GENETIC CONTROL OF GRAIN SIZE AND WEIGHT IN WHEAT– WHERE ARE WE NOW?

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Abstract

Wheat is one of the world's most important food sources, alongside with rice and maize, directly providing about 50% of human food calories. By 2020, it is estimated that the global demand for wheat will increase by a further 40%, due to the increasing world population. Therefore, higher yield is one of the most important goals in wheat breeding.
Larger grains not only directly relate to grain yield but also have favorable effects on seedling vigour and early growth, thereby promoting and stabilizing yielding ability. Large grain size has been an important trait and it is usually measured in plant breeding practice by one thousand grain weight (TGW), mainly determined by grain width (GW), grain length (GL) and grain thickness (GT), but also by grain shape and density.
Milling and baking quality is also influenced by grain size and shape. Geometrical models indicated that changes in grain shape and size could result in increases in flour yield of up to 5%.
Test weight (volumetric weight), a trait largely used in commercial transactions with wheat, also depends on grain size and shape - larger grains, deviating from spherical shape having lower test weight.
Grain size in wheat is a complex character and any information on its genetic control is useful for increasing breeding efficiency. Identifying molecular markers linked to quantitative trait loci (QTLs) controlling seed size would facilitate selection in early generations and may contribute to improved yield and end-use quality in wheat by accumulating such loci into elite backgrounds.
Grain size in wheat is a quantitative trait controlled by quantitative trait loci (QTL), and numerous QTLs for grain size have been reported. Previous research showed important QTLs on all chromosomes, but most significant QTLs were identified on chromosomes 1B, 1D, 2A, 2B, 2D, 3A, 3B, 3D, 4B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B, 7D. Grain size is negatively correlated with grain number, mainly due to competition for available assimilates.
Alleviating this correlation should be facilitated by a more detailed knowledge of grain size genetic control.
In this mini-review we will focus on the latest information about the QTLs and genes involved in genetic control of wheat grain size and weight, and the best molecular markers associated with these traits.

Key words: wheat, grain size, weight, TGW, QTL.

BACKGROUND

Worldwide food production must be raised by 70% from present level to sustain the estimated population of 9.1 billion by 2050 (Patil, 2013). Wheat is one of the most important crops worldwide, alongside with rice and maize directly providing about 50% of human food calories (Lin et al., 2015).

It is estimated that the wheat demand will increase by a further 40% before 2020, as a result of world population increase (Rajaram, 2005; Dixon et al., 2009). Since wheat is one of the most important cereals along with rice and maize, annual increase of 1.6%-2% in grain yield is required in the coming years in order to fulfil the global demand (Patil, 2013; Faris, 2014).

To achieve higher yields in wheat, breeding programs focused on obtaining cultivars with best agronomic traits (disease resistance, protein content, grain size and weight, drought tolerance etc.). This achievement can be made through genetic improvements and enhanced plant biology understanding. Grain yield in wheat is determined by the grain number per spike, spike number per plant and grain weight. Among these, the most reliable trait is grain weight, measured as the 1000-grain weight (TGW). Grain weight has a strong positive

correlation with grain size and shape (Gegas et al., 2010). Also, grain shape is characterized by a combination of grain length, grain width, grain length-to-width ratio, and thickness. The complexity of genetic control for grain size and weigh set in motion many studies that lead to the discovery of important QTLs, on almost all chromosomes. Dissection of these complex traits into individual components using molecular maps is useful to obtain information about genetic control and relationship between the components (Wu et al., 2012; Patil et al., 2012).

Marker association (especially haplotype association analysis) accelerates the process of mapping and detection of important genomic regions and favoured alleles or haplotypes for breeding (Hou et al., 2014).

High-density genetic linkage maps are necessary for precisely mapping QTLs controlling grain shape and size in wheat (Qiu-Honget al., 2015).Advances in field of genetics made possible for the geneticists to identify genes and quantitative trait loci (QTLs) involved in controlling important agronomic traits. Wheat yield, or yield components, is controlled by numerous genes with additive and epistatic effects that are highly interactive with the environment (Zheng et al., 2014).

In this article, we briefly review the current status about the genes/QTLs involved in grain size and weight for yield improvement.

GENETIC ANALYSIS OF WHEAT GRAIN SIZE AND WEIGHT

The domestication of wheat, 10000 years ago, was instrumental in the transition of human behaviour from hunter-gatherer to farmers. One of most important modifications that occurred in wheat and other cereal crops was the increase in size of seeds (Faris, 2014).

Grain size (and weight) is a major component of wheat yield. Larger grains not only directly relate to grain yield but also have favourable effects on seeding vigour and early growth, thereby promoting and stabilizing yielding ability.

Large grain size has been an important trait and it is usually represented in plant breeding practice by one thousand grain weight (TGW), mainly determined by grain width (GW), grain length (GL) and grain thickness (GT) (Zhenqi et al., 2010).

TGW is a complex trait and any information on its genetic control is useful for increasing breeding efficiency (Giura and Saulescu, 1996). TGW, a trait largely used in commercial transactions with wheat, also depends on grain shape, seed number (negative compensation effect between seed size and seed number), spikes per plant, environment conditions, stress tolerance and other factors which make the improvement of this trait a challenge for the geneticists (Zanke et al., 2015; Xuejiao et al. 2015; Weiyu et al., 2015; Quan et al., 2015).

Milling and baking quality is also influenced by grain size and shape. Geometrical models indicated that changes in grain shape and size could result in increases in flour yield of up to 5% (Röder et al., 2008; Rasheed et al., 2014).

Wang et al. (2015) studied the TaGS5 genes (physically mapped on 3AS and 3DS). Analysis of association of *TaGS5-A1* alleles with agronomic traits indicated that cultivars with *TaGS5-A1b* possessed wider grain width and higher TKW (45.8g), as well as significantly lower plant height, spike length, and internode length below spike than those of cultivars with *TaGS5-A1a*(44.9g; P < 0.05) over 3 years.Expression analysis of the *TaGS5-A1* gene indicated that *TaGS5-A1b*allele possessed significantly higher expression level than *TaGS5-A1a* allele in differently developmental seeds.

Another study, focused on the *TaGS5* genes, was carried out by Ma et al. (2015).

In this study, *TaGS5* homoeologues in wheat were isolated and mapped on chromosomes 3A, 3B and 3D (designated as TaGS5-3A, -3B and -3D).

TaGS5-3A was classified as a type II serine carboxypeptidase, whose functions are closely related to cell division. Two alleles of *TaGS53A*, *TaGS5-3A-T* and *TaGS5-3A-G* were identified in wheat accessions, and a functional marker was developed to discriminate them. Association analysis revealed that *TaGS5-3A-T* was significantly correlated with larger grain size and higher thousand grain weight.

The results of Ma et al. (2015) suggests that *TaGS5-3A* is a positive regulator of grain size

and its favoured allele *TaGS5-3A-T*exhibits a larger potential application in wheat high-yield breeding. More recently, Kumar et al., 2016, published their analysis and were showed that grain length and width are genetically independent and the most significant QTL was identified on chromosome 4B, and could be an ortholog of major rice grain size and shape gene *GS3* or *qGL3*. Also, they found major and stable locus on the homeologous region of *TaGASR7* (7A) gene. This gene (*TaGASR7*), which is an ortholog of *OsGASR7*, a gibberellin- regulated gene that controls grain length in rice. Dong et al., (2014) identified *TaGASR7-A1*, in wheat, based on the sequence similarity with rice, and this gene was mapped on the telomeric end of 7AL with strongest effect on grain length. Nevertheless, the study by Kumar et al. (2016) suggested that GASR7 region may play an important role in the genetic control of seed development and grain shape and size in wheat.

Grain filling between anthesis and maturity is the main mechanism that determines the final grain weight. At this stage there are three physiological processes occurring simultaneously: dry matter accumulation, water accumulation and subsequent desiccation, and grain morphological expansion.

Grain filling can be divided into two components: rate and duration. The rate and duration of grain filling both contribute to final grain weight.

Dry matter accumulation is a process of deposition of starch (~60–70% of the mature grain weight), proteins (8–15%), and other nutrients (e.g. minerals, vitamins and fibres) (Quanet al., 2015).

Considering that starch accounts for about 70% of the grain endosperm, Hou et al. (2014), focused on the conversion of sucrose to starch. Sucrose synthase catalysis is the first step in the conversion of sucrose to starch, that is, the conversion of sucrose to fructose and UDP-glucose by the wheat sucrose synthase genes *TaSus1* and *TaSus2* (located on chromosomes 7A/7B/7D and 2A/2B/2D, respectively). Five favoured haplotypes were identified at TaSus2-2A (*Hap-A*), TaSus2-2B (*TaSus2-2B-Hap-H*), TaSus1-7A (*Hap-1* and *Hap-2*), and TaSus1-7B (*Hap-T*) (Hou et al., 2014).

During grain filing stage, drought, heat and other abiotic stresses greatly affect growth and productivity of wheat. Grain filling in wheat depends on two major sources of carbon: current photosynthate in leaves and non-leaf organs; and carbohydrates stored in the stem and leaf sheath from stem elongation to the early phase of grain filling.

Conserved water-soluble carbohydrates (WSC; composed mainly of fructans, sucrose, glucose, and fructose, with the main reserve as fructans at the late stages of WSC accumulation) at early grain filling play an important role in partial compensation of reduced carbon supply (Zhang et al., 2014; Li et al., 2015).

WSC accumulation and utilization depend on growing conditions and genotypes. Among three segments of the main stem (peduncle, penultimate internode and the remainder segments), the remainder segments are the major storage sites and the major source for WSC mobilization during the grain filling period. In general, WSC accumulate until 10–20 days after anthesis, and the reserved WSC can reach more than 40% of total stem dry weight in wheat (Zhang et al., 2014).

Under diverse drought stress conditions, WSC in lower internodes showed significant positive correlations with TGW, especially at the flowering stage under well-watered conditions (WW) and at grain filling under drought stress (DS).

Mobilization of WSC during grain filling can potentially contribute about 10-20% of the final grain weight under non-stress conditions, and up to 70% or more of grain dry matter under drought stress in wheat (Zhang et al., 2014; Li et al., 2015).

Drought tolerant wheat cultivars have a high capability of WSC accumulation, coupled with higher mobilization efficiency, stronger sink activity and longer duration of grain filling.

Zhang et al. (2014) found correlation between TGW and four types of WSC, viz. (1) total WSC at the mid-grain filling stage (14 days after flowering) produced by leaves and non-leaf organs; (2) WSC contributed by current leaf assimilation during the mid-grain filling; (3) WSC in non-leaf organs at the mid-grain filling, excluding the current leaf assimilation; and (4) WSC used for respiration and

remobilization during the mid-grain filling (Remo).

Variation in stem WSC among wheat genotypes is an important genetic factor involving grain weight and yield under drought stress conditions. WSC content is a complex quantitative trait controlled by polygenes, and the small effects of many independent QTL limit their direct use for marker-assisted selection in breeding programs.

QTL associated with stem WSC have been reported in perennial ryegrass, rice, maize, barley, and wheat. In wheat, QTL for WSC were mapped on chromosomes 1A, 2D, 4A, 4B, 5D, 6B, 7B and 7D (Zhang et al., 2014).

Favourable alleles for WSC of Total, Leaf, Non-leaf and Remo highlighted by Bing Zhang et al. in 2014: Xcfd17-2D (Remo, WW) had the same favourable WSC alleles (Xcfd17-2D$_{223}$) in peduncle, lower internode and the whole stem estimates; Xgwm181-3B$_{131}$ and $_{161}$ (Leaf, DS), Xgwm610-4A$_{167}$ (Leaf, WW),Xgwm513-4B$_{144}$ (Leaf, DS), Xgwm165.1-4D$_{199}$ (Non-leaf, WW), Xwmc517-7B$_{188}$ (Non-leaf, WW) had positive effects both in lower internode and the whole stem. Higher WSC were associated with Xgwm169-6A$_{203}$ (Remo, WW) and Xgwm537-7B$_{205}$ (Leaf, DS) in both the peduncle and lower internode. Xbarc125-3D$_{147}$ (Total) contributed to higher WSC in lower internodes, not only under well-watered conditions, but also under drought stress.

WSC alleles that exhibited significantly positive contributions to TGW on an individual basis identified by Zhang et al., in 2014 were Xcfd17-2D$_{223}$, Xcfd53-2D$_{263}$, Xgwm181-3B$_{140}$ and $_{161}$, Xgwm389-3B$_{116}$, Xbarc125-3D$_{147}$, Xgwm358-5D$_{162}$ and Xgwm537 7B$_{205}$.

In Li et al. (2015) study, five of the 16 favorable WSC alleles, individually contributed to significantly higher TKW, respectivelyXbarc181–1B$_{187}$, Xgwm148–2B$_{165}$, Xgwm261–2D$_{203}$, Xgwm149–4B$_{153}$ and Xgwm358–5D$_{162}$.

WSC can make a positive contribution to TKW under different environment conditions. Pyramiding target favourable alleles is not only effective for obtaining genotypes with higher stem water-soluble carbohydrates, but also is effective for enhancing TKW under drought conditions.

High stem WSC has already been suggested as a criterion for wheat breeding under drought stress. With marker-assisted selection, accumulation of favourable alleles for WSC should play an important role in future wheat breeding programs (Li et al., 2015).

Final grain weight (height and volume) is also influenced by the water accumulation during grain filling. Water is essential to transport photo assimilates and other nutrients into developing grains. It also provides a suitable environment for metabolic processes, and directly takes part in the synthesis of storage products (Xieet al., 2015).

Grain morphology changes along with dry matter and water accumulation. Immediately after fertilization, grain length, width, height (thickness), and thus volume increase rapidly. The first dimension to reach its maximum value is grain length (~15 d after anthesis), followed by grain width, height, and volume (~28 d) (Lizana et al., 2010; Hasan et al., 2011), corresponding to the period of endosperm cell enlargement.

A positive relationship between carpel size at anthesis and final grain weight was found, consistent with earlier reports in wheat (Calderini et al., 1999; Hasan et al., 2011), barley (*Hordeum vulgare* L.; Scott et al., 1983), and sorghum (*Sorghum bicolor* (L.) Moench; Yang et al., 2009). Larger carpels accelerated the initial and rapid grain filling rates (mainly the former), advanced the onset of grain filling, and slightly extended grain filling duration, resulting in higher grain weight. Moreover, larger carpels increased maximum grain water content, grain water absorption and loss rates, and grain dimensions.

The carpel size mediates final grain weight mainly through its effects on the initial phase of grain filling.

The significant QTLs identified by Xieet al. (2015) in their study, were scattered on 18 chromosomes, individually explaining 6-39% of the phenotypic variation. Taken together, QTL coincidences among final grain weight, carpel size, grain dry matter and water accumulation, and final grain dimensions were found on 16 chromosomes, with the increasing alleles usually conferred by the same parents, indicating pleiotropy or the tight linkages of functionally related genes. A large number of

coincident QTLs were observed on chromosomes 2A (36 QTLs for 12 traits), 3B (37 QTLs for 13 traits), 4A (39 QTLs for 14 traits), 5A (16 QTLs for 13 traits), 5DL (20 QTLs for 12 traits), and 7B (49 QTLs for 12 traits), which would offer the opportunity for improvement of multiple grain filling traits simultaneously (Xieet al., 2015).

In another study, Yue et al. (2014), focused on the enzymes involved in fructan synthesis in higher plants, emphasizing 6-SFT as a key enzyme in fructan biosynthesis.

Using the genomic sequence of 6-SFT, 6-SFT-A1 locus, was mapped on chromosome 4A, and revealed that SNP in 6-SFT-A1 gene was associated with wheat seedling drought resistance.

Based on sequence differences in 6-SFT among genomes, A genome-specific primer pair was designed for chromosome location. PCR results showed that the 6-SFT-A2 gene was also located on chromosome 4A. Furthermore, three 6-SFT-A2 haplotypes, designated HapI, HapII, and HapIII, were identified based on the 13 SNP/InDel sites.

Yue et al.(2014) developed two cleaved amplified polymorphic sequence (CAPS) markers to distinguish the three haplotypes. The cleaved PCR products were easily distinguished on agarose gels.

The mean TGW of HapIII was higher than that of both HapI and HapII. HapIII haplotype possessed a significantly positive effect on TGW and, therefore, should be a beneficial allele for improving grain yield (Yue et al., 2014).

Jaiswal et al. (2015) analysed sequence polymorphism in the promoter region ofTaGW2-6A (negative regulator of grain-width and grain-weight) and found two novel SNPs (one SNP present in CGCG motif) in the promoter region. Among the five haplotypes identified in this study, Hap5 (G_A_G_A) had significantly higher TGW than other haplotypes except Hap2, which did not show any significant difference from Hap5. A user-friendly CAPS marker for the causal SNP was also developed for exploitation of the variation in *TaGW2-6A* gene for improvement in TGW and other associated agronomic traits through marker-assisted selection (MAS) in wheat.

Qin et al. (2014), analysed haplotypes of *TaGW2-6B* and their effects on TKW and interaction with haplotypes at *TaGW2-6A*.Haplotype association analysis indicated that *TaGW2-6B* has a stronger influence than *TaGW2-6A* on TKW, and *Hap-6B-1* was a favoured haplotype increasing grain width and weight that had undergone strong positive selection in global wheat breeding.

Furthermore, haplotype interaction analysis between *TaGW2-6A* and *TaGW2-6B* showed additive effects between the favoured haplotypes. *Hap-6A-A/Hap-6B-1* was the best combination to increase TKW. Based on the -593 A/G polymorphism a CAPS marker was developed and association analysis indicated that *Hap-6A-A* increased TKW by more than 3.1g.

Recent studies reported that transcript abundance of *TaGW2-6A* is negatively associated with the grain width, but the transcript levels of *TaGW-2B* and *TaGW-2D* were positively associated with the grain width in the same bread wheat accessions, suggesting that triplicate homoeologues of *TaGW2* might have different functions in grain development, and that there is a balance among three genes finally determining the grain size in bread wheat.(Jaiswal et al., 2015).

Lu et al. (2015) studied one of the key phytohormones synthesized in the root, cytokinin (CTK) that regulates many important plant processes by controlling cell division and tissue differentiation.

Cytokinin is one key hormone in controlling grain size and weight by regulating endosperm cell numbers of crops and also can enhance grain weight by regulating grain filling patterns of crops. Seed numbers per plant and seed weight are improved by silencing the *TaCKX1* gene in wheat.

At present, wheat CKX genes have been isolated: *TaCKX1* and *TaCKX4* (Chang et al., 2015) on chromosome 3A, *TaCKX2* on 7A or 7B, and *TaCKX2.1*, *TaCKX2.2*, *TaCKX3*, *TaCKX5*, and *TaCKX6* on 3DS.

The results of Lu et al.,2015 study indicated that the allelic variation of*TaCKX6a02* had significant correlation with grain size, grain weight, and grain filing rate (GFR) in the recombinant inbreed line (RIL) population,

explaining 17.1~38.2% of phenotype variations in different environments.

A specific marker, TKX3D, was designed and can be used in marker-assisted selection (MAS) for grain size, weight, and GFR in common wheat.

Chang et al. (2015) associated the CKX genes with flag leaf chlorophyll content after anthesis, as well as grain weight. In high plant leaves, chlorophyll, including chlorophyll a and b, is the main photosynthetic pigment in chloroplasts, and its amount directly affects plant photosynthetic efficiency. Increased chlorophyll content in crop-species leaves increases in both biomass production and grain yield. As chlorophyll is the main pigment in photosynthesis, its abundance and stability in the leaf significantly affects grain filling and crops yield.

Results of Chang et al. (2015) showed that the variation of *TaCKX4*significantly associate with chlorophyll content and grain weight in the RIL population. Through mapping analysis, *TaCKX4,* was closely linked to Xwmc169 on chromosome 3AL. *TaCKX4* co-segregated with a major QTL for both grain weight and chlorophyll content of flag leaf at 5~15 days after anthesis. This QTL explains 8.9~22.3% phenotypic variations of the two traits across four cropping seasons.

From the three identified genotypes, genotype-A corresponded to higher wheat chlorophyll content and grain yield. Furthermore, the study indicated that copy number variation in *TaCKX4* (not the allelic variation) could significantly influence wheat chlorophyll content and grain weight. The locus linked to *TaCKX4* showed good stability and reliability in varied environments and genetic backgrounds, making this useful for improving the effectiveness of MAS for chlorophyll level and grain weigh in wheat breeding.

Cell wall invertase (CWI) is a critical enzyme for sink tissue development and carbon partition and has a high association with grain weight.

Ma et al. (2012) characterized the CWI genes and designed a pair of complementary dominant markers (CWI21 and CWI22), based on the two allelic variation of at the *TaCWI-A1* locus (*TaCWI-A1a* and *TaCWI-A1b*; chromosome 2A). The lines with *TaCWI-A1a* allele had significant higher TKW (45g) compared to the lines with *TaCWI-A1b* allele (42.6g). QTL analysis indicated that *TaCWI-A1*could explain 4.8% of phenotypic variance for grain over 2 years.

Another study on CWI was carried out by Jiang et al. 2015. This study, based on isolated *TaCWI* genes from chromosomes 4A, 5B and 5D, found two SNPs that were detected in the promoter region of *TaCWI-4A*, and four SNPs and two Indels were present in the *TaCWI-5D* gene. Discrimination of *TaCWI-4A* and *TaCWI-5D* haplotypes was accomplished by CAPS markers, viz.,*caps4A* and *caps5D*. The results indicated that *Hap-5D-C* at *TaCWI-5D* was significantly associated with higher TKW in 348 Chinese modern cultivars grown in multiple environments. In rainfed production regions, *Hap-4A-C* was favoured because it brought more seeds, but in well irrigated conditions, *Hap-4A-T* was favoured in modern breeding because of higher TKW.

The *TGW6* gene encodes a novel indole-3-acetic acid-glucose hydrolase and plays a significant role in improving TGW and yield in rice.

Hanif et al. (2016) isolated and characterized*TGW6*orthologs in bread wheat and developed functional markers to validate the *TaTGW6* gene association with TKW and yield. The analysis of ortholog*TaTGW6-A1* revealed two haplotypes, *TaTGW6-A1a* and *TaTGW6-A1b*. Haplotype *TaTGW6-A1a* identified by the dCAPS conferred higher grain weight and yield (higher TKW).

The QTL for yield at the *TaTGW6-A1* locus explained 17.4% of the phenotypic variance in average yield over four environments.

ADDITIONAL GENES WITH EFFECT ON GRAIN SIZE AND WEIGHT

Zheng et al. (2014) studied a member of the transcript elongation factor gene family, *TaTEF.TaTEF-7A* was located on chromosome 7A and was flanked by markers Xwmc83 and XP3156.3. Subcellular localization revealed that TaTEF-7A protein was localized in the nucleus. This gene was expressed in all organs, but the highest expression occurred in young spikes and developing seeds.

Overexpression of *TaTEF-7A* in Arabidopsis thaliana produced pleiotropic effects on vegetative and reproductive development that enhanced grain length, silique number, and silique length.

Haplotype–trait association analysis of the Chinese wheat mini core collection revealed that *TaTEF-7A*was significantly associated with grain number per spike. Phenotyping of near-isogenic lines (NILs) confirmed that TaTEF-7A increases potential grain yield and yield-related traits.

The presence of favoured haplotype, *Hap-7A-3*, showed a positive correlation with yield in a global set of breeding lines. These results suggest that *TaTEF-7A* is a functional regulatory factor for grain number per spike and provide a basis for marker-assisted selection.

Another interesting gene family with positive effect on TKW encoding for plant stress association proteins (SAPs). Thus, *TaSAP1*, a member of the stress association protein (SAP) gene family from wheat is involved in response to several abiotic stresses, including drought, salt and cold. Chang et al., 2013, found that *TaSAP1-A1* locus, located on chromosome 7A, was significantly associated with TGW, number of grains per spike, spike length, peduncle length and total number of spikelets per spike in multiple environments. Also, this team identified three markers T7AM5, T7AM2606 and T7AM39 located in the promotor region with six haplotypes.

CONCLUSIONS

According to the most recent data, the grain size and weight are under complex genetic control and at the same time influenced by the environment. At present, there are identified genes/QTLs significantly associated with grain shape, size and weight. Moreover, several genes/QTLs are involved in response to several abiotic stresses and associated with grain traits and yield. The presence of molecular markers, associated with grain traits, constitute a premise for the improvement of grain potential, by pyramiding the best alleles with additive effect, using MAS.

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