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Past, Present and Future Molecular Approaches to Improve Yield in Wheat

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Abstract

This chapter addresses the development and use of molecular markers for yield enhancement in wheat. Since their key goal for breeding is to maximize yield, extensive efforts have been made toward the improvement of yield. Agronomic traits related to yield, yield-related, disease resistance, and abiotic stresses are considered to be quantitative traits (QTLs), also known as complex traits, because they are controlled by numerous genes and are affected by environmental factors. Researchers have been studying such traits in the past decades for the development of molecular markers which can be used in various wheat breeding studies mainly involving restriction fragment length polymorphism (RFLP), simple sequence repeat (SSR), single nucleotide polymorphism (SNP), random amplified polymorphic DNA (RAPD), and amplified fragment length polymorphism (AFLP). Furthermore, the advent of next-generation sequencing (NGS) has accelerated the discovery of agronomically important genes. All of the technologies have enabled great advances for increasing the productivity of wheat. Here, the past history of first-generation sequencing, present status of second-generation sequencing, and future potential of translational genomics linked to the yield will be discussed.

Keywords: molecular markers, yield, quantitative traits (QTLs), next-generation sequencing (NGS)

1. Introduction

As the world's population is projected to reach approximately 9 billion by 2050, grain production of major staple crops needs to double to meet global food needs [1]. Together with rice and maize, wheat is one of the major staple crops widely grown in many countries, providing one-fifth of the calories and the protein for the world's population. In addition,

bioethanol is made primarily from wheat in Europe. Wheat starch is a major component for the production of bread, porridge, cakes, biscuits, and cereals which is a highly versatile crop for the human diet. In 2013, wheat was the third most produced cereal crop (713 million tons), after maize (1016 million tons) and rice (545 million tons). There are two distinct types of wheat, spring wheat and winter wheat, cultivated in many countries based on growing seasons, of which spring wheat is planted in most countries except in the United States and Northern Europe where the predominant crop is winter wheat. The global consumption of wheat has increased at a much faster rate than all other crops, because of the scale-up cultivation in developing countries, particularly in China [2]. Currently, out of the total cultivation area of more than 217 million hectares, the European Union countries has the largest area, followed by China, India, Russia, United States, and Canada [3]. Therefore, there has been an extensive effort over the past decades to increase wheat production through the application of molecular techniques which are powerful tools for enhancing effectiveness in breeding.

The most common or bread wheat species, *Triticum aestivum*, is an annual grass cultivated in temperate zones worldwide that belongs to the genus *Triticum* of the tribe *Triticeae*, and the family Poaceae. The most economically important cereals in the Poaceae family are maize, wheat, rice, barley, and millet. In the genus *Triticum*, there are approximately 25 species including wild and domesticated consisting of a series of diploid, tetraploid, and hexaploid forms, including the diploid einkorn wheat, *Triticum monococcum* (AA genome), the diploid wild wheat, *Triticum urartu* (AA genome), the allotetraploid emmer wheat, *Triticum turgidum* var. *durum* (AABB genome), the allohexaploid common wheat, *T. aestivum* L. (AABBDD genome), and the autoallohexaploid *Triticum zhukovskyi* (AAAAGG genome). Of these, *T. aestivum* has 42 chromosome pairs that are derived from two rounds of polyploidization events. Its genome size is approximately 17 Gb, composed of A, B, and D genomes created from the hybridization of three different species. The first hybridization between *T. urartu* ($2n=2x=14$) and a B genome species that has not yet been identified occurred 0.20–1.3 million years ago (MYA) to form the tetraploid *Triticum dicoccoides* ($2n=4x=48$) [4, 5]. The B genome is still unclear and may be extinct, but cytological evidence suggests that the S genome of *Aegilops speltoides* is a closely related species or an ancestral progenitor to the B genome of wheat [6, 7]. The second hybridization event resulted in the complete form of the hexaploid genome *T. aestivum* ($2n=6x=42$), which occurred between the domesticated *Triticum dicoccum* or *T. durum*, a wild goatgrass, and *Aegilops Tauschii* about 8000–10,000 years ago [8–10]. Like most allopolyploid plants, wheat also has the diploid-like chromosome pairing behavior during meiosis, preventing multivalent formation created by multiple homologous or homoeologous chromosomes [11].

In wheat breeding, a strong emphasis has been put toward the improvement of grain yield as it the most important goal in wheat breeding. There have been concerns about the stagnation or decline of the staple crops in some parts of the world. It has been detected that 37% of wheat areas have experienced the yield stagnation [12]. If the breeder develops an improved wheat variety, having a superior of trait, but produces low yields, producers unlikely will grow it because the yield is necessary for economic feasibility. The grain yield is a complex character with low heritability which is influenced not only by genes but also by the effects of the environment. In wheat, it has been documented that the higher yield is inversely related to

the protein content and can also delay maturity. Furthermore, abiotic stress factors including drought, salinity, extreme temperatures, and acidity contribute the most to yield loss, ranging between 60 and 82% [13]. As a consequence, extensive efforts have been made to identify the QTLs associated with the yield and its related traits which can be deployed by breeders through marker-assisted selection (MAS). The first report of the genome-wide assessment of molecular marker-based map in the nuclear genome of wheat began in the 1989 with the use of restriction fragment length polymorphism (RFLP) [14]. Subsequent analyses have been performed for construction of genetic maps to improve the efficiency of conventional breeding based on amplified-fragment-length polymorphism (AFLP), single-nucleotide polymorphism (SNP), diversity arrays technology (DArT), simple sequence repeat (SSR) or microsatellite, random DNA marker (RDM), gene targeted marker (GTM), and functional marker (FM). Based on these markers, there are 180 genetic maps extrapolated in wheat, most of which are developed by SSR markers. For example, molecular markers such as SSR and DArT have been used to detect QTLs for fusarium head blight (FHB) resistance, which can further be implemented in breeding studies [14]. Since 2007, a number of research studies have been taken to identify QTLs related to yield based on different mapping populations such as kernel length, kernel width, spike length, spike number, the grain number of spike, sterile spikelet number per spike, fertile spikelet number per spike, and thousand kernel weight [15–22]. However, the development of molecular markers and their applications in breeding have been relatively difficult in wheat because of its three closely related subgenomes and a large genome size consisted of high amounts (80%) of repetitive sequences. In 2012, the availability of wheat whole genome sequences has provided a framework for understanding of polyploidization, and domestication by comparing its sequences with ancestral and progenitor genomes, enabling us to understand the genetic diversity of wheat, which may help accelerate breeding programs [11]. Up to now, there are a total of 217,907 loci and 273,739 transcripts identified, of which 104,091 have been assigned as coding genes and 10,156 as long ncRNAs, according to Ensembl Plants (www.plants.ensembl.org). The chapter addresses molecular areas of research for yield improvement in wheat, focusing on finding QTLs for traits that affect yield. There are three objectives of this chapter as follows: (1) to explore the use of major molecular markers that have been used to identify yield and its-related QTLs in the past; (2) the current progress of molecular markers for linkage map construction; (3) to assess genomic studies of wheat; and (4) to discuss the potential of translational genomics in wheat using well-studied grasses such as rice and barley.

2. First-generation sequencing resources for yield improvement in wheat

2.1. Restriction fragment length polymorphism (RFLP) markers

Earlier molecular studies in wheat have shown that the RFLP markers are the common tools used as the oldest method of molecular markers for the construction of genetic maps. RFLP are typically inherited as simple Mendelian codominant markers, and are not influence by the environment, which could serve as highly heritable genetic markers for the study of inheritance of a trait. Chao et al. created the first linkage maps of the homoeologous group

7 chromosomes on the wheat genome using 18 cDNA clones across six mapping populations from ten varieties [14]. They mapped 31 RFLP loci on chromosomes 7A, 7B, and 7D. In 1991, detailed linkage maps were constructed with a total size of 1800 cm consisting of 197 RFLP loci [23]. Ma et al. [24] and Anderson et al. [25] identified RFLP markers associated with two Hessian fly resistance genes from *Triticum tauschii*, and preharvest sprouting genes from two recombinant inbred populations of white wheat (*T. aestivum* L. em. Thell.). Based on comparative mapping among cereal species such as wheat, rye, and barley, the development of detailed RFLP maps of the homoeologous group-2 chromosomes has established and showed that they had collinear relationships, indicating the high degree of conservation in gene orders [26]. The RFLP markers flanking the resistance to cereal cyst nematode were identified to be *Xglk605* and *Xcdo588*, which were mapped at 7.3 and 8.4 cm from the *Cre* locus [27]. Later, RFLP-based genetic maps belonging to different homoeologous groups were generated including homoeologous group 1 [28], group 2 [29], group 3 [30], and group 5 [31], and group 6 [32]. During this period, the powdery mildew genes were detected by RFLP probes. Ma et al. [33] reported that the powdery mildew resistant gene *Pm2* was located at 3.5 cm away from the RFLP marker *BCD1871*, and both *Pm1* and *Pm4a* showed cosegregation of markers. In addition, the *Pm1a* and *Pm2* were positioned on the RFLP maps at 3 cm away from *Xwhs178-7A*, at 2.7 cm away from *Whs296*, respectively [34]. To increase the frequency of polymorphism detection in wheat, a non-intervarietal cross (W7984 X Opata85) developed at the International Maize and Wheat Improvement Center (CIMMYT) was used creating a dense map which consisted of about 1000 RFLP loci on group 1 [28], group 2 [29], group 3 [30], and group 6 [35]. Other disease-resistant genes of *Lr9* responsible for leaf rust and *Sr22* responsible for stem rust were characterized and mapped using RFLP markers [36, 37]. Furthermore, the feasibility of the 37 RFLP probes on group 5 chromosomes from Thatcher near isogenic lines (NILs) for leaf rust resistance gene *Lr1* was conducted by Feuillet et al., of which three were investigated to be linked the gene [38]. Galiba et al. analyzed the cross between a frost-sensitive, vernalization-insensitive substitution line, *Triticum spelta* 5A and a frost-tolerant, vernalization-sensitive line, Cheynne 5A and showed cosegregation with *Vrn1* and *Xpsr426* RFLP marker [39]. There was also a linkage detected between *Vrn1* and *Xwg644* in accordance to Korzun et al. [40]. The mapping of a single locus controlling the aluminum tolerance gene *Alt2* was completed on the Chinese Spring chromosome arm 4DL derived from homoeologous recombination between *T. aestivum* cv. Chinese Spring chromosome 4D and *Triticum turgidum* cv. Cappelli chromosome 4B.

Starting from 1998, QTLs for yield and yield-related traits were investigated. The dwarfing genes, *Rht-B1* and *Rht-D1*, associated with plant height in wheat were firstly mapped on the short arms of chromosomes 4BS (*Xfba1-4B*) and 4DS (*Xfba211-4D*) [41]. A year later, thirteen RFLP probes and one morphological marker locus, *Eps*, were used to develop a genetic linkage map and identified that an RFLP marker *Xcdo549* on the short arm of chromosome 3A was associated with plant height, kernel number spike-1, and 1000-kernel weight [42]. Araki et al [43] reported one QTL for yield, *Qyld.ocs-4A.1*, and other yield-related traits of spikelet number ear, *QSpn.ocs-4A.1*, and grain weight/ear *QGwe.ocs.-4A.1*, on chromosome 4A which were detected by the *Xbcd1738* marker. As wheat lodging can result in yield losses, nine

QTLs for lodging resistance were detected with the genetic distance between the flanking RFLP markers, of which seven coincided with QTLs for morphological traits [44]. Since the year 2000, there have been many studies published for loci associated with grain yield, heading date, disease, and spike morphology. Kato et al. conducted mapping of QTLs for grain yield and its components on chromosome 5A and confirmed that the grain-yield QTLs were closely linked to QTLs for yield components [45]. They found RFLP markers associated with grain yield, tiller number/plant, ear grain weight, 50-grain weight, and spikelet number/ear based on a homozygous population of single-chromosome recombinant lines. Genetic mapping of QTLs conferring resistance to stripe (yellow) rust and powdery mildew was performed by Singh et al. [46] and Tao et al. [47]. The resistance gene, *Yr28*, derived from *Ae. tauschii* and the adult-plant resistance (APR) gene *Yr18* were mapped on chromosome arm 4DS and 7DS, respectively. They found that *Yr18* was closely correlated with leaf-rust gene *Lr34*. In addition, the RFLP *xbcd135* and *xbcd266* loci mapped at a genetic distance of 1.6 and 4.8 cm were identified to be closely linked to *Pm6*, a gene conferring resistance to the powdery mildew. Later, two of the powdery resistant genes, *Pm26* and *Pm29*, were mapped on the RFLP linkage map [48, 49]. Several RFLP markers within six major QTL regions have been identified to be tightly linked traits related to compactness such as spike length and number of spikelets [50]. Based on a set of 114 recombinant lines (RILs) of the 'International Triticeae Mapping Initiative' mapping population, morphological, agronomical, and disease resistance traits have been studied. Börner et al. [51] mapped 211 QTLs distributed over 20 chromosomes, of which they detected 64 major QTLs with a LOD score of >3.0 conferring glume color, leaf erectness, peduncle length, ear emergence time, flowering time, plant height, ear length, winter hardiness, grain-filling, grain number, thousand-grain-weight, fusarium resistance, powdery mildew resistance, and leaf rust resistance. The mapping of an earliness *per se* gene in wheat was carried out by Bullrich et al. [52]. This gene was located between the RFLP *Xcdo393* and *Xwgd241* on the long arm of chromosome 1A, which showed a large effect on heading date with a phenotypic variance of 0.47. Despite RFLP markers are highly reproducible and used as the primary way for most genetic work in wheat, it has been difficult to use RFLP markers due to the low levels of polymorphism detected in wheat.

2.2. Random amplified polymorphic DNA (RAPD) markers

The applications of RAPD markers have been beneficial to improve breeding programs in wheat because they are simple and fast PCR based, require no prior knowledge of target DNA sequence, and are analyzed either by the presence or absence of an amplicon via agarose gel electrophoresis. In wheat, RAPD has been used since 1990 [53]. Devos and Gale confirmed that a degree of polymorphism detected by six RAPD primers was comparable with RFLP markers [54]. They identified four RAPD markers with bread wheat cultivar 'Chinese Spring.' The application of both bulk segregant analysis (BSA) and RAPD has started in 1994 by Eastwood et al. [55]. Using BSA on DNA enriched for low-copy sequences by RAPD markers, the *Cre3* gene resistance to cereal cyst nematode (CCN) in *Triticum tauschii*, was mapped on the long arm of chromosome 2D (*Ccn-D2*) [55]. More efforts have been made to distinguish the wheat varieties resistant to cadmium stress [56], powdery mildew [57], and

common bunt [58]. The RAPD marker *OPC20* was closely correlated with a gene controlling cadmium uptake in western Canadian durum wheat (*T. turgidum* L. var. *durum*) [56]. In addition, a RAPD marker *OPH17-1900* located on the chromosome arm 6VS, was detected that could be used for the detection of a powdery mildew resistance gene, *Pm21*, in breeding [57]. For common bunt, also known as stinking smut and covered smut, the polymorphic RAPD marker, *BW553*, was identified between resistant and susceptible NILs [58]. Furthermore, identification of RAPD markers linked to the *Yr15* gene controlling stripe rust resistance was conducted using 340 RAPD primers, six of which were detected to be polymorphic [59]. The *OPB13* RAPD marker was the only one that produced polymorphism in 123 F₂ individuals and showed that it was linked to *Yr15* through screening a series of NILs each consisted of a different gene for Hessian fly resistance using 1600 random 10-mer primers. Another RAPD marker, *OPE-13*, showed the complete cosegregation with the H21 Hessian fly resistance gene in wheat [60]. Dweikat et al. developed RAPD markers linked to 11 different Hessian fly resistance loci that could be used for determining the presence or absence of specific Hessian fly resistance genes [61]. More RAPD markers including *OPX061050*, *OPAG04950*, and *OPAI14600*, was observed to be linked to the new powdery mildew resistance *Pm25* gene, where the linkage distance between them was 12.8, 17.2, and 21.6 cm, respectively [62]. The application of the BSA approach on DNA enriched for low-copy sequences was used by Eastwood et al. [55] and William et al. [63], generating an increased level of polymorphism and in repeatability. Hu et al. [64] identified two RAPD markers, *UBC320420* and *UBC638550*, that cosegregated with *Pm1a* and one RAPD marker, *OPF12650*, tightly linked to the resistance gene. In these studies, it has been observed that RAPD markers also have been difficult to use in wheat like RFLP markers due to the very low level of polymorphism. Furthermore, the reproducibility of this RAPD bands have been found to be questionable. Despite this, continuous efforts have been made to develop RAPD genetic markers for the discrimination of species/cultivars from each other [65, 66].

2.3. Amplified fragment length polymorphism (AFLP) markers

For assessment of large numbers of polymorphic loci, the AFLP technology has been implemented as a powerful tool because of its advantage of having good levels of reproducibility, insensitivity, fast, and no need of sequence information required for primer design [67]. In 1995, a novel PCR-based assay for plant DNA fingerprinting using AFLP markers has resulted in high levels of DNA polymorphism [68]. In fact, the AFLP technique has observed to be more efficient and less expensive and less labor intensive compared to the RFLP technique in wheat [69]. Earlier AFLP-based marker studies have been found to be informative in assessment of genetic diversity in wheat varieties started in 1998 [70, 71]. Regarding the investigation of traits associated with yield, Goodwin et al. [72] and Hartl et al. [73] initiated the AFLP technique to develop an AFLP marker associated with resistance to *Septoria tritici* blotch and powdery mildew, respectively. Hartl et al. identified several AFLP markers closely linked to the *Pm1c* and *Pm4a* [73]. Out of 92 AFLP primer combinations, 31 polymorphic fragments detected between the resistance and susceptible lines, of which eight were found to be the most reliable polymorphic markers. One of the AFLP markers, *18M2*, was detected as being highly specific for the *Pm1c* gene, while the *4aM1* AFLP marker was identified at 3.5 cm

from *Pm4a*. A couple of years later, an AFLP analysis was conducted using NILs of the strip rust resistance gene *Yr10* and designed AFLP primers that can be useful in detecting the *Yr10* gene [74]. Cao et al. analyzed the 119 individuals of H9020-17-5 x Mingxian169 F₂ population to detect AFLP markers linked to the strip rust resistance gene *YrHua* [75]. They found the two markers, *PM14(301)* and *PM42(249)*, of which *PM14(301)* was converted to PCR marker that could be a useful tool for MAS. In 2006, nine AFLP markers that showed polymorphism between the Argentinian wheat cultivar Sinvalocho MA and the rust leaf susceptible cultivar Gamma 6 were used to construct a linkage map of the *Lr3* gene for leaf rust resistance on chromosome 6BL of wheat [76]. The development of AFLP markers was carried out by Li et al. [77]. They detected seven markers linked to *Lr19* resistance to wheat leaf rust using *Mse I* and *Pst I* based on Thatcher, 23 NILs and F₂ generation of TcLr19 x Thatcher. Dhillon et al. detected putative AFLP markers linked to leaf rust resistance genes *Lr9*, *Lr19*, and *KLM4-3B* using NILs of wheat [78]. More likely, the AFLP technique has been approached for developing polymorphic markers underlying a trait.

2.4. Simple sequence repeat (SSR) and intersimple sequence repeat (ISSR) markers

Among all available markers, SSR (or microsatellite) markers have become the best suited tool in plant breeding programs, because they are practical, convenient, easy to use, and inexpensive. Moreover, SSRs with tandem repeats of a motif of <6 bp are the most polymorphic, codominant, easy for scoring banding patterns, and have wide genomic distribution, high reproducibility, and a multiallelic nature [79]. SSR analysis has been conducted in most of the QTL studies for mapping various traits. Up to 2015, there are more than 4000 SSR markers that have been developed and used for the construction of wheat genetic maps [80]. The high level of variability and Mendelian inheritance of SSR DNA markers have been first reported by Devos et al. [81] and Röder et al. [82]. Moreover, Röder et al. [83] and Stephenson et al. [84] placed SSR loci onto the genetic map, providing a starting point for developing a saturated map of the wheat genome. For example, SSR markers have been implemented for tagging and mapping important yield-related genes such as the dwarfing genes *Rh8* [85], *Rht12*, and the vernalization gene *Vrn1* [40], and a gene for preharvest sprouting tolerance [86]. SSR primers also have been used to detect some of the wheat resistance genes. Peng et al. found nine microsatellite loci found to be linked to *YrH52* with recombination frequencies of 0.2–0.35, and LOD scores of 3.56–54.22 [87]. The identification chromosomes with QTLs underlying 1000 grain weight (GW) has conducted by Varshney et al. [88]. They found the SSR marker *Xwmc333* as being linked to GW and the major QTL for GW (*QGw1.ccsu-1A*) with a R² value of 0.1509. Moreover, the SSR markers of *Xgwm210*, *Xgwm296*, and *Xgwm455*, were detected to be polymorphic and linked to the leaf rust resistance gene *Lr39*, of which *Xgwm210* was the closest marker mapped 10.7 cm from *Lr39* [89]. Ammiraju et al. [90] found four intersimple sequence repeat (ISSR) markers, *UBC8181000*, *UBC842600*, *UBC8431200*, and *UBC814750*, controlling seed size in wheat, which can be measured indirectly by 1000-kernel weight (TKW). These markers showed a significant association with gene effects of 84.662.92, and 2.61%, contributing a total of 31% of the phenotypic variance in seed size. The following year, Zhou et al. [91] identified six SSR markers linked to the major QTL for scab resistance, which were *Xgwm389*, *Xgwm533*, *Xgwm493*, *Xbarc75*, *Xbarc88*, and

Xbarc147 spanning a region of approximately 20 cm on chromosome 3BS. Additional SSR markers have been reported for strip rust resistance genes, including the *Xgwm501* marker linked to *Yr5* [92], and the *Xpsp3000* marker linked to *Yr10* [93]. A microsatellite linkage map of the powdery mildew resistance gene *Pm5e* on chromosome 7B has been constructed with 20 microsatellite loci, consisting of two codominant markers *Xgwm783* and *Wgwm1267* located close to *Pm5e* with a linkage distance of 11.0 cm and 6.6 cm, respectively [94]. The detection of QTL linked to FHB resistance has found that two microsatellite loci, *Xgwm533* and *Xgwm*, were significantly associated with QTL for FHB [95]. In 2004, a SSR-based consensus map has been completed by Somers et al. [96] that has been widely used as a reference. Furthermore, five QTLs, *QYld.crc-1A*, *QYld.crc-2D*, *QYld.crc-3B*, *QYld.crc-5A.1*, and *QYld.crc-5A.2*, controlling grain yield have been identified on chromosomes 1A, 2D, 3B, and 5A [97]. Other QTLs associated with 1000 grain weight, spikes meter⁻², seed number spike⁻¹, average seed weight spike⁻¹, harvest index, days to heading, days to maturity, and grain filling time have also been detected in the Superb/BW278 mapping population. Liu et al. [98] performed association mapping by genotyping wheat germplasm accession from China using SSR markers and EST-SSR markers, detecting 10 SSR markers on chromosome 4A associated with plant height, spike length, spikelets per spike, spikelet density, grains per spike and thousand-kernel weight. Even though studies involving RFLP, RAPD, and AFLP markers have only been used for identification and mapping of QTLs and genes, they are less likely to be applied into breeding programs because the application of these markers is likely to be less efficient for MAS [99].

3. Second-generation sequencing resources for yield improvement in wheat

Researchers have focused on discovering SNPs to be used as genetic markers, because they have many advantages. SNPs act as codominant, single-locus, biallelic markers offering a lower error rate, and higher accuracy than SSR markers. However, the nature of polyploidy and having similar sequences among the A, B, and D genomes makes it difficult to identify SNPs [100]. Therefore, progress in SNP detection has been limited, especially related to yield and its related traits. With the advancement in next-generation sequencing (NGS), sequencing has become increasingly popular due to the rapid development of NGS technologies, including SOLiD/Ion Torrent PGM from Life Science, Genome Analyzer/HiSeq 2000/MiSeq from Illumina, and 454 FLX Titanium/GS Junior by Roche [101]. These technologies have led to the implementation of high-density SNP genotyping in wheat [99, 102].

An important milestone in wheat genomic research was accomplished in 2012 with the completion of *de novo* sequencing of bread wheat, the variety Chinese Spring (CS42), facilitating advances in genomic research into the genus *Triticum* and providing insights into the polyploidization and domestication of wheat. Brenchley et al. sequenced the wheat genome using Roche 454 pyro-sequencing technology (GS FLX Titanium and GS FLX+ Platforms [11]). To identify the three component genomes (A, B, and D) of hexaploid wheat, the following technologies have been applied: Illumina sequence assemblies of *Triticum monococcum* (related

to the A-genome donor), *Ae. speltooides* complementary DNA assemblies, and 454 sequences from *Ae. tauschii* (the D-genome donor). Sequence analysis revealed that the A, B, and D genomes have estimated to consist of approximately 28,000, 38,000, and 36,000 genes, respectively. As a consequence, they identified the number of genes in wheat to be between 94,000 and 96,000. Like *G. hirsutum* [103] and soybean [104], wheat also has experienced a recent whole genome duplication (WGD) at 0.5 MYA and about 3.5 MYA. Brenchley et al. also examined gene conservation between wheat and its most closely related species *Brachypodium distachyon* and detected a high degree of conservation between the two species [11]. A large set of SNPs (132,000 SNPs) in A, B, and D genes will enhance future studies aimed at identifying QTLs and discovering associations of traits.

Since the completion of the draft sequence of wheat, extensive efforts have put into the identification of various molecular markers influencing yield to increase MAS efficiency. Based on the genotype by sequencing (GBS) approach, the linkage map of wheat comprised of markers including 538 GBS Bin, 258 AFLPs, 175 SSRs, and an EST has been constructed in 2014 [105]. They identified five QTL regions linked to thylakoid membrane damage (TMD), SPAD chlorophyll content (SCC), and plasma membrane damage (PMD), known as indicatives of high temperature tolerance, on chromosomes 6A, 7A, 1B, 2B and 1D and also detected some of the SSR markers associated with these traits such as the SSR marker *Xbarc121* and *Xbarc49* for all three traits and *gwm18* and *Xbarc113* for SCC. More SNP and SSR markers have been investigated using the 9 K Infinium iSelect Beadchips [106]. The SNP distribution between cultivars and landraces has provided impacts on our understanding of crop improvement on the structure of genetic diversity and insight into signatures of selection. Liu et al. reported six SNPs from two genes, *wsnp_CAP11_c209_198467* and *wsnp_JD_c4438_5568170*, showed significant association with soil-borne wheat mosaic virus (SBWMV) resistant which can be used in MAS to improve SBWMV resistance in wheat breeding [107]. Using the high-density Illumina iSelect 90K SNP assay, a linkage map spanning 3609.4 cm was constructed based on 5636 polymorphic SNP markers, with an average length of 171.9 cm per chromosome and marker density of 0.64 cm [108]. Association of agronomic traits with 1,366 SNP markers in durum wheat has been performed by Hu et al. [109]. By genotyping 150 accessions of durum wheat germplasm based on the Illumina Bead Array platform and Golden Gate Assay, a large amount of SNP markers were detected associated with key yield-related traits including plant height, number of effective spikes, length of main spike, number of spikelets per plant, panicle neck length of main spike, grain number per plant, grain weight per plant, and 1000-grain weight. These SNP markers have enhanced the previous QTL analyses and can be utilized for MAS to improve yield in wheat.

4. Future directions: translational genomics

The wheat genome is very complex as it is a polyploid species consisted of three diploid progenitor genomes. Recent advances in genome sequencing technologies have accelerated efforts to complete genomes of many crop species, which has opened the door for discovery and knowledge of the genetic basis of a number of important agronomic traits, with the final

| Species | | Arabidopsis | Barley | | Rice | | Wheat | | Maize | |
|-----------|------------------|-------------|------------|----------|--------------|----------|------------|----------|------------|----------|
| Trait | | Locus | Locus | Identity | Locus | Identity | Locus | Identity | Locus | Identity |
| Flowering | Early flowering | At1g28380 | KR706151 | 42.43 | XM_015770121 | 36.86 | KX161741.1 | 44.78 | EU241899.1 | 41.78 |
| | | At5g44040 | HM133570 | 43.85 | XM_015777033 | 37.49 | KJ711537 | 43.1 | KP202720.1 | 42.53 |
| | Late flowering | At1g01580 | EU331897.1 | 44.13 | XM_015787003 | 38.04 | KJ711539.1 | 43.16 | | |
| | | At1g04400 | AB476614.1 | 43.88 | XM_015756636 | 36.72 | | | | |
| Growth | Dwarf/small | At5g19530 | AY750996.1 | 42 | AB630963.1 | 43.05 | AY747606.1 | 43.1 | | |
| | | At1g02730 | EU331690.1 | 43.14 | AY747605.1 | 43.1 | KR816810.1 | 42.96 | | |
| | | At4g10180 | KT247893.1 | 42.47 | | | KT750252.1 | 42.82 | | |
| | Growth defective | At4g01690 | | | | | AY244509.2 | 42.97 | | |
| | | At1g02910 | | | | | JF965395.1 | 42.79 | | |
| | | At1g65260 | | | | | | | | |
| Stems | Waxy | At1g09560 | AK366020.1 | 58.91 | FJ487950.1 | 58.98 | KU376264.1 | 58.75 | | |
| | | At1g02205 | AK360068.1 | 58.91 | FJ487949.1 | 58.86 | KU376267.1 | 58.98 | | |
| | Fasciation | At1g64670 | AJ567377.2 | 60.29 | FJ501983.1 | 59.64 | EU981913.1 | 59.82 | | |
| | | | AK354338.1 | 57.95 | EU981914.2 | 60.39 | | | | |
| | | | AK356998.1 | 59.25 | | | | | | |
| | Short petiole | At4g10180 | AK360706.1 | 36.39 | AY585350.1 | 54.03 | M11336.1 | 55.81 | | |
| | | At3g03860 | AK353983.1 | 37.12 | GQ389628.1 | 58.62 | DQ457416.2 | 54.2 | | |
| | Twisted petiole | At4g27060 | | | EF190873.1 | 58.4 | EU189093.1 | 54.23 | | |
| Leaves | Abnormal shape | At3g16830 | | | JX828333.1 | 58.57 | AY831792.1 | 56.52 | | |
| | | At1g61940 | | | | | JX878122.1 | 58.41 | | |

| Species | | Arabidopsis | Barley | Rice | Wheat | Maize |
|---------|----------------|-------------|------------|------------|------------|----------------|
| Flowers | Rough surface | At5g04660 | | | | |
| | | At5g11060 | | | | |
| | | At1g32640 | | | | |
| | Carpel | At4g32551 | AK368072.1 | CT831121.1 | AY887064.1 | NM_001112060.1 |
| | | At5g11320 | AK253078.1 | AK100856.1 | BT008997.1 | AY898650.1 |
| | Stamen | At5g48390 | AB085818.1 | | AK334664.1 | DQ343238.1 |
| | | At1g63990 | | | | |
| | | At1g05160 | | | | |
| | Petal | At4g32551 | | | | |
| | | At1g55320 | | | | |
| Sepal | At2g20860 | | | | | |
| Fruits | Short | At2g02000 | EU333863.1 | AP014958.1 | KP749902.1 | FJ573211.1 |
| | | At1g69180 | AK250398.1 | | KP749901.1 | NM_001151022.1 |
| | | At1g68560 | | | | EU968771.1 |
| | Abnormal shape | At4g05200 | | | | |
| | | At5g04660 | | | | |
| | | At1g74720 | | | | |

Table 1. Comparative analysis of yield-related genes in Arabidopsis, wheat, barley, and maize.

aim of crop improvement and production. Moreover, the completion of sequences has enabled assessment of translational genomics which is an effective way for researchers and breeders to transfer knowledge of genetic and genomic information among related species, such as rice and wheat [110]. The translational genomics tool is known as 'model to crop' translation that can be contributed to the implementation of genetic and genomics in crop species [111]. There are three well-characterized model grass species rice [112, 113], *Brachypodium* [114], and barley [115], which can be used to accelerate the application of translational genomics among the Poaceae family. The large amount of insufficient knowledge such as biological processes that are controlled by genes can be filled from well-studied species through translational biology approach [110]. In translational genomics, comparative genomics studies can take advantage from available genomes and can provide information on the extrapolation of knowledge of gene functions among species [110]. Genome sequences are currently available for wheat, but information QTL mapping as compared to other model grass species have been less reported. Comparative analysis based on the candidate gene approach (CGA) is known as the most powerful tool for exchange information among species. We conducted a brief comparative analysis of yield-related genes in Arabidopsis, barley, rice, wheat, and maize. The 37 Arabidopsis genes controlling flowering, growth, stems, leaves, flowers, and fruits, have been used to investigate homologous sequences in the barley, rice, wheat, and maize genomes using BLAST [116]. Using the detected homologs among the grass species, we found a number of homologous sequences with the sequence identity values ranging between 36.39 and 60.39 based on MUSCLE v3.51 [117] (**Table 1**).

The release of genomic sequence of wheat [11], barley [115], and maize [118], provides a new opportunity for translational genomics. Since comparative genomics focuses on comparing genomes among plant species looking for similarities and differences of DNA sequence, protein sequence, and gene orders, information from well-studied and analyzed species can be applied for less studied crops to improve a specific target trait, which can be implemented in crop breeding and improvement. For example, genome-wide comparative analysis of flowering-related genes in Arabidopsis, wheat, and barley has revealed that there are 900 and 275 putative orthologs in wheat and barley, respectively [119]. In addition, they showed many orthologous genes having similar expression profiles in different tissues of wheat and barley based on their *in silico* expression analyses. Such a work will help researchers to investigate candidate genes controlling the time of flowering in rice and barley which can be incorporated into molecular breeding for early flowering in wheat and barley in short-season cropping region [119].

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