Theoretical and Applied Genetics (2020) 133:1569–1602
https://doi.org/10.1007/s00122-020-03583-3

REVIEW

Genetics of yield, abiotic stress tolerance and biofortification in wheat (*Triticum aestivum* L.)

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Received: 30 August 2019 / Accepted: 13 March 2020 / Published online: 6 April 2020

Abstract

Key message **A review of the available literature on genetics of yield and its component traits, tolerance to abiotic stresses and biofortification should prove useful for future research in wheat in the genomics era.**

Abstract The work reviewed in this article mainly covers the available information on genetics of some important quantitative traits including yield and its components, tolerance to abiotic stresses (heat, drought, salinity and pre-harvest sprouting = PHS) and biofortification (Fe/Zn and phytate contents with HarvestPlus Program) in wheat. Major emphasis is laid on the recent literature on QTL interval mapping and genome-wide association studies, giving lists of known QTL and marker-trait associations. Candidate genes for different traits and the cloned and characterized genes for yield traits along with the molecular mechanism are also described. For each trait, an account of the present status of marker-assisted selection has also been included. The details of available results have largely been presented in the form of tables; some of these tables are included as supplementary files.

Introduction

Wheat is the most widely grown crop globally as well as in Asia, with China ranking first and India ranking second in terms of annual grain production (Supplementary Table 1). Wheat is also a major source of calories for growing world population. It is widely known that in Asia (particularly in China and India), the green revolution of late 1960s was followed by another green evolution during 1980s (Yadav et al. 2019). During these two green revolutions, the rate of annual growth in wheat production globally and in Asia was ~ 3%, which declined to < 0.9% in recent years, thus causing concern. Although currently, the global wheat production has been able to meet the current demand and consumption, there are concerns whether or not we will be able to achieve the targets of at least ~ 858 Mt in 2050, as against current global production of 763 Mt. This amounts to at least ~ 15% desired increase in global wheat production (1.5% annual increase) during the next three decades to feed the global human population, which is estimated to reach ~ 9.7 billion in 2050 (https://population.un.org/wpp/). This increase in production needs to be achieved despite shrinkage in arable land due to urbanization, and the projected impact of expected climate change.

Wheat is one of the most widely studied crops, particularly at the level of cytogenetics and genetics, despite the fact that it is a hexaploid ($2n = 6x = 42$) with three closely related sub-genomes. The hexaploid nature of bread wheat can tolerate major structural and numerical changes in its chromosome constitution. Therefore, it was possible to produce whole sets of aneuploids including monosomics, trisomics, tetrasomics and compensating nullisomic-tetrasomics (NT) in this crop. This became possible mainly due to painstaking efforts of (late) Ernie Sears, who worked in Columbia, Missouri, USA. The two-way classification of wheat with three sub-genomes (each having seven chromosomes) and seven homoeologous groups (each group with three chromosomes) also became possible only due to the availability of complete set of compensating NT lines developed by Sears. These homoeologous relationships were later extended to chromosomes of related alien species also. Later, a set of more than 400 deletion stocks covering the entire genome also became

Communicated by Chun-Hai Dong.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00122-020-03583-3) contains supplementary material, which is available to authorized users.

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available through the research work undertaken at Kansas State University (KSU), USA (Endo and Gill 1996). A variety of aneuploids, NT lines, ditelocentrics and the deletion stocks that are available in wheat made it possible to map genes for phenotypic traits and associated marker loci on individual chromosome arms, and to develop and compare the genetic (linkage) and physical maps. The aneuploids also allowed discovery of a diploidizing system (*Ph1* locus), production of alien addition and substitution lines using a number of alien species including rye (*Secale cereale*), barley (*Hordeum vulgare*) and several species from the genera *Aegilops* and *Agropyron/Thynopyrum/Elymus/Dasypyrum.* The development of alien addition and substitution lines also made it possible to transfer segments of alien chromosomes carrying desirable genes to high-yielding wheat cultivars, so that a large number of current wheat cultivars carry segments of alien chromosomes (see Gupta 2016; Gupta and Vasistha 2018 for details).

During the last three decades, wheat biotechnology also became a major thrust area of research in Asia (particularly in China and India) and elsewhere in the world, so that USA, China and India were the three top-ranking countries in terms of the number of documents published (Giraldo et al. 2019). Initially, during mid-1990s, DNA-based molecular markers were developed, so that significant progress was made in the development of DNA-based molecular markers like SSRs, AFLPs, DArT markers and SNPs. These markers were used for the construction of molecular, genetic and physical maps and for conducting QTL analysis including single-marker analysis (SMA), interval mapping (IM) and genome-wide association studies (GWAS). The traits which received major attention for the study of genetics using QTL analysis (including GWAS) included yield attributes, tolerance against abiotic and biotic stresses, grain quality and biofortification.

Starting in 2005, the research involving whole-genome sequencing also gained momentum. The large size of wheat genome (~ 17 Gb) with major fraction represented as repetitive sequences, made sequencing of the genome of this crop to be the most difficult and therefore the last to be achieved among all major crops. For the purpose of whole-genome sequencing, the availability of ditelocentric stocks allowed separation of individual chromosome arms using flow sorting for the purpose of preparing arm-wise BAC libraries and BAC-based physical maps and optical maps for each of the 40 arms (excluding the chromosome 3B). This exercise allowed completion of high-quality gold-standard whole-genome sequence for wheat cv. Chinese Spring (CS) (IWGSC RefSeq v1.0) followed by identification of core genome (~ 120,000 genes) and pangenome (~ 140,000 genes) of this polyploid species (IWGSC 2018; for a review, see Gupta and Vasistha 2018). More recently, a concept of super-pangenome involving pangenome of a crop along with the pangenomes of alien species has been proposed (Khan et al. 2020). This super-pangenome in wheat may have as many as 200,000 genes. Whole-genome optical maps and contigs assembled from whole-genome-shotgun (WGS) PacBio SMRT reads also allowed release of another improved version of wheat genome sequence (IWGSC RefSeq v2.0) in July 2019; this improved version is being utilized for annotation of all genes, which should become available later in 2020. These resources are now being extensively utilized for in silico identification of genes that were cloned and sequenced in other species. A transcription atlas was also prepared for all genes (Ramírez-González et al. 2018; Xiang et al. 2019), thus paving way for identification of candidate genes for all traits.

In parallel with the progress in wheat cytogenetics and genomics, research activity in the area of genetics of all important agronomic traits in wheat using Mendelian methods of genetics was also in progress in several countries including Asian countries. Thus, genes were identified for all kinds of traits including grain yield and its contributing traits, grain quality traits, tolerance to biotic and abiotic stresses including resistance to a variety of diseases among biotic stresses and heat, drought, salinity and pre-harvest sprouting (PHS) among abiotic stresses. Genetics of nutrient (N/P) use efficiency and also that involved in grain micronutrient contents like Fe and Zn has also been studied in recent years (see later for details).

This article describes the progress made globally in the field of genetics of several traits including yield and its components, tolerance to abiotic stresses including heat, drought, salinity and PHS and biofortification (including content/concentration of Fe, Zn and phytate). The genetics of other traits including quality traits and tolerance to biotic stresses (mainly diseases) is covered in several other articles in this special issue. The literature on cytogenetics will not be covered in this review, since a detailed review on this subject written by one of us appeared recently (Gupta and Vasistha 2018).

Genetics of simple and complex traits

The genetics of different traits in wheat was initially studied using Mendelian approach, which involved intercrossing followed by the study of segregation patterns in the F_2 generation. This was followed by the use of monosomic analysis during 1950s and thereafter. Biometrical approaches were also used during 1960s and 1970s, where genetic variances and effects were estimated without identification of individual genes. Later, starting in 1990s, study of genetics of individual traits involved identification of specific QTL/genes and their locations on specific chromosomes using QTL analysis. With the availability of molecular markers,

three major approaches that could be used for QTL analysis included single-marker analysis (SMA), QTL interval mapping (IM) and genome-wide association studies (GWAS). SMA was initially used in some studies, but this method being inefficient, only the other two approaches were later utilized for identification of thousands of QTL/marker-trait associations (MTAs) involving a variety of traits; these MTAs were later also used for marker-assisted selection (MAS). The knowledge generated globally through the use of these approaches in wheat will be briefly reviewed with emphasis on the work done in Asia including China and India.

Nomenclature for QTL

Before we review the literature on genetics of different traits, we like to briefly discuss the issue of naming QTL. In the published literature on QTL analysis or GWAS, we noticed that QTL have not always been named using standard nomenclature. In some cases, only the associated markers or markers flanking the interval carrying the QTL are given (Rustgi et al. 2013). We also noticed that the results of GWAS are generally reported as MTAs, but in some cases, no distinction is made between MTAs and QTL and the terms are used interchangeably, as done by Julian et al. (2019) in their recent detailed study involving GWAS. We believe that QTL are identified in IM, while only MTAs (and not QTL) are identified during GWAS. Of course, GWAS results can be utilized for further analysis to identify QTL as done in some recent studies (Condorelli et al. 2018; Touzy et al. 2019).

The rules of nomenclature of wheat QTL are available at https://wheat.pw.usda.gov/ggpages/wgc/98/ Intro.htm; these rules require a QTL to be named starting with letter "Q" followed by a trait designator (2–4 letters; the first letter capitalized), a period, a laboratory designator, a hyphen (-) and the symbol for the chromosome on which the QTL is located. Different QTL for the same trait on one chromosome need to be assigned the same symbol except for the addition of a period and an arabic numeral after the chromosome designation. All characters in the locus symbol should be italicized. For example, *QYld.psr-7B.1* and *QYld.psr-7B.2* would designate two yield QTL identified in chromosome 7B by the John Innes Centre, UK. On a map, these could be abbreviated as *QYld.psr.1* and *QYld.psr.2*.

When names are given, the above rules have not always been followed. As an example in a recent important paper by Juliana et al. (2019), QTL are named without specifying the trait for the QTL, thus making the reader find out the trait for which the QTL is referred, as shown in the following examples: *Qcim.2A.1*, *Qcim.3B.2*, *Qcim.6A.7* and *Qcim.4D.1*. This has been done partly because a QTL may control more than one trait (personal communication), although we believe that in cases of a QTL controlling multiple traits, a symbol like *mt* could be used for the trait.

Grain yield and its components

Grain yield is a complex polygenic trait with several component traits. The trait also has low heritability, since it is influenced by environment and exhibits high level of genotype × environment interaction. Also, grain yield-related QTL are present on all the 21 wheat chromosomes. These features make the study of genetic architecture of this trait challenging indeed. Despite this, a large number of genetic studies including QTL analysis have been conducted to study the genetics of grain yield.

During 1950s, initial studies on genetics of yield in wheat involved monosomic analysis and use of intervarietal substitution lines for identification of chromosomes carrying genes for a variety of yield traits. For instance, in a study involving monosomic analysis, chromosomes 6D and 4A were found to carry genes for grain weight, chromosomes 4A, 4B, 2B, 3A and 1B were found to carry genes for grain length, and chromosomes 1A and 1B were found to carry genes for grain width (Giura and Saulescu 1996). Similarly, all 21 chromosomes were found to carry genes influencing grain traits in an important study involving intervarietal chromosome substitutions (Kuspira and Unrau 1957).

Starting in early 1990s, as many as 750 QTL were reported in ~ 26 studies involving IM and ~ 2000 MTAs were identified in ~ 12 studies using GWAS. Some of the QTL for yield and component traits were also pleiotropic in nature affecting more than one grain-related traits. Q × Q and Q × Q × E interactions were also reported (Goel et al. 2019). For IM and GWAS, a large number of mapping populations (mainly DH and RIL populations) and association mapping panels were utilized (Supplementary Table 2). In the studies already conducted, only yield or individual component traits were investigated in some studies, but in majority of cases, yield and its component traits were studied together. An up-to-date information on QTL and MTAs for yield and its component traits reported in different studies involving IM and GWAS are summarized in Supplementary Tables 2 and 3 (see Guan et al. 2018 for some details). Further large-scale genome-wide studies are needed to identify stable MTAs involving large collection of wheat germplasm grown in diverse environments.

Although many reports (as above) are available on QTL analysis involving IM and GWAS for yield and related traits, only limited information has been utilized for MAS leading to selection of superior wheat lines in actual breeding programs. Since yield and component traits are available on all the 21 chromosomes, simple MAS may not be suitable and major concerted efforts involving genomics-based approaches like genomic selection are needed to supplement

conventional wheat breeding for improvement of these traits. Utilization of genomic resources for wheat improvement through genomics-based breeding has recently been demonstrated in a major study conducted jointly by CIMMYT and its research partners from South Asia, Americas and Africa (Juliana et al. 2019). In this study, extensive phenotyping data were collected on 44,624 wheat genotypes using global wheat trials of the CIMMYT. GWAS was conducted using 3485 lines from EYT (Elite Yield Trials) and a number of other panels (ranging from 157 to 7887 lines). Data for as many as 50 important trait-environment combinations were utilized for this GWAS leading to identification of as many as 138 QTL and sub-QTL, which included 131 QTL/MTAs for yield-related traits that were located at 14 genomic regions. The most significant MTAs and the corresponding known QTL or genes were also utilized for developing a reference wheat genotype–phenotype map using IWGSC reference genome RefSeq v 1.0 (see Supplementary Fig. 1); this demonstrated the utility of the RefSeq as a platform for comparing and validating GWAS results.

Genetic studies have also been conducted on all component traits. Following are the three important component traits, which will receive relatively detailed treatment in this section: (1) plant height, involving dwarfing genes; (2) number of productive tillers, fertile spikelets/spike and number of fertile florets or grains per spike or per spikelet; (3) grain weight and grain size (length, width and thickness).

Plant height and dwarfing genes

Plant height is an important trait that influences yield and harvest index, so that much of the green revolution was brought about due to the introduction of dwarf wheat varieties using Rht genes.

Rht genes for reduced plant height Plant height is controlled by as many as 25 Rht genes (*Rht1-Rh25*). Among the commonly used Rht genes, the two common Rht genes that are found in most dwarf wheats include *Rht1* (*Rht-B1b*) and *Rht2* (*Rht-D1b*), which are gibberellin (GA) insensitive, and therefore have a negative impact on yield under conditions of low water supply. Due to insensitivity to endogenous gibberellins, these genes are responsible for decreased cell wall extensibility (Keyes et al. 1990) and reduced epidermal cell length (Keyes et al. 1989; Hoogendoorn et al. 1990). Size and number of epidermal cells are also known to vary in different tissues (Beemster and Masle 1996; Wenzel et al. 1997). The smaller cell size associated with *Rht1* and *Rht2* produces concomitant reduction in sub-crown internode and coleoptile length, and leaf area of wheat seedlings (Allan et al. 1961; Allan 1989; Botwright et al. 2001).

Rht1 and *Rht2* dwarfing genes were also subjected to molecular characterization; it was shown that both encode DELLA proteins, which repress GA-responsive growth, leading to ~ 20% reduction in plant height (Peng et al. 1999). Several mutants of these two Rht genes have been studied and have been shown to confer extreme dwarfism (reduction of 50% in plant height) by producing more active forms of these growth repressors (Pearce et al. 2011). Of these mutants, *Rht1* mutant resulted due to an intragenic insertion, leading to 30-amino acid insertion within the DELLA domain, while *Rht*2 mutant resulted due to an increase in gene copy.

Alternate dwarfing genes Although *Rht1* and *Rht2* have been widely used, they are responsible for reduced yield under dry and hot climate, so that a search was made for alternative GA-sensitive dwarfing genes. As a result, a number of alternate Rht genes have been identified, which are responsible for reduced plant height associated with sensitivity to exogenous gibberellic acid (GA) (Gale and Youssefian 1985; Ellis et al. 2005). Four GA-sensitive genes, which have been subjected to some detailed studies, include *Rht8*, *Rht12*, *Rht14* and *Rht24*, which neither reduce coleoptile length nor seedling vigor (Rebetzke et al. 1999; Botwright et al. 2001; Ellis et al. 2005) under dry and hot conditions. However, there are also other GA-sensitive dwarfing genes (*Rht4*, *Rht5*, *Rht9*, *Rht12*, *Rht13*, *Rht14*), which have not been subjected to similar detailed studies.

Among GA-sensitive Rht genes, *Rht8* is carried by several European cultivars including Cappelle-Desprez, which is a high-yielding European winter wheat with durable adult plant resistance to stripe rust. The gene has been widely used for adaptation to dry climate in several Mediterranean countries in Eastern and Southern Europe. Due to climate change, *Rht8* is also considered to be an important gene for more Northern latitudes in Europe. Plants carrying *Rht8* have semi-dwarf lodging resistance phenotype, which is attributed to short internodal segments associated with reduced cell elongation (Gasperini et al. 2012). The reduction in cell elongation is not due to defective gibberellin biosynthesis or signaling, but possibly due to reduced sensitivity to brassinosteroids (BR). During 1930s, *Rht8* along with early flowering gene *Ppd-D1a* was introduced from the Japanese variety Akakomugi into European wheats. *Rht8* is located on chromosome 2D at a distance of 0.6 cM from the marker *Xgwm261* (Korzun et al. 1998). The gene was subjected to a detailed study including high-resolution fine mapping in view of its potential for more efficient future deployment in international breeding programs (Gasperini et al. 2012). In order to overcome the adverse effects of *Rht1* and *Rht2* under reduced water supply, it is recommended that *Rht8* may be used along with *Rht1* and *Rht2*, which are already present in a number of high-yielding wheat cultivars.

Rht12 was also subjected to a detailed study of its effects on seedling vigor, seedling roots, leaf and stem morphology,

spike development and carbohydrate assimilation and distribution. It was discovered that *Rht12* was responsible for decreased plant height (up to 40%), stem length (48% for peduncle) and leaf length (up to 30% for flag leaf), but the thickness of the internode walls and width of the leaves increased (Chen et al. 2013). The seedling vigor, especially coleoptile length and root traits at the seedling stage, was not adversely affected. There was also an increase in duration of the spike development phase, the proportion of spike dry weight at anthesis and floret fertility (14%) in the autumn sowing experiment. However, anthesis was delayed by ~ 5 days, and the plants had reduced grain size and reduced ability to support spike development after anthesis; even the dominant *Vrn-B1* allele could not compensate for these negative effects. However, despite these negative effects, grain yield was similar between the dwarf and tall lines in the autumn sowing experiment. Thus, *Rht12* could substantially reduce plant height without altering seedling vigor and significantly increased spikelet fertility in the favorable autumn sowing environment and therefore could be utilized for developing dwarf wheat cultivars.

Rht14 also confers semi-dwarf plant height, while retaining longer coleoptiles and early seedling vigor. Using two RIL populations in durum wheat, *Rht14* was mapped on chromosome 6A in the genomic region 383–422 Mbp flanked by the markers *GA2oxA9* and *wmc753* in a Bijaga Yellow/Castelporziano RIL population. *Rht14* has also been recommended for use as an alternative to *Rht1* for development of cultivars suitable for deeper sowing in dry environments and in conditions of conservation agriculture where crop residues are retained (Vikhe et al. 2019).

Rht24 is another newly discovered gene and was first detected as a QTL named *QPH.caas-6A* with flanking markers *TaAP2* and *TaFAR*. The gene is responsible for reduced plant height by an average of 6.0–7.9 cm across environments and was associated with an increased thousand grain weight (TGW) of 2.0–3.4 g. The findings indicate that *Rht24* is a common dwarfing gene in wheat breeding and can be exploited using marker-assisted selection (Tian et al. 2017).

The above account about four specific Rht genes suggests that *Rht8*, *Rht12*, *Rht14* and *Rht24* can certainly be used as alternate GA-sensitive dwarfing Rht genes for wheat improvement without having adverse effect under low moisture or dry and hot conditions. Markers associated with these GA-sensitive dwarfing genes are also available and can be used for MAS. However, the successful utilization of these genes in breeding will require careful selection, since each of these genes may be associated with genes having adverse effect.

Productive tiller number (PTN) and fertile spikelets/grain number per spike (fSNS/GNS)

Productive tiller number (PTN) is defined as the number of tillers that produce spikes and seeds. Similarly, number of fertile spikelets per spike is defined as the number of spikelets (per spike), which bear seeds. The grain number (GN) is directly related to number of only fertile spikelets and not the total number spikelets per spike, which ranges from 24 to 28, each spikelet with several florets (some spikelets would bear no seeds). The number of florets and therefore number of seeds also differ among different spikelets (Li et al. 2016). The size of seeds also differs in different spikelets in a spike, the middle spikelets having more seeds, which are also heavier relative to those in the basal and terminal spikelets (Boz et al. 2012).

Spikelet number per spike and fertile florets (grain number) per spikelet also have a significant effect on TGW, although in a recent study it has been shown that the grain number per spike remains stable despite breeding for high yield (Philipp et al. 2018). The grain number per spikelet is also determined by the fertility of each floret. It has been shown that at the white anther stage, a wheat spikelet normally produces up to 12 florets primordia: However, during development, more than 70% of the florets abort. Recent studies have suggested that wheat grain yield is affected more by variation in grain number per spike than by variation in grain size, the two generally having negative correlation (Lynch et al. 2017; Feng et al. 2018).

A number of QTL have been identified for PTN as well as for fSNS/GNS. QTL associated with PTN were mapped on chromosomes 1D, 2B, 2D,3A, 4D, 5A, 6A and 6B and those for fSNS were mapped on chromosomes 1A, 1B, 2A, 2D, 3A, 3B, 5A, 6A, 7A, 7B and 7D (for details of references, see Wang et al. 2018a, b). Most QTL had additive effects, although QTL with dominant and epistatic effects were also available. QTL for PTN also occur very close to the QTL for fSNS on chromosomes 4A and 6A, suggesting either possible pleiotropic effect of the same QTL or tightly linked QTL. KASP markers were developed for some of the associated markers, which should facilitate their use for MAS.

A number of quantitative trait loci (QTL) affecting fSNS or GNS have also been mapped in wheat. Globally > 100 QTL for GNS have so far been identified using IM and GWAS (see Guan et al. 2018 for references). These QTL are distributed on all the 21 wheat chromosomes, but are primarily located on the following 12 chromosomes: 1A, 1B, 1D, 2A, 2D, 3B, 3D, 4A, 5A, 6A, 7A and 7D. Some of the QTL for GNS are co-located with those for GW on chromosome 4A. However, the gene(s) underlying the above QTL for PTN and fSNS are largely unknown (Wu et al. 2006; Liu et al. 2013; Bhusal et al. 2017; Guo et al. 2017; Sukumaran et al. 2018), although 46 genes have been identified, cloned

and characterized, when we consider all yield and component traits together (see later for some details).

Grain weight and grain size (length, width and thickness)

Detailed studies have also been conducted to identify QTL for grain weight and grain size. As a result, a number of markers associated with grain traits are now available and can be utilized for MAS keeping in mind that often a negative correlation occurs between grain size and grain number.

QTL analysis for grain weight (*GW*) Dozens of studies involving QTL analysis for GW have been conducted in hexaploid wheat (Varshney et al. 2000; Ammiraju et al. 2001; Dholakia et al. 2003; Kumar et al. 2006; Ramya et al. 2010; Mir et al. 2012; Shukla et al. 2015;Tyagi et al. 2015; Bhusal et al. 2017, 2018; Krishanappa et al. 2017; Kumari et al. 2018; Goel et al. 2019). The QTL identified in different environments largely differed, suggesting the presence of significant QTL × environment (Q × E) interactions. However, there were also QTL, which were detected in more than one environment; these are sometimes described as stable QTL (Table 1) and therefore may be important for improving grain traits using MAS. Some QTL were also pleiotropic, affecting more than one grain traits. Q × Q and Q × Q × E interactions were also reported in some studies (Bhusal et al. 2017; Goel et al. 2019). In a recent study, a "QTL hot spot" for GW was identified on chromosome 4B of hexaploid wheat and can be used for MAS. A novel QTL for heat susceptibility index for 1000-grain weight (HSI-TGW) was also identified on chromosome arm 4BL (Guan et al. 2018). In order to bring precision to the markers to be used for MAS, a study involving both CIM and GWAS was also conducted leading to identification of QTL, which were available from both CIM and GWAS (Mir et al. 2012). Similarly, meta-QTL analysis was conducted leading to identification of 23 meta-QTL on 8 chromosomes (Tyagi et al. 2015). Three of these MQTL were also reported earlier by Zhang et al. (2010). Some QTL were also co-localized with QTL for leaf rust resistance gene *Lr22a* and grain weight gene *TsGW2-6A* (Su et al. 2011). Meta-analysis for grain traits has also been conducted in tetraploid wheats, leading to identification of rare alleles of the gene *GRF4* associated with larger grains (Avni et al. 2018).

QTL analysis for GW was also carried out in tetraploid and diploid wheats. In tetraploid durum wheat, using a RIL population derived from the cross PDW233 × Bhalegaon4, Patil et al. (2013) identified 11 main-effect QTL and six digenic interactions for GW. The QTL for test weight (TW) and GW belonged to chromosomes 2A, 2B, 4B and 7A; at least one QTL each for TW and TGW was shown to be co-localized on chromosome arm 2AS. Similarly, in diploid wheat, Yu et al. (2019) identified 42 QTL for GW using 109 RILs derived from the cross, *T. monococcum* ssp. boeoticum (KT1-1) × *T. monococcum* ssp. monococcum (KT3-5), and genotyped for ~ 10,000 SNPs. These 42 QTL were assigned to 17 genomic regions on six chromosomes and accounted for 52.3–66.7% of the PV; candidate genes were also identified. RNA-seq and expression studies were conducted leading to identification of differentially expressed genomic regions in pairs of genotypes which differed for

Table 1 A summary of stable QTL for grain weight reported in wheat

Sr. no.	Stable QTL	Associated marker (cM)	Physical position (Mbp)[a]	References
1.	*QGw.ccsu-2B.1*	*E35/M47–94* (79.21)	ND	Kumar et al. (2006), Gupta et al. (2007)
2.	*QGw.ccsu-7A.1*	*E36/M61–244* (131.3)	ND	
3.	*Gw.ccsu-5A.1*	*E36M6221–E36M6211* (281–284)	ND	Mir et al. (2012)
4.	*QGw.ccsu-6A.2*	*Xbarc3–Xbarc146b* (268)	166.9	
5.	*QGw.ccsu-7A.1*	*E36M6125–E36M6126* (133–136)	ND	
6.	*qTGWWD.3B.5*	*cfb3059–cwem4d*	703.1–707.2	Shukla et al. (2015)
7.	*QGwid.ccsu-7D.1*	*Xgwm635–Xgwm37* (372.5)	17.2	Kumari et al. (2018)
8.	*qKW-2D.1*	*Xcfd168–BobWhite_c7149_371*	580.0	Su et al. (2016)
9.	*qTKW-5A*	–	ND	
10.	*qTKW-5B.2*	*BS00050775_51–Exb_c37146_747*	ND	
11.	*QGws-4D*	*Xbarc105–barc217* (0)	36.5–62.5	Liu et al. (2013)
12.	*QTgw-4D*	*Xbarc1118–Xbarc105* (28)	9.1–36.5	
13.	*QTKW.caas-6A.1*	*Ku_c32392_967-wsnp_RFL_Contig2523_2130662* (73.5)	ND	Gao et al. (2015)
14.	*QTKW.caas-7AL*	*Kukri_rep_c97425_164–RAC875_c18798_103* (172)	ND	

–, Associated marker not available; ND, physical position of QTL could not be determined due to lack of linked marker sequence information

[a]Physical position of QTL is given based on one linked marker if either the second marker or its sequence was not available

GW. These regions contained 20 of the 42 QTL identified using QTL analysis.

Some important genes for yield and its components (including cloned genes)

As many as 46 genes for yield and its component traits (including TGW, grain length/width and grain number) have been identified, cloned and characterized using approaches like fine mapping, map-based cloning and comparative genomics, sometimes using rice orthologues. Of these, as many as > 30 genes belong to TGW, the remaining genes being involved in other component traits. Gene-based markers are also available for many of these genes and can be used for MAS. Wherever markers have not been designed yet, these can be easily developed using variation in gene sequences. Some details about these wheat genes are summarized in Supplementary Table 4.

A summary of the list of some representative genes and their products (proteins) is presented in Table 2, which can be used for understanding the molecular mechanism involved in achieving higher yield. The list of the gene products (proteins) includes a variety of enzymes and DNA binding proteins including transcription factors. Obviously, the mechanism involved in grain production should be complex in nature. The enzymes encoded by these genes include sucrose synthases, cell wall invertases, kinases, phosphatases, transferases, E3 ligase, cytokinin oxygenases/dehydrogenases and an IAA-glucose hydrolase. The list also includes genes encoding transcription factors, like NAC and SPL. The role of some of these genes in determining the level of yield and component traits has been studied at the molecular level and will be briefly described.

The genes encoding sucrose synthase and other synthases facilitate synthesis of sugar and starch, which is a major component of the mature wheat grain. Another two enzymes of starch biosynthesis, namely ADP-glucose pyrophosphorylase (AGPase) and soluble starch (SS) synthase, are involved in grain filling. There are also genes for accumulation of starch and other storage proteins. For instance, the genes like *Flo2* (*FLOURY ENDOSPERM 2*) regulate grain size and starch quality by affecting accumulation of storage substance in the endosperm (She et al. 2010). The recessive *flo2* mutant showed reduced expression of multiple genes involved in storage starch and proteins. Overexpression of *FLO2* leads to a significant enlargement of the size of grains (She et al. 2010). These genes thus provide variation in the capacity for starch synthesis and its transport during grain filling, thus influencing grain weight. Notwithstanding all this, in a recent study, it was shown that final grain weight has no significant correlations with either the activities of these enzymes, or sugar/starch levels during grain filling or

Table 2 Representative genes for grain yield-related traits and their products reported in wheat during the past 10 years

Gene	Protein	References
TaTGW-7A	Indole-3-glycerol-phosphate synthase	Hu et al. (2016)
TaCwi-A1, TaCWI-5D	Cell wall invertase	Ma et al. (2012), Jiang et al. (2015)
TaSus2	Sucrose synthase	Hou et al. (2014), Jiang et al. (2011)
TaTPP-6AL1	Trehalose 6-phosphate phosphatase	Zhang et al. (2017b)
TaFlo2-A1	Tetratricopeptide repeat domain (TPR)-containing protein	Sajjad et al. (2017)
TaSnRK2.3, TaSnRK2.10	Sucrose non-fermenting 1-related protein kinases	Miao et al. (2017), Zhang et al. (2017c)
6-SFT-A2	Sucrose–fructan 6-fructosyltransferase	Yue et al. (2015)
Tabas1-B1	2-Cys peroxiredoxin	Zhu et al. (2016)
TaSPL16, TaSPL 20, TaSPL-21	Squamosa promoter binding protein-like (SPL transcription factor)	Cao et al. (2019), Zhang et al. (2017a)
TaGW2-6A	E3 ubiquitin ligase	Jaiswal et al. (2015), Qin et al. (2014) Yang et al. (2012), Su et al. (2011)
TaCKX6-D1 (*OsGS3*)	Cytokinin oxidase/dehydrogenase	Zhang et al. (2012)
TaGL3-5A	Protein phosphatase with a Kelch-like repeat domain	Yang et al. (2019)
TaSAP1-A1	Stress association protein (homologs of mammalian A20/AN1 zinc-finger protein)	Chang et al. (2013)
TaAPO-A1 (*OsAPO1*)	F-box protein	Muqaddasi et al. (2019)
TaTGW6-A1	Indole-3-acetic acid (IAA)-glucose hydrolase	Hanif et al. (2016)
TaGW8-B1	Squamosa promoter binding protein	Yan et al. (2019)
TaTAR2.1-3A	Tryptophan amino transferase-related	Shao et al. (2017)
TaNAC2-5A	NAC transcription factor	He et al. (2015)
TaGS5-3A	Serine carboxypeptidases	Ma et al. (2016)
TaGS1a	Glutamine synthetase	Guo et al. (2013)

at maturity. It was therefore concluded that neither sugar availability nor enzymatic capacity for starch synthesis during grain filling significantly influence final grain weight. Instead, final grain weight may largely depend on developmental processes prior to grain filling. Starch accumulation then fills the grain to a physical limit set by developmental processes, suggesting that starch level will only indirectly influence grain weight (Fahy et al. 2018).

The gene *TaGS1a* encodes glutamine synthetase, which catalyzes the conversion of NH_4^+ into glutamine, which serves (together with glutamate) as a nitrogen donor for the biosynthesis of all other amino acids. The amino acids thus produced are used for synthesis of other nitrogenous compounds, such as protein, chlorophyll and nucleotides, thus contributing to yield (Wei et al. 2018). The gene encoding cell wall invertase (*TaCwi*) is involved in the development of sink tissue and carbon partitioning, both having strong association with kernel weight (Ma et al. 2012).

The gene *TaTGW-7* encodes indole-3-glycerol-phosphate synthase, which is involved in a number of biological processes including tryptophan biosynthetic pathway, thus indirectly influencing yield. Similarly, *TaTGW-6* encodes IAA glucose hydrolase; its low expression is associated with low IAA content and high grain weight (Hu et al. 2016). There are also at least two genes, which influence grain yield through regulation of components of cell cycle. The *TaCKX* genes encode cytokinin dehydrogenases, which cause dehydrogenation of few or all 20 known cytokinins, and thus influence yield. It was shown that there are as many as 11–14 *TaCKX* genes in each sub-genome of wheat, thus making ~ 35 CKX genes encoding cytokinin dehydrogenases (for a review, see Chen et al. 2019). These enzymes have been shown to influence grain yield through their opposing actions in shoot and root growth due to their effect on cell cycle regulators including cyclins and cyclin-dependent kinases (Cdks). Apparently, this facilitates cell divisions in the endosperm leading to improvement in grain filling. Cytokinin application has actually been shown to result in significant increase in expression of cell cycle regulators like Cdks and cyclins (Zhang et al. 2012). The second gene, which takes part in cell cycle regulation, is *TaGS5-3A*, which encodes serine carboxypeptidase that facilitates production of more cells in the endosperm (Li et al. 2011).

At least two genes encoding TFs also influence yield and related traits through binding specific sites on the promoters of genes, which are involved in yield and contributing traits. The transcription factor *TaNAC2-5A* has been shown to bind to the promoter regions of the genes encoding nitrate transporter and glutamine synthetase and is involved in nitrate signaling. Therefore, it can be utilized for breeding wheat cultivars with higher and efficient use of fertilizer. Another gene *TaSPL16-7A* encodes TF SPL (squamosa promoter binding protein-like), which is involved in plant development, and may thus indirectly influence yield and its component traits.

The genes encoding kinases and phosphatases are supposed to be involved in reversible phosphorylation. A recent study of wheat phosphoproteome under water deficit suggested that 20 proteins in flag leaf and 38 proteins in grain undergo reversible phosphorylation during grain development; the 20 phosphorylated proteins in flag leaf seem to influence grain yield or its component traits through regulation of photosynthesis and starch synthesis, energy metabolism and response to drought stress. Similarly, 38 phosphorylated proteins detected in grain take part in processes like the following: detoxification and defense, protein metabolism; carbohydrate metabolism and energy metabolism (Luo et al. 2018).

There are also genes, which take part in protein degradation, so that the loss of function of these genes seems to be involved in improvement in yield and its component traits. For instance, the gene *TaGW2-6A* encodes E3 ubiquitin ligase and the gene *TaAPO-1* encodes F-box protein with similar activity. These genes cause protein degradation and thus are negative regulators of cell division, so that loss-of-function mutants of these genes give increased grain size (length, width) and grain weight, thus contributing to yield.

Allelic variation for genes affecting yield (to be used for MAS)

Allelic variation and associated markers using diverse genotypes have also been identified for many genes that have been cloned and characterized. This is necessary, if desirable genes are to be used for breeding using MAS. The allelic variation may be recorded either in the form of polymorphic SSRs/SNPs or in the form of haplotypes. For instance, allelic variation has been reported for genes involved in a variety of processes including carbohydrate metabolism (TaSnRKs, *TaFlo2-A1*, *TaSus2-2A*, *TaSus1-7A*, *TaTPP-6AL1*, *TaCWI-4A*), photosynthesis (*Tabas1-B1*), cell division and growth (*TaGS5-3A* and *TaTEF-7A*), ubiquitination (*TaSAP1-A1* and *TaGW2-6A*), dephosphorylation (*TaGL3-5A*), etc. (Table 2). For most of these genes, only 2 alleles in the form of haplotypes were identified suggesting fixation of specific alleles during wheat breeding as a result of selection of favorable alleles. However, maximum number of 6 alleles (haplotypes) were reported for the gene *TaSAP1-A1* associated with TGW and other traits. Using the information on allelic variation, functional markers like cleaved amplified polymorphism sequence (CAPS), allele-specific PCR (AS-PCR) and Kompetitive Allele-Specific PCR (KASP) were developed for these genes. These markers could be used for MAS, while breeding for improvement of yield and component traits.

A recent study involving analysis of allelic variation for 87 functional genes (including many genes for yield) in a

panel of diverse advanced lines (derived from synthetic wheats) also seems to be noteworthy (Khalid et al. 2019). In this study, 124 high-throughput KASP markers were used, which also included markers for water-soluble carbohydrate genes (*TaSST-D1* and *TaSST-A1*) associated with plant height and TGW. It was discovered that beneficial alleles for genes for the following yield-related traits were fixed in diversity panel with frequency ranging from 96.4 to 100%: (1) genes for flowering time (*Ppd-D1* and *Vrn-D3*), (2) genes for 1000-grain weight (*TaCKX-D1*, *TaTGW6-A1*, *TaSus1-7B* and *TaCwi-D1*) and (3) gene for water-soluble carbohydrates (*TaSST-A1*). Allelic variation has also been reported for some major developmental genes such as *Vrn-A1*, *Rht-D1* and *Ppd-B1*. These genes have a confounding effect on several agronomic traits including plant height, grain size and weight, and grain yield in both WW (well-watered) and WL (water-limited) conditions. It was also shown that there was an accumulation of favorable alleles for genes controlling grain size and grain weight; these favorable alleles were additive in nature and gave enhanced grain weight. Accessions with maximum number of favorable alleles were also identified and could be used in future breeding programs.

MAS involving QTL and cloned gene for yield

Some important QTL for grain size and GW are also known and can be utilized for MAS or marker-assisted recurrent selection (MARS). Studies have also been conducted to study polymorphism for the cloned genes, so that this genetic variation may be exploited for yield improvement. Gene-based markers are available for some and can be developed for others, so that these markers will be effective in MAS or MARS for improvement of grain size and grain yield. Gene stacking may also be undertaken using various approaches that are available.

Tolerance to abiotic stresses

In wheat, abiotic stresses have been recognized as a major cause of loss in yield; among abiotic stresses, heat and drought are the two major concerns, so that globally, following two initiatives have been launched to address the issue of improvement of productivity under heat and drought: (1) Heat and Drought Wheat Improvement Consortium–HeDWIC established by Consultative Group on International Agriculture Research (CGIAR) program on wheat (CRP WHEAT) and (2) the global Wheat Yield Consortium (WYC) (Reynolds and Rebetzke 2011; Parry et al. 2011). In addition to these two initiatives, the genetics of tolerance to abiotic stresses has received major attention by individual groups in different parts of the world, so that a large number of QTL/MTAs and associated markers have been identified. A brief summary of these studies is presented in this section.

Heat stress

It has been estimated that 58% of the wheat crop globally experiences heat stress (Kosina et al. 2007). Several model-based studies also suggest frequent future episodes of high temperature during crop season due to climate change (for references, see Bheemanahalli et al. 2019). In India, China and USA, the wheat crop experiences short duration heat episodes coinciding with the reproductive phase and long duration of high-temperature stress during the crop growth (Mondal et al. 2013, 2016; Tack et al. 2015; Liu et al. 2016). The model-based studies and empirical studies have also shown that 1 °C rise in temperature could lead to as much as 6.4–27% reduction in yield in wheat crop (Liu et al. 2016; Bergkamp et al. 2018).

In order to mitigate the negative impact of heat stress on productivity of wheat crop and also to meet the future demand of wheat grain, it is important to develop heat-tolerant wheat varieties using genes for tolerance to heat stress. Therefore, efforts have been made to understand the genetic basis of tolerance to heat stress involving agronomic and physiological traits. Efforts have also been made to understand the molecular basis of tolerance to heat stress (for references, see Gupta et al. 2012; Ni et al. 2017; Pandey et al. 2019). In this section, we will build on our earlier review reporting QTL for different traits in wheat under heat stress (Gupta et al. 2012) and will summarize the available information on important QTL detected using IM, and the MTAs reported using GWAS.

Nearly twenty studies are available, where QTL interval mapping was conducted using phenotypic data recorded on a number of agronomic and physiological traits on mapping populations, grown under conditions of heat stress (Supplementary Table 5). Maximum studies were conducted in Mexico, followed by USA, India, China and other countries (Supplementary Fig. 2). As many as > 300 QTL for 19 agronomic traits and 14 physiological traits (data recorded under heat stress) were reported; the QTL reported in these studies are spread over all the 21 chromosomes. Among the agronomic traits, maximum QTL were reported for TGW followed by grain number per spike, grain yield, grain weight per spike, plant height and others (Fig. 1). The number of QTL reported for physiological traits was fewer relative to those for agronomic traits involved in tolerance to heat stress. However, among physiological traits, maximum number of QTL were reported for canopy temperature followed by normalized difference vegetative index (NDVI), grain filling duration, SPAD/chlorophyll content, water-soluble carbohydrates, flag leaf temperature depression and others. A large number of these QTL for different traits were either minor and/or unstable (detected in only one environment); only 18 major and stable QTL were reported, which included 13 QTL for agronomic traits and 5 QTL for physiological

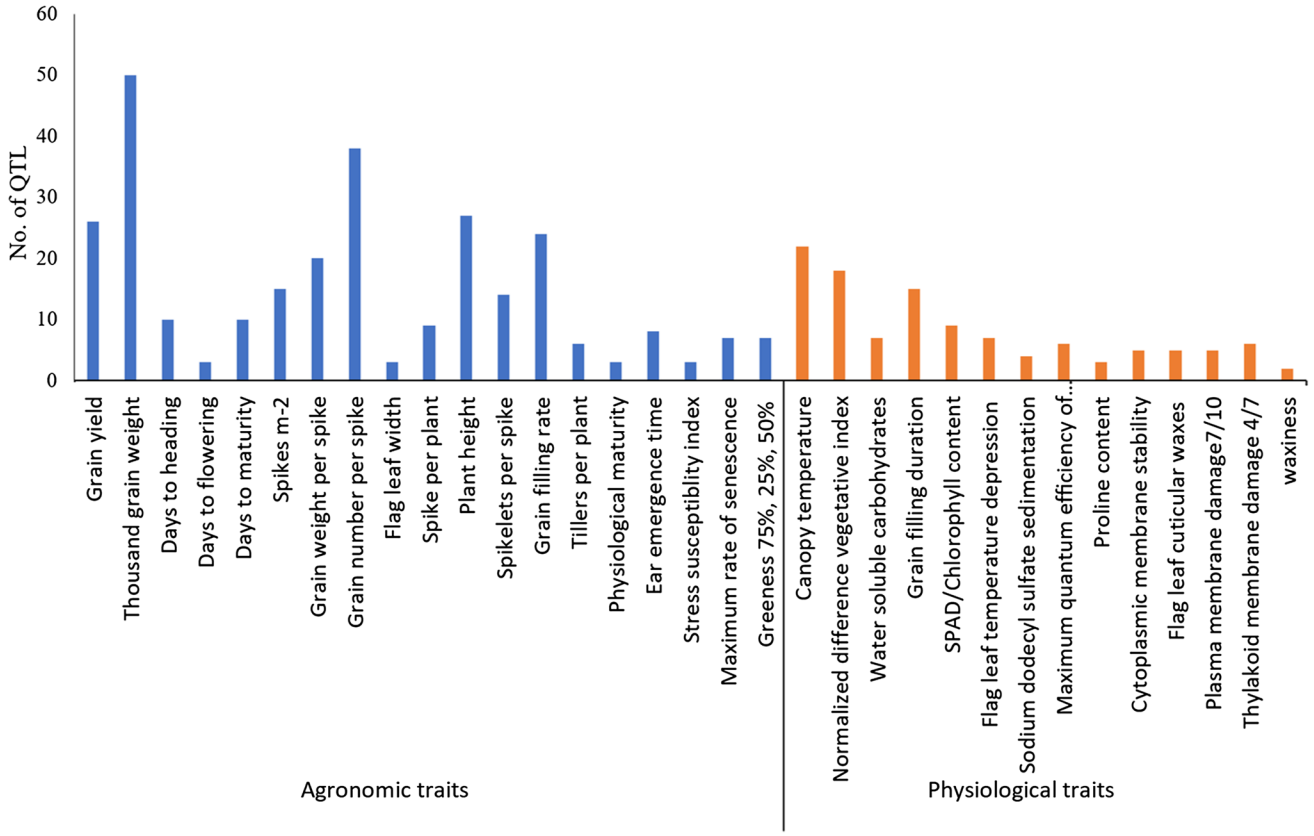

Fig. 1 Histogram showing the number of QTL identified for agronomic and physiological traits related to heat tolerance

traits (≥ 20% PV; detected in ≥ 50% environments) (Table 3). These QTL may prove useful for MAS and deserve further discussion.

Major stable QTL, MQTL, QTL × QTL and QTL × QTL × E interaction The PV explained by the above 18 major stable QTL ranged from 19% to 36% for individual QTL. The PV was relatively low due to QTL for traits like kernel weight per main spike (*QHkwm.tam-3B*) and canopy temperature depression (*QHtctd.bhu-7B*); the PVE of only one QTL (2A) for TGW approached ~36% (Table 3). Canopy temperature has received major attention of the wheat breeders as a selection criterion while breeding for heat tolerance, since cooler canopies contribute to higher yield under heat stress; therefore, major and stable QTL for canopy temperature were also identified (Mason and Singh 2014). Following two stable major QTL were found to be important, since these QTL overlapped the meta-QTL (MQTL) reported by Acuña-Galindo et al. (2015): (1) *Qtgws.iiwbr-2A* for TGW and (2) *Qlgns.iiwbr-2A* for grain number per spike. The remaining stable major QTL for different agronomic and physiological traits and also the other MQTL reported by Acuña-Galindo et al. (2015) can be used for MAS in breeding programs for improvement of heat tolerance in wheat.

Candidate genes have also been identified for heat tolerance. For instance, MQTL10 represents two candidate genes, which encoded acetyl-transferring dehydrogenase and membrane protein (Acuña-Galindo et al. 2015); in future, these genes may be used for studies involving candidate gene-based association mapping in order to identify causal SNPs for MAS. The studies on QTL interval mapping for heat tolerance reported during recent years may also be used for further MQTL analysis to identify more precise and relatively narrow intervals, which will provide more robust markers to be used in MAS.

Epistatic interactions (Q × Q) involving following pairs of QTL were also reported: (1) a QTL for thylakoid membrane damage (TMD) on 7A and a QTL for SPAD chlorophyll content (SCC) on 1B (Talukder et al. 2014); (2) five pairs of QTL involving Fv/FM ratio, grain yield and water-soluble carbohydrates under heat stress (Hassan et al. 2018). Q × Q × E interaction involving a pair of QTL for Fv/FM ratio was also reported. Thus, Q × Q and Q × Q × E interactions should also be taken into account while preparing strategies involving MAS.

Candidate genes underlying QTL About a dozen candidate genes have been identified using heat stress QTL that are associated with phenomena like carbohydrate metabolism,

Table 3 List of major and stable QTL for heat tolerance-related traits in wheat

Sr. no.	Trait/QTL (PVE%)[a]	Linked marker (position in cM)	Physical position (Mbp)[d]	Env.[b]	References
I. Agronomic traits					
1. Grain yield					
a.	*Q.Yld.aww-3B-2* (22)	*XWPT8021-Xgwm0114B* (190.7)	802.3	3/3	Bennett et al. (2012)
2. Thousand grain weight					
a.	*Qtgw.iiwbr-2A* (23.7)	*Xgwm122* (174.41)	80.8	1/2	Bhusal et al. (2017)
b.	*QHthsitgw.bhu-7B* (20.3)	*Xgwm1025–Xgwm745* (144.1)	ND	2/2	Paliwal et al. (2012)
c.	*2A* (36.1)[c]	*224948|F|0-9:T>A-9:T>A-kukri_c22235_1549 (21-24)*	ND	2/3	Liu et al. (2019a, b, c)
3. Grain weight per spike					
a.	*Qtgws.iiwbr-2A* (28.9)	*Xgwm497.1* (41.61)	684	1/2	Bhusal et al. (2017)
b.	*Qgws.iiwbr-2A* (19.9)	*Xgwm122* (171.41)	80.8	2/2	Bhusal et al. (2017)
4. Grain number per spike					
a.	*Qlgns.iiwbr-2A* (23.16)	*Xgwm372* (149.01)	203.3	1/2	Bhusal et al. (2017)
b.	*Qgns.iiwbr-2A* (20.04)	*Xgwm448 (166.51)*	154.4	1/2	Bhusal et al. (2017)
5. Kernel number per spike					
a.	*QHknm.tam-2B* (21.6)	*Xgwm111.2* (36.9)	786.6	2/2	Mason et al. (2010)
6. Kernel weight per main spike					
a.	*QHkwm.tam-3B* (19)	*Xwmc527* (89.8)	540.2	2/2	Mason et al. (2010)
b.	*QHkwm.tam-3B* (21.2)	*Xwmc326* (123.6)	778.7	2/2	Mason et al. (2010)
7. Single kernel weight of main spike					
a.	*QHskm.tam-1A* (22.6)	*Xcfa2129* (43.2)	513.7	2/2	Mason et al. (2010)
b.	*QHskm.tam-2A* (21)	*Xgwm356* (129.5)	670.6	2/2	Mason et al. (2010)
II. Physiological traits					
1. Grain filling duration					
a.	*QHgfd.iiwbr-5A* (22)	*X1079678|F|0* (107.5)	ND	2/2	Sharma et al. (2016)
b.	*QHthsigfd.bhu-2B* (20.2)	*Xgwm935–Xgwm1273* (385.3)	ND	2/2	Paliwal et al. (2012)
2. Ear emergence time					
a.	*Q.Eet.aww-7A-2* (39)	*XPPDD1-XWPT0330* (35)	63.5	3/2	Bennett et al. (2012)
3. Canopy temperature: grain filling					
a.	*Q.Ctgf.aww-3B* (21)	*XWPT-8021–Xgwm0114B* (192.7)	802.3	3/3	Bennett et al. (2012)
4. Canopy temperature depression					
a.	*QHtctd.bhu-7B* (19.8)	*Xgwm1025–Xgwm745* (144.1)	ND	2/2	Paliwal et al. (2012)

[a]Highest PVE (phenotypic variance explained) values under heat stress; [b]Env., number of environments in which QTL was detected/number of total environments; [c]detected under heat and drought stress; [d]position of one flanking marker was given if either the second marker or its sequence was not available

ND, physical position of QTL could not be determined due to lack of marker sequence information

photosynthetic light reaction, metal binding, oxidative stress, etc. (Table 4). These genes include the following: (1) *frk2* (fructose kinase 2), (2) *bglu26* (beta-glucosidase 26), (3) *ndhB2* [chloroplastic NAD(P)H-quinone oxidoreductase subunit 2B], (4) *psaC* (photosystem I iron–sulfur center), (5) *BUD31/G10*-related genes, (6) genes encoding chloroplastic 3-isopropylmalate dehydrogenase 2, (7) *psb28* encoding protein for PSII reaction center, (8) heme peroxidase gene, (9) *α-galactosidase* gene, (10) *psbK* and (11) a gene encoding DNAJ hsp. Among these genes, the genes *ndhB2*, *psaC*, *psb28* and *psbK* are important, since these genes could be involved in maintaining high Fv/Fm during heat stress. The proteins encoded by these genes have a role in the oxygen evolving complex, biogenesis, assembly, stabilization and repair of PSII complex (Bateman et al. 2015). These genes when present in a tolerant genotype help in protecting the oxygen evolving complex and maintain higher Fv/Fm. The other genes like *frk2*, *bglu26* and the gene for heme peroxidase and a heat shock protein DNAJ (Bateman et al. 2015) are also important for providing tolerance against the heat stress. It is possible that these genes act in a coordinated manner to maintain an efficient photosynthesis machinery during heat stress. In future, these genes may be used for

Table 4 Potential candidate genes related to photosynthesis and heat stress localized in three QTL regions in wheat (Sharma et al. 2017)

Name of QTL	Candidate gene	TrEMBL Interpro description of candidate gene
QHst.cph-3B.1 and *QHst.cph-3B.2*	*kf–SCRK2_ORYSJ*	Fructokinase-2, *frk2*
	kf–LEU32_ARATH	3-Isopropylmalate dehydrogenase 2, chloroplastic
	kf–LEU32_ARATH	3-Isopropylmalate dehydrogenase 2, chloroplastic
	kf–BGL26_ORYSJ	Beta-glucosidase 26, *bglu26*
	kf–BGL26_ORYSJ	*BUD31/G10*-related, conserved site (IPR018230)
	kf–NU2C2_LOLP	Chloroplastic NAD(P)H-quinone oxidoreductase subunit 2B, *ndhB2*
	kf–PSAC_VITVI	Photosystem I iron–sulfur center, *psaC*
QHst.cph-3B.3	*kf–PSB28_ORYS*	Photosystem II *Psb28*, class 1 (IPR005610)
QHst.cph-1D	*Peroxidase_WHEAT*	*Heme peroxidase* (IPR010255)
	α*galactosidase_WHEAT*	Glycoside hydrolase family 27
	PSBK_WHEAT	Photosystem II *PsbK* (IPR003687)
	DNAJ hsp_WHEAT	DnaJ domain (IPR001623)

candidate gene-based association analysis for heat stress tolerance in order to develop functional markers.

MTAs identified through GWAS. During the last 5 years, at least 10 GWAS were conducted, which utilized phenotypic data recorded on (1) heat responsive traits in seedling and adult plant and (2) spectral reflectance indices (SRIs) as proxies for agronomic traits including grain yield under heat stress (Liu et al. 2019a). In these studies, the use of association mapping panels ranging in size from 130 to 2111 genotypes allowed identification of 960 MTAs (Supplementary Table 6). Since Bonferroni correction was not applied in majority of these studies, many of these MTAs may be false positives. A number of these MTAs for different traits (including for SRIs) were located in genomic regions that were known to carry QTL identified through IM. Such MTAs may prove useful for MAS after validation. SNPs involved in MTAs were also annotated in a few of these studies and were found to be linked with functional genes for biochemical activities related to abiotic stresses (El Basyoni et al. 2017; Maulana et al. 2018;Jamil et al. 2019) and also with MIP1-like genes having a possible role in enhancing grain yield (Li et al. 2019).

A gene underlying QTL *qYDH.3BL* for yield stability recorded under heat stress was also cloned. The gene is homologous to "*Seven In Absentia"* (*SINA*) genes, a family encoding E3 ubiquitin ligases involved in the ubiquitin pathway for the degradation of target proteins. This gene has an adverse effect on phenotype, so that its loss-of-function mutant may prove useful (Thomelin et al. 2019). In another study, 17 wheat genes exhibiting improved thermotolerance were shown to overexpress in transgenics under heat stress; these genes may also prove useful for providing tolerance to heat stress (for details, see review by Ni et al. 2017).

Drought stress

Drought (water stress) has been shown to affect an estimated 42% of the 218.5 million ha wheat-growing area in the world, leading to major losses in crop productivity (Kosina et al. 2007;Kang et al. 2009). According to some estimates, ~ 50% of wheat cultivated in the developing world (50 million ha) is sown under rainfed conditions and receives < 600 mm of precipitation per annum. This rainfall could be as low as < 350 mm per annum in areas inhabited by the poorest/most disadvantaged farmers of the developing countries (CIMMYT 2005). In India, ~ 66% of the irrigated wheat crop that accounts for 80% of the total wheat area (Rodell et al. 2009) also receives only partial irrigation and is subjected to water stress (Joshi et al. 2007; Kang et al. 2009; Collins et al. 2008). In China, reduced water supply for irrigation is one of the main reasons for not growing wheat crop in a part of the main winter wheat-growing area in North China Plains (Wang and Li 2018). In view of this, genetic improvement of wheat cultivars for drought tolerance is currently receiving worldwide attention.

It is widely known that most of the traits used to measure drought tolerance are complex and polygenic in nature and have low heritability (for details, see reviews by Gupta et al. 2012, 2017; Farooq et al. 2014). Therefore, the genetic dissection of such traits is important for developing superior cultivars through a synergy between molecular and conventional plant breeding. Building on our two earlier reviews (Gupta et al. 2012, 2017), we summarize here the available literature on IM and GWAS for drought stress-responsive traits.

More than 50 studies on IM have been conducted in 13 different countries spread all over the world (Supplementary Fig. 3, Supplementary Table 7). Maximum number of studies have been reported from Australia followed by China and other countries including India. As many as > 1200 QTL

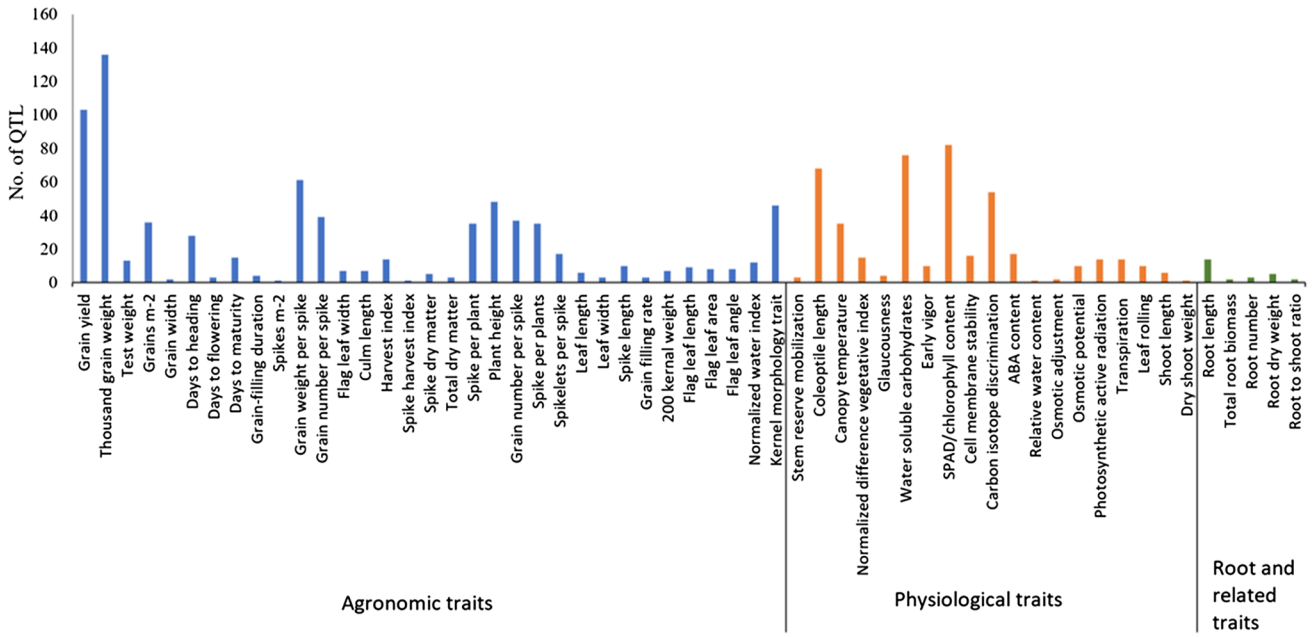

Fig. 2 Distribution of QTL for different agronomic, physiological and root-related traits under drought/water stress in wheat

based on IM, spread over all the 21 wheat chromosomes, have been reported. Maximum number of QTL have been reported for as many as 33 surrogate agronomic traits, followed by 19 physiological traits and five root traits (Fig. 2). Among agronomic traits, maximum QTL are known for TGW followed by grain yield and other traits recorded under drought conditions as well as normal conditions. Among physiological traits, maximum number of QTL are available for SPAD/chlorophyll content (82 QTL) followed by water-soluble carbohydrates (76 QTL), coleoptile length (68 QTL) and others (Fig. 2). Among the root traits, maximum number of QTL are known for root length. Only 70 of these reported QTL are major (explaining ~>20% PVE), and only 19 QTL (including 14 QTL for agronomic traits, 5 for physiological traits) are stable QTL (detected in ≥ 50% environments used for QTL analysis) (Table 5). The root traits exhibit high QTL × environment interaction, which suggests non-availability of stable QTL for these traits; some of the major and stable QTL will be described in greater detail.

Major stable QTL Fourteen stable major QTL were reported for five agronomic traits, with PV for individual QTL ranging from 19.60% (grain yield QTL *qGYWD.3B.2*) to 45.20% (1000-grain weight QTL on 3B) (Table 5). These QTL can be used for improvement of drought tolerance using MAS. Two of the five QTL for grain yield that respond to drought/heat stress overlap a particular MQTL; these two QTL are located one each on chromosomes 4A and 7A (Acuña-Galindo et al. 2015) in regions, which also harbor QTL for the following 14 traits, which contribute to seedling emergence, grain yield and adoption to drought environments: (1) days to heading, (2) days to maturity, (3) stay green habit, (4) biomass, (5) canopy temperature; (6) carbon isotope discrimination, (7) coleoptile vigor, (8) grain filling, (9) plant height, (10) kernel number, (11) spike density, (12) 1000-kernel weight, (13) water-soluble carbohydrates and (14) grain yield. Two other QTL for kernel width/thickness ratio on chromosome 5A overlap a MQTL on 5A which represent QTL for plant height, spike weight and TGW (Acuña-Galindo et al. 2015). The four stable major QTL for drought tolerance include two QTL for grain yield and two QTL for kernel width/thickness ratio. In a recent study, after extensive field experiments conducted under stress conditions in India, Australia and Mexico, a main-effect yield QTL (*QYld.aww-1B.2*) was fine-mapped to 2.9-cM region corresponding to 2.2-Mbp genomic region containing 39 predicted genes (Tura et al. 2020). This QTL could be exploited in wheat breeding.

QTL for other relevant traits included three QTL for TGW, three QTL for days to heading and one QTL for days to maturity. The QTL for TGW, which is a major component of grain yield and have high heritability as well as stability, can be exploited for improvement of grain yield under water stress. Four QTL for days to heading and days to maturity may also be exploited using MAS.

Five major and stable QTL for three physiological traits (SPAD/chlorophyll content, stem reserve mobilization and water-soluble carbohydrates) each explained PV ranging from ~ 20 to ~ 60% (Table 5). These traits contribute to grain filling/development and consequently to grain yield (for

Table 5 A list of major and stable QTL (PVE ranging from 19 to 59%) for agronomic and physiological traits identified under drought/water stress

Sr. no.	Trait/QTL (PVE %)[a]	Linked marker (position in cM)	Physical position (Mbp)[c]	Env.[b]	References
I. Agronomic traits					
1. Grain yield					
(a)	*qGYWD.3B.2* (19.6)	*Xgpw7774* (97.6)	16.2	4/7	Shukla et al. (2015)
(b)	*4A* (20)	*Xwmc420* (90.4)	538.2	Mean/2	Kirigwi et al. (2007)
(c)	*4A-a* (23.9)	*Xgwm397* (6)	708.6	5/6	Pinto et al. (2010)
(d)	*Qyld.csdh.7AL* (20.0)	*Xgwm332* (155.9)	681.6	11/21	Quarrie et al. (2006)
(e)	*6D* (26.6)	*2265648|F|0-60:A > G-60:A > G-RAC875_c57371_238* (73)	ND	2	Liu et al. (2019b)
2. 1000 Grain weight					
(a)	*2A* (36.1)	*2264948|F|0-9:T > A-9:T > A-Kukri_c22235_1547* (21.0-24.0)	ND	5/6	Liu et al. (2019b)
(b)	*3B* (45.2)	*Xbarc101* (86.1)	34.3	Mean/2	Golabadi et al. (2011)
(c)	*QTgw-7D-b* (21.9)	*XC29-P13* (12.5)	ND	10/11	Lopes et al. (2013)
3. Days to heading					
(a)	*QDh-7D.b* (22.7)	*XC29-P13* (12.5)	ND	11/11	Lopes et al. (2013)
(b)	*QHd.idw-2A.2* (32.2)	*Xwmc177* (46.1)	33.7	13/16	Maccaferri et al. (2008)
(c)	*5D* (21.4)	*1126619|F|0-21:A > T-21:A > T-wsnp_Ex_c1278_2449191* (162)	ND	2/5	Liu et al. (2019b)
4. Kernel width/thickness ratio					
(a)	qWTR-5A-1 (33.09)	*Xwmc74-Xgwm291* (61)	702.5–698.1	4/6	Chen et al. (2019)
(b)	qWTR-5A-2 (23.59)	*Xgwm291-Xgwm410* (71)	698.1	3/6	
5. Days to maturity					
(a)	*QDm-7D.b* (22.7)	*X7D-acc/cat-10* (2.7)	ND	10/11	Maccaferri et al. (2008)
II. Physiological traits					
1. Stem reserve mobilization					
(a)	*QSrm.ipk-2D* (42.2)	*Xgwm249a* (142)	141.1	2/2	Salem et al. (2007)
(b)	*QSrm.ipk-5D* (37.5)	*Xfbb238b* (19)	ND	2/2	Salem et al. (2007)
(c)	*QSrm.ipk-7D* (21)	*Xfbb189b* (338)	ND	2/2	Salem et al. (2007)
2. Water-soluble carbohydrates					
(a)	*QWsc-c.aww-3A* (19)	*Xwmc0388A* (64.9)	208	2/2	Bennett et al. (2012)
3. SPAD/chlorophyll content					
(a)	*Qchl.ksu-3B* (59.1)	*Xbarc68* (67.2)	76.1	2/3	Kumar et al. (2012)

[a]PVE, phenotypic variation explained; [b]Env., number of environments in which QTL was detected/number of total environments; [c]Position of linked flanking marker was given if either the second marker or its sequence was not available

ND, physical position of QTL could not be determined due to lack of linked marker sequence information

references, see Gupta et al. 2017). The markers associated with QTL for these traits are also good candidates for MAS.

Meta-QTL and candidate genes Acuna-Galindo et al. (2015) carried out meta-QTL analysis utilizing 502 QTL for drought tolerance; these QTL were available from 30 studies and gave 19 MQTL for 17 different agronomic and physiological traits, each with a narrow interval, having mean length of 5.8 cM. Four individual MQTL (e.g., MQTL2, MQTL11, MQTL29 and MQTL61), each represented six to seven individual QTL for agronomic and physiological traits. Candidate genes for at least one meta-QTL (MQTL2) were also reported, which encode following proteins: ADP-ribosylation factor, prolamin, globulin. These proteins mainly include grain storage proteins or enzymes, which function as molecular switches, thus regulating intracellular vesicular pathway. These genes may be utilized for candidate gene-based association studies for developing useful SNP markers.

A follow-up MQTL study (including identification of candidate genes) is being conducted in our laboratory at Meerut, India, since results on ~ 375 QTL became available from more than two dozen additional studies conducted after 2015, when earlier meta-QTL study was conducted. The markers associated with MQTL and candidate genes reported earlier and those being worked out in our

own laboratory will be used in future MAS programs for improvement of drought tolerance in wheat.

Q × Q, Q × E and Q × Q × E interactions. More than 100 first-order epistatic (Q × Q) interactions were reported for 10 different drought-responsive agronomic and physiological traits (Supplementary Table 8), although the PV for each pair of epistatic QTL was generally low (Yang et al. 2007; Khanna-Chopra et al. 2019). Q × E and Q × Q × E interactions were also reported for three QTL for flag leaf-related traits, four QTL for TGW and one QTL for water-soluble carbohydrates (Table 6; Yang et al. 2007; Khanna-Chopra et al. 2019). The PV explained by these interactions ranged from 2% (flag leaf area) to 21% (flag leaf width). These interactions need to be taken into account along with the main-effect QTL while selecting markers for MAS.

MTAs identified through GWAS. Results of at least 10 reports based on GWAS are also available, each involving an association panel ranging in size from 108 to 382 genotypes that were phenotyped under conditions of drought. The markers utilized in GWAS included SSR, SNP and DArT markers. A total of > 1150 MTAs have been reported for different agronomic and physiological traits (Supplementary Table 9). FDR was applied in five studies for eliminating false positives (Edae et al. 2014; Ain et al. 2015; Qaseem et al. 2018; Ballesta et al. 2020); these MTAs may need to be validated using either QTL interval mapping or through joint-linkage association mapping (JLAM).

In a few studies, MTAs identified through GWAS in the same linkage disequilibrium cluster of SNPs were converted into QTL (Condorelli et al. 2018; Touzy et al. 2019); in this manner, 477 QTL were identified for different traits in drought environments. Some of these QTL were common for different drought environments and for different traits. However, due to lack of shared markers among the above studies on GWAS and those on IM/meta-QTL analyses (discussed above), we could not relate the MTAs/QTL identified through GWAS with the QTL mapped through IM. In some recent studies, high-throughput phenotyping using spectral reflectance indices (SRIs) as proxy traits has also been utilized for drought tolerance. The data on SRIs recorded under drought stress/restricted irrigation in wheat were used for GWAS by Gizaw et al. (2018a, b) leading to identification of 74 MTAs; some of these MTAs overlapped the QTL earlier reported through interval mapping for agronomic traits. Information on PV explained due to MTAs for drought tolerance is available from only some of the above studies (Supplementary Table 9).

Candidate gene-based AM Forty-six (46) candidate genes were also identified using MTAs for different traits (Ain et al. 2015; Qaseem et al. 2018; Bhatta et al. 2018; Gahlaut et al. 2019; Supplementary Table 10). Candidate gene-based association mapping was undertaken for only five of these genes; causal SNPs were identified in each case (for details, see Gupta et al. 2017). Following are some details of the causal SNPs identified for these five different genes: (1) two SNPs for *DREB1A*, one each for days to heading and final biomass; (2) one SNP for *1-FEH-B*, associated with days to maturity; (3) three SNPs for *1-FEH-A*, associated one each with three traits (grain number per spike, NDVI and green leaf area, respectively), and another SNP associated with a solitary trait (green leaf area); (4) two SNPs for *ERA1-B*, associated one each with grain filling duration and spike number per m^2; and (5) four SNPs, detected for *ERA1-D*; one SNP was associated with grain weight per spike and flag leaf width; the remaining three SNPs were associated, one each with flag leaf width, harvest index and leaf senescence. These SNPs may be exploited in MAS, after due validation. The remaining 41 candidate genes may also be utilized in future for gene-based association mapping to identify associated SNP markers.

Table 6 Important epistatic interaction (QTL x QTL x environment) with PVE ≥ 5% reported in wheat under drought/water stress

Trait	QTL-i	Linked marker	Physical position (Mbp)[a]	QTL-j	Linked marker	Physical position (Mbp)[a]	PVE % QQE	References
FLL	*qFLLWD.4B.1*	*gwm495-gpw4079*	482.8–573.9	*qFLLWD.2D.1*	*wmc503-cfd43*	19.6	8	Khanna-Chopra et al. (2019)
FLW	*qFLWWD.2D.1*	*wmc503-cfd43*	19.6	*qFLWWD.5A.1*	*barc40-wmc415*	444.9–535.1	21	
TGW	*QTgwg.cgb-1B*	*P3622-280*	ND	*QTgwg.cgb-5A*	*Xwmc524*	682.7	5.16	Yang et al. (2007)
	QTgwg.cgb-4A.2	*CWM145*	ND	*QTgwg.cgb-4A.3*	*XP4232-260*	ND	8.26	
	QTgwg.cgb-6A.2	*Xgwm334*	9.2	*QTgwg.cgb-6A.3*	*XP3474-260*	ND	5.79	
	QTgwm.cgb-2B.1	*P6411-216*	ND	*QTgwm.cgb-7B.4*	*Xwmc276*	404.3	6.61	
WSC	*QSwscg.cgb-2B*	*WMC441*	598	*QSwscg.cgb-6B*	*Xwmc182*	496.4	5.61	

FLL, flag leaf length; FLW, flag leaf width; TGW, 1000 grain weight; WSC, water-soluble carbohydrates; PVE%, phenotypic variation explained by QQE interaction; ND, physical position of QTL could not be determined due to lack of linked marker sequence information

[a]Position of one flanking marker was given if either the second marker or its sequence was not available

Molecular marker-assisted breeding Despite the availability of a fairly large number of major QTL for drought tolerance, only few of these major QTL have been used for MAS; some details about MABC and MARS utilized for this purpose will be described.

(1) *Marker-assisted backcrossing* (*MABC*) In India, two major MABC projects involving drought tolerance were undertaken: One was supported by the Generation Challenge Programme (GCP) funded by CIMMYT, Mexico, and the other was supported by the National Initiative on Climate Resilient Agriculture (NICRA) Project of ICAR, New Delhi. The program focused on introgression of QTL for the following traits into two elite Indian wheat cultivars, namely HD2733 and GW322: canopy temperature, chlorophyll content, stay green habit, NDVI values, days to anthesis, grain yield and its related traits (for details, see Gupta et al. 2017). Following foreground and background selections, BC_1F_5/BC_2F_4 progenies (containing 90% recurrent parent genome) were developed and evaluated under rainfed condition. One of these high-yielding lines (HD3343) was eventually tested in MABB trial conducted by the ICAR-Indian Institute of Wheat and Barley Research (IIWBR), Karnal. This line, however, could not be released as a cultivar because of its susceptibility to diseases (personal communication, Neelu Jain, ICAR-IARI, New Delhi, India).

In our own laboratory at Meerut, India, we focused on the exploitation of a major QTL (*Qyd.csdh.7AL*) for grain weight per spike that was identified under drought stress (Quarrie et al. 2005, 2006). The marker associated with this QTL was utilized in a restricted backcross program involving foreground MAS for development of lines with improved yield and tolerance to drought. The above QTL has been reported to control grain yield and its components including spike attributes in a number of other studies (for more details, see Su et al. 2016; Kuzay et al. 2019; Voss-Fels et al. 2019). The gene *TaAPO-A1* (an ortholog of rice gene *APO1*), associated with total spikelet number per spike in wheat, was also reported from the genomic region containing the QTL *Qyd.csdh.7AL*, suggesting the importance of this QTL region in wheat breeding (Kuzay et al. 2019; Voss-Fels et al. 2019; Muqaddasi et al. 2019). We introgressed the desirable allele of the above QTL *Qyd.csdh.7AL* for grain weight per spike into four Indian wheat cultivars (HUW234, HUW468, K307 and DBW17) and derived a line with 25.5% higher yield relative to the recipient genotype HUW468 under rainfed conditions (Gautam et al. 2020). This high-yielding line is currently being tested in a variety development program. There are also examples of introgression of desirable alleles for some QTL from wild emmer wheat (*T. turgidum* ssp. dicoccoides) into durum and bread wheat cultivars. For instance, Merchuk-Ovnat et al. (2016) introgressed a QTL on 7AS in common wheat and a QTL on 2BS in durum wheat leading to the improvement of grain yield and biomass under drought stress.

(2) *Marker-assisted recurrent selection* (*MARS*) MARS has also been attempted under collaborative programs involving India, Australia and China for improving water use efficiency and for deployment of QTL for stress adaptive traits (early vigor, SPAD values at vegetative and reproductive stages, NDVI, chlorophyll fluorescence and flag leaf area) (Jain et al. 2014; http://www.generationcp.org/communications/media/feature-stories/breaking-new-ground-in-mars-gcp-launches-challenge-initiative-on-wheat-in-asia.html). Progenies carrying desirable combinations of QTL were developed; some of these progenies showed improvement not only over the parents, but also over the check cv. HD3043. A line HD3296 developed following MARS was tested in central and peninsular zones of India under the rainfed condition in the national initial varietal trials (NIVT) conducted by ICAR-IIWBR, Karnal. This line had the same fate as the improved line HD3343 developed using MABC (described above) and could not be released due to its susceptibility to diseases, although it was highest yielding (personal communication, Neelu Jain, ICAR-IARI, New Delhi, India).

Salinity stress

Salinity stress affects > 800 Mha (6%) of land globally and causes serious losses to wheat production in several countries (Wang and Xia 2018). Among Asian countries, the total land area affected with salinity accounts for 6.73 Mha in India, for 3.1 Mha in Bangladesh and for 36 Mha in China. A substantial part of this land area is under wheat cultivation explaining the importance of the study of genetics of soil salinity tolerance and its use to develop salinity-tolerant wheat cultivars. Therefore, research involving study of the genetics of salinity tolerance in wheat has also been a priority in several countries including India, Pakistan, Bangladesh, China, Egypt, etc.

Like heat and drought tolerance, salinity tolerance is also a complex polygenic quantitative trait, which is also influenced by the environment (Blum 1988; Foolad 2004; Flowers 2004). The mechanism of salinity tolerance involving Na^+/K^+ uptake by the roots and their transport within the plant has been reviewed (Chinnusamy et al. 2005; Pardo 2010; Deinlein et al. 2014); it was shown that salt tolerance is developmentally regulated and that the salinity tolerance increases with the age of a crop like wheat (Foolad 2004). Thus, the QTL for salinity tolerance identified at germination and early growth stages generally differ from those identified at the adult plant stage (Yamaguchi and Bulmwald 2005).

The surrogate traits used for estimation of salinity tolerance differed in different studies and included both root and

shoot traits. Experiments in field and in laboratory (involving hydroponics) have also been used for recording phenotypic data for QTL analysis. High-throughput phenomics data using image analyzers like The LemnaTec Scanalyzer 3D (LemnaTec GmbH, Aachen, Germany) at The Plant Accelerator® in Australia were also used for nondestructive measurements of plant growth under salinity stress.

QTL for salinity tolerance Starting in 2004, > 20 studies for identification of QTL for salinity tolerance have been conducted in different parts of the world including Iran, China and Pakistan. The available studies generally utilized IM and led to identification of ~ 500 QTL (excluding those involved in digenic epistatic interactions and QTL x treatment interactions); these QTL are spread over all the 21 wheat chromosomes (see Supplementary Table 11). The PV explained by individual QTL ranged from 8.4% to 38.0%, and only a dozen major QTL have been reported (Table 7). The traits used for QTL analysis included Na^+ exclusion/content, K^+ content and K^+/Na^+ ratio, etc., both at the seedling and adult plant stages. Since several studies in different plant systems including wheat have demonstrated that Na^+ concentration is not necessarily associated with salinity tolerance, other additional mechanisms (tissue tolerance and osmotic adjustment) may also be examined in future in order to breed for salinity tolerance in bread wheat (for references, see Genc et al. 2019).

Bread wheat has been shown to exhibit low rates of Na^+ transport, which leads to high K^+/Na^+ ratio in leaves. A high K^+/Na^+ discrimination provides tolerance to salinity stress. A locus *Kna1* for Na^+ exclusion was mapped on chromosome arm 4DL (Dubcovsky et al. 1996) and was found to be tightly linked with the SSR markers *Xwg199*, *Xabc305*, *Xbcd.402*, *Xpsr567* and *Xpsr375*. The following eight QTL for salinity tolerance were considered to be important: (1) QTL *QNax.aww-7AS* for Na^+ within the marker interval *Xwmc083-Xcdo595* mapped using two mapping populations (Cranbrook × Halberd and Excalibur × Kukri; this QTL explained up to 40% PV for Na^+ exclusion; Edwards et al. 2008). (2) QTL *qSNAX.7 A.3* contributes ~ 19% to the shoot dry weight, and is used as a direct measure of salinity tolerance (Hussain et al. 2017). (3) QTL *QK.asl-5A* for K^+ accumulation explaining 28% of PV is located in the region of the vernalization response gene (*Vrn-A1*) (Asif et al. 2018) but is independent of the *Vrn-A1* gene; a candidate gene (two-pore potassium channel) underlying this QTL was also identified. (4) Five major QTL for booting, ear emergence time, flowering and maturity were mapped on chromosome 2D (De Leon et al. 2011; for more details, see Table 7). Some of these QTL were coincident. The location

Table 7 A list of major QTL/loci (PVE of ~>20%) for seedling and adult plant traits under salt stress condition in bread and durum wheats

Sr. no.	Trait	QTL/locus (PVE%)	Linked marker	Physical position (Mbp)[a]	References
1.	Na^+ exclusion	*Kna1* (–)	*Xwg199*, *Xabc305*, *Xbcd.402*, *Xpsr567*, Xpsr375	390.2	Dubcovsky et al. (1996)
2.	Na^+ exclusion	*Nax1* (38)	*Xgwm312, Xwmc170*	709.0–711.5	Lindsay et al. (2004)
3.	Dry weight of plumule at germination stage	*Qpdwg-4D.1* (19.8)	*Xfbb226–Xfba177*	ND	Ma et al. (2007)
4.	Na^+ exclusion	*QNax.aww-7AS* {41 (hydroponics/21 (field)}	*Xwmc083–Xcdo595*	89.9	Edwards et al. (2008)
5.	Booting	*QB.uabcs-2D* (23.6)	*Xcdo1379*	ND	De Leon et al. (2011)
6.	Ear emergence time	*QEet.uabcs-2D* (27.1)	*Xcdo1379*	ND	
7.	Flowering	*QFl.uabc-2D* (26.7)	*Xbcd102a*	ND	
8.	Maturity	*QM.uabc-2D* (28.9)	*Xcdo1379*	ND	
9.	Ear length	*QEl.uabc-2D* (21.5)	*Xbcd102a*	ND	
10.	Seedling shoot fresh weight	*3B-1* (19.2)	*wPt-798970-wPt-8303*	ND	Masoudi et al. (2015)
11.	Na^+ exclusion value	*qSNAX.7 A.3* (18.79)	*AX-95248570–AX-95002995*	700.6	Hussain et al. (2017)
12.	3rd leaf Na^+ and K^+ concentration and K^+/Na^+ ratio	*4B* (18, 20, 27)	*Xm564*	657.1	Shamaya et al. (2017)
13.	3rd leaf Na^+ concentration	*3B* (18)	*Xm551*	701.9	
14.	K^+ µmol/g DW	*QK.asl-5A* (28.2)	*Vrn-A1*	587.4	Asif et al. (2018)

PVE, phenotypic variation explained; DW, dry weight; –, PVE% not available; ND, physical position of QTL could not be determined due to lack of linked marker sequence information

[a]Position of one flanking marker was given if either the second marker or its sequence was not available

of at least two of these QTL (*QEet.uabcs-2D* and *QFl.uabcs-2D*) was similar to those reported under non-saline conditions, suggesting that these QTL are constitutive in expression (Börner et al. 2002; Kumar et al. 2007). This QTL region on 2D also contains the gene *Ppd1* responsible for photoperiodic response, which has pleiotropic effect on a number of traits. QTL *QFl.uabc-2D*, along with few QTL for other traits, was present in the most tolerant RIL making this an important candidate for MAS aimed at improvement of salinity tolerance.

In durum wheat, which is more sensitive than the bread wheat due to higher concentration of Na^+ in the shoots (Francois et al. 1986; Maas and Grieve 1990), a land race (Line 149) having high salinity tolerance was used to map two important genes *Nax1* on the chromosome arm 2AL and *Nax2* on chromosome arm 5AL (Lindsay et al. 2004). The *Nax1* is closely associated with SSR markers *Xgwm312* and *Xwmc370* and explains 38% PV for Na^+ exclusion at adult plant stage (Lindsay et al. 2004), and *Nax2* is associated with markers *Xgwm291*, *Xgwm410* and *Xgpw2181* (Byrt et al. 2007). The linked markers were validated in segregating populations, which were shown to discriminate among the lines with high and low Na^+. The *Nax2* region on 5AL seems to be a duplication of a region on chromosome 4DL that contains *Kna1* locus for Na^+ exclusion. These loci seem to correspond to those coding for two Na^+ transporters, namely HKT1;4 (HKT7) and HKT1;5 (HKT8) (Huang et al. 2006a, b; Byrt et al. 2007). Subsequently, using an F_2 population involving a Afghani wheat accession (AUS-14740) and an Australian cv. Jandorai, one QTL each for salinity tolerance-related traits were reported on chromosomes 3B and 4B (Shamaya et al. 2017). The QTL on 4B was responsible for Na^+ (PVE = 18%) and K^+ (PVE = 20%) concentrations and the K^+/Na^+ ratio (PVE = 27%) in the third leaf, while the QTL on 3B (PVE = 18%) was responsible for third leaf Na^+ concentration only. The above QTL could prove useful resource for MAS aimed at improving salt tolerance in durum wheat.

Q × Q, Q × E and Q × Q × E interactions were also identified for seedling traits (measured in hydroponics experiments) using IM involving salinity stress in wheat (Xu et al. 2012a, b, 2013; Masoudi et al. 2015). Some of the digenic epistatic interactions and the interactions involving the QTL and the treatment had additive effects. However, the PV due to these interactions was generally low (0.87–9.12%) for each trait used in these three studies.

MTAs for salt tolerance using GWAS. MTAs for salt tolerance traits have also been detected in wheat using GWAS (Supplementary Table 12); following are some examples: (1) In durum wheat, 12 MTAs for different traits were identified, explaining ~ 13% R^2 for salt tolerance index (STI) for the trait per cent dry leaf mass (Turki et al. 2015). These MTAs identified at the seedling stage and may not be suitable for providing tolerance at adult plant stage. (2) Four important MTAs on 1BS, 2AL, 2BS and 3AL were reported to be associated with salinity tolerance across the three growth stages and with the leaf K^+ and Na^+ contents (Oyiga et al. 2018). The R^2 values for these associations ranged from 12.02 to 30.67%. The associated SNPs also allowed identification of a few candidate genes (*ZIP7*, *Salt 1B*, *SAP8*) for salt tolerance, which were validated through expression analysis using salt-tolerant and sensitive wheat genotypes. (3) MTAs for adult plant leaf Na^+ concentration were also identified in one study (Genc et al. 2019). SNPs associated with seven of these MTAs were mapped on chromosomes 2A, 2B, 2D, 4B, 4D, 5A and 7A. Almost all the MTAs were novel and differed from those earlier reported by Oyiga et al. (2018). This study also reported four candidate genes encoding following proteins with potential function in Na^+ accumulation/exclusion: calcium-transporting ATPase, $Na^{(+)}/H^{(+)}$ antiporter NhaB, aquaporin *TIFI_4* and aquaporin *PIP2*. (4) Haplotype diversity analysis for QTL for salt tolerance was carried out in a set of 30 salinity sensitive and tolerant wheat genotypes and a check cultivar. For this purpose, SSR markers flanking the large effect QTL for salinity tolerance on chromosomes 2A, 3B and 4D were utilized (Sardouie-Nasab et al. 2013). Based on amplification of alleles similar to those in the salt-tolerant check cultivar, it was inferred that SSR markers *Xcfa2121b*, *Xgwm10* and *Xgwm296* on chromosome 2A and markers *Xgwm194* and *Xgwm624* on chromosome 4D had significant association with most of the measured traits. Other suitable associated markers included *Xgwm10, Xgwm445, Xbarc353.2, Xgwm312, Xgwm515 and Xwmc296* on 2A and markers *Xwmc326 and Xgwm345, Xbarc48.4* on 3B.

Breeding for salinity tolerance In India, efforts were made by Central Soil Salinity Research Institute (CSSRI), Karnal, to screen the germplasm for salinity tolerance and to develop salinity-tolerant wheat varieties (no markers were used). The collection of salt-tolerant wheat land races like Kharchia 65 and others proved useful donors for salinity tolerance in wheat breeding programs for salinity tolerance. As a result, following four salt-tolerant varieties were developed and released for cultivation: KRL 1-4, KRL 19, KRL 210 and KRL 213 (STVsinCrops-PlantStress.com.pdf). Some details of these salt-tolerant wheat varieties are given in Supplementary Table 13. The work on breeding strategies for salinity-tolerant wheats at the international level has recently been reviewed (Mujeeb-Kazi et al. 2019).

Pre-harvest sprouting (PHS)

Pre-harvest sprouting (PHS) is characterized by germination of grains within physiologically mature spikes before harvest under conditions of wet weather. PHS adversely affects grain quality, yield and baking quality of dough, thus reducing

the marketability of the grain. This leads to an estimated financial loss of $1 billion annually (https://maswheat.ucdavis.edu/; Buchanan and Nicholas 1980; Bewley et al. 2006; Olaerts and Courtin 2018; for more references, see Ali et al. 2019). The reduction in grain quality is due to the activation of many enzymes including lipases, amylases and proteases, which degrade lipids, starch and proteins in sprouting grains (Andreoli et al. 2006; Simsek et al. 2014). PHS is a major problem in many wheat-growing parts of the world including India, China, USA, Japan, Canada, Australia and Europe (Rajjou et al. 2012). The wheat crop grown in Yangtze River Valley and Yellow and Huai Valley in China suffers from PHS, when rain and humidity coincide with harvest period (Zhou et al. 2017). Similar is the case with the wheat crop grown in the northeast and other wheat-growing regions of India.

In order to mitigate the problem of poor grain quality associated with PHS, the study of genetics and breeding of PHS tolerance/dormancy has attracted worldwide attention. PHS is a typical quantitative trait and polygenic in nature and is often also associated with seed dormancy. Many QTL and genes involved in controlling traits related to PHS have been reported. The results available from studies on QTL analysis, GWAS and identification of candidate genes for PHST will be briefly reviewed.

As many as 47 studies on QTL interval mapping for PHS tolerance and related traits involving ~ 40 different populations derived from bread wheat (including synthetic wheat), durum wheat and *T. monococcum* have so far been conducted (Supplementary Fig. 4). Of these studies, 18 studies were conducted in Asian countries (China, India, Japan, Korea) followed by studies in USA, Australia and Canada. In India, major contribution to the study of the genetics of PHS was made by CCS University, Meerut, and PAU, Ludhiana, as evident from a series of publications (Roy et al. 1999; Kulwal et al. 2004, 2005; Kumar et al. 2009, 2015; Mohan et al. 2009).

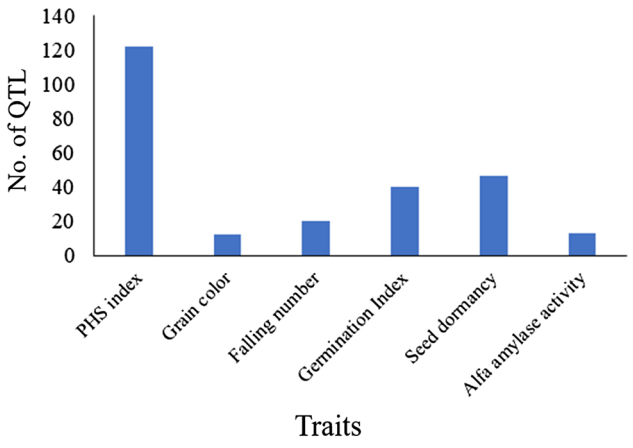

Fig. 3 Number of QTL for five different traits associated with preharvest sprouting tolerance reported in the 47 studies in wheat

QTL for PHS tolerance have been identified using the following parameters: PHS index, grain color, falling number, germination index, seed dormancy and alpha amylase activity (Fig. 3). Maximum number of QTL have been reported for PHS index followed by seed dormancy, germination index, falling number and alpha amylase activity in that order. A total of ~ 250 QTL detected using IM and a similar number of MTAs detected using GWAS for traits associated with PHS tolerance have been reported. These QTL/MTAs are located on all 21 wheat chromosomes (for reviews, see Zhou et al. 2018; Zhu et al. 2019; Ali et al. 2019). A summary of the results of QTL interval mapping (IM) studies is included in Supplementary Table 14.

Stable major QTL. Of the ~ 250 QTL, only 29 QTL were major and stable over environments; these QTL are distributed on 11 different chromosomes (1B, 3A, 4A, 5A, 6A, 2B, 3B, 4B, 7B, 2D, 3D and 7D); the highest PV explained by an individual QTL ranged from 23% to 78.3% (Table 8). Chromosomes from homoeologous groups 3 and 4 together carried 17 of the 29 major and stable QTL (for references, see Mori et al. 2005; Kulwal et al. 2010). The PHS and the germination index (a measure of dormancy) have often been used for estimation of tolerance against PHS. PHS index is an easy to score parameter and is also reliable, so that it has been extensively utilized. The QTL due to seed dormancy, which is defined as the inability of viable seeds to germinate under conditions favorable for germination, is also associated with PHS tolerance (Seshu and Sorrells 1986).

The QTL for PHS tolerance, located on the long arms of chromosomes of homoeologous group 3, have often been reported to be associated with genes for red grain color, which contributes to coat-imposed dormancy. A major stable QTL for PHS (*QPhs.ccsu-3A.1*; 24.68–35.21% PV) was reported from studies conducted in our own laboratory (Kulwal et al. 2005; Mohan et al. 2009). The use of markers associated with this QTL in MAS resulted in high level of PHS tolerance, which was unfortunately associated with red grain color (Kumar et al. 2010). In wheat markets, particularly in Southeast Asia and Middle East, Africa and North America, there is a consumer preference for white grain (Ambalamaatil et al. 2006). Therefore, attempts were later made to produce white-grained PHS-tolerant wheat genotypes; for this purpose, major and stable QTL on chromosomes of group 4 and other chromosomes were recommended. SSR markers are available for almost all major and stable QTL; these SSR markers have been used for introgression of a QTL for PHS/dormancy to derive lines with high degree of PHS tolerance associated with amber grains (our unpublished results).

Meta-QTL analysis, Q × Q, Q × E interactions Meta-QTL analysis for PHS traits was carried out in our laboratory

Table 8 A summary of the major and stable QTL for pre-harvest sprouting/dormancy-related traits in wheat

Sr. no	Trait/QTL (PVE%)[a]	Linked marker	Physical position (Mbp)[c]	Env.[b]	References
1.	FN/5A(26.4)	*Xpsr1194–Xpsr918b*	ND	2, Mean/4	Zanetti et al. (2000)
2.	α-AA/5A(30.0)	*Xpsr1194–Xpsr918b*	ND	3, Mean/4	Zanetti et al. (2000)
3.	SD/4AL(33–77.2)	*Xcdo795/Xpsr115*	ND	3/3	Kato et al. (2001)
4.	PHS/*QPhs.ccsu*-3A.1(78.3)	*Xwmc153–Xgwm155*	701.7–702.9	6, Mean/6	Kulwal et al. (2005)
5.	SD/*QPhs.ocs*-3A.1(23.0–44.8)	*Xbarc310/Xbcd907*	7.1	2/4	Mori et al. (2005)
6.	GI/*QGi.crc*-3B(27.0)	*Xbarc77–Xwmc307*	430.1–783.5	3, Mean/3	Fofana et al. (2009)
7.	SI/*QSi.crc*-3B(24.0)	*Xbarc77–Xwmc307*	430.1–783.5	3, Mean/3	Fofana et al. (2009)
8.	FN/*QFn.crc*-3B(33.0)	*Xbarc77–Xwmc307*	430.1–783.5	3, Mean/3	Fofana et al. (2009)
9.	GI-14/*QPhs.dpivic*-3D.1(26.0–43.0)	*Red Grain Color RGC-wms1200*	ND	2/4	Imtiaz et al. (2008)
10.	VI/*QPhs.dpivic-4A.1* (21.0)	*Xbarc170–Xgwm269c*	605.7–607.8	2/4	Imtiaz et al. (2008)
11.	PHS/*QPhs. pseru*-3AS(31.26–44.96)	*Xbarc12–Xbarc321*	11.7–15.4	2, Mean/3	Liu et al. (2008)
12.	*QPhs.dpi.vic*.4A.2(27.78–39.84)	*Xgwm637–Xgwm937*	617.4	2, Mean/3	Ogbonnaya et al. (2008)
13.	PHS/2DS(25.73-–27.50)	*Xgwm261–Xgwm484*	19.6–48.1	2/2	Xiao-bo et al. (2008)
14.	GI/*QGI.crc*-4B(28.2–66.6)	*Xwmc349*	640.9	3, Mean/4	Rasul et al. (2009)
15.	PHS/*QSI.crc*-4B(6.2–26.9)	*Xwmc349*	640.9	2, Mean/5	Rasul et al. (2009)
16.	PHS/*QPhs.cnl*-2B.1(24.0)	*Xbarc55–Xwmc474*	133.5–172.6	16, Mean/16	Munkvold et al. (2009)
17.	GC/*QGc.ccsu*-3B.1(15.28–40.42)	*Xgwm938–Xgwm980*	ND	4, Mean/4	Kumar et al. (2009)
18.	PHS/*QPhs.ccsu*-6A.1 (12.01–29.47)	*Xgwm1296–Xgwm1150*	ND	3, Mean/4	Kumar et al. (2009)
19.	PHS/*QPhs.caas*-3AS.1 (11.8–27.7)	*Xbarc294–Xbarc57*	7.9–10.3	2, Mean/3	Miao et al. (2013)
20.	GI/*QGi.crc*-4A (27.6–58.1)	–	ND	3/3	Cabral et al. (2014)
21.	PHS(SI)/*QSi.crc*-4A (10.5–32.1)	–	ND	3/4	Cabral et al. (2014)
22.	PHS(SI)/*QSi.crc*-7B (11.8–20.5)	–	ND	1/2	Cabral et al. (2014)
23.	FN/*QFn.crc*-7D (13.2–20.6)	–	ND	1/2	Cabral et al. (2014)
24.	PHS, SD/*Qphs.pseru*-4A (17.2–26.5)	*GBS_212432–GBS_109947*	ND	2, Mean/5	Lin et al. (2015)
25.	*QPhs.spa*-4B (35.0–60.0)	*Xwmc617b–Xwmc48a*	15.7–98.7	7/7	Kumar et al. (2015)
26.	*QPhs.spa*-7D2 (14.0–47.0)	*Xbarc76–Xcfa2257a*	634.0	7/7	Kumar et al. (2015)
27.	GI/3AS (21.6–41.0)	*KASP-222*	7.2	3/3	Shao et al. (2018)
28.	*qPHS.sicau*-3D (8.65–42.47)	*AX-94415259*	562.5–5	7/9	Yang et al. (2019)

PHS, pre-harvest sprouting; α-AA, α-amylase activity; FN, falling number; SD, seed dormancy; GI-14 days, germination index at 14 days; VI, visual index; GI, germination index; –, marker information not available; ND, physical position of QTL could not be determined due to lack of marker sequence information

[a]Phenotypic variation explained, [b]Env. = number of environments in which QTL was detected/number of total environments, [c]physical position of one flanking marker was given (instead of interval), if the second marker or its sequence was not available

utilizing the data for 36 QTL from 15 different studies (Tyagi and Gupta 2012); in this study, a number of MQTL were identified, which included 2 MQTL on chromosomes 3A, 3 MQTL on 3B, 2 MQTL on 3D and one MQTL on 4A, each having a relatively much narrower confidence interval. Two MQTL were also co-localized with genes for dormancy/PHS tolerance on chromosome arms 3AL (*taVP1*) and 4AL (*taGA20-ox1*). Closely linked SSR markers are available with each of these meta-QTL and can be exploited in MAS for improvement of PHS tolerance.

Digenic Q × Q and Q × Q × E interactions involving main-effect QTL and epistatic QTL (E-QTL) for PHS tolerance and related traits were also reported in five studies (Supplementary Table 15); the epistatic interactions accounted for 28.73% PV, which is fixable; Q × Q × E interactions accounted for a meager 3.24% PV (Kulwal et al. 2004). In two other studies, no interactions with environment were reported (Mohan et al. 2009; Kumar et al. 2009). Together, these observations suggested that Q × Q interactions and the main-effect QTL together explain ~ 75% PV for PHS tolerance.

Genome-wide association studies (*GWAS*). A number of GWAS for PHS tolerance and related traits have also been undertaken leading to identification of ~ 250 MTAs (Supplementary Table 16); many of these MTAs were located in the QTL regions earlier identified through IM. In India, a solitary study involved a set of 242 wheat genotypes and 250 SSR markers, where 30 markers associated with PHS tolerance were reported with R^2 values ranging from 0.95 to 3.27 (Jaiswal et al. 2012). Eight of the associated SSRs

Table 9 Candidate genes for traits related to PHS tolerance/dormancy in wheat

Sr. no.	Trait/QTL or gene	Candidate gene in wheat	Chromosome	References
1.	Viviparous/*Vp-1*	*TaVp-A1, TaVp-B1, TaVp-D1*	1A, 1B, 1D	Utsugi et al. (2008)
2.	Dormancy/*DOG-1*	*TaDOG1-like* genes	–	Ashikawa et al. (2010)
3.	Seed Dormancy/*Sdr4*	*TaSdr-A1, TaSdr-B1, TaSdr-D1*	2A, 2B, 2D	Zhang et al. (2014)
4.	Dormancy	*TaMFT-3A*	3A	Nakamura et al. (2011)
5.	Red grain color	*Tamyb10-3A1, Tamyb10-3B1, Tamyb10-3D1*	3A, 3B, 3D	Himi and Nada (2005)
6.	PHS/*phs.pseru-3AS*	(homolog of MOTHER OF FLOWERING TIME (TaMFT)-like gene	3AS	Liu et al. (2013)
7.	Dormancy/*4A-1*	*PM19-A1, PM19-A2*	4AL	Barrero et al. (2015)
8.	Dormancy/*Phs-A1*	*ERF-1B-Like, ASC1* and *PP1-Like*[a]	4AL	Shorinola et al. (2016)
9.	Dormancy/*Phs1*	*TaMKK3-A*	4AL	Torada et al. (2016)
10.	PHS	*TaABI5*	2D, 4D, 6D, 7D	Zhou et al. (2017)
11.	Dormancy	*TaQsd1A, TaQsd1B, TaQsd1D*	1A, 1B, 1D	Onishi et al. (2017)

PHS pre-harvest sprouting

[a]Yet to be confirmed

were found to be located in the marker intervals of the QTL for PHS tolerance reported in earlier studies conducted using IM. Most of these QTL disappeared, when Bonferroni corrections were applied. The reported MTAs should therefore be validated through IM using biparental mapping populations.

Candidate genes for PHS/dormancy Candidate genes for PHS tolerance/dormancy have also been identified (Table 9), although not all of these candidate genes have been functionally characterized (for reviews, see Nakamura 2018; Ali et al. 2019; Vetch et al. 2019a, b). Functional markers for some of these genes (*TaSdr-B1, TaMFT-A1, TaMFT-A1, TaVp-1B* and *TaVp-1B*) have also been developed with a view to stack these genes during marker-assisted breeding for improvement of PHS tolerance (for reviews, see Nakamura 2018; Ali et al. 2019). Recently, a loss-of-function triple mutant for *Qsd1* (which control seed dormancy in barley) has been obtained through *Agrobacterium*-delivered CRISPR/Cas9; the mutant prolongs seed dormancy, suggesting the promise of CRISPR/Cas-mediated gene editing or base editing for improvement of PHS tolerance in wheat (Abe et al. 2019).

MAS for PHS tolerance In our laboratory at CCS University, we have successfully exploited two QTL for PHS, namely *QPhs.ccsu-3A.1* (associated with red grain color) and *QPhs.dpi.vic.4A.2* (associated with white grain color), in MAS for improvement of PHS tolerance in wheat. The QTL *QPhs.ccsu-3A.1* was pyramided with leaf rust resistance genes *Lr24* and *Lr28* in the background of cv. HD2329. The derived lines exhibited high to moderate tolerance to PHS (PHS score of 2–4) and resistance to leaf rust under artificial conditions (Kumar et al. 2010). This QTL (*QPhs.ccsu-3A.1*) was also pyramided with several other grain quality and rust resistance genes [(*Gpc-B1* + HMW glutenin allele *Glu-A1* + high grain weight QTL *QGw.ccsu-1A.3* + three rust resistance genes (*Yr36, Lr24/Sr24*)] in the background of cv. PBW343 (Tyagi et al. 2015). In another study, a QTL for PHS tolerance (*QPhs.dpi.vic.4A.2*), associated with white grain color, was pyramided with genes for high grain protein content and rust resistance (*Gpc-B1/Yr36* + *Lr24*); as a result, lines containing the following genes were developed in the background of cv. Lok1: *Gpc-B1/Yr36* + *Lr24* + a PHS tolerance QTL *QPhs.dpi.vic.4A*.2 (our unpublished results).

Biofortification for Fe and Zn in wheat

Improvement of grain micronutrients did not receive the desired attention in the past, both at the international level and also in Asia (including China and India), leading to significant loss in genetic variability for Fe and Zn among contemporary wheat cultivars (Rawat et al. 2009a, b). Global biofortification research for a number of crops including wheat can be traced back to 1995, when CGIAR launched its "CGIAR Micronutrients Program," which continued till 2002, when CGIAR approved its major "Biofortification Challenge Program" that was later renamed as "HarvestPlus"; the program also covered South East Asia and South Asia including India and China. In particular, studies on genetics and breeding for producing biofortified crops including wheat have been underway in many countries during the last two decades. At the international level, the program on biofortification of wheat was undertaken and coordinated by CIMMYT in Mexico. Consequently, the study of genetics and its use for improvement of grain nutritional composition especially for Fe and Zn content/concentration without any yield penalty received the desired attention during the last ~ 15 years, although much more remains to be

done. The work already done globally and in Asia is briefly summarized.

QTL analysis

Under the biofortification program, globally and particularly in Asia, more than a dozen studies involving QTL analysis have been conducted (Genc et al. 2009; Shi et al. 2008; Peleg et al. 2009; Tiwari et al. 2009, 2016; Xu et al. 2012a, b; Hao et al. 2014; Roshanzamir et al. 2013; Srinivasa et al. 2014a; Pu et al. 2014; Crespo-Herrera et al. 2016, 2017; Velu et al. 2016; Krishnappa et al. 2017; for reviews, see Ozkan et al. 2007; Distelfeld et al. 2007; Pu et al. 2014; Garcia-Oliveira et al. 2018). In these studies, QTL for grain Zn (GZn) and grain Fe (GFe) have been mapped using a variety of populations derived from crosses involving diploid wheat (Tiwari et al. 2009), durum wheat and wild emmer wheat (Peleg et al. 2009), synthetic hexaploid wheats and *T. spelta* (Pu et al. 2014; Krishnappa et al. 2017; Crespo-Herrera et al. 2017) (Supplementary Table 16). These studies identified ~ 80 QTL for GFe and ~ 110 QTL for GZn, which are spread over all the 21 wheat chromosomes. Individual QTL for GFe explained 2.0–47.0% PV while those for GZn explained 1.0–35.9% PV (see Supplementary Table 17). Some of these QTL were major QTL and were therefore detected across environments; QTL for GFe and GZn sometimes also overlapped in the same genomic regions (see later).

Two stable QTL each for GZn (chromosomes 5A and 6B) and GFe (chromosomes 5A and 6A) explained up to 23% and up to 18% PV, respectively (Peleg et al. 2009). Other stable QTL, one each for GZn on chromosomes 2B and that for GFe on chromosome 3A explained up to 15% PV (Hao et al. 2014). QTL for GZn explaining up to 27% PV were also consistently detected on chromosomes 1B and 6B (Velu et al. 2016). Other large effect QTL were also reported, one for GZn (PV = 32.7%) on chromosome 7B and the other for GFe (PV = 21%) on chromosome 4A. A GZn QTL on chromosome 2B was also shown to have pleiotropic effect on the trait TGW.

A QTL controlling both GFe and GZn was mapped on chromosome 5B using two mapping populations (Pu et al. 2014); this QTL may represent the QTL earlier reported by Peleg et al. (2009). In another study, two QTL controlling GFe and GZn were identified, one each on chromosomes 5A and 7A (Krishnappa et al. 2017). Stable QTL for GZn (mean PVE = 36%) and those for GFe (mean PVE = 22%) were sometimes reported to occupy the same genomic regions on chromosome 2B (Tiwari et al. 2016). These genomic regions controlling both GFe and GZn suggest that some specific genomic regions may control both GFe and GZn.

There were also genomic regions, containing QTL for GFe and/or GZn along with those for grain protein content and other micronutrients, as is the case with marker interval *Xgwm359-Xwmc407* on chromosome 2A. Similarly, one genomic region each on 5A (*Xgwm126-Xgwm595*) and 7A (*Xbarc49-Xwmc525*) contained QTL for both GFe and GZn (Krishnappa et al. 2017). Among these studies, a significant positive correlation was also observed between GZn and GFe across different environments indicating co-localization of QTL or pleiotropic effect regulating the concentrations of both GZn and GFe in wheat. Co-localization of QTL for GZn and GFe was also reported on some other chromosomes including 2A (Krishnappa et al. 2017), 2B (Tiwari et al. 2016), 4BS (Crespo-Herrera et al. 2016), 5A (Xu et al. 2012a, b; Krishnappa et al. 2017) and 6B (Velu et al. 2016).

Q × Q epistatic interactions were also reported and involved the following pairs of QTL (Xu et al. 2012a, b): (1) a pair of QTL, located on chromosome 2A (*Xgwm501-Xgwm156.2*; *Xwmc181-Xcfd267.1*) for GZn concentration and (2) a QTL on chromosome 2B (*Xbarc1138.2-Xcfd238*) involved with a QTL (*Xgwm617-Xcfa2114*) on chromosome 6A for GFe.

Genome-wide association studies (GWAS)

MTAs for GZn concentration were also identified using GWAS in the following five studies: (1) a study involving HarvestPlus Association Mapping (HPAM) panel consisting of 330 bread wheat genotypes; this study gave 39 GZn MTAs including two large effect MTA regions, one each on group 2 and 7 chromosomes (Velu et al. 2018). (2) A study involving a Spring Wheat Reference Set (SWRS) consisting of ~ 320 genotypes; in this study, nine most important MTAs were reported for three traits (GPC, GFe content and yield per plot) (Kumar et al. 2018). (3) A GWAS involving a panel of 369 European wheat genotypes; in this study 40 MTAs for GZn were identified on the following 12 chromosomes: 2A, 3A, 3B, 4A, 4D, 5A, 5B, 5D, 6D, 7A, 7B and 7D. Three of these MTAs were most significant and consistent with major effects. These were located on 3B and 5A. Candidate genes involved in the Zn uptake and transport and genes for bZIP and mitogen-activated protein kinase were also located in the above genomic regions (Alomari et al. 2018). (4) In another GWAS conducted using 114 non-redundant *Ae. tauschii* accessions and 5249 genotyping-by-sequencing (GBS) markers (Arora et al. 2019), MTAs were identified on all the seven D genome chromosomes including five for GFe and four for GZn concentrations. (5) A GWAS was also conducted involving synthetic hexaploid wheats, which were genotyped for 35,648 SNPs and phenotyped for 10 grain minerals (Ca, Cd, Cu, Co, Fe, Li, Mg, Mn, Ni and Zn) (Bhatta et al. 2018); 60 novel MTAs and 40 MTAs reported earlier within the genes were identified; these included three MTAs for GFe concentration on chromosomes 1A and 3A,

and 13 MTAs for GZn concentration on eight different chromosomes (1A, 2A, 3A 3B, 4A, 4B, 5A and 6B).

Alien gene transfer

In a study conducted by HS Dhaliwal and his group in India, GFe and GZn contents were examined in the following two sets of germplasm: (1) 15 semi-dwarf cultivars of bread wheat/durum wheat and (2) 80 accessions belonging to nine alien species from the genera *Triticum* and *Aegilops* (Rawat et al. 2009b). Alien species with S, U and M genomes had up to threefold to fourfold higher GFe/GZn contents relative to bread/durum wheat genotypes. Three *Aegilops* species, namely *Ae. longissimi*, *Ae peregrina* and *Ae kotschyi*, were found to be promising for biofortification involving Fe and Zn; major emphasis, however, was laid on *Ae kotschyi*, which was later used in several studies involving biofortification (Table 10; Chhuneja et al. 2006; Rawat et al. 2009b; Neelam et al. 2010a, b). Several alien species were also used for developing amphiploids, with an objective to obtain alien addition and substitution lines (Tiwari et al. 2008).

Three approaches for alien gene transfer Three different approaches were used for transfer of alien segments from chromosomes of *Ae kotschyi*. (1) *Chinese Spring* (*CS*)×*Ae. kotschyi crosses*: The F_1 hybrids were backcrossed and BC_1F_1 and BC_2F_1 plants were selfed; plants with high GFe and GZn concentration were selected, which had 50–120% increase in Fe and Zn contents relative to recipient wheat cultivars. It was also possible to use anchored wheat SSR markers, for transfer of genes/QTL for high GFe and GZn from *Ae. kotschyi* chromosomes belonging to homoeologous groups 2 and 7 (Tiwari et al. 2009, 2010; Rawat et al. 2011). (2) *Use of Ph1 for inducing homoeologous pairing*. The interspecific hybrids lacking 5B chromosome (developed through crosses with monosomic 5B) allowed pairing between wheat and homoeologous alien chromosomes, leading to the transfer of alien segments to wheat chromosomes; selected BC_2F_2 plants showed up to 125% increase in GFe and 158% increase in GZn relative to recipient cv. PBW343 carrying *Lr24* and *Yr36* (Verma et al. 2016b). (3) *Irradiation of pollen from wheat-Aegilops kotschyi substitution lines*: Pollen from wheat-*Ae. kotschyi* 2A/2S^k and 7A/7S^k substitution lines with high GFe and GZn were irradiated with gamma rays using a dose of 40 krads; the irradiated pollen was used for pollinating wheat cultivars WL711 and PBW343 (Verma et al. 2016a; Tiwari et al. 2010). Some of the derivatives had up to 65% higher GFe and up to 54% higher GZn contents coupled with better harvest index relative to the elite wheat cultivars used (Verma et al. 2016a; Sharma et al. 2018). In the derived lines, although the uptake of Zn was slow, its mobilization into grains was more effective relative to that for Fe (Sharma et al. 2017).

Use of alien addition lines In another study, disomic alien addition lines involving six different *Aegilops* species were evaluated for GFe and GZn. The following chromosomes were found to carry genes for higher GFe and GZn concentrations, the increase ranging from 50 to 248% over Chinese Spring recipient cultivar: chromosomes 1S^l and 2S^l of *Ae. longissima*, 1S^S and 2S^S of *Ae. searsii*, 2U and 6U of *Ae. umbellulata*, 4S^v of *Ae. peregrina* and 5M^g of *Ae. geniculata* (Wang et al. 2011).

Prażak and Krzepiłko (2018) detected chromosome fragments specific to *Ae. kotschyi* Boiss ($2n=4x=28$, UUSS) using two ISSR markers (ISSR23690 and ISSR33650) to characterize the hybrid lines derived from *Ae. kotschyi* Boiss.×*T. aestivum* L crosses. In another study, four translocation lines carrying 1S^k fragment in a "Pavon-76" wheat genetic background were found to have significantly higher Zn over the mean of 62 lines that were used for trial. The results of this study demonstrated that large genetic variation

Table 10 A summary of grain Fe and Zn contents and the transfer of alien genes for these traits to wheat from alien species

Alien species	Genomic constitution	Chromosome	Fe increase (%)	Zn increase (%)	References
Ae. kotschyi	$U^kU^kS^KS^k$	$2S^k$, $7U^k$	75, 89	75, 93	Tiwari et al. (2010a), Verma et al. (2016)
Ae. longissima	S^lS^l	$2S^l$	124	132	Tiwari et al. (2008), Sharma et al. (2018)
Ae. longissima	S^lS^l	$1S^l$, $2S^l$	55, 38	124, 74	Wang et al. (2011)
Ae. peregrina	$U^PU^PS^PS^P$	$4S^P$, $7S^P$, $7U^P$	46, 133, 92	125, 107, 251	Neelam et al. (2010a)
Ae. peregrina	$U^PU^PS^PS^P$	$4S^P$	36	69	Wang et al. (2011)
Ae. searsii	SS	$1S^S$, $2S^S$	84, 61	143, 129	Wang et al. (2011)
Ae. umbellulata	UU	2U, 6U	47, 70	79, 32	Wang et al. (2011)
Ae. caudata	CC	B	41	161	Wang et al. (2011)
Ae. geniculata	$M^gM^gU^gU^g$	$5M^g$	14	47	Wang et al. (2011)
Ae. variabilis	UUS^vS^v	Hybrid line*	59	71	Prażak and Krzepiłko (2018)
Secale cereale	RR	1R	–	18	Velu et al. (2019)

**Ae. variabilis* × *T. aestivum*

is available in translocation lines for improving the nutritional quality of wheat and could be used in wheat biofortification program (Velu et al. 2019).

In a recent study, metal homeostasis genes were located on chromosomes of the homoeologous groups 2 and 7 in the tribe *Triticeae* (Sheikh et al. 2018). The derived lines containing group 2 chromosomes contained alien genes *NAS2*, *FRO2*, *VIT1* and *ZIP2*, whereas group 7 derivatives had alien genes *YSL15*, *NAM*, *NRAMP5*, *IRO3* and *IRT2*. Novel DNA-based markers called Intron Targeted Amplified Polymorphism (ITAP) were also developed using bioinformatics approach; these markers were used to verify metal homeostasis genes earlier transferred from the non-progenitor *Aegilops* species into common wheat cv. PBW343 *LrP* (Sheikh et al. 2018).

Bioavailability of Fe and Zn

Low phytic acid (phytate) and high phytase levels have been targeted to improve bioavailability of Zn and Fe through reduction in phytic acid content, which has antinutritional properties (Vashishth et al. 2017a). In a study conducted at ICAR-IIWBR, Karnal, 400 genotypes including some released Indian wheat varieties, advanced lines and synthetic hexaploids were evaluated for the variability in the levels of phytate and phytase in wheat grains (Ram et al. 2010). The Indian wheat varieties and advanced lines were found to carry 3.4-fold variation while the synthetic hexaploid wheat had 5.9-fold variation in phytase level. Similarly, the phytate levels varied from 1.6-fold in the Indian wheat varieties and advanced lines and 2.2-fold in the synthetic hexaploid wheats. Variation in the level of phytic acid was also reported in a study involving 257 wheat genotypes (89 wheat cultivars and 168 synthetic hexaploids) (Vashishth et al. 2017b). This study reported 1.5-fold variation in the level of phytic acid in wheat varieties and 2.1-fold variation in synthetic hexaploid wheats. Sixfold variation in phytase levels was also reported in synthetic wheats (Neeraja et al. 2017). In another study involving 100 advanced breeding lines, phytic acid level varied from 4.97 to 15.02 mg/g (mean of 9.58 mg/g) (Shitre et al. 2015).

Selected synthetic hexaploids with high phytase levels could also be used to improve the level of phytase in common wheat cultivars. Stable high-yielding mutant lines (derived from PBW502) with high level of phytase (750 FTU/Kg), high GFe (47 ppm) and high GZn (45 ppm) were also identified at IIWBR, Karnal, India (Ram et al. 2019). PCR-based markers were also developed for phytase genes and their seed-specific promoters, which can be used for selection of plants with high phytase level in wheat (Vashishth et al. 2018a). It was also shown that the activity of phytase enzyme is primarily controlled at transcriptional level (Vashishth et al. 2018b). In an in silico study, Bhati et al. (2014) identified six wheat genes that might be involved in the biosynthesis of inositol phosphates. A homolog of *Zmlpa-1* encoding an ABCC subclass transporter protein (TaMRP3) was also identified, which is involved in phytic acid transport during wheat grain development leading to phytic acid accumulation (Bhati et al. 2016).

The above account on biofortification suggests that biofortified wheats can be developed using the available genetic variability. It has also been shown that there are significant positive correlations among GZn, GFe and GPC, and a negative correlation between the contents of micronutrients and important agronomic characteristics like plant height, grain yield and 1000-grain weight (Srinivasa et al. 2014b). In some studies, negative correlations between the concentrations of GFe and GZn with grain yield have also been reported, although these correlations are influenced by environment (Oury et al. 2006; Morgounov et al. 2007; Ficco et al. 2009; Zhao et al. 2009; White and Broadley 2009). In some other studies, absence of these negative correlations was observed (Graham et al. 1999; Welch and Graham 2004). Positive correlation of GFe concentration with grain weight has also been reported in several studies (Oury et al. 2006; Morgounov et al. 2007; Peleg et al. 2008). These findings suggest that although it may be difficult to improve GZn concentration and grain yield simultaneously, there is a possibility of simultaneous improvement of GFe and grain weight by traditional breeding. The levels of bioavailability have been shown to be low for GFe (5%) and GZn (25%) in staple food crops (Bouis and Welch 2010). The anti-nutrient factors such as phytic acid and tannins are responsible for reduced bioavailability of micronutrients (Guttieri et al. 2006). Therefore, it is necessary to take into account the bioavailability of micronutrients, while preparing strategies for wheat biofortification.

Biofortified wheat lines/cultivars

During 1990s, a large number of synthetic wheats were produced at CIMMYT to create new genetic variation in wheat. These synthetic wheats were crossed with superior wheat genotypes to improve several different traits including stress tolerance, agronomic and nutritional quality traits. Large variation in GFe and GZn concentrations in wheat and its related wild species was also reported (Çakmak et al. 2004). This variation was exploited by HarvestPlus for development and release of several lines/varieties of wheat with improved GZn (up to 410 ppm). High GZn wheat lines/varieties have been tested in a wide range of environments for adaptation and stability in target locations, so that as many as 17 such high GZn lines/cultivars (6 lines + 11 varieties) were released in some developing countries (Velu et al.

2012, 2015; Baloch et al. 2015; Supplementary Table 18). One variety, namely "Nohely-F2018" was also released from Mexico. All these lines/varieties carry relatively high level of either GZn alone or both GFe and GZn (up to 43 ppm) along with profitable yield potential and some other desirable characteristics. The availability of this material indicates that substantial progress has been made in achieving the ultimate goal of developing biofortified wheat.

In addition to the development of the above biofortified wheat lines/cultivars, the high grain protein content (GPC) gene *Gpc-B1*, cloned from *T. dicoccoides* (Uauy et al. 2006), has also been exploited in breeding (mostly following MAS) for improvement of GFe and GZn along with the improvement of GPC in wheat (for a review, see Tabbita et al. 2017). Introgression of *Gpc-B1* gene involving both durum and bread wheats has been reported in more than two dozen studies from following seven different countries: Argentina, Australia, Canada, India, Israel, Japan and USA. An analysis of these studies suggested that of all the lines carrying above high GPC gene, 95% lines had significantly higher GFe content (on average 12.5 mg kg^{-1}) and 93% lines had significantly higher GZn content (on an average 11.6 mg kg^{-1}) (Tabbita et al. 2017), suggesting that *Gpc-B1* gene may be exploited for improvement of GFe and GZn contents along with improvement of GPC.

Conclusions and perspective

From the account presented in this review, it is apparent that significant progress has been made in our understanding of the genetics of yield and its component traits (including plant height involving Rht genes, TGW, grain size and grain number), tolerance to abiotic stresses (including tolerance to heat, drought salinity and pre-harvest sprouting) and biofortification (including grain Fe, Zn and phytate). A large number of QTL and more than 50 genes have been identified/cloned for all these traits, although all the identified genes have not been functionally validated. A number of reported QTL are major, which are sometimes also stable over environments. These QTL can be introgressed through marker-aided conventional breeding in high-yielding cultivars that are deficient for these traits. Some progress in this direction has already been made, and with the availability of knowledge about QTL and markers, the use of molecular breeding to supplement conventional wheat breeding will certainly increase giving a new direction to global wheat breeding programs. In our laboratory at Meerut, India, we are also in the process of developing a QTL database for wheat, so that wheat geneticists and breeders will have access to complete information on QTL and the associated markers for all traits including those covered in this review; efforts are being made to allow its access in a user-friendly manner.

However, for biofortification (including Fe and Zn contents), adequate necessary genetic variability is not available in wheat germplasm; the contents of these micronutrients in grains of a number of alien species have been shown to be several folds higher relative to that in high-yielding wheat cultivars. Therefore, methods are being developed for utilization of this alien genetic variation for biofortification; these methods and the progress made so far have been briefly described in this review. Further progress in this direction is likely to be made in future. The bioavailability of micronutrients is another issue, which is being addressed through manipulation of phytic acid and phytase contents; this aspect has also been discussed in this review.

In future with climate change, we will also need cultivars with climate resilience, since there is evidence of loss of climate resilience in wheat cultivars during 1991–2014 (Kahiluoto et al. 2019), and also because there is negative correlation between productivity and stress tolerance (Paul et al. 2018). Since the conventional breeding supplemented with MAS may not prove adequate, alternative approaches may have to be used. Modulation of genes involved in carbon and nitrogen metabolism pathways may have to be used for improvement in yield along with resilience against climate change. Following genes have been recommended for this purpose: (1) genes encoding enzymes like phosphoenolpyruvate carboxylase (pepc) and pyruvate orthophosphate dikinase (ppdk); (2) the gene *TaNAC2-5A* for nitrogen accumulation in aerial parts; (3) chloroplastic glutamine synthase gene (*TaGS2*) responsible for prolonged leaf photosynthesis (Hu et al. 2018); and (4) *TaSS* (soluble starch synthase) gene for increased heat stability (Tian et al. 2018). Wherever desirable mutants are not available, genome editing tools involving CRISPR/Cas technology will certainly be utilized for overall improvement of yield and tolerance to biotic and abiotic stresses. The utility of this approach has already been demonstrated through editing of genes such as *TaGW2, TaGARS7* and *TaDEP1* (Liang et al. 2017; Wang et al. 2018a, b; Zhang et al. 2016, 2018). Base editing (a modified CRISPR/Cas approach) has also been recommended for possible use in developing climate-resilient improved wheat cultivars (for a review, see Gupta 2019).

Acknowledgements Thanks are due to the Department of Biotechnology (DBT), Govt of India, and to Indian Council of Agricultural Research (ICAR)-National Agricultural Science Fund (NASF), Govt of India, for providing funds in the form research projects over the years for undertaking the research work described in this review, to Indian National Science Academy (INSA) for the award a position of INSA Honorary Scientist to PKG and that of Senior Scientist to HSB and to the Head, Department of Genetics & Plant Breeding, CCS University, Meerut, India, for providing the necessary facilities. Thanks are also due to Kalpana Singh, Ritu Batra, Gautam Saripalli, Tinku Gautam, Anuj Kumar, Manoj Kumar, Vivudh Pratap Singh, Kuldeep Kumar,

Rakhi, Deepak Kumar, Vikas Kumar Singh, Saksham and Deepti Chaturvedi for their assistance in finalization of the manuscript.

Author contribution statement PKG conceived the review and each author wrote different sections of the review either independently or jointly. The manuscript was read and revised by all the authors and finalised by PKG.

Compliance with ethical standards

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

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