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Genome-Wide Association Studies and Genomic Predictions for Climate Change Resilience in Wheat

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Abstract

Wheat is the most widely grown staple crop as compared to other food crops, covering 250 million hectares area around the world. It is predicted that many wheat-growing regions around the world are likely to face severe water and heat stress due to global climate change in the coming decades. Global climate change is largely assumed to drive the emergence of new abiotic and biotic stresses in wheat. Under such circumstances, understanding the underlying natural genetic variation and identifying novel tolerance alleles is a prerequisite for developing climate-resilient wheat cultivars. The most prevalent abiotic stresses, viz., heat and drought, are complex in genetic regulation and difficult to dissect in terms of high genotype x environment interaction and low heritability. However, the recent advances in wheat genomic approaches like genome-wide association mapping (GWAS) and genomic predictions (GP) can facilitate in understanding the genetic architecture of complex traits and identifying the novel tolerance alleles precisely on a wheat chromosome that are otherwise difficult through biparental mapping. GWAS utilizes the ancestral recombination events through a large population and creates an opportunity to identify closely linked markers,

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where genomic prediction incorporates available linked markers information into the prediction model to predict the breeding value of selected genotypes, which is essential for efficient marker-assisted breeding programmes to develop stress-tolerant wheat cultivars. The application of GWAS and GS is gaining importance in stress-resilient wheat breeding. Here, we summarized the recent application of GWAS and GP in wheat breeding to develop climate-resilient cultivars.

Keywords

Wheat · Climate change · GWAS · Genomic prediction · Mapping population · G × E interaction

3.1 Introduction

Wheat (*Triticum* spp.) is the second most important cereal crop and a major food source for more than 35% of the world population, providing 55% of the carbohydrates and 20% of the food calories consumed globally (Shewry and Hey 2015). Wheat is grown in all the regions of the world, occupying nearly 250 million hectares of area, and is the main source of income to millions of smallholding farmers (https://wheat.org/). It supersedes maize and rice as a source of protein in developing nations and is consumed by more than 2.5 billion people (http://www.fao.org). Urbanization, rising incomes and an increase in per capita wheat consumption are driving a rapid rise in global wheat demand. By 2050, wheat demand is expected to rise by at least 50%; hence the global economies are concentrating on expanding wheat output and production (Enghiad et al. 2017). However, wheat yields continued to increase, and through much of the last century, wheat was the most produced crop in the world. Global wheat-breeding programme with long-term approaches to enhance the grain yield has solved various challenges faced by wheat farmers to ensure the better wheat crop (Ramadas et al. 2019). However, global wheat production faces serious challenges posed by global climate change in terms of many abiotic (environmental factors) and biotic factors (diseases and pests). Wheat breeding programmes all over the world are focusing on developing climate change-resilient varieties that can be grown in harsh climates and have a higher survival rate.

Global climate change has a substantial effect on agricultural productivity. The effect of climate change in the form of enhanced incidence of stresses like high temperature, drought, salinity, waterlogging and mineral toxicity and biotic stresses are the major concerns to wheat scientists. Drought stress can be simply defined as a scarcity of water, leading to dramatic changes in the plants morphological, biochemical, physiological and molecular features (Sallam et al. 2019). Heat stress induced by high temperature is expressed as an increase in air temperature beyond a particular threshold level and period, resulting in irreversible damage to the plant (Farooq et al. 2011). A meta-analysis of 1700 published simulations predicted a rise of 2 °C mean temperature in temperate and tropical regions which results in a significant yield loss in wheat (Challinor et al. 2014). Similarly, modelling studies predicted around 6% decrease in wheat production, which is equivalent to a possible reduction of 42 Mt. per degree rise in temperature (Asseng et al. 2015). In India, climate change is predicted to reduce the wheat yield from 6 to 23% by 2050 and 15 to 25% by 2080 (Kumar et al. 2014). Globally, over 20% of the cultivable land is affected by salinity and which is further expected to increase day by day owing to environmental changes and anthropogenic exercises (Munns and Tester 2008). According to estimates, high salinity affects 20% of cultivated agricultural lands and 33% of irrigated agricultural lands. Additionally, abiotic stress factors such as drought, salinity, extreme temperatures and acidity, account for 60 to 82% of yield loss. The increase or decrease in wheat yield losses due to changing climate will depend on climatic effects on pathogens and the host plant itself (Juroszek and von Tiedemann 2013). The potential risk of climate change may lead to increased losses, decreased resistance effectiveness and evolution of newer pathotypes/pathogens (Chakraborty and Newton 2011). The efficacy of many of the rust resistance genes is driven by temperature. Any change in temperature regimes due to climate change may alter the resistant status of the wheat genotypes carrying these temperature-sensitive resistance genes. Increased CO_2 concentration and elevated temperatures due to climate change may increase wheat biomass which in turn increase the total leaf area available for pathogen/pest attack leading to the build up of more inoculum, which may lead to severe disease epidemics problem in wheat. The conducive environment for rust pathogen may also lead to higher rates of new pathotype evolution in nature, leading to the breakdown of many deployed resistance genes (Chakraborty and Newton 2011). The evolution of newer rust and other pathogen races occurs due to changes in climate, monoculture, cultivation practices, etc. Many newer pathotypes are being continuously evolved in nature. Therefore, sustaining wheat productivity levels is a major challenge in present agriculture, and the mitigation strategies must be streamlined towards boosting grain yield under limited resources environment.

Being a complex trait, the grain yield shows low heritability and is greatly influenced by the G × E and G × E × M interactions.

In some parts of the world, there have been concerns about the stagnation or decline of staple crop production. Wheat yield stagnation has been reported in 37% of wheat-growing regions. Further, in many areas the wheat yields are sustained owing to the availability of genetic resources for crop improvement for introgression of desired target traits through conventional breeding. However, improving stress tolerance through conventional breeding is labour intensive and time consuming as it involves complex genetics owing to multigene families/QTLs mediated molecular and physiological stress responsive mechanisms. Thus, traditional approaches and methods are not enough to resolve global food security issues in changing climatic scenario. Available genetic variability in the primary gene pool has been integrating with long-term traditional breeding methodologies; thus, there is need to create the new variability to improve desired target traits by speed breeding, mutation breeding, rapid generation advancement techniques and genome-wide selection approaches.

Old-generation markers like RFLP, RAPD, AFLP and SSR have served for more than three decades as a tool for marker-assisted selection and QTL identification. Traditional markers have played a key role in the identification and mapping of different QTLs, and marker-assisted selection was accelerated with the identification of different markers like SSR, STS, SNP, DArT, etc. However, the old-generation markers have less genome coverage and less abundance throughout the genome, and their analysis is laborious and requires more time (Desta and Ortiz 2014). The advances in sequencing technology and reduction in cost and time requirement have revolutionized the marker system. Although the bi-parental populations were more popular for the mapping study, but it has weakness in identifying QTL with small effect and methods applied for identifying QTL may also hinder crop improvement. The bi-parental mapping in addition to these also has few limitations: (i) bi-parental population do not possess the same level of allelic diversity throughout the breeding programme which makes them unsuitable as representative of the populations; (ii) developing population and its maintenance become costly affairs; (iii) identified QTLs are needed to be validated which require further efforts; and (iv) QTLs with small effects are entirely missed due to stringent significant threshold. With the availability of the NGS, the bi-parental mapping is being slowly replaced by association mapping, which is more cost-effective as well as precise, for QTL mapping and trait investigations.

Breeding and trait development have been accelerating with recent genomic technologies and resulting cultivars with enhanced environmental resistance and productivity. The quick selection and breeding of elite varieties with new genetic combinations is enabled by the identification of loci that contribute to characteristics and together with genomic-assisted breeding. Further, the availability of NGS approaches made the exploration of genetic diversity at nucleotide-scale precision through genome-wide association and improved phenomics platforms. In addition to genome-wide breeding tools, advances in engineering the spatial and temporal regulation of genes and pathways are increasingly accelerated by the targeted editing of genomes for stress tolerance traits in wheat (Juliana et al. 2019). Wheat breeding, combined with genome-wide studies, enhances the accuracy of breeding practices and saves time to deliver new wheat cultivars to farming community (Ahmar et al. 2020).

3.2 Vulnerabilities of Global Climate Change in Wheat Production

Global climate change in terms of drought and heat stress, particularly at the reproductive stage of the crop, can be a great threat to food security. The yield losses of wheat due to these abiotic stresses vary substantially among the wheat-producing nations. Furthermore, the frequency and magnitude of stress-induced crop losses may increase in the future owing to projected global temperature rise by 0.6–2.5 °C by 2050 and 1.4–5.8 °C by 2100 which are accompanied with increased incidence and severity of drought conditions (IPCC 2007).

According to the global climate model predictions, cereal crops were found to be most affected by drought and heat stress, and drought conditions were found to be more extensive and persistent in the coming future (Seneviratne et al. 2012; Trenberth et al. 2014). However, the effects of these stresses on yield are complex, and stress at any growth stage can affect crop yield. Drought and heat stress can affect wheat germination, vegetative growth, tiller production, dry matter partition, reproductive organ development, grain filling and grain quality (Gooding et al. 2003; Prasad et al. 2008; Sehgal et al. 2017). Studies showed that wheat crop yields are reduced when exposed to heat stress during the growing season due to accelerated crop phenological stages, which affect photosynthesis and respiration (Lobell and Gourdji 2012; Rezaei et al. 2015). A more pronounced effect of these abiotic stresses is observed during the reproductive phase of wheat, i.e. grain filling stages affecting yield in both qualitative and quantitative terms (Sehgal et al. 2017; Kumar et al. 2020). Exposure of wheat crop to heat stress (>25 °C) for 2–5 days at the reproductive stage has resulted in substantial damage to florets' fertility. These stresses will limit the grain filling duration resulting in the reduction of grain weight, grain number and quality of grains (Wardlaw 2002; Farooq et al. 2011). The linear association was observed with increased high-temperature duration at this grain filling stage and the grain weight loss (Prasad and Djanaguiraman 2014). Protein quality of wheat grain under drought stress and heat stress indicates differences in the concentration of total nitrogen, protein and glutenin, gliadin and albumin concentrations compared to grain quality under optimum conditions (Barnabás et al. 2008). Dough quality was found to deteriorate due to a rise in gliadin content compared to glutenin, and the ratio of large polymers was found to decline when exposed to heat stress (Panozzo and Eagles 1998; DuPont and Altenbach 2003). During grain filling stage, the heat stress reduces the non-structural carbohydrates accumulation in the endosperm of wheat grain (Hurkman et al. 2003; Plaut et al. 2004). Along with losses associated with the quality and yield, plant diseases are mostly considered as one of the most formidable obstacles. Climate change is leading to an increase in the CO_2 concentration, which has surpassed 400 ppm, and it can increase the crop yields of C_3 crops and can surge disease severity in wheat (Vary et al. 2015). Few rust resistance genes in wheat are temperature sensitive, and variation in temperatures during the growing season can alter their resistance pattern in the future. Since 2000, the new races of rust fungus *Puccinia striiformis*, which causes yellow rust, have been more aggressive at higher temperatures and are becoming prevalent worldwide (Milus et al. 2009). Elevated CO_2 level has increased the susceptibility of wheat varieties to the fungal pathogen *Fusarium graminearum due to the increase in the virulence of fungus* (Vary et al. 2015). Changes in environmental temperature can modify insect/pest physiology, behaviour, voltinism and distribution (Sandra et al. 2021). With an increase in temperature during wheat crop season, the aphid population and their distribution can be increased, incurring more yield losses (Alford et al. 2014).

3.3 Genetic Behaviour of Complex Traits

Developing abiotic stress resilience especially drought and heat tolerance in wheat is of extreme importance, as wheat is the main contributor to the world food supply. Responses to drought, heat and other abiotic stresses are complex and governed by the up- and downregulation of several genes and pathways, and each may have a minor to major effect on traits (Bernardo 2008). Stress responses are composed of a network of the regulatory process comprised of upstream (stress hormones, reactive oxygen species, gaso-transmitters, polyamines, phytochromes and calcium) and downstream (transcription factors) signalling as well as structural modification (cuticle outside plants, electrolyte leakage) in response to environmental factors (He et al. 2018). Some genes, viz. quantitative trait loci (QTL), show additive and non-additive gene effects. As the responses having polygenic inheritance and genotype adopt by its interaction with the environment, abiotic stress resilience characteristically has little heritability (Mwadzingeni et al. 2016). The genomic-assisted selection has still to contribute for the improvement in the genotypes of wheat for such abiotic stresses due to the polygenic nature of these traits, complexity and large size of the genome (Berkman et al. 2012).

Phenotyping for tolerance against abiotic stresses is also a major challenge due to the complexity of regulatory networks behind tolerance against these stresses (Vandenbroucke and Metzlaff 2013). The phenotype represents the effect of either a single gene or multiple genes, which may express different phenotypic outcomes depending on its interaction with each other and environment. Phenotyping is done at each growth stage under stress, which may also show variation in the crop's tolerance and susceptibility for the stress. The phenotyping techniques also limit the application of genomic tools in these stresses as the phenotyping has not been standardized. However, with the advent of effective high-throughput phenotyping platforms and phenomics tools, it has become possible to screen larger populations for multiple characteristics non-destructively under stress conditions. Further, high-throughput phenomics also enables the genetic dissection of complex stress-tolerant adaptive traits through providing reliable and accurate phenotypic data (Yang et al. 2013).

The precise estimation of the phenotypic response requires sophisticated tools and techniques to analyse the key parameters unique to stress tolerance. Therefore, the degree of stress and extent of resistance or vulnerability of a cultivar have been assessed using several parameters (Collins et al. 2008). The development of a high-throughput phenotyping platform for precise phenotyping is of utmost importance for dissecting these complex traits in developing climate-resilient wheat. The high-throughput phenotyping can aid the application of genomics tools for the improvement of these traits. Consequently, advanced phenotyping and genotyping stand as a tool in precision genomic breeding through genomic-wide characterization, selection and marker discovery, gene/QTL mapping and candidate identification.

3.4 Genomics Opportunities for Climate-Resilient Breeding

Plant breeders have continuously improved the genetic architecture of crops through conventional breeding technologies from many decades; now, breeders need to focus on global climate change and its effects on crop production. The advances in current breeding techniques showed it has the capacity to drastically decrease time to deliver improved crop varieties resilient to recent climate change. These techniques include advanced genomic approaches, which bypass some traditional approaches of the long selection process and indirect selection of beneficial genes and alleles in elite wheat cultivars. Genomics approaches provide an understanding of many phenomena such as genotype × environment interaction, identification and mapping of genes related to environmental stress tolerance, indirect selection of complex abiotic stress-tolerant genes and introduction of valuable alleles from wild relatives to wheat cultivars through marker-assisted selection. Hence, we highlighted the two recent genomics approaches of viz. genome-wide association studies (GWAS) and genomic prediction (GP) in wheat crop for the development of climate-resilient wheat cultivars.

3.4.1 Genome-Wide Association Studies (GWAS)

The genome-wide association studies (GWAS) are used to compute the correlation between single genome positions, primarily SNP (single nucleotide polymorphism) and the phenotype or trait of interest. GWAS is proven to be a very efficient approach for locating marker trait associations (MTAs) in wheat from the last decade due to the decreasing cost of high-throughput genotyping. Thus, GWAS is becoming a powerful tool for detecting QTLs associated with important traits of wheat (Cericola et al. 2017; Lopes et al. 2015), which is also supported by high-density SNP- genotyping platforms developed by Illumina (Wang et al. 2014) and Affymetrix (Allen et al. 2017). Till now, the identification of genetic basis for underlying phenotypic variation in plants has been achieved through traditional linkage mapping based on genetic maps. The diversity of experimental population in traditional linkage mapping ranges from F_2 population to MAGIC (multiparent advanced generation intercross) population (Kover et al. 2009). However, in traditional linkage mapping, the RILs (recombinant inbred lines) are the most widely used population owing to immortal and completely homozygous nature, enabling the replication of each line throughout the locations and environmental seasons (Bergelson and Roux 2010). However, the traditional linkage mapping leads to two drawbacks: the limited genetic diversity, which is in the range of parental lines used to develop segregating populations, and the limited recombination events. These drawbacks can be overcome through GWAS, which takes advantage of ancestral recombination events accumulated over thousands of generations and uses natural linkage disequilibrium (LD) to identify polymorphism ultimately associated with phenotypic variation (Nordborg and Weigel 2010). For successful GWAS studies, it is a prerequisite to have the large diversity panel of germplasm having less similarity in the pedigree as well as with respect to adaptation and photoperiod requirement (Yu and Buckler 2006). GWAS makes use of natural linkage disequilibrium (LD) to identify polymorphism ultimately associated with phenotypic variations.

For successful GWAS studies, there are prerequisites of few important things, which include (1) diverse association mapping panel, (2) high-throughput genotyping platform, and (3) good phenotyping site, especially in the case of abiotic stresses like drought and heat and artificial epiphytotic platform (control environment) in the case of disease studies. The association mapping panel used in GWA mapping should be of appropriate size. The panel size is a very crucial factor in getting meaningful results; increasing population size will improve the power of association as it can define a sufficient portion of the phenotypic and genotypic variation. The individual genotypes of association mapping should represent sufficient diversity in terms of geographic origin, growth habit, etc. The known association mapping panels of wheat used globally includes, the global spring wheat association mapping panel consisting of 882 landraces and 912 improved accessions (493 experimental lines and 419 cultivars) originated from 107 countries which include old and new wheat accession from the year 1920 to 2012. In case of winter wheat the known GWAS panel are, NSGC core panel consist of 4007 accessions and other panel includes hard winter wheat association mapping panel 1 and 2 (HWWAMP 1 and HWWAMP 2). Recently in the case of durum wheat, a global durum wheat panel (GDP) of 1011 genotypes was developed that captures 94–97% of original diversity, and it consists of a wider representation of durum germplasms, landraces along with the selection of primitive tetraploid and emmer wheat (Mazzucotelli et al. 2020).

The second important requirement of GWAS is the high-throughput genotyping platform that can provide complete wheat genome coverage and fast genotyping for a large set of germplasm. The present next-generation sequencing (NGS) provides thousands of SNPs covering most of the genomic region of wheat. NGS techniques provide huge numbers of markers within a short time frame and can genotype a large number of genotypes simultaneously using genotyping arrays or chips. The first high-throughput genotyping array developed in wheat is popularly known as Illumina iSelect 9 K bead chip assay (Cavanagh et al. 2013). Following this high-throughput genotyping array, a 90 K iSelect Assay was developed consisting of allelic ratio deviating between hexaploid and tetraploid wheat, which includes approximately 90,000 gene-associated SNPs covering all 7 groups of wheat chromosomes (Wang et al. 2014). Recently the Breeders' 35 K Axiom® array, a 35,143 SNP-based genotyping assay, was derived from 8,19,517 previously characterized wheat markers and was developed in 384 samples format array. This assay is highly suited for genotyping of elite hexaploid wheat accessions and is most useful to characterize diverse global collections of wheat, including landraces and elite genotypes derived from the commercial breeding programmes. Additionally, Breeders' 35 K Axiom® array is found to be a cost-effective and efficient platform for screening a large number of wheat genotypes (Elbasyoni et al. 2019).

Even though genomics techniques are fast forward and gaining wide importance, the importance of phenotype is still evident from the fact that almost all genomic techniques, including QTL mapping, fine mapping, GWAS and genomic prediction, depend immoderately on precise and accurate phenotyping. The climate change imparts abiotic stress like drought and heat on wheat crop, and this stress creates huge threats to wheat production as its leads to change in plant's basic metabolism which ultimately represents the phenotype of crops; hence precise phenotyping is very much important to get success in both GWAS and genomic prediction. The screening of genotypes under ideal stress conditions will provide a true potential of given genotypes. A recent study by Mamrutha et al. (2020) prioritized hotspot locations in India for drought and heat screening of wheat, which reveals that Indore location in the state of Madhya Pradesh of India (ICAR- IARI, regional station, Indore) has the highest drought stress intensity index of 0.89 among 15 studied locations, and also it is observed that India can be a hub for wheat research across the globe for screening what germplasm for changing climatic conditions like heat and drought stress.

3.4.1.1 GWAS for Heat and Drought Stress in Wheat

Several GWAS studies have been conducted in wheat for climate change-associated stresses, which mostly include global stresses, viz. drought and high temperature. The summary of GWAS studies of wheat, including cultivated hexaploid and tetraploid wheat for both spring and winter wheat, along with synthetic wheat is discussed in this section (Table 3.1). The GWAS panels used in these studies were comprised of diverse genotypes, which include historic genotypes along with advanced cultivars; the diversity was maintained through core collection and pre-breeding lines developed from three-way crosses. The size of GWAS panels used in these studies was in the range of 91–2111 wheat accessions (Ayalew et al. 2018; Elbasyoni et al. 2017). The phenotypic traits or class of traits used in these GWAS studies are related to (i) agronomic traits, viz. grain yield, 1000 grain weight, spike length, tillers number, plant height, days flowering and days to maturity; (ii) physiological traits like normalized difference vegetation index (NDVI), canopy temperature (CT), SPAD, leaf rolling and biomass; (iii) biochemical traits such as cell membrane stability, proline content, etc.; and (iv) seedling traits, viz. seminal root angle, root length, seedling length, root:shoot ratio, days to wilting, number of leaves, water content and chlorophyll content. Most of these studies are conducted under field conditions by creating and maintaining stress conditions through different water regimes for drought stress phenotyping and late sowing for heat stress phenotyping. However, few studies are conducted under controlled environmental conditions by creating artificial drought stress through PEG 6000 solution treatment at the seedling stage (Elbasyoni et al. 2017; Lin et al. 2019) and for heat stress through control environment treatments of 45 °C (Elbasyoni et al. 2017) and 40/35 °C day/night temperature regimes (Maulana et al. 2018). The speed of these GWAS studies was truly accelerated by available NGS and high-throughput genotyping techniques. Millions of SNP markers spread throughout the wheat genome are now available through new genotyping techniques. The wheat GWAS

Table 3.1 List of MTAs identified for drought- and heat-related stress in wheat and its cultivated and wild tetraploid relatives (*T. turgidum* and *T. turgidum* ssp. *dicoccoides*)

S. No.	Trait class/ trait	GWAS panel and markers	Phenotyping condition	No of MTAs	Chromosome	Reference
1	Seedling length, days to wilting, leaf wilting	138 diverse spring wheat genotypes with 407 DArT markers		104	–	Ahmed et al. (2021)
2	Seminal root angle and nodal root angle	393 durum RILs form NAM genotype with 2541 genome-wide DArT markers	"Clear pot" method for root phenotyping	7	6A	Alahmad et al. (2019)
3	Four drought tolerance indices	382 advanced lines of spring wheat genotype with GBS markers	Rainfed condition for two crop seasons	175	4A is most prominent	Ballesta et al. (2020)
4	Cell membrane relative injury (RI%)	2111 spring wheat accession, 9 K SNP wheat iSelect assay	Drought—(60% PEG600) solution for 24 h at 10 °C in the dark Heat water bath at 45 °C for 1 h	Drought (RI %)—15 Heat (RI%) – 16	1A, 1B, 2A, 4A, 6B, 7B 1B, 2A, 4B, 6B, 7B	Elbasyoni et al. (2017)
5	Normalized difference vegetation index (NDVI)	248 elite durum wheat, Illumina iSelect 90 K wheat SNP assay	NDVI—Arial NDVI—Ground based At different growth stages and water regime	NDVI—Arial, 55 MTAs NDVI –ground based 41 MTAs SPAD—39 MTAs Leaf rolling—9 MTAs	1A, 1B, 2B, 4A, 4B, 5A, 6A, 6B, 7A 1A, 3B, 5A, 5B, 7A 3A	Condorelli et al. (2018)

6	Tillers number	92 Iranian wheat genotypes, 6349 SNP from 15 K wheat Infinium array	Two water regimes—Full irrigation and drought	Total tillers number—13 MTAs Fertile tillers number—11 MTAs	1A,2A,6A,6B,6D,7A 1A,2A,2B,5B,7A,7D	Bilgrami et al. (2020)
8	Stress tolerance indices	208 durum lines, 6211 DArTseq SNPs	Three treatments 1. Yield potential (YP) 2. Drought stress (DT) 3. Heat stress (HT)	YP—121 MTAs (8 traits) DT—159 MTAs (8 traits) HT—112 MTAs (7 traits)	All 14 chr. Mostly on 2A & 2B All 14 chr. Maximum on 2B & 5B All 14 chr. Except 3B	Sukumaran et al. (2018)
9	Agronomic traits 1. GY/plant 2. Effective spike no/plant 3. Spikelet no/spike 4. TGW, 5. Plant height 6. Spike length	277 winter wheat accessions, 395681 SNPs derived from transcriptome and genome sequencing	4 treatments (no stress + drought stress + heat stress + combine drought & heat stress) in 30 environments	Drought stress—65 MTAs Heat stress—27 MTAs Combined stress-30 MTAs	–	Li et al. (2019)
10	Stress tolerance indices	290 lines of WAMI population, 15,737 SNP markers	Under drought and irrigated condition	Irrigated—114 MTAs Drought—85 MTAs For 6 traits	1A, 1B, 2A, 2B, 3D, 5A, 6A, 6B, 7B, 7D 1B, 2A, 2B, 3A, 3B, 4B, 5A, 5B, 6A, 6B, 7A, 7B, 7D	Abou-Elwafa and Shehzad (2020)

(continued)

Table 3.1 (continued)

S. No.	Trait class/ trait	GWAS panel and markers	Phenotyping condition	No of MTAs	Chromosome	Reference
11	Agronomic traits (14 traits)	92 diverse bread wheat lines, 9236 polymorphic markers from 15 k Illumina chip	Four different stress treatments	Non stress—148 MTAs, Drought—95, Heat—151 and combined heat and drought—93	All chromosomes except 2A & 4D 1B, 2B, 3D, 4B, 6A, 6B, 6D, 7A, 7B, 7D 2A, 3A, 3D, 5B, 6A, 6D, 7A,7B, 7D	Qaseem et al. (2019)
12	Root length	91 winter wheat collections	Water stress (PEG 6000) and non-stress conditions	Stress—2 MTAs Non-stress—3 MTAs	2B & 3B 3B, 4A, 5B	Ayalew et al. (2018)
13	Seedling data 1. Leaf chlorophyll 2. Shoot length 3. No. of leaves/ seedling 4. Seedling recovery	200 red winter wheat genotypes	Heat stress (40/35 °C) dd Optimal temp (25/20 °C)	Leaf chlorophyll—6QTLs No of leaves/ seedling—3 QTLs Seedling recovery—6 QTLs	2B, 2D, 4A, 4B 3A, 3B, 5A 2A, 2B, 2D, 3A, 7A, 7B	Maulana et al. (2018)
14	Grain yield- and yield-related traits	123 synthetic hexaploidy wheat, 35648 GBS markers	Drought stress condition for 2 years	194 MTAs for GY and yield-related traits	All 21 chromosomes	Bhatta et al. (2018)
15	Drought tolerance indices	290 genotypes of WAMI population, 15735 SNP markers	Drought and irrigated condition	205 MTAs for six drought indices	Well water—1A, 1B, 2A, 2B, 2D, 3A, 3B, 3D, 4D, 5A, 5B, 6A, 6B, 7B, 7D Drought- 1B, 2A, 2B, 3A, 3B, 4B, 5A, 5B, 6A, 6B, 6D, 7A, 7B, 7D	Elwafa and Shehzad (2020)

16	Agronomic and physiological traits	339 pre-breeding lines derived from the three-way top-crosses, 7180 SNP markers	Well water and drought condition for 3 year	Well water—10 MTAs Drought—11 MTAs	NDVI—3A CT– 7B Plant ht.—7A DTH—3A, 6B DTM—1B G Y—4A, 6B Spike Len—2D, 3B No of grains/spike—6B, 3A Kernel abortion—3A, 3B TGW—3B	Shokat et al. (2020)
17	Biomass and agronomic traits	100 wheat genotypes, 15600 DArTseq-derived SNP markers	Drought stress and non-stress	Drought stress—46 MTAs Non-stress—41 MTAs	1B, 1D, 2A,2B,2D, 3B,4A, 4D, 5A,5B, 6A, 6B,7A, 7B, 7D 1A, 1B, 2A, 2B, 2D, 3A, 3B, 4A, 4D, 5A, 5B, 5D	Mathew et al. (2019)
18	Agronomic traits (10 traits) for heat stress	205 wheat accessions, 11911 SNP markers	Heat stress (late sown), 3 locations, 3 years	69 QTLS (10 significant +59 suggestive)	1A,1B,1D, 2A,2B,2D,3A,3B,3D,4D,5B,5D,6A,6B,7A,7B,7D	Kumar et al. (2020)
19	Yield and quality traits	96 bread wheat accessions, Illumina 90 K Infinium SNP array	Normal and water stress condition	28 MTAs—Normal condition 44 MTAs -drought stress condition	1A, 1B, 2A, 2B, 3B, 3D, 4D, 5A, 6B, 7A, 7B 1A,1B,2B,2D,3A,3B,3D,4A,4B,5A,5B5D,6B, 7B,7D	Ahmed et al. (2020)
20	Agronomic traits	320 spring wheat accessions, 9626 SNPs	Irrigated and rainfed	20 MTAs in irrigated, 19 MTAs in rainfed	1A, 1B, 2A, 2B, 2D, 3A, 3B, 4A, 4B, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B (for five traits in both condition)	Gahlaut et al. (2019)

(continued)

Table 3.1 (continued)

S. No.	Trait class/ trait	GWAS panel and markers	Phenotyping condition	No of MTAs	Chromosome	Reference
21	Agronomic traits (7 drought indices)	287 wheat lines (WAMI II), 1863 DArT markers	3 contrasting irrigation condition with 2 locations	11 MTAs	1B, 2B, 6A (5 are unmapped)	Edae et al. (2013)
22	Yield and yield-related traits	123 Pakistan historic wheat cultivars, 14960 SNPs	Rainfed condition for 3 years	44MTAs	1AL, 1BS, 2AL, 2BS, 2BL, 4BL, 5BL, 6AL, 6BL	Ain et al. (2015)

studies for drought and heat stress discussed here also strongly depend on available fast genotyping techniques. The initial GWAS studies in wheat utilised DArTseq SNP markers (Edae et al. 2013), followed by newly developed wheat-specific genotyping assay or chips like 9 K SNP wheat iSelect Assay, Illumina iSelect 90 K, 15 K wheat Infinium array and Breeders' 35 K Axiom$^{®}$ array. All these genotyping platforms provide large number of SNP markers which can cover broad genotypic variations of the GWAS panel. The large SNP data generated through these platforms then need to be filtered based on missing data points, heterozygosity and minor allele frequencies before carrying out GWAS analysis. The different high-throughput techniques available in wheat have specific advantages and limitations (Chawade et al. 2019). Hence, the choice of genotyping platform should be objective specific and should also consider the knowledge about computational techniques for large data analysis. The GWAS studies using a large association panel with millions of SNPs can also have few limitations such as missing data, rare alleles, false discovery rates, etc. These GWAS limitations can be overcome through newer computational methods having improved statistics. The discussed wheat GWAS studies here applied different computational models, and the most used model in these studies was MLM (mixed linear model). The MLM model takes care of multiple levels of relatedness, effectively controls population structure and Type I and Type II error rates (Yu et al. 2006); however, the MLM model can be computational challenging for large datasets. The other analysis models used in these studies were GLM (General Linear Model), CMLM (compressed mixed linear model) and FarmCPU (Fixed and random model Circulating Probability Unification). The FarmCPU is a recent model, which combines both fixed effect and random effects in analysis and improves statistical power with reduced computational times (Liu et al. 2016). In the discussed studies for GWAS in wheat for drought and heat tolerance (Table 3.1), the FarmCPU model was used to identify significant MTAs for tillers number using 92 Iranian wheat genotypes in drought condition which identified 13 significant MTAs for tillers number and 11 MTAs for fertile tiller number on chromosome 1A, 2A, 2B, 5B, 6A, 6B, 6D, 7A, 7B and 7D. (Bilgrami et al. 2020). Another GWA study by Bhatta et al. (2018) using 123 synthetic hexaploid wheat accessions for grain yield and yield-related traits under drought condition using FarmCPU model identified 194 MTAs covering all 21 chromosomes of wheat.

GWAS mapping approaches also have few limitations, of which false positives are considered as the major limitation due to the large genetic diversity of the association panel, and to overcome this limitation, multiple correction methods are used. The significance of MTAs passing the threshold p-value (0.001) is usually determined by using Bonferroni correction (BC) and false discovery rate (FDR). These multiple correction methods were used to test the significance of millions of markers in GWAS mapping. The BC defines the threshold level of significance for several traits at once, while FDR calculates significance for each trait independently. It is suggested that the studies which focused on identifying candidate loci/genes for further genetic and molecular studies should use low FDR values (Alqudah et al. 2018).

Several GWAS studies in wheat have demonstrated the power of association mapping in identifying candidate genes for tolerance to climate change-related drought and heat stress. Alahmad et al. (2019) identified a major QTL region on the distal end of chromosome 6A for seminal root angle in drought condition, which overlaps with the gene model representing a *NAC* transcription factor, a fatty acid hydroxylase family protein and SAWADEE homeodomain protein 2. In the case of durum wheat, a GWAS study using 208 durum lines phenotyped with three different treatments, viz. yield potential, drought and heat stress, identified a QTL hotspot for stress tolerance indices on chromosomes 2A and 2B, and one SNP (100035706) in these regions was related to gene *DMAS1-A,* and the protein is characterised as deoxymgiretic acid syntheses 1 (Sukumaran et al. 2018). The GWAS study of 277 winter wheat accessions under drought and heat stress condition for six agronomic traits identifies haplotype blocks containing candidate gene for stress tolerance, which include a dwarfing gene *Rht-D1* located on haplotype block on chromosome 4D and another three *WRKY* genes (*TaWRKY 8, TaWRKY 45 and TaWRKY 70*) which confirm the genomic region with multiple abiotic stress tolerance on haplotype block on chromosomes 6A and 6D (Li et al. 2019). The GWA study of physiological traits like NDVI and CT under drought condition using 339 pre-breeding lines derived from three-way crosses observed a candidate gene *TauE/SaFE* responsible for taurine metabolism and anion export across cell membrane in stress condition on chromosome 4A; another candidate gene *"Loci09764454"* was observed coding for heat stress protein on chromosome 2D, and on chromosome 7B, two SNPs were associated with the candidate genes coding for Omega *glidin-D1* and asa-like protein of bread wheat (Shokat et al. 2020).

3.4.1.2 Genome-Wide Association Studies for Salinity Stress Tolerance in Wheat

Wheat production is globally hampered by soil salinity and sodicity. Moreover, there is less attention given to salinity stress due to lack of suitable phenotypic methods and lack of diversity with a narrow gene pool for salinity tolerance in wheat, which impaired the progress of salinity tolerance; hence the importance of GWAS comes into the picture to identify novel salinity tolerance genes in wheat. Unlike major abiotic stresses, drought and heat, very few GWA studies for salinity stress in wheat were conducted (Table 3.2). These studies are mainly based on phenotyping of Na^+ and K^+ ions accumulation at germination and seedling stage under salt stress conditions (Oyiga et al. 2018; Genc et al. 2019; Li et al. 2020; Chaurasia et al. 2020), whereas the physiological traits like root and shoot length were used by Liu et al. (2018) and Li et al. (2020) and grain yield in field condition by Hu et al. (2021). These GWA studies utilised diverse association mapping panels, which include exotic wheat cultivars, landraces, double haploids and synthetic wheat lines genotyped with SNP markers in all studies, expect a study by Liu et al. (2018), which used 546 SSR markers for genotyping of 277 wheat accessions for association mapping of salt tolerance indices at germination and seedling stage. The association mapping study by Genc et al. (2019) in 100 bread wheat accessions for leaf Na^+ accumulation in artificial pot treatment with Na^+ humate solution leads to

Table 3.2 List of MTAs identified for salinity stress tolerance in wheat

Sr.	Trait class/trait	GWAS panel and markers	Phenotyping condition	No. of MTAs	Chromosome	Reference
1	Ion traits (Na^+ and K^+ leaf content)	150 winter and facultative wheat, 18085 SNPs	Salt stress (150 mM NaCl) and non salt stress condition (3 location)	37 QTLs	1BS, 1DL, 2AL, 2BS, 3AL	Oyiga et al. (2018)
2	Leaf Na + accumulation	100 bread wheat entries, 41035 SNPs	Pot treatment (8 g/kg, Na^+ humate)	7 MTAs	2A, 2B, 2D, 4B, 4D, 5B, 7A	Genc et al. (2019)
3	Salt tolerance index (germination and seedling)	227 wheat accessions, 546 SSR markers	Artificial seawater solution treatment	24 MTAs (8 MTAs germination +16 MTAs seedling)	1A, 5A, 1B, 2B, 3B, 6B, 7B, 1D	Liu et al. (2018)
4	Yield and yield-related traits	191 wheat accessions, 387657 SNPs	Salt stress condition	48 SNPs for yield	2D, 3A, 5A, 5B, 7A	Hu et al. (2021)
5	Salt tolerance index (germination)	307 wheat accessions, 402176 SNPs	Different salt solutions	117 MTA	Mostly clustered on 1A (72MTAs), 3B (10 MTAs), 6B (20 MTAs)	Yu et al. (2020)
6	Leaf chlorophyll, membrane stability, ion traits (Na^+, K^+)	135 diverse wheat genotypes, 17927 SNPs	Vegetative salt tolerance (hydroponics) 100 mM NaCl	Na^+ (7MTAs) K^+ (5 MTAs) Na/K (4 MTAs)	(Na^+) 1BL, 2BL, 3AL, 3BL, 5Al, 5DL, 7BL (K^+) 2AL, 5AL, 5DL, 7BL	Chaurasia et al. (2020)

identification of 7 MTAs distributed on chromosomes 2A, 2B, 2D, 4B, 4D, 5B and 7A, and further four candidates genes, viz. calcium-transporting ATPase, $Na^{(+)}/H^{(+)}$ antiporter NhaB, AquaporinTIF1–4 and Aquaporin PIP2 having the potential function in Na^+ accumulation, were identified.

3.4.2 Genomic Prediction

Genomic prediction (GP) is widely used in crops nowadays. GP explores available molecular markers to predict genomic estimated breeding values based on new marker-based models (Bhat et al. 2016; Xu et al. 2020). GP approach comprises two populations, viz. training population (reference population) and breeding population (testing population). Training set/population is employed to predict the genomic estimated breeding values for testing set/population based on a marker-based statistical model developed using phenotypic and genotypic information of the training population (Xu et al. 2020). GP for self- and cross-pollinated crops follows the different skim, as the training population and breeding population varies. The GP has two advantages over traditional MAS as there is no need to unearth the QTL related to target traits, and phenotyping for the breeding population can be exempted which reduce the time for GP. Thus, GP provides the opportunities to enhance the genetic gain of multigenic traits per unit time and cost. The high-throughput techniques of the genome-wide association have become cheaper, and several new markers have been developed in a large population with or without the reference genome sequence (Bhat et al. 2016). The next-generation sequencing has provided an SNP genotyping platform through genotyping by sequencing; hence the availability of the SNP markers for genome-wide studies has increased, so the precision in the marker-trait relation has also increased. The availability of such high-precision molecular marker and its platform made the GP routine work for crop improvement in both model and non-model crop species. Genotyping by sequencing using NGS has increased the precision in predicting the genomic-estimated breeding values (Xu et al. 2020). The GP must combine with high-throughput phenotyping to acquire maximum genetic gain from complex traits. The gradual decrease in sequencing cost has made sequencing of complete genome possible for all important crops, which will accelerate the genomic selection in present and future also.

Presently, there are plenty of models available for genomic predictions (Fig. 3.1) depending on the prediction accuracy and genetic gain from the selection. Every model of prediction has different responses due to the variety in assumption(s) for the variance of complex traits (Desta and Ortiz 2014). Several models were already used for prediction in wheat for different complex traits. Saint Pierre et al. (2016) evaluated 803 spring wheat lines at 5 locations with several traits characterized for grain yield and agronomic traits with the best linear unbiased prediction (BLUP) model, which suggested that the best prediction was observed when the genotypic and pedigree data combined in the model and their interaction with the environment. Heffner et al. (2011) used multifamily prediction models to enhance genomic selection accuracy by 28% compared to MAS for 374 winter wheat by comparing

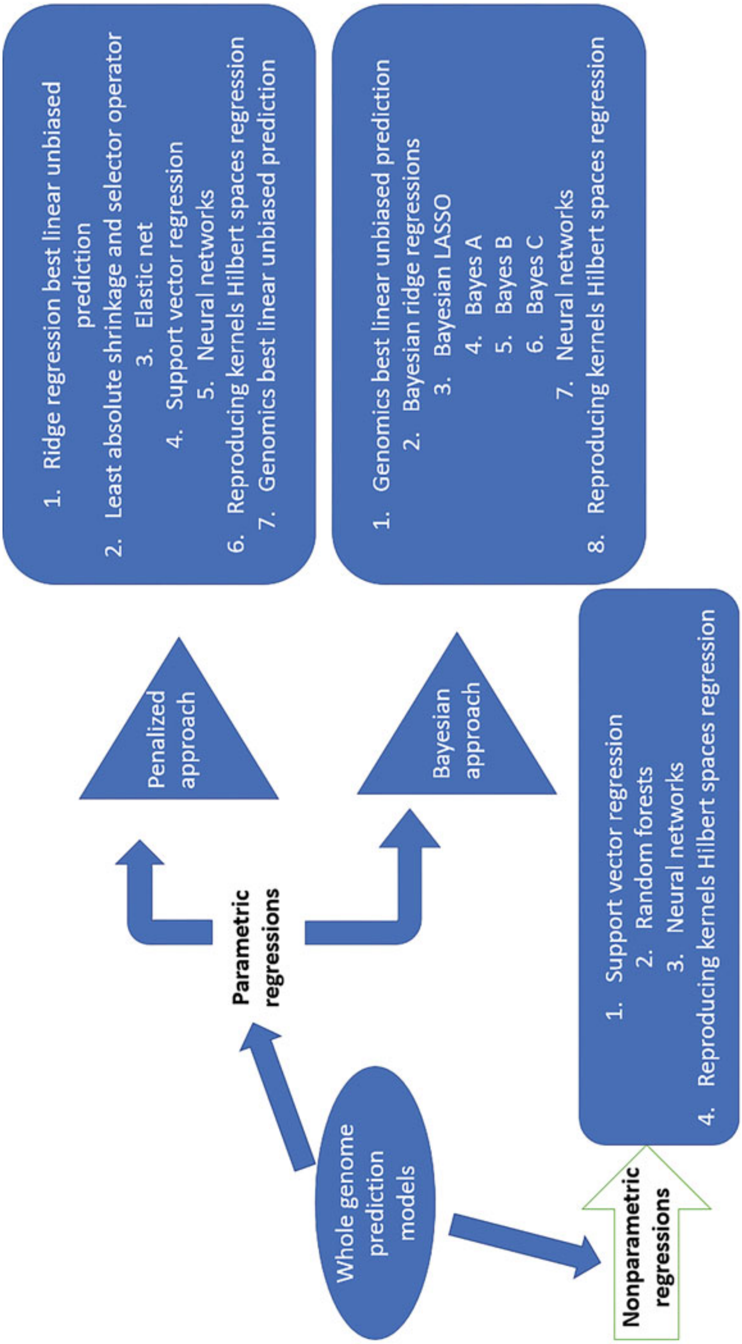

Fig. 3.1 Classification of whole-genome prediction models

13 agronomic traits. Rutkoski et al. (2012) used ridge regression (RR), Bayesian LASSO (BL), reproducing kernel Hilbert spaces (RKHS) regression, random forest (RF) regression and multiple linear regression (MLR) models for genomic prediction of fusarium head blight resistance in wheat and suggested that use of genome-wide marker apart from QTL-targeted marker has higher accuracy for genomic prediction with these models. The genomic best linear unbiased prediction (GBLUP) and a Bayesian regression method (BayesR) were used to predict genomic estimated breeding values (GEBVs) for rust resistance in 206 hexaploid wheat landraces, and the study showed that GBLUP has higher prediction accuracy when training population has a close relationship with reference population (Daetwyler et al. 2014). Sehgal et al. (2020) conducted a study on 4302 advanced bread wheat lines to integrate genetic architecture of grain yield and yield stability into the prediction model to increase the accuracy of the prediction. Though the different models have been evaluated for their prediction accuracy in wheat for different traits, the prediction accuracy may change for the different models based on the assumptions made and markers used.

3.4.2.1 Case Studies of Genomic Prediction for Abiotic Stress Tolerance in Wheat

The changing climate mostly triggers abiotic stresses like heat and drought. These abiotic stresses are quantitative in nature and genetically complex. Hence, these traits are ideal candidates for genomic prediction studies. However, the stress phenotyping requires specialised phenotypic equipments and platforms which restrict breeders with minimal budget and resources. The high phenotyping cost of abiotic stresses and availability of low-cost genotyping platforms in wheat make genomic prediction a more economical and attractive alternative for selection. A genomic prediction was applied in 254 advanced breeding lines of wheat by Poland et al. (2012) for agronomic traits, viz. grain yield, 1000 kernel weight and days to heading in contrasting irrigation conditions; the genomic prediction accuracy and the correlation between GEBV and phenotype were in the range of 0.3–0.5 for all three traits. For complex abiotic traits, indirect selection through secondary traits is common practice; secondary traits become important when they are highly heritable and genetically correlated with target traits. In wheat canopy temperature (CT) and normalized difference vegetation index (NDVI) are excellent secondary traits for genomic prediction for grain yield in heat and drought stress conditions owing to high heritability and genetic correlation with grain yield. Rutkoski et al. (2016) applied genomic selection using 555 bread wheat lines in five environments for secondary traits NDVI and CT to training and test population and grain yield only on training population were modulated as multivariate and compared to univariate models through grain yield only on a training set. The results showed that secondary traits NDVI and CT increase grain yield accuracy by 70% in the genomic prediction model, which indicates that NDVI and CT can be used in genomic selection in wheat during early crop stage under stress condition.

3.5 Prospects

It is long known that the abiotic stress in field conditions often occurs simultaneously rather than individual stress, which may create errors in phenotyping in field conditions. Hence, automated high throughput with high-precision phenotyping should be focused rather than normal field phenotyping with different irrigation and sowing dates. The traits used for phenotyping of stress tolerance should be prioritised based on their correlation with grain yield. Several agronomic, biochemical, physiological traits were used at different growth stages, and their relationship with grain yield is stage-specific, and each trait shows a differential association with grain yield. Hence, the target phenotyping stress indicator traits need to prioritise based on their relationship with grain yield and heritability of the trait(s). Major emphasis is needed to develop user-friendly and economic phenotypic platforms for continuous screening of elite wheat genotypes in breeding programmes and genomics studies. Likewise, the use of possible thermal infrared imaging and multispectral imaging in both ground- and aerial-based phenotypings should be considered.

GWAS has been attempted in wheat from more than a decade, although as stated above, GWAS faces new challenges with complex quantitative traits due to their genetic interaction (epistasis) and G × E interaction; the adoption of new statistical models and experimental design for these interactions should be considered in future. Now there is sufficient availability of stable and major genomic regions identified through GWAS studies for climate stress tolerance. Therefore, it demands the cloning of these genes identified in the genomic regions associated with target traits. The characterization of genes underlying these identified genomic will speed up the breeding programme for climate-resilient breeding.

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