A Review on Major Rust Resistance Gene and Amino Acid Changes on Wheat (*Triticum aestivum* L.)

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Wheat ranks first in the production and productivity of staple cereal crops in the world. Several diseases, including Stripe (*Puccinia striiformis* f. Sp. *tritici*), Black (*Puccinia graminis* f. Sp. *tritici*), and Brown (*Puccinia recondita*), have a major negative impact on wheat output, with 20 to 80% loss annually. Growing rust-resistant varieties is the most durable, cost-effective, and environmentally friendly way to combat rust pathogens. In the present review, we provide updated information on all black stem rust, yellow leaf rust, and brown leaf rust resistance genes including chromosomal position, those derived from different sources, nature of resistance type, and amino acid changes done by this gene against rust pathogen. This study summarized the 68 black stem rust, 101 leaf rust, and 108 stripe rust resistance genes from diverse cultivars of wheat and wheat primary and secondary gene pools. This review will be valuable to wheat breeders in cloning rust-resistant genes and developing leaf as well as stem rust-resistant wheat cultivars using gene pyramiding as well as frequency multiplication through introgression of the gene of interest for disease-free, sustainable grain production of wheat. The success of pyramiding genes from other sources to bread wheat depends on the nature of germplasm, the gap between flanking marker and targeted genes, the selection of genotypes in each generation, large number of genotypes large genotype-environment interaction, etc., which is the future area of study.

1. Introduction

Bread wheat (*Triticum aestivum* L.) is a major staple food that provides significant amounts of nutrition to individuals all around the planet [1]. Bread wheat is a significant crop around the world, providing 20% of the caloric intake [1]. Due to COVID-19 and the Russia-Ukraine war, world wheat production year 2022-23 is expected to be 774.83 million tonnes, lower than 4.46 million tonnes from the prediction for 2021 to 22 [2]. With an estimated 220 million hectares, wheat is the world’s largest acreage crop and 35 percent of the world’s population consumes wheat as a staple grain [1].

Wheat productivity is severely harmed by three rusts: leaf rust (LR, caused by *Puccinia recondita*), stem rust (SR, caused by *Puccinia graminis f. Sp. tritici*), and yellow rust (YR, caused by *P. striiformis f. Sp tritici*) [3]. According to recent research, the average yearly losses from all three rusts go up to 15.04 million tons per year, equating to a cost of roughly US $2.9 billion annually [4]. Wheat yellow and stem rust are two of the most common wheat diseases worldwide [5]. *Leaf rust* produces yield reduction of up to 50% in favorable conditions, Stem rust causes yield reduction of up to 100% during epidemics, and Yellow stripe causes yield reduction of 10–70%, as per available estimates [6]. In these predictions, the magnitude of reduction in yield is sometimes also dependent on the cultivar utilized, the period of infection, the speed of pathogenicity, and the disease duration [7, 8].

The global population is expected to grow to 9.8 billion by 2050 and 11.2 billion by 2100 [9]. According to a new United Nations, the present global population of 7.6 billion is expected to increase to 8.6 billion in 2030, 9.8 billion in 2050, and 11.2 billion in 2100, putting an even bigger need on wheat world production. Rust resistance genes from wild species were studied genetically. Cloned genes give seedling resistance (SR), also known as all-stage resistance (ASR), or
adult plant resistance (APR genes), which is only expressed in the adult plant stage, especially after booting. Resistance is also reported to be provided by ASR genes; however, it only lasts a few years. Cloned genes give seedling resistance (SR), also known as all-stage resistance (ASR), or adult plant resistance (APR genes), which is only expressed in the adult plant stage, especially after booting [10]. ASR genes are also known to generate resistance that lasts only a few years, whereas APR genes provide long-term, permanent resistance [11].

When a plant’s immune system is activated, it can defend itself against pathogen invasion [12]. There are two types of immune systems in plant defense mechanisms called systemic acquired resistance (SAR) and induced systemic resistance (ISR) which are described in salicylic and jasmonic acid pathways [13]. During inoculation of the pathogen in the host surface, significant variations in host plants during pathogen infection include the generation of reactive oxygen species, the activation of defensive machinery of plants including enzymatic and nonenzymatic antioxidative components, secondary metabolites, pathogenesis-related protein expression (e.g., chitinases and glucanases), phytoalexin production, modification in cell wall composition, production of melatonin, accumulation of carotenoids, and altered activity of polyamines. Consequently, disease growth is limited by the changing concentration of metabolic products in hosts [14]. When infections are first identified, several transcription factors inform the rest of the crop it is under attack and trigger signaling systems [15]. Air dissemination of its spores across hundreds or even thousands of km has resulted in its widespread on a regional or worldwide level, allowing the disease to resurface frequently in areas where the climate remains unfavorable throughout the year [8]. The pathogen is hemicyclic, and there is no evidence of a sexual cycle [16]. Up to 88% of the wheat crop is susceptible to yellow rust, while black stem rust causes greater loss in wheat production, as per a conservative estimate [17]. The pathogen damages at least 5 million tons worldwide yearly harvest season [17].

All-stage resistance (ASR) and adult plant resistance (APR) are the two most common types of host defense against rust in wheat [4]. Unlike ASR, which is effective from seedling to mature stages of plant growth, APR is only active in the late stages of plant growth [18]. APR usually only gives partial resistance, although it is more durable and efficient over all or a larger range of Pst races than ASR [19]. Adult plant resistance that gives lasting and nonrace-specific resistance to Pst10 is known as high temperature adult-plant resistance (HTAP) [20]. Using several ASR and HTAP genes to maintain wheat stripe rust resistance looks to be an appropriate strategy in all locations. Stripe rust is a severe foliar disease that is threatening wheat output all over the planet [21]. To control and prevent wheat rust, the most cost-efficient, productive, and ecologically friendly solutions are to breed and plant disease-resistant cultivars [12].

The objectives of this study are (i) understanding the chromosomal location of different LR, SR, and YR resistance series genes like seedling resistance, all-stage resistance, high temperature activating resistance, and adult plant resistance in wheat populations. (ii) Study of these each avirulence genes series from SR, YR, and LR (1 up to identified cloned genes shown in tables) has its own mechanism of amino acid biosynthesis process for triggering the pathogen. Avirulence genes help to sustainable levels of horizontal resistance against the diverse race of rust pathogens. Introgression and frequency multiplication of gene of interest called avirulence genes on different chromosomal locations of bread wheat are useful in breeding for resistance cultivars development against pathogen races. This study assists the breeders and scientists who are looking for a durable resistance gene to combat the rust disease. So, this gap is being filled by gene pyramiding of resistance genes into different cultivars of wheat-growing regions for long-term cultivar development and to ensure global food security.

2. Black Stem Rust Known Gene (*Puccinia graminis Pers. f. sp. tritici*)

When susceptible cultivars are produced, stem rust (caused by *Puccinia graminis Pers. f. sp. tritici*) can result in significant yield losses [22]. It is critical to understand the biological component of stem rust resistance in wheat to increase wheat breeding efficacy [23]. A total of 69 stem rust resistance (Sr) genes have been identified so far. Only 15 all-stage Sr resistance genes have been cloned, with diagnostic markers being produced for only a few of them [24]. The cloned Sr resistance genes include Sr13, Sr21, Sr22b, Sr26, Sr27, Sr33, Sr35, Sr45, Sr46, SrT1A1662, Sr50, Sr60, Sr61, and Sr62 [25]. Some quantifiable APR sources for stem rust have been discovered in nature [25]. It is considered more lasting than the qualitative main gene-based resistance when APR is controlled by numerous genes with minor impacts [25]. Quantitative resistance is typically displayed in mature plants and discovered by field studies of vulnerable seedling lines [25]. Combining race-specific and APR genes can result in increased stem rust resistance [25]. The researchers found more than 16 APR genes and 36 seedling-stage resistance genes [22]. Some of these genes are derived from *monococcum* wheat such as SrTm4 A™, Sr20, Sr21, Sr22b (Sr2+Fhb1 rec), Sr23, Sr35, Sr60, SrTm5, and some of these resistance genes are derived from durum wheat (*Triticum turgidum*) such as Sr2, Sr9e, Sr9g, Sr12, Sr14, Sr17, Sr63; similarly, some genes are derived from hexaploidy wheat of different cultivars such as Sr2, Sr5, Sr6, Sr7a, Sr7b, Sr8a, Sr8b, Sr9a, Sr9b, Sr9d, and some of resistance genes are derived from wild species such as *Secale cereal*, *T. comosa*, *Aegilops speltoides*, *Triticum timopheevii* ssp. *Araraticum*, *Aegilops tauschii*, *Thinopyrum intermedium*, *rye cultivar*, *Aegilops searsii*, *Dasypyrum villosum*, *Aegilops geniculata* such as Sr27, Sr34, Sr32, Sr33, Sr47, Sr53, and whole information is given in Table S1 [26–36].

3. Brown Rust (*Puccinia recondita*) Resistance Gene in Wheat

*Puccinia recondita* causes leaf rust which is one of the most important and widespread diseases in wheat (*Triticum aestivum*). It thrives in a variety of temperatures, may...
be found almost anywhere wheat is farmed, and causes severe yield and economic losses [20]. Leaf rust can result in yield losses of up to 40% in favorable situations [38]. In wheat, up to 100 leaves, rust-resistant strains have been formally designated [39]. The majority of them cause hypersensitivity and interact with the pathogen gene for gene action [40]. Other approaches to extending race-specific resistance include gene pyramiding, strategic gene deployment, and multilinie cultivars [41]. Half of these genes have been introduced from wild and related species, while the rest are native to wheat [42]. As a result, a continuing investigation for novel and efficient resistant strains which can be exploited in wheat genetic improvement is required to fight rust infections [43]. Wheat genetic resources are divided into three categories: primary, secondary, and tertiary gene pools [44]. While transferring genes from primary and secondary gene pools is generally simple, transferring genes from the tertiary gene pool is often complex and needs the employment of chromosomal manipulation techniques [45]. Genes Lr27 and Lr31 in Australian hexaploid wheat types were found to have the best documented complimentary activity [46]. Brown rust, sometimes known as leaf rust, is currently a major wheat disease over the world [4]. Lots of resistance genes are identified and cloned from hexaploidy, monoccocum, and wild species wheat such as Lr1, Lr2, Lr2a-c, Lr3, LrZHB84, Lr10, Lr11, Lr12, Lr13, Lr14a-b, Lr15, Lr16, Lr17a-b, Lr18 from hexaploid wheat species, Lr9, Lr4-6, Lr19, Lr21, Lr22a-b, Lr23, Lr24, Lr25, Lr26, Lr35, Lr36, Lr37, Lr38, Lr39 from wild species such as Secale cereal L, Agropyron elongatum, Secale cereal, Rosen, Secale cereal Petkus, Aegilops speltoides, Aegilops ventricosa, Agropyron elongatum [47]. Some of the resistance genes are derived from monoccocum wheat such as Lr50, Lr63, Lr80, LrX, and LrTM16 in different chromosomal loci [48]. Some of these genes are race-specific adult plant resistance types, some are seedling resistance types, some are all-stage resistance types, and some are field resistance types which are shown in Table S2 [26, 49–69].

4. Yellow Leaf or Stripe Rust Resistance Known Gene (P. striiformis f. sp. tritici)

Wheat stripe rust (also known as yellow rust) is a widespread disease caused by Puccinia striiformis f. Sp. tritici (PST) [70]. The most cost-effective and environmentally friendly way to decrease stripe rust damage is to select resistant cultivars. For extending race-specific resistance, gene pyramiding, gene deployment, and multilinie cultivars are recommended [71]. More than 105 genes for stripe rust resistance have been discovered so far. APR usually only gives partial resistance, although it is more lasting and effective against all or a broader range of Pst races than ASR [72]. A prominent kind of APR is high temperature adult plant (HTAP) resistance, which gives long-lasting and nonrace-specific resistance to Ps [20]. Multiple ASR and HTAP genes appear to be an excellent strategy for sustaining long-term wheat stripe rust resistance [73]. Stripe rust is a major foliar disease that threatens wheat output throughout the world. Leaf rust resistance genes obtained from Triticum aestivum were studied genetically. Many yellow rust resistance genes are derived from hexaploidy wheat [74]. Yr1, YrA, Yr2, Yr3a-c, Yr4a-b, Yr6, Yr11, Yr12, Yr13, Yr14b, etc. are the stripe rust resistance genes; few of these genes show seedling stage resistance, some of them sow high temperature adult plant resistance. Those genes that are cloned and introgressive to bread wheat from wild species such as Secale cereale (Yr9) and Aegilops ventricosa (Yr17) give all-stage resistance against rust pathogen, and double haploid population gives adult stage resistance to wheat cultivar [15]. Yr18, Yr36, and Yr46 confer adult-plant resistance and encode a putative ATP-binding cassette (ABC) transporter a protein with a kinase domain and a lipid-binding domain [75], and a hexose transporter. Yr7, Yr10, Yr15, YrAS2388, and YrU1 are all-stage resistance genes derived from wild species and wheat lines [76]. The list of yellow rust resistance genes is shown in Table S3 [77–92].

5. Amino Acid Changes due to Resistance Gene against Rust Pathogen in Wheat

To combat pathogen infection, plants have developed a variety of defense mechanisms [93]. Rust resistance conferred by the combination of race-specific and nonrace-specific resistance genes is more durable and most preferred in the wheat varieties [94]. Avirulence genes called R-genes in plants, including Lr genes in wheat, are discovered to belong to 104 different families [47]. In wheat cultivars, rust resistance provided by a mix of race-specific and nonrace-specific resistant strains is substantially more persistent and desirable. A nucleotide-binding region and a leucine-rich repeat are found in R genes (NLR), the remaining cloned R genes code for receptor-like proteins (RLPs), and receptor-like kinases (RLKs) (19%), and NLR-ID (NLRs with 106 integrated domains) proteins [95]. Integrated domains (IDs) may be essential in receptor stimulation or signaling downstream [11]. Wheat has 2,151 NLR-like genes, with 1,298 clustered into 547 genes. 1,552 NLR (non-TNL)-like genes encode LRRs, 802 encode CC-domain-encoding (CC-NBS-LRR or CNL) genes, and NLR-ID fusion proteins as potential NLR functional diversifiers, often as kinase and transcription factor domains [96]. Analyses of the IDs revealed that over 80% of amino acid sequence similarity has been conserved over time [10]. 547 gene clusters contain NB-ARC-encoding genes, and they are all quite similar. Genes encoding receptor-like kinases (RLKs) (including ATP binding, serine-threonine kinases) and other kinases were the most commonly affected genes [97, 98]. Many genes encoding transcription factors (TFs) (the most abundant of which are WRKY TFs), ncRNAs, and histone variants were found, as well as genes involved in reactive oxygen species (ROS) homeostasis [98].

5.1. Different Lr Genes and Amino Acids Changes. The wheat leaf rust resistance gene Lr1 produces a 1 344-amino-acid resistance protein with a characteristic coiled-coil nucleotide-binding site leucine-rich repeat (CC-NBS-LRR) [99]. Lr35-induced adult resistance to Puccinia triticina is
mediated by the TaLr35PR5 gene [100]. A full-length TaLr35PR5 gene was identified from wheat near-isogenic line TcLr35, expressing a protein with amino acid and structural similarities to the sweet protein thaumatin. TLPs (thuaamatin-like proteins) overexpression can cause antifungal activity in a variety of transgenic plants [100]. TaLr35PR5 plays a role in the Lr35-mediated defensive response against the leaf rust fungus [101]. Inactivating a pathogenesis-related thaumatin-like protein gene in wheat, TaLr35PR5 limits Lr35-mediated resistance for the first time [100]. During the key grain-filling stage, the Lr34 gene drives senescence-like processes in the flag leaf tips and margins and is particularly effective in the highest leaf, the so-called flag leaf [24, 102]. Understanding the genetic nature of this type of resistance is critical for long-term rust disease management [75].

The Lr34 protein is related to the pleiotropic drug resistance subfamily’s adenosine triphosphate-binding cassette transporters [103]. In the adult plant stage and the flag, Lr34 is active [104]. The Lr34 gene codes for a full-size ABCG (pleiotropic drug resistance) transporter [103]. The transmembrane domain (TMD) and the nucleotide-binding domain (NBD) are two different domains that ABC transporters have in common (NBD) [104]. The predicted 1401-amino acid protein belongs to the pleiotropic drug resistance subfamily of ABC transporters [75]. Pleiotropic drug resistance transporters share a common basic structure containing two cytosolic nucleotide-binding domains and two hydrophobic transmembrane domains [101, 105]. OsPDR23 is the rice homolog of LR34, with 86 percent amino acid similarity [75, 104].

A pectate lyase gene was found to be involved in resistance conferred by Lr34/Yr18, and a 1-proteasome subunit was found to be connected with resistance conferred by Lr46/Yr29, another wheat slow-rusting gene [103]. The wide range of resistance and lack of race specificity resembles systemic-acquired resistance (SAR) linked to pathogenesis-related (PR) protein expression [103].

Induction is highly restricted to those leaf mesophyll cells within and immediately surrounding rust infection sites, according to a-glucuronidase (GUS) reporter gene under the control of the fis1 promoter [40]. The extent of fungal development is reflected in the level of induction [40]. There is very little fungal growth and a microscopic level of GUS expression in a strong resistance reaction, such as the hypersensitive fleck mediated by the Lr6 resistance gene [106]. Wheat (Triticum aestivum; wis1) and Arabidopsis encode proteins that are highly similar (76 percent–82 percent) to the FIS1 protein [40]. It has been discovered that the Arabidopsis homolog encodes a 1-pyrroline-5-carboxylate dehydrogenase, which is involved in the conversion of proline to glutamate [40]. A suitable infection with the matching species-specific rust upregulates it [40].

The accumulation of autotoxic and/or antimicrobial chemicals is suggested by the necrosis and increased resistance of leaf tips [75]. In considering the development of the growing dependence on slow-rusting genes like Lr34/Yr18 cultivars for long-term rust resistance[104]. It is critical to learn more about the resistance process [103]. The most abundant form of 25 immunological receptors in plants, nucleotide-binding leucine-rich repeat receptors (NLRs), can cause fast cell death (hypersensitive) response in response to 26 pathogens [107]. Previously, the wheat NLR Sr35, which encodes a coiled-coil (CC) 27 NLR that confers resistance to the severe wheat stem rust race Ug99, had been cloned [108]. The NBD or ATP-binding cassette (ABC) domain is cytoplasmic and more highly conserved. A characteristic of the NBD domain is its ATP binding [104]. It is the hydrolysis of ATP that powers the substrate transport. In the Lr34 protein, the N-terminal NBD and the C-terminal transmembrane domains form a single polypeptide chain, arranged as NRDTMD-NBD-TMD. NAC (NAM, AFAT1/2, and CUC2) transcription factors play important roles in plant growth and resistance to abiotic and biotic stresses [109].

About 9.2 million bases away from Lr77, Lr79 was discovered. A substantial proportion of Lr genes (28 out of 80) is derived from alien species [6].

In the wheat line Thatcher + Lr14b (TcLr14b), the TaNAC35 gene inhibits leaf rust resistance [110]. The TaNAC35 gene was cloned from this line, and the results revealed that its open reading frame (ORF) was 96.16 percent identical to the NAC35-like sequence reported from Aegilops tauschii, and that it encoded a protein with 387 amino acids (aa), including a conserved NAM domain with 145 aa at the N-terminus and a transcriptional activation domain with 220 AA at the C-terminus. Inhibition of TaNAC35 reduced the production of haustorial mother cells (HMC) and mycelial proliferation [111]. Histological tests show that the TaNAC35 gene plays a negative role in TcLr14b’s response to the Pt (Puccinia triticic) pathotype [112].

5.2. Different Yr Genes and Amino Acid Changes. The gene LHY (late elongated hypocotyl) regulates and governs biological rhythms in plants. TalHY’s DNA is also 3085 base pairs long, with a 1947 base pair open reading frame [113]. TalHY is thought to encode a 648-amino-acid, 70.3 kDa protein with one typical plant MYB-DNA-binding domain [114]. They may play a role in wheat heading and resistance to stripe rust infection [10].

On the long arm of chromosome 2B, Yr5 resistance is found [115]. These wheat sequences were matched with the 5’ and 3’ ends of rice loci that had a considerable resemblance to NB-LRR type R-genes using nucleotide and amino acid sequence searches [12]. These rice loci were found on rice chromosomes 4 and 7, which are syntenic with wheat group 2 chromosomes [116].

At relatively high temperatures (25° to 35°C), Yr36 (WKS1) gives resistance to a broad spectrum of stripe rust races. A kinase and a putative START lipid-binding domain are found in this gene [12]. Because Yr36 is found in wild wheat but not in commercial pasta and bread wheat varieties, it can now be employed to improve stripe rust resistance in a wider range of cultivars [102]. The high temperature adult plant resistance gene Yr36 was identified as a single locus [45]. All three Yr genes are members of a complex resistance gene cluster on chromosome 2B that
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...nucleotide-binding and leucine-rich repeat proteins (NLRs) with a noncanonical N-terminal zinc-finger BED domain that differs from that found in non-NLR wheat proteins [108].

By amplifying the polymorphic region of a putative gene encoding wheat copper-binding protein (WCWP1), researchers were able to localize WCWP1 to a 0.64 cM genomic interval [117]. WCWP1 is the probable candidate gene of YrLe693, which was engaged in leaf senescence and photosynthesis associated to plant responses to stripe rust infection during the grain-filling stage on chromosome 1A, based on its unique chromosomal position and expression manner [117].

Two key disease resistance signaling pathways in plants are (salicylic acid) SA- and JA (Jasmonic Acid)-dependent signaling pathways [118]. The cellular concentration of SA was significantly reduced in TaTrxh1-silenced plants, implying that TaTrxh1 may regulate wheat resistance to stripe rust via the SA-associated defense signaling pathway [119]. Trxs have been described as a key component of SA-mediated immune signal transduction cascades, implying a link between redox-based processes and hormone signaling in response to pathogen infection [120, 121].

Genes encoding receptor-like kinases (RLKs) (including ATP binding, serine-threonine kinases) and other kinases were the most commonly affected [98]. Many genes encoding transcription factors (TFs) (the most abundant of which are WRKY TFs), ncRNAs, and histone variants, as well as genes involved in reactive oxygen species (ROS) homeostasis, have been found [122]. Others, such as Yr15, which encodes a protein with kinase-pseudokinase domains, encode a variety of nucleotide-binding sites and leucine-rich repeat (NBS-LRR) proteins [123]. Superoxide dismutase, catalase, peroxidase, and phenyl ammonia-lyase activity were found to be significantly higher in medicated leaves in comparison to healthy leaves, and resistant genotypes exhibited better activity compared to susceptible genotypes, implying that higher activity was induced to detoxify ROS production during leaf rust infection, causing the plant to protect itself from oxidative damage in resistant genotypes [124]. There was a small decline in nitrate and nitrite reductase activity when resistant genotypes were compared to susceptible genotypes, demonstrating that susceptible genotypes cannot maintain nitrogen metabolism under leaf rust infection [124].

5.3. Reactive Oxygen Species and SAR Activating Gene against Biotic Stress. Plant immunity depends on reactive oxygen species (ROS), and controlling their generation is critical for plant health [125]. BdWRKY19 acts as a negative regulator of ROS production, and knocking it out increases resistance to the rust fungus Puccinia brachypodii [118]. By increasing the amount of ROS produced by the host plant, T. mutans in all three TaWRKY19 copies conferred high resistance to Pst. TaWRKY19 is a transcriptional repressor that binds to a W-box element in the promoter of TaNOX10, an NADPH oxidase that is needed for ROS production and Pst resistance [118]. TaWRKY19 has been identified as a potential target for improving wheat resistance to the economically significant wheat stripe rust fungus [118].

Plant disease resistance specialized in systemic-acquired resistance (SAR) has been linked to the production of pathogenesis-related (PR) proteins in response to pathogen attack [110]. Inhibitors of cinnamyl-alcohol dehydrogenase were found to be more efficient than inhibitors of phenylalanine ammonia-lyase, which are inhibitors of lignification in rust [126]. PRs (pathogenesis-related proteins) play a variety of roles in the plant’s defense response to pathogen attack [103]. Molecular mechanisms of Plant Rust Resistance genes implicated in stripe rust resistance in adult wheat plants require searching of genes and gene products [93]. The TaPR10 gene is thought to code for a 160-amino-acid protein [127]. TaPR10’s DNA sequence indicated the presence of one 84 bp intron with GT-AT bi-nucleotide sequence splicing sites between 188 and 271 bp [127]. TaPR10 may play a role in APR’s response to stripe rust in wheat [127].

In plant-pathogen interactions, calcineurin B-like interacting protein kinase (CIKPs) is essential for biotic stress tolerance [112]. TaCIKPK10, a wheat CIK homolog gene, was cloned. Inoculation with Puccinia striiformis f. Sp. tritici (Pst) and treatment with salicylic acid (SA) resulted in rapid induction of TaCIKPK10. Knockdown TaCIKPK10 decreased wheat resistance to Pst, but TaCIKPK10 overexpression increased wheat resistance to Pst by inducing defense responses in various aspects, such as hypersensitive cell death, ROS buildup, and pathogenicity—gene expression concerning other genes [126]. TaBCATI is required for the infection of yellow and stem rust, and it is considered to be involved in the metabolism of branched-chain amino acids (BCAAs), as TaBCATI disruption mutants had increased BCAA levels [119]. TaBCATI mutants also showed increased levels of SA and higher expression of associated defense genes, suggesting that TaBCATI-mediated BCAA regulation is necessary for SA-dependent defense activation [119]. TaBCATI mutants also showed increased levels of SA and higher expression of associated defense genes, suggesting that TaBCATI-mediated BCAA regulation is necessary for SA-dependent defense action [119]. BCAA levels have been linked to wheat resistance to yellow rust infestation [119]. These findings add to our understanding of SA-mediated wheat defensive responses and stress the role of BCAA metabolism in the defense response. TaBCATI could also be changed to provide resistance to two of the most economically destructive wheat diseases [128].
After infection with AMT members (hereinafter TaAMTs) were discovered [136]. Using a protein homology search in the wheat genome, TaAMT2;3a, which may contribute to rust fungus infection [136], may engage in Ca2+-regulated signaling [112]. The general scheme of defending mechanism against biotic and abiotic stress in plant is shown in Figure S1.

5.4. Some Sr Genes and Amino Acid Changes. TmNLRI is an orthologue of Sr22, a cloned stem rust resistance gene, and hence a good candidate gene for SrTm5 [48]. TmNLRI gene in PI 306540 has four exons and spans 19715 bp from start to stop codons, including the insertion of a 13.8 kb gypsy-like retrotransposon in the second intron [48]. A typical CC-NBS-LRR protein of 938 amino acids is encoded by the 2817 bp coding sequence, and six previously known Sr22-resistant protein haplotypes share 95.7%–96.7% of their amino acid composition in Sr22-mediated resistance plants [48, 131]. The SrTm5 gene encodes a characteristic coiled-coil nucleotide-binding leucine-rich repeat protein from diploid wheat Triticum monococcum accessions [70], Sr22b is a novel allele of Sr22 with a rare 13.8 kb retrotransposon insertion into its second intron [48].

The Sr2 gene and a dark pigmentation feature called pseudo-black chaff (PBC) were previously found on chromosome 3B’s short arm [4]. The stripe rust resistance gene is the only member of the 250 START family that has been identified [8]. Sr15 is temperature-sensitive. The effectiveness of Sr15 to specific Pgt races and temperatures makes it a less-desirable TTKSK-effective gene [42]. Wheat lines assayed as resistant to race TTKSK at the seedling stage may possess. Sr15 and breeders should be aware of the limitations of Sr15 for conferring stem rust resistance [42, 132]. These accessions were susceptible as seedlings at high temperatures (22–25°C) [133].

Med15 is a constituent of the Mediator complex, a conserved protein complex that regulates the expression of protein-coding genes in eukaryotes [134]. Wheat stem rust resistance is activated by a mutation in Sur-D1. Sur-D1 is a single dominant gene on wheat chromosomal arm 7D that suppresses stem rust resistance [135]. Med15b.D is a subunit of the conserved Mediator complex, which regulates the transcription of protein-coding genes in eukaryotic organisms [134]. Sur-D1 encodes Med15b.D. Med15 is a potential target for gene editing to improve disease resistance while causing minimal morphological changes [134].

The level of NH4+ in wheat leaves reduced after infection with Puccinia striiformis f. Sp. tritici (Pst), the cause of stripe rust. Pst’s nitrogen uptake from wheat leaves may be aided by the AMT2-type ammonium transporter gene TaAMT2;3a, which may contribute to rust fungus infection [136]. Using a protein homology search in the wheat genome, 23 AMT members (hereinafter TaAMTs) were discovered [136]. After infection with Puccinia graminis f. Sp. tritici, rust-resistant wheat plants cultivated under N-free circumstances had a lower disease index than plants grown with NH4+ as the sole N source in the medium, implying that NH4+ and its transport may enhance the infection of wheat stem rust disease [136, 137]. This suggests that the effective infection of uredinio spores into plant leaves may be required for TaAMT1;1a, TaAMT1;1b, and TaAMT1;3a induction [136, 137]. Numerous transcription factor family members, including WRKYs, MYBs, and bZIPs, were found to be potential hotspots in the wheat resistance response to Pst infection. In an in vitro assay, HGA decreased the germination of stripe rust fungus uredinio spores and lowered the incidence of wheat stripe rust. Proteins containing nucleotide-binding sites (NBS) and leucine-rich repeat (LRR) domains are important in the plant immune system [116]. They usually mediate resistance to a subgroup of races of a single disease [101].

6. Conclusion
Wheat rust is a globally destructive disease. Concerning this pathogen, we reviewed 286 rust resistance genes, including 68 black stem rust, 101 leaf rust, and 108 stripe rust, their chromosomal positions, generated from various unique species, and important amino acid changes during rust resistance due to this resistance gene. It would be helpful to generate long-term and nonrace-specific resistant wheat cultivars by pyramiding various resistance genes. Previously, less than 210 rust resistance genes are updated but not the summarized view of biochemical changes like biosynthesis of different amino acids for triggering the rust pathogen. We updated the information on more than 70 rust-resistance novel genes which are valuable for the breeders for cloning and introgression in wheat lines for developing rust-resistant wheat genotypes to ensure food security in an ever-changing world. Cassette breeding of rust resistance genotypes has several difficulties and requirements, including the need to clone numerous, R, (ASR, and APR) genes that have to find effective and efficient ways to insert numerous alleles at a specific locus. The nature of polygenic resistance is additive; thus, the expression of the many resistance genes is environment sensitive called genotype-environment interaction (GE) which needs further investigation.

Data Availability
All data are included within the manuscript.

Conflicts of Interest
The authors declare that they have no conflicts of interest.

Authors’ Contributions
BB created the idea about manuscript, wrote the paper, revised the paper, and submitted to the journal. JP helped to revise and gave suggestion about the manuscript. KB and UU helped for the download of the paper and wrote some points. BB is the major ideal contributor to this paper.
Supplementary Materials

Here is the list of figures and tables which are cross-ref in the main manuscript file. Table S1: stem rust resistance genes derive from hexaploidy, diploid wheat, and wild species. APR = adult plant resistance, SR = seedling resistance, ASR = all-stage resistance, APRsus = adult plant stage susceptible. Figure S1: General scheme of defending mechanism against biotic stress in plant. Systemic acquired resistance (SAR) and induced systemic resistance (ISR) are governed by ethylene and salicylic acid (SA)+jasmonic acid (JA). Table S2: list of all leaf rust resistance genes derived from different wheat and wild species. APR = adult plant resistance, ASR = all-stage resistance, SR = seedling stage resistance, HTAP = high temperature adult plant resistance, rs = race-specific. Table S3: identified stripe rust gene and their chromosomal location. APR = adult plant resistance, ASR = all-stage resistance, SR = seedling stage resistance, HTAP = high temperature adult plant resistance, rs = race-specific. (Supplementary Materials)

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