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Novel genes for quality in rice: A review

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Abstract

Rice is rich in germplasm resources, including naturally occurring and artificially modified germplasms. The International Rice Research Institute (IRRI) maintained 110 000 rice germplasm accessions, which is the world's largest and most diverse collection. In India, Indira Gandhi Krishi Vishwavidyalaya, Raipur is maintaining 23,250 rice germplasm resources which is the largest collection of active germplasm in India. Acceptance of new rice genotypes by producers and consumers hinges not only on their potential for higher yield but recent emphasis has also been on premium-value genotypes that have the ability to satisfy consumer preferences for grain quality. This review article provides insights into how to link grain quality attributes and sensory perception to support breeding superior rice varieties. Recent advances in quality profiling and omics technologies have provided efficient approaches to identify the key genes and biochemical markers involved in rice quality traits. Emphasis has been given to the upcoming area of holistic understanding of grain quality and attributes derived from sensory evaluation to leverage integrative gene discovery strategies that enable breeding programs to efficiently tap the huge genetic diversity in rice for novel genes that enhance rice quality.

Keywords: Genes for quality, noble genes, *Oryza sativa* L.

Introduction

Rice is the staple food of India as well as of Chhattisgarh State. Chhattisgarh is blessed with a wide variability in rice. More than 23,000 different rice germplasm accessions are present in Indira Gandhi Krishi Vishwavidyalaya, Raipur, Chhattisgarh which is the largest germplasm collection in India. Market survey data suggest that efforts to develop varieties with improved cooking and eating quality have high economic returns (Son *et al.* 2014) [30]. Even though grain quality strongly drives the market value of rice (Dalton 2004) [12], varietal improvement programs have largely focused on enhancing yield with a lag in focusing on grain quality. Grain yield and key grain quality traits are complementary beneficial traits. However, breeding varieties with both higher yield potential and superior grain quality traits have not had much historical success (Peng *et al.* 2008) [27]. Low- to moderate-yielding varieties that have the best organoleptic properties consistently have higher end-consumer acceptability than high-yielding varieties that lack premium attributes. Examples of these are the IRRI mega-varieties developed from the late 1960s to 1980s that remain popular today (Leung *et al.* 2002) [22]. Breeding therefore has to leverage recent scientific advancements to achieve adequate cooking and eating quality of rice and introgress these genetic regions (reflected by grain quality and sensory evaluation preferences) into high-yielding varieties through marker-assisted selection. Rice varieties can be grouped into several quality classes based on consumer preferences. These quality classes are based on physical properties:

- head rice recovery
- chalkiness
- grain size
- grain shape
- grain color
- starch quality influencing cooking and
- organoleptic properties

Above all, aroma is regarded as a premium quality trait that gives higher economic gains to rice farmers (Champagne 2008; Chen *et al.* 2008; Fitzgerald *et al.* 2008; Huang *et al.* 2008; Kovach *et al.* 2009) [9, 10, 13, 15, 20]. Several methodologies for measuring rice quality indicators are established and are currently being used to screen rice breeding lines (Mariotti *et al.* 2010; Vilaplana *et al.* 2012) [25, 34].

In this review, we summarize the links from the genetics of rice grain quality to consumer preferences and propose to explore modern tools to

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- tap into the genetic diversity within the rice breeding pool using grain quality phenotypic plasticity to identify superior lines,
- validate grain quality (proxy) measurements further through sensory profiling,
- widen the breadth of phenotypic assessments of grain quality preferences by unraveling metabolic signatures, and
- associate various levels of phenotypic measurements with high-throughput genotypic data to mine the genome hot-spots related to grain quality (including sensory attributes) that would potentially lead to the identification of diagnostic markers reflecting consumer preferences. This integrative knowledge needs to be used in marker assisted selection and genomic selection technologies to hasten the progress in rice breeding pipelines.

Genetic variations in rice grain aroma and its contribution to premium quality

In certain markets, fragrance in rice is a highly valued characteristic (Buttery *et al.* 1983) [7], and thus aroma is treated as a premium trait. Aroma in rice grains, as indicated by the quantity of 2-acetyl-1-pyrroline (2-AP), is routinely tested by gas chromatographic (GC) approaches (Bergman *et al.* 2000; Grimm *et al.* 2001) [3, 14]. Probing aroma is carried out by (i) a GC-MS technique implemented to quantify volatile compounds contributing to aroma in rice (Bergman *et al.* 2000; Grimm *et al.* 2001; Maraval *et al.* 2008) [3, 14, 24] and (ii) sensory panel analysis to correlate aroma descriptors with the volatile composition of aromatic rice (Champagne *et al.* 2004; Yang *et al.* 2008a) [8, 35]. The popcorn-like smell of aromatic rice, mostly due to 2-AP, is a strong flavor that appeals to a wide consumer base (Buttery *et al.* 1983) [7]. The aroma attribute in rice is not just about 2-AP. Though 2AP predominates, it is accompanied by a wide array of other maillard reaction products depending on the levels of other metabolites in the genotype (Bradbury *et al.* 2008) [6]. Jasmine- and basmati-type rice both have 2-AP, but they have distinct sets of volatile compounds that make their aroma profiles distinguishable. 2-AP has the lowest reported odor threshold (0.02 ng L⁻¹ in air) among odorants found in six rice varieties (Yang *et al.* 2008b) [36], which explains the sensitivity of rice consumers to 2-AP and hence its association with high-quality rice. 2-AP is reported to be in raw grain as a precursor derived from metabolism [reviewed in (Bradbury *et al.* 2005; Fitzgerald *et al.* 2008)] [5, 13] and as by-product of cooking or heat processing of various food materials presumably through a Maillard reaction (Adams and De Kimpe 2006) [1].

The synthesis of 2-AP in one pathway is via the expression of the recessive for allele located on chromosome 8 (Bradbury *et al.* 2005; Lorieux *et al.* 1996) [5, 23]. The gene encodes an aldehyde dehydrogenase annotated as a betaine aldehyde dehydrogenase (BADH2) in indica (Bradbury *et al.* 2005) [5] and in japonica (Bourgis *et al.* 2008) [4] rice types. The dominant functional *Badh2* allele inhibits the synthesis of 2-AP by metabolizing γ -aminobutyraldehyde, the precursor of 2-AP, to γ -aminobutyric acid. The nonfunctional form of BADH2 is brought about by mutations of *fgr/badh2*, which lead in the most common allele to shifts in reading frame and premature transcription termination and then to a truncated BADH2 protein. Studies have mapped insertions, deletions, and polymorphisms resulting in the discovery of multiple alleles of *badh2* across the different subpopulations of rice (Amarawathi *et al.* 2008; Bourgis *et al.* 2008; Bradbury *et al.*

2005; Kovach *et al.* 2009; Myint *et al.* 2012) [2, 4, 5, 20, 26]. These reports identified *badh2* as the candidate locus responsible for aroma in japonica also, which presented exactly the same mutation as that identified in basmati and jasmine rice of indica varieties. It has been observed that *OsBADH2* is expressed constitutively with less expression in mature roots, and the disrupted *OsBADH2* leads to increased 2-acetyl-1-pyrroline production. Reports show that, aside from *fgr/badh2*, QTLs on chromosomes 3, 4, 8, and 12 are associated with 2-AP synthesis. *BADH1* is reportedly mapped on chromosome 4, and it has 15 exons and 14 introns. Rice varieties could be classified into four main SNP haplotypes. Haplotypes 3 and 4 translate to a potential decrease in or loss of substrate binding capacity of BADH1 protein and to the production of 2-AP akin to the mechanism of *badh2* (Singh *et al.* 2010) [29]. The synthesis of 2-AP can also occur without the involvement of either BADH1 or BADH2. In an alternate pathway, 2-AP synthesis in rice callus was associated with concentrations of Δ 1-pyrroline-5-carboxylic acid, through the activity of Δ 1-pyrroline-5-carboxylic acid synthetase (P5CS) and ornithine aminotransferase (OAT), and methylglyoxal. Enhanced activity of these enzymes was observed in calli of Tainung 71 and 72. P5CS is reportedly controlled by two genes: *P5CS1* and *P5CS2*, whose expression levels were significantly higher in aromatic rice than in non-aromatic rice. This contributes to the increase in P5C, thus leading to the accumulation of 2-AP. The close association of the enzymes involved in this stress response pathway may explain the preponderance of aromatic rice varieties that are susceptible to abiotic stresses.

Application of resequencing and high-throughput genotyping data for precision breeding to improve grain quality traits

Desirable variations in quality that have been lost during domestication can now be introduced into elite lines by targeted analysis of loci of interest from novel or wild germplasm (Krishnan *et al.* 2014) [21]. Resequencing of rice germplasm (Subbaiyan *et al.* 2012) [32]

allows the identification of the allelic variation found in key rice quality genes. The genes of starch metabolism have been early targets for this type of approach. More extensive analysis of diversity of all of these loci in the domesticated rice gene pool should provide an explanation for most if not all of the variation in rice quality traits related to starch composition and its influence on cooking quality. A study of the allelic variation in 18 starch metabolism genes in Australian rice breeding germplasm allowed association between specific alleles and rice starch properties to be established (Kharabian-Masouleh *et al.* 2012). Analysis of rice genotypes with differing combinations of alleles at each starch gene loci allows determination of the roles of each allele of each gene in determination of starch chemistry. Evaluation of the wider gene pool of wild rice relatives (Kasem *et al.* 2012) [17] may allow expansion of the range of starch types that can be bred to satisfy consumer demand. Differences in fine structure of starches from Asia and Africa have recently been defined. This insight should allow redesign of starches for a wider range of nutritional and functional consumer traits.

Ultimately, it should be possible to completely predict all of the starch properties of a rice breeding line by analysis of the DNA with highthroughput sequencing or genotyping tools. Associating the grain quality and sensory phenotyping data with highthroughput genetic markers by cloning high-value

genes from grain quality traits will remain pivotal. The beneficial alleles could be used to develop lines with superior grain quality. Understanding the contribution of these alleles and the interactions between them will require ongoing research but will be increasingly possible with the ongoing advances in sequencing technologies for efficient breeding of superior quality lines in high-yielding background. Advances in rice science have typically veered toward increasing food production to feed a growing population by focusing on replacing low-yielding varieties with higher yielding ones (Khush 2005) [19], as well as on addressing tolerance to biotic and abiotic stresses that are key drivers to increased rice productivity. A large number of breeders' materials are discarded if varieties do not meet requirements on yield potential, abiotic and biotic stress resistance, and ability to match quality preferences. A traditional pedigree breeding scheme adopted over decades in IRRI's breeding program resulted in generating advanced lines from the F2 to F7 generation with extensive screening of lines for optimizing yield and grain quality being checked at the end of pipeline (Collard and Mackill 2008; Khush 2001) [11, 18].

Grain quality screening starts at F5 for physical dimensions, chalkiness, amylose, and starch-modulated properties such as GC and gelatinization temperature. HRY analysis is done when yield testing commences, usually at F7. Despite these advances, attaining superior quality grains in the high-yielding background is lagging behind thus leaving farmers with varieties that, though high-yielding, are of sub-optimal commercial value because consumers find them unappealing to eat. These breeding materials could then be used to fine-tune the genetic gains and pyramid multi-trait grain quality targets in optimized high-yielding lines through precision breeding. Studying genomic landscapes of large number of hybrids and its corresponding inbred parents suggest that most indica hybrids possess superior alleles for higher potential for grain yield but with substantial disadvantages with grain quality attributes such as elevated chalk rate (Huang *et al.* 2015) [16]. Surprisingly, the yield advantage seen in hybrids could be related to few loci with heterotic phenomenon and larger contribution of more superior alleles within GWAS peaks of yield traits (Huang *et al.* 2015) [16]. These results shed interesting insights to the possibility of fixing the superior alleles of yield in inbred and fine-tune grain quality targets by introgressing major effect QTLs into important crop species through marker assisted selection (MAS). Progress made in the area of molecular breeding that address yield, biotic and abiotic stress tolerance, and grain quality is a key to ensure success in breeding (Rao *et al.* 2014). Cloned genes for disease resistance (*Pik*, *Pita*, and *Xa23*) and grain quality (*fgr*, *Wx*) were pyramided into elite lines that included Nipponbare japonica group) and Basmati 370 (*indica* group) cultivars. Submergence tolerance has been successfully conferred into mega-varieties with good grain quality background lines from India, Philippines, Laos, and Bangladesh.

Complex traits like yield and grain quality are influenced by not only major QTLs but also many minor effect genes or small-effect QTLs contribute in combination, which could be predicted by techniques such as genomic selection (GS). This emerging potential of GS technology is a special kind of MAS wherein all uncorrelated markers are used as predictors of the trait of interest and is believed to bring about highly accurate predictions with the right set of statistical methods addressing small-effect QTLs as well. The GS application in rice breeding has been successfully applied with the recent

available genomic resources to predict yield performance. This methodology resulted to a more accurate prediction of breeding line performance than pedigree data alone (Spindel *et al.* 2015) [31]. Further improvement of rice productivity and grain quality through breeding requires the combination of proven conventional breeding methods and genomic knowledge to break down linkage blocks and select favorable alleles for traits of interest. This approach enables structured breeding programs to develop top-quality lines through grain quality genomics knowledge within a minimal time. The use of modern approaches such as GS and MAS to estimate the genetic merit of candidate genotypes for the selection of key grain quality traits is required. Carefully selected superior lines for grain quality, high yield, and stress tolerance need to be used as parents to generate crosses to create desired recombinations among these superior lines with desirable grain quality alleles. This genetic gain could be systematically explored in breeding through the use of recurrent selection (RS), the MAGIC population, and GS (Varshney *et al.* 2014) [33]. This approach will help create stable high-yielding populations with desired grain quality traits. Through GS, the length of breeding cycles in both population improvement and line development could be shortened in order to achieve higher genetic gain in combining various quantitative traits, such as grain yield, stress tolerance, and quality. Furthermore, the development of high-throughput DNA markers enables the rapid introgression of major genes/QTLs (e.g., quality) via marker-assisted backcrossing and gene pyramiding. This allows the selection of key target loci in early generation breeding material through these cutting-edge aids to undertake genomic-estimated breeding. Such a systematic process identifies the link from grain quality to sensory attributes to define consumer preferences. These events enable breeders to tailor new varieties with superior grain quality fine-tuned according to consumer demand.

Conclusions and future outlook

Knowledge of the genes that control various grain quality attributes and the influence of the specific alleles present in domesticated rice gene pools provides a robust platform for marker-assisted selection in breeding to fine-tune grain quality traits in high-yielding genetic backgrounds. This kind of approach can be used to further explore sensory attributes of rice that are not currently measured in rice quality evaluation programs. Knowledge of all of the alleles in the rice gene pool at all of the loci influencing major quality traits is an achievable objective with the resequencing technologies be available to rice researchers. Alternative uses of rice and its processed by-products, and their corresponding quality requirements, have not

been explored as much as the quality parameters of milled rice. Hence, market research needs to be conducted to explore this area and determine the suitability of rice lines that have superior quality and nutritious rice grains for alternative uses. There is a growing demand for specialty foods such as those that cater to the health needs of people. The target of healthier traits to alleviate malnutrition in Asia and Africa includes high-amylose foods, suitable for alleviating type II diabetes; gluten-free protein-rich foods (for those with celiac disease or allergy to certain cereals); and foods enriched with micronutrients and antioxidants. Rice can potentially be used as an alternative ingredient in these aims. Demand is also increasing for nutritious rice by-products such as rice bran (processed into oil and food supplements, among other options) or its use in processed food products. We need to

create new state-of-the-art breeding programs to combine these “nutritious and premium” traits as part of grain quality traits to improve the health status of the Asian population.

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