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Wheat seed transcriptome reveals genes controlling key traits for human preference and crop adaptation

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Analysis of the transcriptome of the developing wheat grain has associated expression of genes with traits involving production (e.g. yield) and quality (e.g. bread quality). Photosynthesis in the grain may be important in retaining carbon that would be lost in respiration during grain filling and may contribute to yield in the late stages of seed formation under warm and dry environments. A small number of genes have been identified as having been selected by humans to optimize the performance of wheat for foods such as bread. Genes determining flour yield in milling have been discovered. Hardness is explained by variations in expression of *pin* genes. Knowledge of these genes should dramatically improve the efficiency of breeding better climate adapted wheat genotypes.

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Introduction

The useful part of the wheat plant is the seed. Analysis of the transcriptome of the developing seed allows analysis of processes involved to seed formation. Recent RNA-Seq experiments with diverse genotypes [1••] are an extensive resource and when combined with phenotypic data associated with contrasting grain traits can be used to identify genes controlling those traits (Figure 1). Differences in gene expression contribute to grain hardness [2••], the yield of flour obtained when the wheat is milled [3••], and the quality of end products such as bread [4••] (Table 1). Photosynthesis is active in the pericarp of the seed at mid-development but declines towards seed maturity. This photosynthesis involves the expression of genes for a C4 pathway of photosynthesis specific to the seed in wheat [5••,6] (Table 1). The exact role of these genes is not resolved but has been proposed to involve re-fixation of CO_2 produced by respiration associated with grain filling with this seed photosynthesis possibly differing significantly from leaf photosynthesis [7].

Importance of wheat

Wheat is the most important food grain in temperate regions complementing rice production in more tropical regions. Wheat is generally lower yielding than rice and is grown over a larger area. Climate change is threatening food security by reducing crop yields [8]. Global warming is resulting in wheat experiencing higher temperatures during grain development with potential consequences for both gain quality and yield. With the availability of a whole genome sequence of wheat [9,10], it is much easier to position the genes underlying yield [11•] and quality [12] traits. This helps to identify and target genes for manipulation to achieve improved productivity and grain quality using present day molecular tools. Genomics tools [13] have been considered as a key approach to climate change adaptation [14] especially for a polyploid crop with very large genome like wheat.

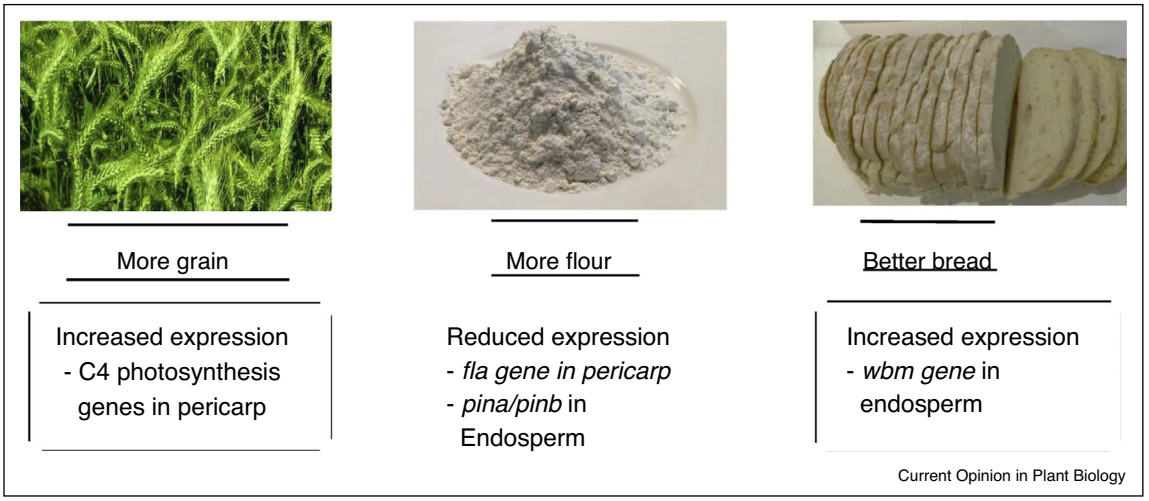
Seed biomass equals yield

The yield of wheat is a product of the number of grains and the size of the grains. Major genes controlling yield-related genes in wheat, identified by means other than seeds transcriptome sequencing/profiling, have been reported at the whole plant level as reviewed in [11•] and in seeds (Table 1) controlling grain size [15–18] and length [19,20] (Table 1). In addition, genes controlling spike architecture leading to grain yield improvement have also been reported [21,22]. Domestication of wheat has involved human selection for these traits to deliver high grain yield. While the plant captures carbon by photosynthesis in the leaves the amount reaching the seed is critical for grain yield. The fate of sugars arriving in the seed may also be highly significant with respiration and capture of additional carbon by photosynthesis in the seed [5••] also contributing to the final seed biomass.

Seed composition equals grain quality

The nutritional and functional quality of wheat is determined by the composition of the grain. Human selection for ease of processing and end product quality has resulted in hexaploid wheat genotypes specifically suited to different products such as bread, chapatti or noodles,

Figure 1



Grain quality and yield-related genes recently identified by transcript profiling of developing wheat seed. Photosynthesis genes expressed in the grain may lead to higher yields of grain. Mutant puroindoline (*pin*) genes or reduced expression of *pin* genes or reduction in the expression of the fasciclin-like arabinogalactan protein (*fla*) genes resulting in lower cell adhesion may lead to higher flour yield. High expression of *wbm* a gene encoding a small protein with four cysteine residues with potential to form cysteine linkages with glutenin and gliadin proteins may lead to better bread quality.

while durum (tetraploid) wheat has been developed for pasta production.

Seed transcriptome analysis

The construction of the grain is largely determined by genes expressed in the various tissues of the grain during seed development acting on the substrates flowing from the vascular system into the grain. This determines grain composition (quality) and influences biomass (yield). Greater knowledge of the patterns of gene expression during seed development and maturation, their variation between genotypes and response to environment will explain the molecular basis of much of the variation in yield and quality in wheat [13].

Transcriptome analysis of diverse wheat genotypes by RNA-Seq [1••] has provided a platform for research on grain development and the determination of grain yield and grain composition that controls functional and nutritional properties [23]. The polyploidy genome of hexaploid wheat results in a complex transcriptome with the potential for highly sub-genome specific expression [24–26]. Nearly 80% of the genes in hexaploid wheat are preferentially expressed at the sub-genome level (A or B or D) during various developmental stages [24,27]. Due to the polyploid nature of wheat, many alleles with trait favourable mutations lie redundant and as a result remain unexploited. A transcriptomic approach [28] may uncover such hidden variation for use in crop improvement. This indicates, targeted (sub-) genome editing tools may become a method of choice for increased productivity in wheat. The availability of long read (Iso-Seq) sequencing should enhance the value of transcriptome analysis especially in polyploid plants [29–31] like wheat.

Grain hardness

The hardness of wheat has been considered a key attribute and used to name wheat classes with hard wheats preferred for breads and soft wheats for cakes and cookies. This is due to the higher degree of starch damage associated with the milling of hard wheats. In hard wheats starch granules are broken providing a greater opportunity for water adsorption by the starch during dough making while in soft wheats the starch granules are more easily separated from the protein matrix allowing milling without starch damage and resulting in lower levels of water adsorption. The hardness locus in wheat includes the *pin* genes encoding the puroindoline proteins (Figure 1) and the gene encoding the grain softness protein. The grain softness protein was named because it was found associated with the surface of the starch granules in the flour of soft but not hard wheats. The grain softness protein (GSP-1) was only recently identified as being encoded by a gene that also encodes an arabinogalactan protein [32•]. The pre-protein translated from this gene is cleaved in the vacuole to generate an AGP and the grain softness protein.

Analysis of *pin* alleles has been used to select for hardness. Mutations in these genes are associated with hardness. However, wheat genotypes with hard grain texture were found without mutations in the *pina* or *pinb* genes. Transcriptome analysis has shown that hardness is associated

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Table 1

Recently identified associations between gene expression in wheat grain and processing, yield and quality traits

Trait	Gene/trait correlation	Description	Reference
Grain hardness Flour yield	*Pina* and *Pinb* negative	• Expression in endosperm • Reduced/no expression/non-functional *PinB* due to mutant *PinA* or *PinB* alleles correlates with genotypes with hard grain • PINA and PINB known to interact with starch	[2••]
Bread quality Loaf volume	*wbm* positive	• Expressed in endosperm • High expression due to promoter variant correlates with genotypes with good bread quality • WBM is a small sulphur-rich protein which potentially cross-links with glutenins and gliadins leading to good bread quality • Rare allele in A/D-sub-genome	[4••]
Milling quality Flour yield	*fla* negative	• Expression in pericarp • Low expression possibly due to promoter variants correlates with genotypes with good milling quality • FLA8 is a cell adhesion protein likely resulting in tight-attachment of bran to endosperm leading to poor flour quality and yield	[3••]
Grain yield	*ppc*, *aat*, *mdh2*, *me2*, *gpt*, *ppdk* positive	• Expression in pericarp • Enhanced expression in grains • Grain C4 photosynthesis for higher grain yield	[5••]
Grain size and weight (positive)	*TaGS5-3A (-T)* positive	• Expression in developing grains and young spike • High expression correlates with genotypes with larger grain size and higher grain weight • Encodes a type II serine carboxypeptidase possibly involved in cell division and rapid cell proliferation	[15]
Grain size and weight (positive and negative)	*TaGW2-6A* positive and negative	• Constitutive expression in plant • Low expression/non-functional protein due to Promoter/coding region variants, correlates with genotypes with larger grain size and higher grain weight • Encodes a functional E3 RING-type ubiquitin ligase possibly upregulating the expression of cytokinins and starch biosynthesis related genes via the ubiquitin–proteasome system; and simultaneously downregulating the cytokinin degradation genes	[16–18]
Grain width, weight and length	*TaGW2-6A1* negative	• Expresses in grains and leaves • G to A transition in the splice acceptor site of exon 5 leads to mis-splicing in *TaGW2-6A1*, resulting in premature truncation with 134 AA correlates with increase in grain width, weight and length	[19]
Grain length and weight	*TaGW7* negative	• Expression in spike and stem with low expression in grain • *TaGW7* likely plays a key role in the development of tissues in vegetative and reproductive organs especially by regulating cell elongation	[20]

Pin: puroindoline, *fla*: fasciclin like arabinogalactan, *wbm*: wheat bread making gene, *ppc*: PEP carboxylase (PPC, EC 4.1.1.31), *aat*: aspartate aminotransferase (AAT, EC 2.6.1.1), *mdh2*: malate dehydrogenase (MDH, EC 1.1.1.31), *me2*: NAD-dependent-malic enzyme (ME2, 1.1.1.39), *gpt*: alanine aminotransferase (GPT, EC 2.6.1.2), *ppdk*: pyruvate orthophosphate dikinase (PPDK, EC 2.7.9.1).

with the levels of expression of the pin genes rather than just the sequences of the proteins themselves [2••].

Flour yield in milling

The genetic control of flour yield has been considered complex. Recently transcriptome analysis indicated that high flour yield was associated with reduced expression of fasciclin-like arabinogalactan proteins (FLAs) in the pericarp and possibly outer endosperm/aleurone [3••]. The FLAs are cell adhesion proteins and reduced expression apparently results in the endosperm breaking up and separating more easily from the bran (pericarp). Major loci controlling flour yield in different populations have been associated with the locations of FLA encoding genes (Figure 1) on chromosomes 2B and 4B. These are distinct probably cell wall associated AGPs rather than from the arabinogalactan proteins found inside the cell and encoded by the gene encoding the grain softness proteins.

Bread quality

A long history of research [33•] has linked bread quality closely with the presence of HMW glutenins.

More recently, analysis of the transcriptome from diverse wheat genotypes has identified a highly significantly differentially expressed gene, the wheat bread making gene, *wbm* [4••]. This gene encodes a small sulphur containing protein that is expressed at very high level in wheat genotypes with good bread quality (Figure 1). It is possible that small proteins may interact to cross-link the gluten and stabilize the bubbles that are the key to a risen bread product.

Chapatti quality

The production of end-products other than bread appears to require very different wheat. The bread and chapatti quality of wheat genotypes was found to be negatively

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correlated [34]. The transcriptome of wheat has been explored for a single genotype known for good chapatti making [35] while studies on a larger set of good and poor chapatti-making genotypes should reveal the identity of the genes that need to be expressed to produce these products with the required quality.

Photosynthesis in the seed

Analysis of changes in gene expression from mid seed development to seed maturity in wheat has revealed that photosynthesis genes in the pericarp are those that change most as the high levels of photosynthesis in mid seed development decline. The novel discovery that has flowed from this is that photosynthesis in the seed is apparently very different to that in the leaf [7]. While wheat is a C3 plant the seed expresses a complete C4 pathway. This has proven to be controversial despite experiments targeting the pericarp showing flux through a C4 pathway experiments with intact ears have been confounded by the respiration of the endosperm and C3 photosynthesis in the glumes [7]. Natural selection [36] may have favoured a C4 pathway later in wheat seed development when temperatures are usually much higher. Photosynthesis in the pericarp may have a key role in the re-capture of CO_2 generated by respiration to support the requirements of the large amounts of starch and protein synthesis in the endosperm in the active stages of grain filling.

Impact of heat stress on yield and quality

Heat has been shown to alter the composition of the wheat grain and thereby its quality [37]. Hotter growing conditions resulted in higher levels of secondary metabolites and saturated fats [38] that will alter nutritional value and functional quality for various end-uses. The transcriptome has been used to study the response of wheat genotypes to heat stress during seed development [39]. Genotypes differ widely in the extent to which gene expression is altered and the consequent impact of heat stress on grain yield and quality.

Prospects for increasing the rate of genetic gain in wheat

Genomics has the potential to enhance the breeding of high quality cereals [40]. A wider gene pool [41] may be accessed with great knowledge of the molecular basis of quality. Due to the requirement of large amount of grain sample, current selection tests for wheat grain quality (hardness, milling yield and end-product quality), can only be applied at later stages in wheat breeding [12]. However, molecular tools for analysis of genes associated with quality traits enable selection for quality traits at any stage in wheat breeding and can potentially accelerate the rate of genetic gain in wheat breeding [42•]. Elimination of large numbers of poor quality wheat early will allow greater selection pressure for yield to be applied to populations that have acceptable grain quality. Selection for photosynthetic efficiency in the seed may also deliver higher yielding wheat especially in hot dry environments or when wheat is subjected to heat stress during grain filling.

Successful gene editing in hexaploid wheat with three sub-genomes [43•,44,45] has opened up the possibility of using this technology for the rapid improvement of wheat by regulating the transcription of target genes. The down-regulation of gliadins using to generated low-gluten wheat is an exciting application of this technology [46]. The rapid pace at which gene editing technology has progressed needs to be matched by the pace at which genomic technologies will identify candidate genes which after validation can be utilized for trait improvement. Assessment of the contribution of the *wbm* gene to bread making was undertaken at CIMMYT with significant correlation with bread making quality reported [47••]. Gene targets can be converted to markers for rapid selection in breeding [48] and be used in conjunction with speed breeding [49] or used for trait improvement using gene editing technologies. Gene editing technologies could be used to accelerate the validation of candidate genes for manipulation [50].

Conclusions

Analysis of the transcriptome of the developing seed has provided many insights into the biology of this critical organ. This may be extended by more critical analysis of the sub-genome specificity of expression in these tissues, analysis of specific tissues, at a wider range of developmental stages and of more genotypes. This should yield more information on how the plant assembles the grain and how genetic and environmental factors influences the final size of the grain (yield) and the composition of the grain (establishing the nutritional and functional characteristics of wheat-based foods).

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- • of special interest
- •• of outstanding interest

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