

Genetic bases of rice grain shape: so many genes, so little known

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Rice (*Oryza sativa*) grain shape is a key determinant of grain yield and market values. Facilitated by advancements in genomics and various molecular markers, more than 400 quantitative trait loci (QTLs) associated with rice grain traits have been identified. In this review, we examine the genetic bases of rice grain shape, focusing on the protein products of 13 genes that have been cloned and the chromosome locations of 15 QTLs that have been fine mapped. Although more genes affecting grain traits are likely to be cloned in the near future, characterizing their functions at the biochemical level and applying these molecular data to rice breeding programs will be a more challenging task.

Grain shape is a key determinant of rice yield

Rice has become a useful model system for monocot plant research, largely because it has a small genome (400 Mb) compared with other major crops and because of the availability of a high-precision genomic sequence and highly saturated molecular markers [1,2]. The high degree of conservation in genome structure between rice and other important cereal crops also offers an opportunity to disseminate knowledge gained in rice genetic research to experimental work on other crop plants [3]. Rice is one of the most important cereal crops in the world, providing more than 21% of the food for the world population and up to 76% of the calorific intake in Southeast Asia [4,5]. It has been estimated that a 40% increase in rice production by 2030 will be needed to meet the predicted demand of the growing world population [6]. Among the strategies proposed for improving rice yield, the development and application of superior rice varieties is one of the most effective, sustainable, and economical approaches [7]. An ideal superior rice cultivar should have high grain-yield potential with improved grain shape, nutritional value, disease resistance, and stress tolerance. Grain yield in rice is determined by three major components: number of panicles per plant, number of grains per panicle, and grain weight. Among these, the most reliable trait is grain weight, which is measured as the 1000-grain weight (KGW). Grain shape is characterized by a combination of grain length, grain width, grain

length-to-width ratio, and grain thickness. These four parameters are positively correlated with grain weight [8].

Besides its contribution to grain yield, grain shape is an important quality trait that has a major impact on the market values of rice grain products. A long, slender grain of rice is generally preferred by consumers in Southern

Glossary

Additive effect: contribution of two or more genes to the phenotype of a trait in an additive manner.

Brassinosteroid (BR) signaling pathway: a sequence of processes by which the signal of the plant hormone BR is relayed to downstream responses including cell expansion and elongation, and vascular differentiation.

Collinearity: used in comparative genomics to describe conservation in the order of gene arrangement on a chromosomal segment of common evolutionary ancestry among phylogenetically related species.

Dominant effect: the phenotype of one allele masks the phenotype of another allele of the same locus in heterozygotes. The allele that is masked is known as the recessive allele.

Epistatic effect: contribution of two or more genes to the phenotype of a trait in a manner where the effect of one gene is modified by another gene. The gene that exerts its genetic effect is known as the epistatic gene, whereas the one whose genetic effect is suppressed is called the hypostatic gene.

Floral meristem identity: characteristic anatomical structures of a flower primordium.

Heterotrimeric G protein: a GTP-binding protein complex of three subunits. The α -subunit is largest in molecular mass and binds GTP. The β - and γ -subunits form a tight protein complex. On activation by G protein-coupled receptors, the α -subunit dissociates from the β - γ complex, the two halves of which stimulate downstream enzymes of the signal transduction pathway.

Next generation sequencing (NGS): DNA sequencing technologies by which hundreds of thousands of single-stranded DNA molecules are immobilized on a solid surface and their sequences are determined in a parallel manner. NGS differs fundamentally from the traditional Sanger sequencing technology.

Pleiotropic effect: genetic contribution of one gene to the phenotype of more than one trait.

Polygene: one group of non-allelic genes that together contribute to the phenotype of a trait.

Quantitative trait locus (QTL): a genetic locus responsible for phenotypic variation of a quantitative trait. A quantitative trait is typically affected by multiple QTLs, some having a larger effect than others.

Syntenic: was originally introduced in cytogenetics to describe the presence of a set of genes located on the same chromosome regardless of their genetic linkage and physical location order. The term is now used widely in comparative genomics to indicate similarity in location and organization of a set of genes on a chromosome region of common evolutionary ancestry among different species.

Transgressive segregation: a genetic population that has offspring individuals with extreme phenotypes exceeding the phenotypic values of their two parental lines.

Ubiquitin-proteasome pathway: a multiple enzyme system that labels unwanted peptides with ubiquitin and delivers them to proteasomes for protein degradation.

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China, the USA, and South and Southeast Asian countries, whereas consumers in Japan, Korea, and Northern China prefer a rice grain that is short and round [9,10].

Most of these agronomically important traits are known to be genetically controlled by multiple genes [8], referred to as quantitative trait loci (QTLs) (see Glossary). Although some of the QTLs may have a dominant effect on one grain trait, most have been found to affect more than one trait. The identification of major QTLs for grain shape and grain weight is an important objective of rice genetic research and breeding programs. The rapid development of DNA markers and the completion of rice genome sequencing have greatly facilitated the discovery and mapping of QTLs for rice grain traits. Over the past two decades, many QTLs associated with these traits have been identified in primary and fine-mapping experiments and 13 have recently been cloned. This review focuses on the recent progress in cloned genes and fine-mapped QTLs associated with grain traits in rice. The challenges and opportunities for rice geneticists and breeders in the post-genomic era are also discussed.

Genetic analysis of grain shape and weight

Grain length, length-to-width ratio, and grain weight are three components that can vary dramatically depending on the rice variety (Figure 1). Grain length can be as short as 6 mm or over 15 mm, and the KGW can vary from 10 g to 70 g. However, the grain width and grain thickness of different rice varieties are much less variable (Figure 1). Data from genetic studies conducted more than a decade ago [11–16] suggested that rice grain length, grain width, length-to-width ratio, grain thickness, and grain weight are controlled by QTLs. Grain length has been shown to be controlled by three to five major QTLs [16] that often exhibit additive effects, although dominant effects have also been detected in some studies [12,14]. However, the epistatic effects of genes for grain length have rarely been observed. Grain width has also been shown to be controlled by polygenes with either an additive effect or a dominant effect [13,15,16]. Grain thickness has been demonstrated to be determined by polygenes with additive effects, but an additional maternal effect may exist as well. Grain thickness is believed to vary, to a certain extent, depending on

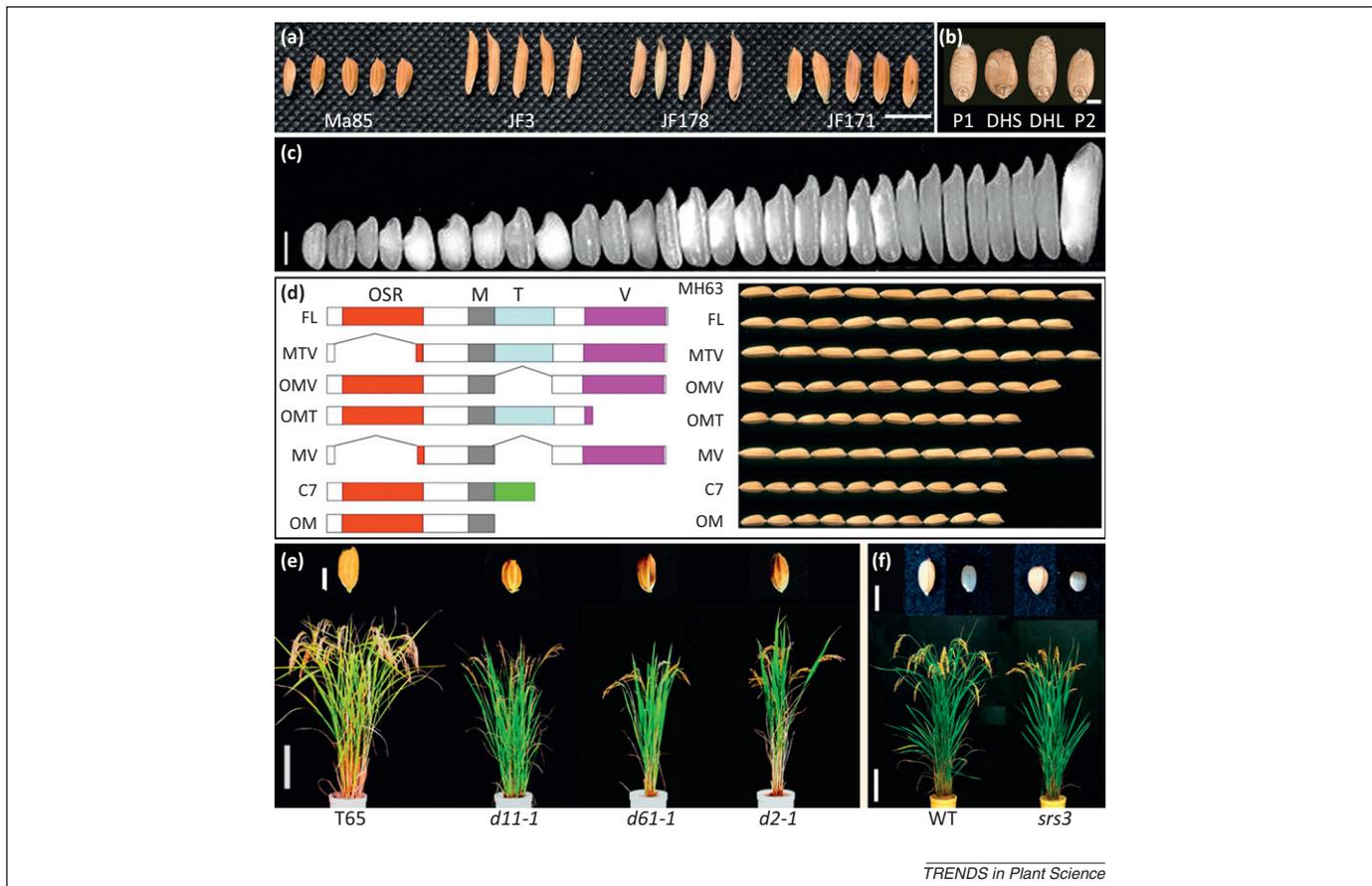


Figure 1. Rice grain traits and their genetic bases. (a) Isolation of long-grain mutants through mutagenesis of a short-grain cultivar. Ma85 is an *indica* rice cultivar grown in Fujian Province, China. Mature pollen grains of Ma85 were treated with γ -rays from cobalt-60 and used to pollinate the parental plants. Seeds with long grains (JF3, JF178, and JF171) were selected from the M_2 population and maintained for more than 10 generations. A major quantitative trait locus (QTL) affecting grain length has been mapped to chromosome 2 [20] and the candidate gene has been cloned (R. Huang *et al.*, unpublished). (b) In contrast to the highly variable grain length of rice, domesticated wheat cultivars vary only slightly in grain length. Shown are representative images of a cross used for selection of grain shape in wheat. P1, parental line Avalon; P2, parental line Cadenza; DHS, the doubled haploid (DH) line with the shortest grain; DHL, the DH line with the longest grain [104]. (c) Domesticated rice (*Oryza sativa*) grain ranging in length from 3 mm to 11 mm and in width from 1.2 mm to 3.8 mm [4]. (d) Dissection of the functional domains of the *GS3* gene. The full-length (FL) or truncated cDNA sequences of *GS3* are expressed in the MH63 cultivar. Grains of T_1 transgenic plants are compared with those of MH63 [27]. Domain abbreviations: OSR, organ size regulation domain; M, putative transmembrane domain; T, TNFR/NGRF domain; V, VVFC domain. The green box represents the polypeptide sequence resulting from a frameshift. (e) Mutations in the Dwarf (*D*) genes result in dwarf plants (*d11-1*, *d61-1*, and *d2-1*) with pleiotropic effects on grain length and size [22]. T65 is the wild type parent cultivar. (f) Mutations in the *SRS3* gene result in the formation of short and round grains (*srs3*) with pleiotropic effects on the development of other organs [34]. Scale bars: (a) 10 mm; (b,c) 2 mm; (e,f) upper, 5 mm, lower 200 mm. © Elsevier, the Crop Science Society of America, American Society of Plant Biologists, National Academy of Sciences, and Oxford University Press; adapted, with permissions, from [4,20,22,27,34,104].

the environmental conditions [13,16]. Grain length-to-width ratio is a compound trait of grain length and width [15,16] and is controlled by several genes with either an additive or a dominant effect. Grain weight is one of the key determinants of rice yield and genes associated with grain weight are mostly additive, although genes with dominant effects may also exist. Transgressive segregation has often been observed in genetic populations [16,17]. In these studies, quantity traits are usually treated as a whole and are not dissected into individual QTLs.

Correlations among the five grain traits have been analyzed in many studies [1,13,16–19]. Grain length, grain width, length-to-width ratio, and grain thickness have all been shown to correlate positively with grain weight, although different studies by different groups have shown some variation in the degree of correlation. Grain length has been shown to contribute more to grain weight than other grain shape traits in some studies [1,17,19,20].

Cloned genes underlying grain shape and weight

Over the past 20 years, the development of DNA markers and genomic sequencing technology have led to rapid progress in the mapping and cloning of genes underlying grain shape and grain weight in rice [2]. To date, 13 genes associated with grain shape and weight have been isolated by map-based cloning strategies. Most of them are still poorly understood, particularly with regard to their functions at the biochemical and cell biological levels [21–34]. These cloned genes can be divided into three functional groups on the basis of the phenotypes of the mutants (Table 1).

The first group of cloned genes associated with grain shape and weight comprises *Dwarf1* (*D1*), also known as the rice heterotrimeric G protein alpha subunit (*RGA1*), *D2*, *D11*, and *D61*. Mutations in these genes result in dwarf plants and have detrimental pleiotropic effects on organ growth, including a reduction in seed size. *D1/RGA1* was

the first gene to be cloned that had substantial effects on seed-size regulation [21,35]. An 833-base pair (bp) deletion of *D1* disrupts the coding region of the heterotrimeric G protein alpha subunit and results in dwarf plant phenotypes with smaller grain. Genes affecting brassinosteroid (BR) biosynthesis and signal transduction have also been shown to regulate grain size in rice. *D2* and *D11* encode two cytochrome P450 oxidoreductase enzymes involved in BR biosynthesis [22,23] and *D61* encodes a BR receptor, an ortholog of *BRI1* in *Arabidopsis* (*Arabidopsis thaliana*) [25]. The *D2* protein represents a novel type of P450 (CYP90D2) that catalyzes the steps from 6-deoxoteasterone to 3-dehydro-6-deoxoteasterone and from teasterone to 3-dehydroteasterone in the late BR biosynthesis pathway [23]. The *D11* P450 (YP724B1) enzyme is required for the supply of 6-deoxytyphasterol and typhasterol in the BR biosynthesis network [22].

The second group of cloned genes associated with grain shape and weight comprises genes that appear to specifically affect grain traits. *GRAIN SIZE 3* (*GS3*) is a major QTL for grain length and weight and a minor QTL for grain width and thickness and functions as a negative regulator for grain size [26,36]. *GS3* was originally detected from the progeny produced by a cross between Minghui 63 and Chuan 7. The *GS3* protein contains an organ size regulation (OSR) domain in the N terminus, a transmembrane domain, a tumor necrosis factor receptor/nerve growth factor receptor (TNFR/NGFR)-like domain, and a von Willibrand factor type C (VWFC) domain in the C terminus. The OSR domain functions as a negative regulator of grain length and deletion mutants of this domain result in the formation of long-grain rice. The C-terminal TNFR/NGFR and VWFC domains act as positive regulators of grain length and loss-of-function mutations of these domains lead to the development of very short grain [27,37]. A molecular marker based on *GS3* has been developed for the selection of long-grain lines in rice breeding programs

Table 1. Cloned genes associated with grain shape and weight in rice

Gene	Trait	Gene difference ^a	Encoded protein	Refs
<i>D1</i>	Seed size	833-bp deletion	Heterotrimeric G protein α	[21]
<i>D2</i>	Seed size	Nonsense mutation in <i>d2-1</i> ; missense mutation in <i>d2-2</i>	Cytochrome P450 (CYP90D) enzyme	[23]
<i>D11</i>	Seed size	1-bp deletion in <i>d11-1</i> ; 1-bp insertion in <i>d11-2</i> ; missense mutation in <i>d11-3</i> ; abnormal splicing in <i>d11-4</i>	Cytochrome P450 (CYP724B1) enzyme	[22]
<i>D61</i>	Seed size	Missense mutation in <i>d61-1</i> and <i>d61-2</i>	BR insensitive (BRI)-like leucine-rich repeat (LRR) receptor kinase	[25]
<i>GS3</i>	Grain length	Nonsense mutation	Membrane protein with multiple domains	[26,27]
<i>GW2</i>	Grain width	1-bp deletion	RING-type E3 ubiquitin ligase	[28]
<i>GW5/qGW5</i>	Grain width	1212-bp deletion	Arginine-rich protein of 144 amino acids	[29,42]
<i>GIF1</i>	Grain filling	1-bp deletion	Cell wall invertase	[30,43]
<i>GS5</i>	Grain shape	6-bp insertion	Serine carboxypeptidase	[32]
<i>GW8/SPL16</i>	Grain width	10-bp deletion in the promoter	SQUAMOSA promoter-binding protein-like 16	[31]
<i>SRS1/DEP2</i>	Seed size	Deletion in <i>srs1-1</i> and <i>srs1-4</i> ; nonsense mutation in <i>srs1-3</i> ; abnormal splicing in <i>srs1-2</i> and <i>srs1-5</i>	Protein of 1365 amino acids with unknown function	[33]
<i>SRS3</i>	Seed size	Missense mutation in <i>srs3</i> ; nonsense mutation in TCM768; abnormal splicing in TCM2092	Kinesin 13 protein	[34]
<i>SRS5</i>	Seed size	Missense mutation	Alpha-tubulin protein	[24]

^aGenetic mutations and natural variations.

[38]. The *GS3* ortholog in maize (*Zea mays*) has also been cloned and characterized. *ZmGS3* has functional domains in common with the rice *GS3* protein and *ZmGS3* has been shown to be involved in maize kernel development [39].

GRAIN WIDTH 2 (GW2), a major QTL for rice grain width and weight, encodes a RING-type E3 ubiquitin ligase [28]. *GW2* was initially detected from a cross between a large-grain *japonica* rice variety, WY3, and a small-grain *indica* rice variety, Fengaizhan-1. A 1-bp deletion in the *GW2* gene in WY3 results in the introduction of a premature stop codon in its exon 4, causing the large-grain phenotype in WY3. *GW2* negatively regulates cell division by targeting its substrates to proteasomes for regulated proteolysis; loss of *GW2* function results in an increase in cell number in the spikelet hull and acceleration of the grain-milk filling rate, thus enhancing grain width, weight, and yield. There are two homologs of the rice *GW2* in maize, referred to as *ZmGW2-CHR4* and *ZmGW2-CHR5*, both of which contribute to the phenotypic variation in kernel size and weight [40].

GRAIN WIDTH 5 (GW5) has been identified as a major QTL for *Seed Width on chromosome 5 (qSW5)* for the determination of rice grain width and weight [29,41,42]. A survey of *GW5/qSW5* polymorphisms in various rice landraces has revealed that deletions in this gene may have played an important role in the selection of increased grain size from artificial and natural crossings during rice domestication [29]. The *GW5/qSW5* gene encodes a nuclear protein of 144 amino acids with an arginine-rich domain. Because *GW5/qSW5* physically interacts with polyubiquitin, it is likely to act as a regulator in the ubiquitin-proteasome pathway and regulates cell division of the outer glume of the rice spikelet [29,41,42].

The *grain incomplete filling 1 (gif1)* mutant was isolated from a screen for mutants with grain-filling defects. The *gif1* mutant also has more grain chalkiness as a result of loosely packed starch granules. *GIF1* encodes a cell-wall invertase required for carbon partitioning during early grain filling [30]. A frameshift mutation caused by a 1-bp nucleotide deletion in *GIF1* results in premature termination of its open reading frame. The *GIF1* gene is expressed in a more restricted pattern in the flowers of cultivated rice varieties than in the flowers of wild rice, which is apparently a consequence of accumulated changes in the regulatory sequence of the promoter as a result of domestication [30]. Its paralog *CIN1* appears to have evolved through segmental duplication of chromosome 4. In contrast to *GIF1*, which has a domestication trace in nucleotide change in the promoter region, *CIN1* contains a distinct mutation in the coding region in cultivated rice cultivars that is absent in wild-rice germplasm resources [43].

GRAIN SIZE ON CHROMOSOME 5 (GS5) is a major QTL affecting grain width, grain filling, and grain weight [32]. It encodes a serine carboxypeptidase and functions as a positive regulator of grain size. Analysis of genomic DNA sequences and promoter swaps in transgenic plants reveals that nucleotide changes in three segments of the *GS5* promoter seem to be responsible for the variations in grain width [32].

GRAIN WIDTH 8 (GW8) was identified from a cross between HXJ74 and Basmati385 as a major QTL affecting

grain width and grain yield [31]. A recent gene-cloning project has revealed that *GW8* encodes SQUAMOSA promoter-binding protein-like 16, referred to as *OsSPL16*, which belongs to the protein family of SBP domain-containing transcription factors. There are six polymorphisms in the DNA sequence of *OsSPL16* between HXJ74 and Basmati385. Among them, a 10-bp deletion in the promoter region has been shown to be responsible for the slender grain trait of Basmati385 [31].

Given that *GS3*, *GW2*, and *GW5/qSW5* act as negative regulators of grain size, *GS5* and *GW8*, which act as positive regulators of cell proliferation, may have a more important role in future hybrid rice breeding programs. What will complicate these studies, however, is that all of the genes studied to date appear to have pleiotropic effects on grain shape and grain weight. For example, *GS3* controls grain length, weight, width, and thickness [26]; *GW2* substantially increases grain width and weight but has much less effect on grain thickness and length [28]; *GW5/qSW5* affects grain width and weight [29,42]; and *GS5* and *GW8* control both grain width and weight [31,32]. With regard to the gene expression patterns, *GS3*, *GS5*, and *GW8* are expressed specifically and at a high level in young panicles, whereas *GW2* is ubiquitously expressed in all organs tested [27,28,31,32].

The third group of cloned genes associated with grain shape and weight includes the *SMALL AND ROUND SEED (SRS)* loci identified in the *japonica* rice subspecies. Mutations in *SRS1* result in reduction in both cell length and cell numbers in the longitudinal direction, and elongation of the cells in the lateral direction of the lemma of rice flowers. Deletions of 38 bp in *srs1-1* and 31 bp in *srs1-4* disrupt the coding region. Other *srs1* mutant alleles are caused by alterations in the stop codon and mRNA splicing sites [33]. The *SRS1* mRNA and proteins are abundant in young leaves, internodes, and panicles. *SRS1* encodes a protein of 1365 amino acids with no known functional domains [33]. The small and round seed phenotype of *srs3* is a result of the reduction in cell length of the lemma. The *SRS3* protein contains a kinesin motor domain and a coiled-coil structure and is a member of the kinesin 13 subfamily [34]. The cell length of the lemma in *srs5* mutants is shorter than that in the wild type plants. A 1-bp substitution in the fourth exon of *SRS5* is responsible for the phenotype. *SRS5* encodes alpha-tubulin and may regulate cell elongation in a pathway independent from the BR signaling network [24].

Genetic mapping of QTLs affecting grain shape and weight

In addition to the cloned genes discussed above, over 400 QTLs associated with rice grain shape and grain weight have been mapped on chromosomes in independent studies [19,44–84]. There are at least 167 QTLs that have been associated with KGW, 103 QTLs associated with grain length, and 95 QTLs associated with grain width (Figure 2a and Tables S1–S3 in the supplementary material online). The number of QTLs for grain length-to-width ratio and for grain thickness is relatively low. All of these QTLs have been integrated into the public Simple Sequence Repeat (SSR) genetic map of rice [85–87] and are unevenly

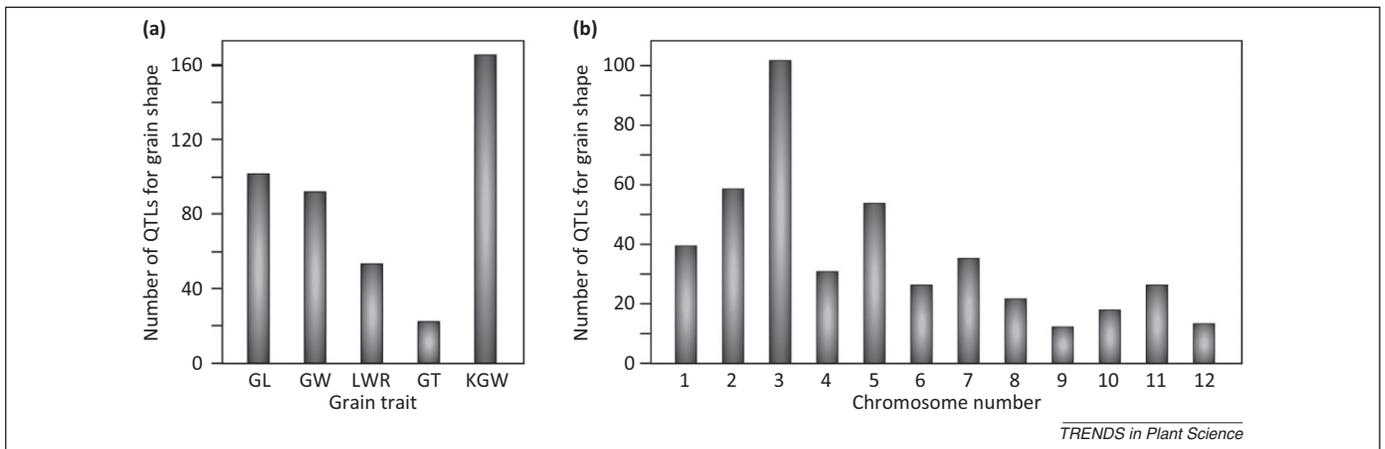


Figure 2. Number and distribution of quantitative trait loci (QTLs) for rice grain traits. (a) Number of QTLs associated with grain length (GL), grain width (GW), length-to-width ratio (LWR), grain thickness (GT), and 1000-grain weight (KGW). Data were collected from all accessible public references. (b) Distribution of QTLs for grain shape on the 12 rice chromosomes. Data on the QTLs associated with rice grain shape and weight were collected from all published references.

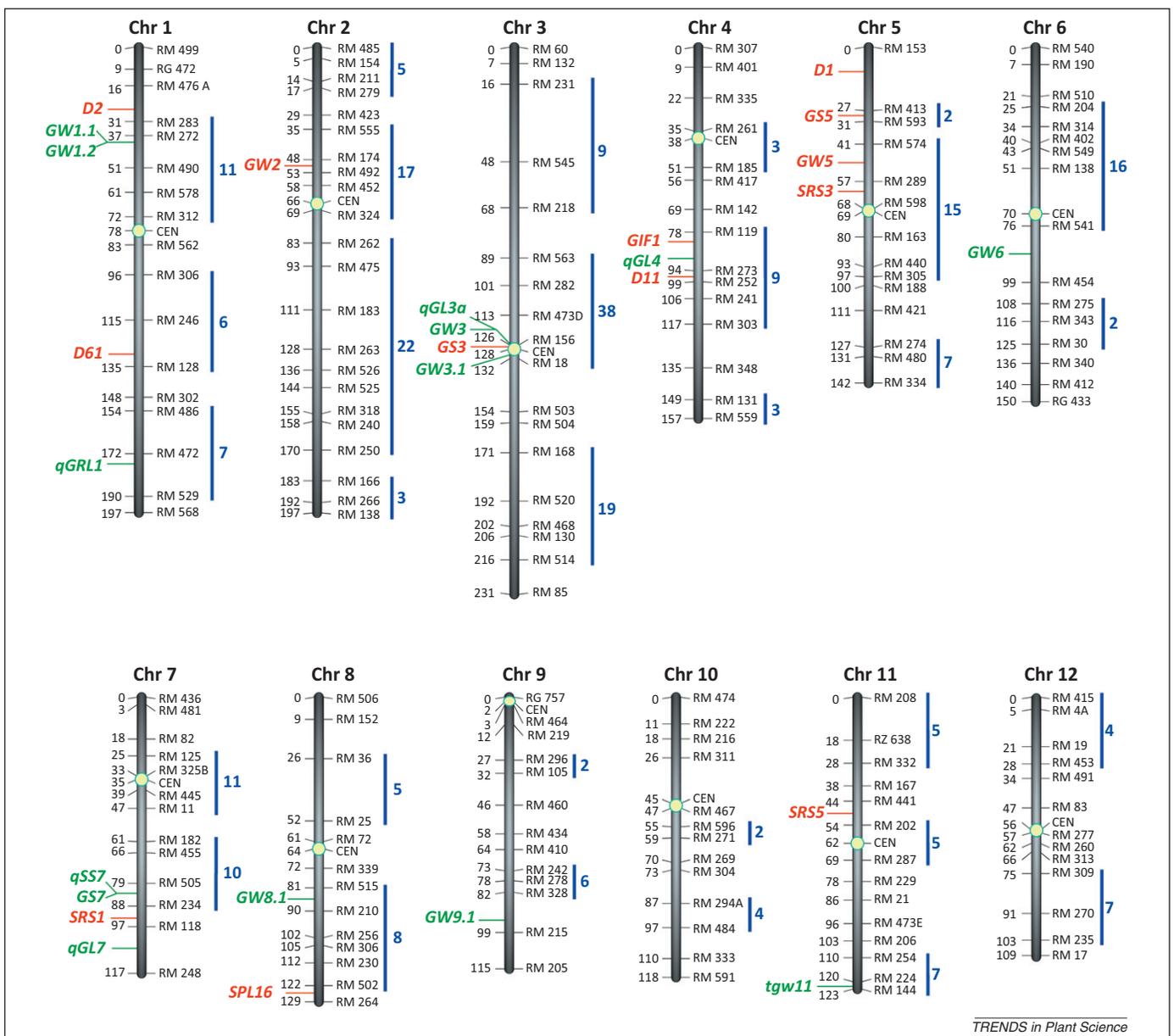


Figure 3. Distribution of quantitative trait loci (QTLs) for grain traits on rice chromosomes. The positions (cM) of the SSR markers of rice chromosomes are derived from the Cornell SSR 2001 (<http://www.gramene.org>). Major QTLs associated with grain shape and weight that have been characterized by gene cloning (labeled in red) (Table 1) or by fine mapping (labeled in green) (Table 2). The locations of QTLs affecting grain shape and weight that have been identified only in primary mapping experiments are indicated by blue bars with the corresponding number of QTLs. Some segments of the chromosomes have more QTLs affecting grain shape and weight than others.

Table 2. Fine-mapped QTLs associated with grain shape in rice

Trait	QTL	Chromosome	Marker interval	Distance ^a	Parents and population ^b	Refs
GL ^c	<i>qGL-3a</i>	3	RMw357–RMw353	87.5 kb	Asominori/IR24 RILs, CSSLs, BC ₄ F ₂ , BC ₄ F ₃	[58]
GL	<i>qGL4b</i>	4	RM5586–RM3524	3 Mb	Cytoto/kasalath F ₂ –F ₅	[92]
GL	<i>qGL7</i>	7	RID711–RM6389	258 kb	Nanyangzhan/Chuan7 RILs and NIL-F ₂	[88]
GL	<i>GS7</i>	7	Indel3–Indel5	4.8 kb	D50/HB277 RHL	[90]
GL	<i>qSS7</i>	7	GL293–GL285	23 kb	ZS97/Cypress CSSL	[91]
GL	<i>qGRL1</i>	1	RM431–CHR1.1	108 kb	Pusa1121/Pusa1342 RIL F ₆	[84]
GL	<i>LGS1</i>	2	RM13838–RM13840	0.2 cM	JF171/Samba BC ₂ F ₂	[20]
KGW	<i>gw3.1</i>	3	JL123–JL109	93.8 kb	Jefferson/ <i>Oryza rufipogon</i> BC ₂ F ₂	[62]
KGW	<i>GW3</i>	3	WGW16–WGW19	122 kb	Baodali/Zhonghua 11 F ₂ , F ₃ , BC ₂ F ₂	[93]
KGW	<i>GW6</i>	6	RM7179–RM3187	4.7 cM	Baodali/Zhonghua 11 F ₂ , F ₃ , BC ₂ F ₂	[93]
KGW	<i>gw8.1</i>	8	RM23201.CNR15–RM30000.CNR99	306.4 kb	Hwaseongbyeol/ <i>O. rufipogon</i> BC ₃ F ₄	[94]
KGW	<i>gw9.1</i>	9	RM24718.CNR11–RM30005.CNR142	37.4 kb	Hwaseongbyeol/ <i>O. rufipogon</i> BC ₃ F ₄ NIL	[95]
KGW	<i>tgw11</i>	11	RM224–RM27358	900 kb	Hwaseong/ <i>Oryza grandiglumis</i> NIL	[96]
KGW	<i>GW1-1</i>	1	RM10376–RM10398	329.9 kb	ZS97B/MY46 RHLs	[97]
KGW	<i>GW1-2</i>	1	RM10404–RM1344	308.5 kb	ZS97B/MY46 RHLs	[97]

^aDistance: genetic distance (cM) or physical distance (kb).

^bParents and population: parents used for crossing and genetic populations used in quantitative trait locus (QTL) mapping.

^cAbbreviation: GL, grain length; KGW, 1000-grain weight.

distributed among the twelve rice chromosomes (Figure 2b). As shown in Figure 3, most of the major QTLs for grain traits that have been fine mapped or cloned are located in regions that have a high concentration of QTLs.

Among the QTLs that have been detected in genetic analyses but have not been cloned, 15 loci have been fine mapped on chromosomes (Table 2). *qGL7*, a QTL for grain length on chromosome 7, has been shown to cosegregate with InDel markers RID710 and RID76 and has been mapped to a 258-kb fragment of genomic DNA between InDel marker RID711 and the SSR marker RM6389 [88]. *qGL7* exhibits pleiotropic effects on grain length, grain width, grain thickness, and KGW. Another major QTL for grain length, *qGL7-2*, was originally mapped to a 278-kb interval of chromosome 7 between markers of Indel1 and RM21945 at a location 13.2 cM from *qGL7* [89]. The interval has recently been narrowed down to a 4.8-kb genomic DNA fragment that contains two open reading frames encoding proteins with unknown functions. *qGL7-2* has been renamed *GS7* for its pleiotropic effects on grain shape traits [90]. Another major QTL for grain length, *qSS7*, has been mapped to a 23-kb interval between GL293 and GL285 that contains two open reading frames [91]. A QTL for grain length, *qGL4b*, has recently been fine mapped to a 3-Mb segment between RM5586 and RM3524 on chromosome 4, using a population derived from a cross between the *japonica* cultivar 'Cytoto' and the *indica* variety 'Kasalath' [92]. A major QTL for grain length, *qGRL-1.1* has been mapped to a 108-kb region between markers RM431 and CHR1.1 on chromosome 1 [84]. *GW3* and *GW6* are major grain weight QTLs that have been fine mapped on chromosome 3 and 6, respectively. *GW3* has been narrowed down to a 122-kb physical distance containing 16 open reading frames. The cloned *GS3* gene is located in this region and it remains to be determined whether they represent the same locus. *GW6* has been localized to an interval between the SSR marker RM7179 and RM3187 [93]. *GW8.1*, a QTL for grain weight, has been mapped to a 306-kb interval between RM23201.CNR151 and RM30000.CNR99 on chromosome

8 [94]. Another grain weight QTL, *GW9.1*, has been mapped to a 37.4-kb region containing seven predicted open reading frames [95]. A QTL for grain weight, *tgw11*, has been mapped to a 900-kb interval between markers RM224 and RM27358 [96]. Two QTLs for grain weight, *GW1-1* and *GW1-2*, have been mapped on chromosome 1 [97]. *GW1-1* is located in a 329.9-kb region between markers RM10376 and RM10398, whereas *GW1-2* is mapped to a 308.5-kb interval between RM10404 and RM1344. They are likely to represent two tightly linked genes. Candidate genes for some of these fine-mapped QTLs have already been isolated but have not been confirmed and are regarded as fine-mapped loci in this review. Supporting evidence from functional complementation tests remains the gold standard for verification of these cloned candidate genes. The remaining fine-mapped QTLs are likely to be cloned in the near future.

Genes associated with seed size in other plants

In contrast to the rapid progress that has been made in cloning QTLs for rice grain shape and weight, our knowledge about the molecular mechanisms underlying the control of seed size and weight in other crops remains limited. Compared with rice, the molecular cloning of genes responsible for seed weight in other cereal crops, such as wheat (*Triticum aestivum*), maize, and sorghum (*Sorghum bicolor*), is lagging behind. *ZmGS3* and *ZmGW2* have recently been identified in maize; the approach adopted for these investigations was based largely on the cloning results of orthologous genes in rice [39,40]. Several key genes associated with seed size and seed mass control have been cloned and studied in *Arabidopsis*, a non-crop dicot model plant [98–102]. *Arabidopsis APETALA2* (*AP2*) encodes a transcription factor that is involved in the specification of floral organ identity and development of the ovule and seed coat [101]. Loss-of-function *ap2* mutations cause an increase in seed mass [100,101]. *Arabidopsis DA1*, encoding a ubiquitin receptor, has been shown to set final seed and organ size [102]. *MINI3* and *IKU2* have also been

identified as regulators of seed size in *Arabidopsis* [103]. An *Arabidopsis* seed contains mostly the embryo, whereas a rice grain is filled mainly with the endosperm. Thus, caution must be exercised when applying knowledge gained from *Arabidopsis* research to rice.

Concluding remarks

Facilitated by the recent development of molecular biotechnology, genomics, and bioinformatics, the fine mapping and gene cloning of major QTLs associated with rice grain shape and weight has proceeded at a rapid pace for the past 20 years. Of the several hundred QTLs that have been detected by primary mapping (Figure 3 and Tables S1–S3 in the supplementary material online), only 13 genes have been cloned (Table 1) and 15 have been fine mapped (Table 2). There remains a long way to go to complete the cloning work for most clonable QTLs. The completion of highly accurate rice genome information, development of high-throughput sequencing and genotyping technologies, and a drastic reduction in the cost of whole-genome sequencing using the next-generation sequencing technology will accelerate the pace of gene cloning in rice. The plan to sequence 10 000 rice accessions and the development of extensive single nucleotide polymorphism (SNP) chips are just two examples of current efforts in the rice research community to decipher the complexity of rice germplasm. The successful completion of these projects will allow rice researchers to pinpoint specific genes that confer desirable traits and to accelerate the pace of fine-mapping and rice-breeding work. It is likely that many genes associated with rice grain development will be cloned in the near future. However, the successful cloning of a locus is not the end of the quest for that genetic element, but the start of a new journey to determine how the gene works. Elucidating the biochemical pathways and understanding the molecular mechanisms underlying rice grain development is likely to remain a challenging task for rice researchers for many years to come.

As a model crop that shares close synteny and collinearity with other agronomically important cereals, rice offers a great opportunity for understanding how grain development is regulated, which should benefit breeding programs and the biotechnology industry in their attempts to improve the yield and quality of food crops. A close collaboration between rice geneticists and breeders will facilitate transfer of the achievements gained from genetic and genomic studies into breeding programs. There have been recent successes using cloned gene-based markers for the breeding of rice varieties with improved yield, grain shape, and nutritional quality [36,38]. As more genes are cloned and the interactions among these genes are identified and their biochemical pathways elucidated, the ultimate goal of integrating multiple favorable genes in one rice variety will become possible.

Acknowledgments

We thank Allan Caplan for critical reading of this manuscript. This work was supported by grants from the National Natural Science Foundation of China (31100866), Fujian Province Science and Technology Major Projects (2008NZ0001-1), and the Basic Research Funds for Central Universities (2010121088). R.H. was supported by fellowships from Xiamen University and Quanzhou city for visiting research abroad.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.tplants.2012.11.001>.

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