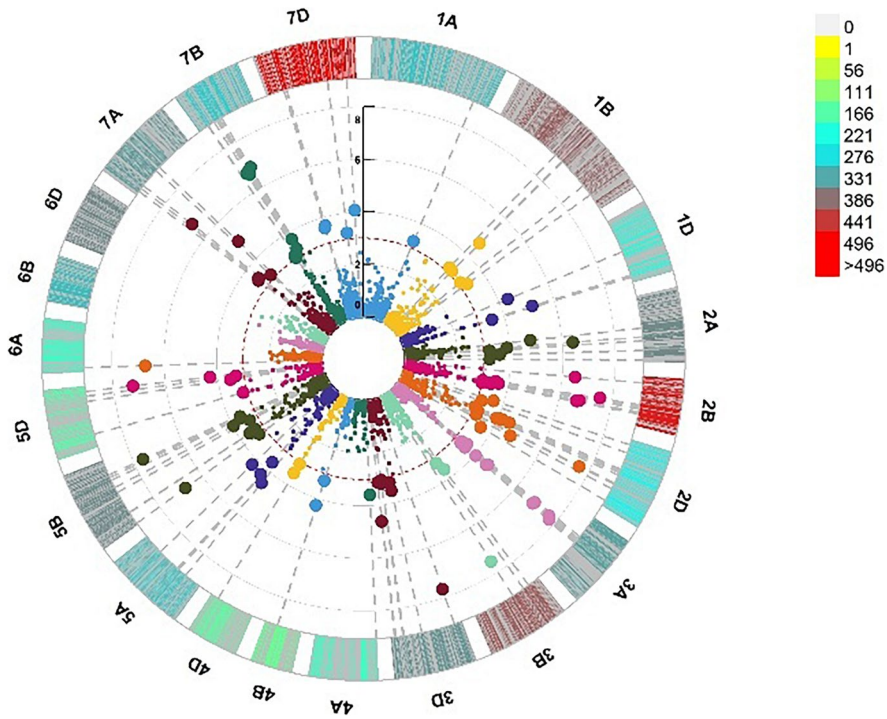

Fig. 9 Genome-wide scan of Yr_IT (inner circle) in the form of a circle. Circular Manhattan plots display the chromosomes along the outermost ring. A thin, dotted red line marks the statistical significance threshold ($p < 0.001$, corresponding to $-\log10 \geq 3$), beyond which black-highlighted dots represent true marker-trait associations. The scale between chromosomes 7D and 1 A denotes the LOD threshold. Additionally, the colored bar located at the upper right side of the plot reflects SNP density across the genome, ranging from white (low density) to pink (high density)

of great importance for combining resistance genes (pyramiding) in advanced breeding studies (Table 2).

The wide range of phenotypic scores and the widespread distribution of QTL regions across multiple chromosomes indicate that a polygenic resistance model is appropriate for rust diseases. This suggests that significant genes, minor-effect genes, and environmental interactions shape resistance. The heterogeneous infection responses observed in some lines should not necessarily be interpreted as evidence of residual segregation, as heterogeneous reactions are commonly reported in rust field evaluations under natural infection conditions due to environmental variation and pathogen diversity. In addition, the CIMMYT-derived wheat lines used in this study represent advanced breeding materials that have undergone several generations of selection and are generally considered genetically stable and highly inbred.

Some of the MTA identified through GWAS analyses overlap with previously reported resistance genes (e.g., Yr7, Yr18, Yr38), supporting the consistency of this study with the literature.

Several marker–trait associations identified in the present study correspond to chromosomal regions previously reported for well-known rust resistance genes. For example, loci located on chromosome 2B may correspond to the Yr7 resistance gene, which has been widely studied in wheat breeding programs (Zhang et al., 2009). Similarly, the Yr18/Lr34 locus, located on chromosome 7D, confers durable adult-plant resistance to multiple rust diseases (Kolmer et al., 2008; Wang et al., 2009). In addition, resistance regions reported in previous studies for Yr38,

Table 2 Number of lines resistant to yellow and leaf rust

	Number of Lines with DS < 5 and IT < 2
Yellow Rust	Line # 3, 27, 108 and 146
Leaf Rust	Line # 4, 40, 56, 65, 67, 70, 83, 84, 86, 88, 89, 98, 100, 106, 107, 108, 109, 110, 111, 112, 114, 115, 116, 137, 138, 142, 143, 144, 145, 146, 154, 167 and 169
Both	Line # 69 and 164

originally transferred from Aegilops ventricosa, may overlap with some of the loci detected in our GWAS analysis (Marais et al., 2005). These findings support the biological relevance of the identified markers and suggest that some of the detected loci may correspond to previously characterized resistance genes. However, identifying new potential resistance loci, particularly on chromosomes 3D and 7D, enhances the contribution of this study.

The presence of markers on all chromosomes (1D–7D) belonging to the D-genome again demonstrates that this genome plays a fundamental role in resistance to leaf rust. This finding is consistent with previous studies emphasizing the importance of the D-genome in hexaploid wheat (Singh et al., 2020; Wang et al., 2024).

Since this study was conducted only in Faisalabad (Central Punjab), it should be noted that the resistance characteristics obtained may be specific to regional pathotypes. Therefore, multi-location trials in different agroecological regions (e.g., Sindh and Northern Punjab) are recommended to verify the stability of resistance.

Conclusion

This study is one of the few studies that integrates comprehensive phenotypic screening conducted under natural field conditions with molecular genotyping. In the study, 33 wheat lines were identified as resistant to leaf or stripe rust; lines 69 and 164 stood out in particular because they simultaneously showed resistance to both diseases. A total of 176 MTAs were identified, and these markers were mapped to important QTL regions that could be involved in resistance to rust diseases. Most of these MTAs overlap with previously reported gene regions, while the remaining portion could be considered new genetic resources.

These data, which can be integrated into molecular marker-assisted selection (MAS) applications in wheat breeding, will shorten the classical breeding period and accelerate the development of more resistant varieties. The results strategically contribute to sustainable wheat production in countries like Pakistan, where rust epidemics are prevalent. The resistant lines identified in the study represent a valuable genetic resource, especially in regions such as Bahawalpur and Faisalabad, where leaf rust is prevalent.

Looking ahead, the wheat lines identified in this study represent valuable genetic resources for breeding programs targeting resistance to leaf and stripe rust. However, it should be noted that the present study was conducted under a single environmental condition during one growing season. Therefore, the detected marker–trait associations should be interpreted as environment-specific and require validation across multiple environments and years to confirm their stability and broader applicability. Future studies integrating multi-location field trials and comprehensive agronomic performance evaluations will be essential for confirming the robustness of these associations and for facilitating the potential registration of new resistant varieties. Despite this limitation, the genotypes identified here provide an important foundation for marker-assisted selection and represent strategic genetic resources that may help strengthen national wheat production and food security.

Authors contributions AJ: Conducted the overall execution of the experiments, collected data, organized and presented the results, interpreted the findings, and was responsible for the writing and revision of the manuscript. WM: Contributed to data collection, presentation of results, and the writing and revision of the manuscript. YEA: Assisted in experiment management, performed analytical work, and contributed to the writing and revision of the manuscript. CE: Assisted in experiment management and contributed to the writing of the manuscript. MARA: Planned and designed the research, provided wheat germplasm, supervised the experiments, conducted analytical work including GWAS and QTL mapping, organized the research workflow, and revised the manuscript to its final version. All authors contributed to the article and approved the, submitted version.

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Data availability The author confirms that the data supporting the findings of this study are available within the article and its Supplementary Material.

Declarations

Ethical This study did not involve any procedures requiring ethical approval. No human participants or animals were used in this research.

Consent to participate Not applicable. The authors conducted the study and did not involve additional participants.

Consent to publish This study does not involve any experiments on humans or animals.

Conflict of interest The author declares no potential conflict of interest.

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