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DEPLOYING GENETIC CONTROL OF WHEAT LEAF RUST: A QTL-BASED APPROACH FOR SUSTAINABLE YIELD

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Abstract

Leaf rust (caused by *Puccinia recondita* f. sp. *tritici*) is the most widespread and regularly occurring rust on wheat. In most parts of the world, wheat production is significantly threatened by leaf rust (LR). For sustainable yield, the most effective approach of disease control is the incorporation of resistance LR genes into superior wheat gene pool. Identifying and characterizing new sources of LR resistance are crucial. Although numerous significant, LR genes for qualitative resistance have been found in wheat. Along with this, more beneficial quantitative resistance sources are still being explored to combat LR. This review refers to 249 LR resistance QTL and covers studies reported from January 1971 to January 2024. Reviewing the QTLs for LR resistance found in bi-parental and association-mapping (AM) studies, we evaluate them in comparison with those found in a 2015 QTL meta-analysis (Vasistha *et al.,* 2024). We have assessed the progress made in locating the molecular markers for the quantitative trait loci (QTL) with respect to adult plant resistance (APR) for LR, which were mostly found in field research. Over the last fifty years, resistance loci for LR were mapped to genomic locations using chromosomal analysis and genome sequencing in bi-parental mapping populations, studies that encompass seventy-nine different donor lines for LR resistance. Furthermore, associations between adult-plant and seedlings resistance marker trait for LR have been found in overall seven association mapping studies in over 4,000 wheat genotypes. All twenty-one chromosomes of hexaploid (6x) wheat have adult plant LR resistance QTLs, with B genome harboring the most QTLs. Additionally, LR resistance QTLs are notably prevalent on the group 2 chromosomes. The A genome has the fewest QTLs linked with resistance LR.

Key words: *Puccinia tritici*; Molecular markers; Adult plant resistance; Leaf rust resistance; Hexaploid wheat

Materials and Methods

Host-leaf rust resistance mechanism: Hexaploid (6x) wheat evolved almost ten thousand years back (Levy and Feldman 2022) from one or more infrequent autonomous crosses between tetraploid emmer wheat (*Triticum dicoccoides*) and the diploid grass *Aegilops tauschii* (Soares *et al.,* 2021). Wheat contributes significantly to global food security by providing 20% of the calories consumed by the world's population (Food and Agriculture (Mottaleb *et al.,* 2024). Mycological diseases, particularly rusts such as LR (brown rust) i.e. Leaf or brown rust (caused by *Puccinia triticina*), Stripe or yellow rust (caused by *P. striiformis f.* sp. *tritici*) and Stem or black rust (caused by *P. graminis f.* sp. *tritici*) are a noteworthy factor affecting the cereal production and are therefore, considered the main problems throughout the world (Fig. 1). The Bible's Old Testament and ancient Roman writings both make mention to wheat rust, demonstrating historically how problematic these diseases have been for the production of cereals (Oliver, 2024). While Leaf rust (LR) is more pervasive and persistent compared to stem and yellow rust, which are thought to be more harmful, it is also a substantial issue year after year (Abdelrahman *et al.,* 2024). As per Belay *et al.,* (2024) statement, *P. triticina* infections typically cause yield losses in wheat by reducing seed weight as well as grains number per spike. Presently, fungicides are a common tool for managing all the three rusts. Nevertheless, in almost all wheat growing areas, inadequate availability of necessary fungicides and improper spraying can significantly reduce the efficacy of fungicide, have a severe impact upon human health as well as the ecosystem, and raise production cost (Ceresini *et al.,* 2024). As a result, the most efficient, economical and ecologically benign method of rust control is to introduce efficacious and durable genetic resistance into the new germplasm of wheat (Pramanik *et al.,* 2024).

Wheat leaf or brown rust resistance: Numerous loci in wheat have been identified that provide resistance to the three rusts pathogens (Tong *et al*., 2024). The loci which are identified as LR resistance, being distinct genetically from loci that currently exist, unique loci are identified with a specific *Lr* number. All stages resistance (abbreviated as ASR) are what most of LR resistance genes with *Lr* gene numbers given. ASR is efficient during the whole span of a plant life. It is frequently qualitative or significant resistance and connected to a protective or defense mechanism known as hypersensitive immunity that causes programmed cell demise. Nevertheless, ASR normally turns out as race

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specific, the resistance is only efficient against the isolates of *Puccinia triticina* that carry a respective a-virulence gene and are short lived, increase mutation-frequency and variation in virulence present within the populations of *P. triticina* which results in the ineffectiveness of these LR resistance genes (Kangara, 2021).

As a result, it has proven challenging to develop wheat varieties with durable LR resistance utilizing ASR genes alone. Numerous *Lr* ASR genes, like as the *Lr10* or *Lr16* used in the Canadian wheat variety Selkirk, have shown to be inefficient after only a few years of cultivation. While virulence to *Lr10* increased quickly following Selkirk introduction, virulence to *Lr16* began to rise in less than a decade after Selkirk has been extensively grown (Bokore *et al.,* 2022). The combination of all stage resistance (ASR) genes can extend the useful lifespan of rust resistant varieties, though doing so increases the possibility of producing races of isolates of rust with different levels of susceptibility, which could result in populations of hyper-virulent pathogens. Presently, 15 LR genes for adult-plant resistance (APR) have been assigned specific *Lr* gene numbers. According to Sheng *et al.,* (2022), seven of the *Lr* genes i.e., *Lr12; Lr13; Lr22a/b; Lr35; Lr37; Lr48* and *Lr49* were shown to be race specific, whereas other 8 are concontinuing be regarded as being racially nonspecific (Table 1). According to Kokhmetova *et al.,* (2023) only later in the plant development do the race specific loci for adult plant resistance genes; *Lr12, Lr13*, and *Lr22b* express themselves and are qualitatively linked to a hyper-sensitive cell death response. Even though certain APR genes partially protect against LR, and are efficacious when used extensively, for a long time, and in LR-friendly locations. For instance, the APR gene *Lr34*, has been widely used in spring wheat varieties in CIMMYT, has demonstrated its durability (Bräunlich *et al.,* 2021). The special properties of *Lr34, Lr46,* and APR *Lr67* include temporary resistance to all species of powdery mildew as well LR, which is brought on by *B. graminis f. sp. tritici*. Additionally, several of these APR genes, including *Lr34,* display a gradual rusty phenotype. Resistance slows the pathogen growth, causing rust pustules to form later and generally smaller and develop only several urediniospores (Osuna-Caballero *et al.,* 2022).

Subsequently, the groundbreaking research of R. M. Caldwell in USA that today acts as a leading concept in most breeding and research projects, the worth of adult plant resistance to impart persistent protection against the cereal rusts has attracted tremendous interest. New quantitative trait loci (QTL) have been found more rapidly because of the resurgence of interest in APR genes, several of which confer resistance to all rust types (Kangara, 2021). A cluster of 4 or 5 QTLs or genes is needed in order to develop appropriate levels of LR resistance, nevertheless, just a single quantitative trait locus seldom transmits significant resistance, particularly when there is intense pressure of disease (Bräunlich *et al.,* 2021) (Fig. 2). It's crucial to comprehend how each QTL is affected by environmental factors, as well as how the QTL interact to affect the ultimate phenotype of rust resistance. Recent studies have explored the potential of natural products and biofertilizers in enhancing crop health and disease resistance, offering insights relevant to sustainable yield strategies (Rafiq *et al.,* 2024a; Rafiq *et al.,* 2024b).

Therefore, it is crucial to consider the expression of QTL throughout a diverse kind of settings, different seasons, and under varied amounts of disease severity when estimating the usefulness of a QTL for LR resistance breeding. We concentrate on the quantitative LR resistance in hexaploid (6x) wheat that was established via field tests in this review. This review refers to 249 LR resistance QTL and covers studies reported from January 1971 to January 2024. Reviewing the QTLs for LR resistance found in bi-parental and association-mapping (AM) studies, we evaluate them in comparison with those found in a 2015 QTL meta-analysis (Vasistha *et al.,* 2024). Therefore, the purpose of this study is to recapitulate and sum up the field and APR QTLs for LR.

APR Loci with race non-specific *Lr* Identifications: *Lr34, Yr18, Sr57, Pm38* (hence referred to as *Lr34*) has initially been discovered in Canada by Radchenko *et al.,* (2022). Since the beginning of the 20th century, wheat germplasm harboring *Lr34* has been used to create new cultivars. Even though the *Lr34* resistant phenotype might change depending on the environment and genetic makeup, *Lr34* has maintained resilience for more than five decades (Spychała *et al.,* 2023). First ever cloned APR gene was *Lr34* (Khan *et al.,* 2024). Presently, 2 of *Lr34* dominant alleles have already been identified, differing only by 2 exon polymorphisms and they both encode an ATP binding-cassette (ABC) transporter (Li *et al.,* 2023).

For *Lr34*, 3 more haplotypes have been reported, with 2 being regarded as unusual (Tong *et al.,* 2024). Studies indicate that *Lr34*, positioned upon the shorter arm of 7D, is unique to the wheat D-genome and chronologically the vulnerable haplotypes are older than the resistant. Owing to the development of gene-specific DNA markers, *Lr34* could be coupled with other QTL/desired genes which were made possible by the cloning of the gene (Cloutier *et al.,* 2023) (Table 1). This provides wheat breeders a quick and effective tool for marker assisted selection (MAS).

This APR gene *Lr46/Yr29/Sr58/Pm39* (hence referred to as *Lr46*) was found in CIMMYT wheat material (Zelba *et al.,* 2024). For the very first time, it was discovered in Pavon 76 (a wheat cultivar) and was found upon the longer arm of 1B. (Fan *et al.,* 2024). In MAS, *Lr46* locus is marked by the marker called csLV46 (E.S. Lagudah, personal comm./unpublished data). According to Zelba *et al.,* (2024), *Lr46* and *Lr34* both confer multiple-pathogen resistance, while resistance of *Lr46* is less pronounced in some situations than that of *Lr34* (Spychała *et al.,* 2024).

Lr67/Yr46/Sr55/Pm46 (hence referred to as *Lr67*) was initially found in PI250413 (Pakistan wheat accession) which was then moved to Thatcher for creating RL6077, an isogenic line (Bapela *et al.,* 2023). *Lr67* was first positioned to the longer arm of 4D by Li *et al.,* in 2023. Huerta-Espinol *et al.,* (2020) reported *Lr67* in Yaqui53, Chapingo48, and Chapingo53 (CIMMYT cultivars), whereas Milne *et al.,* (2024) identified it in Sujata (an indian wheat cultivar). The *Lr67* has been cloned which was very similar to a hexose transporter called *LR67res*.

Although rust infection upregulates both the susceptible allele, *Lr67sus*, and the resistant allele, *Lr67res*, only *Lr67res* confers resistance. In a region shared by orthologous hexose transporters, *LR67res* and *LR67sus* differ by two amino acids, which lowers the protein affinity for glucose. Through heterodimerization, *LR67res* is considered to have a dominant-negative effect that lowers glucose uptake and prevents biotrophic pathogens from colonizing plant tissues (Milne *et al.,* 2023). According to him, the advent of gene-specific-DNA-markers for marker assisted selection was made possible by the cloning of *Lr67*.

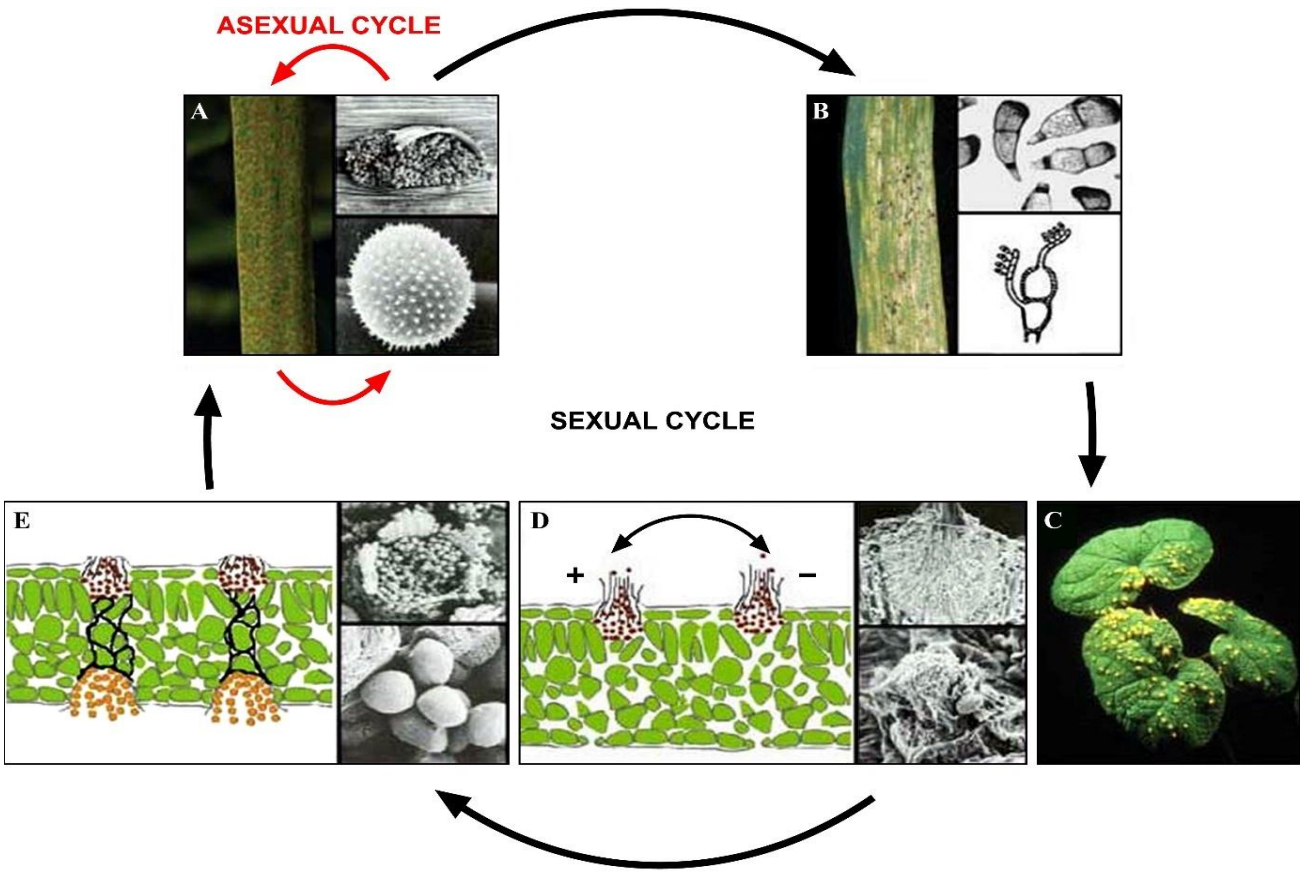

Fig. 1. Life cycle of *Puccinia triticina*. (A) Uredinia and urediniospores on wheat leaf; (B) Telia and teliospores initiating sexual reproduction; (C) Pycnia on Thalictrum leaves from basidiospore infection; (D) Cross-section of pycnia with pycniospores and hyphae in nectar; (E) Cross-section showing aecia and aeciospore formation after fertilization. Insets show microscopic details (Zhao & Kang, 2023).

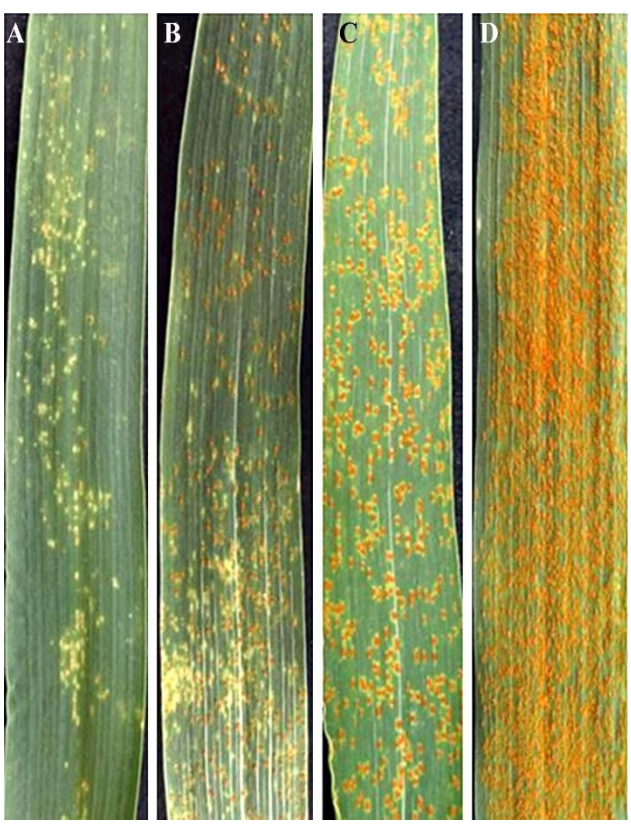

Fig. 2. Modified Cobb Scale; severity of wheat LR categorized as: A, resistant; B, moderately resistant; C, moderately susceptible; D, susceptible.

Several other APR genes were assigned *Lr* numbers namely *Lr68; Lr74; Lr75; Lr77* and *Lr78*. Tong *et al.,* (2024) identified *Lr68* upon the longer arm of 7B. It might be originated from Frontana (a Brazilian cultivar) which also has the APR genes *Lr13* and *Lr34* as its ancestor. *Lr68* locus is flanked by two marker loci *Xgwm146* (0.6 cM) as well as *Psy1-1* (0.5 cM), but they are not appropriate for MAS. Who found out that a dominant marker called *csGS* (1.2 cM) and a co-dominant marker called *cs7BLNLRR* (0.8 cM) were created for APR *Lr68*.

The APR gene *Lr74* on chromosome 3BS that was initially discovered in the wheat cultivars Caldwell and Spark as well as the selection BT-Schomburgk (Kolmer *et al.,* 2018a) The shorter arm of 1B contains the LR APR *Lr75*, which was initially discovered in Forno, a Swiss cultivar (Singla *et al.,* 2017). There are six LR resistance QTLs including *Lr34* in Forno, according to Farooq *et al.,* (2023). In Switzerland, *QLr.sfr-1BS* (*Lr75*) accounted from 29 and 33 percent of phenotypic variance. Singla *et al.,* (2017) reported that the actual mapping population developed from Arina Forno cross was reassessed, and *QLr.sfr1BS* was designated as *Lr75*.

According to Kolmer *et al.,* (2018b), on the longer arm of 3B, *Lr77* from Santa Fe (a winter wheat cultivar) was discovered. An SNP marker *IWB10344* which defines the locus, imparts r^2 values ranging from 0.24 to 0.81. The APR gene *Lr78* has been discovered in Toropi (a Brazilian wheat cultivar) on 5D shorter arm which is recognised by *IWA6289*. Spychała *et al.,* (2024) also reported that *Lr78* conferred up to 0.54 r^2 values LR resistance.

Table 1. List of DNA markers for LR gene identification in wheat.

Marker	Species/Origin	Gene	Chromosome	Reference
RFLP, STS	*Triticum aestivum*	*Lr*1	5DL	Song *et al.,* 2023
RFLPcMW684	*Aegilops umbellulata*	*Lr*9	6BL	Wang *et al.,* 2023
RFLP, STS	*Triticum aestivum*	*Lr*10	1AS	Yuan *et al.,* 2021
RFLP	*Triticum aestivum*	*Lr*13	2BS	Kumar *et al.,* 2017
RFLP, RAPD	*Agropyron elongatum*	*Lr*19	7DL	Xu *et al.,* 2023
RFLP	*Triticum aestivum*	*Lr*23	2BS	Ren *et al.,* 2023
RFLP, PSR1205	*Agropyron elongatum*	*Lr*24	3DL	Chhuneja *et al.,* 2016
SCAR	*Agropyron elongatum*	*Lr*24	3DL	Li *et al.,* 2024
RAPD, DGGE	*Secale cereal*	*Lr*25	4AL/2RS	Chelkowski *et al.,* 2001
RFLP	*Triticum aestivum*	*Lr*27	1BL/1RS	Ren *et al.,* 2023
RAPDOPJ-01, STS	*Aegilops speltoides*	*Lr*28	4AL	Xu *et al.,* 2023
RAPD, DGGE	*Agropyron elongatum*	*Lr*29	7DS/Ae#1S	Chelkowski *et al.,* 2001
RFLP	*Triticum aestivum*	*Lr*31	4BS	Ren *et al.,* 2023
RFLP	*Triticum aestivum*	*Lr*34	7DS	Ren *et al.,* 2023
RFLP, STS	*Triticum speltoides*	*Lr*35	2B	Kumar *et al.,* 2017
RAPD, SCAR	*Aegilops ventricosa*	*Lr*37	2A	Ren *et al.,* 2023
CAPS	*Triticum speltoides*	*Lr*47	7AS	Li *et al.,* 2023

Since all these genes only provide a small amount of resistance, they can be coupled with other ASR and/or APR genes to provide a greater level of resistance. For instance, the QTL *QLr.cdl-5BL* and the APR gene *Lr46* together showed an improved additive resistance (Rosa *et al* 2019). Even while *Lr16* and *Lr23* (ASR genes) alone do not offer a substantial level of LR resistance, clubbed with *Lr34,* they have shown considerable LR resistance to the hard red wheat cultivar called Norm for a number of years (Rosa *et al.,* 2019; Kumar *et al.,* 2022). The ideal ASR and APR gene combination is typically thought to provide the most effective field-level LR resistance while perhaps preserving long lasting resistance (Rani *et al.,* 2019).

Mapping of LR resistance QTLs: A quantitative trait locus (QTL) is a segment of the genome that has one or more genes that impart a quantitative phenotype. The gene (in question) manifestation may be impacted by other gene(s) in the genetic background through interactions called epistasis or environmental variables (Mackay & Anholt, 2024). A population of plants with the QTL denoted by various alleles, each one of which confers a discernible but distinct phenotypic, is necessary for QTL identification. There is a discernible difference in the average resistance phenotype among plants bearing various alleles at that locus, the QTL is said to exist.

Additionally, the population must have enough genetic diversity to identify polymorphic-DNA-markers associated or linked to the QTL(s). For mapping of the LR resistance QTL, a variety of population types have been used, namely backcrosses (BCs), F_2, recombinant inbred line (RILs), doubled haploid (DH), multi-parent advanced generation intercrosses, near isogenic line, and association mapping populations (AMP). All kinds of populations have both advantages as well as disadvantages. The amount of phenotypic genetic variability present in the two parents of the initial cross limits the ability to find QTL in mapping populations resulting from bi-parental crossings (Dash & Mishra, 2024). Moreover, they typically reflect brief recombination's, enabling the localization of QTL to intervals of no more than 10-20 cM. (Dash & Mishra, 2024).

To get around bi-parental populations' drawbacks, multi-parent mapping populations have been developed. Recurrent crossings, increase the amount of recombination's, allowing for higher mapping-resolution, and different parents utilized to produce the population allow the incorporation of numerous QTLs and QTL alleles.

Until now, bi-parental mapping populations have been utilized to identify the majority of LR resistance QTL. Association Mapping (AM) panels have more recently been employed to broaden the new wheat germplasm search for LR resistance QTL. Large collections of varied germplasms can be processed using AM, although MTA validation typically requires follow-up confirmation, frequently using biparental mapping (Bekele *et al.,* 2022). Association Mapping (AM) is predicated on the idea that the association between genes and markers has been severed during a few recombination generations, and any correlations that still exist are the result of relative proximity.

Thus, AM circumvents two key drawbacks of bi-parental mapping i.e. the restricted recombination amount that takes place in growth of a bi-parental mapping population, which then affects the positioning resolution for QTL and the slight allelic variation that assorts during a bi-parental cross. According to Jain & Sevanthi (2024), Association Mapping (AM) is vulnerable for the identification of false positive QTL because of population structure and is unable to identify uncommon 5% alleles in the Association Mapping (AM) panel.

Gostel & Kress (2022) reported that now the modern DNA marker tools have made it potentially possible to create accurate maps of different organisms with huge genomes e.g. hexaploid (6x) wheat, with most of its chromosomes having strong marker coverage, but owing to the DNA polymorphism, the D-genome still has a low level of representation. We found that the use of SSR-markers in wheat is still a common choice given their good genome coverage, co-dominant inheritance, reproducibility, high information content, and easy detection after analyzing and reviewing 66 LR resistance studies. SSR markers are useful for comparing different genomic maps. Nevertheless, Next Generation Sequencing (NGS) SNP-marker technologies like the 90K SNP-arrays or Illumina iSelect 9K usage (Kumar *et al.,* 2022), are already replacing SSR-markers in studies that map the resistance to LR (Kumar *et al.,* 2021; Chhetri *et al.,* 2016). After the orientation of the wheat RefSeq-v1.0 genome and these novel marker technologies, precise approaches for finding QTLs and comparing QTL positions between wheat cultivars or genotypes are now available.

To find QTL, several statistical techniques have been reported (Wang *et al.,* 2022). Centimorgans (cM) on a genetic marker linkage map, % PVE (percentage of phenotypic variation explained) which is denoted as $r^{2,}$ and logarithm of the odds (LOD) score are used to define a QTL. The overall phenotypic variance percentage indicates the impact of the QTL on the phenotype. The statistical significance of the QTL evidence at a certain place is measured by the LOD score (Si *et al.,* 2023).

Major QTL is commonly referred to as such because it has a significant impact on phenotypic and is typically found in multiple environments. When a QTL accounts for a minimum 15-20 percent of PVE to segregate in the test population, some authors classify it as "major" (Dong *et al.,* 2024). However, depending on the study, the population, and the growing environment, the phenotypic variance may be affected differentially by the same QTL.

Discussion

In this study, we observed 249 LR resistance QTLs found in 79 different donor lines and 70 bi-parental mapping populations covering all 21 wheat chromosomes (Table 3) by 35 meta-QTL (MQTL) and approximately 200 MTA/QTL found in 7 Association Mapping (AM) studies. Vasistha *et al*., (2024) conducted a MQTL study that included 144 LR resistance QTLs found in 20 bi-parental mapping populations. The thirty-three parental lines comprising bread and durum wheat cultivars were examined in 52 locations between 1999 and 2015 making the mapping populations. According to Wen *et al*., (2017), the results of three different QTL investigations were combined in this MQTL analysis, which projected each distinct QTL on a consensual map using the QTL related markers shared by the mapping-populations. Ng *et al*., (2017) reported that MQTL study boosted statistical strength and enabling a more accurate evaluation of genetic changes or effects by combining the findings of much research. The MQTL study found 48 loci upon 17 chromosomes, out of which 13 regions had a single QTL and the remaining 35 regions had 2 or more than 2 closely connected QTLs for LR resistance (out of 144 QTLs, 128 were included in the MQTL study). Vasistha *et al*., (2024) discovered that 7 of the MQTLs were co-localized with the 11 identified *Lr10; Lr13; Lr14; Lr19; Lr23; Lr27; Lr34; Lr46; Lr67; Lr68* and *Lr71*.

LR resistance association mapping (AM) studies were conducted on 3640 genotypes of spring wheat genotypes (Beral *et al.,* 2022; Semagn *et al.,* 2021; Yan *et al.,* 2023; Pu *et al.,* 2022), including 96 genotypes of winter wheat (Zhou *et al.,* 2022), 295 lines of mixed type wheat (Daskalova *et al.,* 2022), and 173-synthetic hexaploid wheat across 20 wheat chromosomes. These studies found 175 MTA/QTLs, while chromosome 3D did not show any associations (Table 3).

About 133 QTLs, the B genome has the most LR resistance, chiefly found on 1B and 2B. B genome contains about 53 percent of the 249 QTLs while 20 MQTLs are identified in bi-parental mapping studies. A genome has the fewest QTLs linked with LR resistance. The chromosomes with fewest LR resistance QTLs are 4A, 5D, 6D and 7A. Chromosome 2B is widely recognized for harbouring resistance loci for diseases like powdery mildew, yellow and black rust. Chromosomes of group 2 contain 66 LR resistance QTLs and 6 MQTLs (Sheng *et al.,* 2022). The B genome (largest of all wheat genomes), which differs greatly from the genome A and D, is quite enormous. Locus is also associated to leaf tip necrosis (Ltn2), a condition in which leaf tips prematurely senesce, accomplished that the 3 ancestral genomes, which are homologous chromosomes capable of pairing during meiosis and are genetically related, have experienced significant alterations after the production of the maiden hexaploidy (Kozub *et al.,* 2022).

D-genome exhibits minimum DNA polymorphism in hexaploid wheat, perhaps because of restricted polyploidization with emmer wheat (*T. dicoccoides*) throughout its development, but according to Biradar *et al*., (2022), it differs the least from its parent *A. tauschii*. Although D genome-donor no more exists, *A. tauschii* provides a promising extensive genetic variation source which can be utilized in the hexaploid (6x) wheat because of its wide geographical distribution stretching from Iraq, Iran, Syria to the western Himalayan slopes of China (Jhala *et al.,* 2017). He also reported that uncertainty exists over the exact progenitor of the B-genome of hexaploid wheat. According to Mirzaghaderi & Mason (2019), the A-genome donor is thought to have been associated to *Triticum urartu* (the diploid wild einkorn wheat) despite substantial gene loss on A-genome compared to *T. urartu*.

The A-genome in hexaploid wheat has much fewer loci for LR resistance compared to B and D genomes that may be explained by the gene loss. The remaining sections of this study cover the LR resistance QTLs found in bi-parental mapping studies and the chromosome-group-specific MQTL-analysis. Although it must be kept in mind that other factors like genes for LR resistance assorting in population, where QTL was mapped, could impact the percent PVE of a QTL, it is important to note that the percent phenotypic variance provide the researchers an indication of the “potential power" for LR resistance. The majority of studies could not prove that a QTL was located at what seemed to be the same chromosome position, despite the fact that multiple marker methods have been employed over the course of the evaluation period. We could determine that the similar LR resistance QTL was being described when QTLs were reported as being associated with particular *Lr* genes like *Lr34* (7DS).

Recent advancements in QTL mapping have significantly enhanced our understanding of genetic resistance to wheat LR. Notably, adult plant resistance genes such as Lr34, Lr46, and Lr67 have been identified and cataloged, contributing to durable resistance in wheat cultivars (Zhang *et al.,* 2017). The integration of these genes into breeding programs has led to the development of wheat varieties with long-lasting resistance to LR (Bokore *et al.,* 2020). Furthermore, the advent of next-generation sequencing (NGS) technology has enabled high-throughput and cost-effective genotyping systems, facilitating faster and more accurate mapping using single nucleotide polymorphism (SNP) markers (Tong *et al.,* 2024). These technological advancements underscore the potential of QTL mapping as a cornerstone for achieving sustainable yield in wheat production (Sanjay & Prakash, 2024).

LR-linked QTLs in chromosome group one: The homologs of 1A, 1B and 1D have 48 QTLs as well as 5 MQTLs. Out of these QTLs, chromosome 1A has 11, 1B has 32 and 1D has 5 QTLs as reported. One MQTL has been identified upon chromosome 1A while 4 upon chromosome 1B. Wheat genotypes Sujata, Luke, Catbird, Shanghai 3, Chapio, Syn022L, 842-2, Opata 85 and Apache are the source of the 11 QTLs and one MQTL found on 1A (Liu *et al.,* 2020). As per Gao *et al.,* (2024) report, when bred with Aquileja, *QLr.cau-1AS* accounted for 44.3-52.6% PVE for LR in a cultivar Luke but only 22.3-32.8% after crossing with the cultivar AQ24788-83. When cultivated in China, RIL harbouring *QLr.cau1AS* showed a 55.5% decline in the severity of LR in comparison to control lines. A recombinant inbred line having *Lr34* and *QLr.cau-1AS* exhibited a decline of 78.5% in the severity of final LR (Gao *et al.,* 2024).

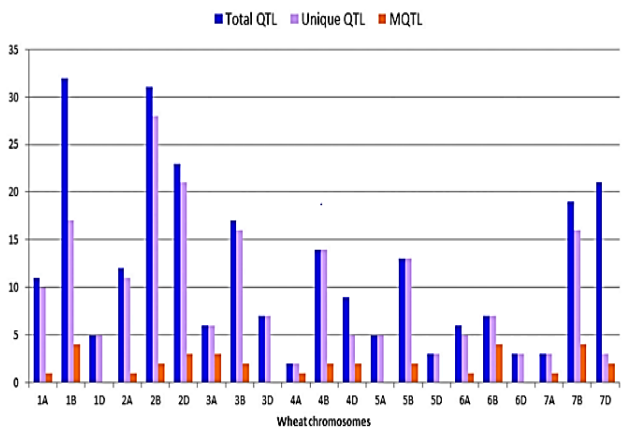

Fig. 3. Total no. of QTL identified on each hexaploid wheat chromosome, as documented in 70 biparental mapping studies (blue columns) and one LR QTL meta-analysis (MQTL; orange columns). Certain QTLs may be reported more than once, as different markers were used in each mapping study, making comparison of genome locations difficult. We confidently identified QTLs in independent studies as having the same chromosomal location, also reported the unique QTL number on each chromosome (light purple columns).

An ASR gene *Lr10* colocalized with the MQTL1 on 1A. (According to Pinto *et al.,* 2018), the CIMMYT wheat germplasm, *Lr46*, which is located on chromosome 1B long arm, is frequently found. Khan *et al.,* (2024) reported that, all rust causing pathogens *P. triticina* (*Lr46*), *P. graminis f. sp. tritici* (*Sr58*), *P. striiformis* (*Yr29*) possessed broad-spectrum resistance. Locus is also associated to leaf tip necrosis (*Ltn2*), a condition in which leaf tips prematurely senesce (Kozub *et al.,* 2022). *Lr46* (from 19 different donor genotypes of wheat) was reported in almost 20 studies. This APR gene has been linked to *csLV46* marker and is utilized in marker assisted selection for *Lr46*, in 13 studies. The existence of *csLV46* led us to believe that a particular QTL was a strong candidate for *Lr46* (Fig. 3) Moreover, *Lr46* is highly influenced by the genetic make-up as well as environment (Milne *et al.,* 2024) and higher temperatures also reduce its effectiveness.

In various mapping-populations and trials, *Lr46* predicted anywhere between 2.9 and 74.5% of the overall PVE. *Lr46* colocalized with the MQTL5 on chromosome 1B (Vasistha *et al* 2024). The SSR loci *Xgwm604* and *Xswm27* surround the *Lr75* (*QLr.sfr-1BS*), which was likewise localized to the shorter arm of 1B (Singla *et al.,* 2017). When cultivated in Switzerland, APR *Lr75* accounted for 28-32% PVE in the Arina Forno cross (Farooq *et al.,* 2023).

Based on the wheat genotypes Kenya Kongoni, Quaiu 3, Avocet-YrA and Syn022L, 5 QTLs have been identified on 1D in 4 studies (Kumar *et al.,* 2021). ASR genes *Lr21* and *Lr42* were subsequently discovered to be two of these QTLs (Xu *et al.,* 2021). Diéguez *et al.,* (2021) identified a QTL on 1D which was mapped adjacent to *Xbarc149* while dealing with a backcross population produced from a synthetic cultivar Syn022L. According to Diéguez *et al.,* (2021), this locus reduced the symptoms of LR by 46.3 and 43.6%, respectively in both seedlings as well as in the field (*QLr.B22-1D*). Even though the seedling (*QLrs.B22-1D*) shared a chromosomal region with *Lr21.* When it was treated with the same isolate of *P. triticina*, various seedling morphologies were seen. This would imply either the existence of a novel *Lr21* allele or a new, isolated ASR gene adjacent to Lr21 (Diéguez *et al.,* 2021).

LR-Linked QTLs in chromosome group two: With 66 QTLs and six MQTLs, the group two chromosomal homeologs have the most LR resistance genes. Of these 66 QTLs, 12 are located on 2A chromosome; 31 upon 2B chromosome; and 23 upon 2D chromosome. 1 MQTL has been reported on chromosome 2A, 2 MQTLs on chromosome 2B while other 3 MQTLs have been found on chromosome 2D. Group two chromosomes currently contain about 20 identified *Lr* genes and are mostly ASR genes (Sheng *et al.,* 2022). *Lr37* from *T. ventricosum* has been moved to the shorter arm chromosome 2A (Li *et al.,* 2023). According to Dhillon *et al.,* (2020), *Qlr.inra-2Ab* which accounts for 5.6-12.2% of PVE and is associated with *Lr37*, was discovered in the cultivar Apache while *QLr.hbau-2AS* originated from Weimai8 (a cultivar), found between *Xcfd36* as well as *Xbarc1138*, within a range of 2.58 cM and described 25.79-71.55% of PVE.

Upon 2B, 7 *Lr* genes have been discovered. Out of these 7 *Lr* genes, 3 are the race specific adult plant resistance genes i.e. *Lr13, Lr35*, and *Lr48* as reported by Sheng *et al.,* (2022). Both *Lr13* as well as *Lr48* occur upon the shorter arm of the chromosome 2B, while *Lr35* is adjacent to the centromere (Sheng *et al.,* 2022). In Australia and Canada, *Lr13* tends to maintain LR resistance while in South America and Mexico, it has lost its effectiveness (Zhang *et al.,* 2016). Vasistha *et al* (2024) reported that Creso and Apache (wheat cultivars) were used in all 7 studies that make up MQTL8, which is most likely related to the gene *Lr13*. *Lr48* being a recessive race-specific gene linked to a hypersensitive-response (Bansal *et al.,* 2008).

Likewise, *Lr35* (conferring a hypersensitive response) following infection with *P. triticina*, was moved from *A. speltoides* to hexaploid (6x) wheat (Nsabiyera *et al.,* 2020). Location wise, the occurrence of *QLr.hebau-2BS* (a significant QTL mapped on 2BS) is different from the genes *Lr13* and *Lr48* (Zhou *et al.,* 2022). With the loci *XwPt8548* and *XwPt2314* on either side, this QTL was mapped while crossing Shanghai3 and Catbird and

imparted between 15.3-37.4% PVE. *QLr.inra-2B* (located on the longer arm of the 2B) accounts for 15-35.6% PVE for LR resistance in cultivar Apache (Dhillon *et al.,* 2020).

As reported by Sheng *et al.,* (2022), 8 identified *Lr* genes existing on chromosome 2D carrying *Lr22a* from *Aegilops tauschii*, whereas *Lr22b* from *Triticum aestivum*, giving race specific adult plant resistance. A couple of QTLs that best described 34.6-48.2% and 4.4-46.4% of the PVE, respectively, of the 23 QTLs found on chromosome 2D were *QLr.inra-2D* (cultivar Balance) and *QLr.lp.osu-2DS* (CI-13227). With a long latent period, the phenotype with *QLrlp.osu-2DS* displays slow rusting. The mean latent duration for RILs carrying *QLrlp.osu-2DS* was 13 days, compared to 7.5 days for lines lacking the QTL.

LR-Linked QTLs in chromosome group three: Overall, 7 identified genes have been documented on chromosomes of group 3 with *Lr24, Lr27, Lr32, Lr63* and *Lr66* are ASR, whereas *Lr74* and *Lr77* are APR genes (Sheng *et al.,* 2022). 6 QTLs on 3A, 17 QTLs on 3B, and 7 QTLs on 3D are among the 30 QTLs and 5 MQTLs that have been found on group three chromosomes. 3 MTQLs on 3A while 2 on 3B were found. According to Chu *et al.,* (2009), a significant QTL called *QLr.fcu-3AL*, produced from TA4152-60 (a hexaploid wheat line), demonstrated LR resistance in seedling trails and accounted for 10 and 18% PVE in field experiments, suggesting a viable ASR gene. Chhetri *et al.,* (2016) identified that *QLr.sun-3BS* on 3B described 2.3 to 35.7% of overall PVE in BT-Schomburgk selection, whereas the QTL *QLr.ifa-3BS* accounted for 4.2 to 40.3 of PVE in the wheat cultivar Capo. The multi-pathogen resistance gene *QLr.cin-3BS* has been discovered in Chapio (a wheat cultivar), may be sharing the same locus with *Sr2* (He *et al.,* 2020). A Locus called *QLr.hwwg-3B.1* upon chromosome 3B which described 16.6-19.2% PVE and was earlier identified as *Lr74* was mapped by Ye *et al.,* (2022).

Being the highly efficient LR adult plant resistance locus upon 3D chromosome, *QLr.cim-3DC* described 17.8-25.4% PVE in a cultivar Francolin#1 (Ren *et al.,* 2023). Barely 4-7.1% of the LR PVE in Quaiu 3 (a wheat line) was explained by *QLr.tam-3D*, but it did co-occur along with a stripe rust locus called *QYr.tam-3D* as reported by Xu *et al.,* (2021).

LR-Linked QTLs in chromosome group four: On the group four chromosomes, 25 QTLs and 5 MQTLs have been reported. 2 QTLs were identified on 4A chromosome, 14 on 4B chromosome whereas, 9 on 4D chromosome. Similarly, one MQTL was documented on 4A, two on 4B whereas, two on 4D. *Lr28* and *Lr30* being the ASR genes, two identified genes were mapped on 4A. (Sheng *et al.,* 2022). 3.4-7.5% PVE was described by a small QTL called *QLr.hebau-4AL* which was found in Chinese Spring (Kumar *et al.,* 2022). *Lr12* is located on chromosome 4B. The *Lr12* gene co-segregates with the *Lr31* ASR gene.

Although Ye *et al.,* (2022) described that *Lr31* could offer LR resistance in the presence of gene *Lr27* only, located on chromosome 3BS. Prior studies caused a slight doubt regarding the position of *Lr31* and *Lr12* on 4B (Ye *et al.,* 2022). However, more recent research documented by Kokhmetova *et al.,* (2023) revealed a new location of gene *Lr12* upon the longer arm of 4B, surrounded by both markers *Xgwm149* as well as *Xgwm251*.

A total of 14 QTLs are associated with LR resistance upon 4B chromosome having PVE between 5.4 (*QLr.spa-4B*) to 24.4% (*QLr.hebau4B*). The QTL *QLr.spa-4B*, which is derived from Carberry (cultivar), is surrounded by marker loci *wPt-5303* and *wPt-1849*. Both markers *BS00022181 51* as well as Excalibur *c37565 709*, shared the same locus corresponding to APR *Lr12* on 4B, were found to be associated with the *QLr.hebau-4B* of cultivar Chinese Spring. It is believed that *QLr.cim-4BS* (discovered in Chapio) lies in the *Lr12* region (He *et al.,* 2020). A hypersensitive reaction is linked to *Lr49*, which corresponds to chromosome 4B. (Nsabiyera *et al.,* 2020). The APR *Lr67* on 4D, was first inserted in Thatcher NIL RL6077 from PI250143 (Bapela *et al.,* 2023). As documented by Dubey *et al.,* (2020), *Lr67* is linked to leaf tip necrosis (*Ltn3*). Moreover, according to Vasistha *et al* (2024), *Lr67* co-localizes with MQTL20, a collection of three QTLs from Sujata, TA4252-60 and PI250143. In the field tests, both Sujata and W195 (a wheat line) had a PVE of 20-44.5% and 33.6-57.9% that *Lr67* explained, respectively (Chhetri *et al.,* 2016). On chromosome 4D, the minor effect *QTLs QTL-4DL, QLr.fcu-4-DL, QLr.B22-4D* and *QLr.inra-4Da* were discovered.

LR-linked QTLs in chromosome group five: On the group five chromosomes, 20 QTLs and 2 MQTLs were discovered, with 5 QTLs on 5A, 13 on 5B, 3 on 5D, and 2 MQTLs on 5B. Although small LR resistance QTL has been found, but, presently no defined *Lr* genes are catalogued on chromosome 5A (Sheng *et al.,* 2022). Several studies have discovered two QTLs *QLr.cim-5AC* and *QLr.cimmyt-5AL* originating from the cultivar Avocet which according to Rollar *et al.,* (2021) accounted for 5% and 5.2 to 7.4% PVE, respectively. On 5A, the two of them were located near the centromere. Singh *et al.,* (2009), Messmer *et al.,* (2000) and Li *et al.,* (2017) documented that all the three QTLs i.e., *QLr.hwwg5AS* in Ning7840, *QLr.sfrs-5AS* in Forno and *QLr.pbi-5AS* in Beaver are localized on the shorter arm and describe 7.5, 7.7, and 11.2% of the PVE, respectively.

Two small QTLs for APR on chromosome 5B in wheat cultivar Opata85, *QLr.ccsu-5B.4* describing 2.5-8.4% PVE and *QLr.ccsu-5B.5* describing 4.4-7.3% PVE, were discovered by Kumar *et al.,* (2022) and were consistently seen across several years different environments in India. The cultivar Jamestown also contained two regularly expressed APR QTLs namely, *QLr.vt-5B.1* explaining 1.7- 22.1% and *QLr.vt-5B.2* explaining 3.3-5.5% of the overall PVE, respectively. According to Vasistha *et al* (2024), both MQTL22 as well as MQTL23 on 5B are made up of QTLs identified in Americano 25e, Kariega, Capo, SHA3/CBRD, TA4152-60 and Carberry, respectively.

On 5DS, Kumar *et al.,* (2021) discovered *QLr.cim-5DS*, a substantial QTL ca in Chilero (a cultivar) for LR resistance that explained 5.2-34% PVE. It is co-localized with *QYr.cim-5DS* which is a yellow rust resistance QTL. An APR *Lr78* was discovered in Toropi (Brazilian wheat cultivar). In a recent study Spychała *et al.,* (2024), *Lr78* described 37-53% of PVE for LR resistance in Toropi.

LR-Linked QTLs in chromosome group six: With only 16 QTLs and 5 MQTLs, the group 6 chromosomes have several documented LR resistance QTLs. On chromosome 6A there are 6 QTLs, on 6B 7, and on 6D 3. Chromosome 6A and 6B each have 1 MQTL and 4 MQTLs, respectively. In two different studies, two QTLs *QLr.cimmyt-6AL* and *QLr.cim-6AL* were discovered in Avocet accounting for 4.2-6.3% PVE (William *et al.,* 2006) and 8.5-12.6%, respectively (Ren *et al.,* 2017). *QLr.cim-6AL* shares the same locus with *QYr.cim-6AL* (a yellow rust resistance QTL). In cultivar Clark, Li *et al.,* (2017) documented *QLr.hwwg-6AS* on chromosome 6AS that accounted for 5-7.1% PVE. On 6B, the QTL *QLr.inra-6B*, generated from Balance (a cultivar), segregated with *QYr.sun-6B* (a stripe rust resistance QTL) and described 3.4-29.2% PVE for LR resistance (Dhillon *et al.,* 2020).

Genotypes of hexaploid wheat where quantitative resistance for LR is discovered on chromosome 6D are the Syn022L (a synthetic wheat) and HD29 (a wheat line). According to Diéguez *et al.,* (2021), the *QLr.B22-6D* from synthetic wheat Syn022L is an all-stage resistance QTL even with a barely 3.2% PVE in seedling experiments and just 2% PVE in field trials.

LR-linked QTLs in chromosome group seven: On chromosomes 7 homeologs, 43 QTLS have been documented and 7 MQTLS. 3 QTLs are localized on 7A chromosome, 19 upon 7B chromosome, whereas 21 upon 7D chromosome. Likewise, 1 MQTL is found on 7A, 4 on chromosome 7B, whereas 2 on chromosome 7D. Nevertheless, *Lr34* is associated with 19 of the 21 QTL found on 7D. *QLr.inra-7Aa* on 7A in Balance which described 10-69.4% PVE has later been determined as *Lr20* ASR gene (Dhillon *et al.,* 2020). Tsilo *et al.,* found a small QTL on 7A that was taken from MN98550-5 (a wheat breeding line) and imparted 2.2-8.1% of PVE.

Lr68 is the most likely present in four of the 19 identified QTLs on 7B. When combined with *Lr68*, *QLr. hbu-7BL* generated from Fuyu 3 (a wheat cultivar) and *QLr. Hwwg-7BL* derived from CI13227 (a wheat line) accounted for 4.1-4.3% and 6.3-13.9% PVE, respectively. A list of key APR genes and their respective chromosomes and cultivars is provided in Table 2. Both *QLr.sfr-7B.1* generated from wheat cultivar Forno as well as *QLr.ksu-7BL* derived from wheat cultivar Opata 85 are substantial adult plant resistance QTLs that describe 11-42.2% and 35.8% PVE, respectively (Xu *et al.,* 2024). Eleven QTLs from the cultivars Creso, Colosseo, and Sujata made up the MQTL33 on 7B (Vasistha *et al*., 2024). *Lr14* and *Lr19* being the ASR genes and the APR *Lr68* co-localize with MQTL33.

Table. 2 Adult plant resistance (APR) genes list with identified LR numbers in hexaploid wheat (*Triticum aestivum* L.)

APR genes	Chromosome ID	Hexaploid wheat cultivars
Lr67	4DL	Pl-250413
Lr68	7BL	Parula and Frontana
Lr77	3BL	Santa-Fe
Lr78	5DS	Toropi
Lr46	1BL	Pavon-76
Lr34	7DS	Mentana and Ardito
Lr74	3BS	BT Schomburgk
Lr75	1BS	Forno

According to the cross and environment, *Lr34* (located on 7DS) has been documented in 19 research publications, accounting for 8-75.2% PVE. Its origin was initially noted in Frontana and later in Mentana, an Italian cultivar (Li *et al.,* 2023). *Lr34* and *MQTL34* were matched in meta-analysis (Vasistha *et al*., 2024). Additionally, two other minute APR QTLs, that is, *QLr.cim-7DS* mapped in wheat cultivar Francolin#1 as well as *QLr.hebau-7DS* found in wheat cultivar Naxos, have been identified on 7D.

Table 3. List of major LR resistance marker trait associations in hexploid wheat by association mapping.

Germplasm	Genotypes	Chromosome	Markers	QTLs	Genes found	References
Spring wheat	1032	All chromosomes (other than 3D, 7B, 6B, and 1D)	5732	37	*Lr35, Lr46, Lr67, Lr74, Lr11, Lr17, Lr34, Lr63, Lr27, Lr28, Lr30, Lr66, Lr10*	Yan *et al.,* 2023
Spring wheat	159	3B, 4A, 1D, 5B, 6D, 7A,1B, 6A, 6B	6176	23	*Lr68, Lr74 Lr46, Lr67, Lr34*	Semagn *et al.,* 2021
Spring wheat	2111	5B, 6A, 5A, 7A2A, 2B, 1A, 2D, 3A	3215	36	*Lr11, Lr52, trp-1, Lr47*	Pu *et al.,* 2022
Winter wheat	96	2A, 2B, 1D, 2D, 1B, 3B, 5B, 7D,7B, 4A, 6A, 6B	874	13	*Sr7, Lr28, Lr22, LrSV1, LrSV2, Lr27*	Zhou *et al.,* 2022
Hexaploid wheat	295	1B, 2A, 5B, 6A, 6B, 7A, 5A, 7B, 2B, 3A, 1A, 3B,7D, 4A	10748	31	*Lr3, LrBi16, Lr64, Lr14b, LrFun, Lr34, Lr68*	Daskalova *et al.,* 2022
Elite Spr. wheat lines	338	All chromosomes (other than 5A and 3D)	18924	46	*Lr64, Lr68, Lr26, Lr28, Lr14, Lr17, Lr30, Lr34, Lr38, Lr42, Lr3, Lr9, Lr11, Lr21, Lr1, Lr72*	Beral *et al.,* 2022
Syn. Hexaploid wheat	173	1D, 2D,7D, 1B, 6D	6176	5	*Lr42, Lr39, Lr38, Lr19, Lr46*	Noweiska *et al.,* 2022

Conclusion

Wheat production is seriously threatened globally by LR. To date, the application of fungicides and important ASR genes have been the principal methods for controlling LR. The increased reliance on ASR, though, is leading to pathogen populations with an ever more complicated virulence profiles and is proving to be insufficient to obtain a potentially durable and meaningful resistance over the course of a cultivar's commercial life.

Wheat breeders are focusing on sources of quantitative LR resistance as more ASR genes are rapidly losing their effectiveness and very few new ASR genes are being discovered to substitute them. According to research of CIMMYT (Bräunlich *et al.,* 2021), combining 4 to 5 quantitative resistance QTL can result in efficient LR resistance. Nevertheless, it is crucial to consider whether the existing wheat breeding materials already have the same/different disease resistance sources, how viable or stable is the expression/behavior of each source in diverse

environmental conditions, or if an interaction exists between different genes or QTLs for resistance in selecting desirable resistance genes or QTLs to integrate.

In a broad range of wheat germplasm, extensive field studies/research, quantitative LR resistance have been reported. These findings, which summarize the genetic variation generating quantitative resistance in wheat to *P. triticina* that causes LR, are hardly ever subjected to systematic analysis. In this study, Source of quantitative LR resistance in wheat that has demonstrated efficacy in natural environmental conditions has been listed.

The contingent value of every reported resistance QTL for LR is evaluated as the proportion of PVE in a particular wheat cross (described by the QTL), as well as in several locations and testing years, where applicable. To help wheat pathologists and breeders choose the QTLs most suitable to their requirements, this review summarizes the possible quantitative resistance sources for LR that may occur in a variety of wheat genotypes.

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