



# Genetic and genomic approaches for breeding rust resistance in wheat

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**Abstract** Wheat rusts are considered major biotic stresses due to immense yield losses incurred by the rust pathogens. Continuous incursions and evolution among populations of rust pathogen have challenged several resistance genes deployed in wheat megavarieties. A substantial amount of wheat production is being saved by rust resistance wheat varieties. Breeding for rust resistance aimed to transfer potential genes in wheat elite lines and discover novel alleles to diversify resistance gene stock for future wheat breeding. This class of research was initiated worldwide after the discovery of mendelian genetics. Over a century, several genetic and genomic approaches were discovered and subsequently applied in wheat research to better understand the nature of rust pathogens and accordingly deployed major and minor rust resistant genes in combination in wheat varieties. Over 240 rust resistance genes have been catalogued and several alleles/QTL have been reported. Various statistical tools and consensus maps have been designed to precisely allocate novel alleles,

as well as known genes on the wheat physical map. With the advancement in genomics and next generation sequencing (NGS) technology, more than 20 rust resistance genes have been cloned in the last two decades. The mutational genomics approach was found competitive and parallel to modern NGS technology in isolating rust resistance loci. In this review, evolutionary trends of rust pathogens, source of rust resistance genes, methodology used in genetic and association mapping studies and available cutting-edge techniques to isolate disease resistance genes have been summarised and discussed.

**Keywords** Consensus map · Fine mapping · Genomics · GWAS · *Puccinia*

## Introduction

Common wheat is an allohexaploid with a vast genome size (~15.8 Gb). It constitutes 85 per cent of highly repetitive sequences (Wicker et al. 2018). The wheat genome was evolved through two continuous polyploidisation events accommodating three diploid progenitors (AA, BB, DD). Million years ago, wild tetraploid emmer wheat (AABB genome; *Triticum turgidum* ssp. *dicoccoides* L.) was originated after a primary hybridisation between two diploid AA (*T. urartu* L.) and BB (closely related to *Aegilops speltoides*, *Ae. longissima*, *Ae. sharonensis*, *Ae. searsii* and *Ae. bicornis*) genome progenitors (Jordan et al.

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2015; Avni et al. 2017). The derived emmer wheat (AABB) faced a secondary hybridisation around 10,000 years ago with the DD genome donor (*Ae. tauschii*). With the origin of agriculture, manifold changes had occurred in wheat biology (Preece et al. 2017). This resulted in the cultivation of domesticated wheat in the Fertile Crescent (Nevo et al. 2013) and led to the evolution of common wheat (Salamini et al. 2002).

Wheat production attains a milestone level of 761 million tons which supplies one-fifth of the total protein and calorific requirements of mankind (USDA 2020). Global wheat production should be increased around 60 to 70 per cent to feed 10 billion people by 2050 (Ray et al. 2013; Ranganathan et al. 2018). To meet the requirement, wheat production in developing countries needs to be double (Ray et al. 2013). The crop encounters numerous biotic and abiotic stresses that continuously challenge its sustainable production. Fungal diseases are considered one of the most serious threats. Rust diseases of wheat are of major concern due to the rapidly evolving nature of the fungal pathogens and their potential to adapt to diverse environments. It afflicts up to 30 per cent of wheat yield (Juliana et al. 2018). Potential losses from stem rust race Ug99 are three billion USD per year (Pardey et al. 2013) and annual yield losses due to stripe rust are estimated 5.47 million tonnes globally which is equivalent to 979 million USD (Beddow et al. 2015). Deployment of stripe rust resistant varieties in Australia alone has saved around one-billion-dollar annually (Murray and Brennan 2009).

#### Wheat rusts and their evolution

Three species of the genus *Puccinia* namely *Puccinia graminis* f. sp. *tritici* (Pgt), *Puccinia triticina* (Pt) and *Puccinia striiformis* f. sp. *tritici* (Pst) are the causal organisms for stem rust, leaf rust and stripe rust, respectively (Roelfs et al. 1992). A conducive environment is needed for the proliferation of rust inoculum and their dispersal occurs via wind (Singh and Rajaram 1992). Stem rust propagates well under warm and humid climates ( $\leq 30$  °C). However, leaf rust pathogen proliferates under 15–20 °C and humid condition. In contrast, most stripe rust races prefer a cool climate (12–20 °C) (Singh et al. 2011).

Incursion and evolution of rust pathogens stress to study of their evolutionary nature. Pathogens

have gained the capacity of migrating long-distance (Brown and Hovmøller 2002), mutational changes from avirulence to virulence (Hovmøller and Justesen 2007), acclimatise to fluctuating climatic conditions (Milus et al. 2009) and creating new variants through a sexual cycle and somatic hybridization (Ali et al. 2017). The evolutionary nature of rusts has been understood at a substantial level, answered and summarised by Jin et al. (2009), Singh et al. (2011), Patpour et al. (2018), Li et al. (2019) and Pinto da Silva et al. (2018).

#### Identification of rust resistance genes

##### *Multi-pathotype tests*

Comparison of infection types (ITs) produced by test entries against an array of pathotypes of the target rust pathogen on differential genotypes carrying known genes facilitates gene postulation (McIntosh et al. 1995). Several studies reported results on the postulation of rust resistance genes in different sets of wheat genotypes. For example, Singh et al. (2008) reported the presence of *Sr5*, *Sr8a*, *Sr9g*, *Sr12*, *Sr30*, *Sr31*, *Sr36* and *Sr38* in British wheat cultivars. Stem rust resistance genes *Sr7b*, *Sr8a*, *Sr8b*, *Sr9b*, *Sr9g*, *Sr11*, *Sr15*, *Sr17*, *Sr29*, *Sr31*, *Sr31*, *Sr36* and *Sr38* were reported in European wheat cultivars (Pathan and Park 2007). Similarly, *Sr5*, *Sr7a*, *Sr7b*, *Sr8a*, *Sr9e*, *Sr11*, *Sr21*, *Sr27*, *Sr29*, *Sr30* and *Sr37* have been postulated in Ethiopian durum and common wheat cultivars (Admassu et al. 2012). Randhawa et al. (2016) postulated the presence of *Sr7b*, *Sr8a*, *Sr12*, *Sr15*, *Sr17*, *Sr23*, *Sr30*, *Lr1*, *Lr3a*, *Lr13*, *Lr14a*, *Lr16* and *Lr20* either in combinations or singly among 87 Nordic spring wheat genotypes. DNA markers confirmed the presence of *Sr2*, *Lr34/Yr18/Sr57*, *Lr68* and *Yr48* in this collection (Randhawa et al. 2016). Singh and Rajaram (1992) postulated the presence of *Lr3*, *Lr10*, *Lr13*, *Lr26* and *Lr34* in CIMMYT wheat genotypes. A collection of European winter wheat carried *Lr1*, *Lr3a*, *Lr3ka*, *Lr10*, *Lr14a*, *Lr17b*, *Lr20*, *Lr26* and *Lr37* (Winzeler et al. 2000). Chinese wheat lines are likely to carry *Yr2*, *Yr3a*, *Yr4a*, *Yr6*, *Yr7*, *Yr9*, *Yr26*, *Yr27* and *YrSD* genes based on rust tests (Li et al. 2006). Two CIMMYT and one Australian wheat nurseries including 153 entries were screened against *Pst* pathotypes to postulate major and minor genes (Singh et al. 2014) and

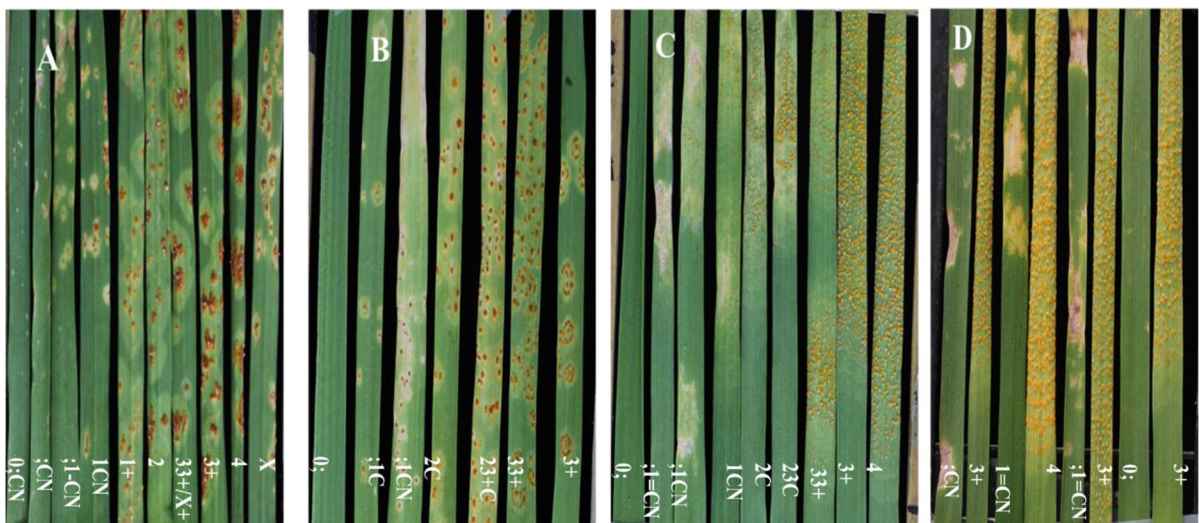
around half of the entries did not carry any effective ASR against Australian *Pst* pathotypes. *Yr6*, *Yr7*, *Yr9*, *Yr17* and *Yr27* were detected either singly or in combinations in these nurseries. Based on their resistance level, some entries were postulated to carry uncharacterised resistance genes and known APR genes *Yr18*, *Yr29* and *Yr30* (Singh et al. 2014). Figure 1 shows the range of rust reactions (immune to very susceptible) of a diversity panel screened against stem rust (A), leaf rust (B) and stripe rust pathotypes (C). For example, the test response of four genotypes against Pst110 E143A+ (all resistant(R); avirulent on *Yr9* and *Yr17*) and Pst134 E16A+17+27 (all susceptible(S); virulent on *Yr9* and *Yr17*) is shown in Fig. 1d. These differences revealed the presence of *Yr9* and/or *Yr17* in these entries.

#### Alien introgression from wild relatives

Diploid progenitors of wheat and wild relatives are the major contributors to the rust resistance gene pool. It has been argued to enhance the deployment of short alien segments in modern wheat to overcome the forbidden challenge posed by evolving rust fungi as the large alien segment is associated with yield penalty (Friebe et al. 1996; Qureshi et al. 2018a). Hybridization among species sharing homologous wheat genomes is feasible. It covers the primary

gene pool of common wheat and includes landraces, the cultivated and wild forms of *T. turgidum* L., and the diploid progenitors *T. monococcum* L. (AA), *T. boeoticum* (AA) and *T. urartu* (AA), and *Aegilops tauschii* (DD) (Sharma and Gill 1983). Several rust resistance genes namely *Sr2*, *Sr12*, *Sr13*, *Sr14*, *Sr21*, *Sr22*, *Sr35*, *Lr14a*, *Lr21*, *Lr22a*, *Lr23*, *Lr39*, *Lr53/Yr35*, *Lr61*, *Yr15*, *Yr28* and *Yr36* have been introgressed in wheat and their utilisation is under progress (McIntosh 1991; Marais et al. 2005a, b; Riar et al. 2012; Tables 1 and 2). The progress on marker development and characterization of some genes has been summarised in Table 2.

The secondary gene pool includes the *Triticum* and *Aegilops* species that share at least one homologous genome in common with common wheat. Gene transfer via homologous recombination from these species is possible if the target gene is also placed on a homologous chromosome. This group mainly includes the tetraploid species *T. timopheevii* Zhuk. and the diploid SS-genome species having *Aegilops* section *Sitopsis* (related to the B genome). This SS genome includes *Ae. sharonensis*, *Ae. speltoides*, *Ae. longissima*, *Ae. searsii* and *Ae. bicornis*, two tetraploid species *Ae. peregrina* (*Ae. variabilis*) and *Ae. kotschyi* and hexaploid *Ae. vavilovii*. This group offers various resistance genes namely *Sr32*, *Sr36*, *Sr37*, *Sr39/Lr35*, *Sr40*, *Lr28*, *Lr36*, *Lr51*, *Lr56/Yr38*



**Fig. 1** Rust reaction against different pathotypes **a** Pgt 34–1,2,3,6,7,8,9, **b** Pt 104–1,3,4,6,7,8,9,10,12+Lr37 and **c**, Pst 239 E237A-17+33+, **d** Contrasting rust reaction of

four genotypes against Pst 110E 143A+ (all resistant; CN, 0; ;1=CN) and 134E 16A+17+27 (all susceptible; 3+, 4), respectively

**Table 1** List of some outsourced wheat rust gene deployed in common wheat (*T. aestivum* L.)

SN	Outsourced wheat rust genes	Source/Origin	References
1	<i>Sr21<sup>#</sup></i> (2A <sup>ML</sup> ), <i>Sr22<sup>#</sup></i> (7AL), <i>Sr35<sup>#</sup></i> (3AL) and <i>SrTm4<sup>#</sup></i> (2AL) and <i>Lr63</i> (3AS), <i>Sr60</i> (5A <sup>MS</sup> )	<i>T. monococcum</i> L	Gerechter-Amitai et al. (1971), McIntosh et al. (1984), Kolmer et al. (2008) and Briggs et al. (2015)
2	<i>Sr33</i> (1DL), <i>Sr45</i> (1DS), <i>Sr46</i> (2DS), <i>SrTA10171<sup>#</sup></i> (7DS), <i>SrTA10187<sup>#</sup></i> (6DS), <i>SrTA1662<sup>#</sup></i> (1DS), <i>Lr21</i> (1DS), <i>Lr22a</i> (2DS), <i>Lr32</i> (3D), <i>Lr39</i> (2DS), <i>Lr40-42</i> (1D), and <i>Yr28</i> (4DS)	<i>Ae. tauschii</i> Coss	Kerber and Dyck (1979), McIntosh et al. (2014) and Olson et al. (2013a, b)
3	<i>Sr32</i> (2A, 2B), <i>Sr39/Lr35<sup>*</sup></i> (2B), <i>Sr47</i> (2BL), <i>Lr28</i> (4BL), <i>Lr36</i> (6BS), <i>Lr51</i> (1BL) and <i>Lr66</i> (3A)	<i>Ae. speltoidea</i> Tausch	McIntosh et al. (1995), Faris et al. (2008) and Chemayek et al. (2016)
4	<i>Sr36</i> (2BS), <i>Sr37</i> (4BL), and <i>Sr40</i> (2BS)	<i>T. timopheevii</i> (Zhuk.) Zhuk	McIntosh et al. (1971), Dyck (1992)
5	<i>Lr24/Sr24</i> (Ug99 susceptible; 3DL), <i>Lr29</i> (7DS) and <i>Sr25/Lr19<sup>**</sup></i> (7DL), <i>Sr26<sup>#</sup></i> (6AL)	<i>Agr.elongatum</i> (syn. <i>Thinopyrum ponticum</i> )	Mago et al. (2005a), Knott (1968), Sears (1973, 1977), McIntosh et al. (1977) and Jin et al. (2007)
6	<i>SrR</i> and <i>Sr31/Lr26/Yr9/Pm9</i> (Ug99 susceptible; 1BL)	<i>Secale cereale</i>	Mago et al. (2005b)
7	<i>Sr2<sup>#</sup>/Lr27/Yr30/Pbc1</i> (3BS) <i>Sr9d</i> (2BL; <i>Sr1</i> ) and <i>Sr17</i> (7BL)	<i>T. turgidum</i> var <i>dicoccoides</i> cv <i>Yaroslav</i>	McFadden (1930) and McIntosh (1988)
8	<i>Sr34/Yr8</i> (2A, 2D)	<i>T. comosa</i>	McIntosh et al. (1995)
9	<i>Sr38/Lr37/Yr17</i> (2AS)	<i>Ae. ventricosa</i>	Molnár-Láng et al (2015)
10	<i>Lr9</i> (6BL), <i>Lr76/Yr70</i> (5DS)	<i>Ae. umbellulata</i>	Bansal et al. (2017)
11	<i>Lr38</i> (2AL)	<i>Th. intermedium</i>	Riar et al. (2012)
12	<i>Lr57/Yr40</i> (5DS), <i>Sr53</i> (T5DL-5MgL-5MgS)	<i>Ae. geniculata</i>	Liu et al. (2011), Riar et al. (2012)
13	<i>Lr58</i> (2BL)	<i>Ae. triuncialis</i>	Molnár-Láng et al (2015)
14	<i>Yr15</i> (1BL), <i>Yr36</i> (6BS), <i>Yr84</i> (1BS), <i>Lr53/Yr35</i> (6BS) and <i>Lr64</i> (6AL)	<i>T. dicoccoides</i>	Marais et al. (2005a, b), Riar et al. (2012) and Klymiuk et al. (2022)
15	<i>Sr9f</i> (2BL), <i>Sr9g/Yr7</i> (2BL), <i>Sr11</i> (6BL; cv. Gaza), <i>Sr12</i> (3BS; cv. Iumillo)	<i>T. turgidum</i> var. <i>durum</i>	Knott and Anderson (1956), Sheen and Snyder (1964), McIntosh and Luig (1973) and Loegering (1975)
17	<i>Sr13</i> (6AL; cv. Khapli) <i>Sr14<sup>#</sup></i> (1BL; cv. Khapli), <i>Sr17</i> (7BL; cv. Yaroslav)	<i>T. turgidum</i> var. <i>dicoccum</i>	Knott (1962)
18	<i>Lr14a</i> (7BL), <i>Lr23</i> (2BS), <i>Lr61</i> (6BS), <i>Sr9e</i> (2BL, <i>SrV</i> ; cv. Bernalemmmer) <i>Srdp2</i>	<i>T. turgidum</i>	McIntosh and Dyck (1975), Herrera-Foessel et al. (2008) and Rondon et al. (1966)
19	<i>Lr62/Yr42</i> (6A)	<i>Ae. neglecta</i>	Marais et al (2008)
20	<i>Lr54/Yr37</i> (2DL)	<i>Ae. kotschy</i>	Marais et al. (2005b)
21	<i>Lr56/Yr38</i> (6AL)	<i>Ae. sharonensis</i>	Marais et al. (2010)
22	<i>Sr52</i> (T6AS.6 V#3L)	<i>Dasypyrum villosum</i> (L.) Candargy	Qi et al. (2011)
23	<i>Yr50</i> (4BL)	<i>Thinopyrum intermedium</i>	Liu et al. (2013)

<sup>#</sup> Ug99 resistant loci; <sup>\*</sup>Tight repulsion phase linkage with *Sr36*; <sup>\*\*</sup>Increasing Yield

and *Lr66* that are being deployed in wheat cultivar (McIntosh 1991; Marais et al. 2008, 2010; Tables 1 and 2).

Distantly related species do not have homology with the wheat. However, the *Ph1* (pairing homoeologous) gene, placed on chromosome arm 5BL,

ensures chromosomal pairing and recombination between homologous chromosomes in wheat (Riley and Chapman 1958). Other options are the transfer of whole chromosome arms, the centric breakage-fusion mechanism of univalents at meiotic metaphase I can be exploited (Sears 1950; Friebe et al. 1996).

**Table 2** List of markers associated with some outsourced wheat rust genes deployed in common wheat (*T. aestivum* L.)

SN	Genes	Associated markers	Approach	Nature of cloned genes	References
1	<i>Sr21</i>	<i>CJ961291</i> and <i>Cscnl20</i>	Map-based cloning	Coiled-coil, nucleotide-binding leucine-rich repeat protein (NLR)	Chen et al. (2018)
2	<i>Sr22</i>	<i>S22GMF</i> and <i>S22GMR</i>	MutRenSeq	NLR	Steuernagel et al. (2016)
3	<i>Sr45</i>	<i>S45F1/S45R1</i>	MutRenSeq	NLR	Steuernagel et al. (2016)
4	<i>Sr35</i>	<i>AK331487</i> and <i>AK332451</i>	Map-based cloning	NLR	Saintenac et al. (2013)
5	<i>Sr33</i>	<i>BE405778</i> and <i>BE499711</i>	Map-based cloning	NLR	Periyannan et al. (2013)
6	<i>Sr46</i> ; <i>SrTA1662</i>	<i>S46ConsFA</i> and <i>S46PREVR</i> ; <i>R1.F3</i> and <i>R1.R3</i>	AgRenSeq	NLR	Arora et al. (2019)
7	<i>SrTA10171</i> ; <i>SrTA10187</i>	<i>gdm88-F</i> and <i>gdm88-R</i> ; <i>6DS0027</i> and <i>6DS0039</i>	–	–	Olson et al. (2013a)
8	<i>Sr32</i>	<i>csSr32#1-F</i> and <i>csSr32#1-R</i>	–	–	Mago et al. (2013)
9	<i>Sr36</i>	<i>STM773-2F</i> and <i>STM773-2R</i>	–	–	Hayden and Sharp (2001)
10	<i>Sr39/Lr35</i>	<i>Sr39#22r-F</i> and <i>Sr39#22r-R</i>	–	–	Mago et al. (2009)
11	<i>Sr47</i>	<i>gpw4043-F</i> and <i>gpw4043-R</i> ; <i>gpw4165-F</i> and <i>gpw4165-R</i>	–	–	Klindworth et al. (2012)
12	<i>Sr24/Lr24</i>	<i>Sr24#12-F</i> and <i>Sr24#12-R</i>	–	–	Mago et al. (2005a)
13	<i>Sr25/Lr19</i>	<i>PSY-E1</i> and <i>PSY-D1</i>	–	–	Zhang and Dubcovsky (2008)
14	<i>Sr26</i>	<i>sunKASP_224</i> and <i>sunKASP_225</i>	–	–	Qureshi et al. (2018a)
15	<i>Sr31/Lr26/Yr9/Pm9</i>	<i>iag95-F</i> and <i>iag95-R</i>	–	–	Mago et al. (2002, 2005b)
16	<i>Sr2/Lr27/Yr30/Pbc1</i>	<i>csSr2-F</i> and <i>csSr2-R</i>	–	–	Mago et al. (2011)
17	<i>Sr50</i>	<i>Sr50-5p-F3</i> and <i>Sr50-5p-R2</i>	Comparative genomics and complementation tests	CNL	Mago et al. (2015)
18	<i>Sr60</i>	<i>ucw530</i> and <i>ucw540</i>	Map-based cloning	<i>wheat tandem kinase2</i>	Chen et al. (2020)
19	<i>Sr38/Lr37/Yr17</i>	<i>Ventrip</i> and <i>LN2</i>	–	–	Helguera et al. (2003)
20	<i>Sr53</i>	<i>Xbe442600</i> and <i>Xbe443201</i>	–	–	Liu et al. (2011)
21	<i>Sr12</i>	<i>IWA610</i> and <i>IWA537</i>	–	–	Hiebert et al. (2016)
22	<i>Sr13</i>	<i>cnl2</i> and <i>CJ641478</i>	Map-based cloning	CNL	Zhang et al. (2017)
23	<i>Sr52</i>	<i>BE497099-STS-F</i> and <i>BE497099-STS-R</i>	–	–	Qi et al. (2011)
24	<i>Lr21</i>	<i>KSUD14</i> , and <i>KSU936</i>	Map-based cloning	CNL	Huang et al. (2003)
25	<i>Lr22a</i>	<i>SWSNP4</i> and <i>SWSNP6</i>	Targeted chromosome-based cloning via long-range assembly (TACCA)	CNL	Thind et al. (2017)



**Table 2** (continued)

SN	Genes	Associated markers	Approach	Nature of cloned genes	References
26	<i>Lr51</i>	<i>S30-13L and AGA7-759R</i>	–	–	Helguera et al. (2005)
27	<i>Lr76/Yr70 and Lr57/Yr40</i>	MAS-CAPS16	–	–	Kuraparthi et al. (2009); Bansal et al. (2017)
28	<i>Lr23</i>	<i>sunKASP_16</i>	–	–	Chhetri et al. (2017)
29	<i>Yr15</i>	<i>kinI and kinII</i>	Map-based cloning	<i>wheat tandem kinase 1</i>	Klymiuk et al. (2018)
30	<i>Yr84</i>	<i>usw312-usw317</i>	–	–	Klymiuk et al. (2022)
31	<i>Yr36</i>	<i>Xucw129 and Xucw148</i>	Map-based cloning	<i>kinase-START gene protein</i>	Fu et al. (2009)

When a univalent of homoeologous wheat chromosome and alien target chromosome are together, chances of recovery of compensating whole-arm translocations are high (Marais and Marais 1994). To introgress smaller non-homologous alien segments, Sears (1956) preferred ionizing radiation treatment to cause chromosome breaks followed by transferring a novel *Lr* gene from *Ae. umbellulata* Zhuk. to wheat. Another approach is to disrupt the normal meiotic chromosome pairing of wheat using a high pairing line of *Ae. speltoides* Tausch followed by introgression of *Yr* gene from *Ae. comosa ssp. comosa* Sm. to wheat through induced homoeologous recombination (Riley et al. 1968a, b). Successful transfer of the alien segments can be confirmed by meiotic-chromosome pairing, phenotypic assays, monosomic analysis, telocentric mapping, C-banding and genome-in-situ hybridization (GISH) (Friebe et al. 1996).

#### Genetic analysis of rust resistance

Host resistance has been categorised into two broad classes: ASR/qualitative resistance and APR/field resistance/quantitative resistance (Bariana 2003; Bariana et al. 2007). ASR is conditioned by major genes (R) effective from seedling to adult plant stage and this type of resistance is often matched by virulence in the corresponding pathogen. In contrast, APR is governed by minor genes effective at the post-seedling stages and it generally retards pathogen development and is hence referred to as partial resistance/slow rusting. It is assumed to be race non-specific (Bariana et al. 2007). However, some APR genes express hypersensitive responses at adult plant stages

and show pathotypic specificity, for example, *Lr22b* (McIntosh et al. 1995).

The resistant parent (carrying ASR and/or APR) is crossed with a susceptible parent to develop a biparental population to determine the inheritance of resistance and genomic location of the underlying resistance gene(s). Although several studies involved tests on individual F<sub>2</sub> plants, tests on F<sub>3</sub> families are preferred for their amenability for checking the reproducibility of results (Bariana 2003). Population advancement to the F<sub>6</sub> generation can be conducted through the single seed/head method to create recombinant inbred lines (RILs) and alternatively the doubled haploid approach (Ahmed and Trethowan 2020). F<sub>3</sub> populations carrying ASR gene(s) are classified into three categories using phenotypic responses: 1. homozygous resistant (HR), 2. segregating (Seg) and 3. homozygous susceptible (HS) and phenotypic data are subjected to Chi-squared analysis to determine the number of resistance loci controlling the target trait. An F<sub>3</sub> population can be used for preliminary genetic analysis, however, a good number of seeds is required to study the segregation pattern. A RIL population has an advantage over an F<sub>3</sub> generation as RILs are fixed after many recombination events and few seeds are needed for genetic analysis and it allows endless screening for different traits segregating among the target population. The segregation ratios for the involvement of a different number of genes are listed in Bariana (2003). Wright's formula is used to estimate the number of loci governing rust resistance based on phenotypic evaluation under field conditions (Wright 1968).

The presence of more than one gene in a biparental population requires the development of

single gene segregating populations to precisely locate genes conferring resistance. For example, an  $F_3$  family of Aus27858/Westonia showed segregation of two seedling stripe rust resistance genes (Randhawa et al. 2014, 2015). Families showing single gene segregation based on ITs were advanced separately to generate  $F_6$  RIL populations. Molecular mapping of two  $F_6$  RILs revealed two new ASRs; *Yr51* (;n-;1-nn) on chromosome arm 4AL (Randhawa et al. 2014) and *Yr57* (0; ) on 3BS (Randhawa et al. 2015). Australian wheat cultivars Sunco and Kukri expressed a high level of stripe rust resistance (Bariana et al. 2001). Two  $BC_1F_2$  populations derived from each cultivar and a common susceptible parent Avocet 'S' confirmed the presence of three independent loci each (1HR:6Seg:1HS) in Sunco and Kukri. The wheat cultivar Sunco was reported to carry *Yr18* (Kolmer et al. 2008) and *YrCK* (Bariana et al. 2001) on chromosome 2D. To map the third gene, a Sunco/2\*Avocet S-derived  $BC_1F_2$  line SA65 (a resistant line) was crossed with a susceptible sib (SA67) and 123 RILs of cross SA65/SA67 was generated (Bariana et al. 2016). Monogenic segregation among derived RILs was demonstrated and the resistance locus was named *YrSA3*. Further selective genotyping using a 90 K SNP array and SSRs placed the *YrSA3* gene on chromosome 3D and was catalogued as *Yr71* (Bariana et al. 2016).

Developing bi-parental mapping population using parents showing moderate resistant to moderate susceptible reaction can help to detect transgressive segregant. Chhetri et al. (2016) developed a low-resolution RIL population from a cross of W195 with BTSS. This population expressed transgressive segregation for each rust confirmed the contribution of both parents. Another phenomenon is known as segregation distortion where the segregation of individual alleles does not follow the mendelian inheritance. For instance, QTL *QYr-3BL* detected in durum wheat Stewart, on chromosome arm 3BL showed distorted segregation in  $F_2$  and later generations of cross Stewart/Bansi (Li et al. 2020a). Markers associated with the *QYr-3BL*-Stewart allele were overrepresented compared with the *QYr-3BL*-Bansi allele in  $F_5$  families and the 4:1 segregation ratio was observed instead of the expected 1:1 ratio (Li et al. 2020a). The same region of chromosome 3BL also harboured powdery mildew locus *Pm41* which expressed a preferential inheritance of the susceptible locus of tetraploid

emmer Langdon in a cross Langdon×IW2 (Li et al. 2009). However, *Yr80* and *Yr82* loci detected on the same arm showed mendelian inheritance (Nsabiyeera et al. 2018; Kandiah et al. 2019).

Mapping populations segregating for *Yr34* (synonym *Yr48*) showed suppression of recombination in the distal region of chromosome arm 5AL (Lowe et al. 2011; Lan et al. 2017; Qureshi et al. 2018b). This kind of suppression may occur due to inverted chromosomal segments or alien introgression. Lan et al. (2017) reported a slight segregation distortion for *Yr48* and comparatively more representation of markers linked to the resistance allele (67% vs. expected 50%). Chen et al. (2021) confirmed that restricted recombination events in the *Yr34*-carrying population occur due to the distal translocation of chromosome arm 5AL of *T. monococcum* into common wheat. Segregation distortion among outsourced rust resistance genes namely *Lr53/Yr35* (Marais et al. 2005a), *Lr54/Yr37* (Marais et al. 2005b), *Lr19* (Prins and Marais 1999) and *QYrtb.pau-5A* (Chhuneja et al. 2008) were also observed.

## Mapping of rust resistance genes

### *Bi-parental mapping*

Precise mapping of rust resistance loci became more convenient with the availability of high throughput genotyping platforms including DArTseq (<http://www.diversityarrays.com>), genotyping-by-sequencing (Poland and Rife 2012) and SNP arrays including 90 K (Wang et al. 2014), 820 K (Winfield et al. 2015), 660 K (Cui et al. 2017) and 35 K chips (Allen et al. 2017). These platforms are frequently used for bulked segregant analysis (BSA; Michelmore et al. 1991), selective genotyping (SG; Lebowitz et al. 1987) and whole population genotyping. For BSA, equal amounts of genomic DNA from 20 resistant and 20 susceptible RILs is pooled separately to constitute resistant and susceptible bulks, respectively. DNA samples from up to forty randomly selected RILs should also be pooled to prepare an artificial  $F_1$  sample. One  $\mu$ g DNA sample of both parents, the constituted resistant and susceptible bulks and an artificial  $F_1$  sample are being used for genotyping using the 90 K SNP array to detect linkage of resistance loci and their position in the wheat genome. GenomStudio software (Illumina Ltd) is being used in

detecting putatively linked SNPs using their normalised theta value (Wang et al. 2014). Associated SNPs can be converted into kompetitive allele-specific PCR (KASP) assays using the bioinformatics pipeline, Polymarker (<http://www.polymarker.info>). The KASP assay includes two allele-specific forward primers that are labelled with specific sequences that correspond to two universal fluorescence resonant energy transfer (FRET) cassettes labelled with FAM™ and HEX™ dye and a common reverse primer (<http://www.lgcgroup.com>). It allows accurate bi-allelic discrimination of known SNPs. The BSA was used to map major genes, for example, *Sr49* (Bansal et al. 2015), *Yr47* (Bansal et al. 2011), *Yr51* (Randhawa et al. 2014) and *Yr57* (Randhawa et al. 2015). It was also used in saturating the *Lr79*-region (Qureshi et al. 2018c) and SG to map the APR gene *Yr71* (Bariana et al. 2016). Polymorphic markers can be recommended to deploy targeted genes in the wheat background.

Several software programs namely QTL IciMapping (Meng et al. 2015), Map Manager QTX20 (Manly et al. 2001) are routinely being used in gene mapping using putatively linked markers and phenotypic responses using the Kosambi and Haldane mapping function (Haldane 1919; Kosambi 1943). A map chart can be used to draw the genetic map (Voorrips 2002).

Sixty genes for stem rust, 80 for leaf rust and 83 for stripe rust resistance has been catalogued using bi-parental populations (McIntosh et al. 2017; Li et al. 2020b). In a study, a Portugees landrace Aus27969 expressed a high level of stripe rust resistance at the seedling and adult plant stage in the field. Kandiah et al. (2019) observed monogenic segregation at the seedling stage against three *Pst* pathotypes in the Aus27969/AvS RIL population. The BSA using the 90 K SNP Infinium array placed this locus on chromosome arm 3BL. The seedling gene was catalogued as *Yr82* and linked markers were identified.

Many methods namely Single-Marker Analysis (SMA), Composite Interval Mapping (CIM) and Multiple Interval Mapping (MIM) have been reported for QTL mapping (Bernardo 2020). However, the CIM function of QTL Cartographer was frequently used and offered a platform to align genome-wide markers and phenotypic data together to detect resistance gene loci using default parameters (Wang et al. 2012).

Several studies focus on mapping QTL underpinning rust resistance (Rosewarne et al. 2013;

Maccaferri et al. 2015; Babu et al. 2020). A RIL population from a cross of the CIMMYT line Arableu#1 (source of APR) and Apav#1 (susceptible line) was derived to identify QTL for leaf rust and stripe rust (Yuan et al. 2020). Further QTL analysis detected four and six genomic regions governing leaf rust resistance and stripe rust resistance, respectively. A new pleiotropic locus *QLr.cim-1BL.2/QYr.cim-1BL.2* was reported that is 37 cM (~6 Mb) far from the known pleiotropic APR locus *Lr46/Yr29*. They found *QLr.cim-3DS*, *QYr.cim-2AL*, *QYr.cim-4BL*, *QYr.cim-5AL*, and *QYr.cim-7DS* as putatively new loci after comparing them with the published literature (Yuan et al. 2020).

#### *Consensus maps and their application in fine mapping and cloning of rust resistance genes*

Integration of known stripe rust resistance loci resulted in two consensus maps (Rosewarne et al. 2013; Maccaferri et al. 2015). The first map included 49 chromosomal regions covering 140 stripe rust resistance QTL from thirty bi-parental mapping studies (Rosewarne et al. 2013). The second map incorporated 56 stripe rust resistance genes and 169 QTL from ten Genome wide association studies (GWAS; Maccaferri et al. 2015). Similarly, a consensus map of stem rust resistance loci was drafted that included 24 bi-parental populations, two backcross populations and three association mapping panels (Yu et al. 2014). This study identified 141 stem rust resistance loci effective against Ug99 and reported linked markers. In more than 50 publications, 80 QTL for leaf rust and 119 QTL for powdery mildew were reported on 16 and 21 chromosomes, respectively (Li et al. 2014). Eleven loci on 10 chromosome arms (1BS, 1BL, 2AL, 2BS, 2DL, 4DL, 5BL, 6AL 7BL and 7DS) showed potential pleiotropic effects including known multi-pathogenic resistance genes *Lr34/Yr18/Sr57*, *Lr46/Yr29/Sr58*, *Lr67/Yr46/Sr55* and *Lr27/Yr30/Sr2* (Li et al. 2014).

Genetic mapping of an individual gene is usually carried out in low-resolution populations. To delimit the gene region, a high-resolution family (HRF) is the prerequisite. HRF can help to develop closely linked markers (<0.1 cM) (Singh and Singh 2015). Flanking markers from the low-resolution mapping are tested for initial screening of a large population, preferably F<sub>2</sub> or backcross population. Progeny testing of these



individuals helps in confirming marker positions. Screening of recombinants with additional markers specific to underlying candidate genes can offer a platform to initiate cloning work (Periyannan et al. 2013; Klymiuk et al. 2018; Zhang et al. 2019). A high level of sequence similarity between homoeologous genomes (95–99% in coding sequences) and over 80% of repetitive DNA had posed challenges to clone rust resistance genes in wheat (Borrill et al. 2015). To fine map and clone a gene, several modern genomic approaches amenable to sequence similarity and repetitiveness in the wheat genome have been undertaken (Keller et al. 2018; Steuernagel et al. 2020).

A comparative study of DNA markers in related taxa originated from a similar ancestor and their arrangement in different maps is known as comparative mapping (Singh and Singh 2015). An orthologous and conserved marker, especially complementary DNA sequences (cDNA) across the taxa, are more useful in a comparative mapping. This can reveal genome organisations of diploid progenitors and common wheat. The orthologous genes and conserved marker sequences located in the same chromosome is referred to as synteny. However, the arrangement of DNA markers in the same linear order in two different chromosomes of the same or different species is termed collinearity (Singh and Singh 2015).

The orthologous region of *Brachypodium distachyon* L. was used in developing a high-resolution map of *Lr52/Yr47* (Qureshi et al. 2017). The *B. distachyon* and related genera *Oryza sativa* L. and *Sorghum bicolor* L. were explored in a collinearity study to saturate the *Yr15*-region flanked by markers *uhw264* and *uhw258* (Klymiuk et al. 2018). Gene annotation studies using *Ae. tauschii* genomic resources inferred *NLR1* as *Lr22a* (Thind et al. 2017). To saturate the pleiotropic APR *Lr67*-region, additional markers were designed using conserved orthologs and its collinear sequences in *B. distachyon* and *O. sativa* (Moore et al. 2015). A high-density map of *Yr36* was drafted using collinear gene regions in *O. sativa* that confirmed the gene to be in a 0.14 cM interval spanned by markers *ucw113* and *ucw111* (Fu et al. 2009). Similarly, collinear region sequences of *B. distachyon* were used to narrow down the *Sr35*-region with markers *AK331487* (0.02 cM proximal) and *AK332451* (0.98 cM distal) (Saintenac et al. 2013).

To reduce genome complexity, the chromosome flow-sorting technology (Vrána et al. 2012) was

employed to dissect individual chromosomes based on their relative DNA content followed by their sequencing individually. A high-resolution map of *Lr49* was prepared using this approach (Nsabiyaera et al. 2020). The largest wheat chromosome 3B was separated easily with this approach, however isolation of the remaining chromosomes was challenging due to similar sizes (Shatalina et al. 2013). Wide application of chromosomes specific labelled repetitive DNA as a probe assisted in isolation of 21 bread wheat and seven barley chromosomes, individually (Giorgi et al. 2013). Sánchez-Martín et al. (2016) demonstrated the importance of flow cytometry-based chromosome sorting of derived mutants followed by alignment of their sequences as a robust and unbiased approach for reduction of genome complexity.

The whole-genome shotgun (WGS) approach has assembled ‘long’ sequence reads using 454 technology and published the first draft sequence of the wheat genome in 2012 (Brenchley et al. 2012). However, this approach failed to overcome the sequence similarity issues between homoeologous genomes and their mis-assembly. Another WGS approach using large-insert sequencing libraries was undertaken to draft assemblies of each of the three homoeologous genomes of synthetic hexaploid wheat ‘Synthetic W7984’ (Chapman et al. 2015). These large insert genomic libraries or Bacterial Artificial Chromosome (BAC) libraries represented in-depth genome coverage and have been used in the cloning of *Yr36* (Fu et al. 2009), *Sr33* (Periyannan et al. 2013), *Sr35* (Saintenac et al. 2013), *Sr50* (Mago et al. 2015) and *Yr15* (Klymiuk et al. 2018). Mascher et al. (2013) have anchored both CSS and W7984 scaffolds into a high-density genetic map using population sequencing (POPSEQ). In POPSEQ, several individuals from a bi-parental population were sequenced to low coverage (c.1.5x) followed by SNP calling to parental lines and in silico mapping of the sequenced contigs associated with the identified SNPs. Through the POPSEQ analysis, 80–90 doubled haploid individuals of synthetic W7984 x Opata M85 (Sorrells et al. 2011) were anchored on a high-density genetic map covering 4.5 Gb (CSS) and 7.1 Gb (W7984) of the wheat genome. POPSEQ relies on meiotic recombination that occurs frequently in the distal ends of wheat chromosomes (Anderson et al. 2006; Saintenac et al. 2009). Due to uneven recombination, POPSEQ generates a distorted assignment of scaffolds

concentrated in centromeric regions with much lower resolution than in the more recombinogenic distal regions of the chromosome. Over 600,000 SNPs from 820 K Axiom and 90 K iSelect SNP platforms have been integrated into the Chinese Spring survey sequence assembly. However, most of the SNPs were mapped in silico by genome browser Ensembl (<http://www.cerealsdb.uk.net/>; <https://plants.ensembl.org>).

A reference wheat genome sequence assembly, derived from one wheat cultivar Chinese Spring, was generated by Appels et al. (2018) and widely used as an annotated reference wheat genome in the mapping and cloning projects. However, one wheat cultivar cannot capture available diversity, rearrangement and historical variations of the hexaploid wheat genome (Walkowiak et al. 2020). To expand the genome assemblies of wheat, Walkowiak et al. (2020) generated five scaffold-level assemblies and ten reference-quality pseudomolecule assemblies (RQAs) of wheat and used them in the validation of each result. A universal single-copy orthologue (BUSCO) analysis showed a high level of completeness of the genomes and identified over 97% of the expected gene content in each genome. Arrangement of over 94% of the scaffolds, three-dimensional chromosome conformation capture sequencing (Hi-C) and 10×genomics linked reads revealed twenty-one pseudomolecules of wheat genomes. Genome size and collinearity were highly similar to the reference genome assemblies of Chinese Spring (Walkowiak et al. 2020).

#### *Application of mutational genomics in isolating rust resistance genes*

The fine mapping approach in wheat delimits the target gene region with the closely linked markers and the delimited gene-region can be annotated to reveal underlying candidate genes using bioinformatic approaches (Appels et al. 2018). However, this approach seeks specific expertise, state of the art resources, cutting-edge technologies and biosafety approval. In general, a candidate gene can be used to transform the susceptible wheat variety like Fielder or Bobwhite to confirm the role of candidate genes in conditioning resistance to the target pathogen (Chen et al. 2020). It is a time consuming and laborious method. Therefore, the mutational genomics approach is preferred to detect the target gene via induced loss-of-function in the parental stock.

Ethyl methane sulfonate (EMS; CH<sub>3</sub>SO<sub>3</sub>C<sub>2</sub>H<sub>5</sub>) is a chemical mutagen that is frequently used in wheat for generating mutants (Acquaah 2009). EMS produces C/G to T/A transitions (Ashburner 1989). It results in impaired complementary base-pairing followed by a series of allelic mutations that are required for comprehensive structural and functional studies (Silme and Çağiran 2007). A low concentration (0.2–0.6%) of EMS has been used to knock out the target gene in rust research; however, kill curve using LD-50 threshold is the most recommended protocol (Acquaah 2009; Periyannan et al. 2013; Thind et al. 2017). The detailed procedure of mutagenesis has been described by Mago et al. (2017).

Rust resistance genes *Lr1* (Qiu et al. 2007), *Lr10* (Feuillet et al. 2003), *Lr21* (Huang et al. 2003), *Lr22a* (Thind et al. 2017), *Sr13* (Zhang et al. 2017), *Sr22*, *Sr45* (Steuernagel et al. 2016), *Sr33* (Periyannan et al. 2013), *Sr35* (Saintenac et al. 2013), *Sr50* (Mago et al. 2015), *Yr5*, *Yr7*, *YrSP*, (Marchal et al. 2018), *Yr10* (Liu et al. 2014) and *YrAS2388R* (Zhang et al. 2019) have been cloned successfully and belong to nucleotide-binding and leucine-rich repeat protein (NLR) or its variants. Of them, *Lr1*, *Lr10* and *Lr21* were cloned a decade ago using a conventional map-based cloning approach. Isolation of *Lr34* (encodes an *ATP binding cassette transporter*), *Lr67* (encodes a *Hexose transporter*), *Yr15* (encodes a *wheat tandem kinase 1*), *Yr36* (encodes a *Kinase-START* gene) and *Sr60* (encodes a *wheat tandem kinase 2*) were successfully executed by map-based cloning (Fu et al. 2009; Krattinger et al. 2009; Moore et al. 2015; Klymiuk et al. 2018; Chen et al. 2020).

Steuernagel et al. (2016) demonstrated a rapid gene isolation approach called MutRenSeq. It combines chemical mutagenesis followed by capturing NLRs (nucleotide-binding leucine-rich repeats) via exome capture to explore pan-genome variation that existed in wild diploid wheat relatives (*Ae. tauschii*, *T. boeoticum* and *T. monococcum*). Arora et al. (2019) developed the AgRenSeq approach using a diversity panel of *Ae. tauschii* ssp. *strangulate*. It is based on R-gene enrichment followed by extraction of NLR k-mers from each accession and k-mers based association mapping to report resistance gene. *Sr46* and *SrTA1662* (both encode NLR) were cloned via the AgRenSeq approach. To validate this approach, they used *Sr33* and *Sr45* (previously cloned) as positive controls, a fine map of *Sr46* and three *Sr46* mutants

(Arora et al. 2019). It indicates that the success of both technologies depends directly or indirectly on the mutational genomics approach. MutRenSeq and AgRenSeq can be used to isolate only NLR-class of genes and the probability of missing NLR during R-gene enrichment, alignment and annotation are the limitations of both technologies. Steuernagel et al. (2020) compared and aligned NLR loci identified via NLR annotator with automated gene annotation used in IWGSC RefSeq v1.0. Of 3,400 loci predicted by NLR annotator, 2,955 NLRs match with genes annotated in IWGSC RefSeq v1.0. Of these NLRs, 578 correspond to two or more genes annotated in IWGSC RefSeq v1.0. They hypothesized three major factors for these poor gene calling and false annotations: 1. gaps (stretches of unassigned nucleotides) in the wheat genome assembly, 2. a potential overextension of the NLR locus carrying at least three consecutive NB-ARC motifs and 3. a stop-codon in the coding sequence interrupting the open reading frame in the transcript. One of the possible hypotheses was verified after cloning of *Pm2* from wheat cultivar Ulka (Sánchez-Martín et al. 2016). *Pm2* confers resistance to powdery mildew caused by *Blumeria graminis*. This encodes a full-length NLR, and the corresponding allele in IWGSC RefSeq v 1.0 substitutes five bases with a stretch of twelve bases resulting in a premature stop codon. In a multi-genome comparison study, NLR gene families were characterised and examined to reveal gene expansion in nucleotide-binding leucine-rich repeat (NBS-LRR) protein group (Walkowiak et al. 2020). This class of proteins are major causal genes for disease resistance and the innate immune system in plants (Steuernagel et al. 2016; Keller et al. 2018). The de novo annotation of loci containing conserved NLR motifs revealed around 2,500 loci with NLR signatures in each assembly of ten reference-quality pseudomolecule (RQ). And NLRs counts in the studied 16 wheat cultivars ranged from 2326 to 2701. Of them, only 31–34% of the NLR signatures were common across the genomes; the number of unique signatures varied from 22 to 192 per wheat cultivar (Walkowiak et al. 2020).

Complex genome and suppressed recombinogenic regions challenge the identification of point mutations in wheat and barley genomes. To overcome these obstacles, a complexity reduction approach MutChromSeq was developed that relies on flow sorting,

sequencing of mutant chromosomes and referencing this with a parental chromosome (Sánchez-Martín et al. 2016). This technique is equally applicable to all classes of genes. Single candidate genes of barley *Eceriferum-q* gene and wheat *Pm2* were identified using six mutants and verified by Sanger sequencing of additional mutants (Sánchez-Martín et al. 2016).

The presence of introns or repetitive regions hindered the progress to clone underlying genes. Therefore, the targeted chromosome-based long-range assembly (TACCA) approach was used to clone *Lr22a* (Thind et al. 2017). These genes were isolated and validated either by developing loss-of-function mutants or transgenesis and/or gene silencing. These studies demonstrated the importance of the mutational genomics approach in positional cloning. However, *Yr10* was cloned using a transgenesis and gene silencing approach (Liu et al. 2014) and *Sr60* was isolated using a transgenesis approach (Chen et al. 2020).

#### Association mapping for gene discovery

Linkage disequilibrium (LD) is the non-random co-occurrence of two or more gametes/alleles in a mapping population. LD occurs between loci placed in proximity, and recombination can break it down (Korte and Farlow 2013). Population structure and selection can maintain higher than expected LD across the different chromosomes (Bernardo 2020). LD is estimated by the observed frequency of an allele in a population deducted by the product of the frequencies of the corresponding alleles (Bernardo 2020). Linkage helps in restoring parental allelic combinations.

The GWAS offer high-resolution mapping due to the exploitation of higher levels of allelic diversity at a locus coupled with ancestral/historical recombination events that are represented in a diversity panel (Yu and Buckler 2006). Rust resistance genes/alleles are reported in various germplasm collections including old and modern wheat cultivars, synthetic hexaploid wheat, diploid and tetraploid wheat progenitors/relatives and wild relatives (Yu et al. 2014; Maccaferri et al. 2015; Pinto da Silva et al. 2018). GWAS has played a key role to dissect various complex traits in wheat. Five GWAS (Maccaferri et al. 2015; Gao et al. 2016; Jighly et al. 2016; Pasam et al. 2017; Turner et al. 2017) based on high throughput marker

**Table 3** Identification of new rust resistance alleles in key GWAS studies

Reference	Maccaferri et al. (2015)	Gao et al. (2016)	Jighly et al. (2016)	Pasam et al. (2017)	Turner et al. (2017)
Genotyping platforms	9 K SNP array *(4585)	90 K SNP array *(18,924)	DArT and DArT-Seq *(6176)	90 K SNP array *(51,208)	9 K SNP array *(5732)
Materials	Spring wheat accessions	Elite wheat Lines	Synthetic wheat	Watkin's collection	Spring wheat
No. of entries	1000	338	173	676	1032
Novel alleles	<b>Stripe rust</b> 1B- <i>IWA3892</i> 1D- <i>IWA980</i> 2A- <i>IWA422</i> 2A- <i>IWA424</i> 3B- <i>IWA5202</i> 4A- <i>IWA1034</i> 4D- <i>IWA5375</i> 5A- <i>IWA6988</i> 6B- <i>IWA7257</i> 6D- <i>IWA167</i>	<b>Leaf rust</b> 3B- <i>IWB74350</i> 4A- <i>IWB40915</i> 4A- <i>IWB7998</i> 6A- <i>IWA7764</i> 6A- <i>IWB40242</i> 6B- <i>IWB65148</i>	<b>Stem rust</b> 2D- <i>1101415</i> 2D- <i>1102301</i> <b>Stripe rust</b> 2B- <i>wPt-8776</i> 3D-100136169 3D-1267912	<b>Stem rust</b> 3A- <i>IWB8720</i> 3B- <i>IWA1196</i> 4B- <i>IWB59588</i> 5A- <i>IWB46277</i> 6A- <i>IWA5781</i> <b>Leaf rust</b> 1B- <i>IWA5474</i> 2B- <i>IWB35072</i> 5A- <i>IWB34703</i> <b>Stripe rust</b> 1A- <i>IWB766</i> 1B- <i>IWB44883</i> 3A- <i>IWA7440</i> 5B- <i>IWB10356</i> 5D- <i>IWB73687</i> 6A- <i>IWB48922</i> 6B- <i>IWB 68,655</i> 7A- <i>IWB60768</i> 7B- <i>IWA1971</i>	<b>Leaf rust</b> 2BS- <i>IWA8221</i> 2BS- <i>IWA4894</i> 2BL- <i>IWA5177</i> 2DL- <i>IWA5637</i> 4AS- <i>IWA1900</i> 4DS- <i>IWA5375</i> 5DS- <i>IWA6289</i> 5DL- <i>IWA1429</i> 7AS- <i>IWA1277</i>

\*Number of polymorphic markers; SNP, Single nucleotide polymorphism; DArT, Diversity Array Technology

platforms have uncovered novel rust resistance alleles (Table 3). The success of GWAS in uncovering new genetic variation relies on the diversity at the genotypic level and resultant phenotypic differences between individuals (Korte and Farlow 2013). It can detect marker-trait associations for the phenotype of interest. Although several major QTL identified through GWAS have not been functionally characterised and validated for their application in wheat breeding programs, IWGSC RefSeq v1.0 can be used to investigate precise locations of QTL identified using high throughput genotyping platforms (Appels et al. 2018).

The LD decay usually drops at 2–8 cM across the three (AA, BB and DD) genomes (Gao et al. 2016; Riaz et al. 2018). GWAS studies can consider the marker trait associations (MTAs) corresponding to 5 cM region and/or higher LD  $r^2$  value (squared

correlation coefficient) as an independent QTL. Identified MTAs deviating from known genes/QTLs by more than 5 cM interval could be treated as new in the case of ASRs/APRs. However, further validation using bi-parental populations and physical positions of underlying rust resistance alleles is essential to catalogue candidate genes. Zhang et al. (2014) developed a customized scale to linearised the 0–4 IT scale into a 0–9 scale for GWAS analysis. This customised scale accommodates complex infection types like “;13+” and calculate the weighted arithmetical mean. It is available in R packages ([https://github.com/umngao/rust\\_scores\\_conversion](https://github.com/umngao/rust_scores_conversion)).

Statistical software like TASSEL, and a few R based programs like rrBLUP, mrMLM, and rMVP targeting single locus and multiple loci mixed linear model (SL-MLM and ML-MLM) are used in GWAS (Yu et al. 2006; Endelman 2011; Yang et al. 2014;

Liu et al. 2016). The SL-MLM tests each marker one by one, however, ML-MLM incorporates multiple markers simultaneously as covariates in a stepwise manner to overcome the confounding effects between kinship and testing markers (Liu et al. 2016). The GWAS highlights the significant MTAs using  $-\log_{10}(p)$  that can result in four possible outcomes while considering the null hypothesis ( $H_0$ ) that the marker under investigation is unlinked to a single QTL; 1. False positive, when a QTL is incorrectly reported, 2. True positive, when a QTL is correctly reported, 3. False negative, when a QTL is incorrectly unreported and 4. True negative, when a QTL is correctly unreported (Bernardo 2020). Type I error rate or significance level ( $\alpha$ ) is the probability of rejecting the null hypothesis in case  $H_0$  is true. However, the type II error rate ( $\beta$ ) equates to the probability that a false  $H_0$  is not rejected. High precision mapping experiments can lower the values of  $\alpha$  and  $\beta$ . To specify experiment-wise control rate ( $\alpha_E$ ) and comparison wise significance level ( $\alpha_C$ ), Bonferroni correction, permutation testing and false discovery rate (FDR, Benjamini and Hochberg 1995) have been used to attain higher stringency. For instance, 5,000 ( $n$ ) unlinked markers,  $\alpha_E$  of 0.05 resulted in  $\alpha_C$  of  $1 \times 10^{-5}$ , where  $\alpha_C = \alpha_E/n$ . In addition to controlling false positives, it can reduce the power of QTL detection and may not be a more robust criteria to detect true QTL (Bernardo 2020). One may prefer a high FDR threshold when aiming to discover the genetic architecture of a trait and a low FDR to identify candidate loci for subsequent studies and validation (Korte and Farlow 2013).

Several GWAS studies have been conducted to detect significant MTAs for rust resistance using mixed linear model (MLM-Q+K) accounting principal component (Q) and kinship matrix (K) that cluster individuals into a subset to minimise the effective sample size (Table 3; Zhang et al. 2010; Pasam et al. 2017; Juliana et al. 2018). A complementary approach, ‘population parameters previously determined’ (P3D) was preferably used in some studies to circumvent re-computing variance components (Zhang et al. 2010). Juliana et al. (2018) applied a GWAS approach to identify leaf rust and stripe rust resistance alleles in International Bread Wheat Screening nurseries. In this study, the POPSEQ map and Ensembl plants were used to report candidate genes associated with significant MTAs. Genomic regions conferring rust resistance on chromosomes

1DS, 2AS, 2BL, 2DL, 3B, 4AL, 6AS, 6AL and 7DS were identified. Maccaferri et al. (2015) performed GWAS using a worldwide collection of 1,000 spring wheat accessions and a 9 K SNP Infinium assay. A greater level of *Pst* resistance was observed in a sub-population from southern Asia. Ten significant MTAs explained 15% of the phenotypic variation (PVE) individually for stripe rust resistance, however, the PVE increased up to 45% when combining the effect of all QTL. Kankwatsa et al. (2017) evaluated 159 old wheat cultivars and landraces against 35 Australian rust pathotypes and postulated several known ASRs, APRs and a few uncharacterised APRs. Similarly, Bansal et al. (2013) screened 205 wheat land pathotypes against rust isolates and high-throughput DArT genotyping using a single marker scan and identified 68 significant MTAs. They reported linked stripe rust-leaf rust resistance loci on chromosome arms 1AL, 2BS, 2BL, 3DL, 5BS, 6BS and 7DL and linked stripe rust-stem rust resistance loci on chromosome arms 4BL and 6AS.

#### *Bi-parental mapping (BM) versus association mapping (AM)*

QTL can be identified using BM and AM approaches. It raises the question about the choice of one of these methods (Bernardo 2020). When population development is challenging, AM is the obvious choice. For instance, developing segregating progeny from a clonal selection of tuber crops is tedious due to their mode of propagation and AM can be chosen in this instance. The probability of detecting rare variants using AM is however lesser than BM. For example, among a diverse wheat collection of 300 accessions, only three lines carried the same resistance allele for pathotype Ug99, while the remaining lines of the panel carried the susceptible allele. The AM approach is less likely to detect the rare variants due to lower frequency (1%). In BM, out of three lines, one accession with a good agronomical background (resistant parent) crossed with the susceptible parent and 200 RILs are developed. In this case, the frequency of resistance allele would be 50% in the population that increases the power of QTL detection.

If an AM panel has 30 resistant lines and 270 susceptible lines that means the frequency of the resistance allele is 10% and QTL can be detected using



GWAS. However, a challenge for the breeder would be to determine a resistant line with better agronomical performance as well as a closely linked marker to expedite the deployment of QTL in the elite cultivars (Bernardo 2020).

### Delivering rust resistance in wheat

Since nineteenth century, wheat crop had been affected by rust diseases. Conventional breeding approaches have incorporated resistance genes in the wheat varieties through hybridization followed by field selection and greenhouse assays. Available genomic technologies have supplemented traditional rust resistant breeding program to address pressing challenges (Babu et al. 2020). Modern wheat breeding approaches rely on qualitative/major (R) and quantitative/minor genes. In general, major gene offers complete resistance and likely to breakdown, and acquisition of virulence in corresponding pathogen populations renders this resistance type ineffective (Sucher et al. 2017). In contrast, a minor gene is assumed to be long-lasting as it does not completely curtail pathogen growth. These genes have been incorporated into wheat that recognizes different races of a pathogen; pyramiding these genes in future varieties is vital for attaining durable resistance (Singh and Rajaram 1992; Bariana et al. 2007).

Australian wheat breeder William Farrer noticed that Indian wheat was early in maturity resulting in rust escape as compared to Canadian wheat var. Fife which was delayed in maturity and exposed to rust. Two new cultivars Yandilla and Comeback were derived from the Indo-Canadian wheat hybridization program. Farrer crossed European-derived purple straw variety with Yandilla and selected a new wheat cultivar namely 'Federation' in honour of the creation of the Australian nation in 1901 (<http://nma.gov.au/defining-moments/resources/federation-wheat>). Virulence in *P. triticini* to *Lr10* was evident after the introduction of rust resistant Canadian wheat cultivar 'Selkirk' (*Lr10+Lr14a*+heterogeneous for *Lr16*), whereas virulence to *Lr16* occurred after 8 years of cultivation of 'Selkirk' (Samborski 1985; Martens and Dyck 1989). Virulence for *Lr13* had appeared after the introduction of Canadian wheat variety 'Manitou' (Samborski 1985). Few mega varieties namely 'CDC Teal' (*Lr1, Lr13, Lr34*) (Hughes and

Hucl 1993; Liu and Kolmer 1997), 'Roblin' (*Lr1, Lr10, Lr13, Lr34*) (Dyck 1993), 'Glenlea' (*Lr1, Lr13, Lr34*) (Dyck et al. 1985), 'AC Domain' (*Lr10, Lr12, Lr16*), 'AC Karma' (*Lr13, Lr16, LrTb*) (Kolmer and Liu 2002) and 'Laura' (*Lr1, Lr10, Lr34*) (Kolmer 1994) were released. Different rust resistant genes have been reported into Indian wheat varieties namely PBW343 (*Sr2+Sr5+Sr31/Lr26/Yr9+Yr27*), RAJ3765 (*Sr2+Lr10+Lr13+Yr2ks*), DBW17 (*Sr31/Lr26/Yr9+Lr23*), PBW550 (*Sr31/Lr26/Yr9+Sr57/Lr34/Yr18*), HD2967 (*Sr2+Sr8a+Sr11+Lr23+Yr2*), HD2733 (*Sr31/Lr26/Yr9+Sr57/Lr34/Yr18*) and HD3086 (*Sr2+Sr7b+Lr10+Lr13+Yr2*) (Babu et al. 2020). Marker assisted pyramiding of effective rust resistant genes is a continuous process, and wheat researchers across the world are actively engaged in this approach.

### Conclusions

From the findings highlighted in the review, it is obvious that significant progress has been made to understand the evolutionary nature of rust pathogens, characterising rust resistance sources, and fine mapping and cloning of rust resistance genes. Over hundreds of genes/QTL along with associated DNA markers for individual rust have been mendelised in bi-parental mapping populations; some of these genes/QTL have qualified to catalogue them as genes. However, over 20 rust resistance genes have been successfully isolated using available genomic technology which represents only one-tenth of the total catalogued genes. This little progress highlighted the barriers associated with gene isolation like size and complexity of the wheat genome, structural rearrangement and lacking genome-assembly data of multiple wheat lines. In the last couple of years, significant progress has been made to deliver reference-quality genome-assembly data of few wheat lines (10+ genome project) which can solve some challenges like deletion/rearrangement in targeted genes' corresponding region in Chinese Spring based wheat genome reference. In perspectives of delivering high yielding wheat varieties, comprehensive studies should be performed to demonstrate the durability of disease resistance genes as well as associated yield penalty and quality constraints. As we have a consensus that

promoting wheat varieties tagged with effective disease resistance genes is a crucial step toward food security, especially for the developing world.

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**Code availability** Publicly available software are used in this study.

#### Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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