Genetic analysis of rust resistance genes in global wheat cultivars: an overview

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ABSTRACT
Rust is the most devastating fungal disease in wheat. Three rust diseases, namely, leaf or brown rust caused by Puccinia triticina Eriks, stem or black rust caused by Puccinia graminis f. sp. tritici West, and stripe or yellow rust caused by Puccinia striformis f. Triticum Eriks, are the most economically significant and common diseases among global wheat cultivars. Growing cultivars resistant to rust is the most sustainable, cost-effective and environmentally friendly approach for controlling rust diseases. To date, more than 187 rust resistance genes (80 leaf rust, 58 stem rust and 49 stripe rust) have been derived from diverse wheat or durum wheat cultivars and the related wild species using different molecular methods. This review provides a detailed discussion of the different aspects of rust resistance genes, their primitive sources, their distribution in global wheat cultivars and the importance of durable resistant varieties for controlling rust diseases. This information will serve as a foundation for plant breeders and geneticists to develop durable rust-resistant wheat varieties through marker-assisted breeding or gene pyramiding.

Introduction
Wheat cultivation represents approximately 19% of global major cereal crop production [1]. Rust diseases are among the most economically important diseases affecting wheat because they cause significant yield losses worldwide. Among the rust diseases, leaf rusts are very common in global wheat production, and yield losses greater than 50% have been recorded in susceptible cultivars [2]. Yield losses of approximately 20%–30% caused by stem or black rust were recorded in the mid-twentieth century in Eastern and Central Europe [3], and notable losses have also been reported in many other countries, including Australia, China and India [4]. The most virulent stem rust race, Ug99, emerged first in Uganda in 1999, then in Kenya, Ethiopia, Yemen, the Middle East and South Asia, and the associated losses were estimated at USD 3 billion.

Two methods have been used for controlling rust diseases: chemical and genetic control. Genetic control, or the growing of resistant cultivars or varieties, is the most effective, economically safe and environmentally friendly approach, as this method eliminates the need to use fungicides and reduces the cost of production. Farmers in the developing world prefer the use of resistant cultivars to fungicides due to the possibility that rust pathogens might develop resistance to fungicides [5]. Using variety to prevent or avoid rust diseases at early stages or to minimize disease impact is known as varietal resistance [1].

To ensure genetic resistance, identification of new or effective resistance genes in different germplasms of global wheat cultivars or wheat relative species is essential [6]. Identification of Lr genes by multipathotype testing or gene postulation is labour-intensive and time-consuming. Furthermore, appropriate pathotype(s) may not be available to identify the resistance genes present in a genotype, or a pathotype may not have the ability to detect rust resistance genes [7]. Therefore, it can be difficult to detect a single gene of interest within a complex background of other resistance genes [8]. In addition, the use of cultivars with single-gene resistance permits the rapid selection of mutations that reduce resistance at an individual resistance locus. Moreover, due to evolution and the loss of variation and selection pressure, new virulent races of fungus have appeared, increasing the need to develop durable resistance [1]. Hence, using combinations of resistance genes is the best method for achieving adequate genetic control of diseases affecting wheat, including rust diseases [9]. Consequently, plant pathologists and breeders have
prioritized the development of disease-resistant varieties with high-yielding capacity through pyramiding effective resistance genes with durable resistance [10] because the expression of individual resistance genes is difficult to monitor in the field [1]. This gene pyramiding strategy, also known as multigenic resistance, has been used to enhance the durability of resistance [10]. In this method, a cultivar with a combination of several effective genes, especially those from wild relatives and related species, is developed [11]. Durable rust resistance is a mechanism conferring resistance to a cultivar for a long period of time during its widespread cultivation within environments that harbour favourable conditions for disease spread [12]. This type of resistance is mainly associated with minor genes, which are also known as slow rusting genes. However, introgression of different resistance genes to a single variety and monitoring in the field are very difficult to accomplish using traditional phenotypic methods. In addition, this approach is limited because screening for one resistance gene interferes with the ability to screen for another, which is a frequent problem in breeding for disease resistance [13].

Recent advances in molecular marker technology have created effective tools for solving such complex problems. For example, the use of polymerase chain reaction (PCR)-based DNA molecular markers has several advantages over traditional phenotype trait selection [1]. Marker-assisted selection (MAS) breeding has also been widely used to target rust resistance genes. These techniques can improve selection efficiency in plant breeding, especially by providing pathways to overcome some of the problems associated with classical phenotypic screening approaches [14,15]. For example, to facilitate breeding for durable resistance to stem rust, molecular markers are useful for developing resistant cultivars, especially in addition to the pyramiding of several disease-resistance genes [14]. MAS can be used at an early stage of plant development, with multiple DNA markers being used to screen several genes simultaneously [16]. In addition, neutral markers, such as iso-enzymes, can also be used to characterize and compare rust populations.

The aim of the present review is to describe the most recently developed approaches for introducing rust resistance genes into bread and durum wheat cultivars and their related species. To accomplish this, we collected current information on rust disease-resistance genes (leaf, stem and stripe), including their primitive sources and their chromosomal positions, and discuss their potential applications for developing durable resistant wheat varieties through MAS.

**Leaf rust fungus characteristics and behaviour**

Wheat leaf rust (caused by *Puccinia triticina* Eriks) is the most destructive and prevalent rust disease [17] and has adapted to a wide range of environments, allowing it to coexist with wheat in all growing environments [18]. The disease continuously evolves and forms novel virulent races [17,19], causing direct yield losses and decreased yield quality. Therefore, management of the disease, such as through the application of chemical fungicides, is necessary to ensure that wheat cultivation remains a profitable endeavour [20]. Yield losses of up to 70% have been recorded in durum wheat fields subject to a severe epidemic of wheat leaf rust [21].

Wheat leaf rust fungus can easily spread thousands of kilometers from the initial infection site through its dikaryotic urediniospores, which have been documented to spread both within and between continents [22]. This widespread dispersal has led to the occurrence of epidemics on a continental scale [9]. Therefore, it is essential to document genetic changes that occur in rust populations over large geographic areas to facilitate the development of rational strategies for achieving durable resistance.

**Genetic characterization of leaf rust resistance genes**

Approximately 100 years ago, the wheat cultivars Malakof and Webster were submitted to genetic studies of leaf rust resistance [23]. It was discovered that these cultivars possessed genes, later designated *Lr1* and *Lr2*, that confer resistance to leaf rust [24]. Following these studies, Soliman et al. [25] identified the chromosomes that carry the leaf rust resistance genes *Lr1*, *Lr3*, and *Lr11*. Approximately 80 leaf rust resistance genes or alleles [26], designated *Lr1* to *Lr78*, *Lrac104* and *Lrac124*, have been identified and characterized in bread wheat, durum wheat and diploid wheat species [27] using different enzymatic, PCR-based DNA molecular and microsatellite markers. These genes are located on 20 of the 21 chromosomes found in hexaploid wheat [26-28]. The genetic resistance conferred by rust resistance genes has been characterized in the seedling and adult stages of plants. Seedling resistance is monogenic, race-specific, vertically controlled by major genes and hypersensitive in nature. Conversely, adult plant resistance (APR) is polygenic, race-nonspecific, horizontally controlled by minor genes and non-hypersensitive, slow rusting or partial and durable in nature. However, most *Lr* genes confer major, seedling or race-specific resistance and follow the gene-for-gene concept, leading to a hypersensitive response (HR) or programmed cell death [29-31]. A
small number of APR genes, such as Lr34 and Lr46, are very important for breeding because they have been shown to confer durable, long-term resistance in different environments and against diverse fungus pathotypes [32].

**Genetic analysis of leaf rust resistance genes derived from Triticum aestivum**

More than 81 leaf rust resistance genes, including Lr1 [33], Lr2, Lr2a to Lr2c, Lr3 to Lr6, Lr8, [34] Lr7 [35], Lr10 to Lr13, Lr14a, Lr15 to Lr18 [34], Lr20 [34,36], Lr22b, Lr23, Lr27, Lr30 [37], Lr31, Lr33, Lr40, [34] Lr46, [35] Lr48 [34], Lr49, Lr52, Lr67, Lr68, [38] trp1, trp29 [39], Lract104, and Lract124 [40], have been derived directly from common wheat (Triticum aestivum) cultivars. Their chromosomal locations, resistance types and presence in cultivars around the world are presented in Table 1.

**Genetic analysis of leaf rust resistance genes originating from wild species**

Some wild cultivars of wheat or wild grasses, such as Aegilops tauschii Coss., Aegilops squarrosa L. and Triticum tauschii, are major sources of many resistance genes to major wheat diseases [53]. Leaf rust resistance genes were initially introduced into common wheat cultivars from these wild accessions. One gene (Lr9) was derived from the wild species Aegilops umbellulata, three (Lr19, Lr24, and Lr29) from Aegilops elongatum, five (Lr28, Lr35, Lr36, Lr47, and Lr51) from Aegilops speltoides, one (L37) from Aegilops ventricosa [1], one (Lr37) from Agropyron intermedium, seven (Lr21, Lr22a, Lr32, Lr35, Lr36, Lr47, and Lr51) from Aegilops speltoides, one (L37) from Triticum monococcum [50,59], one (Lr33) from Triticum dicoccoides [50] and one

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**Table 1. List of identified leaf rust (Lr) resistance genes originating from Triticum aestivum and their chromosomal locations, resistance types and presence in existing cultivars in global germplasms.**

| Genes  | Chromosomal location | Resistance types | Cultivars/varieties with country of origin                                                                 | References |
|--------|----------------------|------------------|----------------------------------------------------------------------------------------------------------|------------|
| Lr1    | 5DL                  | SR               | Sonora 64, Pavon F 76 (Mexico), Dollarbird (Australia), American soft red wheat                           | [22,33,41,42] |
| Lr2    | 7BL                  | SR               | –                                                                                                        | [34]       |
| Lr2a-c | 2DS                  | SR               | –                                                                                                        | [34]       |
| Lr3    | 6BL                  | SR               | –                                                                                                        | [34]       |
| Lr4-6, Lr8 |                  | SR               | –                                                                                                        | [34]       |
| Lr7    | APR                  | –                | –                                                                                                        | [35]       |
| Lr10   | 1AS                  | SR               | Pavon F 76 (Mexico), Punjab (Pakistan, India), Dollarbird (North America), BIOINTA 1004, INIA Churrinche, INIA Torcaza, Cronox Buck Baqueano, Buck Ranquel (Argentina) | [22,34,43-45] |
| Lr11   | 2A                   | SR               | –                                                                                                        | [34]       |
| Lr12   | 4B                   | SR               | –                                                                                                        | [34]       |
| Lr13   | 2BS                  | SR               | Giza164 (Egypt), Gemeaeza 7 (Europe), Ara (Argentina), Punjab 81 (Pakistan)                              | [46,47]    |
| Lr14a-b| 7BL                  | SR               | Hope and its related lines (Argentina, France, Ethiopia)                                                 | [34]       |
| Lr15   | 2DS                  | SR               | –                                                                                                        | [34]       |
| Lr16+Sr23 |                  | SR               | –                                                                                                        | [34]       |
| Lr17a-b| 2AS                  | SR               | –                                                                                                        | [34]       |
| Lr18   | 5BL                  | SR               | –                                                                                                        | [34]       |
| Lr20 + Pm1*+Sr15 |                  | SR               | Trizo (Ethiopia) British, Russia, Thatcher                                                            | [34]       |
| Lr22b  | 2BS                  | SR               | –                                                                                                        | [34]       |
| Lr23   | 2BS                  | APR              | –                                                                                                        | [37]       |
| Lr27+Sr2 + Pm8 | 3BS,1BL/1RS      | APR              | Frontana (Mexico) ACA801 (Iran), Klein Castor (Argentina)                                              | [34,37,49] |
| Lr30   | 4AL                  | SR               | –                                                                                                        | [34,37]    |
| Lr31   | 4BL                  | SR               | –                                                                                                        | [34,37,48] |
| Lr33   | 1BL                  | SR               | –                                                                                                        | [34]       |
| Lr34+Yr18+Pm38 | 7DS                | APR              | Frontana (Mexico) ACA801 (Iran), Klein Castor (Argentina)                                              | [34,37,49] |
| Lr40   | APR                  | –                | –                                                                                                        | [34]       |
| Lr46+Yr29* | 1B                  | APR              | Pavon 76 (Mexico)                                                                                       | [35,48,50] |
| Lr48   | 4BL                  | –                | –                                                                                                        | [34]       |
| Lr49   | 2AS                  | –                | –                                                                                                        | [34]       |
| Lr52 or LrW | 5B                  | APR              | R6107 (North American)                                                                                  | [34]       |
| Lr63+Yr46 | 4DL                | SR               | Toropi (Brazilian wheat cultivar)                                                                       | [51]       |
| Lr68   | 7BL                  | APR              | Parula                                                                                                  | [52]       |
| trp-1  | 1A                   | APR              | Toropi (Brazil)                                                                                        | [39]       |
| trp-2  | 4D                   | APR              | Toropi (Brazil)                                                                                        | [39]       |
| Lract104 | 6B                  | APR              | Emmer wheat (South Africa)                                                                             | [40]       |
| Lract124 | 4A                  | APR              | Emmer wheat (South Africa)                                                                             | [40]       |

Note: APR-adult plant resistance; SR-seedling resistance.
Genetic analysis of leaf rust resistance genes originating from wild species with their chromosomal locations, resistance types and presence in global wheat cultivars.

Table 2. List of leaf rust resistance genes originating from wild species with their chromosomal locations, resistance types and presence in global wheat cultivars.

| Genes          | Source               | Chromosomal location | Resistance type | Cultivars/varieties with country of origin                  | References |
|----------------|----------------------|----------------------|-----------------|-------------------------------------------------------------|------------|
| Lr9            | Aegilops umbellulata | 6BL                  | SR              | Biointa 1000 (Argentina), Europe, USA                      | [34]       |
| Lr19+Sr25      | Agropyron elongatum  | 7DL                  | SR              | ProINTA Gaudo, Agrus, Sids 1, Sids 12 (Argentina), Egypt, Russia | [13,60,61] |
| Lr24           | Agropyron elongatum  | 3DL                  | SR              | BIONTA 1004, INIA Churrinche, INIA Torcaca, Cronox (Argentina), Australia | [43,60,62] |
| Lr29           | Agropyron elongatum  | 7DL                  | APR             |                                                      | [60,63]   |
| Lr28           | Aegilops speltoides  | 4AL                  | SR              | Russian cultivars                                          | [13]       |
| Lr35           | Aegilops speltoides  | 2B                   | APR             |                                                      | [48,30]   |
| Lr36           | Aegilops speltoides  | 6BS                  | SR              |                                                      | [34]       |
| Lr47           | Aegilops speltoides  | 7AS                  | APR             | BIONTA 2004 (Argentina)                                   | [45,64]   |
| Lr51           | Aegilops speltoides  | 1BS                  | APR             | Europe, USA                                                | [65]       |
| Lr37+Yr17+Sr38 | Aegilops ventricosa  | 2AS                  | APR             |                                                      | [66]       |
| Lr38           | Agropyron intermedium | 1DL /2AL/3DS/5AS/6DL | APR             |                                                      | [34]       |
| Lr21           | T. tauschii          | 1DS                  | APR             | [56-58,67]                                                 |            |
| Lr22a          | T. tauschii          | 2D                   | SR              | [55,58]                                                   |            |
| Lr22           | T. tauschii          | 3DS                  | APR             | [57,58,67]                                                 |            |
| Lr23           | T. tauschii          | 2DS                  | APR             | [48,50,59]                                                 |            |
| Lr41           | T. tauschii          | 1D                   | APR             | [56-58,67]                                                 |            |
| Lr42           | T. tauschii          | 1D                   | APR             | [57,58]                                                   |            |
| Lr43           | T. tauschii          | 7DS                  | APR             | [57,58]                                                   |            |
| Lr44           | T. spelta            | 1B                   | APR             | [34]                                                      |            |
| Lr25+Pm7       | Secale cereale Rosen | T1B:T1R              | APR             | Argentinia, Russia, BIONTA 1001, Buck Guapo, Klein Escudo, Klein Zorro (Argentina) Chinese, British, Iran | [50,59]   |
| Lr26+Yr9+Sr31  | Secale cereale Petkus | T2AS                 | APR             |                                                      | [34]       |
| Lr45           | Secale cereale       | T2AS                 | APR             | [50,59]                                                   |            |
| Lr50           | T. monococcum        | 2BL                  | APR             | [50,59]                                                   |            |
| Lr53+Yr35      | T. turgidum subsp. dicoccoides | 6BS | APR | Avocet ‘S’, Emmer wheat, (South African and Canadian, Chinese cultivars) | [68,69] |
| Lr54+Yr37      | Aegilops kotschyi    | 2DL                  | APR             | Northern Africa, and Mid-East and Western Asia (Chinese Spring wheat) | [69,70]   |
| Lr56 +Yr38     | Aegilops sharonensis | 6AL                  | APR             | Chinese spring wheat                                       | [71,72]   |
| Lr59           | Aegilops peregrina   | 1AL                  | APR             | Israel, Chinese spring wheat cultivars                     | [73,74]   |
| Lr62+Yr42      | Aegilops neglecta    | 6AS                  | APR             | California wheat cultivars                                 | [75,76]   |

Note: APR-adult plant resistance; SR-seedling resistance.

(Lr54) from Aegilops kotschyi. Their chromosomal locations, resistance types and presence in wheat cultivars around the world are presented in Table 2.

Genetic analysis of leaf rust resistance genes originating from durum wheat

The leaf rust resistance genes Lr14a (on 7BL) and Lr23 (on 2BS) were transferred to common wheat from the durum wheat cultivar ‘Hope’ and the related line ‘Gaza’, respectively, and their detailed information is presented in Table 3. A characteristic feature of durum wheat leaf rust races is virulence to most durum wheat lines and avirulence to most Lr genes present in common wheat lines [77,78]. Thus, the resistance genes that are effective in durum wheat germplasms could be widely ineffective in common wheat lines [79]. In addition, the seedling resistance genes Lr23, Lr10, and Lr33 are not considered effective due to frequent virulence among P. triticina races [78].

Genetic analysis of stem rust resistance genes

Among the fungal diseases that affect wheat, stem rust caused by Puccinia graminis Pers. f. sp. tritici (Pgt) is a major biotic constraint in most of the wheat-growing areas in the world and causes yield losses of up to 100% during epidemic outbreaks [85]. Ug99, a new virulent stem rust race, was first identified in Uganda in 1999 [86] and then spread to Kenya in 2001 and to Ethiopia in 2003, following the migration path suggested by Singh et al. [87]. Currently, it is a major threat to global wheat cultivation. According to the Farm and Ranch Guide report, 50% of winter wheat and 70%–80% of spring wheat varieties currently grown in the USA are susceptible to Ug99. Furthermore, 75%–80% of breeding
materials are susceptible to Ug99, and most stem rust resistance genes deployed in breeding programmes have been overcome by this new fungus [1]. For this reason, current research on stem rust has focused on identifying additional resistance genes to control Ug99. To date, approximately 58 stem rust resistance (Sr) genes have been identified [88,89] and numerically designated as Sr1 to Sr58 as part of the International Wheat Genetics Symposium Gene Catalog [26,90]. Among these genes, at least 27 genes, including Sr2 (Yr30), Sr13, Sr21, Sr22, Sr24, Sr25, Sr26, Sr27, Sr28, Sr32, Sr33, Sr35, Sr36, Sr37, Sr39, Sr40, Sr42, Sr44, Sr45, Sr46, Sr47, Sr51, Sr52, Sr53, Sr55 (Lr67/Yr46/ Pm46), Sr57 (Lr34/Yr18/Pm38), and Sr58 (Lr46/Yr29/Pm39), are effective or partially effective against the Ug99 race group [91-100]. Among these 27 genes, Sr2, Sr13, Sr22, Sr25, Sr26, Sr35, Sr39 and Sr40 were reported to be the most effective against Ug99 [87,101-103]. A brief description of the details of these genes is given in Table 4.

Understanding the genetic basis for durable resistance to stem rust disease is necessary for improving the efficiency of wheat breeding [88]. Detailed genetic characteristics of the above-described stem rust resistance genes are shown in Table 4. One of the more effective stem rust resistance genes Sr2 is a catalogued adult plant stem rust resistance gene in wheat [34] and has been shown using SSR markers to be located in a region on the short arm of chromosome 3B [125] that is derived from the variety ‘Hope’ and commonly known as the ‘Sr2-complex’ (Sr2+Yr30+Lr27+Pbc) [87,126]. Due to its ability to confer durable and broad-spectrum resistance, the Sr2 gene has been used to improve resistance against stem rust diseases in several popular International Maize and Wheat Improvement Centre (CIMMYT) varieties cultivated worldwide [129]. Generally, Sr2 confers moderate levels of resistance against Ug99 (generating an approximate 30% reduction in disease severity); however, strong resistance can be achieved when it is combined with other unknown genes, such as the Yr30, Lr27 and Pbc genes of the Sr2-complex. These Sr2-complex resistance genes are currently effective against all isolates of Pgt throughout the wheat-growing regions of the world [130].

Stem rust resistance gene Sr13 was first identified in the germplasm of Triticum dicoccon (emmer or Khapli wheat) but is also present in several Triticum durum cultivars [77]. Sr13 is located on the long arm of chromosome 6A. Sr22 is located on the long arm of chromosome 7A [106]. Hexaploid lines with Sr22 are partially effective in producing resistance to Ug99 [107]. The stem rust resistance genes Sr25 and Sr26 were derived from the common wheat Agropyron elongatum and are located on chromosome segments 7DL and 6AL, respectively [34,109]. The resistance gene Sr35 was originally

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**Table 4.** List of stem rust resistance genes effective against Ug99 race (P. graminis f. p. tritici) with their sources, chromosomal locations and presence in existing cultivars worldwide.

| Gene | Source | Chromosomal location | Cultivars with country of origin | Reference |
|------|--------|----------------------|--------------------------------|-----------|
| **A. Seedling resistance gene** | | | | |
| Sr13 | Triticum dicoccon Triticum durum Triticum turgidum | 6AL | K hapli | [89,104,105] |
| Sr22 | Triticum monococcum | 7AL | Sebatel, Boohai (Ethiopia) | [106-108] |
| Sr25 | Agropyron elongatum | 7DL | | [34,47,109] |
| Sr26 | Agropyron elongatum | 6AL | Eagle (Australia) | [34,109,110,111] |
| Sr27 | Secale cereale | 3A | | [112] |
| Sr28 | Triticum aestivum | 2BL | | [95,100,113] |
| Sr32 | Aegilops speltoides | 2A, 2B, 2D | | [87,95,114-116] |
| Sr33 | Aegilops tauschii | 1DS | | [95,117,118] |
| Sr35 | Triticum monococcum | 3AL | | [34,95] |
| Sr37 | Triticum timopheevii | 4BL | | [118,119] |
| Sr39 +Lr35 | Aegilops speltoides | 2B | Canadian cultivars | [34,110,102,120,122] |
| Sr40 | Triticum timopheevii ssp. araraticum | 2BS | | [34,95,121,122] |
| Sr42 | Triticum aestivum | 6DS | | [92] |
| Sr44 | Thinopyrum intermedium | 7DS | | [95,122] |
| Sr45 | Aegilops tauschii | 1DS | | [112,117] |
| Sr46 | Aegilops tauschii | 2DS | | [99,112] |
| Sr47 | Aegilops speltoides | 2BL | | [91,123] |
| Sr51 | Aegilops searsii | 3A | | [96] |
| Sr52 | Dasyypyrum villosum | 6AL | | [124] |
| Sr53 | Aegilops geniculata | 5DL | | [96] |
| **B. Adult plant resistance genes** | | | | |
| Sr2+Lr27+Yr30 | Triticum aestivum Triticum turgidum | 3B | Hope, Sebatel (Ethiopia) | [87,113,125–127] |
| Sr25+Lr67+Yr46+Pm46 | | 4DL | RL 6077 | |
| Sr57+ Lr34+Yr18+Pm38 | | 7DS | Parula | [128] |
| Sr58+ Lr46+Yr29+Pm39 | | 18L | Pavon 76 (Mexico), Lalbahadur (India) | [88] |
transferred from *Triticum monococcum* to hexaploid wheat [36] and is effective against the TTKSK (*Ug99*) race of *P. graminis* f. sp. *tritici* [64] and its variants. This gene was mapped to the long arm of chromosome 3AL. The *Sr40* gene, located on chromosome 2BS, was transferred from *Triticum timopheevii* ssp. *araraticum* to hexaploid wheat [34,96,121,122].

**DNA markers and identification of rust resistance genes (Lr, Sr)**

The MAS has produced very favourable results in facilitating new gene deployment and gene pyramiding for quick release of rust-resistant cultivars. In contrast, gene pyramiding using conventional methods is difficult, time-consuming and requires concurrent tests of the same wheat breeding materials with several different rust races before making a selection [131]. It is not feasible for a regular breeding programme to maintain all necessary rust races needed for this type of work [132]. However, with the advent of MAS, gene pyramiding, in which genes identified in different genotypes are deployed into a single cultivar that contains the desired alleles at more than one locus, has become efficient [133]. Selectively neutral markers, such as isozymes or more recently developed types of molecular markers, such as random amplified polymorphic DNA (RAPD), simple sequence repeat (SSR) markers and amplified fragment length polymorphism (AFLP), can also be used to characterize and compare rust populations [134]. Molecular markers such as STS or SCAR and CAPS are available for the leaf rust resistance genes *Lr1, Lr9, Lr10, Lr19, Lr21, Lr24, Lr25, Lr28, Lr29, Lr34, Lr37, Lr39, Lr47* and *Lr51* [1] (Table 5). An enzymatic marker (endopeptidase Ep-D1c) for *Lr19* has also been developed [135]. Microsatellite (SSR, single sequence repeats), restriction fragment length polymorphism (RFLP), and AFLP markers have been developed for *Lr* genes, including *Lr2, Lr22* [32], *Lr3bg, Lr18, Lr40, Lr46* and *Lr50* [136]. The STS marker was first developed by Schachermayer et al. [43] for the *Lr9* gene derived from *Aegilops umbellulata*. Currently, numerous leaf rust resistance genes, including *Lr1, Lr10, Lr13, Lr16, Lr19, Lr20, Lr21, Lr24, Lr25, Lr26, Lr28, Lr29, Lr35, Lr34, Lr37, Lr39, Lr46, Lr47, Lr50, Lr51* and *LrW*, have been identified using the STS, SCAR and CAPS markers (Table 5) [48,50,60,61,65,110,137-140]. The leaf rust resistance genes *Lr1* [141], *Lr10* [142] and *Lr21* [143] have been isolated by cloning and sequenced. Molecular markers are also available for stem rust resistance genes, such as *Sr2* [144], *Sr9a* [145], *Sr22* [146,147], *Sr24, Sr26, Sr31, Sr36* and *Sr39* [22] (Table 6). Several DNA markers linked to various stem rust resistance genes in wheat have been identified and developed. For example, STS, SSR, and CAPS molecular markers have been developed for the identification of the seedling resistance genes *Sr22* [107,108], *Sr24* [47,148], *Sr25* [102,128] *Sr26* [47,102], and *Sr46* [109] and the APR gene *Sr2* [111,144] (Table 6). Microsatellite markers are closely linked to the resistance genes *Sr6* [107,112] and *Sr40* [8]. The STS marker has been used to detect the stem rust resistance genes *Sr22* [106] and *Sr24* [148], and the SCAR markers have been used to detect the *Sr39* gene in Canadian wheat [149]. Improved DNA markers were identified for the stem rust resistance genes *Sr13, Sr21, Sr22, Sr28, Sr33, Sr35, Sr42, Sr44, Sr45, Sr55, and Sr56*. In addition to these, more markers have been developed to identify several stem rust resistance genes, such as *Sr9a* [145], *Sr35* [150], *Sr36* [151], *Sr38* [152], *Sr40* [153], *SrCad* [154], *SrWeb* [124], *Sr51* [97], *Sr52* [124], and *Sr53* [65] (Table 6).

**Table 5.** List of leaf rust resistance genes and molecular methods used to identify them.

| Genes | Molecular methods | References |
|-------|-------------------|------------|
| *Lr1, Lr10, Lr13, Lr19, Lr20, Lr21, Lr24, Lr25, Lr28, Lr29, Lr34, Lr37, Lr39, Lr47, Lr51* | RFLP, STS, SCAR and CAPS | [22,41,42,47,155,156-159] |
| *Lr46* | AFLP, STS, SCAR and CAPS | [48,50,65,140,160] |
| *Lr27, Lr25* | RAPD, SCAR, STS and CAPS | [50,63] |
| *Lr16, Lr20, Lr35, Lr47, Lr51, Lr21, Lr39, Lr26, Lr50* | STS, SCAR and CAPS | [34,36,48,45,50,56-59,65] |
| *Lr7, Lr67, Lr3bg, Lr18, Lr40, Lr46, Lr50, Lr52 or LrW, and Lr53* | Microsatellites (SSR), and AFLP | [51,146,136] |
| *Lr9* | RFLP cMW 684, STS, RAPD, RFLP PSR 546 | [34] |
| *Lr19* | RFLP, RAPD, STS, SCAR and CAPS | [13,60,61] |
| *Lr24* | RFLP PSR 1205, PSR 1203, PSR 388, PSR 904, PSR 931, PSR 1067 RAPD | [43,62,60] |
| *Lr29* | RAPD, DGGE, STS, SCAR and CAPS | [61,63] |
| *Lr28* | RAPD OPJ-01, STS, SCAR and CAPS | [13] |
| *Lr14* | AFLP | [78] |
| *Lr23, Lr27, Lr31, Lr34, Lr13, Lr35, Lr53* | RFLP | [37,69,155] |
| *Lr25, Lr29* | RAPD, DGGE | [63] |
| *Lr51* | RFLP, STS | [43] |
| *Lr59, Lr62* | Microsatellites, SCAR | [74] |
| *Lr68* | SSR | [52] |
| *trp-1, trp-2* | SSR, AFLP | [39] |
| *Lrac104, Lrac124* | | [40] |
The concept of durable resistance was initially introduced by Johnson [165,166] and defined as 'resistance that remains effective when deployed over extensive acreage and time, in an environment favorable for the disease'. Therefore, durable resistance remains effective after widespread deployment over a considerable period of time. This type of resistance is mainly associated with minor genes, also known as slow rusting genes, and is generally controlled by more than one gene during the adult-plant stage rather than the seedling-resistant stage, and shows non-HRs to infection [22]. In wheat cultivars, the presence of a single resistance gene is generally less effective for controlling rust disease, whereas the combination of two or more genes enhances resistance durability. The genetic basis of durable resistance is the additive effect of partially resistant minor genes, and it is usually polygenic in nature and active in the adult-plant stage [22]. A group of CIMMYT germplasms involving 10–12 different genes were developed by pyramiding 4–5 minor genes; this resulted in a degree of resistance against rust that approaches immunity [22]. The Pakistani variety Lyalpur 73 and the South American wheat cultivar are good examples of durable resistance varieties that were developed over 50 years ago and remain rust resistant almost everywhere in the world.

### Genetic studies of stripe rust resistance genes

Stripe or yellow rust caused by *Puccinia striiformis* f. *Tritici* Eriks is also a destructive disease of wheat and can cause significant yield losses during severe epidemics due to reductions in kernel number and size [164]. Yield losses of up to 100% have been recorded in severe epidemics; however, yield losses between 10 and 70% are more common [134]. The pathogen *Puccinia striiformis* f. *Tritici* Eriks is highly aggressive and variable, quickly evolving new races that overcome existing resistance [134]. Historically, stripe rust was widespread in the northwestern USA, and infection has typically been associated with cool weather conditions, although new races tolerant to higher temperatures were recently identified [134,165], which presents a great threat to spring wheat-production areas. Currently, more than 49 stripe rust resistance genes [26], designated Yr1 to Yr49, have been catalogued in different hexaploid bread, durum wheat, and wild species backgrounds. Most of the stripe rust resistance genes were derived from common wheat (*Triticum aestivum*), although some were derived from different wild species, such as *Triticum spelta album*, *Triticum dicoccoides*, *Triticum spelta*, *Secale cereale*, *Aegilops comosa*, *Aegilops ventricosa*, *Triticum tauschii* and *Haynaldia villosa* (Table 7).

### Concept and genetic basis of durable resistance genes

The concept of durable resistance was first introduced by Johnson [165,166] and defined as 'resistance that remains effective when deployed over extensive acreage and time, in an environment favorable for the disease'. Therefore, durable resistance remains effective after widespread deployment over a considerable period of time. This type of resistance is mainly associated with minor genes, also known as slow rusting genes, and is generally controlled by more than one gene during the adult-plant stage rather than the seedling-resistant stage, and shows non-HRs to infection [22]. In wheat cultivars, the presence of a single resistance gene is generally less effective for controlling rust disease, whereas the combination of two or more genes enhances resistance durability. The genetic basis of durable resistance is the additive effect of partially resistant minor genes, and it is usually polygenic in nature and active in the adult-plant stage [22]. A group of CIMMYT germplasms involving 10–12 different genes were developed by pyramiding 4–5 minor genes; this resulted in a degree of resistance against rust that approaches immunity [22]. The Pakistani variety Lyalpur 73 and the South American wheat cultivar are good examples of durable resistance varieties that were developed over 50 years ago and remain rust resistant almost everywhere in the world.

### Durable resistance breeding for the development of rust-resistant wheat cultivars

The APR genes *Lr12* [167], *Lr13* [156,168], *Lr22a*, *Lr22b* [169], *Lr34* [170,168], *Lr35* [171], *Lr37* [172], *Lr46* [173], *Lr67* [51,154], *Lr68* [52], *trp-1* and *trp-2* [40] are considered durable resistance genes. Among these genes, *Lr13* and *Lr34* appear to be the main source of durable leaf rust resistance [168]. The combined effects of the adult resistance genes *Lr11*, *Lr12*, *Lr13*, *Lr22b*, *Lr35*, and *Lr37* have been reported in 55% of European wheat cultivars [18]. The combined effects of seedling resistance genes, such as *Lr16*, *Lr47*, *Lr19*, *Lr41*, *Lr21*, *Lr25* and *Lr29*, with APR genes, such as *Lr34*, *SV2*, *Lr46*, might explain the highly durable and effective leaf rust control that has been achieved in Argentinean wheat cultivars [45]. The combination of *Lr35* with seedling and/or other adult-plant leaf rust resistance genes should facilitate more efficient breeding for durable resistance [155]. Genes *Lr34*, *Lr46* and *Lr67* provide partial or slow resistance to

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### Table 6. List of stem rust resistance genes and different molecular approaches used to identify them.

| Genes | Molecular markers | References |
|-------|-------------------|------------|
| S52, S22, S24, S25, S26, S26, S26 and S46 | STS, SSR, CAPS | [47,107,108,109,110,111,114,148,150,161] |
| Sr31 | STS, SCAR | [59,162] |
| Sr29 | SCAR | [8] |
| Sr6, Sr40 | Microsatellite | [110,148,163] |
| Sr57+ Lr67+Yr46+ Pm46 | SNP | |
| Sr58+ Lr46+Yr29+Pm39 | STS, SNP | [128] |
| Sr48+ Lr67+Yr28+Pm46 | CAPS | [88] |

### Table 7. List of stripe rust resistance genes with their source species and chromosomal locations [34].

| Source | Genes with their chromosomal locations |
|--------|--------------------------------------|
| *Triticum aestivum* | Yr1(2AL), Yr2(7B), Yr3a<1(B), Yr4a<6(6B), Yr6(7BS), Yr7(2BL), Yr11,Yr12, Yr13, Yr14, Yr16(2D), Yr18 (7DS), Yr19(3B), Yr20(6D), Yr21(1B), Yr22(4D), Yr23(6D), Yr24(1BS), Yr25(1D), Yr27+Lr13(2BS), Yr29+Lr46(1BL), Yr30+Sr2+Lr27(3BS), Yr31(2BS), Yr32 (2BS), Yr41(2B) |
| *Triticum spelta album* | Yr5(2BL) |
| *Aegilops comosa* | Yr8(2D = T2DS-2M#1L2M#1S) |
| *Secale cereale* | Yr9(1RL. 1BS) |
| *Triticum spelta* | Yr10(1BL) |
| *Triticum dicoccoides* | Yr15(1BS) |
| *Aegilops ventricosa* | Yr17(2AS) |
| *Haynaldia villosa* | Yr26(6AS) (6AL.6VS) |
| *Triticum tauschii* | Yr28(4DS) |
leaf rust and are considered more durable than seedling resistance genes [173]. The mode of action of these genes is characterized by a longer latent period, lower infection frequency, smaller uredinia size, shorter period of sporulation and lower spore density [46]. Among these genes, Lr34 has been shown as not only durable but also capable of acting synergistically with other leaf rust resistance genes [174] in addition to having a pleiotropic effect on other diseases [157,161]. The combined effect of the leaf rust resistance gene Lr19 with the stem rust resistance gene Sr25 causes wheat flour to appear yellow and enhances the durability of leaf rust resistance in wheat cultivars [26]. When Sr2 is present alone, it does not provide a sufficient level of resistance; however, in combination with the Lr27 gene, it provides a desirable level of stem rust resistance in tall Kenyan cultivars such as Kenya plume and semi-dwarf CIMMYT cultivars Pavon F76, Parula, Kingbird, and Dollarbird [22]. Similarly, the combined effect of Lr34 and Yr18 in the Italian varieties Mentana and Ardito [175] has lead to effective durable resistance to stem rust. The combination of the leaf rust resistance gene Lr46 and the yellow rust resistance gene Yr29 is tightly linked and pleiotropic [160], producing durable and effective control for leaf rust [164].

Distribution of Lr genes in global wheat cultivars

Among the leaf rust resistance genes, Lr1, Lr3, Lr10 and Lr20 have been the most frequently identified and widely distributed genes in global wheat cultivars. The Lr1 and Lr2 are the most common leaf rust resistance genes in American soft red winter wheat [33,41]. The Lr20 gene dominates in African germplasms, followed by South American and Asian germplasms [176]. It is also very frequent in Ethiopian wheat germplasm [177] but is found at a very low frequency in North American and British wheat germplasms [178]. The Lr1, Lr10 and Lr20 genes are the most frequent in Europe, while Lr1, Lr3, Lr10 and Lr20 are found at higher frequencies in Oceania [176]. The Lr20 gene is very rare in Australian germplasm, American soft red winter wheat, and Argentinian germplasm [41,122]. The Lr1 gene has been most frequently recorded in Australian wheat cultivars, American hard red spring wheat, Mexican bread wheat, Chinese cultivars, and Indian and Pakistani wheat cultivars [122,179,180-182], while this gene is rare in Argentinian germplasm [45]. The Lr10 is very common in international winter wheat nurseries, Indian and Pakistani wheat cultivars, Mexican bread wheat, and Brazilian and Argentinian wheat cultivars [44,45,181–183]. Soft red winter wheat cultivars from the southeastern USA bearing the leaf rust resistance genes Lr9, Lr11, Lr18, Lr24 and Lr26 can be infected by selected races with virulence against these genes [184]. Similarly, the leaf rust resistance genes Lr3ka, Lr11, Lr24, and Lr26 have been recorded in hard red winter wheat cultivars from the southern Great Plains region of Texas, Oklahoma, and Kansas since the late 1980s. [185,186]. However, the Lr17 gene is most commonly identified in southeastern US, Great Plains, Ohio Valley, and California wheat cultivars in the USA, while the Lr16 gene is common in the north-central states in the USA, where spring wheat cultivars are grown. Lr16 is more effective than Lr17 against various virulent races of leaf rust disease [187]. Conversely, Lr24 is widely ineffective in North and South America and in South Africa but is effective in Australia and the Indian sub-continent [188] as well as in European wheat cultivars. The resistance genes Lr3a, Lr10, Lr13, Lr14a, Lr20, Lr26 and Lr37 are the most common in the modern European winter wheat germplasm [18]; specifically, eastern European wheat cultivars carrying Lr26 show good resistance against leaf rust disease and are therefore popular options [189]. The Lr3, Lr3ka, Lr3bg, and Lr26 genes are most frequently found in Western European wheat cultivars [190]. The Lr26 is most commonly found in Argentinean germplasm [45], British cultivars [178] and Chinese wheat germplasm. Due to its durable resistance ability, Lr13 is the most widely distributed Lr gene in world wheat cultivars [26]. The Lr13 was recorded in approximately 58% of European wheat genotypes either alone or in combination with other genes, and it is now ineffective in several countries, including Mexico [142]; however, it is still considered effective in cultivars from Australia [9,26], India [178], Brazil, Argentina and the United States [9] and also in cultivars derived from CIMMYT germplasms [182].

The genes Lr13, Lr24, Lr34, and Lr36 are the most common resistance genes among all Egyptian wheat cultivars [191]. Of the non-specific genes, the Lr34/Yr18 complex [192], Lr46 [130] and Lr67 [131] are the most commonly introduced genes in global wheat. The Lr34 gene has been present in Chinese, Italian, and South American varieties for much longer than the others [193]. The juvenile genes Lr25, Lr29, and Lr39 and APR genes Lr21, Lr35, and Lr37 (http://maswheat.ucdavis.edu/protocols) are not found in Russian varieties. However, more than 15% of winter and 40% of spring varieties in Russia are protected from leaf rust disease by the Lr10 gene [137]. Moreover, only one spring wheat, Trizo, was found to carry the Lr20 gene and was recommended for release as a variety in the Northwestern, Central, and Central Chernozem regions of Russia [39,194]. Lr53 [68], Lr54 [69], and Lr56 [161] have been recorded in spring wheat cultivars from Chinese origin and are closely linked with Yr35, Yr37, and Yr38, respectively, and Lr62 [162] was recorded in California wheat cultivars linked with the stripe rust resistance gene Yr42. The adult-plant leaf rust resistance genes Lr34,
**Global distribution of wheat cultivars containing the Sr gene**

The *Sr2* is present in approximately 60% of current CIMMYT spring wheat germplasms [101], including some high-yielding wheat varieties that also have high levels of resistance to leaf rust and stripe rust, as well as desirable end-use quality characteristics. Similarly, more than 50% of International Centre for Agriculture Research in the Dry Areas (ICARDA) and South African wheat germplasms have shown an SSR haplotype association with the durable stem rust resistance gene *Sr2* [195]. The combination of *Sr2* with the uncharacterized slow-rusting genes commonly known as the *Sr2*-complex has provided the foundation for durable resistance to stem rust in most parts of the world [126,196]. The stem rust resistance gene *Sr24* has effectively conferred resistance against most races of *Pgt* and is present in most commercial wheat cultivars worldwide [148,197]. More than 20% of the germplasms and elite lines of South African wheat carry *Sr24* as a major resistance gene [198]. The stem rust resistance genes *Sr25* and *Sr26* are effective against variants of *Ug99*, TTKST and TTTSK [87,95]. The stem rust resistance gene *Sr31* is very common in world wheat varieties. Before the emergence of *Ug99*, stem rust resistance was maintained mainly by *Sr31* in most countries around the world, except for Australia [101].

**Conclusions**

Knowledge regarding the characteristics and distribution of rust resistance genes is essential for developing new wheat varieties with resistance. Gene pyramiding through MAS and the use of different molecular approaches is essential for ensuring the sustainability of long-term resistance in wheat cultivars and for controlling these widespread and dangerous wheat diseases. Consolidating information on durable resistance varieties and their mechanisms for controlling rust disease, which is the focus of this paper, is also important for the development of new disease-resistant varieties with high-yielding capabilities. Overall, this work aims to support wheat researchers, students, academics, plant breeders and pathologists by enhancing understanding of the current state of the field of wheat research.

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**Disclosure statement**

No potential conflict of interest was reported by the authors.

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