Genetic and genomic approaches for breeding rust resistance in wheat

Deepak Baranwal

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 mega-varieties. 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.
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, *Pst* are the causal *f. sp. tritici* *P. tritici* and *f. sp. Puccinia triticina* *Pgt*, *P. triticina* *P. tritici*. The rust pathogens and their dispersal occurs via wind (Singh and Rajaram 1992). Stem rust propagates well under warm and humid climates (≤ 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, 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 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. *Yr*6, *Yr*7, *Yr*9, *Yr*17 and *Yr*27 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 *Yr*18, *Yr*29 and *Yr*30 (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 *Pst*110 E143A + (all resistant(R); avirulent on *Yr*9 and *Yr*17) and *Pst*134 E16A +17 +27 (all susceptible(S); virulent on *Yr*9 and *Yr*17) is shown in Fig. 1d. These differences revealed the presence of *Yr*9 and/or *Yr*17 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 *Sr*2, *Sr*12, *Sr*13, *Sr*14, *Sr*21, *Sr*22, *Sr*35, *Lr*14a, *Lr*21, *Lr*22a, *Lr*23, *Lr*39, *Lr*53/*Yr*35, *Lr*61, *Yr*15, *Yr*28 and *Yr*36 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 *Sr*32, *Sr*36, *Sr*37, *Sr*39/*Lr*35, *Sr*40, *Lr*28, *Lr*36, *Lr*51, *Lr*56/*Yr*38

![Fig. 1 Rust reaction against different pathotypes](image-url)
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 1
List of some outsourced wheat rust gene deployed in common wheat (*T. aestivum* L.)

| SN | Outsourced wheat rust genes | Source/Origin | References |
|----|-----------------------------|---------------|------------|
| 1  | *Sr21* (2A*α*), *Sr22*(7AL), *Sr35*(3AL) and *SrTm* (2AL) and *Sr63*(3AS), *Sr60*(5A*α*), *Sr66*(3BS) | *T. monococcum L.* | Gerechter-Amitai et al. (1971), McIntosh et al. (1984), Kolmer et al. (2008) and Briggs et al. (2015) |
| 2  | *Sr33* (1DL), *Sr45* (1DS), *Sr46* (2DS), *SrTAA10171* (7DS), *SrTAA10187* (6DS), *SrTA662* (1DS), *SrL21* (1DS), *SrL22a* (2DS), *SrL32* (3D), *SrL39* (2DS), *SrL40* (42D), and *Yr28*(4DS) | *Ae. tauschii Coss* | Kerber and Dyck (1979), McIntosh et al. (2014) and Olson et al. (2013a, b) |
| 3  | *Sr32* (2A, 2B), *Sr39* (2B), *Sr47*(2BL), *Lr28*(4BL), *Lr36*(6BS), *Lr40* (2B), and *Yr28*(4DS) | *Ae. speltoides Tausch* | McIntosh et al. (1995), Faris et al. (2008) and Chemayek et al. (2016) |
| 4  | *Sr36* (2BS), *Sr37* (4BL), and *Sr40* (2BS) | *T. timopheevii (Zhuk.) Zhuk* | McIntosh et al. (1971), Dyck (1992) |
| 5  | *Sr24*/*Sr26* (Ug99 susceptible; 3DL), *Sr46* (1DS), *Sr47* (2BL), *SrL28* (4BL), *SrL36* (6BS), *SrL51* (1BL) and *SrL66*(3A) | *Ae. elongatum (syn. Thinopyrum ponticum)* | Mago et al. (2005a), Knott (1968), Sears (1973, 1977), McIntosh et al. (1977) and Jin et al. (2007) |
| 6  | *SrR* and *Sr31*/*Sr32* (3BS) | *T. turgidum var dicoccoides cv Yaroslav* | Mago et al. (2005b) |
| 7  | *Sr27*/Yr30//Sr32* (3BS) | *T. turgidum var dicoccoides cv Yaroslav* | Li et al. (2011), Riar et al. (2012) |
| 8  | *Sr34*/*Yr8* (2A, 2D) | *T. comosa* | McIntosh et al. (1995) |
| 9  | *Sr38*/*Lr37*/*Yr17* (2AS) | *Ae. ventricosa* | Molnár-Láng et al. (2015) |
| 10 | *Lr9*(6BL), *Lr76*/*Yr70*(5DS) | *Th. intermedium* | Bansal et al. (2017) |
| 11 | *Lr38* (2AL) | *Ae. geniculata* | Riar et al. (2012) |
| 12 | *Lr57*/Yr40*(5DS), *Sr53*(T5DL-5MgL-5MgS) | *Secale cereale* | Riar et al. (2012) |
| 13 | *Lr58*(2BL) | *Ae. triuncialis* | Molnár-Láng et al. (2015) |
| 14 | *Yr15*(1BL), *Yr36*(6BS), *Yr84* (1BS), *Lr53*/Yr35*(6BS) and *Lr64*(6AL) | *T. dicoccoides* | Marais et al. (2005a, b), Riar et al. (2012) and Klymiuk et al. (2022) |
| 15 | *Sr9f* (2BL), *Sr9g*/*Yr7* (2BL), *Sr11* (6BL; cv. Gaza), *Sr12*(3BS; cv. Iumillo) | *T. turgidum var. durum* | Knott and Anderson (1956), Sheen and Snyder (1964), McIntosh and Luig (1973) and Loegering (1975) |
| 16 | *Sr13* (6AL; cv. Khapli)/*Sr14a* (1BL; cv Khapli), *Sr17*(7BL) | *T. turgidum var. dicoccum* | Knott (1962) |
| 17 | *Lr14a*(7BL), *Lr23*(2BS), *Lr61*(6BS), *Sr9e*(2BL; *SrV*; cv. Bernalemmer) | *T. turgidum* | McIntosh and Dyck (1975), Herrera-Foessel et al. (2008) and Rondon et al. (1966) |
| 18 | *Sr62*/*Yr42* (6A) | *Ae. neglecta* | Marais et al (2008) |
| 19 | *Lr54*/*Yr37*(2DL) | *Ae. kotschyi* | Marais et al. (2005b) |
| 20 | *Lr56*/*Yr38*(6AL) | *A. sharonensis* | Marais et al. (2010) |
| 21 | *Sr52*(T6AS.6 V#3L) | *Dasypyrum villosum (L.) Candargy* | Qi et al. (2011) |
| 22 | *Yr50*(4BL) | *Thinopyrum intermedium* | Liu et al. (2013) |

* Ug99 resistant loci; *tight repulsion phase linkage with Sr36; **Increasing Yield
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  | Sr21  | CJ961291 and Cscnl20 | Map-based cloning | Coiled-coil, nucleotide-binding leucine-rich repeat protein (NLR) | Chen et al. (2018) |
| 2  | Sr22  | S22GMF and S22GMR | MutRenSeq | NLR | Steuernagel et al. (2016) |
| 3  | Sr45  | S45F1/S45R1 | MutRenSeq | NLR | Steuernagel et al. (2016) |
| 4  | Sr35  | AK331487 and AK332451 | Map-based cloning | NLR | Saintenac et al. (2013) |
| 5  | Sr33  | BE405778 and BE499711 | Map-based cloning | NLR | Periyannan et al. (2013) |
| 6  | Sr46; SrTA1662 | S46ConsFA and S46PREVR; R1.F3 and R1.R3 | AgRenSeq | NLR | Arora et al. (2019) |
| 7  | SrTA10171; SrTA10187 | gdm88-F and gdm88-R; 6DS0027 and 6DS0039 | – | – | Olson et al. (2013a) |
| 8  | Sr32  | csSr32#1-F and csSr32#1-R | – | – | Mago et al. (2013) |
| 9  | Sr36  | STM773-2F and STM773-2R | – | – | Hayden and Sharp (2001) |
| 10 | Sr39/Lr35 | Sr39#22r-F and Sr39#22r-R | – | – | Mago et al. (2009) |
| 11 | Sr47  | gpw4043-F and gpw4043-R; gpw4165-F and gpw4165-R | – | – | Klindworth et al. (2012) |
| 12 | Sr24/Lr24 | Sr24#12-F and Sr24#12-R | – | – | Mago et al. (2005a) |
| 13 | Sr25/Lr19 | PSY-E1 and PSY-D1 | – | – | Zhang and Dubcovsky (2008) |
| 14 | Sr26  | sunKASP_224 and sunKASP_225 | – | – | Qureshi et al. (2018a) |
| 15 | Sr31/Lr26/Yr9/Pm9 | iag95-F and iag95-R | – | – | Mago et al. (2002, 2005b) |
| 16 | Sr2/Lr27/Yr30/Pbc1 | csSr2-F and csSr2-R | – | – | Mago et al. (2011) |
| 17 | Sr50  | Sr50-5p-F and Sr50-5p-R2 | Comparative genomics and complementation tests | CNL | Mago et al. (2015) |
| 18 | Sr60  | ucv530 and ucv540 | Map-based cloning | wheat tandem kinase2 | Chen et al. (2020) |
| 19 | Sr38/Lr37/Yr17 | Ventrip and LN2 | – | – | Helguera et al. (2003) |
| 20 | Sr53  | Xbe442600 and Xbe443201 | – | – | Liu et al. (2011) |
| 21 | Sr12  | IWA610 and IWA537 | – | – | Hiebert et al. (2016) |
| 22 | Sr13  | cnl2 and CJ641478 | Map-based cloning | CNL | Zhang et al. (2017) |
| 23 | Sr52  | BE497099-STS-F and BE497099-STS-R | – | – | Qi et al. (2011) |
| 24 | Lr21  | KSUD14, and KSU936 | Map-based cloning | CNL | Huang et al. (2003) |
| 25 | Lr22a | SWSNP4 and SWSNP6 | Targeted chromosome-based cloning via long-range assembly (TACCA) | CNL | Thind et al. (2017) |
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 \textit{Lr} gene from \textit{Ae. umbellulata Zhuk.} to wheat. Another approach is to disrupt the normal meiotic chromosome pairing of wheat using a high pairing line of \textit{Ae. speltoides} Tausch followed by introgression of \textit{Yr} gene from \textit{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, \textit{Lr22b} (McIntosh et al. 1995).

The resistant parent (carrying ASR and/or APR) is crossed with a susceptible parent to develop a bi-parental population to determine the inheritance of resistance and genomic location of the underlying resistance gene(s). Although several studies involved tests on individual \textit{F2} plants, tests on \textit{F3} families are preferred for their amenability for checking the reproducibility of results (Bariana 2003). Population advancement to the \textit{F6} 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). \textit{F3} 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 \textit{F3} 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 \textit{F3} 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 bi-parental population requires the development of

| SN | Genes | Associated markers | Approach | Nature of cloned genes | References |
|----|-------|-------------------|----------|------------------------|------------|
| 26 | \textit{Lr51} | S30-13L and AGA7-759R | – | – | Helguera et al. (2005) |
| 27 | \textit{Lr76/Yr70} and \textit{Lr57/Yr40} | MAS-CAPS16 | – | – | Kuraparthy et al. (2009); Bansal et al. (2017) Chhetri et al. (2017) |
| 28 | \textit{Lr23} | \textit{sunKASP}_16 | – | \textit{wheat tandem kinase 1} | Klymiuk et al. (2018) |
| 29 | \textit{Yr15} | \textit{kin1} and \textit{kinII} | Map-based cloning | \textit{wheat tandem kinase 1} | Klymiuk et al. (2022) |
| 30 | \textit{Yr84} | usw312-usw317 | – | – | |
| 31 | \textit{Yr36} | \textit{Xucw129} and \textit{Xucw148} | Map-based cloning | \textit{kinase-START gene protein} | Fu et al. (2009) |
single gene segregating populations to precisely locate genes conferring resistance. For example, an F₂ 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 F₆ RIL populations. Molecular mapping of two F₆ 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 BC₁F₂ populations derived from each cultivar and a common susceptible parent Avocet ‘S’ confirmed the presence of three independent loci each and a common susceptible parent Avocet ‘S’ derived BC₁F₂ line SA65 (a resistant line) was some 2D. To map the third gene, a Sunco/2*Avocet (Bariana et al. 2001) on chromosome 2008) and YrCK locate genes conferring resistance. For example, an F₃ single gene segregating populations to precisely Euphytica (2022) 218:159 1 3 Two BC₁F₂ 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 confirmed the presence of three independent loci each and a common susceptible parent Avocet ‘S’ constituted resistant and susceptible bulks and an artificial 3BS (Randhawa et al. 2015). Australian wheat cultivars Sunco and Kukri expressed a high level of stripe rust resistance (Bariana et al. 2001). Two BC₁F₂ populations derived from each cultivar and a common susceptible parent Avocet ‘S’ confirmed the presence of three independent loci each and a common susceptible parent Avocet ‘S’ constituted resistant and susceptible bulks and an artificial chromosome 2D. To map the third gene, a Sunco/2*Avocet S-derived BC₁F₂ 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 Yr5A3. Further selective genotyping using a 90 K SNP array and SSRs placed the Yr5A3 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 F₂ 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 F₂ 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 (Nsabiyera 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 QYr‌_rb.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 F₁ sample. One µg DNA sample of both parents, the constituted resistant and susceptible bulks and an artificial F₁ 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. Genom-eStudio 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 competitive 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.1gcgroup.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 Yr77 (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 biparental populations (McIntosh et al. 2017; Li et al. 2020b). In a study, a Portugeese 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 F2 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 termed collinearity (Singh and Singh 2015). However, the arrangement of different maps is known as comparative mapping (Singh and Singh 2015). An 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 (Third 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 (Nsabiyera 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 cyometry-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 sequencing of chromosomes specific labelled repetitive DNA to similar sizes (Shatalina et al. 2013). Wide applicability of the remaining chromosomes was challenging due to similar sizes (Shatalina et al. 2013). However, due to uneven recombination, 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; CH3SO3C2H5) 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 Çağırgan 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. *strangulatum*. 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.
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 \textit{Pm2} from wheat cultivar Ulka (Sánchez-Martín et al. 2016). \textit{Pm2} confers resistance to powdery mildew caused by \textit{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 \textit{Eceriferum-q} gene and wheat \textit{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 \textit{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, \textit{Yr10} was cloned using a transgenesis and gene silencing approach (Liu et al. 2014) and \textit{Sr60} was isolated using a transgenesis approach (Chen et al. 2020).

\textit{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
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).

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; Maccaferri et al. 2015; Gao et al. 2016; Jighly et al. 2016; Pasam et al. 2017; Turner et al. 2017)

| Reference               | Genotyping platforms | Materials          | No. of entries | Novel alleles |
|-------------------------|----------------------|-------------------|----------------|---------------|
|                         | 9 K SNP array *(4585)| Elite wheat Lines | 1000           | String rust   |
| Maccaferri et al. (2015)| 90 K SNP array *(18,924) | Synthetic wheat | 338            | Leaf rust     |
| Gao et al. (2016)       | DArT and DArT-Seq *(6176) | Watkin’s collection | 173           | Stem rust     |
| Jighly et al. (2016)    | 90 K SNP array *(51,208) | Spring wheat | 676            | Stem rust     |
| Pasam et al. (2017)     | 9 K SNP array *(5732) |                   | 1032           | Leaf rust     |
| Turner et al. (2017)    |                      |                   |                |               |

*Number of polymorphic markers; SNP, Single nucleotide polymorphism; DArT, Diversity Array Technology
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-parenatal 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 definining-moments/resources/federation-wheat). Virulence in P. tritici 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.

Acknowledgments The first author would like to thank Australian Centre for International Agricultural Research (ACIAR) for the award of John Allwright Fellowship. The author duly acknowledges the contribution of Associate Professor Urmil Bansal and Professor Harbans Bariana, the University of Sydney, Plant Breeding Institute, Australia for their critical inputs to finalise the manuscript. The manuscript bears the BAU communication number 995/210805.

Authors’ contributions DB collected and collated relevant literature and edited the final draft of the manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. There is no separate funding for this project.

Data availability and material All data are given in the manuscript.

Code availability Publicly available software are used in this study.

Declarations

Conflicts of interest The authors declare that they have no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Acquaah G (2009) Principles of plant genetics and breeding. Wiley, New York, pp 1–540

Admassu B, Friedt W, Ordon F (2012) Stem rust seedling resistance genes in Ethiopian wheat cultivars and breeding lines. Afric Crop Sci J 20:149–162

Ahmed NU, Trethewan RM (2020) A rapid breeding technology of wheat. Science and technology innovation for a sustainable economy. Springer, Berlin, pp 109–119

Ali S, Rodriguez-Algaba J, Thach T, Sørensen CK, Hansen JG, Lassen P, Nazari K, Hodson DP, Justesen AF, Hovmöller MS (2017) Yellow rust epidemics worldwide were caused by pathogen races from divergent genetic lineages. Front Plant Sci 8:1057–1062

Allen AM, Winfield MO, Burridge AJ, Downie RC, Benbow HR, Barker GL, Wilkinson PA, Coghill J, Waterfall C, Davassi A (2017) Characterization of a Wheat Breeders’ Array suitable for high-throughput SNP genotyping of global accessions of hexaploid bread wheat (Triticum aestivum). Plant Biotechnol J 15:390–401

Anderson LK, Lai A, Stack SM, Rizzon C, Gaut BS (2006) Uneven distribution of expressed sequence tag loci on maize pachypete chromosomes. Genome Res 16:115–122

Appels R, Eversole K, Stein N, Feuillet C, Keller B, Rogers J, Pozniak CJ, Choulet F, Distelfeld A, Poland J, Ronen G, Sharpe AG, Barad O, Baruch K, Keesle-Gagnère G, Mascher M, Ben-Zvi G, Josselin A-A, Himmelbach A, Balfourier F, Gutierrez-Gonzalez J, Hayden M, Koh C, Muehlbauer G, Pasam RK, Paux E, Rigault P, Tittis J, Tiwari V, Spannagl M, Lang D, Gundlach H, Haberer G, Mayer KFX, Ormanbekova D, Prade V, Šimková H, Wicker T, Swabreck D, Rimbert H, Felder M, Guhlhot N, Kaithakottigal K, Keilwagen J, Leroy P, Lux T, Twardziok S, Venturini L, Juhasz A, Abrouk M, Fischer I, Uauy C, Borrill P, Ramírez-Gonzalez RH, Arnald D, Chalabi S, Chalhoub B, Cory A, Datra LA, Davey MW, Jacobs J, Robinson SJ, Steuernagel B, Van Ex F, Wulff BBH, Benhamed M, Bendahmame A, Concia L, Latrasse D, Bartos J, Bellac A, Berges H, Doležel J, Frenkel Z, Gill B, Korol A, Letellier T, Olsen O-A, Singh K, Valár M, van der Vossen E, Vautrin S, Weining S, Fahima T, Glikson V, Raats D, Čihalíková J, Toegelevá H, Vrána J, Sourdille P, Darrier B, Barabaschi D, Cattivelli L, Hernández P, Galvez S, Budak H, Jones JGD, Witek K, Yu G, Small I, Melonek J, Zhou R, Belova T, Kanyuka K, King R, Nilsen K, Walkowiak S, Cuthbert R, Knox R, Wiebe K, Xiang D, Rohde A, Golds T, Čížková J, Akpinar BA, Biyiklioglu S, Gao L, N’Daiye A, Kubaláková M, Šafář J, Alfama F, Adam-Blondon A-F, Flores R, Guerche C, Looae M, Quesneville H, Condie J, Ens J, Maclachlan R, Tan Y, Alberti A, Aury J-M, Barbe V, Couloux A, Cruaud C, Labadik K, Mangenot S, Wincker P, Kaur G, Luo M, Sehgal S, Chhuneja P, Gupta OP, Jindal S, Kaur P, Malik P, Sharma P, Yadav B, Singh NK, Khurana JP, Chaudhary C, Khurana P, Kumar V, Mahato A, Mathur S, Sevanthi A, Sharma N, Tomar RS, Holušová K, Plihal O, Clark MD, Heavens D, Kettleborough G, Wright J, Ballaré C, Rung Y, Salina E, Ravin N, Skryabin K, Beletsky A, Kandikov N, Mardanov A, Nesterov M, Rakitin A, Sergeeva E, Handa H, Kamamori H, Katagiri S, Nasuda S, Tanaka T, Wu J, Cavetano M, Jiumeng M, Kugler K, Pfeifer M, Sandve S, Xun X, Zhan B, Batley J, Barker GL, Wilkinson PA, Coghill J, Waterfall C, Davassi A, Admassu B, Friedt W, Ordon F, Ahuja NU, Trethewan RM.

Arora S, Steuernagel B, Gaurav K, Chandramohan S, Long Y, Matny O, Johnson R, Enk J, Periyannan S, Singh N

Euphytica (2022) 218:159
Borrill P, Adamski N, Uauy C (2015) Genomics as the key to
Benjamini Y, Hochberg Y (1995) Controlling the false discov-
Beddow JM, Pardey PG, Chai Y, Hurley TM, Kriticos DJ,
Bariana H, Forrest K, Miah H, Singh D, Bariana H (2011) Characterisation of a new stripe rust resistance gene Yr47 and its genetic association with the leaf rust resistance gene Lr52. Theor Appl Genet 122:1461–1466
Bansal UK, Arief VN, DeLacy IH, Bariana HS (2013) Exploring wheat landraces for rust resistance using a single marker scan. Euphytica 194:219–233
Bansal UK, Muhammad S, Forrest KL, Hayden MJ, Bariana HS (2015) Mapping of a new stem rust resistance gene Sr49 in chromosome 5B of wheat. Theor Appl Genet 128:2113–2119
Bansal M, Kaur S, Dhaliwal H, Bains N, Bariana H, Chhuneja P, Bansal U (2017) Mapping of Aegilops umbellulata-derived leaf rust and stripe rust resistance loci in wheat. Plant Pathol 66:38–44
Bariana HS, Hayden MJ, Ahmed N, Bell J, McIntosh R (2001) Mapping of durable adult plant and seedling resistances to stripe rust and stem rust diseases in wheat. Crop past Sci 52:1247–1255
Bariana H (2003) Breeding for disease resistance. In: Thomas B, Murphy DJ, Murray BG (eds) Encyclopedia of applied plant sciences Harcourt. Academic Press, Cambridge, pp 244–253
Bariana H, Brown G, Bansal U, Miah H, Standen G, Lu M (2007) Breeding triple rust resistant wheat cultivars for Australia using conventional and marker-assisted selection technologies. Crop past Sci 58:576–587
Bariana H, Forrest K, Qureshi N, Miah H, Hayden M, Bansal U (2016) Adult plant stripe rust resistance gene Yr71. Mol Breed 36:1–10
Beddow JM, Pardey PG, Chai Y, Hurley TM, Kriticos DJ, Braun H-J, Park RF, Cuddy WS, Yunow T (2015) Research investment implications of shifts in the global geography of wheat stripe rust. Nature Plants 1:1–5
Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc Ser B (methodol) 57:289–300
Bernardo R (2020) Breeding for quantitative traits in plants, 3rd edn. Stemma Press, Woodbury, pp 1–411
Borrill P, Adamski N, Uauy C (2015) Genomics as the key to unlocking the polyploid potential of wheat. New Phytop 208:1008–1022
Brenchley R, Spannagl M, Pfeifer M, Barker GL, D’Amore R, Allen AM, McKenzie N, Kramer M, Kerhornou A, Bolser D (2012) Analysis of the bread wheat genome using whole-genome shotgun sequencing. Nature 491:705
Briggs J, Chen S, Zhang W, Nelson S, Dubcovsky J, Rouse MN (2015) Mapping of Sr7M1, a recessive stem rust resistance gene from diploid wheat effective to Ug99. Phytopathology 105:1347–1354
Brown JK, Hovmöller MS (2002) Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. Science 297:537–541
Chapman JA, Mascher M, Buluç A, Barry K, Georgianas E, Session A, Strnadova V, Jenkins K, Sehgal S, Oliker L (2015) A whole-genome shotgun approach for assembling and anchoring the hexaploid bread wheat genome. Genom Biol 16:26–32
Chemayek B, Bansal UK, Qureshi N, Zhang P, Wagoire WW, Bariana HS (2016) Tight repulsion linkage between Sr36 and Sr39 was revealed by genetic, cytogenetic and molecular analyses. Theor App Genet 130:587–595
Chen S, Zhang W, Bolus S, Rouse MN, Dubcovsky J (2018) Identification and characterization of wheat stem rust resistance gene Sr27 effective against the Ug99 race group at high temperature. PLoS Genet 14(e1007287):1–8
Chen S, Rouse MN, Zhang W, Zhang X, Guo Y, Briggs J, Dubcovsky J (2020) Wheat gene Sr60 encodes a protein with two putative kinase domains that confers resistance to stem rust. New Phytol 225:948–958
Chen S, Hegarty J, Shen T, Hua L, Li H, Luo J, Bai S, Zhang C, Dubcovsky J (2021) Stripe rust resistance gene Yr34 (synonym Yr48) is located within a distal translocation of Triticum monococcum chromosome 5AmL into common wheat. Theor Appl Genet 134:2197–2211
Chhetri M, Bansal U, Toor A, Lagudah E, Bariana H (2016) Genomic regions conferring resistance to rust diseases of wheat in a W195/BTSS mapping population. Euphytica 209:637–649
Chhetri M, Bariana H, Wong D, Sohail Y, Hayden M, Bansal U (2017) Development of robust molecular markers for marker-assisted selection of leaf rust resistance gene Lr22 in common and durum wheat breeding programs. Mol Breed 37:21–26
Chhuneja P, Kaur S, Garg T, Ghai M, Kaur S, Prashar M, Bains N, Goel R, Keller B, Dhaliwal H (2008) Mapping of adult plant stripe rust resistance genes in diploid A genome wheat species and their transfer to bread wheat. Theor Appl Genet 116:313–324
Cui F, Zhang N, Fan X-l, Zhang W, Zhao C-h, Yang L-j, Pan R-q, Chen M, Han J, Zhao X-q (2017) Utilization of a Wheat 660K SNP array-derived high-density genetic map for high-resolution mapping of a major QTL for kernel number. Sci Rep 7:1–12
Dyck P (1992) Transfer of a gene for stem rust resistance from Triticum araraticum to hexaploid wheat. Genome 35:788–792
Dyck PL (1993) Inheritance of leaf rust and stem rust resistance in ‘Roblin’ wheat. Genome 36:289–293
Dyck PL, Samborski DJ, Martens JW (1985) Inheritance of resistance to leaf rust and stem rust in the wheat cultivar Glenlea. Can J Plant Pathol 7:351–354
Endelman JB (2011) Ridge regression and other kernels for genomic selection with R package rrBLUP. Plant Genome 4:250–255
Faris JD, Xu SS, Cai X, Friesen TL, Jin Y (2008) Molecular and cytogenetic characterization of a durum wheat—Aegilops speltoides chromosome translocation conferring resistance to stem rust. Chrom Res 16:1097–1105

Feuillet C, Travella S, Stein N, Albar L, Nublat A, Keller B (2003) Map-based isolation of the leaf rust disease resistance gene Lr10 from the hexaploid wheat (Triticum aestivum L.) genome. Proc Natl Acad Sci 100:15253–15258

Friebe B, Jiang J, Raupp W, McIntosh R, Gill B (1996) Characterization of wheat-allein translocations conferring resistance to diseases and pests: current status. Euphytica 91:59–87

Fu D, Uauy C, Distelfeld A, Blechl A, Epstein L, Chen X, Sela H, Fahima T, Dubcovsky J (2009) A kinase-START gene confers temperature-dependent resistance to wheat stripe rust. Science 323:1357–1360

Gao L, Turner MK, Chao S, Kolmer J, Anderson JA (2016) Genome-wide association study of leaf rust resistance in elite wheat breeding lines. PLoS ONE 11(6):e0148671:1–7

Gerechter-Amitai Z, Wahl I, Vardi A, Zohary D (1971) Transfer of stem rust resistance from wild diploid einkorn to tetraploid durum wheat by means of a tripod hybrid bridge. Euphytica 20:281–285

Giorgi D, Farina A, Grosso V, Gennaro A, Ceoloni C, Lucretti S (2013) FISHIS: fluorescence in situ hybridization in suspension and chromosome flow sorting made easy. PLoS ONE 8(5):e59974:1–4

Haldane J (1919) The probable errors of calculated linkage values, and the most accurate method of determining gametic from certain zygotic series. J Genet 8:291–297

Hayden MJ, Sharp PJ (2001) Sequence-tagged microsatellite profiling (STMP): a rapid technique for developing SSR markers. Nucleic Acids Res 29:e43–e43:1–6

Helguera M, Khan I, Kolmer J, Lijavetzky D, Zhong-Qi L, Dubcovsky J (2003) PCR assays for the Lr37-Yr17-Sr38 cluster of rust resistance genes and their use to develop isogenic hard red spring wheat lines. Crop Sci 43:1839–1847

Helguera M, Vanzetti L, Soria M, Khan IA, Kolmer J, Dubcovsky J (2005) PCR Markers for Triticum speltoides Leaf Rust Resistance Gene Lr51 and their use to develop isogenic hard red spring wheat lines. Crop Sci 45:728–734

Herrera-Foessel SA, Singh RP, Huerta-Espino J, Crossa J, Djurle A, Yuen J (2008) Genetic analysis of slow-rusting resistance to leaf rust in durum wheat. Crop Sci 48:2132–2140

Hiebert CW, Kolmer JA, McCartney CA, Briggs J, Fetch T, Bariana H, Choulet F, Rouse MN, Spielmeyer W (2016) Major gene for field stem rust resistance co-locates with resistance gene Sr12 in ‘Thatcher’ wheat. PLoS ONE 11:1–10

Hovmøller MS, Justesen AF (2007) Rates of evolution of avirulence phenotypes and DNA markers in a northwest European population of Puccinia striiformis f. sp. tritici. Mol Ecol 16:4637–4647

Huang L, Brooks SA, Li W, Fellers JP, Trick HN, Gill BS (2003) Map-based cloning of leaf rust resistance gene Lr21 from the large and polyploid genome of bread wheat. Genetics 164:655–664

Jighly A, Alagu M, Makdis F, Singh M, Singh S, Emebiri LC, Ogbonnaya FC (2016) Genomic regions conferring resistance to multiple fungal pathogens in synthetic hexaploid wheat. Mol Breed 36:127–131

Jin Y, Singh R, Ward R, Wanyera R, Kinyua M, Njau P, Fetch T, Pretorius Z, Yahayaoui A (2007) Characterization of seedling infection types and adult plant infection responses of monogenic Sr gene lines to race TTKS of Puccinia graminis f. sp. tritici. Plant Dis 91:1096–1099

Jin Y, Szabo LJ, Rouse MN, Fetch T Jr, Pretorius Z, Wanyera R, Njau P (2009) Detection of virulence to resistance gene Sr36 within the TTKS race lineage of Puccinia graminis f. sp. tritici. Plant Dis 93:367–370

Jordan KW, Wang S, Luna Y, Gardiner L-J, MacLachlan R, Hucl P, Wiebe K, Wong D, Forrest KL, Sharpe AG (2015) A haplotype map of allohexaploid wheat reveals distinct patterns of selection on homoeologous genomes. Genome Biol 16:48–52

Juliana P, Singh RP, Singh PK, Poland JA, Bergstrom GC, Huerta-Espino J, Bhavani S, Crossa J, Sorrells ME (2018) Genome-wide association mapping for resistance to leaf rust, stripe rust and tan spot in wheat reveals potential candidate genes. Theor Appl Genet 131:1405–1422

Kandiah P, Bariana H, Qureshi N, Wong D, Hayden M, Bansal U (2019) Identification of a new source of stripe rust resistance Yr82 in wheat. Theor Appl Genet 132:3169–3176

Kankwatsa P, Singh D, Thomson PC, Babiker EM, Bonman JM, Newcomb M, Park RF (2017) Characterization and genome-wide association mapping of resistance to leaf rust, stem rust and stripe rust in a geographically diverse collection of spring wheat landraces. Mol Breed 37:113–117

Keller B, Wicker T, Krattinger SG (2018) Advances in wheat and pathogen genomics: implications for disease control. Ann Rev Phytopath 56:67–87

Kerber E, Dyck P (1979) Resistance to stem and leaf rust of wheat in Aegilops squarrosa and transfer of a gene for stem rust resistance to hexaploid wheat. In: Proceeding of the 5th international wheat genetic symposium, New Delhi, India, pp 358–364

Klindworth DL, Niu Z, Cai X, Xu SS (2012) Introgression and characterization of a goatgrass gene for a high level of resistance to Ug99 stem rust in tetraploid wheat. G3 GenesGenomesGenet 2:665–673

Klymiuk V, Chawla HS, Wiebe K, Ens J, Fatiuinka A, Govta L, Fahima T, Pozniak CJ (2022) Discovery of stripe rust resistance with incomplete dominance in wild emmer wheat using bulked segregant analysis sequencing. Commun Biol 5:1–9

Klymiuk V, Yaniv E, Huang L, Raats D, Fatiuinka A, Chen S, Feng L, Frenkel Z, Krugman T, Lizdbarsky G (2018) Cloning of the wheat Yr15 resistance gene sheds light on the plant tandem kinase-pseudokinase family. Nat Commun 9:3735–3740

Knott D, Anderson R (1956) The Inheritance of rust resistance: I. The Inheritance of stem rust resistance in ten varieties of common wheat. Can J Agri Sci 36:174–195
Knott D (1962) The inheritance of rust resistance: IX. The inheritance of resistance to races 15B and 56 of stem rust in the wheat variety Khapstein. Can J Plant Sci 42:415–419

Knott D (1968) Translocations involving Triticum chromosomes and Agropyron chromosomes carrying rust resistance. Can J Genet Cyto 10:695–696

Kolmer JA (1994) Genetics of leaf rust resistance in three western Canada spring wheats. Plant Dis 78:600–602

Kolmer JA, Liu JQ (2002) Inheritance of leaf rust resistance in the wheat cultivars AC Majestic, AC Splendor, and AC Karma. Can J Plant Pathol 24:327–331

Kolmer JA, Singh RP, Garvin DF, Viccars L, William HM, Huerta-Espino J, Ogbonnaya FC, Raman H, Orford S, Bariana HS, Lagudah ES (2008) Analysis of the Lr34/ Yr18 rust resistance region in wheat germplasm. Crop Sci 48:1841–1852

Korte A, Farlow A (2013) The advantages and limitations of trait analysis with GWAS: a review. Plant Methods 9:1–9

Kosambi D (1943) The estimation of map distances from recombination values. Ann Hum Genet 12:172–175

Krattinger SG, Lagudah ES, Spielmeyer W, Singh RP, Huerta-Espino J, McFadden H, Bossolini E, Selter LL, Keller B (2009) A putative ABC transporter confers durable resistance to multiple fungal pathogens in wheat. Science 323:1360–1363

Kuraparthy V, Sood S, Gill BS (2009) Molecular genetic description of the cryptic wheat–Aegilops geniculata introgression carrying rust resistance genes Lr57 and Yr40 using wheat ESTs and synteny with rice. Genome 52:1025–1036

Lan C, Hale IL, Herrera-Foessel SA, Basnet BR, Randhawa MS, Huerta-Espino J, Dubcovsky J, Singh RP (2017) Characterization and mapping of leaf rust and stripe rust resistance loci in hexaploid wheat lines UC1110 and PI610750 under Mexican environments. Front Plant Sci 8:1450–1455

Lebowitz R, Soller M, Beckmann J (1987) Trait-based assays for the detection of linkage between marker loci and quantitative trait loci in crosses between inbred lines. Theor App Genet 73:556–562

Li Z, Xia X, Zhou X, Niu Y, He Z, Zhang Y, Li G, Wang D, Chen X (2006) Seedling and slow rusting resistance to leaf rust and powdery mildew in wheat. Theor Appl Genet 119:531–539

Liu J, Chang Z, Zhang X, Yang Z, Li X, Jia J, Zhan H, Guo H, Wang J (2013) Putative Thionin protein intermediate-derived stripe rust resistance gene Yr50 maps on wheat chromosome arm 4BL. Theor Appl Genet 126:265–274

Liu W, Rouse M, Friebe B, Jin Y, Gill B, Pumphrey MO (2011) Discovery and molecular mapping of a new gene conferring resistance to stem rust, Sr53, derived from Aegilops geniculata and characterization of spontaneous translocation stocks with reduced alien chromatin. Chr Res 19:669–682

Liu W, Frick M, Huel R, Nykiforuk CL, Wang X, Gaudet DA, Eudes F, Conner RL, Kuzyk A, Chen Q (2014) The stripe rust resistance gene Yr10 encodes an evolutionary-conserved and unique CC–NBS–LRR sequence in wheat. Mol Plant 7:1740–1755

Liu X, Huang M, Fan B, Buckler ES, Zhang Z (2016) Iterative usage of fixed and random effect models for powerful and efficient genome-wide association studies. PLoS Genet 12(10):e1006763

Liu JQ, Kolmer JA (1997) Inheritance of leaf rust resistance in wheat cultivars Grandin and CDC Teal. Plant Dis 81:505–508

Loegering W (1975) An allele for low reaction to Puccinia graminis tritici in Chinese Spring wheat. Phytopathology 65:925–927

Lowe I, Jankuloski L, Chao S, Chen X, See D, Dubcovsky J (2011) Mapping and validation of QTL which confer partial resistance to broadly virulent post-2000 North American races of stripe rust in hexaploid wheat. Theor Appl Genet 123:143–157

Maccarelli M, Zhang J, Bulli P, Abate Z, Chao S, Cantu D, Bossolini E, Chen X, Pumphrey M, Dubcovsky J (2015) A genome-wide association study of resistance to stripe rust (Puccinia striiformis f. sp. tritici) in a worldwide collection of hexaploid spring wheat (Triticum aestivum L.). G3: Genes Genomes Genet 5:449–465

Mago R, Bariana H, Dundas I, Spielmeyer W, Lawrence G, Pryor A, Ellis J (2005a) Development of PCR markers for the selection of wheat stem rust resistance genes Sr24 and Sr26 in diverse wheat germplasm. Theor Appl Genet 111:496–504

Mago R, Miah H, Lawrence G, Wellings C, Spielmeyer W, Bariana H, McIntosh R, Pryor A, Ellis J (2005b) High-resolution mapping and mutation analysis separate the rust resistance genes Sr31, Lr26 and Yr9 on the short arm of rye chromosome 1. Theor Appl Genet 112:41–50

Mago R, Spielmeyer W, Lawrence G, Lagudah E, Ellis J, Pryor A (2002) Identification and mapping of molecular markers linked to rust resistance genes located on chromosome 1RS of rye using wheat-rye translocation lines. Theor Appl Genet 104:1317–1324

Mago R, Tabe L, McIntosh RA, Pretorius Z, Kota R, Paux E, Wicker T, Breen J, Lagudah ES, Ellis JG, Spielmeyer W (2011) A multiple resistance locus on chromosome arm 3BS in wheat confers resistance to stem rust (Sr2),
leaf rust (Lr27) and powdery mildew. Theor Appl Genet 123:615–623

Mago R, Verlin D, Zhang P, Bansal U, Bariana H, Jin Y, Ellis J, Hoxha S, Dundas I (2013) Development of wheat-Aegilops speltoides recombinants and simple PCR-based markers for Sr32 and a new stem rust resistance gene on the 2SL1 chromosome. Theor Appl Genet 126:2943–2955

Mago R, Zhang P, Bariana H, Verlin D, Bansal U, Ellis J, Dundas I (2009) Development of wheat lines carrying stem rust resistance gene Sr39 with reduced Aegilops speltoides chromatin and simple PCR markers for marker-assisted selection. Theor Appl Genet 119:1441–1450

Mago R, Zhang P, Vautrin S, Šimková H, Bansal U, Lao M-C, Rouse M, Karaoğlu H, Periyannan S, Kolmer J (2015) The wheat Sr50 gene reveals rich diversity at a cereal disease resistance locus. Nature Plants 1:15186–15190

Manly KF, Cudmore RH Jr, Meer JM (2001) Map Manager QTX, cross-platform software for genetic mapping. Mam Genom 12:930–932

Marais G, Marais A (1994) The derivation of compensating translocations involving homoeologous group 3 chromosomes of wheat and rye. Euphytica 79:75–80

Marais G, Pretorius Z, Wellings C, Marais A (2005a) Leaf rust and stripe rust resistance genes transferred to common wheat from Triticum dicoccoides. Euphytica 143:115–123

Marais GF, McCallum B, Snyman JE, Pretorius ZA, Marais AS (2005b) Leaf rust and stripe rust resistance genes Lr54 and Yr37 transferred to wheat from Aegilops kotschyi. Plant Breed 124:538–541

Marais F, Marais A, McCallum B, Pretorius Z (2008) Leaf rust and stripe rust resistance genes Lr62 and Yr42 transferred to common wheat from Aegilops neglecta. Req. ex Bertol. Crop Sci 49:871–879

Marais G, Badenhorst P, Eksteen A, Pretorius Z (2010) Reduction of Aegilops sharonensis chromatin associated with resistance genes Lr56 and Yr38 in wheat. Euphytica 171:15–22

Marchal C, Zhang J, Zhang P, Fenwick P, Steuernagel B, Adamski N, Boyd L, McIntosh R, Wulff BBH, Pfeifer M, D’Ascenzo M (2013) Barley whole exome capture: a tool for genomic research in the genus Hordeum and beyond. Plant J 76:494–505

Martens JW, Dyck PL (1989) Genetics of resistance to rust in cereals from a Canadian perspective. Can J Plant Pathol 11:78–85

Mascher M, Richmond TA, Gerhardt DJ, Himmelbach A, Clissold L, Sampath D, Ayling S, Steuernagel B, Pfeifer M, D’Ascenzo M (2013) barley whole exome capture: a tool for genomic research in the genus Hordeum and beyond. Plant J 76:494–505

McFadden ES (1930) A successful transfer of emmer characters to vulgare wheat. J Am Soc Agro 22:1020–1034

McIntosh RA (1988) The Catalogue of gene symbols in wheat. In: Miller TE, Koeber RMD (eds), Proceedings of the 7th international wheat genetics symposium, vol 2, Institute of Plant Science Research, Cambridge, pp 1225–1323

McIntosh R (1991) Alien sources of disease resistance in bread wheats. In: Proceedings of Dr H Kihara Memorial international symposium on cytoplasmic engineering in wheat, pp 3–6

McIntosh R, Luig N (1973) Linkage of genes for reaction to Puccinia graminis f. sp. tritici and P. recondita in Selkirk wheat and related cultivars. Aus J Biol Sci 26:1145–1152

McIntosh R, Dyck P (1975) Cytogenetical studies in wheat. VII gene Lr23 for reaction to Puccinia recondita in Gabo and related cultivars. Aust J Biol Sci 28:201–212

McIntosh R, Dyck P, Green G (1977) Inheritance of leaf rust and stem rust resistances in wheat cultivars Agent and Agatha. Aust J Agri Res 28:37–45

McIntosh R, Dyck P, Cusick J, Milne D (1984) Cytogenetical studies in wheat. XIII: Sr35—a third gene from Triticum monococcum for resistance to Puccinia graminis tritici. Z Für Pflanzenzücht 92:1–14

McIntosh R, Wellings CR, Park RF (1995) Wheat rusts: an atlas of resistance genes. CSIRO Publishing, Melbourne, pp 1–204

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, Appels R, XC X (2014) Catalogue of gene symbols for Wheat: 2013–14 suppl pp 10–40

McIntosh RA, Dubcovsky J, Rogers WJ, Morris C, XC X (2017) Catalogue of gene symbols for wheat. pp 1–148

Meng L, Li H, Zhang L, Wang J (2015) QTL IciMapping: integrated software for genetic linkage map construction and quantitative trait locus mapping in biparental populations. The Crop J 3:269–283

Michelmore RW, Paran I, Kesseli R (1991) Identification of markers linked to disease-resistance genes by bulked segregant analysis: a rapid method to detect markers in specific genomic regions by using segregating populations. Proc Nat Acad Sci 88:9828–9832

Mítulo EA, Kristensen K, Hovmøller MS (2009) Evidence for increased aggressiveness in a recent widespread strain of Puccinia striiformis f. sp. tritici causing stripe rust of wheat. Phytopathology 99:89–94

Molnár-Láng M, Cereola C, Doležel J (2015) Alien introgression in wheat: cytogenetics, molecular biology, and genomics. Springer, Berlin, pp 1–213

Moore JW, Herrera-Foessel S, Lan C, Schnippenkoetter W, Ayliffe M, Huerta-Espino J, Lillemo M, Viccars L, Milne R, Periyannan S (2015) A recently evolved hexose transporter variant confers resistance to multiple pathogens in wheat. Nat Genet 47:1494–1498

Murray GM, Brennan JP (2009) Estimating disease losses to the Australian wheat industry. Austr Plant Path 38:558–570

Nevo E, Korol AB, Beiles A, Fahima T (2013) Evolution of wild emmer and wheat improvement: population genetics, genetic resources, and genome organization of wheat’s progenitor, Triticum dicoccoides, vol 10. Springer, Berlin, pp 364–368. https://doi.org/10.1007/978-3-662-07140-3

Nsabiyera V, Bariana HS, Qureshi N, Wong D, Hayden MJ, Bansal UK (2018) Characterisation and mapping of adult
plant stripe rust resistance in wheat accession Aus27284. Theor Appl Genet 131:1459–1467

Nsabiyera V, Baranwal D, Qureshi N, Kay P, Forrest K, Valárik M, Doležel J, Hayden MJ, Bariana HS, Bansal UK (2020) Fine mapping of Lr49 using 90K SNP chip array and flow-sorted chromosome sequencing in wheat. Front Plant Sci 10:1–10

Olson EL, Rouse MN, Pumphrey MO, Bowden RL, Gill BS, Poland JA (2013a) Introgression of stem rust resistance genes SrTA10187 and SrTA10171 from Aegilops tauschii to wheat. Theor Appl Genet 126:2477–2484

Olson EL, Rouse MN, Pumphrey MO, Bowden RL, Gill BS, Poland JA (2013b) Simultaneous transfer, introgression, and genomic localization of genes for resistance to stem rust race TTKSK (Ug99) from Aegilops tauschii to wheat. Theor Appl Genet 126:1179–1188

Pardey PG, Beddow J, Kriticos D, Hurley T, Park R, Duveiller E, Sutherst R, Burdon J, Hodson D (2013) Right-sizing stem-rust research. Science 340:147–148

Pasam RK, Bansal U, Daetwyler HD, Forrest KL, Wong D, Petkowskki J, Willey N, Randhawa M, Chhetri M, Miah H (2017) Detection and validation of genomic regions associated with resistance to rust diseases in a worldwide hexaploid wheat landrace collection using BayesR and mixed linear model approaches. Theor Appl Genet 130:777–793

Patpour MSH, Hansen JG, Justesen AF, Thach T, Rodriguez-Algab J, Hodson D, Randazzo B (2018) Epidemics of yellow and stem rust in southern Italy 2016–2017. https://globalrust.org/content/epidemics-yellow-and-stem-rust-southern-italy-2016-2017 Poster Accessed 3 July 2021

Periyannan S, Moore J, Ayliffe M, Bansal U, Wang X, Huang L, Deal K, Luo M, Kong X, Bariana H (2013) The gene Sr33, an ortholog of barley Mla genes, encodes resistance to stem rust race Ug99. Science 341:786–788

Pinto da Silva GB, Zanella CM, Martinelli JA, Chaves MS, Hiebert CW, McCallum BD, Boyd LA (2018) Quantitative trait loci conferring leaf rust resistance in hexaploid wheat. Phytopathology 108:1344–1354

Poland JA, Rife TW (2012) Genotyping-by-sequencing for plant breeding and genetics. Plant Genome 5:92–102

Preece C, Livarda A, Christin PA, Wallace M, Martin G, Poland JA, Rife TW (2012) Genotyping-by-sequencing for plant breeding and genetics. Front (2020) Fine mapping using 90K SNP chip array Lr49 and flow-sorted chromosome sequencing in wheat. Theor Appl Genet 131:1091–1098

Randhawa M, Bansal U, Valárik M, Klocová B, Doležel J, Bariana H (2014) Molecular mapping of stripe rust resistance gene Yr51 in chromosome 4AL of wheat. Theor Appl Genet 127:317–324

Randhawa MS, Bariana HS, Mago R, Bansal UK (2015) Mapping of a new stripe rust resistance locus Yr57 on chromosome 3BS of wheat. Mol Breed 35:1–8

Randhawa M, Bansal U, Lillemo M, Miah H, Bariana H (2016) Postulation of rust resistance genes in Nordic spring wheat genotypes and identification of widely effective sources of resistance against the Australian rust flora. J Appl Genet 57:453–465

Ranganathan J, Waite R, Searchinger T, Hanson C (2018) How to sustainably feed 10 billion people by 2050, in 21 charts. https://www.wri.org/blog/2018/12/how-sustainably-feed-10-billion-people-2050-21-charts. Accessed on 1 July 2020

Ray DK, Mueller ND, West PC, Foley JA (2013) Yield trends are insufficient to double global crop production by 2050. PLoS ONE 8(e66428):1–7

Riar AK, Kaur S, Dhaliwal H, Singh K, Chhuneja P (2012) Introgression of a leaf rust resistance gene from Aegilops caudata to bread wheat. J Genet 1–7

Riaz A, Athiyannan N, Periyannan SK, Afanasenko O, Mitrofanova OP, Platz GJ, Aitken EA, Snowden RJ, Lagudah ES, Hickey LT (2018) Unlocking new alleles for leaf rust resistance in the Vavilov wheat collection. Theor Appl Genet 131:127–144

Riley R, Chapman V (1958) Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature 182:713–715

Riley R, Chapman V, Johnson R (1968a) The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synopsis. Genet Res 12:199–219

Riley R, Chapman V, Johnson R (1968b) Introduction of yellow rust resistance of Aegilops comosa into wheat by genetically induced homeoeologous recombination. Nature 217:383–384

Qureshi N, Bariana H, Forrest K, Hayden M, Keller B, Wicker T, Faris J, Salina E, Bansal U (2017) Fine mapping of the chromosome 5B region carrying closely linked rust resistance genes Yr47 and Lr52 in wheat. Theor Appl Genet 130:495–504

Qureshi N, Kandiah P, Gessese MK, Nsabiyera V, Wells V, Babu P, Wong D, Hayden M, Bariana H, Bansal U (2018a) Development of co-dominant KASP markers co-segregating with Ug99 effective stem rust resistance gene Sr26 in wheat. Mol Breed 38:1–9

Qureshi N, Bariana H, Zhang P, McIntosh R, Bansal U, Wong D, Hayden M, Dubcovsky J, Shankar M (2018b) Genetic relationship of stripe rust resistance genes Yr34 and Yr48 in wheat and identification of linked KASP markers. Plant Dis 102:413–420

Qureshi N, Bariana H, Kumran VV, Muruga S, Forrest KL, Hayden M, Bansal U (2018c) A new leaf rust resistance gene Lr79 mapped in chromosome 3BL from the durum wheat landrace Aus26582. Theor Appl Genet 131:1091–1098

Randhawa M, Bansal U, Valárik M, Klocová B, Doležel J, Bariana H (2014) Molecular mapping of stripe rust resistance gene Yr51 in chromosome 4AL of wheat. Theor Appl Genet 127:317–324

Randhawa MS, Bariana HS, Mago R, Bansal UK (2015) Mapping of new stripe rust resistance loci Yr57 on chromosome 3BS of wheat. Mol Breed 35:1–8

Randhawa M, Bansal U, Lillemo M, Miah H, Bariana H (2016) Postulation of rust resistance genes in Nordic spring wheat genotypes and identification of widely effective sources of resistance against the Australian rust flora. J Appl Genet 57:453–465

Ranganathan J, Waite R, Searchinger T, Hanson C (2018) How to sustainably feed 10 billion people by 2050, in 21 charts. https://www.wri.org/blog/2018/12/how-sustainably-feed-10-billion-people-2050-21-charts. Accessed on 1 July 2020

Ray DK, Mueller ND, West PC, Foley JA (2013) Yield trends are insufficient to double global crop production by 2050. PLoS ONE 8(e66428):1–7

Riar AK, Kaur S, Dhaliwal H, Singh K, Chhuneja P (2012) Introgression of a leaf rust resistance gene from Aegilops caudata to bread wheat. J Genet 1–7

Riaz A, Athiyannan N, Periyannan SK, Afanasenko O, Mitrofanova OP, Platz GJ, Aitken EA, Snowden RJ, Lagudah ES, Hickey LT (2018) Unlocking new alleles for leaf rust resistance in the Vavilov wheat collection. Theor Appl Genet 131:127–144

Riley R, Chapman V (1958) Genetic control of the cytologically diploid behaviour of hexaploid wheat. Nature 182:713–715

Riley R, Chapman V, Johnson R (1968a) The incorporation of alien disease resistance in wheat by genetic interference with the regulation of meiotic chromosome synopsis. Genet Res 12:199–219

Riley R, Chapman V, Johnson R (1968b) Introduction of yellow rust resistance of Aegilops comosa into wheat by genetically induced homeoeologous recombination. Nature 217:383–384
Krasileva K, Kuo T, McKenzie N, Murata K, Nabeka Y, Paape T, Padmasaru S, Percival-Alwyn L, Kagale S, Scholz U, Sese J, Juliana P, Singh R, Shimizu-Inatsugi R, Swarbreck D, Cockram J, Budak H, Tameshige T, Tanaka T, Tsuji H, Wright J, Wu J, Steuernagel B, Small I, Cloutier S, Keeble-Gagnère G, Muehlbauer G, Tibbets J, Nasuda S, Melonek J, Hulj PJ, Sharpe AG, Clark M, Legg E, Bharti A, Langridge P, Hall A, Uauy C, Mascher M, Krattinger SG, Handa H, Shimizu KK, Distelfeld A, Chalmers K, Keller B, Mayer KFX, Poland J, Stein N, McCartney CA, Spannagl M, Wicker T, Pozniak CJ (2020) Multiple wheat genomes reveal global variation in modern breeding. Nature 588:277–283

Wang S, Basten C, Zeng Z (2012) Windows QTL Cartographer 2.5. Department of Statistics, North Carolina State University, Raleigh, NC http://statgen.ncsu.edu/qtlcart. WQTLCarthm

Wang S, Wong D, Forrest K, Allen A, Chao S, Huang BE, Maccaferri M, Salvi S, Milner SG, Cattivelli L (2014) Characterization of polyploid wheat genomic diversity using a high-density 90 000 single nucleotide polymorphism array. Plant Biotech J 12:787–796

Wicker T, Gundlach H, Spannagl M, Uauy C, Borrill P, Ramirez-Gonzalez RH, De Oliveira R, Mayer KF, Paux E, Choulet F (2018) Impact of transposable elements on genome structure and evolution in bread wheat. Genome Biol 19:103–110

Winfield MO, Allen AM, Burridge AJ, Barker GL, Benbow HR, Wilkinson PA, Coghill J, Waterfall C, Davassi A, Scopes G (2015) High-density SNP genotyping array for hexaploid wheat and its secondary and tertiary gene pool. Plant Biotech J 14:1195–1206

Winzeler M, Mesterházy Á, Park R (2000) Resistance of European winter wheat germplasm to leaf rust. Agron 20:783–792

Wright S (1968) Evolution and The Genetics of populations. In: Genetic and biometric foundations, vol I. The University of Chicago Press, Chicago. pp 1–48

Yu J, Presoir G, Briggs WH, Bi IV, Yamasaki M, Doebley JF, McMullen MD, Gaut BS, Nielsen DM, Holland JB (2006) A unified mixed-model method for association mapping that accounts for multiple levels of relatedness. Nat Genet 38:203–208

Yu L-X, Barbier H, Rouse MN, Singh S, Singh RP, Bhavani S, Huerta-Espino J, Sorrells ME (2014) A consensus map for Ug99 stem rust resistance loci in wheat. Theor Appl Genet 127:1561–1581

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.