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Rice grain quality—traditional traits for high quality rice and health-plus substances

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Abstract Rice grain quality is a complex trait that reflects the opinions of producers, processors, sellers and consumers in regard to production, processing, marketing and consumption of the grain. It can be roughly divided into milling quality, appearance quality, cooking and sensory quality, nutrition quality and hygiene quality. Milling quality indicates level of recovery of grain products in order of value; appearance quality is reflected in ability to attract buyers; sensory quality and nutritional quality relate to the edible characteristics, and hygiene quality relates to freedom from internal and external contamination. With improving living standards, access to food has shifted from grain to meat, milk, eggs, vegetables and fruits. The demand for food is no longer simply "enough," but is increasingly "delicious" and "healthy." In order to meet the needs of consumers and producers, scientists have to understand the genetic basis that determines quality in rice, and breeders and seed companies have to develop rice varieties with high yield, good quality and health benefits. This paper summarizes progress in understanding rice quality by addressing aspects of consumer demand, classification and importance, functional genomics, genetics, breeding and, finally, future challenges.

Keywords Functional genomics · Genetic improvement · Grain quality · Health benefits · *Oryza sativa*

Consumer demand for and classification of rice quality

Rice grain quality in the narrow sense usually refers to eating quality or palatability, while rice grain quality in the broad sense includes many aspects.

Generally, rice grain quality encompasses milling quality, appearance quality, and cooking and sensory quality, as well as nutrition and hygiene quality (Fig. 1). The term 'rice quality' means different things to different people. For some, it refers to the amount of whole grain rice (polished rice) left after milling. For others, it is the visual appeal of rice flour, and for still others, it relates to palatability of the rice compared with local preferences.

Common characteristics of good quality rice

Rice quality evaluation standards of each country reflect consumer demand for grain quality. Rice quality evaluation standards in China, Thailand and USA are summarized in Supplemental Table 1. Polished rice yield and appearance form the most important standards in each country. Processed white rice is the main form of

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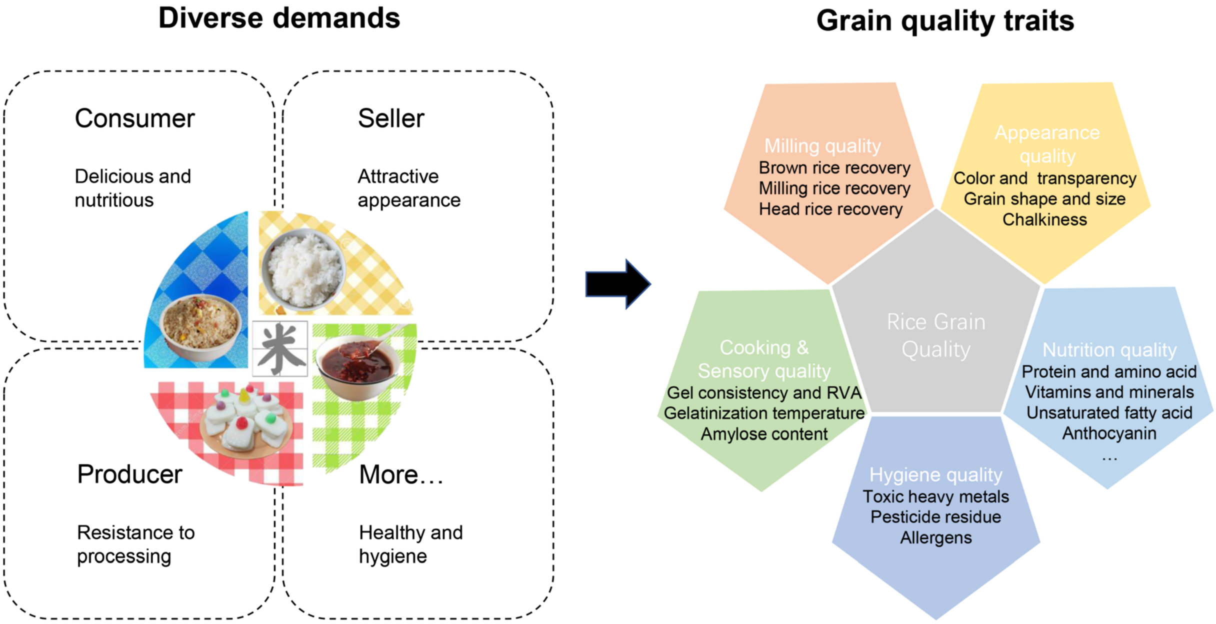


Fig. 1 Demands for and classification of rice grain quality traits

rice as a commodity, so appearance is also the main standard for consumers to assess quality. Excessive broken and variously colored grain affects the appearance of cooked rice and may also affect taste. Changes in national rice standards in China also reflect changes in consumer demand for rice quality over time.

Examples of traditional rice types grown in China, Japan, India and Thailand, the major rice producing countries, are shown in Table 1. Khao Dawk 105 (KDML 105) is the best Thai jasmine rice cultivar, known for its strong aroma (Vanavichit et al. 2018). It has a long grain shape and, after cooking, has luster, soft taste and high viscosity as well as strong aroma. Daohuaxiang 2 is a Chinese medium grain rice cultivar with good quality. It has a strong flavor, luster, sweet taste and soft and chewy texture after being cooked and remains soft after cooling. Koshihikari, which is the most widely planted cultivar in Japan for more than 40 years, has short grain, high luster after cooking, superior whiteness, soft taste, high viscosity and light fragrance and maintains a soft texture after cooling (Kobayashi et al. 2018). It can be seen from these descriptions that luster, fragrance and taste are general indicators of good quality rice. Meullenet et al. (2001) studied the preferences of Asian consumers living in the USA for quality, and found that the most important indicators were appearance and aroma, with most consumers liking jasmine rice from Thailand. Their results suggested that the main drivers for consumers were (in order) color, flavor, aroma, viscosity and hardness. In other words, consumers prefer rice types that are high in whiteness, strong in aroma, low in bitterness, tight in texture, and soft but not sticky.

Regional characteristics of good quality rice

Compared with the above three cultivars, the quality of cultivar Pusa 1121 (Table 1) is quite distinct (Singh et al. 2018). Pusa 1121 is a leading Basmati rice cultivar and has extra-long grain (9 mm) and medium to solid texture. It is dry, non-sticky, tasty and easily digested after cooking and has a popcorn-like aroma. The most significant characteristic of Pusa 1121 is its cooked kernel elongation factor of 2.5-fold, that is, a cooked length of up to 22 mm, a fourfold expansion in volume. Indian and Pakistani consumers usually consume this type of rice. Clearly, people from different places have different standards for rice quality.

Calingacion et al. (2014) investigated the three most popular varieties in different countries and analyzed their grain shape, amylose content, gel consistency, gelatinization temperature and flavor. Their research provides a holistic view of regional differences in consumer preference for quality

Table 1 Quality characteristics of four famous rice varieties from different countries

Variety	Origin	Grain shape	Chalkiness	Texture	Amylose	Aroma
Koshihikari	Japan	Short	Small	Soft	Low	Slight
Daohuxiang 2	China	Medium	Small	Medium	Medium	Strong
KDML 105	Thailand	Long	None	Soft	Medium	Strong
Pusa 1121	India	Very long	Small	Firm	High	Medium

around the world. For example, consumers in Southeast Asia preferred long slender grains, whereas consumers in northern Asia preferred short bold grains, and people in India and Pakistan preferred longer grains. Differences also occur within a country. Consumers in southern China prefer slender rice, whereas those in northern China prefer short round rice.

There was a similar pattern of differences in amylose content. In rice, amylose content is positively correlated with hardness, and negatively correlated with viscosity and water absorption. Consumers in Laos and parts of Thailand prefer glutinous or sticky rice, and, in northern China, Japan, and Thailand, there is a preference for low amylose rice. Consumers in southern China, Iran, Pakistan, Malaysia, the Philippines, Vietnam, Indonesia and Uruguay prefer rice with moderate amylose contents. High-amylose varieties are popular in Burma, Sri Lanka, Indonesia, many states of India, Ghana, Senegal, Suriname and Colombia. These differences reflect consumer preferences in regard to appearance and taste of rice in different regions.

Increasing health awareness

During milling, bran is removed from the grain along with many of the non-starch nutrients; this also changes the sensory quality of cooked rice. Although consumers tend to choose rice with or without a small amount of bran (Lyon et al. 1999), increasing health awareness in Asian countries is leading to greater use of brown rice and even germinated brown rice and consideration of other value-added benefits (Son et al. 2013). Son et al. (2014) investigated consumer perception of "good rice" in South Korea, Japan, Thailand and France, and consumers in all countries emphasized taste, health and processing as leading factors.

Classification and importance of rice quality

Milling quality refers to the proportion of economic product recovered from milling, firstly in brown rice and then in white rice. Unbroken white rice is the main form of refined rice sold as a commodity. Milling quality includes brown rice rate (BRR), white rice rate (WRR) and head rice rate (HRR). The milling quality overall mainly refers to the head rice yield, namely the head rice rate.

Appearance quality refers to the appearance of polished rice and includes color, shape, chalkiness, and transparency (Zhou et al. 2019). Grain shape and chalkiness are the main traits that determine appearance quality. Grain shape-related traits include grain length, grain width, grain thickness and length/width ratio, and chalkiness can be divided into white core, white belly and white back according to location.

Cooking and sensory quality refers to the comprehensive evaluation of the smell, color, shape, palatability, taste and other sensory indicators after cooking under specific conditions. Current evidence suggests that the main indicators affecting cooking and sensory quality are amylose content, protein content, fat content, gel consistency, gelatinization temperature and cooking method.

Rice mainly consists of starch, with very low amounts of other nutrients. But, in a staple food, the additional nutrients might be critical for maintenance of human health (Bhullar and Gruissem 2013; Birla et al. 2017). It is generally accepted that those key nutrients are protein and the amino acid lysine. Minerals and vitamins are also important nutrients in areas where trace elements are scarce. Rice bran is rich in polyunsaturated fatty acids, crude fiber and anthocyanins, so there are health benefits in eating white rice with lower milling extraction levels or, alternatively, brown rice, which contains more of the outer brown bran that is rich in fiber, vitamins, minerals and amino acids. With increasing standards of living and education, people are realizing the benefits of some healthy substances such as resistant starch and anthocyanins.

Consumers now pay more attention to food safety, and rice as a main food component is increasingly being questioned. While rice contains various nutrients, it may also contain toxins such as heavy metals (arsenic, cadmium, lead and mercury), pesticide residues and allergens.

Genes and QTL for grain quality

With the rapid development of functional genomics, more than 2000 genes controlling important agronomic traits have been cloned in plants and some molecular mechanisms have been characterized. In this section, we review important genes and QTL affecting rice quality, as well as some regulatory networks. It is expected that achievements in functional genomics research will greatly promote improvements in rice quality.

Genetic studies on milling quality

BRR, WRR and HRR are all complex quantitative traits easily affected by environment. At present, no major gene has been cloned, so the research on the functional genomics of milling quality has made limited progress. A large number of QTL for milling quality have been detected in genetic studies. This has improved our understanding of the genetic basis of milling quality of rice and provided useful molecular markers for improving rice quality in breeding programs.

Genetic effects on milling quality

Gravois (1994) predicted the combining ability effect of milled rice recovery (MRR) and head rice recovery (HRY) by using an 8-parent diallel hybrid population and found that general combining ability is more important for HRY than specific combining ability. Shi and Zhu (1998) used an incomplete diallel hybrid population of *Xian* rice to analyze cytoplasmic effects, maternal effects and seed effects on milling quality. The maternal effects were more important for BRR and MRR, whereas the seed effect was more important for HRY.

With developments in quantitative genetics, linkage analysis was used for QTL localization and analysis of gene effects. Various studies identified many QTL for milling quality and found QTL co-located with the cloned GS3 and Waxy genes. Only two other QTL for milling quality have been precisely localized (Ren et al. 2016; Sater et al. 2017), and neither has been cloned.

QTL for BRR

Twenty six QTL for BRR have been identified, many of which are co-located with grain shape QTL, but no study has shown that a particular gene affects BRR. Ren et al. (2016) used a DH population derived from cross *Xian* rice cultivar Taizhong 1 × *Geng* rice cultivar Chunjiang 6 to locate a brown rice extraction rate QTL on chromosome 10, named *qBRR-10* (LOD = 5.95), explaining 23.1% of the phenotypic variation. The allele from Chunjiang 6 increased BRR by about 7%. By fine mapping, they localized *qbrr*-10 to a 39.5-kb region and predicted that LOC_Os10g32124 or LOC_Os10g32190 might be the candidate gene for this QTL. By cytological analysis, they found that *qBRR-10* reduced glume thickness by reducing cell size, leading to a decreased glume proportion in the milled grain, thus increasing the yield of brown rice.

QTL for WRR and HRR

Totals of 41 and 35 QTL were identified for MRR and HRR, respectively, many of which are co-located with cloned genes for grain shape or chalkiness. *Chalk5* is a cloned major chalkiness gene that increases chalkiness and decreases HRR in rice (Li et al. 2014). Lou et al. (2009) showed that *GS3* affected both grain length and HRR, indicating a negative correlation between grain length and head rice yield. These results reflect not only an effect of appearance quality on milling quality but also the complexity of quality traits and pleiotropy of genes related to quality traits.

Fissure is another trait besides grain shape and chalkiness with a significant effect on HRR. The high milling quality cultivar Cypress is well known for its extensive fissure resistance. Using a Cypress × Lagrue RIL population Pinson et al. (2013) located three QTL for crack resistance and named them *qFIS1–1*, *qFIS1–2* and *qFIS8* according to chromosome location. *qFIS1–2* at the end of chromosome 1 L had the largest effect, explaining 13% of the phenotypic variation with the allele from Cypress reducing crack rate by 12%. Sater et al. (2017) narrowed *qFIS1–2* to the RM1361 - RM3482 region of about 640 kb.

Genetic and functional studies on appearance quality

Grain shape and chalkiness are major components of rice appearance quality (Zhou et al. 2019). In the past decade, many grain shape and chalkiness genes were cloned. Functional studies of these genes provided insights on molecular mechanisms underlying grain shape and chalkiness.

GS3 and GW5 define the length and width of grain

Grain length and grain width of cultivated rice are mainly determined by *GS3* and *GW5* (Zhou et al. 2017). Fan et al. (2006) first used a backcross population of *Xian* varieties Chuan 7 and Minghui 63 to identify and clone *GS3*, which negatively regulates grain length. Takano-Kai et al. (2009) subsequently analyzed the natural variation of *GS3* and found that a C > T mutation in the second exon originated from temperate *Geng* rice and was strongly artificially selected in tropical *Geng* and *Xian* rice varieties. This discovery also explains why most *Xian* rice genotypes have long grain. Mao et al. (2010) found that *GS3* had four functional domains and formed multiple alleles; wild-type *GS3* (*GS3–1*) had a medium-length grain shape, typified by cv. Zhenshan 97; *GS3–3* conferred long grain, as in cv. Minghui 63; and *GS3–4* with loss of the C-terminal functional domain had much stronger function and ultra-short grains, such as in Chuan 7. Trusov et al. (2012) identified the G protein gene in rice and found that it was encoded by *GS3*, hence showing that *GS3* is a G protein γ subunit gene. Sun et al. (2018) showed how *GS3* regulates grain length through the G protein pathway (Fig. 2). Three Gγ subunits are involved; DEP1 and GGC2 bind to Gβ to increase rice grain length. GS3 itself does not affect grain length but inhibits the functions of DEP1 and GGC2 by competitively binding to the Gβ subunit, thus negatively regulating the grain length.

GW5 is the main gene affecting variation in rice grain width. Weng et al. (2008) identified *GW5* as a major QTL for grain width and weight and showed that a 1212-bp deletion in cv. Assominori was associated with increased grain width. Shomura et al. (2008) pointed out that this deletion led to a significant increase in grain width in cultivated rice and played a historical role in rice domestication. Duan et al. (2017) cloned *GW5*; it encodes a plasma membrane–associated protein with an IQ domain. Analysis of the natural variation of *GW5* revealed three haplotypes, including wild type, the 1212-bp deletion haplotype in *Geng* rice, and a 950-bp deletion and 370-bp insertion haplotype in *Xian* rice. Liu et al. (2017) further found that *GW5* interacts with *GSK2*; they proposed a regulation model for the effect of *GW5* on grain width and pointed out that GW5 participated in the brassinosteroid pathway by regulating grain growth through inhibition of the kinase activity of GSK2 on OsBZR1 and DLT.

Other genes controlling grain shape

In addition to *GS3* and *GW5*, many other genes affecting grain shape have been cloned from natural variations, including *GS2*/*GL2*, *GL3.1*, *GS5*, *GW2*, *GW8*, *GL7*/*GW7*, *GLW7* and *GL3.3* (Hu et al. 2015; Li et al. 2011; Qi et al. 2012; Song et al. 2007; Wang et al. 2015; Wang et al. 2012; Xia et al. 2018). Analyses of the mechanisms of these genes revealed five regulatory pathways, among which plant hormone pathways had profound effects on grain shape (Fig. 2). Genes such as *GW5*, *D2*, *D11*, *TGW6* and *TGW3* are all involved in phytohormone pathways (Hu et al. 2015; Ishimaru et al. 2013; Liu et al. 2017; Ying et al. 2018). The G protein signaling pathway is another important pathway that determines grain shape; in addition to the G protein subunit genes *GS3*, *DEP1* and *D1*, *LGY3* plays a role in regulation of the G protein pathway through interaction with *DEP1* and *GS3* (Liu et al. 2018). *GW2* encodes a RING-type E3 ubiquitin ligase highlighting the important role of proteasome degradation in regulation of grain shape (Song et al. 2007); deubiquitinase activity of WTG1 affected grain shape and plant type by proteasome degradation (Huang et al. 2017). *GLW7*, *GW8*, *GS2* and *GS9* serve as transcriptional regulators affecting the expression of other grain size genes to regulate grain size (Wang et al. 2012; Hu et al. 2015; Si et al. 2016; Zhao et al. 2018). Additionally, *SMG1/OsMKK4* and *SMG2/OsMKKK10* participate in the mitogen-activated protein kinase (MAPK) signaling pathway to control grain size (Xu et al. 2018).

Chalk5 regulates grain chalkiness

Chalkiness is a complex trait that is sensitive to the environment and controlled by multiple genes. Among

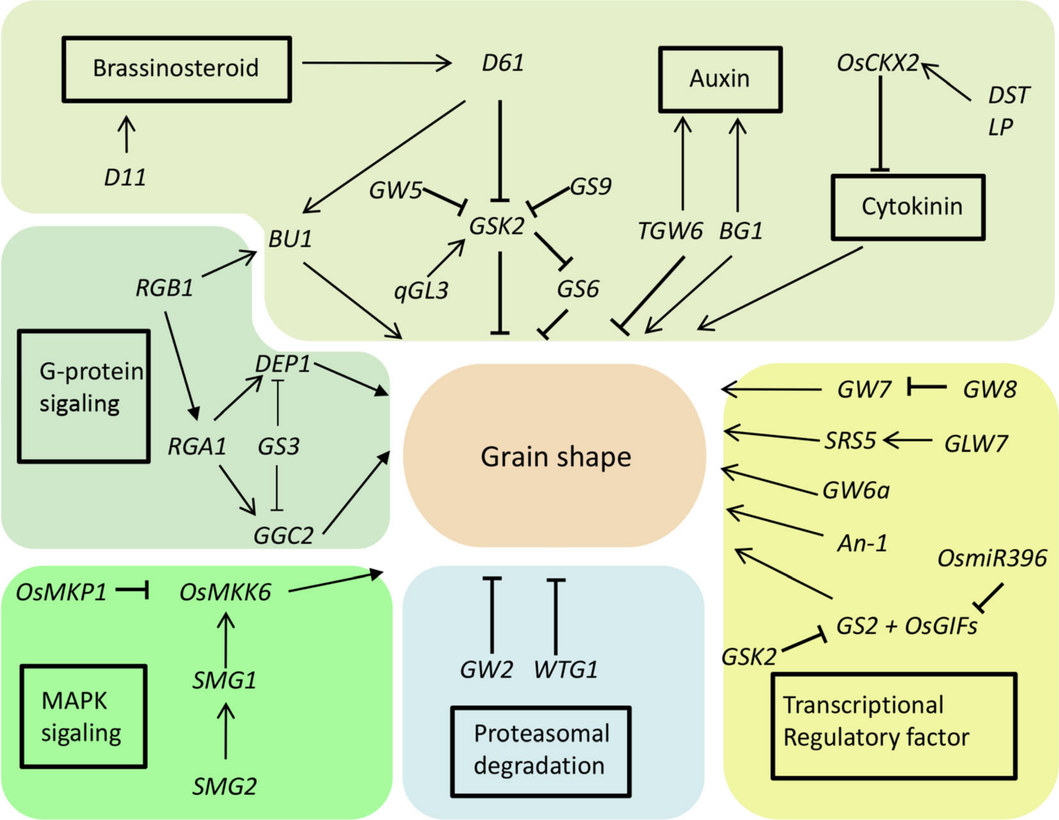


Fig. 2 The major signaling pathways of seed size control in rice

the many QTL related to chalkiness, only *Chalk5* has been cloned from natural variants, and almost all of the remainder were identified as mutants (Li et al. 2014). *Chalk5* encodes a vacuole H$^+$-translocating pyrophosphatase (V-PPase), specifically expressed in the endosperm and a positive regulator of the rate white belly chalkiness. Polymorphisms in the promoter region of *Chalk5* were associated with expression level and amount of chalkiness. Analysis of natural variation showed that variation of chalkiness in *Xian* rice was mainly caused by polymorphism in the promoter region.

Other genes related to chalkiness

Many chalkiness-related genes were cloned from floury endosperm mutants, most of which were related to starch synthesis or starch quality. *FLO5/SSIIIa* regulates short amylopectin elongation, and knockout of this gene led to formation of white core (Ryoo et al. 2007a). *FLO2* is involved in the regulation of grain shape and starch quality; *flo2* mutants displayed decreased expression of storage starch-related genes, and overexpression of *FLO2* increased grain size (She et al. 2010). The starch content in the grain of *flo6* mutants was reduced, and the physicochemical properties were changed. Peng et al. (2014b) found that *FLO6* may be involved in starch synthesis and formation of starch granules as a starch-binding protein. *FLO7* encodes a functionally unknown protein harboring an N-terminal transit peptide capable of targeting functional FLO7 fused to green fluorescent protein to amyloplast stroma in developing endosperm cells. Mutant *flo7* has floury-white endosperm with reduced amylose content and an abnormal amylopectin structure (Zhang et al. 2015).

Functional genes for cooking and sensory quality

Measures of cooking and sensory quality include amylose content, gel consistency or RVA, gelatinization temperature and aroma. Cooking and eating quality is mainly influenced by the composition and structure of starch. The pathway of starch synthesis in rice has been clearly elucidated (Bao 2019). GBSS is responsible for synthesis of amylose in the grain, whereas SS, BE and

DBE are involved in the synthesis of amylopectin. *Waxy*/*GBSSI* and *ALK*/*SSIIa* determine most of the natural variation in cooking and eating quality. Aroma is mainly regulated by the protein *OsBADH2* encoded by gene *frg*. Artificial sensory evaluation is more accurate than human taste panels for evaluation of taste quality, but as a genetic trait, it remains too complex to apply in genetic research and breeding (Lyon et al. 1999; Limpawattana and Shewfelt 2010).

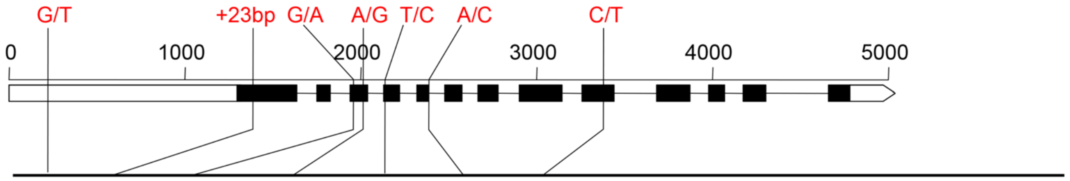
Waxy determines amylose content and gel consistency

The endosperm of rice is mainly composed of starch; the composition and structure of the starch determines the physical and chemical characteristics before and after cooking. The *Waxy*/*GBSSI* gene, located on chromosome 6 and specifically expressed in the endosperm, encodes a granule-bound starch synthase that controls the synthesis of amylose. There are many natural variants of *Waxy*, and 7 functional variations have been reported to control the apparent amylose content within a range of 0~30% (Fig. 3). Duplication of a 23-bp sequence in the second exon leads to a premature termination codon, resulting in loss of function of *Waxy* ing synthesizing amylose and the phenotype known as Waxy (Wanchana et al. 2003). A G > T mutation in the splice site of the 5'UTR region causes a decrease in mRNA expression and represents a major site for variation in amylose content in nonwaxy accessions (Cai et al. 1998). An A > C variation in exon 6 causing a tyrosine to serine substitution is a secondary site for variation in amylose content in non-glutinous rice (Larkin and Park 2003). A C > T SNP in exon 10 causes a serine to proline change that affects gel consistency and RVA characteristics (Tran et al. 2011; Traore et al. 2011; Zhang et al. 2019). Teng et al. (2012) identified five *Waxy* alleles in cultivated varieties based on these four variants and confirmed their effects on starch content by constructing chromosome fragment substitution lines of the five alleles.

There are several rare variations in addition to the four described above. The G > A base replacement in exon 4 resulted in the amino acid variation from aspartic acid to threonine, which does not affect the enzyme activity of GBSSI but reduces the binding ability of GBSSI to granulated starch and eventually leads to decreased amylose content and an opaque phenotype (Mikami et al. 2008). SNP variants G > T in exon 4 and G > A in exon 5 were identified in cv. Milky Queen, a low-amylose Japanese variety (Sato et al. 2002).

ALK determines gelatinization temperature

The *ALK*/*SSIIa* gene, located on chromosome 6 and specifically expressed in the endosperm, encodes an amylopectin synthase that elongates short chains with a degree of polymerization (DP) < 10 in amylopectin to medium-long chains with a DP between 12 and 24 (Nakamura et al. 2005). *ALK* is the main gene regulating gelatinization temperature (GT). Previous studies identified four SNP variants causing amino acid substitutions, two of which affected ALK function (Nakamura



5'UTR	Exon2	Exon4-1	Exon4-2	Exon5	Exon6	Exon10	Wx allele	Amylose (%)	References
G	-	G	A	T	A	C	Wx^{lv}	25-30	Zhang et al. 2019
G	-	G	A	T	A	T	Wx^{a}	25-30	Mikami et al. 2008
G	-	G	A	T	C	C	Wx^{in}	18-22	Mikami et al. 2008
T	-	G	A	T	A	C	Wx^{b}	15-19	Mikami et al. 2008
T	-	A	A	C	A	C	Wx^{mq}	8-12	Sato et al. 2002
T	-	A	A	T	A	C	Wx^{mp}	8-12	Yang et al. 2013
G	-	G	G	T	A	C	Wx^{op}	12-14	Mikami et al. 2008
T	-	G	G	T	A	C	Wx^{hp}	9-10	Li et al. 2009
T	+23bp	G	A	T	A	C	*wx*	0-2	Mikami et al. 2008

Fig. 3 Seven variations at the *WAXY* locus affecting amylose content in rice

et al. 2005). A GC > TT mutation in exon 8 causing substitution of leucine by phenylalanine had a major effect on GT (Bao et al. 2006). A G > A change in exon 8, causing a replacement of glycine by serine, is a second site of variation affecting GT. These two SNP mutations lead to inactivation of *SSIIa*, reduced long chains in amylopectin and reduced gelatinization temperature.

Other starch synthesis-related genes

The starch synthesis pathway in rice is mainly based on four enzymes (AGP enzyme, starch synthase, branching enzyme and debranching enzyme). Discovery and functional analysis of related genes were mostly based on mutant studies. The *SSIIIa* gene, located on chromosome 3, is specifically expressed in the endosperm and encodes an amylopectin synthase whose main function is to elongate chains with DP of 15~24 to long chains with DP > 30 (Fujita et al. 2007; Ryoo et al. 2007b). Loss of function of *SSIIIa* leads to formation of chalky endosperm and increased expression of the *SSI* and *Waxy* genes (Crofts et al. 2012; Zhou et al. 2016b). Gene *BEIa* encodes a starch branching enzyme, mutation of which caused a decrease in long chains with DP > 30 in amylopectin, and decreased gelatinization temperature, but endosperm morphology and total starch content were normal (Satoh et al. 2003).

OsBADH2 determines aroma

Aromatic compound 2-acetyl-1-pyrrolidine (2-AP) is the main component of the popcorn-like smell of cooked rice. Earlier studies identified a recessive fragrance QTL (*fgr*) on chromosome 8 (Lorieux et al. 1996). Bradbury et al. (2005) suggested that *OsBADH2* encodes a betaine aldehyde dehydrogenase (BADH) and is the most likely product of *fgr*. Chen et al. (2008) confirmed that an *OsBADH2*-encoded BADH protein inhibited biosynthesis of 2-AP by consuming the precursor of 2-AP, 4-aminobutyraldehyde (AB-ald), thus causing rice to lose its fragrance. Recessive alleles of *OsBADH2*, *badh2-E2* and *badh2-E7* have 7 bp and 8 bp deletions, respectively, in exon 2 and exon 7 (Bradbury et al. 2005; Shi et al. 2008b).

Other genes or QTL for sensory quality

Lin et al. (2014) reported a mutant, SA0420, whose fragrance was not dependent on *fgr*. The *OsGAPDHB* gene was identified as a functional gene responsible for the creamy popcorn flavor of SA0420 by proteomic analysis and transgenic verification (Lin et al. 2014).

Genetic and functional genomic studies on nutrition quality

Rice has many nutrients, but mostly at very low levels. Most of the genes related to nutrient synthesis were identified in mutants or predicted by homology. Identification of these genes provided a valuable resource for improving nutritional quality.

Proteins and amino acids

Fifteen glutelin genes (Kawakatsu et al. 2008), 34 prolamin genes (Xu and Messing 2009), 3 globulin genes (Nakase et al. 1996b; Sun et al. 1996) and 7 albumin genes (Alvarez et al. 1995) have been identified in rice, predominantly predicted by homology. Many QTL for rice storage proteins were identified by genetic methods, but few have been confirmed by fine mapping and cloning. Peng et al. (2014a) cloned the *OsAAP6* gene by positional cloning. This gene encodes an amino acid transport protein and positively regulates the contents of four kinds of storage proteins. Chen et al. (2018) identified many known and unknown QTL by genome-wide association analysis of storage proteins in 527 cultivars. They analyzed the effects of different haplotypes of the cloned protein genes *OsAAT2*, *RA17*, *RM1* and *RP6* and cloned starch metabolism related genes *AGPS2a*, *ISA2*, *PUL* and *Waxy* on contents of various storage proteins. Yang et al. (2019) found that natural variation of *OsGluA2* contributed to the protein content differences between *Xian* and *Geng*.

Among the nine essential amino acids, rice storage proteins are deficient in lysine and tryptophan. Lysine-ketoglutarate reductase/saccharopine dehydrogenase (LKR/SDH) is a bifunctional lysine-degrading enzyme and one of the key regulators of free lysine content in plants (Kemper et al. 1999). In rice, *OsLKR/SDH* is regulated by the *bZIP* transcription factor *RISBZ1* and DOF transcription factor RPBF (Kawakatsu and Takaiwa 2010). Down-regulation of *RISBZ1*, or *RPBF*, decreases the level of *OsLKR/SDH* and results in increased free lysine content in rice grains. A key step in the synthesis of plant tryptophan is the conversion of chlorate and glutamine into anthranilate, glutamate and pyruvate (Li and Last 1996). Anthranilate synthase (AS) is an important enzyme in this process, which is feedback-regulated by tryptophan content. Two genes in rice synthesize AS, *OASA1D* and *OASA2* (Tozawa et al. 2001). The tryptophan content in seeds was increased 230-fold by inhibited expression *OASA2* in the endosperm (Saika et al. 2011).

Minerals

The mineral elements in rice are mainly iron, zinc, copper and selenium, among which iron and zinc are very important micronutrients for human health (White and Broadley 2009). Metabolism of metal elements in rice involves absorption and transport. Iron uptake in rice requires transport to other tissues by binding insoluble Fe(III) to the family of iron carriers known as mugineic acid phytosiderophores (MAs). Iron transporters in rice include the Yellow Stripe-Like (YSL) family, rice iron-regulated transporters (OsIRT1 and OsIRT2) and citrate transporters (Santos et al. 2017). Sperotto et al. (2010) found that Fe concentration in rice grain was positively correlated with the expression of *OsYSL14* and *OsNAC5* and negatively correlated with expression of *OsNRAMP7, OsNRAMP8* and *OsFRO1*. On the other hand, *OsFER1, OsNRAMP4, OsNRAMP5, OsNRAMP6, OsYSL6, OsYSL12, OsYSL4, OsZIP8* and *OsZIP10* are related to the iron content in seeds. Lee et al. (2009a) found that *OsYSL15* was related to Fe absorption, and its overexpression improved the Fe content in leaves and seeds. Zinc uptake can be either as Zn^{2+} or MA complexes, depending on particular transporters. In rice, zinc-regulated transporters and iron-regulated transporter-like protein (ZIP) were identified as zinc transporters (Bashir et al. 2012). Current ZIP proteins reported in rice include OsIRT1, OsIRT2, OsZIP1, OsZIP3, OsZIP4, OsZIP5, OsZIP7 and OsZIP8, among which OsZIP4 and OsZIP8 are particularly important for Zn transport to seeds. Overexpression of OsZIP1 increased the zinc contents in roots, shoots and grains (Lee and An 2009).

Vitamins

Rice seeds contain vitamins B1, B2, B3, B4, B6, B7, B9 and E but do not contain vitamins A, C and D (Champagne et al. 2004). Tan et al. (2005) screened a large number of rice germplasms and found no accession with high β-carotene (vitamin A precursor) content in the endosperm, indicating an absence of endogenous genes for vitamin A improvement. However, introduction of exogenous genes to improve β-carotene levels has been achieved by genetic engineering (see 3.3). Expression of the rice dehydroascorbate reductase (dhar) gene in maize increased the ascorbic acid level in transgenic maize by 6-fold (Naqvi et al. 2009). A similar approach could be used for the development of high vitamin C rice. The metabolic pathways and physiological functions of vitamin D in plants are not well understood.

Unsaturated fatty acids

The fatty acids in rice are mainly palmitic acid (C16:0), oleic acid (C18:1) and linoleic acid (C18:2) and are mainly present in the bran. Unsaturated fatty acids, especially linolenic acid (C18:3), are very beneficial to human health. Several genes important for the synthesis of unsaturated fatty acids have been identified in rice. Fatty acid dehydrogenase OsFAD2 converts C18:1 into C18:2 (Shi et al. 2012), and fatty acid dehydrogenase OsFAD3 converts C18:2 into C18:3 (Liu et al. 2012). In addition, ketolisyl synthase OsKASI regulates the contents and components of fatty acids in roots and seeds (Ding et al. 2015).

Resistant starch

Resistant starch can help to control type 2 diabetes and prevent obesity and other diseases. The recommended intake of resistant starch is 18–20 g per day, but cooked rice contains less than 3%. Zhou et al. (2016a) found that *SSIIIa* interacts with the *Waxy* gene, and, in the presence of a strong *Waxy* allele, the resistant starch content in *SSIIIa* mutant lines was much higher than that of the wild type, reaching 6%. Bao et al. (2017) performed a genome-wide association analysis of rice resistant starch and identified four genes (*Waxy*, *SSIIa*, *ISA1* and *AGPS1*) in the starch synthesis pathway affecting natural variation in resistant starch levels.

Anthocyanins

Anthocyanins are water-soluble pigments with high antioxidant activity; antioxidants are beneficial to human health (Wang and Stoner 2008). Anthocyanin biosynthesis in rice tissues is primarily controlled by three types of dominant genes: C (chromogen), A (activator) and P (tissue-specific regulator). C and A are fundamental for the formation of anthocyanin pigments, and P is a tissue-specific regulator of C and A (Sakamoto et al. 2001). Pro-anthocyanidins and anthocyanins in rice are present in the pericarps of red and black rice, respectively. Red pericarp is controlled by genes *Rc* on chromosome 7 and *Rd* on chromosome 1. When *Rc* is functional, the pericarp is brown; when *Rd* is functional, the pericarp has no color; but, when *Rc* and *Rd* are both functional, the pericarp is red. Black grains in rice are due to accumulation of anthocyanin in the pericap and are determined by three dominant genes, namely, *kala1* (*Rd*), *kala3* and *kala4* (*OsB2*) (Maeda et al. 2014; Oikawa et al. 2015). *Rd* is an anthocyanin synthesis gene, *kala3* is an R2R3-Myb transtription factor and *OsB2* is a bHLH transcription factor, corresponding to the determinant factors P, C and A for anthocyanin biosynthesis.

Genes related to hygiene quality

Heavy metals

Arsenic and chromium are the main toxic elements found in rice. Arsenic mainly occurs in the form of arsenite and arsenate. Arsenite enters the root system through water channels (Ma et al. 2008). The specific transporter responsible for arsenite uptake is LSi1, and another transporter, LSi2, mediates accumulation of arsenic in roots and seeds. As arsenate is an analogue of phosphate, the phosphate transporter OsPT8 regulates both arsenate and phosphate uptake (Wu et al. 2011).

Cadmium exists in soil as cadmium sulfide, cadmium carbonate or Cd^{2+} ions, and their absorption and transport mechanisms overlap in many ways with iron and zinc. Rice iron transporters OsIRT1 and OsIRT2 have been reported to transport Cd^{2+} ions (Nakanishi et al. 2006). Another transport vector associated with cadmium accumulation is the natural resistance-associated macrophage protein (NRAMP) family (Ishimaru et al. 2012). OsNRAMP5 enhances the ability of roots to absorb cadmium, and OsHMA3 participates in transportation of cadmium from roots to shoots (Miyadate et al. 2011).

Allergens

The allergens in rice are mainly proteins. Analysis of serum lgE binding in allergic patients showed that the proteins included α-amylase/trypsin inhibitors (14–16 kDa), α-globulin (26 kDa) and β-glyoxalase I (33 kDa) (Urisu et al. 1991; Mills et al. 2004). *RAG2* encodes one of the14–16 kda albumins (Kurokawa et al. 2014). The major globulin gene, *Glb-1*, encodes the endosperm-specific 26 kDa α-globulin (Nakase et al. 1996a). In addition, 52 kDa globulin-like protein (identical to REG2), 63 kDa embryo globulin (possibly identical to REG1), about 90 kDa α-glucosidase and 55 kDa protein disulfide isomerase have been identified as high–molecular weight allergens (Satoh et al. 2011).

Genetic improvement of grain quality in rice

Milling quality, appearance quality and cooking and sensory quality are correlated with each other, and several major genes explaining much of the genetic variation are suitable for molecular marker-assisted selection (MAS). The nutritional quality and hygiene quality of rice are more complex because the beneficial and harmful substances may be interrelated. The very low levels of most nutrients in rice limit exploitation of natural variation in breeding programs whereas transgenic methods offer promising opportunities. Mutation breeding may be an attractive way to address problems of harmful metabolites.

Breeding for improved rice grain shape, amylose content, gelatinization temperature and aroma using MAS

MAS is the application of molecular markers in plant breeding. MAS is simpler to conduct than phenotypic screening, can be carried out at the seedling stage and allows single plants to be selected with high reliability, making for higher efficiency and accelerated line development in plant breeding. Reliable molecular markers allow MAS to be used effectively in backcross breeding, forward selection, reverse selection, gene pyramiding and background screening.

Four genes, *GS3*, *Waxy*, *ALK* and *fgr*, determine most of the natural variation in grain length, amylose content, gelatinization temperature and aroma and are key targets for improvement of rice quality. Fan et al. (2006) cloned grain-length gene *GS3* and developed molecular marker SF28 based on its functional variation. Wang et al. (2012) utilized SF28 in MAS to pyramid the non-functional alleles *gs3* and *gw8* into the short grain variety HJX74. This changed the grain shape forming a long grain shape similar to Basmati 385. Pyramiding of the *GW7* and *gs3* alleles promoted development of high yielding *Xian* hybrids (e.g., Taifengyou 55 and Taifengyou 208) with high grain quality (Wang et al. 2015).

Cooking and sensory quality are the most important aspects of rice quality. Most consumers prefer rice with medium or low amylose content, low gelatinization temperature and fragrance. The *Waxy* gene controlling amylose content has multiple alleles, among which WX^a confers high amylose content, WX^b produces medium amylose content and *wx* has no amylose (Fig. 3). Ayres et al. (1997) developed molecular markers for the *Waxy* locus from analysis of amylose content and *Waxy* sequence variation in 92 cultivars. Molecular marker-assisted selection of the Wx^b allele was used to improve grain quality in breeding (Liu et al. 2006; Gao et al. 2009; Yi et al. 2009). *ALK* has two non-functional alleles that reduce the gelatinization temperature, and markers developed from them have been used to improve gelatinization temperature (Bao et al. 2006). *fgr* has two non-functional alleles that permit aroma; molecular markers have been developed for breeding (Shi et al. 2008a). Utilizing markers for these various major genes Jin et al. (2010) simultaneously improved amylose content, gelatinization temperature and aroma of maintainer line II-32B. Clearly, MAS breeding can be a very effective method for improving quality traits regulated by combinations of several major genes.

Transgenic breeding to improve vitamin A, Zn, Fe, anthocyanin and lysine contents

Many molecular markers have been developed for rice breeding. The use of molecular markers is currently limited to the availablilty of suitable traits within the rice species. However, genetic engineering by means of transgenics could target genes from other species. Some possibilities are discussed below.

Vitamin A deficiency is a worldwide problem. In the last decade, through a combination of molecular biology and genomics, great progress has been made in the genetic engineering of biosynthesis genes for phytocarotenoids (precursors of vitamin A). Ye et al. (2000) developed Golden Rice No.1 with a grain carotenoid content of 1.6 mg/g by expression of the daffodil phytoene synthase gene bacterial phytoene desaturase and lycopene β-cyclase in the endosperm. Paine et al. (2005) transformed rice plants with a maize lycopene synthetase gene instead of the daffodil source to develop Golden Rice No. 2, with total endosperm carotenoids content reaching 37 mg/g. Carotene is easily degraded during rice storage, and Gayen et al. (2014) solved this problem by regulating the expression of a lipoxygenase gene.

Two of the most important microelements for human health, iron and zinc, are found in very low levels in rice. Nicotianamine (NA) is a metal chelator that is involved in the transport of metals in plants. Endosperm-specific overexpression of *OsNAS1* resulted in polished grain with significantly increased concentrations of NA and Zn, but Fe concentration was not increased. By overexpressing NA synthase genes, *OsNAS2* and *OsNAS3*, Lee and co-workers (Lee et al. 2009b; Lee et al. 2012) increased Fe and Zn levels in rice seeds. Johnson et al. (2011) constitutively overexpressed the *OsNAS* gene family and obtained *OsNAS2* overexpression lines with 19 μg/g Fe in polished grain. Two-fold increases of Zn concentration were also observed in the *OsNAS2* lines.

Anthocyanins are beneficial to human health by reducing the risk of certain cancers, cardiovascular diseases, diabetes and other chronic diseases (Wang and Stoner 2008). Anthocyanins in rice are found only in the pericarp but not in the endosperm and therefore are lost in highly polished rice. Zhu et al. (2017) made a construct containing eight anthocyanin-related genes (two regulatory genes from maize and six structural genes from Coleus) driven by an endosperm-specific promoter, as well as a selectable marker and a gene for marker excision to transform rice. The transgenic lines, Purple Endosperm Rice (called “Zijingmi” in Chinese), had high anthocyanin content and antioxidant activity in the endosperm.

Essential amino acids in rice can be increased by knockdown of some storage proteins and then increasing the contents of other storage proteins through proteome rebalancing. Kawakatsu et al. (2010) constructed transgenic knockout lines of glutenin, globulin and prolamin and found that the lysine content in transgenic lines lacking the 13 kDa prolamin was increased by 56% compared with the wild type. Corn lysine ketoglutarate reductase/saccharopine dehydrogenase (LKR/SDH) is a bifunctional lysine-degrading enzyme that accumulates mainly in the endosperm (Kemper et al. 1999). Suppression of *ZmLKR/SDH* by RNAi under control of the embryo-specific *Glb-1* promoter led to a 10-fold increase in free lysine content in corn grains compared with the control (Reyes et al. 2009). The same technique to downregulate *OsLKR/SDH* was applied in rice, and the level of free lysine also increased 10-fold relative to the wild type (Long et al. 2013). Yang et al. (2018) bred a High Free Lysine (HFL) line by pyramiding overexpression lines of feedback-insensitive bacterial AK and DHPS (35S) and downregulation line of LKR/SDH (Ri or GR) with an aim to breed Lys-rich rice.

Mutation breeding to reduce heavy metal and allergen contents

Mutation is considered the ultimate cause of variation. Without variation, plant breeding is impossible. To initiate a breeding program, breeders must find an appropriate genotype containing the desired genes from existing germplasm resources or create variation if none is found in nature. Mutation breeding is the process of producing new alleles.

Ishikawa et al. (2012) generated three mutant lines that reduced grain cadmium content (< 0.05 mg/kg) compared with the wild type (1.73 mg/kg) by carbon ion-beam irradiation. The mutation in all three lines was associated with *OsNRAMP5*. Cadmium was barely detectable in grains of these mutants that had no obvious agricultural or economic defects. Ishikawa et al. (2016) also proposed a method to simultaneously reduce cadmium and arsenic in rice by using mutants of the OsNRAMP5 gene. Following alternate wetting and drying (AWD), the milled grain of *OsNRAMP5* mutant plants was free of cadmium and had a 27% reduction in arsenic content compared with the control.

Six kinds of allergenic proteins are present in rice (see “Allergens”). Iida et al. (1998) screened an allergen mutant Gbn-1 lacking the 26 kDa allergen protein. Wakasa et al. (2011) used RNAi to inhibit expression of the 14–16 kDa and 33 kDa allergic protein genes in the background of Gbn-1, and obtained lines with downregulated contents of all three proteins. Ogo et al. (2014) utilized RNAi to construct transgenic lines in which 52-, 63- and 90-kDa proteins were simultaneously downregulated. The two lines were hybridized to produce a new derivative with reduced levels of all six allergens (Ogo et al. 2014). Immunodot blotting showed that the binding of seed protein to IgE in sera from allergic patients was significantly reduced in the new strain, compared with non-transgenic rice. Such a line could be beneficial for people who are allergic to rice.

Challenges and prospects of rice grain quality improvement

Consumer demand for quality rice varies with local preferences, but accurate evaluation of consumer preference is key to rice grain quality for breeding programs. Actual sensory evaluation is currently only implemented during identification of parental traits or at release of newly developed varieties. In the early stages of breeding and genetic studies on quality traits, indirect traits, such as amylose content, RVA and aroma, are used to measure sensory quality. Panel-based sensory evaluation (Lyon et al. 1999; Limpawattana and Shewfelt 2010), which needs a number of professional tasters and a large amount of rice, cannot be used in breeding or scientific research. Therefore, instruments that can replace artificial sensory evaluation are very important for genetic improvement of rice quality. The correlation between instrument and panel-based sensory analyses can be verified by different samples with local preferences (Kwak et al. 2015; Lu et al. 2016). The establishment of a rapid and effective sensory evaluation system will provide an understanding of why some classical varieties continue to be widely used by farmers in major rice-growing areas and are preferred by a majority of rice consumers despite the availability of newer, more productive cultivars (Sudha et al. 2013; Kwak et al. 2015). Market research on the preferred distribution and clustering of consumer demand for different quality and sensory attributes will be crucial for objective approaches in breeding for rice quality.

The existing rice cultivars with good quality are climatically and locally adapted, and interaction between quality characteristics and environment needs to be studied. Cultivar Koshihikari is favored by consumers worldwide for its quality and therefore has been planted in various locations outside Japan, such as the USA, Australia and China (Kobayashi et al. 2018). Although there is an expectation that the high eating quality of Koshihikari will be retained in these areas, environmental conditions such as high temperature and low humidity tend to prevent it from achieving the same quality as in Japan. In fact, even when grown in different parts of Japan, Koshihikari varies in grain quality. According to the assessment results of the Japan Grain Inspection Association, Koshihikari is grown in 39 of 113 rice production areas in Japan, but only Koshihikari from Niigata-ken in Uonuma-shi has obtained the special A evaluation for 27 consecutive years (Liu 2016). Therefore, studying the influence of environment on rice quality and understanding the interaction between rice quality and environment is key to improving rice quality, and future climate change will also make an impact.

It is difficult to combine quality, yield and abiotic and biotic resistances in rice breeding. Many high-quality rice varieties have defects, for example, Koshihikari has no resistance to lodging and blast and KDML 105 is low-yielding and has no resistance to brown planthopper (Kobayashi et al. 2018; Vanavichit et al. 2018). Although functional genomics have made progress (Li et al. 2018), it has not been applied effectively in breeding. Traditional molecular marker-assisted selection systems are time- and labor-consuming for improving multiple traits. High-throughput sequencing technology and chip technology can effectively solve this problem (Varshney et al. 2009; Thomson 2014). Breeding chips, products of combinations of functional genomic research and high-throughput genotyping, have three advantages (Yu et al. 2014). The first is that breeding chips can quickly identify favorable alleles in populations. The second is that background selection can assist in selecting the required genetic background. Thirdly, breeding chips are fast and efficient. Large-scale screening can be carried out in the laboratory to exclude over 95% of individual plants, leaving a smaller population (or a larger number of highly selected plants) to be planted in the field, greatly reducing the workload in the field.

To sum up, a more systematic and comprehensive strategy should be adopted in rice breeding to pyramid more favorable genes for quality. In order to achieve this goal, a recent study showed that systematic pyramiding of multiple genes with major effect was effective in producing both high yield and good quality (Zeng et al. 2017). In the future, the systematic design rice genotypes with high-yield and high-quality rice will depend on the outcomes of genetics and genomics research, adoption of high-throughput genotyping technologies and refinement of instruments for evaluation of quality.

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