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Review

Genetics of Resistance to Leaf Rust in Wheat: An Overview in A Genome-Wide Level

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Abstract: Due to the global warming and dynamic changes in pathogenic virulence, leaf rust caused by *Puccinia triticina* has greatly expanded its epidermic region and become a severe threat to global wheat production. Genetic bases of wheat resistance to leaf rust mainly relies on the leaf rust resistance (*Lr*) gene or quantitative trait locus (*QLr*). Although these genetic loci have been insensitively studied during the last two decades, an updated overview of *Lr*/*QLr* in a genome-wide level is urgently needed. This review summarized recent progresses in genetic studies of wheat resistance to leaf rust. Wheat germplasms with great potentials in genetic improvement of resistance to leaf rust were highlighted. Key information about the genetic loci carrying *Lr*/*QLr* were summarized. A genome-wide chromosome distribution map for all the *Lr*/*QLr* was generated based on the released wheat reference genome. In conclusion, this review has provided valuable sources for both wheat breeders and researchers to understand the genetics of resistance to leaf rust in wheat.

Keywords: wheat; resistance; leaf rust; genetic loci; genome-wide

1. Introduction

Leaf rust, caused by biotrophic fungal pathogen *Puccinia triticina*, is one of the most wide-spread and severe diseases in wheat all over the world [1]. The yield loss caused by leaf rust ranges from 5% to 20%, and reaches about 50% during epidemics [2]. Compared with other rust diseases such as stripe rust and stem rust, leaf rust adapts to a more moderate temperature (10–25 °C). However, due to the global warming, leaf rust has greatly expanded its epidermic region and advanced its occurrence period [3]. Generally, seedling plants of wheat are more vulnerable to rust diseases, and all these changes have made leaf rust become a new threat to global wheat productions.

2. Pathogenic profile

Leaf rust has a complicated life cycle including asexual stage on wheat and sexual stage on alternative hosts (**Figure 1**) [1]. At the asexual stage, leaf rust infects wheat plant via its urediospores (**Figure 1a**). Urediospores can spread high distance with air flow and re-infect wheat plants multiple times. Since leaf rust has a broad host range including wheat, barley, and their wild relatives, it can easily over-summer on grasses and volunteer crops. On the other hand, it normally over-winter on wheat as latent hypha or urediospores. At the sexual stage, leaf rust produces telia on wheat leaves in the late growing

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season (**Figure 1a**); teliospores from telia further infects alternative hosts including *Thalictrum* spp. or *Leptopyrum fumarioides*; pycnia/pycniospores and aecium/aeciospores can be formed on the alternative hosts; fertilization occur between pycniospores and receptive hyphae with opposite mating type combinations; aeciospores infect back to the host plants of wheat and produce uredium/urediospores to complete the life cycle (**Figure 1b**).

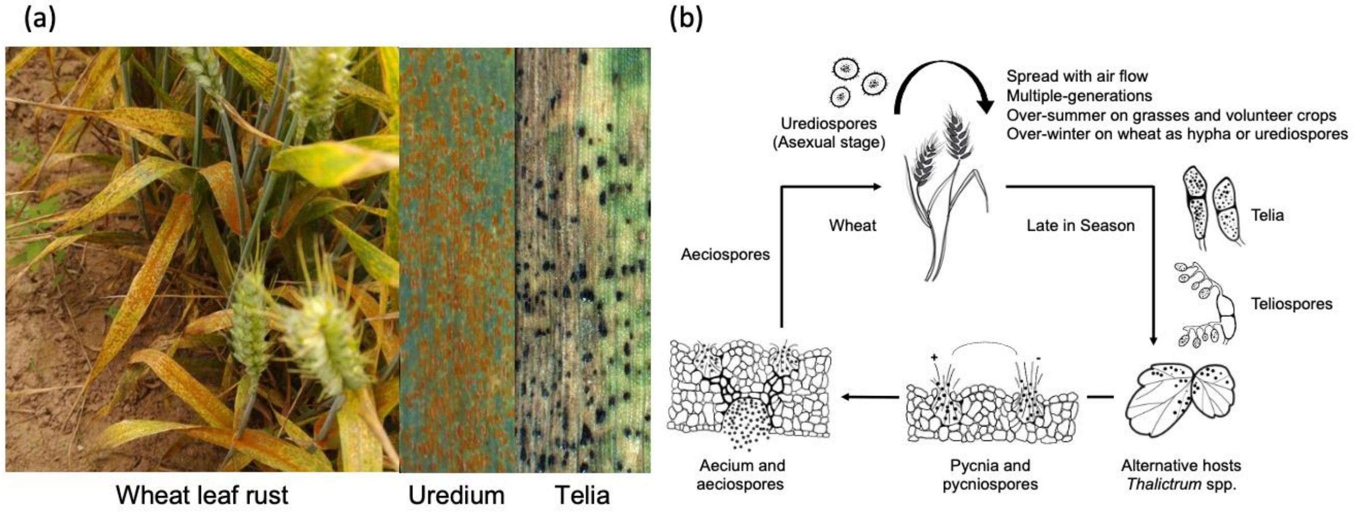

Figure 1. Pathogenic profile of *Puccinia triticina.* **(a)** Leaf rust infects wheat leaves via its urediospores at the asexual stage. Telia is produced on wheat leaves in the late growing season. **(b)** Life cycle of *P. triticina* can be divided into asexual stage on wheat and sexual stage on alternative hosts. Teliospores infects alternative hosts *Thalictrum* spp. and later produces pycnia and aecium. Aeciospores infects back to wheat plants to complete the life cycle.

3. Types of wheat resistance to leaf rust

Based on the physiological features, genetic determinations, and molecular mechanisms, wheat resistance to leaf rust can be classified into two types (**Table 1**): race-specific resistance and slow rusting resistance. The race-specific resistance follows the gene-for-gene theory. Currently, most of the cloned *Lr* genes controlling this type of resistance, including *Lr1*, *Lr10*, *Lr13*, *Lr21*, *Lr22a*, and *Lr42*, encode nucleotide binding site leucine-rich repeat (NBS-LRR) proteins [4-9]. As modeled in *Arabidopsis*, upon directly or indirectly recognition of avirulence (Avr) proteins secreted from phytopathogens, NBS-LRR proteins form a homo-pentamer called resistosome, which penetrates the cell membrane of the responsive cells and eventually results in the observed hypersensitive responses (HR) or necrosis on wheat leaves [10]. A recent protein crystallization study on wheat stem rust resistance protein Sr35 and its corresponding avirulent protein AvrSr35 revealed a similar resistosome structure [11]. Besides these NBS-LRR proteins, another race-specific resistance gene, *Lr14a*, encodes a membrane-localized protein containing multiple ankyrin repeats and Ca^{2+} channels [12]. And the other recently cloned high-resistant gene *Lr9*/*Lr58* encodes a tandem kinase fusion protein [13]. Notably, certain race-specific resistance genes are functioning only at seedling stage but lost their resistance against multiple *Pt* pathotypes in the field at the adult plant stage. Others may keep their high resistance to leaf rust at the adult plant stage as hypersensitive adult plant resistance (APR) or all-stage (AS) race-specific resistance.

Slow rusting resistance, also considered as APR in most cases, provides a lower level but more durable resistance in a non-race-specific manner only at the adult plant stage. Compared with the mentioned hypersensitive APR, rust infection and sporulation can be accomplished in a much delayed and reduced manner. It is normally controlled by quantitative trait loci (QTL) and provides broad-spectrum resistance to multiple pathogens. For instance, the first cloned leaf rust APR gene *Lr34* encoding an ATP-binding cassette (ABC) transporter controls resistance to stripe rust, stem rust, powdery mildew, and spot blotch [14]. The other cloned leaf rust APR gene *Lr67* encodes a hexose transporter that forms heterodimer with other functional transporters to reduce the uptake of glucose [15].

Table 1. Types of wheat resistance to leaf rust

Type of resistance	Resistance stage	Resistant features	Cloned resistance genes
Race-specific resistance	Seedling stage	Seedling resistance. Immune or hypersensitive response (cell death/necrosis) observed on the leaf surface. May be lost at adult plant stage against multiple *Pt* pathotypes in the field.	*Lr1*, *Lr10*, *Lr13*, *Lr21*, *Lr22a*, *Lr42* (NBS-LRR) *Lr14a* (Ankyrin repeats and Ca2+ channels) *Lr9*/*Lr58* (Tandem kinase)
	Adult plant stage	Hypersensitive adult plant resistance (APR) / All-stage (AS) race-specific resistance. Immune or hypersensitive response (cell death/necrosis) observed on the leaf surface.	
Slow rusting	Adult plant stage	Non-race-specific resistance. A lower level but more durable resistance. Rust infection and sporulation can be accomplished in a much delayed and reduced manner.	*Lr34* (ATP-binding cassette transporter) *Lr67* (Hexose transporter)

With advances in techniques of genomic sequencing and molecular biology, cloning of *Lr* genes or leaf rust resistance QTL (*QLr*) has become a more implementable task. It can be accomplished following multiple strategies such as classical map-based positional cloning, capture sequencing, or even whole genome sequencing [16]. In this review, we have mainly focused on the research progresses in genetic determinations of wheat resistance to leaf rust during the last two decades. Genetic loci carrying *Lr*/*QLr* are summarized and introduced following a sub-genome and chromosome order to provide an overview in a genome-wide level.

4. Genetic loci carrying *Lr*/*QLr* in A sub-genome

4.1. Lr/QLr on chromosome 1A

A tall Indian bread wheat cultivar “Sujata” displayed high resistance to leaf rust at adult plant stage in the field. Two novel significant resistance loci on chromosomes 1AS (*QLr.cim-1AS*) and 7BL (*QLr.cim-7BL*), in combination with *Lr46* and *Lr67*, were identified using single sequence repeat (SSR) markers [17]. A major QTL, *QLr.cau-1AS*, for slow rusting in wheat cultivar “Luke” was mapped to chromosome 1AS using SSR markers [18]. A genome-wide association study (GWAS) on a panel of 483 spring wheat genotypes revealed major QTLs for APR against leaf rust on chromosome 1A (*QLr.ramp-1A.2*), 1B (*QLr.ramp-1B.3*), and 6A (*QLr.ramp-6A.1*) [19]. Seedling/all-stage leaf rust resistance (AS) gene *Lr10* was also located on the chromosome 1AS [5]. *Lr10* was successfully cloned and encoded a typical NBS-LRR protein. Interestingly, two different CC-NBS-LRR proteins were discovered to be essential for the *Lr10*-mediated resistance [20].

A collection of 331 diverse wheat genotypes were inoculated with four prevalent *Pt* pathotypes at seedling stage and a further GWAS revealed novel QTLs on chromosomes 1AL (*QLr.uga-1AL*), 4AS (*QLr.uga-4AS*), 5AS (*QLr.uga-5AS*), 5AL (*QLr.uga-5AL*), and 7AS (*QLr.uga-7AS*) [21]. Another GWAS was performed on a diverse 385 germplasms including 27 different *Triticum* and *Aegilops* species at both seedling and adult plant stages. For the APR phenotype, significant associations were detected on chromosomes 1A (*QLr.fiz-1AL*), 2D (*QLr.fiz-2D*), and 5B (*QLr.fiz-5B*) [22]. Leaf rust resistance of another 338 spring wheat breeding lines developed in the Americas were evaluated at the seedling stage and in the field. A further GWAS revealed two potentially novel QTLs (*QLr.umn-1AL* and *QLr.umn-4AS*) for variations of the APR phenotype [23]. A haplotype-based GWAS was conducted on 133 wheat collections and 1,574 their hybrids to reveal the associations between high-quality single nucleotide polymorphisms (SNPs) and APR phenotypes. Five major QTLs on chromosomes 1A (*QLr.liu-1AL*), 3D (*QLr.liu-3D*), 4A (*QLr.liu-4A*), 6B

(*QLr.liu-6B*), and 7A (*QLr.liu-7A*) were detected [24]. A novel APR QTL *Lr2K38* (*QLr.ags-1AL*) from soft red winter wheat cultivar "AGS 2038" was mapped on chromosome 1AL [25].

4.2. *Lr/QLr on chromosome 2A*

Great number of genetic loci carrying *Lr/QLr* were enriched on chromosome 2A. *Lr65* originated from spelt wheat (*Triticum spelta*) was recently fine mapped within a 0.8 cM interval on chromosome 2AS, corresponding to a 60.11 Kb region in the Chinese Spring (CS) wheat reference genome [26]. *Lr37* introgressed from *Aegilops ventricosa* was initially mapped on the chromosome 2AS using restriction fragment length polymorphism (RFLP) and cleaved amplified polymorphic sequence (CAPS) markers [27]. The chromosome 2AS-located *Lr17a* gene was widely presented in wheat varieties adapted to North America and its resistance has been overcome by newly merged *Pt* pathotypes [28]. Seedling resistance gene *Lr81* was identified in a Croatian breeding line "PI 470121" and mapped to an approximately 100 Kb genomic region on chromosome 2AS using Kompetitive allele-specific PCR (KASP) markers [29]. A novel leaf rust resistance gene *LrM* introgressed from *Aegilops markgrafii* provides high degree of resistance against multiple *Pt* pathotypes. *LrM* was mapped on chromosome 2AS using SSR- and SNP-based PCR markers [30]. Seedling resistance gene *Lr45* was derived from *Secale cereale* and introgressed to chromosome 2AS [31].

A GWAS on 496 accessions of worldwide durum wheat collection revealed significantly associated SNPs on chromosomes 2AL (*Lr.locus-2AL*) and 2BL (*Lr.locus-2B5*) [32]. Several APR QTLs on chromosomes 2AL (*QLr.ifa-2AL*), 2BL (*QLr.ifa-2BL*), and 3BS (*QLr.ifa-3BS*) were identified from an Australian winter wheat cultivar "Capo" using biparental mapping populations [33]. A Chinese wheat cultivar "Zhou 8425B" showed relative high resistance to leaf rust at both seedling and adult plant stages. A genetic study using constructed mapping population identified novel QTLs on chromosomes 2AL (*QLr.hebau-2AL*), and 4AL (*QLr.hebau-4AL*) [34]. Two Canadian wheat cultivars "AC Cadillac" and "Carberry" showed relatively high resistance to leaf rust in the field. A further genetic study identified an APR QTL on chromosome 2A (*QLr.spa-2A*) from "AC Cadillac" and two APR QTLs on chromosomes 2B (*QLr.spa-2B*) and 4B (*QLr.spa-4B*) [35].

4.3. *Lr/QLr on chromosome 3A*

Seedling resistance gene *Lr63* derived from *Triticum monococcum* was mapped to chromosome 3AS using SSR markers [36]. A Uruguayan wheat landrace "Americano 44" exhibited long lasting resistance to leaf rust. Three major QTLs including *QLr.cdl-3A*, *QLr.cdl-3D*, and *QLr.cdl-6D* were identified to be interactively responsible for the variation of APR phenotype [37]. Another AS gene on chromosome 3AS, *Lr66*, was introgressed from *Aegilops speltoides* and initially mapped using microsatellite and diversity array technology (DArT) markers [38]. A constant major QTL *QLr.sfrs-3AL* inherited from "Forno" was detected on chromosome 3AS [39]. A major QTL *QLr.fcu-3AL* from a synthetic hexaploid wheat line TA4152-60 (× *Aegilotriticum* spp.) was associated with APR to leaf rust [40].

4.4. *Lr/QLr on chromosome 4A*

A novel seedling resistance gene *Lr.ace-4A* for multiple *Pt* isolates was initially detected on chromosome 4A from a Portuguese durum landrace "PI 192051" [41]. A diversity panel of 268 wheat lines were evaluated for leaf rust resistance at both seedling and adult plant stages. A GWAS using 90K SNP array revealed novel QTLs for APR on chromosomes 4AL (*QLr.zha-4AL*) and 1DL (*QLr.zha-1DL*) [42]. Seedling resistance gene *Lr28* derived from *Ae. speltoides* was mapped to chromosome 4AL, and a microsatellite marker was validated to be closely linked to this gene [43]. Moreover, the possible molecular mechanism of *Lr28* has been intensively investigated during the last decade with emphasis on its transcriptional responses [44,45].

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4.5. Lr/QLr on chromosome 5A

A major QTL for APR to leaf rust from the European winter wheat cultivar "Beaver", *QLr.pbi-5AS*, was mapped to chromosome 5AS using multiple molecular markers [46]. A collection of 100 Russian varieties of spring wheat was phenotyped for leaf rust resistance in the field and subsequent GWAS using 15K SNP assay identified two new APR QTLs on chromosomes 5AS (*QLr.leo-5AS*) and 1BL (*QLr.leo-1BL*) [47]. A total of 676 pre-Green Revolution common wheat landraces were evaluated for their APR responses to leaf rust in the field. Associations of SNPs on chromosomes 5A (*QLr.aus-5A*) and 1B (*Lr33*) were detected and further validated using a recombinant inbred line (RIL) population of "Aus28230 × Yitpi" [48]. The APR of a Brazilian wheat cultivar variant "Toropi-6.4" was investigated and several major QTLs were identified using 90K SNP array, including *QLr.crc-1BL/Lr46* on chromosome 1BL and *QLr.crc-5AL* on chromosome 5AL [49]. Two novel APR QTLs on chromosomes 5AL (*QLr.hebau-5AL*) and 3BL (*QLr.hebau-3BL*) were identified from a wheat cultivar "SW 8588" using 55K SNP array and SSR markers [50].

4.4. Lr/QLr on chromosome 6A

Seedling resistance gene *Lr62* was transferred from *Aegilops neglecta* and mapped to chromosome 6AS using microsatellite markers [51]. The *Aegilops sharonensis*-derived seedling resistance gene *Lr56* was translocated to the telomeric region of chromosome 6AL [52]. Another AS gene *Lr64* initially introgressed from *Triticum dicoccoides* was also mapped to chromosome 6AL with SNP and KASP markers [53].

4.5. Lr/QLr on chromosome 7A

Seedling resistance gene *Lr47* was introgressed from *Ae. speltoides* to chromosome 7AS [54]. Grain yield and flour quality were negatively influenced by the introgression of chromosome segment carrying *Lr47* [55]. Nevertheless, this gene still showed high resistance to most of the collected *Pt* pathotypes in China and its transcriptional regulatory network was profiled [56]. A recent study developed new KASP markers for the *Lr47* gene [57]. A large scale association study using 1,032 spring wheat accessions and 9K SNP array revealed QTLs on chromosome 7AS (*QLr.tur-7AS*) and 2DL (*QLr.tur-2DL*) contributed for both seedling resistance and APR to leaf rust [58]. Seedling resistance gene *Lr20* was localized in the distal region of chromosome 7AL [59]. Recombination of the genetic locus carrying *Lr20* was significantly suppressed, indicating this chromosome segment may be introgressed from unidentified wild relative species.

Information for all the genetic loci carrying *Lr* and major *QLr* in A sub-genome were summarized in **Table 2**.

Table 2. Genetic loci carrying *Lr*/*QLr* in A sub-genome

Chromosome	*Lr* gene/ major QTL	Resistance type	Donor	Associated markers or SNPs	Reference
1AS	*QLr.cim-1AS*	APR	*T. aestivum*: Sujata	***wPt-9752***, *Xgdm33*, *Xcfd15*	[17]
1AS	*QLr.cau-1AS*	APR	*T. aestivum*: Luke	***Xgpw2246***	[18]
1AS	*QLr.ramp-1A.2*	APR	*T. aestivum*: spring wheat collection (GWAS)	***AX-95080736***	[19]
1AS	*Lr10*	AS	*T. aestivum*: TcLr10	*Lrk10D1*, *Xgwm136*, ***Xpsr596***	[5]
1AL	*QLr.uga-1AL*	AS	*T. aestivum*: wheat genotypes collection (GWAS)	***IWA1952***	[21]
1AL	*QLr.fiz-1AL*	APR	*Triticum* and *Aegilops* species collection (GWAS)	***Excalibur_c33567_363***	[22]
1AL	*QLr.umn-1AL*	APR	*T. aestivum*: spring wheat breeding lines (GWAS)	***IWB48030***	[23]
1AL	*QLr.liu-1AL*	APR	*T. aestivum*: wheat collections and their hybrids (GWAS)	***SNP532737351chr1A***	[24]
1AL	*Lr2K38/QLr.ags-1AL*	APR	*T. aestivum*: AGS 2038	***IWB20487***, *IWA4022*	[25]
2AS	*Lr65*	AS	*T. spelta*: Altgold Rotkorn	*Xbarc124*, ***Xbarc212***, *Xgwm614*	[26]
2AS	*Lr37*	AS	*Ae. ventricosa*: Madsen	***Xcmwg682***, *Xbcd348*, *Xpsr933*	[27]
2AS	*Lr17a*	AS	*T. aestivum*: Klein Lucero (CI 14047) *T. aestivum*: Maria Escobar (PI 150604)	***Xgwm614***, *Xgwm614*, *Xwmc407*	[28]
2AS	*Lr81*	AS	*T. aestivum*: PI 470121	***Xstar-KASP320***, *Xstar-KASP323*	[29]
2AS	*LrM*	AS	*Ae. markgrafii*: ER9-700	***Xgwm512***, *Xcfd36*	[30]
2A	*Lr45*	AS	*S. cereale*: TcLr45	***Xcfd168***, *Xgwm372*	[31]
2AL	*Lr.locus-2AL*	AS	*T. turgidum*: durum wheat collection (GWAS)	***Xgwm1045***	[32]
2AL	*QLr.ifa-2AL*	APR	*T. aestivum*: Capo	***Xgwm312***	[33]
2AL	*QLr.hebau-2AL*	APR	*T. aestivum*: Zhou 8425B	***wmc181,*** *BS00057060_51*	[34]
2AL	*QLr.spa-2AL*	APR	*T. aestivum*: AC Cadillac	***rPt-9611***	[35]
3AS	*Lr63*	AS	*T. monococcum*: RL6137	*Xbarc321*, ***Xbarc57***	[36]
3AS	*QLr.cdl-3AS*	APR	*T. aestivum*: Americano 44d	***Xbarc321***	[37]
3AS	*Lr66*	AS	*Ae. speltoides*	***Xgwm674***, *Xbarc57*	[38]
3AL	*QLr.sfrs-3AL*	APR	*T. aestivum*: Forno	***Xpsr570***, *Xpsr543*	[39]
3AL	*QLr.fcu-3AL*	APR	Synthetic hexaploid wheat: TA4152-60	*Xcfa2183*, *Xgwm666*, ***Xfcp586***	[40]
4AS	*QLr.uga-4AS*	AS	*T. aestivum*: wheat genotypes collection (GWAS)	***IWA1766***	[21]
4AS	*QLr.umn-4AS*	APR	*T. aestivum*: spring wheat breeding lines (GWAS)	***IWB59410***	[23]

4AS	*Lr.ace-4A*	AS	*T. turgidum*: PI 192051	***IWA232***, *IWA603*, *IWA4657*	[41]
4AL	*QLr.hebau-4AL*	APR	*T. aestivum*: Zhou 8425B	***Xwmc617***, *BobWhite_c15697_675*	[34]
4AL	*QLr.zha-4AL*	APR	*T. aestivum*: wheat lines collection (GWAS)	***Tdurum_con-tig93100_149***	[42]
4AL	*QLr.liu-4AL*	APR	*T. aestivum*: wheat collections and their hybrids (GWAS)	***SNP713087672chr4A***	[24]
4AL	*Lr28*	AS	*Ae. speltoides*	***Xwmc313***, *SCS421*	[43]
5AS	*QLr.pbi-5AS*	APR	*T. aestivum*: Beaver	***wPt-1931***, *wPt-8756*	[46]
5AS	*QLr.uga-5AS*	APR	*T. aestivum*: wheat genotypes collection (GWAS)	***IWA2143,*** *Xwmc47*, *Xbarc122*	[21]
5AS	*QLr.leo-5AS*	APR	*T. aestivum*: Spring wheat collection (GWAS)	***GENE-3321_201***	[47]
5AL	*QLr.aus-5AL*	APR	*T. aestivum*: wheat landrace collection (GWAS)	***IWB23955***, *IWB34703*	[48]
5AL	*QLr.crc-5AL*	APR	*T. aestivum*: Toropi-6.4	***Excalibur_rep_c111129_125***	[49]
5AL	*QLr.hebau-5AL*	APR	*T. aestivum*: SW 8588	***AX-110679506,*** *AX-110996595*	[50]
5AL	*QLr.uga-5AL*	AS	*T. aestivum*: wheat genotypes collection (GWAS)	***IWA5929***, *Xgpw2273*	[21]
6AS	*Lr62*	AS	*Ae. neglecta*: 03M119-71A	***Xgwm334***, *Xcfd190*, *Xcfa2173*	[51]
6AL	*Lr56*	AS	*Ae. sharonensis*	***Xgwm427***, *Xwmc59*	[52]
6AL	*Lr64*	AS	*T. dicoccoides*: RL6149	***K-IWB59855***	[53]
6AL	*QLr.ramp-6A.1*	APR	*T. aestivum*: spring wheat collection (GWAS)	***AX-94653398***	[19]
7AS	*Lr47*	AS	*Ae. speltoides*: Pavon	***Xgwm60***, *PS10*	[54]
7AS	*QLr.tur-7AS*	AS/APR	*T. aestivum*: spring wheat collection (GWAS)	***IWA1277***	[58]
7AS	*QLr.uga-7AS*	AS	*T. aestivum*: wheat genotypes collection (GWAS)	***IWA7201***	[21]
7AS	*QLr.liu-7AS*	APR	*T. aestivum*: wheat collections and their hybrids (GWAS)	***SNP126914404chr7A***	[24]
7AL	*Lr20*	AS	*T. aestivum*: Thew	***Xpsr148***, *Xcdo347*, *STS638*	[59]

5. Genetic loci carrying *Lr*/*QLr* in B sub-genome

5.1. Lr/QLr on chromosome 1B

Genetic loci carrying *Lr*/*QLr* were intensively distributed on chromosome 1B. Seedling resistance gene *Lr55* derived from *Elymus trachycaulus* was mapped to chromosome 1BS using microsatellite and DArT-based markers [60]. A recent study revealed that *Lr33* on chromosome 1BL conferred resistance to leaf rust at both seedling and adult plant stages [61]. Interestingly, *Lr44* originated from spelt wheat "Accession 7831" was reported as recessive or partially dominant to *Lr33* [62]. Seeding resistance gene *Lr71* was identified from spelt wheat cultivar "Altgold Rotkorn". It was initially mapped close to the centromere of chromosome 1B using SSR markers and deletion lines [63]. A major QTL *QLr.sfr-1BS* was discovered in winter wheat cultivar "Forno" for APR to leaf rust in a series of genetic studies and eventually designated as *Lr75* [64,65]. Interestingly, a consistently detected QTL *QLr.pser-1BL* controlling phenotype of lesion mimics in wheat cultivar "Ning7840" was also responsible for seedling resistance and APR to leaf rust [66]. A seedling resistance gene *LrZH84* was identified from a widely planted wheat cultivar "Zhou 8425B" in China and mapped to chromosome 1BL using multiple molecular markers [67,68].

Lr46 was another slow rusting gene that conferred broad-spectrum resistance to multiple fungal diseases, including stripe rust (*Yr29*), powdery mildew (*Pm39*), and spot blotch (*Qsb*). Various molecular markers have been developed to map this genetic locus or utilize it in breeding programs [69,70]. Major QTLs for slow rusting detected in wheat cultivars "Bainong 64" and "Attila" were both initially mapped to chromosome 1BL and further predicted as *Lr46* [71,72]. Seedling resistance gene *Lr51* introgressed from *Ae. speltoides* was mapped to chromosome 1BL and its associated CAPS marker was designed [73]. Seedling resistance gene *Lr26* was derived from rye (*Secale cereale*) and located on the 1BL/1RS translocation in wheat [74]. The recent released high-quality genome assembly of rye may greatly facilitate the cloning of *Lr26* in the coming future [75]. A multiple-year stable major QTL *QLr.pbi-1B* for APR of wheat cultivar "Beaver" was mapped to chromosome 1BL and estimated to be associated with the 1BL/1RS translocation [46].

5.2. Lr/QLr on chromosome 2B

Chromosome 2BS is a hot zone enriched with large number of *Lr*/*QLr* loci. Three wheat cultivars from different regions, including "Saragolla" from Italy, "Gaza" from Middle East, and "Arnacoris" from France, expressed high levels of resistance to Mexican races of *P. triticina*. Further genetic investigation revealed major APR QTLs on chromosomes 2BS (*QLr.usw-2BS*), 6BS (*QLr.usw-6BS*), 6BL (*QLr.usw-6BL*), and 7BL (*QLr.usw-7BL*) [76]. *Lr16* was a seedling resistance gene previously mapped to the telomeric region of chromosome 2BS [77]. A recent genetic study using four mapping populations developed resistance gene analog (RGA)-based SNP markers associated with *Lr16* to facilitate the marker-assisted selection (MAS) [78]. A major QTL *QLr.csiro-2BS* on chromosome 2BS for slow rusting was discovered in wheat cultivar "Attila" [72]. *Lr48* was designated as a hypersensitive APR gene and mapped to chromosome 2BS using SSR markers [79]. An International Maize and Wheat Improvement Center (CIMMYT) spring wheat line "Shanghai 3/Catbird" showed a high level of APR to Chinese *P. triticina* pathotypes in the field. A major QTL *QLr.hebau-2BS* was detected on chromosome 2BS using SSR markers [80]. Seedling resistance gene *Lr23* on chromosome 2BS was initially identified in a synthetic hexaploid wheat "W-7984" produced from the cross between durum wheat cultivar "Altar 84" and *Ae. tauschii* [81]. A further investigation discovered a major QTL *QLr.ksu-2BS* for APR in "W-7984" close to *Lr23* [82].

The chromosome 2BS-located *Lr13* was sufficient to provide seedling resistance at relatively high temperature around 25℃ and APR in the field. This gene encoding a typical NBS-LRR protein also controlled hybrid necrosis as a specific allele of *Necrosis 2* (*Ne2*) [6,83]. An Argentinean wheat cultivar "Klein Proteo" showed broad-spectrum resistance to most of Chinese *P. triticina* pathotypes at seedling stage. A single-dominant gene *LrKP* was mapped near the *Lr13* region on chromosome 2BS. Its relationship with *Lr13* remained to be explored [84]. The APR gene *Lr35* was introgressed from *T. speltoides* and showed broad resistance to different *Pt* pathotypes. The *Lr35* gene was mapped to chromosome 2BS using RFLP and STS markers [85]. Several pathogenesis-related protein (*PR*) genes including *PR1*, *PR2*, and *PR5* were reported to be involved in the *Lr35*-mediated APR response [86-88]. A chromosome 2BS-located major QTL *QLr.osu-2B* for slow rusting was consistently detected from wheat line “CI 13227” in multiple environments [89].

A diversity panel of 196 spring wheat genotypes was phenotyped for the leaf rust resistance in the field. A GWAS approach using 90K SNP array revealed significant association of multiple SNPs on chromosomes 2B (*QLr.dms-2B.2*) and 2D (*QLr.dms-2D*) [90]. An AS gene *LrNJ97* was identified from a Chines wheat line “Neijiang 977671” and linked with SSR markers on chromosome 2BL [91]. Seedling resistance gene *Lr50* was introgressed *T. timopheevii* subsp. *armeniacum* and initially mapped on chromosome 2BL using SSR markers [92].

5.3. Lr/QLr on chromosome 3B

An APR gene *Lr74* from soft red winter wheat cultivar “Caldwell” was mapped to chromosome 3BS using 90K SNP array and SSR markers [93]. A genetic study on a RIL population developed from a cross of “Ning7840 × Clark” revealed major APR QTL *Lr74/QLr.hwwg-3BS.1* on chromosome 3BS from “Clark” and *Lr34* on chromosome 7DS from “Ning7840” [94]. Several slow rusting QTLs were identified from wheat cultivar “Francolin#1”, including *Lr46/QLr-cim-1BL* on chromosome 1BL and *QLr-cim-3BS.1* on chromosome 3BS [95]. A race-specific APR gene *LrSV2* on chromosome 3BS was isolated from a durable resistant Argentinean wheat variety “Sinvalocho MA” using SSR markers [96].

A major QTL *QLr.fcu-3BL* for seedling resistance to *Pt* pathotype MFPS was discovered in the synthetic hexaploid wheat line “TA4152-60” (× *Aegilotriticum* spp.) and was mapped to chromosome 3BL [40]. A panel of 96 wheat cultivars were evaluated for their APR response to leaf rust in the field and genotyped with DArT markers. Novel associations were detected against markers on chromosomes 3BL (*QLr.wpt-3BL*), 6B (*QLr.wpt-6BS.1*), 1DS (*QLr.wpt-1DS*) and 7DS (*QLr.wpt-7DS*) [97]. The seedling resistance gene *Lr79* was identified from a durum wheat landrace “Aus26582” and initially mapped to chromosome 3BL using DArT markers [98].

5.4. Lr/QLr on chromosome 4B

A major QTL *QLr.sfrs-4B* for APR in wheat cultivar “Forno” was detected on chromosome 4B [39]. *Lr12* on chromosome 4BL provides adult-plant race-specific resistance to leaf rust. It is completely linked or identical to *Lr31*, whose seedling resistance is associated with another complementary gene *Lr27* [99]. A recent study detected a major QTL *QLr.hebau-4B* on chromosome 4BL for APR in wheat cultivar “Chinese Spring” and its relationship with *Lr12* remained to be tested in the future [34]. The seedling resistance gene *Lr25* was originally transferred from *Secale cereale* and linked with SSR markers on chromosome 4BL [100]. The APR gene *Lr49* was discovered in wheat recombinant inbred line “VL404” and also mapped to chromosome 4BL using SSR markers [79].

5.5. Lr/QLr on chromosome 5B

The AS gene *Lr52* provides broad-spectrum resistance to multiple *Pt* pathotypes. It was mapped to chromosome 5BS using cytogenetic method [101]. Two durum wheat lines “Heller#1” and “Dunkler” from CIMMYT exerted moderate and stable APR to leaf rust in the field. Multiple QTLs were detected on chromosomes 1BL (*Lr46*), 5BL (*QLr.cim-5BL*) and 6BL (*QLr.cim-6BL*) from these resistant lines [102]. The AS gene *Lr18* was transferred from *Triticum timopheevii* to chromosome 5BL [103].

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5.6. Lr/QLr on chromosome 6B

The seedling resistance gene *Lr53* was transferred from *T. dicoccoides* to chromosome 6BS [104]. A major QTL *QLr.caas-6BS.1* for APR was identified from wheat cultivar "Bainong 64" and mapped to the chromosome 6BS using bulk segregant analysis (BSA) [71]. Also in the distal region of chromosome 6BS, another AS gene *Lr61* was identified from *Triticum turgidum* subsp. *durum* cultivar "Guayacan INIA" [105]. AS gene *Lr59* derived from wheat wild relative *Aegilops peregrina* was recently mapped to chromosome 6BS using microsatellite markers [106]. The seedling resistance gene *Lr36* was derived from *Ae. speltoides* and mapped between SSR markers *Xgwm88* and *Xcfd13* on chromosome 6BS [107].

The *Aegilops umbellulata*-derived *Lr9* was introgressed to chromosome 6BL and recently cloned using mutagenesis and transcriptome sequencing. It encoded an unusual tandem kinase fusion protein, and the coding sequence was identical to *Lr58* introgressed from *Aegilops triuncialis* on chromosome 2BL [13,108]. Two consistent major QTLs for APR was detected in wheat cultivar "Pastor" on chromosomes 6BL (*QLr.cimmyt-6BL.1*) and 7BL (*QLr.cimmyt-7BL*) [109]. The chromosome 6BL-located *Lr3* had three alleles as *Lr3a*, *Lr3bg* and *Lr3ka*. Since this gene has not been cloned yet, it was difficult to distinguish different alleles. A recent investigation has mapped an allele at the *Lr3* locus to chromosome 6BL using DArT markers [110].

5.7. Lr/QLr on chromosome 7B

The seedling resistance gene *Lr72* was discovered in durum wheat cultivar "Atil C2000" and mapped to chromosome 7BS using SSR markers [111]. A consistently detected QTL *QLr.sfrs-7B.2* was discovered to confer the APR in wheat cultivar "Forno" [39]. A major QTL *QLr.cimmyt-7BL.1* for slow rusting in wheat cultivar "Parula" was detected on chromosome 7BL as a possible homoallele to *Lr34* [112]. Wheat line "CI 13227" showed a high leveled slow rusting resistance. A stable QTL *QLr.osu-7BL*/*QLrlp.osu-7BL* on the chromosome 7BL was consistently detected in a series of studies [89,113]. The chromosome 7BL-located AS gene *Lr14a* has been cloned recently with support from genome assembly of wheat line "Arina*LrFor*". It encoded a membrane-localized protein containing twelve ankyrin repeats and Ca^{2+}-permeable non-selective cation channels-like structures. Its unique mechanism controlling race-specific disease resistance remained to be explored [12]. The slow rusting gene *Lr68* was isolated from wheat cultivar "Parula" and mapped to the distal region of chromosome 7BL [114]. *QLr.ubo-7B.2* was a major QTL on chromosome 7BL responsible for both seedling resistance and APR in durum wheat cultivar "Colosseo" [115]. A postulated novel seedling resistance gene *LrFun* from wheat cultivar "Fundulea 900" was also mapped to the distal region of chromosome 7BL [116]. A cluster of defense response genes including catalase, chitinase, thaumatin, and ion channel regulator on chromosome 7BL was associated with APR of wheat cultivar "Opata 85" to leaf rust as a major QTL *QLr.ksu-7BL* [82].

Information for all the genetic loci carrying *Lr* and major *QLr* in B sub-genome were summarized in **Table 3**.

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Table 3. Genetic loci carrying *Lr*/*QLr* in B sub-genome

Chromosome	Gene/QTL	Resistance type	Donor	Associated markers or SNPs	Reference
1BS	*Lr55*	AS/APR	*E. trachycaulis*: KS04WGRC45	*Xgwm374*, ***Xwmc406***	[60]
1BL	*Lr33*	AS/APR	*T. aestivum*: PI 58548, KU168-2	***Xgwm413***	[61]
1BL	*Lr44*	AS	*T. spelta*: Accession 7831	Linked with *Lr33*	[62]
1B	*Lr71*	AS	*T. spelta*: Altgold Rotkorn	***Xgwm18***, *Xbarc187*	[63]
1BS	*Lr75*/*QLr.sfr-1BS*	APR	*T. aestivum*: Forno	***Xgwm18***, *Xpsr949*, *Xgwm604*	[64,65]
1BL	*QLr.pser-1BL*	AS/APR	*T. aestivum*: Ning7840	*Xscm9*, ***Xwmc85.1***	[66]
1BL	*LrZH84*	AS	*T. aestivum*: Zhou 8425B	***Xgwm582***, *barc8*, *BF474863*, *BE497107*	[67,68]
1BL	*QLr.leo-1BL*	APR	*T. aestivum*: Spring wheat collection (GWAS)	***tplb0023b14_704***, *wsnp_Ra_c8484_14372815*, *BobWhite_c1456_615*	[47]
1BL	*QLr.wpt-1BL*	APR	*T. aestivum*	***wPt-9809***	[97]
1BL	*Lr46*/*QLr.caas-1BL*/*QLr.csiro-1BL*/ *QLr.cim-1BL*	Slow rusting	*T. aestivum*: Pavon 76, Bainong 64, Attila, Toropi-6.4, Francolin#1	*Xwmc719*, *Xgwm140*, ***Xwms259*** *Xgwm153.2*, *Xwmc44* *Excalibur_c35888_208*, *csLV46*, *wPt-9028*, *wPt-1770*	[49,69-72,95]
1BL	*Lr51*	AS	*Ae. speltoides*: F-7-3	***Xcdo393***	[73]
1BL	*Lr26*	AS	*S. cereale*: Petkus	1BL/1RS translocation	[74]
1BL	*QLr.pbi-1B*	APR	*T. aestivum*: Beaver	1BL/1RS translocation	[46]
1B	*QLr.ramp-1B.3*	APR	*T. aestivum*: Spring wheat collection	*AX-94517050*	[19]
2BS	*QLr.usw-2BS*	APR	*T. turgidum*: Saragolla	***Tdurum_contig76118_145***, *wsnp_Ex_c18354_27181086*	[76]
2BS	*Lr16*	AS	*T. aestivum*: BW278, AC Majestic, AC Domain, Kenyon	***Xwmc764,*** *Xgwm210*, *Xwmc661*, *kwm677*, *kwm744*	[77,78]
2B	*QLr.spa-2B*	APR	*T. aestivum*: Carberry	*wPt-732018*, ***wPt-7883***	[35]
2BS	*QLr.csiro-2BS*	*APR*	*T. aestivum: Attila*	***Xwmc154***, *Xgwm682*, *XP32/M62*	[72]
2BS	*Lr48*	APR	*T. aestivum*: CSP44	***Xgwm429b***, *Xbarc07*	[79]
2BS	*QLr.hebau-2BS*	APR	*T. aestivum*: Shanghai 3/Catbird	*wPt-8548*, ***wPt-2314***	[80]
2BS	*Lr23*/*QLr.ksu-2BS*	AS/APR	Synthetic hexaploid wheat: W-7984	*Xtam72*, *Per2*, ***Xcdo405***	[81,82]
2BS	*Lr13*	HTAS/APR	*T. aestivum*: TcLr13	***TraesCS2B02G182800***	[6,83]
2BS	*LrKP*	AS	*T. aestivum*: Klein Proteo	*Lrkp2B114*, ***LrkpF299R300***	[84]

2BS	*Lr35*	APR	*T. aestivum*: TcLr35	*Xwg996*, *Xpsr540*, ***Xbcd260***	[85]
2BL	*QLr.osu-2B*	Slow rusting	*T. aestivum*: CI 13227	***Xbarc167***, *Xagc.tgc135*, *Xcatg.atgc60*	[89]
2BS	*QLr.ifa-2BS*	APR	*T. aestivum*: Capo	***Xgwm120***	[33]
2BL	*Lr.locus-2B5*	AS	*T. turgidum*: durum wheat collection (GWAS)	*IWA1765*, ***wmc332***	[32]
2B	*QLr.dms-2B.2*	APR	*T. aestivum*: spring wheat collection (GWAS)	***Excalibur_c62234_105***	[90]
2BL	*LrNJ97*	AS	*T. aestivum*: Neijiang 977671	***Xwmc317***, *Xbarc159*	[91]
2BL	*Lr50*	AS	*T. timopheevii*: TA 870, TA 874, KS96WGRC36	*Xgwm382*, *Xgdm87*	[92]
3BS	*QLr.ifa-3BS*	APR	*T. aestivum*: Capo	***Xgwm389***	[33]
3BS	*Lr74/ QLr.hwwg-3BS.1*	APR	*T. aestivum*: Caldwell, Clark	*gwm533*, *cfb5006*, ***barc75***, *IWA4654*, *IWA1702*, *Xgwm389*	[93,94]
3BS	*QLr.cim-3BS.1*	APR	*T. aestivum*: Francolin#1	***wPt-6945***, *wPt-664393*, *wPt-5390*	[95]
3BS	*LrSV2*	APR	*T. aestivum*: Sinvalocho MA	***Xpsr598***, *swm13*, *gwm533*	[96]
3BL	*QLr.fcu-3BL*	AS	Synthetic hexaploid wheat: TA4152–60	***Xbarc164***, *Xfcp544*	[40]
3BL	*QLr.wpt-3BL*	APR	*T. aestivum*: wheat cultivar collection (GWAS)	***wPt-7502***	[97]
3BL	*QLr.hebau-3BL*	APR	*T. aestivum*: SW 8588	*AX-111014259*, ***AX-111534420***	[50]
3BL	*Lr79*	APR	*T. turgidum*: Aus26582	*sun770*, *sun786*	[98]
4B	*QLr.sfrs-4B*	APR	*T. aestivum*: Forno	***Xpsr921***, *Xpsr953b*	[39]
4BL	*Lr12/Lr31/QLr.hebau-4B*	APR	*T. aestivum*: Chinese Spring	***gwm149***, *BS00109813_51*	[34,99]
4BL	*Lr25*	AS	*Secale cereale*: TcLr25	***Xgwm251,*** *Xgwm538*, *Xgwm6*	[100]
4BL	*Lr49*	APR	*T. aestivum*: VL404	***Xbarc163***, *Xwmc349*	[79]
4BL	*QLr.spa-4B*	APR	*T. aestivum*: Carberry	***wPt-5303***, *wPt-1849*	[35]
5BS	*Lr52*	AS	*T. aestivum*: RL6107	*Xwmc149*, *Xtxw200*, ***Xgwm234***	[101,117]
5BL	*QLr.cim-5BL*	APR	*T. aestivum*: Heller#1, Dunkler	*AX-94480675f*, *AX-94394039f*, ***AX-94962653***	[102]
5BL	*QLr.fiz-5B*	APR	*Triticum* and *Aegilops* species collection (GWAS)	***wsnp_Ex_c6548_11355524***	[22]
5BL	*Lr18*	AS	*T. timopheevii*	***Xwmc75***, *Xgpw7425*	[103]
6BS	*QLr.usw-6BS*	APR	*T. turgidum* ssp. *durum*: Gaza	***CAP7_c10772_156***	[76]
6BS	*QLr.wpt-6BS.1*	APR	*T. aestivum*: wheat cultivar collection (GWAS)	***wPt-3116***	[97]
6BS	*Lr53*	AS	*T. dicoccoides*: 98M71	***Xwmc487***, *Xcfd1*, *Xgwm508*	[104]
6BS	*QLr.caas-6BS.1*	APR	*T. aestivum*: Bainong 64	***Xwmc487***, *Xcfd13*	[71]

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6BS	*Lr61*	AS	*T. turgidum* ssp. *durum*: Guayacan INIA	***Xwmc487***, *Xwmc104*, *Xwmc398*	[105]
6BS	*Lr59*	AS	*Ae. peregrina*	***Xgwm518***, *Xdupw217*	[106]
6BS	*Lr36*	AS	*Ae. speltoides*: ER84018	***Xgwm88***, *Xcfd13*	[107]
6B	*QLr.liu-6B*	APR	*T. aestivum*: wheat collections and their hybrids (GWAS)	***SNP459220281chr6B***	[24]
6BL	*Lr9/Lr58-2BL*	AS	*Ae. umbellulate* *Ae. triuncialis*: TA10438	*Xpsr546*	[13,108]
6BL	*QLr.cimmyt-6BL.1*	APR	*T. aestivum*: Pastor	*wPT6329*, *wPt-5176*, ***Xgwm219***	[109]
6BL	*Lr3*	AS	*T. aestivum*: RL6062	***wPt-6878***	[110]
6BL	*QLr.usw-6BL*	APR	*T. turgidum*: Gaza	***wsnp_Ex_c45713_51429315***, *GENE-3689_293*	[76]
6BL	*QLr.cim-6BL*	APR	*T. aestivum*: Heller#1, Dunkler	***AX-95155193***, *AX-94469158*	[102]
7BS	*Lr72*	AS	*T. durum*: Atil C2000	***barc279***, *wmc606*	[111]
7BL	*QLr.sfrs-7B.2*	APR	*T. aestivum*: Forno	*Xpsr593c*, ***Xpsr129c***	[39]
7BL	*QLr.cimmyt-7BL*	APR	*T. aestivum*: Pastor	***wPt-4342***, *wPt-8921*	[109]
7BL	*QLr.osu-7BL/QLrlp.osu-7BL*	Slow rusting	*T. aestivum*: CI 13227	*Xaca.cacg126*, ***Xbarc50***, *Xbarc182*, *Xcatg.atgc125*	[89,113]
7BL	*QLr.cim-7BL*	AS	*T. aestivum*: Sujata	*Xcfa2040*, ***Xwmc526***	[17]
7BL	*Lr14a*	AS	*T. aestivum*: Selkirk *T. aestivum*: Arina*LrFor*	***Xgwm146***, *gwm344*	[12]
7BL	*Lr68*	Slow rusting	*T. aestivum*: Parula	***Xgwm146***, *csGS*, *cs7BLNLRR*, *Psy1-1*	[114]
7BL	*QLr.ubo-7B.2*	APR	*T. durum*: Colosseo	*Xbarc340.2*, ***Xgwm146***, *Xgwm344.2*	[115]
7BL	*LrFun*	AS	*T. aestivum*: Fundulea 900	*Xgwm344*, ***Xwmc70***	[116]
7BL	*QLr.ksu-7BL*	APR	*T. aestivum*: Opata 85	*Cht1b*, *Tha1*, *Cat*, *Xfbb189*	[82]
7BL	*QLr.cimmyt-7BL.1*	Slow rusting	*T. aestivum*: Parula	*Xcmtg05-500*, *Xcmti16–1500*	[112]
7BL	*QLr.usw-7BL*	APR	*T. turgidum*: Arnacoris	*Tdurum_contig30545_715*, *Bobwhite_c42202_158*	[76]

6. Genetic loci carrying *Lr*/*QLr* in D sub-genome

6.1. Lr/QLr on chromosome 1D

There were several seedling resistance *Lr* genes in the distal region of chromosome 1DS. Both *Lr21* and *Lr40* were introgressed from *Aegilops tauschii*, and later they were proved to be allelic to each other [118]. *Lr21* was then successfully cloned and encoded a typical NBS-LRR protein [7]. By developing a virus-induced gene-silencing (VIGS) system, a protein complex of RAR1-SGT1-HSP90 was proved to be essential for the full function of *Lr21* [119]. *Lr60*, also known as *LrW2*, was mapped to a nearby region of *Lr21* on chromosome 1DS using microsatellite markers [120]. Seedling resistance gene *LrTs*$_{276-2}$ was derived from *T. spelta* and initially mapped to chromosome 1DS using BSA [121]. Another *Ae. tauschii*-derived seedling resistance gene *Lr42* located in this region was recently cloned using BSR-seq on constructed *Ae. taushchii* population [9]. The *Lr42* gene also encoded a typical NBS-LRR protein and was widely employed in wheat breading practice.

6.2. Lr/QLr on chromosome 2D

Large number of genetic loci carrying *Lr*/*QLr* were distributed on chromosome 2D, particularly in the distal region of the short arm. AS gene *Lr11* in common wheat cultivar "Buck Poncho" was recently re-mapped to chromosome 2DS using BSR-seq and multiple molecular markers [122]. Two major QTLs, *QLrlp.osu-2DS* and *QLrid.osu-2DS*, for slow rusting in the recombinant inbred line "CI 13227" were mapped to the distal region of chromosome 2DS [89,113]. AS gene *Lr80* showed widely effective resistance to multiple *Pt* pathotypes and was initially mapped to the chromosome 2DS using SSR and 90K SNP markers [123]. Both seedling resistance genes *Lr39* and *Lr41* were transferred from *Ae. tauschii* and reported later as the same or closely linked genes on chromosome 2DS [124,125]. Another study predicted that *Lr39*, although introgressed to a different chromosome, was an allelic gene to *Lr21* [118]. An APR locus *QLr.cim-2DS* contributed by an adapted common wheat line "UC1110" was genetically mapped to chromosome 2DS using a segregation population [126]. *Lr2a* located on chromosome 2DS was reported to be involved in both seedling resistance and APR (*QLr.mna-2DS*). A major QTL *QLr.inra-2D* on chromosome 2DS was responsible for the APR in wheat cultivar "Balance" [127]. The seedling resistance gene *Lr22a* derived from *Ae. tauschii* was successfully cloned using "targeted chromosome-based cloning via long-range assembly (TACCA)"[8]. The *Lr22a* gene encoded an intercellular immune receptor with an NBS-LRR structure. Seedling resistance gene *Lr15* was also mapped to chromosome 2DS using SSR markers [128]. A major QTL *QLr.hwwg-2DS* responsible for slow rusting was detected in the U.S. winter wheat line "CI13227" using 90K SNP and SSR markers [129]. AS gene *Lr54* was introgressed from *Aegilop kotschyi* to chromosome 2DL. A dominant sequence characterized amplified region (SCAR) marker and three microsatellite markers were developed to detect *Lr54* [130].

6.3. Lr/QLr on chromosome 3D

AS gene *Lr32* introgressed from *Ae. tauschii* was mapped to the short arm of chromosome 3D [131]. A Chinese wheat cultivar "Pingyuan 50" showed APR to multiple fungal diseases including stripe rust, powdery mildew, and leaf rust. A major QTL *QLr.hebau-3DS* was stably detected in six experimental environments using 55K SNP array and additional SSR markers [132]. In wheat cultivar "UC1110", besides *QLr.cim-2DS*, there was a co-located APR locus *QLr.cim-3DC*/*QYr.cim-3DC* on centromere region of chromosome 3D to both leaf rust and stripe rust [126]. Moreover, *QLr.cim-3DC* and *QLr.cim-2DS* showed marginally significant interaction for APR in "UC1110". AS gene *Lr24* derived from *Agropyron elongatum* was mapped in the distal region of chromosome 3DL [133]. A further study developed SCAR markers co-segregating with the *Lr24* gene [134] and this gene was widely used in breeding practice.

6.4. Lr/QLr on chromosome 4D

The *Lr67* gene on chromosome 4DL provided slow rusting resistance to leaf rust and was successfully cloned recently [15]. It encoded a hexose transporter to block the uptake of glucose by rust fungus. A major QTL *QLr.sfrs-4DL* for APR in wheat cultivar "Forno" was constantly detected on chromosome 4DL in different environments [39].

6.5. Lr/QLr on chromosome 5D

Several AS genes were mapped to chromosome 5D. Seedling resistance gene *Lr70* was discovered in common wheat accession "KU3198" and mapped to chromosome 5DS using BSA [135]. An *Aegilops umbellulate*-derived AS gene *Lr76* was transferred to the telomeric region of chromosome 5DS [136]. The *Lr78* gene was identified as an APR gene controlling slow rusting in wheat cultivar "Toropi". It was also mapped to chromosome 5DS using SSR and KASP markers [137]. The *Lr57* gene derived from *Aegilops geniculata* conferred both seedling resistance and APR to leaf rust. It was introgressed to chromosome 5D and co-segregated RFLP markers were developed for this gene [138]. The chromosome 5DL-located *Lr1* has been successfully cloned using classical map-based positional cloning strategy [4]. The seedling resistance *Lr1* gene also encoded an NBS-LRR protein, and its function was validated using a VIGS assay.

6.6. Lr/QLr on chromosome 6D

The Chinese wheat landrace "Bai Qimai" showed a slow rusting phenotype at the adult plant stage, and a major QTL *QLr.cau-6DL* on chromosome 6DL was recently identified using 90K SNP chip and SSR markers [139]. The *Agropyron intermedium*-derived *Lr38* on chromosome 6DL provided a stable seedling and APR to multiple *Pt* pathotypes [140].

6.7. Lr/QLr on chromosome 7D

A multiparent advanced generation intercross (MAGIC) wheat population was prepared using 394 F6:8 RILs and a total of 19 QTLs were detected on 11 distinct chromosomal regions. Among these QTLs, a major QTL *QLr.jki-7D.1* on chromosome 7D explained 28% of the phenotypic variance with "BAYP4535" as the most resistant founder [141]. There were three designated *Lr* genes on chromosome 7D. The slow rusting gene *Lr34* located on chromosome 7DS was successfully cloned and widely used in wheat breeding all over the world [14]. It encoded an ABC transporter and was associated with leaf tip necrosis. Phytohormone abscisic acid (ABA) was recently revealed as a substrate of the ABC transporter encoded by *Lr34*, and the re-distribution of ABA in the *Lr34*-expressing plant greatly influenced the transcriptional response [142]. Moreover, *Lr34* also showed excellent potentials in genetic improvement of disease resistance in several other crops, including maize to common rust and northern corn leaf blight [143], sorghum to anthracnose and rust [144], and rice to blast disease [145].

Both seedling resistance genes *Lr29* and *Lr19* were transferred from *Agropyron elongatum* to chromosome 7D. *Lr29* was mapped to chromosome 7DS using random amplified polymorphic DNA (RAPD) and SCAR markers [146]. *Lr19* located on chromosome 7DL still provided high resistance to major *Pt* pathotypes in worldwide, and various molecular markers were developed for this gene to facilitate its usage in breeding practice [147,148]. Notably, the same *Ag. elongatum*-derived chromosome segment carrying *Fusarium* head blight resistance gene 7 (*Fhb7*) was successfully decoded recently, which might greatly facilitate the cloning of *Lr19* in the future [149].

Information for all the genetic loci carrying *Lr*/*QLr* in D sub-genome were summarized in **Table 4**.

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Table 4. Genetic loci carrying *Lr*/*QLr* in D sub-genome

Chromosome	Gene/QTL	Resistance type	Donor	Associated markers or SNPs	Reference
1DS	*Lr21/40*	AS	*Ae. tauschii*: TA1649 *Ae. tauschii*: KS89WGRC7	*Xksud14*, *Xksu936*, *Xksu937*, *Xksu027*, *Gli-D1*, ***Xbcd1434***	[7,118]
1DS	*Lr60*	AS	*T. aestivum*: RL6172	***barc149***, *WMC432*, *CFD61*	[120]
1DS	*LrTs276-2*	AS	*T. Spelta*: TSD276-2	***Xcfd15***	[121]
1DS	*Lr42*	AS	*Ae. tauschii*: TA2450	*Xwmc432*, *Xgdm33*, ***Xcfd15***	[9]
1DS	*QLr.wpt-1DS*	APR	*T. aestivum*: wheat cultivar collection (GWAS)	*wPt-0413*	[97]
1D	*QLr.zha-1D*	APR	*T. aestivum*: wheat lines collection (GWAS)	*BS00014671_51*	[42]
2DS	*Lr11*	AS	*T. aestivum*: Buck Poncho	*Xscar32/35*, ***wmc574***, *wms1099*	[122]
2DS	*QLrlp.osu-2DS*	Slow rusting	*T. aestivum*: CI 13227	*Xactg.gtg185*, ***Xbarc124***	[113]
2DS	*Lr80*	AS	*T. aestivum*: Hango-2	*Cau96*, ***gwm210***, *barc124*	[123]
2DS	*Lr39/41*	AS	*Ae. tauschii*: TA4186 *Ae. tauschii*: TA2460	***Xgwm210***, *Xgwm296*, *Xgwm455*, *Xbarc124*, *Xgdm35*, *Xcfd36*	[124,125]
2DS	*QLr.cim-2DS*	APR	*T. aestivum*: UC1110	***cfd51***, *cfd36*	[126]
2DS	*Lr2a/QLr.mna-2DS*	AS/APR	*T. aestivum*: MN98550-5/MN99394-1	*wmc453*, *wPt-0330*, ***barc95***	[150]
2DS	*QLr.inra-2D*	APR	*T. aestivum*: Balance	*gpw3320*, ***cfd36***	[127]
2DS	*Lr22a*	AS	*Ae. tauschii*: RL6044	*gwm455*, ***gwm296***, *gwm261*	[8]
2DS	*QLrid.osu-2DS*	Slow rusting	*T. aestivum*: CI 13227	***Xgwm261***	[89]
2DS	*Lr15*	AS	*T. aestivum*: TcLr15	*Xgwm4562*, ***Xgwm102***	[128]
2DL	*Lr54*	AS	*Ae. kotschyi*: CS-Lr54/Yr37	***Xcfd50***, *Xgdm6*	[130]
2DS	*QLr.hwwg-2DS*	APR	*T. aestivum*: CI13227	*IWB8545*	[129]
2DL	*QLr.tur-2DL*	AS/APR	*T. aestivum*: spring wheat collection (GWAS)	*IWA5637*	[58]
2D	*QLr.fiz-2D*	APR	*Triticum* and *Aegilops* species collection (GWAS)	*Kukri_c59403_339*	[22]
2D	*QLr.dms-2D*	APR	*T. aestivum*: spring wheat collection (GWAS)	*RAC875_c52856_250*	[90]
3DS	*Lr32*	AS	*Ae. tauschii*: RL5497-1	***barc135***	[131]
3DS	*QLr.hebau-3DS*	APR	*T. aestivum*: Pingyuan 50	***AX-109395143***	[132]
3DC	*QLr.cim-3DC*	APR	*T. aestivum*: UC1110	***gwm341***, *barc1119*	[126]
3DL	*Lr24*	AS	*Ag. elongatum*: Agent	*Xpsr904*, ***Xpsr931***, *Xpsr1205*	[133,134]

3D	*QLr.liu-3D*	APR	*T. aestivum*: wheat collections and their hybrids (GWAS)	*SNP597179288chr3D*	[24]
3D	*QLr.cdl-3D*	APR	*T. aestivum*: Americano 44d	*wPt-741949*	[37]
4DL	*Lr67*	Slow rusting	*T. aestivum*: RL6077	*csSNP856*, *gwm4670*, ***cfd71***	[15]
4DL	*QLr.sfrs-4DL*	APR	*T. aestivum*: Forno	*Xglk302b*, *Xpsr1101a*	[39]
5DS	*Lr70*	AS	*T. aestivum*: KU3198	***wmc233***, *gwm190*	[135]
5DS	*Lr76*	AS	*Ae. umbellulate*: IL 393-4	*Xcfd18*, *Xwmc233*, ***Xgwm190***	[136]
5DS	*Lr78*	Slow rusting	*T. aestivum*: Toropi (PI 344200)	*IWA6289*, ***cfd189***, *wmc233*	[137]
5D	*Lr57*	AS/APR	*Ae. geniculata*: TA6675	*Xbcd1087*, *Xabg705*, ***Xpsr128***	[138]
5DL	*Lr1*	AS	*T. aestivum*: 87E03-S2B1	***Xgwm272***, *Xgwm65*	[4]
6D	*QLr.cdl-6D*	APR	*T. aestivum*: Americano 44d	***wPt-664670***	[37]
6DL	*QLr.cau-6DL*	APR	*T. aestivum*: Bai Qimai	***Cfd188***	[139]
6DL	*Lr38*	AS/APR	*Ag. intermedium*: RL6079	*Xwmc773*, ***Xbarc273***	[140]
7DS	*QLr.jki-7D.1*	APR	*T. aestivum*: MAGIC population	***AX-94930280***	[141]
7DS	*Lr34*	Slow rusting	*T. aestivum*: SAAR	*Xgwm37*, *XcsLV34*, ***Xgwm295***	[14]
7DS	*Lr29*	AS	*Ag. Elongatum*: RL6080	*OPY10*$_{950}$, *UBC219*$_{1000}$	[146]
7DS	*QLr.wpt-7DS*	APR	*T. aestivum*: wheat cultivar collection (GWAS)	*wPt-2565*	[97]
7DL	*Lr19*	AS	*Ag. elongatum*: TcLr19	*Xwmc221*, *Xgdm46*, ***Xgdm67***	[147,148]

7. Discussion

Chromosome distributions for these genetic loci were estimated based on the positions of associated molecular markers in the common wheat Chinese Spring reference genome v1.1 (**Figure 2**). As indicated on the genome-wide scale map, several hot zones enriched with *Lr*/*QLr* were distributed on chromosomes 2AS, 2BS, 7BL, and 2DS. Rational pyramiding of these leaf rust resistance loci with balanced seedling resistance and slow rusting resistance relies on further development of high-throughput SNP-based molecular markers. With advanced techniques in genome sequencing and molecular biology, more *Lr* genes or dominant genes in *QLr* loci are expected to be cloned in the coming future. Transgenic expression of clustered *R* gene cassette is another strategy to provide broad-spectrum resistance to multiple rust pathotypes [151]. On the other hand, gene-editing on susceptible genes or negative regulatory genes of plant defense responses shows great potentials in improvement of wheat resistance to fungal diseases [152].

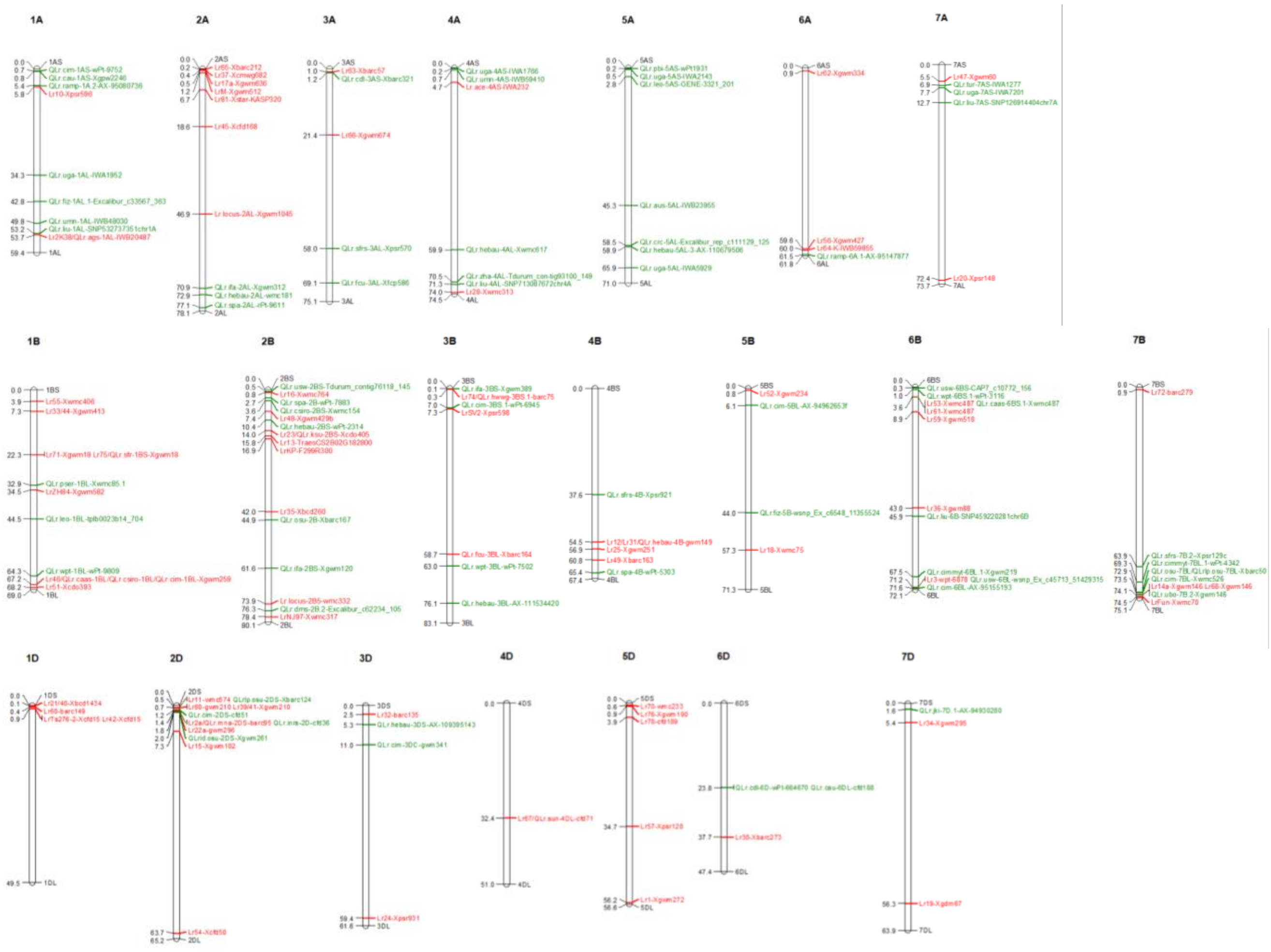

Figure 2. Genome-wide distribution of genetic loci carrying *Lr*/*QLr* in wheat. Molecular markers, SNPs, and genes associated with *Lr*/*QLr* were collected from previous publications and searched against the reference genome of common wheat "Chinese Spring" v1.0. Corresponding physical position for each *Lr*/*QLr* was estimated, and a distribution map was generated using MapChart software v2.32. Numbers on the leaf side of each chromosome indicated physical locations in units of 10,000,000 bp. Formally designated *Lr* genes are highlighted in color of red, and stable QTLs with large effect are in green.

8. Conclusions

In conclusion, this review summarized recent progresses on genetics of wheat resistance to leaf rust in a genome-wide perspective. It will serve as a valuable resource for both researchers and breeders to follow-up studies on various genetic loci controlling resistance of wheat to leaf rust.

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Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: Estimated physical positions for all the identified *Lr*/*QLr* loci.

Author Contributions: Conceptualization, X.W. and S.C.; formal analysis, X.R., C.W., and Z.R.; visualization, J.W.; software, S.Z., M.L. and M.Y.; data curation, P.Z., X.Y. and Z.L.; writing—original draft preparation, X.R., C.W., and Z.R.; writing—review and editing, X.W. and S.C.; supervision, X.W. and S.C.; project administration, X.W. and S.C.; funding acquisition, X.W. and S.C. All authors have read and agreed to the published version of the manuscript.

Funding: Work at X.W. lab was supported by Provincial Natural Science Foundation of Hebei (C2022204010 and C2021204008). Work at S.C. lab was supported by the Provincial Natural Science Foundation of Shandong (ZR2021MC056), the Young Taishan Scholars Program of Shandong Province and the Open Project Funding of the State Key Laboratory of Crop Stress Adaptation and Improvement. Work at Z.L. lab was supported by the National Natural Science Foundation of China (32161143007 and 32001538). Work at X.Y. lab was supported by the Provincial Natural Science Foundation of Hebei (C2020204050).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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