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Intelligent reprogramming of wheat for enhancement of fungal and nematode disease resistance using advanced molecular techniques

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Wheat (*Triticum aestivum* L.) diseases are major factors responsible for substantial yield losses worldwide, which affect global food security. For a long time, plant breeders have been struggling to improve wheat resistance against major diseases by selection and conventional breeding techniques. Therefore, this review was conducted to shed light on various gaps in the available literature and to reveal the most promising criteria for disease resistance in wheat. However, novel techniques for molecular breeding in the past few decades have been very fruitful for developing broad-spectrum disease resistance and other important traits in wheat. Many types of molecular markers such as SCAR, RAPD, SSR, SSLP, RFLP, SNP, and DArT, etc., have been reported for resistance against wheat pathogens. This article summarizes various insightful molecular markers involved in wheat improvement for resistance to major diseases through diverse breeding programs. Moreover, this review highlights the applications of marker assisted selection (MAS), quantitative trait loci (QTL), genome wide association studies (GWAS) and the CRISPR/Cas-9 system for developing disease resistance against most important wheat diseases. We also reviewed all reported mapped QTLs for bunts, rusts, smuts, and nematode diseases of wheat. Furthermore, we have also proposed how the CRISPR/Cas-9 system and GWAS can assist breeders in the future for the genetic improvement of wheat. If these molecular approaches are used successfully in the future, they can be a significant step toward expanding food production in wheat crops.

KEYWORDS

wheat diseases, marker assisted selection, quantitative trait locus, genome wide association studies, CRISPR/Cas-9 system

Introduction

Wheat (*Triticum aestivum* L.) is one of the most widely cultivated cereal grain crops and is a major source of calories for the world's ever-increasing population (Gupta et al., 2020). Wheat yield enhanced significantly as a result of the green revolutions of the 1960s and 1980s, mainly in Southeast-Asia. In 2020-2021, global wheat production was 772.6 million tons (Nigus et al., 2022). However, current wheat production patterns do not give the impression of feeding the estimated population of nine billion people by 2050 (Curtis and Halford, 2014). The production of wheat grain per unit area must expand to meet increasing human demands, as expansion in the area under cultivation seems impossible due to urbanization and other problems, i.e., drought, water logging and salinity. Hence, significant work has been done in the past to increase the productivity of wheat worldwide after the green revolution. Despite this significant enhancement in wheat production, crop yield remains sensitive to several biotic and abiotic diseases (Jabran et al., 2021). Plant diseases are the key players affecting the yield of cereal food crops and have remained the main hindrance in achieving food security and safety (Montesclaros and Teng, 2021). Pests and pathogens damage 40–50% of crop yields. (Khan et al., 2021). A brief survey of the peer-reviewed literature showed that major wheat fungal diseases such as bunts, smuts, and rusts are difficult to manage due to the alternate existence of wheat pathogens on weeds or other host plants (Figueroa et al., 2018). Elimination of the fungus is difficult due to the ability of spores to remain viable for longer periods of time in the soil and air (Eversmeyer and Kramer, 2000). Similarly, the occurrence of diseases fluctuates greatly from season to season, depending on the conduciveness of environmental conditions, nature of pathogen, and host susceptibility (Jevtić et al., 2020). Furthermore, the intensive use of synthetic fertilizers over the years has taken a toll on the health of soil and has badly affected the environment as well as food quality. Fungal diseases such as rusts are extremely adaptive, and new races emerge quickly, infecting previously disease-resistant plants. Therefore, enhancement of plant resistance against the diseases caused by fungi, nematodes, viruses, and bacteria has great potential to increase crop production per unit area through resistance breeding approaches. These breeding systems were built on simple theories, which include identification of novel variation through sexual recombination and selecting offspring with the most desired traits. This all began as a visual selection, but as science progressed, it became convincing to utilize scientific data to select better plants for the development of disease resistant/tolerant crop varieties. The genetics of some types of plant defense against pathogens is simple and has been extensively studied using conventional phytopathology, breeding, and genetics approaches. Classical quantitative genetics has provided the tools for research related to complicated disease resistance in the past. However, quantitative genetics deals with the inheritance of complex traits in plant populations. In the context of plant disease resistance, it involves the use of statistical methods to analyze the genetic basis of resistance to various diseases (Fischer et al., 2004). Furthermore, conventional wheat breeding is a process to control major diseases in wheat by selecting and developing disease-resistant varieties through crossbreeding and hybridization. The main diseases are rusts, smuts, and leaf and stem diseases, and breeding for resistance involves selecting for plants with resistance genes to overcome the disease. This is done by identifying resistant plants and crossing them with other plants to create new varieties with the desired traits. The development of leaf rust-resistant, powdery mildew-resistant, and FHB-resistant cultivars is done by crossing wheat varieties with natural resistance and selecting for the most resistant progeny. However, this process can take multiple years and generations to produce a cultivar with the desired level of resistance.

To address and manage these biotic issues, molecular marker approaches are a breakthrough genomic tool for producing disease-resistant germplasm with high production (Mores et al., 2021). Likewise, new molecular approaches must be included in plant breeding programs to enhance resistance against wheat diseases (Ali et al., 2019). Many researchers have explored the potential of molecular markers for enhancing the speed and proficiency of breeding program (Bhanu et al., 2016), and there is a large body of literature available on the topic of how to use markers in breeding assessment to support a variety of tasks such as trait mapping, germplasm evaluation, and cultivar identification. Similarly, markers can be used to identify the genetic loci that control traits of interest such as disease resistance, yield, or seed size. This information can then be used to select plants with desirable traits for breeding purposes (Collard et al., 2005). Therefore, marker-assisted selection (MAS) has been established as a promising breeding strategy using molecular markers. Conventional simple sequence repeats (SSRs) have remained the most prevalent technology utilized by the public sector in breeding programs. They have been applied in cross-population meta-analyses (Swamy and Sarla, 2008), allelic diversity evaluations and biparental mapping research such as quantitative trait loci (QTL) mapping and fine-mapping (Yadaw et al., 2013). QTL mapping depends upon the application of DNA markers to identify genomic regions associated with complicated and polygenic types of disease resistance (Young, 1996). Furthermore, novel pathogen mutations frequently cause a higher risk to crops. For instance, Ug99 is the most virulent fungal strain of wheat stem rust disease (Singh et al., 2011), and wheat blast (Ceresini et al., 2018) severely harms wheat productivity in different countries. These ever-mutating pathogens have diverted the attention of plant breeders to constantly seek novel resistance gene for the management of crop disease. To combat this problem, partial/polygenic resistance has been defined as more durable and broad-spectrum resistance (BSR) against multiple pathogen species/strains or races that is modulated by QTLs (Li S. et al., 2021).

Abbreviations: A. M. C, Associated Marker category; DArT, Diversity array technology; SNP, Single nucleotide polymorphism; RAPD, Random amplified polymorphic DNA; RFLP, Restriction fragment length polymorphism; AFLP, amplified fragment length polymorphism; ISSR, Inter Simple Sequence Repeat markers; SSLPs, Microsatellites or simple sequence length polymorphisms; SCAR, Sequence Characterized Amplified Region; SSR, Simple sequence repeat marker; DH, Double Haploid; HIGS, Host-induced gene silencing; PTGS, posttranscriptional gene silencing; VIGS, virus-induced gene silencing; SIGS, Spray-induced gene silencing.

Most of the modern MAS research has concentrated on novel single nucleotide polymorphism (SNP) technologies following recent advancements in next-generation sequencing that reveal the entire genomes of crop plants for SNP identification (Liu et al., 2022). Genotyping by sequencing followed by SNP identification is a high throughput genomics approach that has been largely used for genome-wide association studies (GWAS) in relation to disease resistance in crop plants (Begum et al., 2015). Similarly, genome editing technology alters a specific sequence of DNA in the genome. A restriction enzyme that can identify the specific sequences in the host genome is required for genome editing. These enzymes act like molecular scissors that not only locate the genomic position but also cut specific sequences (Khalil, 2020). Among genome editing tools, an efficient and easy technique is the CRISPR/Cas9-system multiplex genome editing technique, which has been particularly important for understanding the complicated features of wheat disease resistance (Zhang et al., 2021). Using the CRISPR/Cas9 system, mutations in host susceptibility (S) genes provided broad-spectrum disease resistance against plant pathogens (Ahmad et al., 2020). Crop disease resistance and/or tolerance to major biotic (e.g., bacterial blight of rice and rice blast) and abiotic stresses (e.g., drought and salinity) have both been improved using CRISPR-based genome editing (Jaganathan et al., 2018). Likewise, (Baltes et al., 2015) illustrated the use of CRISPR/Cas9 technology to generate *geminivirus* resistant plants, and this technology has great potential for improving disease resistance in wheat. Furthermore, molecular technology has played an important role in the development of disease-resistant wheat cultivars. Scientists around the world have worked to combat various diseases affecting wheat crops such as Fusarium head blight, *Septoria tritici* blotch, leaf rust, and stem rust. By introducing genes that confer resistance to these diseases, they have developed cultivars that are now widely grown by farmers, such as "Avocet R" for FHB resistance, "Condor" for STB resistance, "Zambezi" for leaf rust resistance, and "Moleleka" for stem rust resistance. These efforts aim to provide farmers with crops that are more productive and sustainable, contributing to the overall growth of the agriculture industry (McLaughlin et al., 2021). In this review, we provide a detailed and comprehensive account of research advancements in QTL mapping, GWAS and genome editing technologies for the enhancement of resistance against wheat bunts, rusts, smuts, nematodes, and other important diseases. We have further reviewed most of the QTLs identified and found to be associated with resistance against major diseases of wheat. The general idea of molecular approaches to develop resistance against major wheat diseases is shown in Figure 1.

Marker assisted selection of wheat resistance

Marker Assisted Selection (MAS) of wheat resistance is a plant breeding technique that uses molecular markers to select for resistance to specific diseases. This technique combines traditional plant breeding practices with modern molecular biology tools. In MAS, molecular markers that are associated with a particular trait of interest (such as disease resistance) are identified and used to screen a large number of wheat varieties. This allows plant breeders to identify individuals with the desired trait more efficiently and speeds up the breeding process by reducing the amount of time required to test each variety in the field (Francia et al., 2005). The most broadly utilized application of DNA markers is marker-

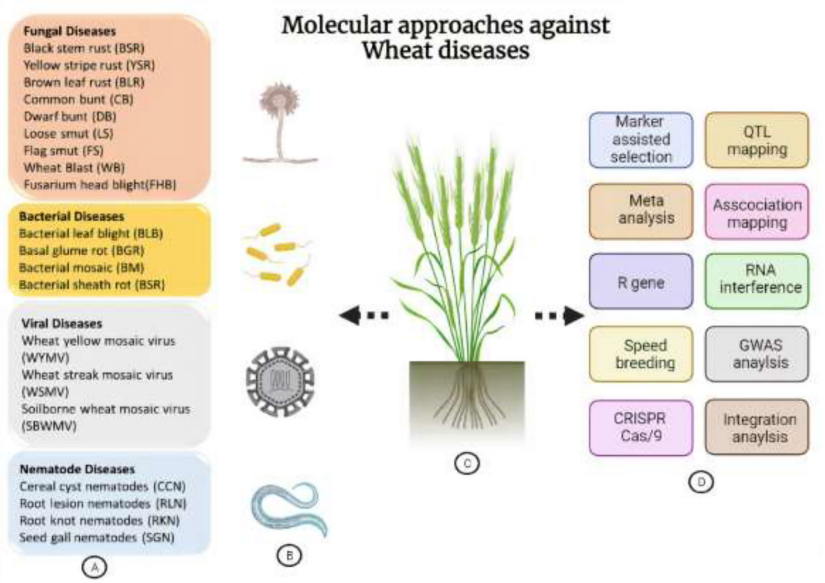

FIGURE 1
Overview of destructive wheat diseases and molecular approaches to develop resistance against them. **(A)** Categorical description of wheat pathogens. **(B)** Schematic representation of different classes of pathogens. **(C)** A wheat plant demonstrating its different pathogens and approaches. **(D)** Representation of various genome-editing, genomics, conventional breeding-based techniques and being employed for the execution of wheat immunity against pathogens.

assisted selection (MAS), which is a type of indirect selection. Once plant physical attributes have been mapped, a closely related DNA marker can be used to screen many samples for progeny with appropriate characteristics (Miedaner and Korzun, 2012). Advances in molecular genetics have led to the invention of DNA tags and marker assisted selection procedures for resistant cultivars (Collard and Mackill, 2008). The introduction of marker-assisted molecular breeding in the context of worldwide climate change and water constraints in arid and semiarid countries coupled with expanding global populations is a prerequisite for crop improvement (Hickey et al., 2019). Molecular markers are obviously not impacted by environmental factors and unchanged by plant developmental stages and can be detected at any stage of plant growth. MAS has become accessible for qualities regulated by most important genes along with quantitative trait loci (QTLs) and ease of use of molecular markers and genetic maps (Hasan et al., 2021). Sequence Characterized Amplified Region (SCAR) (Gold et al., 1999), Simple-sequence repeats SSRs (Wang et al., 2002), random amplified polymorphic DNA (RAPD) (Qi et al., 1996), microsatellites or simple sequence length polymorphisms (SSLPs) (Ma et al., 2001), restriction fragment length polymorphism (RFLP) (Metakovsky et al., 2021) and novel single-nucleotide polymorphism, (SNP) (Wu et al., 2018) are the different molecular markers that have been reported for the molecular identification of plant pathogens and widely used in plant breeding (Thomson, 2014). Hence, MAS could be useful in helping traditional plant breeding procedures in selecting phenotypic features for disease resistance screening (Todorovska et al., 2009). Accordingly, conventional plant breeding approaches, as well as functional genetic equipment and existing molecular markers (Gupta et al., 2010), can assist a breeder in producing advanced wheat genotypes that are resistant to fungal pathogens in order to reduce production losses. Hence, high costs in MAS that requires specialized laboratory equipment and skilled personnel, which can be expensive. The cost of the molecular markers, DNA extraction, and genotyping can also add to the cost of MAS. Any errors in any of these steps can impact the accuracy of the results.

Quantitative trait loci for plant disease resistance in wheat

QTLs (quantitative trait loci) and genes are related, but they are not the same thing. A gene is a segment of DNA that codes for a specific protein or RNA. Each gene contains the information needed to make one or more specific proteins, and these proteins determine the traits of a plant, such as height and susceptibility to certain plant diseases. While QTLs are specific locations on a chromosome that are associated with a particular trait and often influenced by multiple genes. They are used to map and study the genetic basis of complex traits in plants. The identification of QTLs can provide insights into the genetic basis of a trait and can be used to improve breeding programs for disease resistance in plants (Vinod, 2009). QTLs are mapped by the identification of molecular markers that are linked with a certain trait. QTL mapping mainly involves the crossing of contrasting parents (resistant and susceptible) to develop the mapping population. This mapping population is subjected to the measurement of disease response, i.e., phenotyping, and is assessed for its genetic makeup through genotyping, i.e., amplification of DNA markers. The whole process of QTL mapping is shown in Figure 2.

Many quantitative plant attributes are regulated by several genes. With the rapid improvement of molecular technology, it is feasible today to map significant QTLs on chromosomes using molecular marker information (Phipps et al., 2022). Various statistical techniques have been developed for investigating mapping data and searching for important QTLs in crop plants. It is possible to select for a resistance gene without exposing the plant to the pathogen, disease, or harmful substance if the QTLs associated with that resistance are known in the same crop species. Successful association between a molecular marker and a QTL makes the selection more effective, reliable, and faster (Reynolds and Borlaug, 2006). Resistance to wheat diseases such as dwarf bunt, leaf rust, stripe rust, stem rust, and spot blotch is often controlled by one to three or more genes that can be identified with several DNA markers, which are particularly based on PCR technology (Randhawa et al., 2013). Seed storage protein loci, genome identification, protein sequences, resistance gene positions, intrachromosomal mapping of genes for dwarfing and vernalization, characterization of genes and QTLs controlling tissue culture response, resistance against nematodes, and production level have all been mapped using molecular markers in wheat crops. There are various kinds of molecular markers that have their own set of benefits and drawbacks. However, most scientists are now aware of the limitations of RAPDs and other molecular markers with less frequent use. The amplified fragment length polymorphism (AFLP) technique uses PCR to selectively amplify DNA segments that have been processed with one or two restriction enzymes (Amom and Nongdam, 2017). Soon after, microsatellite markers, also known as SSRs (simple sequence repeats), were developed to replace RAPD and RFLP (Harshitha and Sandal, 2022). SSRs have been the most developed and used DNA markers for the characteristics associated with disease resistance in crop plants, especially wheat. For instance, several nematode resistance QTLs based on SSR markers have been previously reviewed (Seid et al., 2021). SNP data are widely utilized to detect marker-trait relationships in quantitative trait locus (QTL) mapping research (Rajesh et al., 2021). A large number of QTLs associated with resistance to important diseases have been identified and mapped on different chromosomes of wheat. However, it also has some limitations such as QTL analysis can only identify the general location of the genes associated with a particular trait, but not the specific genes themselves. This can make it difficult to identify the exact genes responsible for disease resistance. The detailed accounts of these mapped QTLs associated with bunts, rusts, smuts, and wheat parasitic nematodes are given below.

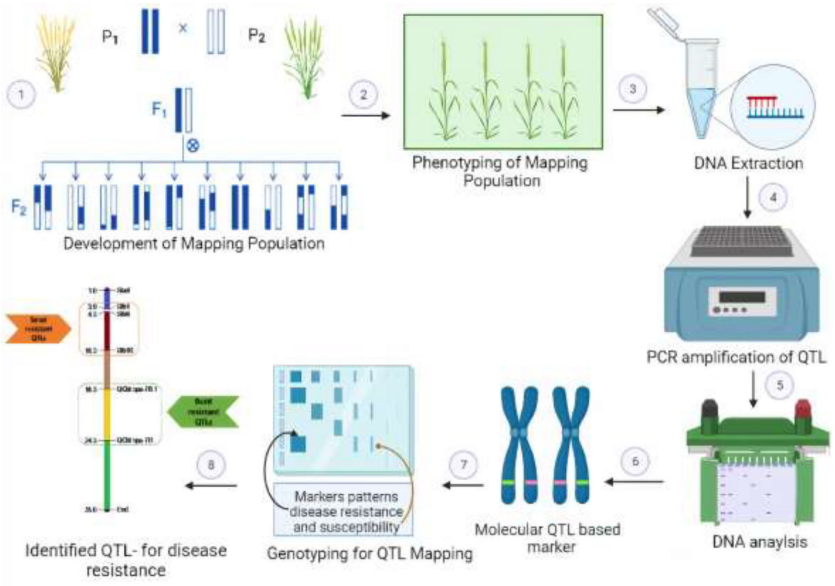

FIGURE 2
Scheme of marker-assisted selection (MAS) and identification of quantitative trait loci (QTLs) involved in wheat disease resistance. 1: Biparental mapping population development, i.e., F_2 plants, NILs, RILs, BILs, etc., segregating for disease resistance. 2: Precise phenotyping for resistance scaling to a specific pathogen. 3: Genomic DNA isolation from selected plants. 4-6: Evaluation of genome-wide distributed polymorphic DNA markers and construction of linkage maps. 7, 8: Statistical modeling of linkage groups using phenotypic-genotypic data followed by mapping of resistance-associated QTLs.

Mapped QTLs for bunt diseases

Dwarf bunt (*Tilletia controversa* J.G. Kühn) and common bunt (*T. caries* and *T. foetida*) are important global quarantine diseases that decrease the quality and quantity of wheat grains (Gao et al., 2014). Teliospore germination and the development of both pathogens on wheat plants are favored by continuous snow cover in the field (Wilcoxson, 1996; Rush et al., 2005). These seed and soil-borne diseases are usually sufficient to produce unpleasant flour odors that reduce grain quality and cause yield losses of more than 80% (Castlebury et al., 2005). However, dwarf and common bunt fungal diseases are difficult to characterize due to their similar morphology and ecology (Li et al., 2018). Bunt diseases of wheat can effectively be controlled by different measures, such as systemic fungicides, e.g., difenoconazole. Hence, most scientists' interest is diverted to genetic resistance to bunt diseases due to attention to organic farming and a focus on more sustainable agricultural production practices. Recent research has attempted to find and map host resistance by using a gene mapping strategy (Zou et al., 2017) and genome-wide analysis (Mourad et al., 2018). Several QTLs have been identified in wheat that are associated with bunt resistance. Similarly, some molecular markers have also been developed for pathogen identification in bunt diseases. Sixteen resistance genes (*Bt1–Bt15*) and BtP have been listed, and several resistance sources are accessible for bunt of wheat (Muellner et al., 2020).

For instance, a specific SCAR marker was developed to detect *Tilletia foetida* (Zhang et al., 2012). Therefore, the application of molecular approaches for the development of bunt-resistant germplasm is essential in many wheat-growing countries, mainly where organic wheat is farmed. Few molecular markers have been discovered to be associated with bunt resistance (Wang et al., 2019). For instance, (Fofana et al., 2008) mapped QTLs associated with resistance to common bunt in a doubled haploid population derived from the cross of two spring wheat accessions RL4452 x AC Domain. They found one QTL on 1BS that was linked to common bunt disease. Furthermore, QTLs were discovered on chromosomes 7A (Dumalasová et al., 2012) and 7B (Knox et al., 2013). Earlier, the genes present in breeding lines were identified and germplasm was based on their response to certain pathogen strains. These pathogen strains have been discovered based on their virulence in the current collection of differential lines. There is much evidence that the current set of differential lines is not always monogenic for bunt pathogenic races. Race D-18 showed minimal virulence toward the Bt8 differential line, but races L-18 and D-19 were virulent toward the *Bt8* differential line. Similarly, the D-7 strain is not virulent against the *Bt8* line, while it is virulent against CI 9342 and PI 636146, which are thought to contain Bt8 based on their responses to L-18, D-18, and D-19 (Goates, 2012). *Bt8* gene is highly resistant to dwarf bunt disease and developed from wheat cultivar PI 178383 in the United States. *Bt8* gene is a well-known gene from cultivars that does not cooperate with known strains of dwarf bunt disease in the United States (Goates, 2012). Similarly, amplified fragment length polymorphism (AFLP) was used to examine a total of 30 primer combinations for detecting DNA polymorphisms in *T. controversa* and related species. According to preliminary findings, the Bt11 gene is found on chromosome 3B and may be linked to QTLs such as Xbarc180, Xwmc623, Xwmc808, and Xgwm285. By employing 1R-specific markers, the bunt resistance gene introduced from Triticale (Line F00628G34-1-

containing a 1A/1R translocation) may lead to successful MAS (Ciucă, 2011). SYBR Green I and TaqMan real-time polymorphic chain reaction analyses were established to identify TCK with a finding limit of 0.1 fg (Gao et al., 2014). Likewise, the Diversity Arrays Technology (DArT) and Illumina Infinium 9K iSelect marker platforms were used to genotype the population. Three Utah State University (USU) experiments discovered a QTL Q. ui-1A on 1A that explained 11–15% of phenotypic variation for resistance to dwarf bunt in recombinant inbred line (IDO444) of wheat (Chen et al., 2016). Likewise, Diversity Arrays Technology (DArT) and Illumina Infinium 9K iSelect marker platforms were used to genotype the population. Three Utah State University (USU) experiments discovered a QTL Q.ui-1A on 1A that explained 11–15% of phenotypic variation for resistance to dwarf bunt in a recombinant inbred line (IDO444) of wheat [63]. Likewise, the study was undertaken for DB resistance across four growing seasons in a field nursery in Logan, Utah. The Illumina 90 K SNP iSelect marker platform was used to genotype the population. On chromosomes 6DL and 7AL, the two most important QTLs were recognized (Q.DB.ui-6DL) and (Q.DB.ui-7AL), respectively. Comparative research proposed that Q.DB.ui-6DL was found in the same location as the Bt9 gene of CB resistance, and Q.DB.ui-7AL was discovered at a new bunt resistance locus. Both resistance QTLs were mapped against bunt disease resistance in the wheat line 'IDO835' in gene-rich (NBS-LRR and kinase genes) areas using the Chinese Spring reference sequence and annotations (Wang et al., 2019). An inter simple sequence repeat (ISSR) molecular marker was reported for the first time by (Yao et al., 2019) and is a quick diagnostic approach for the detection of teliospores of *Tilletia laevis* Kühn. Similarly, SYBR Green I real-time PCR and sequence characterized amplified region (SCAR) is fast and highly specific for the identification of the teliospores of *T. laevis* depending upon the ISSR tool. This technique enables efficient and correct differentiation among pathogens, particularly the pathogens *T. tritici* and *T. controversa*, which are very similar (Li et al., 2018). Similarly, dwarfism and common QTLs for bunt resistance were found on chromosomes 1AL, 1BS, 7AL, and 7DS. Kompetitive allele-specific PCR (KASP) was successfully employed for QTL validation. These KASP markers have the potential to aid targeted QTL introgression into superior wheat germplasm and speed up bunt resistance breeding. The combination of multiple resistance genes in the same genetic background can provide long-term protection against both common and dwarf bunts (Muellner et al., 2021). Various QTLs associated with bunt resistance are given in Table 1.

Mapped QTLs for rust diseases

Wheat rust pathogens are host specific and macrocyclic. Leaf rust, stem rust, and stripe rust are important diseases of wheat worldwide (Sinha and Chen, 2021). Wheat rusts are caused by obligate, biotrophic fungal pathogens belonging to the family *Puccinacae* that can spread thousands of miles by wind and cause significant economic losses around the globe (Kolmer, 2013). For instance, only yellow or stripe rust of wheat causes up to 100% yield losses to susceptible varieties (Chen, 2005).

Additionally, (Park et al., 2011) proved the value of genetic resistance in the management of rust pathogens in their studies. The availability of various resistance genes is a requirement for producing cultivars with long-term rust resistance. Rust infection has become more common in the recent years, producing epidemics in wheat-growing areas across the United States and world (Jamil et al., 2020). This is mainly caused by substation changes in climatic

TABLE 1 QTLs reported to be associated with bunt disease resistance genes in wheat, their origin, chromosomal positioning and linked molecular markers.

Sr. No.	QTLs	Origin	Position	A. M. C	Source
1	Q.DB.ui-7DS	(RIL) Idaho 444	7DS	DArT marker	(Chen et al., 2016)
2	Bt12	(RIL) PI119333	7DS	SNP (KASP)	(Muellner et al., 2020)
3	Bt10	*T. aestivum*	6D	microsatellite markers	(Menzies et al., 2006)
4	Bt9	*T. aestivum*	6DL	SSR	(Steffan et al., 2017)
5	Bt1	*T. aestivum*	2B		(Al-Maaroof et al., 2016)
6	Bt4	*T. aestivum*	1B		(Briggs, 1933)
7	QCbt.crc-1B.1	*T. aestivum*	1BS	SSR	(Fofana et al., 2008)
8	QCbt.crc-1B.2	*T. aestivum*	1BL	SSR	(Fofana et al., 2008)
9	QCbt.spa-1B	*T. aestivum*	1B	microsatellite and DArT	(Singh et al., 2016)
10	QCbt.spa-4B	*T. aestivum*	4B	microsatellite and DArT	(Singh et al., 2016)
11	QCbt.spa-4D	*T. aestivum*	4D	microsatellite and DArT	(Singh et al., 2016)
12	QCbt.spa-7B.1	*T. aestivum*	7B	SSR	(Knox et al., 2013)
13	QCbt.spa-7D	*T. aestivum*	7D	microsatellite and DArT	(Singh et al., 2016)
14	Bt11	*T. aestivum*	3B	Xwmc808, Xgwm285	(Ciucă, 2011)
15	Bt13				(Dumalasová et al., 2012)

conditions, which lead the pathogen to alter its genetic makeup and break resistance in the host. Ug99, a novel strain of stem rust, was discovered in Uganda in 1999, and its variants are pathogenic to approximately 80–90% of wheat cultivars and germplasm (Singh et al., 2011; Bhardwaj et al., 2014). Stripe rust has also appeared as the most harmful grain rust in several parts of the globe caused by *Puccinia striiformis* (Wellings, 2011). Spring wheat landrace PI 480035 proved highly resistant against stripe rust (Sthapit et al., 2014). In 2013 and 2014, the population was assessed in the research area, and seedling responses against three pathogen races (PSTv-14, PSTv-37, and PSTv-40) were tested under a controlled environment (Wan et al., 2017). Genotyping by sequencing and microsatellite markers were used to genotype the population within the entire wheat genome. On chromosome 1B, an important QTL (QYr.wrsggl1-1BS) was discovered. The nearest molecular markers included Xgwm273, Xgwm11, and Xbarc187 1.01 cM distal to QYr.wrsggl1-1BS, Xcfd59 0.59 cM proximal to QYr.wrsggl1-1BS, and XA365 3.19 cM proximal to QYr.wrsggl1-1BS, respectively (Sthapit Kandel et al., 2017). On 3B, a different QTL (QYr.wrsggl1-3B) was detected that was only significant for PSTv-40 and not in the field, showing that it negotiates race-specific resistance. When compared to markers linked with earlier studied Yr genes on 1B (Yr64, Yr65, and YrH52), QYr.wrsggl1-1BS appears to be a new resistance gene to yellow stripe rust. This novel gene can be adapted into modern breeding systems and resistance genes of adult plants to create cultivars with long-lasting resistance (Sthapit Kandel et al., 2017). The Yr15 gene has been finely mapped to a 0.77 cM area using BSR-Seq, which confers resistance to yellow rust in wheat, allowing the creation of effective MAS markers (Ramirez-Gonzalez et al., 2015). In diploid wheat species of both common wheat and durum wheat, more than 65 leaf rust resistance (Lr) genes have been reported through different molecular techniques (Bansal et al., 2008). The wild wheat relative *Aegilops tauschii* has been shown to contain most of these genes (Hiebert et al., 2007). In a study using the IWGSC RefSeq v2.0 physical map, 82 QTLs were mapped in two hexaploid wheat populations for resistance to leaf spot, leaf rust, stripe rust, and common bunt. 29 QTLs were associated with all combined environments, and 14 were stable across most environments. Ten chromosome arms had QTL clusters for resistance to 2-4 diseases, providing a resource for comparing QTLs in different populations based on physical information of all markers. A total of 82 QTLs related to resistance against Yr (36), Ls (18), Lr (15), and Cbt (13) were discovered by analyzing both individual and combined data from all environments (Iqbal et al., 2023).

The study led to determine the frequency of Iranian Pt races causes leaf rust of wheat, their virulence to key resistance genes and map quantitative trait loci (QTL) for resistance to different Pt races from 185 globally diverse wheat genotypes. Results showed that some Pt races were relatively frequent in Iran and that certain resistant genes were still effective against the pathogen population. Genome-wide association study (GWAS) resulted in the identification of 62 significant marker-trait associations (MTAs) belonged to 34 QTLs across 16 chromosomes. The known and novel QTLs associated with different Pt races can be used in future wheat breeding programs for durable resistance (Talebi et al., 2023). Furthermore, a study evaluated 441 synthetic hexaploid wheat (SHW) accessions for resistance to spot blotch (SB) caused by *Bipolaris sorokiniana*. The panel showed high resistance, with 250 accessions being resistant and 161 showing moderate resistance. A genome-wide association study (GWAS) revealed 41 significant marker-trait associations for SB resistance, located on different chromosomes, but none had a major effect. This is the first GWAS to identify markers and resistant SHW lines for SB resistance in wheat breeding (Haugrud et al., 2023). Various QTLs linked to rust resistance are given in Table 2.

Mapped QTLs for smut diseases

Smut diseases are another important challenge faced by wheat crop. The pathogens causing smut diseases in wheat belong to the family *Ustilaginaceae* and order, *Ustilaginales*. Wheat is mainly infected by two smut diseases namely loose smut of wheat (*Ustilago tritici*) and flag smut disease (*Urocystis agropyri*) (Ram and Singh, 2004). However, loose smut is more serious than flag smut. Flag smut disease of wheat has been a serious issue leading to reduced yield. However, with the adoption of resistant cultivars and seed dressings, the prevalence has decreased (Toor and Bariana, 2012). A doubled haploid (DH) population was generated by crossing an Australian variety with high levels of tolerance against flag smut 'Diamondbird' with the susceptible Chinese landrace TH3929 (Murray and Brennan, 2009). Diamondbird identification of chromosomal position affecting flag smut resistance was recognized using a linkage map of 386 markers. Five quantitative trait loci (QTL) with significant impacts on flag smut resistance were discovered. The QTLs exposed by Diamondbird included QFs.sun-3AL, Qfs.sun6AS, Qcs.sun1BL, Qfsun5BS, and Qqs.sun3AS. Sequences of three or more QTLs were found in DH lines with low flag smut levels (Toor et al., 2013). In a high-density genetic map, the SNPs and 426 SSRs were mapped to 16 linkage groups spanning 3008.4 cM with an average intermarker gap of 0.2 cM. The blackbird variety of Nevski was crossed with the loose smut-sensitive durum (*Triticum turgidum* L.) Strongfield cultivar. This study has found three significant quantitative trait loci (QTL) to produce resistance against loose smut of wheat. The major QTL on 6B was stable to produce 74% phenotypic variation against all different races. The QTL QUt.spa-6B.2 could be useful to generate resistance against multiple strains of loose smut disease (Kumar et al., 2018). Six genes for loose smut resistance (Ut1-Ut6) were detected and reported based on the information provided by (Kassa et al., 2014). In the literature, from 34 genotypes of wheat, Krivchenko and Bakhareva identified 52 genes for resistance against loose smut; there were 11 recessive genes, and the remainder were dominant (Krivchenko and Bakhareva, 1984). Furthermore, Ut8, Ut9, and Ut10 on chromosomes 3A, 6B and 6D were also discovered (Knox et al., 2014). In the differential line TD-14, Ut11 was found and recognized as a strong resistance gene to loose smut disease. Thambugala et al. (2020) suggested that Ut11 showed resistance to *U. tritici* race T2, whereas races T9 and T39 did not. QUt.mrc-5B was responsible for the semi-resistant to smut phenotype and indicated resistance to all three races; however, it

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TABLE 2 QTLs reported to be associated with rust disease resistance genes in wheat, their origin, chromosomal positioning and linked molecular markers.

Sr. No.	QTLs	Origin	Position	A. M. C	Source
Leaf rust (Puccinia triticina)					
1	*Lr1*	*T. aestivum*	7BL	RFLP/STS	(Akın et al., 2013)
2	*Lr3*	*T. aestivum*	6BL	RFLP	(Herrera-Foessel et al., 2007)
3	*Lr9*	*Aegilops umbellulata*	6B	RAPD/STS, RFLP	(Autrique et al., 1995)
4	*Lr10*	*T. aestivum*	1AS	RFLP/STS, STS	(Feuillet et al., 2003)
5	*Lr12*	*T. aestivum*	4B	SSR	(Singh and Bowden, 2011)
6	*Lr13*	*T. aestivum*	2BS	RFLP, SSR	(Bansal et al., 2008)
7	*Lr14*	*T. aestivum*	7BL	SSR	(Herrera-Foessel et al., 2007)
8	*Lr14a*	*T. durum*	7BL	SNP	(Terracciano et al., 2013)
9	*Lr15*	*T. aestivum*	2DS	SSR	(Dholakia et al., 2013)
10	*Lr16*	*T. aestivum*	2BS	SSR	(Kassa et al., 2017)
11	*Lr19*	*Agropyron elongatum*	7DL	STS, RAPD/SSR	(Zhang et al., 2011)
12	*Lr20*	*T. aestivum*	7AL	RFLP	(Neu et al., 2002)
14	*Lr21*	*T. tauschii*	1DS	RFLP; KASPar	(Huang and Gill, 2001)
15	*Lr22*	*T. tauschii*	2DS	SSR	(Hiebert et al., 2007)
16	*Lr23*	*T. turgidum*	2BS	RFLP	(Nelson et al., 1997)
17	*Lr24*	*Agropyron elongatum*	3D	RFLP, RAPD/STS, SCAR	(Gupta et al., 2006)
18	*Lr25*	*S. cereale*	4BS	RAPD/SSR	(Singh et al., 2012)
19	*Lr26*	*Secale cereale*	1B	SCAR, SSR	(Zhou Y. et al., 2014)
20	*Lr27*	*T. aestivum*	3BS	RFLP, SSR	(Aravindh et al., 2020)
21	*Lr28*	*T. aestivum*	4AL	STS, SCAR	(Sohail et al., 2014)
22	*Lr29*	*Agropyron elongatum*	7DS	RAPD	(Vanzetti et al., 2011)
23	*Lr31*	*T. aestivum*	4BL	RFLP, SSR	(Nelson et al., 1997)
24	*Lr32*	*T. tauschii*	3DS	RFLP	(Autrique et al., 1995)
25	*Lr34*	*T. aestivum*	7DS	STS	(Dakouri et al., 2010)
26	*Lr35*	*A. speltoides*, *T. speltoides*	2BL	SCAR, STS	(Gold et al., 1999)
27	*Lr37*	*A. ventricosa*	2AS	STS/CAPS, ISSR	(Bulos et al., 2006)
28	*Lr38*	*Thinopyrum intermedium*	2AS	SSR	(Mebrate et al., 2008)
29	*Lr39*	*T. Tauschii*	2DS	SSR	(Raupp et al., 2001)
30	*Lr41*	*T. Tauschii*	1D		(Sun et al., 2009)
31	*Lr45*	*T. aestivum*	2A	AFLP, SSR	(Naik et al., 2015)
32	*Lr46*	*T. aestivum*	1BL	STS	(Mateos-Hernandez et al., 2006)
33	*Lr47*	*T. speltoides*	7AS	RFLP, CAPS	(Helguera et al., 2000)
34	*Lr48*	*T. aestivum*	2BS	SSR	(Bansal et al., 2008)
35	*Lr49*	*T. aestivum*	2AS, 2BL	SSR	(Bansal et al., 2008)

(Continued)

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TABLE 2 Continued

Sr. No.	QTLs	Origin	Position	A. M. C	Source
36	*Lr50*	*T. timopheevii*	2BL	SSR	(Brown-Guedira et al., 2003)
37	*Lr51*	*T. speltoides*	1BL	STS	(Helguera et al., 2005)
38	*Lr52*	*T. aestivum*	5BS	STS	(Bansal et al., 2011)
39	*Lr 58*	*T. aestivum*	Ncw1	SSR	(Kuraparthy et al., 2007)
40	*Lr60*	*T. aestivum*	1DS	SSR	(Hiebert et al., 2008)
41	*Lr63*	*T. monococcum*	3AS	SSR	(Kolmer et al., 2010)
42	*Lr64*	*T. dicoccoides*	1DS	SSR	(Kolmer et al., 2019)
43	*Lr67*	*T. aestivum*	4D	SSR	(Hiebert et al., 2010)
44	*Lr68*	*T. aestivum*	7BL	SSR, CAPS	(Herrera-Foessel et al., 2012)
45	*LrM*	*Aegilops markgraffii*	2AS	SNP based PCR markers	(Rani et al., 2020)
46	*TaCN-R with Lr13*	leaf rust in wheat	QLr.hnau-2BS	Linkage mapping	(Hou W. et al., 2023)
Stem rust (Puccinia graminis f. sp. tritici., P. recondita)					
1	*Sr2*	*T. turgidum*	3BS	STS, CAPS	(Mago et al., 2014)
2	*Sr9a*	*T. aestivum*	2BL	SSR	(Tsilo et al., 2007)
3	*Sr22*	*T. monococcum*	7AL	RFLP	(Periyannan et al., 2011)
4	*Sr24*	*Agropyron elongatum*	3DL	STS	(Mago et al., 2005)
5	*Sr25*	*Thinopyrum ponticum*	7BL	STS	(Liu et al., 2010)
6	*Sr26*	*Agropyron elongatum,*	6AL	STS	(Mago et al., 2005)
7	*Sr28*	*T. aestivum*	2BL	PCR	(Rouse et al., 2012)
8	*Sr35*	*T. aestivum*	3AL	SSR	(Zhang et al., 2010)
9	*Sr38*	*A. ventricosa*	2AS	STS/CAPS	(Helguera et al., 2003)
10	*Sr39*	*A. speltoides*	2B	STS	(Yu et al., 2014)
11	*Sr36*	*T. timopheevi*	2BS	SSR	(Yu et al., 2014)
12	*Sr47*	*Aegilops speltoides*	2B	SSR	(Klindworth et al., 2017)
13	*Sr52*	*D. villosum*	6AL	STS	(Yu et al., 2014)
14	*Sr R*	*Secale cereale*	1D	STS	(Mago et al., 2002)
15	*Sr32*	*A. speltoides*	2DS	SSR	(Mago et al., 2013)
16	*Sr43*	*T. aestivum*	7D	SSR	(Niu et al., 2014)
17	*Sr45*	*T. aestivum*	1DS	SSR/AFLP	(Periyannan et al., 2014)
18	*Sr54*	*Ae. tauschii*	2DL	SSR	(Ghazvini et al., 2013)
19	*Sr56*	*T. aestivum*	5BL	STS and SSR	(Bansal et al., 2014)
20	*QSr.dms-2B*	Stem rust of wheat	2B	SNPs	(Ciechanowska et al., 2022)
Stripe rust – (Puccinia striiformis)					
1	*Yr5*	*T. spelta*	2BL	STS	(Yan et al., 2003)
2	*Yr10*	*T. aestivum*	1BS	SSR, STS	(Yuan et al., 2018)

(Continued)

TABLE 2 Continued

Sr. No.	QTLs	Origin	Position	A. M. C	Source
3	*Yr15*	*T. dicoccoides*	1BS	SSR	(Sun et al., 1997)
4	*Yr17*	*A. ventricosa*	2AS	STS/CAPS, SCAR	(Robert et al., 1999)
5	*Yr26*	*H. villosa*,	1B	SSR, EST-STS	(Wang et al., 2008)
6	*Yr28*	*T. aestivum*	4DS	RFLP	(Zheng et al., 2020)
7	*Yr50*	*T. aestivum*	4BL	SSR	(Liu et al., 2013)
8	*Yr51*	*T. aestivum*	4AL	DArT (Marker sun104)	(Randhawa et al., 2014)
9	*YrH52*	*T. dicoccoides*	1B	SSR	(Yan et al., 2011)
10	*Yr53*	*T. aestivum*	2B	RGAP/SSR	(Xu et al., 2013)
11	*Yr59*	*T. aestivum*	7BL	RGAP and SSR	(Zhou X. et al., 2014)
12	*Yr61*	*T. aestivum*	7AS	STS5467, STS5765b,	(Zhou X. et al., 2014)
13	*Yr64*	*T. durum*	1B	SSR	(Cheng et al., 2014)
14	*Yr65*	*T. durum*	1B	SSR	(Cheng et al., 2014)
15	*YrSD*	*T. aestivum*	5B	SSR	(Jing et al., 2013)
16	*YrHA*	*T. aestivum*	1AL	SSR	(Ma et al., 2013)
17	*YrSN104*	*T. aestivum*	1BS	SSR	(Asad et al., 2012)
18	*QYr.sicau*	Stripe rust of wheat	6B	SSR and KASP	(Hou S. et al., 2023)
19	*Yrpd.swust*	Stripe rust of wheat	7A	90K SNP	(Zhou et al., 2022)
20	*QYr.rcrrc*	Stripe rust of wheat	1B, 2A, 7D	SNP	(Tehseen et al., 2022)

was less efficient against race T2. The genes and SNP markers linked with the QUt.mrc-5B, and Ut11 QTLs could be used in spring wheat breeding programs for marker-assisted selection. Many QTLs linked to smut disease resistance are given in Table 3.

Mapped QTLs for wheat nematodes

Plant parasitic nematodes (PPNs) are significant pathogens of wheat and cause various diseases with substantial economic losses (Ali et al., 2019). Several nematode species have been reported in wheat. For instance, cereal cyst nematodes (*Heterodera* spp.), root lesion nematodes (*Pratylenchus* spp.), root knot nematodes (*Meloidogyne* spp.), seed gall nematodes (*Anguina* spp.) and ring nematode (*Mesocriconema* spp.) (Seid et al., 2021). These parasitic nematodes use their stylet to enter the root cortex and release important enzymes in the form of secretions causing rupture of the cell wall (Ali et al., 2017). Plants are unable to adequately absorb water and nutrients from the soil due to the establishment of feeding sites on the vasculature of plant roots, resulting in water shortage and subsequent wilting. Nematodes of wheat cultivation have been recorded in Syria, Mexico, Canada, China, Yugoslavia, Morocco, Iran, India, Turkey, Pakistan, Algeria, Bangladesh, Australia, and the United States. Nematologists in cereal research prioritize enhancing nematode resistance in wheat for higher production. This generally concerned natural breeding selection of resistant germplasm and the discovery of QTLs linked to resistance genes. To improve resistance to *Heterodera avenae*, (Barloy et al., 2007) found that 9 resistance genes (e.g., Cre1 and Cre8 from *T. aestivum*; Cre3 and Cre4 from *Ae. tauschii* Coss.; Cre2, Cre5 and Cre6 from *Ae. ventricosa* (Zhuk.); Cre7 from *Ae. triuncialis* L.; CreR from rye and CreV from *Dasypium villosum* L.) were moved into common wheat from wild taxa such *Aegilops* and some other *Triticum* spp. However, *Rlnn1* is the only resistance gene identified in wheat that confers resistance to root knot lesion nematodes (Seid et al., 2021). The QTLs associated with CCN resistance are found on hexaploidy wheat chromosomes 1A, 1D, 4D, 5A, 5B, 5D, 6A, 6B, 7A, and 7D (Mulki et al., 2013). Likewise, Baloch et al. (2015) analyzed and provided complete data on the transfer of these genes and their related QTLs from wild relatives to common wheat. Consequently, MAS for cereal cyst nematode resistance in wheat is now widely utilized to discover resistant genotypes in Australia (Smiley et al., 2017). The Cre2 and Cre4 genes of *Aegilops* spp., as well as an unknown gene from the wheat line AUS4930, offered broad-spectrum resistance against multiple *Heterodera* species and pathotypes. CIMMYT coordinated the establishment of these loci in wheat in several parts of the globe, including Cre1 to Cre7, with a high level of resistance to CCNs. In addition, 11 DArT markers linked to CCN resistance have been identified, which can lead to the discovery of additional resistance loci and implements that could be

TABLE 3 QTLs reported to be associated with smut disease resistance genes in wheat, their origin, chromosomal positioning and linked molecular markers.

Sr. No.	QTLs	Origin	Position	A. M. C	Source
1	*Stb1*	*T. aestivum*	5BL	qRT-PCR, SSR	(Karlstedt, 2020)
2	*Stb18*	*T. aestivum*	6DS	SSR	(Tabib Ghaffary et al., 2011)
3	*StbSm3*	*T. aestivum*	3AS	–	(Brown et al., 2015)
4	*StbWW*	*T. aestivum*	1BS	–	(Raman et al., 2009)
5	*Stb6*	*T. aestivum*	3AS	–	(McCartney et al., 2003)
6	*Stb16q*	*T. aestivum*	3DL	–	(Ghaffary et al., 2012)
7	*Qsng.sfr.3BS*	*T. aestivum*	3BS	–	(Schnurbusch et al., 2003)
8	*Qsnb.fcu-1A*	*T. aestivum*	1A	–	(Abeysekara et al., 2009)
9	*Fhb1*	*T. aestivum*	3BS, 5AS	–	(Cuthbert et al., 2007)
10	*Fhb2*	*T. aestivum*	6BS	–	(Cuthbert et al., 2007)
11	*Fhb3*	*Leymus racemosus*	7AL	SSR	(Guo et al., 2015)
12	*Fhb4*	*T. aestivum*	4BL	SSR	(Guo et al., 2015)
13	*Fhb5*	*T. aestivum*	5AS	SSR	(Guo et al., 2015)
14	*Fhb6*	*Elymus tsukushiensis*	1AS	SSR	(Guo et al., 2015)
15	*Fhb7*	*Thinopyrum ponticum*	7DS	SSR	(Guo et al., 2015)

valuable in wheat breeding programs (Dababat et al., 2016). In Australia, a combination of pot testing and MAS has been utilized to effectively decrease CCN infestation levels and losses (Ogbonnaya et al., 2009). Several studies suggest that using resistant cultivars can inhibit nematode reproduction and densities, while a wheat cultivar tolerant to *P. thornei* conserves development and production (Robinson et al., 2019). The GS50a bread wheat line is the first reported source of partial resistance against P. *thornei* produced from a highly infested wheat field (Thompson et al., 1999). In wheat, several QTLs have been discovered, and these resistance sources could be used for breeding attempts (Zwart et al., 2010). Furthermore, (Toktay et al., 2006) discovered resistance QTLs for *P. thornei* on chromosomes 1B, 2B, 3B, 4D, and 6D. Many QTLs linked to nematode disease resistance are given in Table 4.

Mapped QTLs for tan spot of wheat

Tan spot of wheat is a fungal disease caused by *Pyrenophora tritici-repentis*, which affects wheat plants and can lead to significant yield losses if left untreated. The disease is common in wheat-growing regions worldwide and can be identified by small, dark, oval-shaped lesions with tan centers on the lower leaves of the plant, which can eventually lead to large necrotic spots and yellowing of the leaves (Muqaddasi et al., 2021). The disease cycle of tan spot involves the overwintering of the pathogen in crop debris and its survival in soil for several years. In the spring, spores are produced, and infection can occur at any growth stage, favored by warm and humid conditions (Istifadah and McGee, 2006). Effective management of tan spot in wheat involves the integration of disease management practices but the most effective way to manage tan spot disease is to plant resistant wheat cultivars. The identification of quantitative trait loci (QTLs) associated with tan spot resistance has facilitated the development of new resistant wheat cultivars. Research has identified several QTLs associated with tan spot resistance in wheat, including chromosomes 1B, 2B, 2D, 3A, 3B, 4A, 4B, 4D, 5A, 5B, 6A, 6B, and 7D. However, the degree of resistance conferred by these QTLs varies, and breeders must carefully select which QTLs to incorporate into their breeding programs to achieve the desired level of resistance (Phuke et al., 2020). In the study, a group of wheat recombinant inbred lines were examined for their response to various tan spot disease isolates, with the lines originating from resistant and susceptible varieties. The Tsn1 locus was found to be significantly linked to the disease caused by ToxA-producing isolates, although the extent of the association differed among the isolates. Another locus on chromosome arm 7DS was identified as being specifically related to an isolate that did not produce ToxA. In addition, other QTL on 5DL and 7BS were discovered to be race-nonspecific and linked to tan spot caused by multiple isolates. These findings suggest that the wheat-tan spot patho system is more intricate than previously thought, and that race-nonspecific resistance QTL plays an important role in controlling the response to tan spot (Faris et al., 2012). Further, the study was conducted to assess the reaction of a population of recombinant inbred lines derived from a cross between Grandin and BR34 wheat varieties to different races of the tan spot pathogen. The study identified QTLs on chromosomes 1B and 3B that were significantly associated with resistance to all four races, with varying effects for each race. The 1B QTL explained 13% to 29% of the variation, and the 3B QTL explained 13% to 41%. Although minor QTLs were detected, they were not linked to resistance to all races.

TABLE 4 QTLs reported to be associated with plant parasitic nematodes resistance genes in wheat, their origin, chromosomal position and linked molecular markers.

Sr. No.	QTLs	Origin	Position	A. M. C	Source
1	*Cre1*	*T. aestivum*	2BL	microsatellite XGWM 301	Barloy et al., 2007
2	*Cre8*	*T. aestivum, Aegilops ventricosa*	6B	RFLP	(Williams et al., 2003)
3	*Cre3*	*Aegilops tauschii*	2DL	SSR (Xgwm301)	(Al-Doss et al., 2010)
4	*Cre4*	*Aegilops tauschii*	2DL		(Eastwood et al., 1991)
5	*Cre7*	*Aegilops triuncialis*	2BL		(Montes et al., 2008)
6	*Cre5*	*Aegilops ventricosa*	2AS	Microsatellite	(Williams et al., 2006)
7	*Cre6*	*Aegilops ventricosa*	5N		(Ogbonnaya et al., 2001)
	Cre8	*T. aestivum, Aegilops ventricosa*	6B	RFLP	(Williams et al., 2003)
8	*QRlnt.lrc*	*T. aestivum*	6DS	(AFLP)	(Zwart et al., 2005)
9	*QRlnn.lrc*	*T. aestivum*	6DS	(AFLP)	(Zwart et al., 2005)
10	*Cre2*	*Aegilops ventricosa*			(Delibes et al., 1993)
11	*QRlnt.sk-2B*	*T. aestivum*	2B	SSR and SNP	(Rahman et al., 2020)
12	*QRlnt.sk-6D*	*T. aestivum*	6D	SSR and SNP	(Rahman et al., 2020)
13	*QCre-ma7D*	*Triticum aestivum*	7DL	KASP (SNP)	(Cui et al., 2020)
14	*QCre-ma2A*	*T. aestivum*	2AS	KASP (SNP)	(Cui et al., 2020)
15	*QCcn-1B*	*F4 wheat population*	1BS	SSR (Xwmc85-1B)	(Al-Ateeq et al., 2021)
16	*TaPrx113-F*	*T. aestivum*		SSR and RAPD	(Al-Doss et al., 2010)
17	*TaPrx112-D*	*T. aestivum*	2B	SSR and RAPD	(Al-Doss et al., 2010)
18	*CreY*	*T. aestivum*	3BL	Microsatellite (OPY16)	(Dababat et al., 2016)
19	*Rlnn1*	*T. aestivum*	7AL	AFLP (Xcdo347-7A)	(Williams et al., 2002)
20	*CreX*	*Variabilis L.*			(Cui et al., 2020)
21	*CreR*	*Secale cereale L.*			(Cui et al., 2020)
22	*CreV*	*Dasypyrum villosum L.*	6VL	STS	(Zhang et al., 2016)
23	*CreZ*	*T. aestivum*	EU327996	Real time PCR	(Dababat et al., 2016)

Surprisingly, the production of Ptr ToxA by races 1 and 2 did not contribute significantly to disease development. The race-nonspecific resistance derived from BR34 may be more important than the gene-for-gene interaction typically associated with the wheat-Ptr system (Faris et al., 2012).

Genome wide association studies for disease-resistance in wheat

Although bi-parental QTL mapping has been successful, it usually takes years to develop a mapping population, and gene discovery is limited to the genetic background of only two parents (Cockram and Mackay, 2018). The more recent techniques used to understand natural variations and associate a particular character to a particular genotype are genome-wide association studies (GWAS), also known as genome-wide association mapping (Baloch et al., 2015). The latest progress and accessibility of genotyping by sequencing (GBS) techniques in wheat, which was used to characterize a wide array of hexaploid cultivars from many parts of the world, is facilitating the use of SNPs in GWAS (Muhammad et al., 2020). Different technologies have been used for the identification of SNPs after sequencing approaches. For instance, SNP arrays, such as 90K arrays, have been used in genome-wide association studies to identify genomic regions and/or markers for several traits, such as grain asparagine contents, resistance to Hessian flies, disease resistance, grain yield and frost tolerance in wheat (Muhu-Din Ahmed et al., 2022).

GWAS is a useful technique to identify significant markers for characteristics in wheat (Verges et al., 2021). GWASs have been reported against the most threatening fungal diseases to wheat production, including rust, smut, and bunt diseases (Goutam et al., 2015). Leaf rust is the most common among all wheat rust which infect most wheat growing fields (Vanzetti et al., 2011). Leaf

resistance (*Lr*) genes have been reported to be linked with a wide range of markers (Imbaby et al., 2014). GWAS also reported in fusarium head blight (FHB) (Verges et al., 2021) resistance in winter wheat lines, suggesting that GWAS is the most effective approach for FHB resistance (Savadi et al., 2018). Furthermore, there are sixteen race-specific resistance genes to common bunts from Bt1 to Bt15 that have been reported (Goates, 2012). Furthermore, 123 SNPs were shown to be linked with resistance on fourteen chromosomes in a genome-wide association study (Mourad et al., 2018). This GWAS and molecular markers could be useful tools for the characterization of DB resistance in bread wheat. A QTL that had been previously identified on chromosome 6DS, as well as a newly discovered locus on the same chromosome, were shown to explain 9-15% of phenotypic variation (Gordon et al., 2020).

GWAS could be a potential technique for identifying marker trait relationships for biotic and abiotic resistance (Ali et al., 2019). There have not been many GWAS reports in wheat of resistance to nematodes (Würschum et al., 2012), as only one gene, *Rlnn1*, came from an Australian spring wheat cultivar (Williams et al., 2002). Additionally, (Dababat et al., 2016) discovered nine significant marker trait associations (MTAs) on chromosomes 1D, 2A, 3B, 5B, and 7A related to *P. thornei* resistance using GWAS. Genome-wide association analyses have been routinely used to link nematode resistance or susceptibility to specific genomic areas. It is commonly known that different resistance sources against different diseases in common wheat are derived from wild wheat families by breeding strategies. These advancements were made possible by the crop plants' genetic variety (Ogbonnaya et al., 2001). Furthermore, R genes encode surface immune receptor-like kinases (RLKs), and intracellular immune receptors include nucleotide-binding leucine-rich repeat proteins (NLRs) that can identify toxic molecules or avirulence (*Avr*) proteins in pathogens directly or indirectly (Monteiro and Nishimura, 2018). Most resistance genes (*R*-genes) are linked to race-specific interactions, also known as "gene for gene" interactions (Flor, 1971), which are easily broken down within the field, as pathogens can change to avoid host identification by modifying the homologous avirulence gene. The use of high-density single nucleotide polymorphism (SNP) maps in genome-wide association studies (GWAS) has proven successful in discovering many important marker traits linked to Fusarium head blight (FHB) traits (Khan et al., 2020). Different important steps of GWAS for disease resistance in wheat are shown in Figure 3.

CRISPR/Cas-9 mechanism- a breakthrough genome editing tool for enhancing wheat resistance to diseases

Wheat hexaploidy (2n = 6x = 42, AABBDD genome) and gene functions make it difficult to choose a suitable phenotype through genetic advances (Adamski et al., 2020). To achieve worldwide food and environmental security, genomic approaches must be used to improve wheat yield and resistance (Li J. et al., 2021). Genome-editing techniques have transformed plant studies and have a great capacity for crop enhancement. In the agriculture sector, disease-resistant varieties in breeding programs are the most cost-effective and environmentally friendly approach to disease management (Figure 4) (Choudhary et al., 2022). As a result, increasing crop

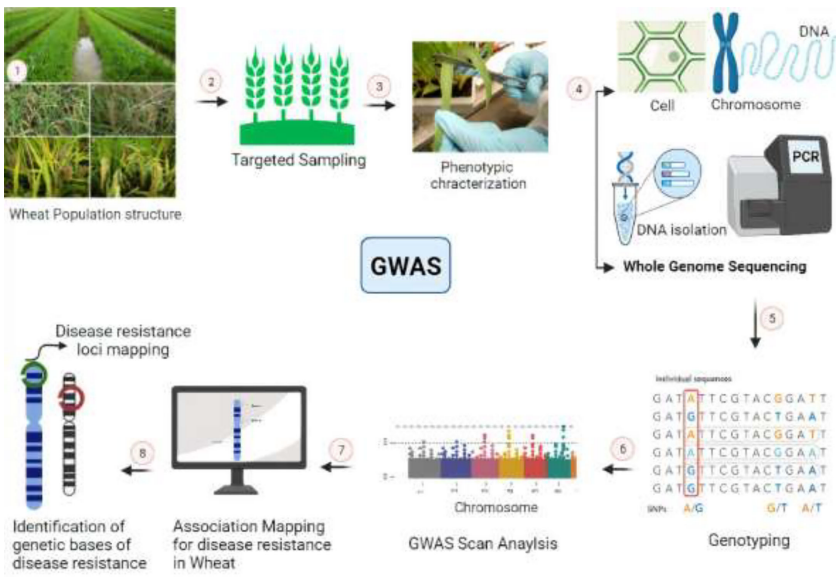

FIGURE 3
Genome-wide association studies demonstrating work scheme for the development of disease resistance in wheat. 1, 2: Cultivation of wheat for large scale field trials and pathogen application. 3: Phenotypic evaluation and measurement of disease resistance in wheat-pathogen reactions. 4: Whole-genome sequencing, assembly, and annotation of selected lines. 5: Alignment of reads with reference genome and identification of molecular markers i.e., SNPs. 6: Statistical data analysis and predictions of associated markers with QTLs of interest. 7, 8: Chromosomal mapping of identified QTLs and their further functional validation.

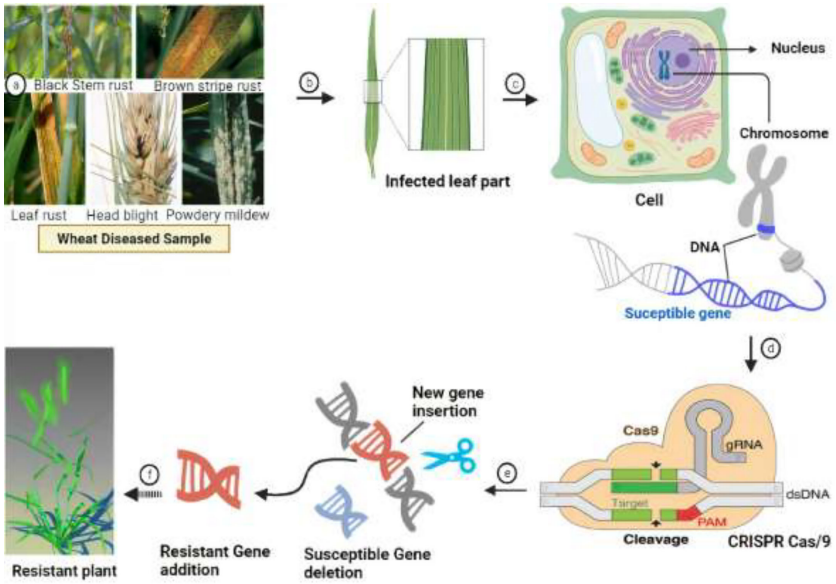

FIGURE 4
Overview of the CRISPR-Cas9 genome editing system and figurative description of how it works for the development of disease resistance in wheat. **(A, B)** Identification and assessment of wheat germplasm susceptible to pathogens. **(C)** In-depth molecular analysis of the wheat genome *via* various genomics-transcriptomics techniques and identification of susceptible/Avr genes that favor pathogen growth on wheat plants. **(D)** Description of the molecular mechanism depicting how the CRISPR-Cas9 construct identifies the Avr genes scanning the wheat genome. **(E)** Deletion or replacement of Avr genes with resistant R genes that hinder pathogen colonization. **(F)** Development of healthy and resistant wheat plants for future cultivation.

breeding policies that promote disease resistance require an awareness of plant–pathogen interactions and crop immune mechanisms (Li J. et al., 2021). Among genome editing tools, CRISPR/Cas9 is a promising gene editing technology in crop plants because it is specialized, highly specific, a multigene editor, and highly useful (Rao and Wang, 2021). Compared to other gene editing methods, such as transcription activator-like effector nucleases (TALENS) (Sun and Zhao, 2013) and zinc finger nucleases (ZFNs) (Townsend et al., 2009), CRISPR/Cas9 is an RNA-guided apparatus enabling efficient and accurate genome editing. CRISPR (clustered regularly interspaced palindromic repeats) Cas9 (CRISPR-associated protein) is a new wave of genome editing that is quick, easy, and cheap. For a long time, it has been utilized as a bacterial immune system and has recently made a significant advancement in the field of genome editing (Figure 5) (Yang et al., 2022). In 2012, CRISPR Cas9 was first

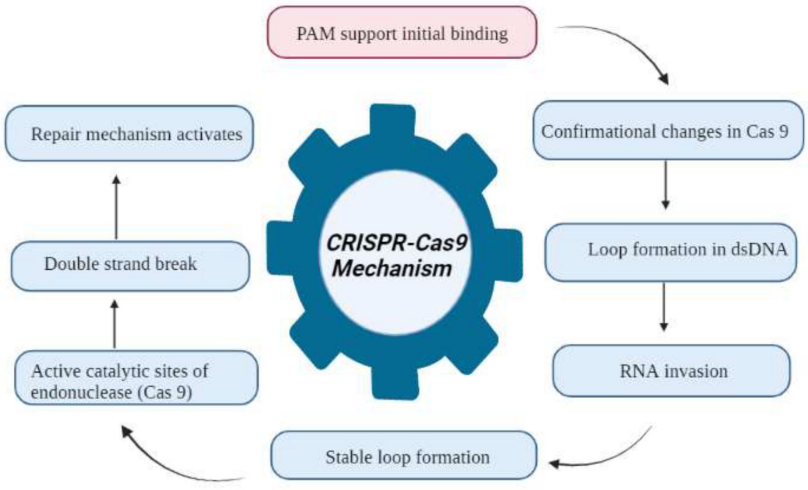

FIGURE 5
Flowchart of the CRISPR Cas9 mechanism for the development of disease resistance in wheat. The recognition, cleavage, and repair phases are the main stages of the CRISPR/Cas-9-based genome editing system. The PAM sequence is present on the noncomplementary strand, and it is on the strand of DNA that contains the same DNA sequence as the target crRNA. After initial recognition at the target locus, CRISPR/Cas9 causes precise double-strand breaks in the target DNA, which is further followed by DNA repair processes.

described for genome editing by American scientist Doudna and French microbiologist Emmanuelle Charpentier (Cohen, 2017). In addition to wheat, many other crop species have benefited from the CRISPR/Cas9-based genome editing system. For example, this system is employed in more than 20 crop species to improve production, biotic and abiotic stress management, and other features (Farooq et al., 2021). As in rice, CRISPR-mediated targeting of the OsERF922 gene has led to resistance against bacterial blight and rice blast (Romero and Gatica-Arias, 2019). The ARGOS8 gene in maize has been mutated to improve grain yield during drought stress (Chilcoat et al., 2017). The *ALS1* gene in potatoes was also targeted for resistance to herbicides (Danilo et al., 2019). Because CRISPR/Cas9 is a sequence specific nuclease, it could be used to influence plant defensive mechanisms against invading pathogens (Tyagi et al., 2021).

Wheat production and disease resistance have both benefited from the adoption of CRISPR/Cas9. The use of CRISPR/Cas9 technology has significantly impacted the production of wheat and improved its resistance to diseases. Additionally, CRISPR/Cas9 can be used to introduce new traits into wheat, such as improved grain quality, higher yield potential, or tolerance to abiotic stress. By combining these traits with disease resistance, the overall productivity of the crop can be increased (Zhang et al., 2021). For instance, lipoxygenase (LOX) has various roles in plant growth and development and resistance against diseases. *TaLOX2* knockout improves wheat shelf life by altering grain size and weight (Shan et al., 2014). The RING-type E3 ligase-encoding gene *TaGW2* was knocked out, resulting in longer and wider wheat grains and higher grain yields (Zhang et al., 2018). Multiplexed gene editing (MGE) based on CRISPR-Cas9 is an effective is an effective tool for modifying many genomic zones at the same time to control diverse agronomic traits. The MGE created by combining tandemly arrayed tRNA–gRNA units resulted in genetic mutations in the wheat genes *TaGW2, TaLpx-1, and TaMLO* (Wang et al., 2018). The desired mutation and resistance in wheat plants altered by CRISPR/Cas9 in one of the three MLO homoalleles (*TaMLO-A1*) demonstrated increased resistance against *Blumeria graminis* f. sp. *tritici* infection. This finding explains the importance of *TaMLO* genes against powdery mildew disease once again (Wang et al., 2014). Likewise, resistance is improved to powdery mildew disease (*Blumeria graminis* f. sp) of wheat TaEDR1/cds area CRISPR/Cas9 (Zhang et al., 2017). Wheat dwarf virus (WDV) is an economically significant virus that is spread by insects (Kis et al., 2019). In model plants, direct use of CRISPR/Cas9 technology against *geminivirus* replication has been explained (Zaidi et al., 2016). WDV Guide4-Guard Lines 1, 3, and 4 showed no signs of viral infection, and neither northern blot nor PCR testing revealed the virus's existence. These findings suggested that these lines are completely resistant to WDV infection (Kis et al., 2019). Similarly, in the free-living nematode *Caenorhabditis elegans*, genome editing utilizing the CRISPR/Cas9 system has newly been recognized (Paix et al., 2017). This breakthrough would lead to the identification of numerous key genes participating in several nematode physiological systems (Ullah et al., 2020). However, the CRISPR/Cas9 process can be complex and time-consuming, especially when multiple genes are targeted. There is also a risk of off-target effects, where the CRISPR/Cas9 system may edit unintended regions of the genome.

Reprogramming of wheat genome through gene pyramiding/stacking using molecular markers

Gene pyramiding is an important breeding strategy in wheat breeding programs that involves the integration of multiple resistance genes into a single cultivar to enhance resistance against biotic and abiotic diseases. This strategy is particularly useful in the development of cultivars that can withstand multiple stresses, thus providing farmers with more resilient and productive crops (Dormatey et al., 2020). One suitable way to achieve functional gene pyramiding is using molecular markers. Markers are DNA sequences that can be used to identify genes associated with specific traits or to track the inheritance of these genes during breeding programs. By using markers, breeders can identify plants that have multiple resistance genes and select them for further breeding (Ye and Smith, 2008). Many global and key national wheat breeding programs have adopted functional gene stacking strategy using markers to develop wheat cultivars with improved resistance to multiple stresses. For example, in India, the Indian Council of Agricultural Research (ICAR) has developed wheat cultivars with resistance to multiple diseases, including rusts and powdery mildew, using functional gene pyramiding. These cultivars have been widely adopted by farmers and have contributed to increased wheat productivity and food security in the country (Kumaran et al., 2021). Similarly, the Chinese Academy of Agricultural Sciences (CAAS) has also developed wheat cultivars with multiple disease resistances using functional gene pyramiding. These cultivars have been widely adopted by farmers in China and have contributed to increased wheat yields and improved food security (Li et al., 2014). Likewise, gene pyramiding has been used to develop cereal cyst nematode resistance with multiple genes in wheat. This involved combining resistance genes from various origins, such as Cre1 located on the 2BL chromosome arm, Cre3 found on the 2DL chromosome arm, and Cre8 situated on the 6BL chromosome arm. Specific molecular markers linked through PCR were then utilized to track each gene individually (Barloy et al., 2007; Ogbonnaya et al., 2009). Overall, functional gene pyramid using markers is an effective breeding strategy for developing wheat cultivars with improved disease resistance. It has been successfully adopted by many global and key national wheat breeding programs, and it is likely to continue to play an important role in the development of resilient and productive wheat cultivars in the future.

Concluding remarks and perspectives

The objective of this review was to provide an overview of reported whole effective QTLs and an understanding of numerous modern molecular techniques that could be used to improve pathogen resistance in bread wheat. It is concluded that the best strategy to manage major wheat diseases is to develop modern genetic resistance, which can be achieved by identifying genes/quantitative trait loci (QTLs) and molecular markers. Overall, innovative genetic methods based on molecular marker tools are

a recommended viable option for improving resistant cultivars against diseases. Wheat genomics has been revolutionized by the advancement of molecular markers such as SSLPs, RFLPs, SSRs, ISSR, AFLPs, SCAR, SNPs, and DArT within the previous two decades. Marker-assisted selection and functional genomics techniques are both efficient approaches for developing resistant germplasm. Among them, QTL mapping is the most effective approach to determine the exact position of a gene. Furthermore, one of the most widely used transgenic methods for silencing the gene expression of pathogen effector-encoding genes is RNA interference (RNAi) to improve disease resistance and different traits in crop plants (Majumdar et al., 2017). By introducing specific dsRNA sequences to confer resistance in host plants, RNAi could be used to downregulate pathogen genes involved in invasion, growth, and pathogenicity in plants. This approach is mostly used as host-induced gene silencing (HIGS) to suppress wheat pathogens, i.e., nematodes. In recent years, resistance engineering has focused on identifying and silencing genes that contribute to facilitating pathogen attack, as these factors may provide more persistent resistance than R genes (Schaefer et al., 2020). Furthermore, the nucleotide-binding site and leucine-rich repeat (NBS-LRR or NLR) proteins are encoded by the largest family of R genes (Gururani et al., 2012). Most R genes, as well as linked components, aid pathogen detection and provide resistance to a subset of pathogens, or races, that produce certain effector proteins gene-for-gene. The discovery, conservation, and effective transfer of R genes between plant species has resulted in the development of long-lasting resistance and crop protection against a variety of infections. Engineered R genes for conferring resistance to a broad variety of pathogens (Jiang et al., 2020) could be a potential method to improve disease resistance in wheat. Molecular markers provide several advantages over traditional phenotype-based alternatives, including that they are stable and detectable in all defensive statuses. A microarray-based approach throughput high molecular marker has been established for evaluating thousands of DNA samples using a co-dominant molecular marker on a glass slide.

They are valuable tools not only for whole-genome transcript profiling but also for the identification of genotypes and polymorphisms. The microarrays used in DNA-chip technology are microscopic arrays of nucleic acid molecules immobilized on a solid surface, typically glass, for biochemical examination. DNA technologies are favorable and powerful means for identifying taxa at different taxonomic levels, including species, subspecies, variety, and strain, because they produce consistent results regardless of tissue origin, physiological conditions, environmental factors, sample harvest, storage, and processing. With the growing demand for high-quality herbs, the requirement for DNA verification to ensure plant effectiveness will increase. The European Union (EU) has created microarrays to speed up the discovery of DNA polymorphisms in plants. According to the EU, the technique could be used to diagnose plant diseases as well as improve crop breeding. The risk of reduced genetic diversity in the wheat crop if only a small number of resistance genes are used in breeding programs.

Future scenarios and recommendations

Regarding the future recommendations for the above data analysis, several additional potentially helpful study directions for proper identification and early detection of wheat pathogens are important to prevent the spread of the fungus that causes major diseases in wheat. The development of disease-resistant cultivars is insufficient to save plants and feed a rising population, particularly in developing nations. Major diseases of wheat result in significant production losses, forcing researchers to generate multiple pathogen-resistant varieties of wheat. Multiple disease resistance is a vital tool against pathogens in sustainable agriculture, it is cost-effective for both farmers and the environment. Similarly, remote sensing technology could increase the depth and dependability of disease surveys conducted annually. Future tasks include acquiring more suitable markers to enhance wheat breeders' strengths. In the literature, integrating molecular breeding works among a few national program partners is also seen as an important issue. One of the main priorities of wheat researchers is making wheat globally competitive by lowering cultivation costs and enhancing farmer profitability. On the other hand, genomic transformation will continue to be a vital tool for studying gene functions and evaluating the value of new sequences. In addition, the peptide method keeps only one functional domain to interfere with the target functions. Additionally, the mechanism of pathogen-derived resistance known as posttranscriptional gene silencing (PTGS) has been discovered. PTGS-based resistance traits are typically strong. The technique represents a potential novel concept that could be utilized for yeast two-hybrid systems to select target-specific peptides ("aptamers") to modify block protein functions *in vivo*. Additionally, in the early days, traditional plant breeding techniques were used in the field of agriculture. However, some drawbacks are that they cannot transfer specific traits to species. Hence, new agricultural enhancement approaches can transfer genes between different species, including vegetatively reproducing plants. It is critical to uncover novel resistance genes/gene families to attain the goal of obtaining disease-resistant plants (Vega-Arreguín et al., 2017). For the identification of novel genes, advanced approaches such as virus-induced gene silencing (VIGS), host-induced gene silencing (HIGS), and mutant screening have been widely used (Sawyer and Labbé, 2021). Host-induced gene silencing (HIGS) is a transgene-based strategy with highly specific siRNA design, off-target effects, and productive technology. By altering gene expression in a precise way, these approaches can provide plant protection against a wide range of plant pathogens. Additionally, spray-induced gene silencing (SIGS) is a nontransgenic technique that uses a spray of tiny RNA molecules to regulate the target gene (s) in a highly targeted manner (Taning et al., 2020). Moreover, sequence-specific nucleases (SSNs) could be utilized to create a broad spectrum of sequence alterations for disease resistance in plant genes. Moreover, the most effective way to reduce the impact of plant diseases is to contain the pathogens at their birthplace. New plant biotechnologies can detect a wide range of uncharacterized pathogens, posing a major task for quarantine standards. The laws of plant quarantine can be administered both at the national level and

at the regional level within a country. The molecular breeding of highly wanted wheat cultivars will undoubtedly benefit from the incorporation of developing novel biotechnologies.

Author contributions

MJ wrote the manuscript and worked on figures. MA and AZ edited and reviewed the manuscript. GM-U-D worked on the tables and revised the manuscript. LG founded, supervised, edited, reviewed and approved the final manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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