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REVIEW

Prospects of breeding high-quality rice using post-genomic tools

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Abstract

Key message **The holistic understanding derived from integrating grain quality and sensory research outcomes in breeding high-quality rice in the light of post-genomics resources has been synthesized.**

Abstract 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 food quality.

Introduction

Rice (*Oryza sativa* L.) belongs to the family *Poaceae* and tribe *Oryzeae*. It has two cultivated species and 22 wild species and possesses huge diversity for grain quality traits. Market survey data suggest that efforts to develop varieties with improved cooking and eating quality have high economic returns (Son et al. 2014). Even though grain quality strongly drives the market value of rice (Dalton 2004), 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). Low- to moderate-yielding varieties that have the best organoleptic

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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). 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 (Calingacion et al. 2014). These quality classes are based on physical properties (head rice recovery, chalkiness, grain size and shape, and grain color) and starch quality influencing cooking and organoleptic properties (Champagne et al. 2010, 2004b; Fitzgerald et al. 2009b; Foegeding and Davis 2011; Juliano 1979, 2001; Juliano and Villareal 1993; Pandey et al. 2012; Siebenmorgen et al. 2013; Sreenivasulu et al. 2015). 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). Several methodologies for measuring rice quality indicators are established and are currently being used to screen rice breeding lines (i.e., Cagampang et al. 1973; Champagne et al. 2004b; Fitzgerald et al. 2009a; Mariotti et al. 2010; Vilaplana et al. 2012). However, in these assessments, individual grain quality traits are often considered separately rather than in a multi-dimensional holistic overview (Figs. 1, 2). Moreover, organoleptic parameters that influence consumer preferences are not entirely captured by current grain quality measurements made using physical and biochemical methods. For instance, several varieties that are within the same range of starch quality classes (Ayabe et al. 2009) can be further differentiated by rice consumers into premium and second-grade classes (Champagne et al. 2010). Sensory profiling that includes texture, organoleptic properties, and aroma is deemed important in certain market segments but is not fully implemented as a screening parameter in rice breeding because of the lack of high-throughput technologies. It is crucial in rice improvement programs to close this gap. Thus, the genetic and biochemical bases of sensory attributes need to be interlinked to the wide array of grain quality traits to help breeding programs to efficiently predict the quality of their newly developed breeding lines (Fig. 3).

Success in developing new food products has always been measured in terms of consumer acceptance. The holistic understanding that can be derived from integrating grain quality (physical and biochemical) and sensory (taste preferences) research outcomes in breeding high-quality rice in the light of the vast post-genomics resources available in rice has not been synthesized. In this review, we summarize the links from the genetics of rice grain quality to consumer preferences and propose to explore modern tools to

- 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.

Capturing grain quality phenotypic plasticity

Constant human intervention in grain traits has contributed to the domestication and diversification of Asian rice that is believed to have begun in southern China and in India (Fuller 2011; Huang et al. 2012). Rice may very well be the most diverse among food crops because varieties differ widely in cooking and organoleptic properties (Calpe 2003; Juliano 2001). This diversity in rice is exemplified by a large collection of 120,000 rice accessions maintained in the T.T. Chang Genetic Resources Center of the International Rice Research Institute (IRRI). Despite such diversity and IRRI's history of breeding for specific market niches and consumer needs, less than 5 % of these accessions are used in breeding programs (Sackville-Hamilton, personal communication, 2013).

Grain shape (measured as the grain length-to-width ratio) and starch-based qualities are the main properties used for selecting breeding lines based on quality attributes. Most mega-varieties in South Asia have been fixed at intermediate amylose and intermediate gelatinization temperature to meet the preference for non-sticky long slender grains (Calingacion et al. 2014). In Japan, Korea, and northern China, sticky, short, and bold rice with a length of 5.50 mm and length-to-width ratio of less than 2.0 is valued (Juliano and Villareal 1993). Systematic profiling of current breeding progress at IRRI in terms of grain quality was undertaken to find high-quality lines suitable for

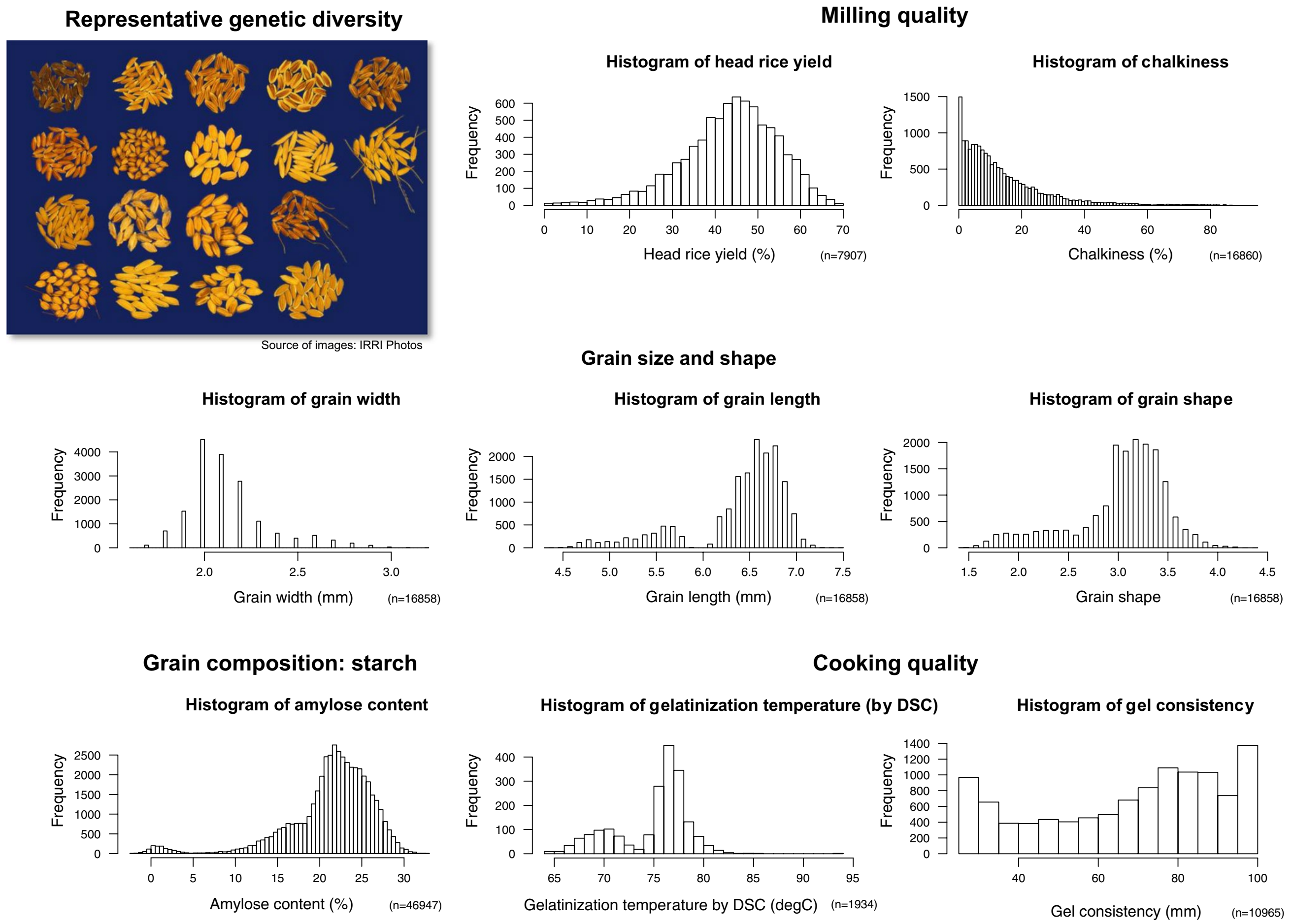

Fig. 1 Histograms of data taken from each of eight grain quality traits. The histogram of head rice yield shows the current average to be approximately 45 % and chalkiness to be mostly controlled within 0–15 %. The grain dimension and amylose content histograms reveal which target market drives most breeding programs at IRRI in terms of grain quality. The gelatinization temperature (GT) by differential scanning calorimetry (DSC) histogram reveals a bimodal distribution that roughly corresponds to low-GT and high-GT values. The gel consistency histogram reveals that a majority of consumers prefer rice that does not harden quickly upon cooling. (The *inset* shows images of paddy grains of selected accessions to illustrate diversity in grain morphology)

different market niches in South and Southeast Asia. To gain a comprehensive overview, 80,661 records of grain quality profiling of 13 grain quality parameters covering physical, biochemical, and cooking quality traits were considered from breeding materials. These lines show substantial genetic diversity for various grain quality traits (Fig. 1). The phenotypic measurements taken from 1500 landraces from the IRRI gene bank were added to the large collection of breeding materials to establish the progress of the current breeding pipelines. Furthermore, multiple pair-wise correlations of all pairs of variables from this very large dataset were performed to obtain inter-relationships between grain quality traits (Supplementary Fig. S1). This approach allows multiple combinatory variables to be evaluated as selection criteria for identifying lines with superior grain quality.

Physical dimensions and head rice yield

Grain quality phenotypic data assessment of physical traits shows that IRRI's breeding focus was on long and slender grains having grain length within the range 6.6–7.5 mm and grain length-to-width ratio greater than 3.0 (Fig. 1). Among physical traits, grain shape is positively correlated with grain length ($\rho = 0.75$). Those lines that are greater than 7.5 mm in length are basmati types. There is a negative correlation ($\rho = -0.47$) between grain length and grain width, implying that long grains (>7.5 mm) tend to be slender (grain shape >3.0) in this set of 17,000 samples (Supplementary Fig. S1). The major market segments in the world cover long non-sticky slender grains, those with length of 6.61 mm and length-to-width ratio of 3 and above, and these are preferred in the southern parts of India, Southeast

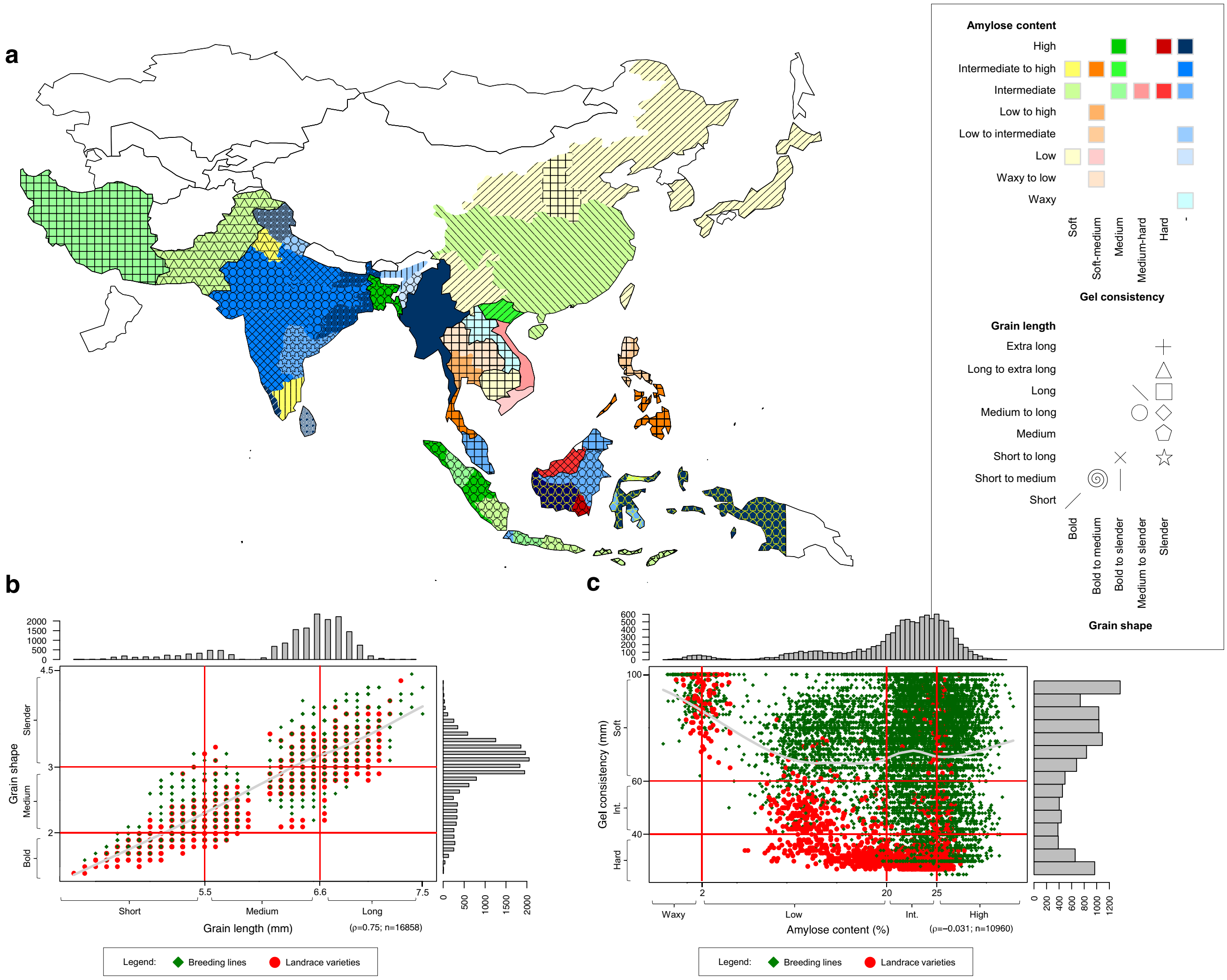

Fig. 2 Quality preferences for consumers in Asia identified based on a survey conducted for mega-varieties (Calingacion et al. 2014) have been used as a guide to map the breeding progress made at IRRI to target specific market niches in South Asia and Southeast Asia using combinatory traits between amylose content and gel consistency, as well as grain length and grain shape. Larger countries such as China and India have a more diverse range of consumer preferences

Asia, Europe, and the United States (Calingacion et al. 2014).

The average head rice yield (HRY) was low with 43.5 % from IRRI's breeding programs, and therefore this trait should be improved further as the prime target of future breeding by minimizing the broken grains during milling (Fig. 1). Interestingly, in breeding material, the mean chalkiness value was 13.9 %. Those lines with less than 10 % chalkiness have 45.5 % HRY. We did not observe any significant inverse relationship between HRY and chalkiness (see Supplemental Fig. S1). These observations made from a large collection of data contradict the existing notion that area of chalkiness substantially increases breakage during milling and thus decreases HRY (Lisle et al. 2000).

Biases may arise in estimating chalkiness in rice seeds using the current imaging technology that is used to process milled grains. The current automated method for assessing chalkiness in rice grain uses a Cervitec 1625 Grain Inspector (Foss Tecator, Sweden) that measures translucency of the milled endosperm from the whole grain. Broken grains are not included to avoid clogging the notches on the wheel of the imager. This sampling bias has the potential to underestimate the proportion of chalky grains because chalky broken grains are discarded prior to the actual measurement. To address this concern, newer imaging and visualization methods are being developed to accurately quantify chalk and broken grains in rice (Kaur and Singh 2013; Liu 2011; Mingyin et al. 2010; Verma 2010) in order to

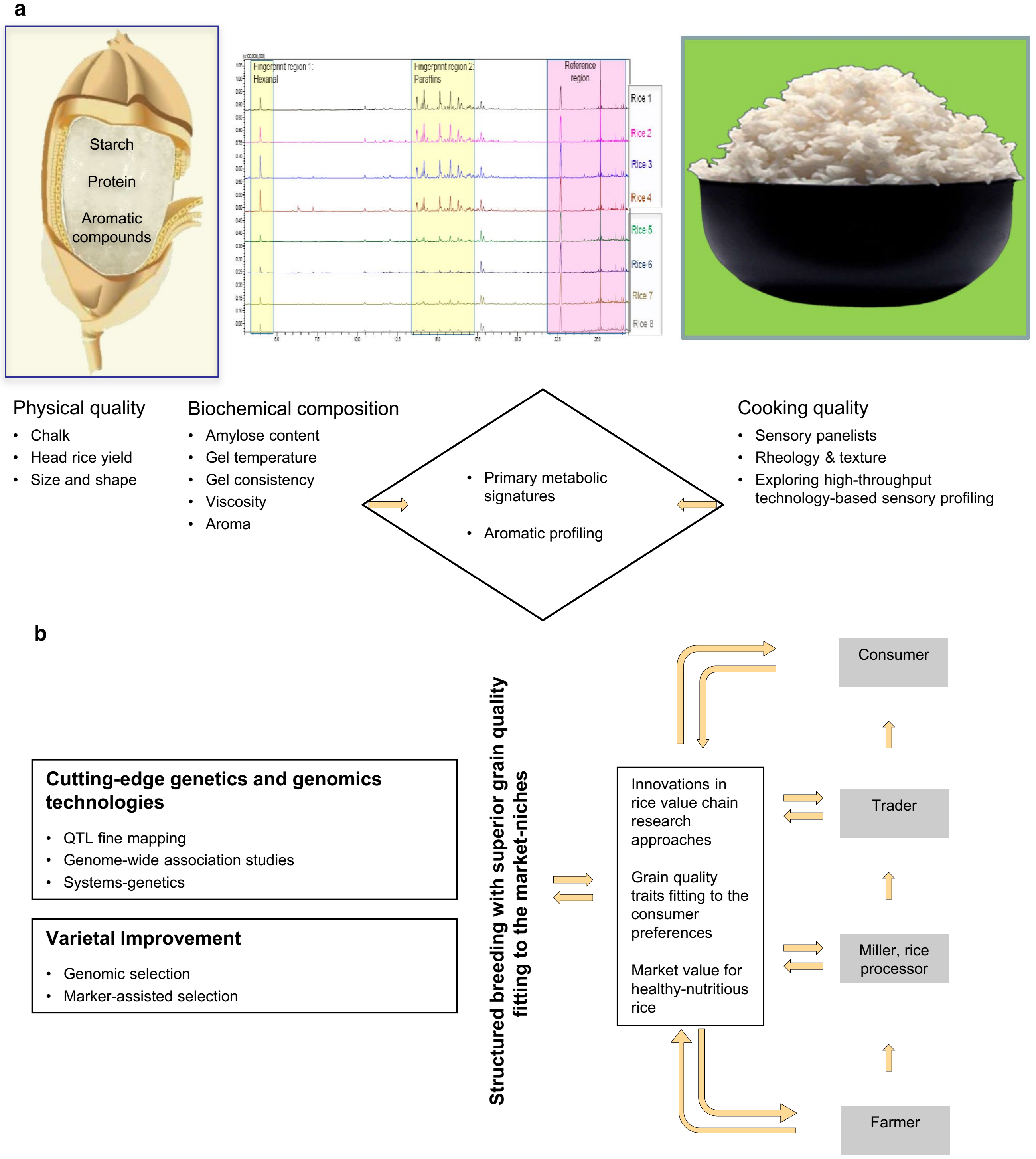

Fig. 3 Multi-layered phenotyping tools covering traditional grain quality attributes reflecting physical and biochemical traits to capture sensory preferences and the use of metabolomics platforms to capture the metabolic fingerprints of primary metabolism and volatiles from mature grain and cooked rice grain. Associating multi-layered phenotypic measures with genotypic data through genetics helps unravel quality preferences (**a**). Schematic representation of the present perspectives of the genomics revolution in breeding to explore the potential of existing intraspecific variation (**b**)

improve the correlation between chalkiness and head rice recovery.

Starch quality inferences related to cooking and taste properties

Milled rice grain is composed of 90 % starch, which makes it a key contributing factor for many grain quality attributes. Starch is composed of two homopolymers: (a) amylose, which is composed of long linear chains of α-1,4-linked glucose units with a few α-1,6 branches; and (b) amylopectin, which is believed to be organized into blocklets [it has shorter glucan chains attached by more branch points of α-1,6 glycosidic bonds (Kowittaya and Lumdubwong 2014)], with amylose molecules filling the spaces surrounding these blocklets (Ridout et al. 2006; Tang et al. 2006). The properties of these two starch polymers are associated with the cooking and eating quality of rice, routinely indicated by apparent amylose content (AC), gelatinization temperature (GT), and gel consistency (GC). Rice varieties are grouped into defined quality ideotypes based on the different combinations of these three traits.

An inspection of the large breeding collection of IRRI material reflects that breeders mostly breed for intermediate- to high-amylose varieties. Rice that cooks relatively fast and remains soft upon cooling is a desirable trait to lower cooking energy, and this has been successfully implemented in breeding, as indicated by the significant proportion (47 % for intermediate class and 33 % for low/intermediate) belonging to low to intermediate GT (Fig. 1). Rice samples with low-GT values showed a bimodal distribution of amylose ranging from intermediate to higher values (see Supplementary Fig. S2). These results suggest that some breeding programs aimed to have high-amylose rice varieties with low to intermediate GT.

High-amylose varieties are distributed across all GC categories (Fig. 2). It is interesting to note that, for pre-breeding lines obtained from the IRRI gene bank, a number of low-amylose lines (AC ranging from 10 to 15 %) were noted to have hard GC. For this same range of amylose classes, breeding lines are already in the vicinity of soft GC. Early on, most of the high-yielding varieties developed by breeders were of the high-amylose type such as IR8 and IR5. Further improvement in these high-yielding varieties by conventional breeding through the years has led to a mix of diverse lines with contrasting traits (such as high-AC rice with both hard and soft GC, etc.). These observations show that some high-amylose varieties remain relatively soft upon cooling. These findings suggest that breeders were able to come up with more high-amylose lines that are “soft” (GC >61 mm) than “flaky” (GC ranging from 41 to 60 mm).

In summary, consumers’ preferences for several quality classes from different market niches for grain size and shape and biochemical parameters (AC, GC, and GT properties) that are associated with cooking properties within non-sticky long slender grains could be captured within the breeding pool of IRRI by multi-dimensional grain quality inferences. Within the IRRI breeding material, (i) we identified a large set of lines fixed at intermediate amylose and intermediate GT reflecting the matching quality suite of a mega-variety such as IR64 likely to cater to the grain quality preferences of Southeast Asia, and (ii) we also captured high-amylose lines (suited for Bangladesh and the northern and western part of India) with hard GT and GC, as well as (iii) high-amylose lines with intermediate GT and GC to meet the preferences of the Middle East and Indonesia.

Advances made in correlation methods and data analysis techniques made it feasible to obtain comprehensive information from a grain quality matrix by analyzing diversity from breeding pipelines. This provides a robust platform to move from single-dimensional traits to multi-dimensional association traits to infer grain quality insights. Although numerous rice quality measures are in place, a gap still exists between how scientists quantify and understand quality through genetic means and how consumers describe the sensory experience of eating cooked rice (Zader 2011). Such a gap could exist because of the trait-wise approach used in understanding quality. In addition, suitable methods have not yet been developed to match consumer vocabulary to textural attributes, thus presenting another huge gap in quality evaluation programs because of routine physico-chemical properties. Varieties that have similar measures of quality in terms of AC, protein content, and GT may still be strongly distinguishable by consumers through taste (Champagne et al. 2010). In our breeding stocks, more than 10,000 lines similarly have intermediate amylose and intermediate GC (Fig. 2c), but with possibly differing organoleptic properties. Only a very few of them will be released as new varieties to meet specific consumer preferences. We need to close this gap between quality evaluation parameters and what people sense as they eat rice by understanding organoleptic properties.

Sensory evaluation as an additional phenotyping tool for selection in breeding high-quality rice

Sensory evaluation has not yet been optimized as a routine tool in rice improvement programs because of its current limitations as being tedious, highly subjective, and overly time-consuming. Here, we update the sensory evaluation methodologies applicable to rice breeding (Box 1) and review the limitations of sensory evaluation in a product development context. We summarize inferences from previously reported associations of organoleptic attributes with grain quality indicators.

Box1: sensory evaluation methodologies

Various classes of methodologies are used in conducting sensory evaluation by a set of panelists, which includes affective tests, discrimination tests, and descriptive profiling. Affective tests deal mainly with measuring the acceptability of a product or a consumer's degree of liking or preference. In the rice breeding context, affective testing may come in the form of participatory varietal selection (PVS). PVS elicits farmers' preferences in evaluating newly developed breeders' lines, and it has been applied by IRRI in nine countries in South and Southeast Asia and African breeding programs. For example, results for sensory evaluation (preference and acceptability) have been reported in four countries where the quality of submergence-tolerant rice mega-varieties was evaluated (Manzanilla et al. 2013). Affective tests can also be applied in measuring the acceptance of rice products by non-farmer rice consumers (Kam et al. 2012; Kaminski et al. 2013; Kwak et al. 2013) and to identify preference, purchase intent, acceptability, and attribute intensity perception (Meilgaard et al. 2007). Although these responses are highly subjective, they are heavily relied upon to determine the needs of target consumers in assessing the potential market demand for new products.

Discrimination tests are conducted to determine whether there are perceptible differences between samples and attributes that contribute to differentiation between samples. These types of tests can be conducted to determine whether panelists can differentiate between products of slightly different formulations or to determine whether panelists can perceive changes in processing methods. These tests have been previously applied to determine rice fortification efforts (Beinner et al. 2010; Moretti et al. 2006; Shrestha et al. 2003). In rice breeding programs, discrimination tests can be used similarly as in industry-oriented product development programs to determine whether new breeding lines are perceivably similar to or different from quality benchmarks.

Descriptive tests are conducted to describe products based on different attributes and their intensities. Descriptive profiling is normally conducted to determine the sensory profiles of different products, which can be compared with those of other brands or with the profiles of product benchmarks and references (Meilgaard et al. 2007). Once a lexicon is developed, this can be used not only for characterization purposes but also as a screening tool for determining the organoleptic properties of new rice materials. Descriptive profiling is therefore particularly useful in rice breeding programs in which descriptions of new products play a decisive role, particularly when there are no established quality benchmarks. In addition, descriptive profiling can be used to distinguish rice samples within the same quality class.

Case studies of sensory evaluation in rice breeding

The factors that affect acceptability of rice include raw grain attributes for which buying is initially influenced by grain size, shape, and translucency (Tomlins et al. 2007). Consumers then proceed to assess rice quality after the grains have been cooked. In a survey participated in by consumers from different countries, it was determined that consumers differentiate rice varieties based on hardness, stickiness, color, and aroma of cooked grain (Suwannaporn and Linnemann 2008). These are the easily perceivable traits that can be correlated with instrument-based approaches that are guaranteed to give objective and reproducible results. For instance, studies have looked into the correlations between instrument measurements and sensory perceptions of texture [i.e., hardness (Perez et al. 1993; Sowbhagya et al. 1987)]. In the past, efforts have been made to understand the effects of environmental variations between cropping seasons, the effects of genotype, the effects of post-harvest practices, the effects of cooking methods, and the effects of serving temperature on the sensory quality of cooked rice (Champagne et al. 1999, 1997, 2004a; Meullenet et al. 2000; Yau and Huang 1996). Associations between the chemical composition of the rice grain and the texture of cooked rice (Gonzalez et al. 2004; Ramesh et al. 1999; Singh et al. 2005) as well as those between 2-AP levels and the pandan-like or popcorn-like aroma in rice are established (Buttery et al. 1988; Grimm et al. 2001). Studies have shown that rice with similar AC may have different textural properties (Champagne et al. 2010, 1999), while fragrant rice samples containing 2-AP could have distinct aroma profiles because of the presence and varying concentrations of other volatile compounds (Fitzgerald et al. 2009a; Mahattanatawee and Rouseff 2014; Mathure et al. 2014). Thus, it is crucial in rice improvement programs to close the gap between biochemical bases of cooking quality (as proxy traits) and sensory attributes, which can ultimately help breeding programs predict the quality of their newly developed breeding lines.

Sensory evaluation is a highly valuable tool in rice breeding for selecting high-quality rice lines. As of now, sensory evaluation is conducted only on advanced breeding material to be released to farmers and we continue to rely on proxy measures of grain quality attributes as a screening tool to test early generation material. The wider application of sensory evaluation in rice breeding programs is yet to be seen because sensory evaluation is slow, tedious, subjective, and costly (Chen and Opara 2013). To address the limited application of sensory evaluation, we need to explore the option of using instrument-based methods for attributes that can increase throughput and be quantified and compared with sensory evaluation data with fewer panel biases.

Naive rice eaters normally describe cooked rice quality with dichotomies such as hard/soft and sticky/not sticky (Suwannaporn and Linnemann 2008). In contrast, the lexicon developed by sensory rice scientists proves that a rice eater's vocabulary has the potential to expand to more than 20 flavor notes (Bett-Garber et al. 2012; Limpawattana and Shewfelt 2010) and to at least 10 textural attributes (Bett-Garber et al. 2001; Goodwin et al. 1996). Numerous attributes and adjectives can be used to describe the flavor and *mouth–feel* characteristics of cooked rice (Goodwin et al. 1996; Limpawattana and Shewfelt 2010). Most of these are left unarticulated by consumers but possibly influence consumer preferences and quality grading of rice samples (Champagne et al. 2010). Identifying and understanding these subtle sensory attributes shaping consumer purchase decisions (i.e., consumer preference) are important in increasing market share (Thompson et al. 2004) and in maximizing farmer adoption of new rice varieties because of the value-added characteristics. Hence, appropriate care needs to be taken to build the panel for descriptive profiling or discrimination tests, and their performance needs to be constantly monitored (Meilgaard et al. 2007; Stone et al. 2012).

The relationship between data derived by instrumental techniques and sensory evaluation has been studied. Firmness and elastic recovery, measured by the Chopin-INRA Viscoelastograph, were reported to be negatively correlated with tenderness, moisture, and stickiness (Sowbhagya et al. 1987), while Instron measurements of hardness were positively correlated with sensory scores (Perez et al. 1993). In contrast, Rapid Visco Analyzer (RVA) data were not associated with textural parameters evaluated via instrumental texture profile analyses or descriptive sensory evaluation (Champagne et al. 1999). On the other hand, near-infrared spectroscopy (NIR), a technique already used to rapidly measure quality for different cereals (Barton et al. 1998), was shown to be able to predict initial tactile and oral parameters such as stickiness, hardness, manual and visual adhesiveness, initial starchy coating, surface slickness, and roughness of cooked rice (Lapcharoensuk and Sirisomboon 2014; Windham et al. 1997). Apart from these existing technologies, scientists are looking into simulations of human perceptions, such as eye-tracking software and the use of electric noses and tongues. These instruments have been applied to food products with strong flavors, such as coffee and wine, and have seen limited application as of now in materials with subtler flavors, such as rice. Olfactometers attached to gas chromatography equipment can be used to describe individual volatile compounds that are detected in different samples. Through GC–olfactometry, numerous volatiles were determined to contribute to the aroma of cooked grains of different rice varieties (Bryant and McClung 2011; Mahattanatawee and Rouseff 2014; Maraval et al. 2008). In rice, the e-nose and e-tongue have yet to see wider application; however, the e-nose has been reported to be sensitive to volatile differences between parboiled rice and non-parboiled rice obtained from the market (Zheng et al. 2009). To improve rice breeding programs, it is better to ensure that instrument-based assessments and sensory evaluation techniques complement each other in developing new rice lines with premium quality. Such combinatory technologies could be applied to a carefully selected core collection representing the highest diversity within the breeding pool.

Metabolic fingerprinting to capture grain quality preferences in breeding

Large datasets have been reported in assessing the heritability of metabolites using metabolite (m)-QTL analysis to identify the molecular background of quality traits using predictive models and to unravel health and nutritional benefits (Heuberger et al. 2010; Liu et al. 2013; Matsuda et al. 2012; Redestig et al. 2011). Implementation of multivariate dimension reduction techniques (MVDRT) such as principal component analysis, artificial neural networks, and correlation measures to process metabolomics data to predict quality may help identify phenotypic trends (Redestig et al. 2011). Overlaying this phenotypic plasticity with genotyping data (SNP matrix) of the population helps relate the genetic structure of the population with observed phenotypic divergence using MVDRT and STRUCTURE programs (Heuberger et al. 2010). These strategies help (i) capture the phenotypic plasticity and thereby overcome the narrow genetic diversity observed in breeding programs due to long domestication history and (ii) allow the investigation of combinatory multiple variables as selection criteria for identifying lines with superior grain quality within a core collection (Fig. 3). Lines with distinct features of contrasting grain quality exhibiting the highest genetic diversity within breeding pipelines of core collections could be subjected to fingerprinting defining the metabolic signatures to derive metabolome-grain quality predictive models.

This unique approach has been implemented to derive predictive metabolome-trait models in a core collection of 68 diverse rice varieties (subtypes indica and japonica) to relate the quantitative metabolome data obtained from the multiple platforms of gas chromatography (GC) or liquid chromatography (LC) to various grain quality attributes

(Redestig et al. 2011). Screening the trait-associated metabolites using Spearman's correlation (Redestig et al. 2011) suggests the presence of a feedback control with the composition of starch (amylose) and starch-bound fatty acids influencing physicochemical properties of the rice grain. The quantitative phenotypic data obtained from 759 metabolite signals from a mapping population (backcrossed inbred lines derived from Sasanishiki × Habataki) were used to calculate the mQTL loci. The hot-spot genetic region encodes genes for amino acids and triacyl glycerol clustered in a region on chromosome 3 (Matsuda et al. 2012). The large number of metabolic traits is affected by environmental factors, and thus validation of the stability of these traits will remain important. From this perspective, it will be interesting to discover the metabolome responses of developing seeds during the peak of seed filling to understand the genetic background of metabolite association with grain quality traits.

In addition to the value of grain quality attributes, there is a need to enhance health and nutritional benefits in rice through the application of systematic metabolite profiling of secondary metabolism in breeding. Ten varieties belonging to three cluster groups (indica, japonica, and aus) were identified based on genotype clustering, and their cooked grains were profiled for phenolic compounds and tocopherol using a UPLC-MS system. Aus and japonica subtypes contained higher levels of total phenolics than indica (Heuberger et al. 2010). In contrast, popular breeding material, IR64 from indica and Nipponbare from japonica, exhibited lower nutritional value in terms of total phenolics (Heuberger et al. 2010). The mQTL inferences drawn from germinating seeds of rice identified the genetic basis of the nutritionally important flavonoid pathway and linked the functional relevance to Os11g26950 and Os07g01020 genes (Gong et al. 2013). In addition, mQTL results unraveled the importance of flavones from secondary metabolism in rice (Matsuda et al. 2012). Many metabolites derived from secondary metabolism in mature grains are more stable than ones derived from primary metabolism. In summary, exploring the use of different complementary analytical techniques is highly recommended (i) to capture the metabolic signatures of primary as well as secondary metabolites and (ii) to analyze the spectrum of volatiles from mature grain and cooked rice to infer food quality (Box 2).

Box2: overcoming technical limitations of metabolomics to address grain quality research

Studies reported in this review demonstrated the useful approach of metabolomics platforms to gain inferences by characterizing germplasm with highly diverse lines or mapping populations by relating the quantitative metabolome response to achieve the breakdown of complex grain quality traits (Calingacion et al. 2012; Heuberger et al. 2010; Matsuda et al. 2012; Redestig et al. 2011). Nevertheless, appropriate care needs to be implemented to obtain meaningful biological insights. This includes considering the size of the populations, identifying false-positive correlations by removing the low-heritability metabolites from genotype–phenotype associations, and overcoming technological limitations using combinatory metabolomics platforms.

Among the available mass analyzer platforms, a gas chromatograph with a mass spectrometry detector (GC–MS) is the most widely used platform so far to analyze metabolic responses of rice grain and cooked samples. This allows monitoring of hundreds of metabolites, including volatile compounds (without the feasibility of quantification). The sensitivity of GC–MS for the analysis of volatiles in rice can now be improved by techniques that require little or no sample preparation. Direct and automated methods such as static headspace sampling, dynamic headspace sampling, and solid phase micro extraction (SPME) can be used to determine volatiles from samples without the use of any solvent. The sensitivity in the SPME mode was better than with headspace for the detection of 2-AP and most of the other volatile metabolites (unpublished data). It is known that a host of other volatile compounds may contribute to the distinct aroma and taste of certain rice varieties. GC–MS can be used to identify these other volatiles associated with the distinct sensory traits of some rice varieties. However, GC–MS using full scan (FS) has sensitivity limitations, especially for trace amounts of small molecules such as the flavor compounds found in rice. GC–MS using selected ion monitoring (SIM) can help improve sensitivity, but small molecules such as some of the volatile compounds found in rice are likely to fragment into smaller ions that are usually common to both analyte and matrix. Hence, SIM is likewise susceptible to ion interferences from the matrix.

As part of technology advancement, a novel high-throughput analytical method has been developed for metabolomics using gas chromatography coupled with triple-quadrupole mass spectrometry (GC-QqQ/MS). The main advantage lies in its capability for both untargeted metabolites profiling as well as for accurate quantification of hundreds of targeted metabolites in one GC-QqQ/MS run. Using the selected reaction monitoring (SRM) or multiple reaction monitoring (MRM) of unique and timed precursor ion-product ion transitions for metabolites of interest, interferences from noise are eliminated, and intensity ratios of differentially expressed metabolites in diverse rice species can be accurately measured (Matthews et al. 2014). These platforms have potential to contribute to biomarker discoveries and quality evaluations in food science and technology (Tsugawa et al. 2014).

Interfacing rice grain quality genetics with sensory knowledge

In market-driven product development, associating multiple parameters of grain quality, including sensory attributes at a genetic level, can enable breeders to tailor new varieties according to consumer demand (Fig. 3). Exploration of rice grain quality traits and sensory properties at the genetic level requires the identification and fine mapping of quantitative trait loci (QTL) of true quality indicators. Exploring genetic diversity using a bi-parental mapping population resulted in the identification of more than 600 grain quality QTLs in rice, which can be browsed in the Gramene grass-genome database (http://www.gramene.org). The most important trends in the research of linking sensory properties to grain quality metrics lie in the deeper understanding of the starch structures, the biochemistry, and the rice grain components which alter under stress prone environments that affect consumer perceptions (Cuevas et al. 2010b; Mestres et al. 2011). This paradigm encompasses (i) the genetic associations between grain quality indicators and cooking and textural properties; (ii) identifying the overlapping genetic hot-spots for grain quality and sensory traits; and (iii) the genetic contributors of rice grain components that contribute to the quality of the aroma.

Associating grain quality genetics with texture and cooking properties

Consumers articulate the quality of cooked rice texture mainly based on hardness (or firmness) and stickiness (Suwannaporn and Linnemann 2008). Although magnitudes of textural attributes such as hardness and stickiness can be identified via a sensory panel, these mechanical properties can be quantified only via instrument-based approaches. Associations between the chemical composition of the rice grain and texture of cooked rice have been reported (Gonzalez et al. 2004; Ramesh et al. 1999; Singh et al. 2005). For instance, stickiness is negatively correlated to AC, while firmness attributes are positively correlated to AC (Mestres et al. 2011; Perez et al. 1979). Currently, 51 QTLs for AC have been mapped across many chromosomes, but the major QTL identified so far has been fine mapped on chromosome 6 and is linked to the granule-bound starch synthase 1 (*GBSS 1* or *Wx*) gene, which is associated with amylose synthesis and cooking properties (Septiningsih et al. 2003; Su et al. 2011; Tan et al. 1999; Tran et al. 2011). Additional QTLs located on different chromosomes are also associated with the functional properties of the cooked grain (GC and GT), and this requires further attention (Aluko et al. 2004; Sabouri et al. 2012; Sun et al. 2006). Chain-length distributions have been associated with starch synthase IIa (SSIIa), the enzyme responsible for elongating the chains within the crystalline lamella (Nakamura et al. 2005; Umemoto et al. 2004). Functional single-nucleotide polymorphisms in the *SSIIa* gene (on chromosome 6) have been identified and can be used to group rice samples into high- and low-GT classes (Cuevas et al. 2010a; Nakamura et al. 2005; Waters et al. 2006). Aside from linking *SSIIa* to GT (Cuevas and Fitzgerald 2012), QTLs for GT have been reported from other rice chromosomes in different populations (He et al. 2006; Lanceras et al. 2000; Sabouri et al. 2012). The roles of the enzymatic processes originating from these QTLs have not been elucidated yet. Genetic factors other than *SSIIa* alleles, such as those that code for enzymes involved in amylopectin chain termination, that is, starch branching enzymes (Butardo et al. 2011; Castro et al. 2005), may be responsible for the development of intermediate-GT rice commonly found in Philippine rice materials (Juliano et al. 2009).

Genetic hot-spot regions overlapping for grain quality and sensory attributes

The genetic understanding of sensory attributes can ultimately help breeding programs predict the quality of their newly developed breeding lines. Relatively high-throughput biochemical indicators of rice cooking and eating quality such as AC, GC, and viscosity profiles need to be associated with various textural attributes of cooked rice grains (Cagampang et al. 1973; Champagne et al. 1999; Perez et al. 1979). Associations of grain quality indicators and sensory attributes through genetic means have been addressed by studying 192 recombinant inbred populations, which resulted in identifying 21 QTLs on chromosomes 1, 4, 6, 7, 8, and 11. Among these, chromosome 8 represents a hot-spot for QTLs representing both sensory taste and grain quality parameters such as AC, protein content, alkali digestion, and glossiness of cooked rice (Kwon et al. 2011). The QTL map indicated 132 stable genetic regions in eight environments for percentage grain chalk, area of chalky endosperm, amylose content, protein content, viscosity properties, and the integrated values of organoleptic evaluation (Liu et al. 2011). As a result, the stable and major QTL cluster on chromosome 8 was emphasized as the main genetic basis for the traits of rice chalkiness, amylose, protein, and eating quality of cooked rice (Liu et al. 2011). It therefore appears that this QTL cluster is a novel gene resource for controlling rice grain quality traits. Map-based cloning of some of the genes underlying these important traits needs to be conducted to support improvement of these traits.

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), 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). 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) and (ii) sensory panel analysis to correlate aroma descriptors with the volatile composition of aromatic rice (Champagne et al. 2004a; Yang et al. 2008a). Although a mixture of more than a 100 compounds that contribute to the aroma of rice have been identified in the flavor of cooked rice (Tsugita 1985; Widjaja et al. 1996), many of them may not contribute to consumer acceptance. 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). 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. 2008b). 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 $\eta g\ L^{-1}$ in air) among odorants found in six rice varieties (Yang et al. 2008b), which explains the sensitivity of rice consumers to 2-AP and hence its association with high-quality rice (Juliano et al. 1990). While distinguishing aromatic rice from non-aromatic rice, alcohols, aldehydes, ketones, furans, esters, and other potentially aroma-inducing compounds were found in cooked and uncooked rice (Fig. 3) (Bryant and McClung 2011; Calingacion et al. 2012; Yang et al. 2008a, b; Zheng et al. 2009).

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)] and as by-product of cooking or heat processing of various food materials presumably through a Maillard reaction (Adams and De Kimpe 2006). The synthesis of 2-AP in one pathway is via the expression of the recessive *fgr* allele located on chromosome 8 (Bradbury et al. 2005; Lorieux et al. 1996). The gene encodes an aldehyde dehydrogenase annotated as a betaine aldehyde dehydrogenase (*BADH2*) in indica (Bradbury et al. 2005) and in japonica (Bourgis et al. 2008) 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 (Bradbury et al. 2008a; Chen et al. 2008). On the other hand, the loss of function of BADH2 allows an accumulation of the precursor and triggers the synthesis of 2-AP (Bradbury et al. 2008a), and thus several haplotypes have been identified based on SNP (Jin et al. 2003) and microsatellite markers associated with loss of BADH2 function (Cordeiro et al. 2002). 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; Niu et al. 2008; Shao et al. 2011; Shi et al. 2008). 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 (Niu et al. 2008). Reports show that, aside from *fgr*/*badh2*, QTLs on chromosomes 3, 4, 8, and 12 (Amarawathi et al. 2008; Lorieux et al. 1996) 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).

The synthesis of 2-AP can also occur without the involvement of either BADH1 or BADH2. In an alternate pathway (Huang et al. 2008), 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 (Bradbury et al. 2005; Fitzgerald et al. 2008, 2010; Huang et al. 2008).

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

Although the identification of major grain quality QTLs (refer above) including the development of the first set of molecular markers for aroma (Ahn et al. 1992) and AC (Shimada et al. 1993) was achieved in the last decade, the identified major haplotypes has not been systematically explored in breeding applications via marker-assisted selection to develop lines with superior rice grain quality in high-yielding background. In this context, genome-wide association studies (GWAS) provide a promising tool for fine mapping of the major QTLs underlying complex traits of grain quality from untapped germplasm (Bandillo et al. 2013). The available post-genomics tools can be applied to clone both major and minor grain quality QTLs at a high-throughput level to unravel allelic variations caused by these polymorphisms. As the costs of genome sequencing continue to drop, this will become an attractive way to define all of the variation in plant genomes (Edwards et al. 2012; Li et al. 2014) and will provide the tools required to identify many other genes responsible for wider volatile compounds (beyond 2-acetyl-1-pyrroline) influencing distinct aroma differentiating between jasmine and basmati type. The resulting accumulation of the substrate, 4-aminobutyraldehyde allows reaction of this compound with other metabolites to form a wide range of compounds in different genotypes. 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).

Resequencing of rice germplasm (Subbaiyan et al. 2012) 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 (Kharabian-Masouleh et al. 2011). 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 (Kharabian-Masouleh et al. 2011; Wang et al. 2014; Waters et al. 2006). Evaluation of the wider gene pool of wild rice relatives (Kasem et al. 2012) 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 high-throughput sequencing or genotyping tools. Associating the grain quality and sensory phenotyping data with high-throughput 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), 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 F_2 to F_7 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). Grain quality screening starts at F_5 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 F_7. 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). 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). 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 (Luo et al. 2014). Submergence tolerance has been successfully conferred into mega-varieties with good grain quality background lines from India, Philippines, Laos, and Bangladesh (Septiningsih et al. 2009).

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 (Heffner et al. 2009; Jannink et al. 2010). 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). 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). 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 and sensory) 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

An essential component to improve the efficiency of breeding operations is to integrate multi-tiered fingerprinting data (grain quality, sensory, and metabolome inferences) from breeding material with the underpinning value of genetics and genomics to ensure the breeding of mega-varieties with superior grain quality and optimum yield. This holistic approach helps (i) identify and measure the sensory attribute of interest, (ii) relate quality indicators associated with the sensory attribute in a high-throughput manner, and (iii) trace the metabolic pathways leading to the grain quality associations. The genetic linkages derived from multi-tiered phenotypic data covering metabolic (m-QTL) and overlaying genetic information with quality preferences (grain quality and sensory, as g-QTLs) are used to identify valuable markers reflecting consumers' choices. 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 re-sequencing 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. The integration of this set of metrics is expected to generate a breakthrough in our understanding of the economics of rice quality by identifying quality cues that drive the value chain throughout

Southeast Asia. With this approach, a thorough understanding can be gained of (i) how rice quality is perceived and experienced by various actors throughout the value chain (farmers, traders, processors, wholesalers, retailers, exporters, consumers, and others), across socioeconomic classes, and (ii) how rice quality with a focus on improving healthy and nutritious traits can be deployed as an "engine" to upgrade rice value chains in Southeast Asia.

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References

Adams A, De Kimpe NG (2006) Chemistry of 2-acetyl-1-pyrroline, 6-acetyl-1,2,3,4-tetrahydropyridine, 2-acetyl-2-thiazoline, and 5-acetyl-2,3-dihydro-4H-thiazine: extraordinary Maillard flavor compounds. Chem Rev 106:2299–2319

Ahn S-N, Bollich CN, Tanksley SD (1992) RFLP tagging of a gene for aroma in rice. Theor Appl Genet 84:825–828

Aluko G, Martinez C, Tohme J, Castano C, Bergman CJ, Oard JH (2004) QTL mapping of grain quality traits from the interspecific cross *Oryza sativa* × *O. glaberrima*. Theor Appl Genet 109:630–639

Amarawathi Y, Singh R, Singh A, Singh V, Mohapatra T, Sharma T, Singh NK (2008) Mapping of quantitative trait loci for basmati quality traits in rice (*Oryza sativa* L.). Mol Breed 21:49–65

Ayabe S, Kasai M, Ohishi K, Hate K (2009) Textural properties and structures of starches from indica and japonica rice with similar amylose content. Food Sci Technol Res 15:299–306

Bandillo N, Raghavan C, Muyco PA, Sevilla MA, Lobina IT, Dilla-Ermita CJ, Tung CW, McCouch S, Thomson M, Mauleon R, Singh RK, Gregorio G, Redona E, Leung H (2013) Multi-parent advanced generation inter-cross (MAGIC) populations in rice: progress and potential for genetics research and breeding. Rice 6:11

Barton FE, Windham WR, Champagne ET, Lyon BG (1998) Optimal geometries for the development of rice quality spectroscopic chemometric models. Cereal Chem 75:315–319

Beinner MA, Velasquez-Melendez G, Pessoa MC, Greiner T (2010) Iron-fortified rice is as efficacious as supplemental iron drops in infants and young children. J Nutr 140:49–53

Bergman CJ, Delgado JT, Bryant RJ, Grimm CC, Cadwallader KR, Webb BD (2000) Rapid gas chromatographic technique for quantifying 2-acetyl-1-pyrroline and hexanal in rice (*Oryza sativa* L.). Cereal Chem 77:454–458

Bett-Garber KL, Champagne ET, McClung AM, Moldenhauer KA, Linscombe S, McKenzie KS (2001) Categorizing rice cultivars based on cluster analysis of amylose content, protein content, and sensory attributes. Cereal Chem 78:551–558

Bett-Garber KL, Lea J, Champagne ET, McClung AM (2012) Whole-grain rice flavor associated with assorted bran colors. J Sens Stud 27:78–86

Bourgis F, Guyot R, Gherbi H, Tailliez E, Amabile I, Salse J, Lorieux M, Delseny M, Ghesquiere A (2008) Characterization of the major fragrance gene from an aromatic japonica rice and analysis of its diversity in Asian cultivated rice. Theor Appl Genet 117:353–368

Bradbury LMT, Fitzgerald TL, Henry RJ, Jin Q, Waters DLE (2005) The gene for fragrance in rice. Plant Biotechnol J 3:363–370

Bradbury LMT, Gillies S, Brushett D, Waters DLE, Henry RJ (2008a) Inactivation of an aminoaldehyde dehydrogenase is responsible for fragrance in rice. Plant Mol Biol 68:439–449

Bradbury LME, Henry RJ, Waters DLE (2008b) Flavor development in Rice. In: Havkin-Frenkel D, Belanger FC (eds) Biotechnology in flavor production. Blackwell Publishing Ltd, Oxon, pp 130–142

Bryant RJ, McClung AM (2011) Volatile profiles of aromatic and non-aromatic rice cultivars using SPME/GC-MS. Food Chem 124:501–513

Butardo V Jr, Fitzgerald MA, Bird AR, Gidley MJ, Flanagan BM, Larroque O, Resurreccion AP, Laidlaw HK, Jobling SA, Morell MK, Rahman S (2011) Impact of down-regulation of starch branching enzyme IIb in rice by artificial microRNA- and hairpin RNA-mediated RNA silencing. J Exp Bot 62:4927–4941

Buttery RG, Ling LC, Juliano BO, Turnbaugh JG (1983) Cooked rice aroma and 2-acetyl-1-pyrroline. J Agric Food Chem 31:823–826

Buttery RG, Turnbaugh JG, Ling LC (1988) Contribution of volatiles to rice aroma. J Agric Food Chem 36:1006–1009

Cagampang GB, Perez CM, Juliano BO (1973) A gel consistency test for eating quality in rice. J Sci Food Agric 24:1589–1594

Calingacion MN, Boualaphanh C, Daygon VD, Anacleto R, Sackville-Hamilton NR, Biais B, Deborde C, Maucourt M, Moing A, Mumm R (2012) A genomics and multi-platform metabolomics approach to identify new traits of rice quality in traditional and improved varieties. Metabolomics 8:771–783

Calingacion MN, Laborte A, Nelson A, Resurreccion A, Concepcion JC, Daygon VD, Mumm R, Reinke R, Dipti S, Bassinello PZ, Manful J, Sophany S, Lara KC, Bao J, Xie L, Loaiza K, El-hissewy A, Gayin J, Sharma N, Rajeswari S, Manonmani S, Rani NS, Kota S, Indrasari SD, Habibi F, Hosseini M, Tavasoli F, Suzuki K, Umemoto T, Boualaphanh C, Lee HH, Hung YP, Ramli A, Aung PP, Ahmad R, Wattoo JI, Bandonill E, Romero M, Brites CM, Hafeel R, Lur H-S, Cheaupun K, Jongdee S, Blanco P, Bryant R, Thi Lang N, Hall RD, Fitzgerald MA (2014) Diversity of global rice markets and the science required for consumer-targeted rice breeding. PLoS One 9:e85106

Calpe C (2003) Status of the world rice market in 2002. 20th Session of the International Rice Commission. Food and Agriculture Organization, Bangkok

Castro JV, Dumas C, Chiou H, Fitzgerald MA, Gilbert RG (2005) Mechanistic information from analysis of molecular weight distributions of starch. Biomacromolecules 6:2248–2259

Champagne ET (2008) Rice aroma and flavor: a literature review. Cereal Chem 85:445–454

Champagne ET, Bett KL, Vinyard BT, Webb BD, McClung AM, Barton FE, Lyon BG, Moldenhauer KA, Linscombe S, Kohlwey

DE (1997) Effects of drying conditions, final moisture content, and degree of milling on rice flavor. Cereal Chem 74:566–570

Champagne ET, Bett KL, Vinyard BT, McClung AM, Barton FE, Moldenhauer KA, Linscombe S, McKenzie KS (1999) Correlation between cooked rice texture and rapid visco analyser measurements. Cereal Chem 76:764–771

Champagne ET, Thompson J, Bett-Garber KL, Mutters R, Miller JA, Tan E (2004a) Impact of storage of freshly harvested paddy rice on milled white rice flavor. Cereal Chem 81:444–449

Champagne ET, Wood DF, Juliano BO, Bechtel DB (2004b) The rice grain and its gross composition. In: Champagne ET (ed) Rice chemistry and technology. American Association of Cereal Chemists Inc, Minneapolis, pp 77–107

Champagne ET, Bett-Garber KL, Fitzgerald MA, Grimm CC, Lea J, Ki Ohtsubo, Jongdee S, Xie L, Bassinello P, Resurreccion AP, Ahmad R, Habibi F, Reinke RF (2010) Important sensory properties differentiating premium rice varieties. Rice 3:270–281

Chen L, Opara UL (2013) Texture measurement approaches in fresh and processed foods: a review. Food Res Int 51:823–835

Chen S, Yang Y, Shi W, Ji Q, He F, Zhang Z, Cheng Z, Liu X, Xu M (2008) *Badh2*, encoding betaine aldehyde dehydrogenase, inhibits the biosynthesis of 2-acetyl-1-pyrroline, a major component in rice fragrance. Plant Cell 20:1850–1861

Collard BCY, Mackill DJ (2008) Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. Philos Trans R Soc B 363:557–572

Cordeiro GM, Christopher MJ, Henry RJ, Reinke RF (2002) Identification of microsatellite markers for fragrance in rice by analysis of the rice genome sequence. Mol Breed 9:245–250

Cuevas RP, Fitzgerald MA (2012) Genetic diversity of rice grain quality. In: Caliskan M (ed) Genetic diversity in plants. InTech, Rijeka, pp 285–310

Cuevas RP, Daygon VD, Corpuz HM, Reinke RF, Waters DLE, Fitzgerald MA (2010a) Melting the secrets of gelatinisation temperature in rice. Funct Plant Biol 37:439–447

Cuevas RP, Gilbert RG, Fitzgerald MA (2010b) Structural differences between hot-water-soluble and hot-water-insoluble fractions of starch in waxy rice (*Oryza sativa* L.). Carbohydr Polym 81:524–532

Dalton T (2004) A household hedonic model of rice traits: economic values from farmers in West Africa. Agric Econ 31:149–159

Edwards D, Henry RJ, Edwards KJ (2012) Advances in DNA sequencing accelerating plant biotechnology. Plant Biotechnol J 10:621–622

Fitzgerald MA, Sackville-Hamilton NR, Calingacion MN, Verhoeven HA, Butardo V Jr (2008) Is there a second fragrance gene in rice? Plant Biotechnol J 6:416–423

Fitzgerald MA, Bergman CJ, Resurreccion AP, Moller J, Jimenez R, Reinke RF, Martin M, Blanco P, Molina F, Chen M-H, Kuri V, Romero MV, Habibi F, Umemoto T, Jongdee S, Graterol E, Reddy KR, Bassinello PZ, Sivakami R, Rani NS, Das S, Wang Y-J, Indrasari SD, Ramli A, Ahmad R, Dipti SS, Xie L, Lang NT, Singh P, Toro DC, Tavasoli F, Mestres C (2009a) Addressing the dilemmas of measuring amylose in rice. Cereal Chem 86:492–498

Fitzgerald MA, McCouch SR, Hall RD (2009b) Not just a grain of rice: the quest for quality. Trends Plant Sci 14:133–139

Fitzgerald TL, Waters DLE, Brooks LO, Henry RJ (2010) Fragrance in rice (*Oryza sativa*) is associated with reduced yield under salt treatment. Environ Exp Bot 68:292–300

Foegeding EA, Davis JP (2011) Food protein functionality: a comprehensive approach. Food Hydrocoll 25:1853–1864

Fuller DQ (2011) Pathways to Asian civilizations: tracing the origins and spread of rice and rice cultures. Rice 4:78–92

Gong L, Chen W, Gao Y, Liu X, Zhang H, Xu C, Yu S, Zhang Q, Luo J (2013) Genetic analysis of the metabolome exemplified using a rice population. Proc Natl Acad Sci USA 110:20320–20325

Gonzalez RJ, Livore A, Pons B (2004) Physico-chemical and cooking characteristics of some rice varieties. Braz Arch Biol Technol 47:71–76

Goodwin HL Jr, Koop LA, Rister ME, Miller RK, Maca JV, Chambers E, Hollingsworth M, Bett KL, Webb BD, McClung AM (1996) Developing a common language for the U.S. rice industry: Linkages among breeders, producers, processors, and consumers. TAMRC Consumer Product Market Research Report. Texas Agricultural Market Research Center, p 43

Grimm CC, Bergman CJ, Delgado JT, Bryant RJ (2001) Screening for 2-acetyl-1-pyrroline in the headspace of rice using SPME/GC-MS. J Agric Food Chem 49:245–249

He Y, Han Y, Jiang L, Xu C, Lu J, Xu M (2006) Functional analysis of starch-synthesis genes in determining rice eating and cooking qualities. Mol Breed 18:277–290

Heffner EL, Sorrells ME, Jannink J-L (2009) Genomic selection for crop improvement. Crop Sci 49:1–12

Heuberger AL, Lewis MR, Chen M-H, Brick MA, Leach JE, Ryan EP (2010) Metabolomic and functional genomic analyses reveal varietal differences in bioactive compounds of cooked rice. PLoS One 5:e12915

Huang T-C, Teng C-S, Chang J-L, Chuang H-S, Ho C-T, Wu M-L (2008) Biosynthetic mechanism of 2-acetyl-1-pyrroline and its relationship with Δ^1-pyrroline-5-carboxylic acid and methylglyoxal in aromatic rice (*Oryza sativa* L.) callus. J Agric Food Chem 56:7399–7404

Huang X, Kurata N, Wei X, Wang Z-X, Wang A, Zhao Q, Zhao Y, Liu K, Lu H, Li W, Guo Y, Lu Y, Zhou C, Fan D, Weng Q, Zhu C, Huang T, Zhang L, Wang Y, Feng L, Furuumi H, Kubo T, Miyabayashi T, Yuan X, Xu Q, Dong G, Zhan Q, Li C, Fujiyama A, Toyoda A, Lu T, Feng Q, Qian Q, Li J, Han B (2012) A map of rice genome variation reveals the origin of cultivated rice. Nature 490:497–501

Huang X, Yang S, Gong J, Zhao Y, Feng Q, Gong H, Li W, Zhan Q, Cheng B, Xia J, Chen N, Hao Z, Liu K, Zhu C, Huang T, Zhao Q, Zhang L, Fan D, Zhou C, Lu Y, Weng Q, Wang ZX, Li J, Han B (2015) Genomic analysis of hybrid rice varieties reveals numerous superior alleles that contribute to heterosis. Nat Commun 6:6258

Jannink J-L, Lorenz AJ, Iwata H (2010) Genomic selection in plant breeding: from theory to practice. Brief Funct Genomics 9:166–177

Jin Q, Waters DLE, Cordeiro GM, Henry RJ, Reinke RF (2003) A single nucleotide polymorphism (SNP) marker linked to the fragrance gene in rice (*Oryza sativa* L.). Plant Sci 165:359–364

Juliano BO (1979) The chemical basis of rice grain quality. Workshop on chemical aspects of rice grain quality. International Rice Research Institute, Los Banos

Juliano BO (2001) Asian perspective on rice sensory quality. Cereal Foods World 46:531–535

Juliano BO, Villareal CP (1993) Grain quality evaluation of world rices. International Rice Research Institute, Los Banos

Juliano BO, Perez CM, Kaosa-Ard M (1990) Grain quality characteristics of export rices in selected markets. Cereal Chem 67:192–197

Juliano BO, Perez CM, Resurreccion AP (2009) Apparent amylose content and gelatinization temperature types of Philippine rice accessions in the IRRI Gene Bank. Philippine Agric Sci 92:106–109

Kam K, Murray JM, Arcot J, Ward RM (2012) Fortification of parboiled rice with folic acid: consumer acceptance and sensory evaluation. Food Res Int 49:354–363

Kaminski TA, Brackmann A, da Silva LP, Nicoletti AM, Roberto BS (2013) Changes in culinary, viscoamylographic, and sensory characteristics during rice storage at different temperatures. J Stored Prod Res 53:37–42

Kasem S, Waters DLE, Henry RJ (2012) Analysis of genetic diversity in starch genes in the wild relatives of rice. Trop Plant Biol 5:286–308

Kaur H, Singh B (2013) Classification and grading rice using multiclass SVM. Int Sci Res Publ 3:1–5

Kharabian-Masouleh A, Waters DLE, Reinke RF, Henry RJ (2011) Discovery of polymorphisms in starch related genes in rice germplasm by amplification of pooled DNA and deeply parallel sequencing. Plant Biotechnol J 9:1074–1085

Kharabian-Masouleh A, Waters DLE, Reinke RF, Ward R, Henry RJ (2012) SNP in starch biosynthesis genes associated with nutritional and functional properties of rice. Sci Rep 2:557. doi:10.1038/srep00557

Khush GS (2001) Green revolution: the way forward. Nat Rev Genet 2:815–822

Khush GS (2005) What it will take to feed 5.0 billion rice consumers in 2030. Plant Mol Biol 59:1–6

Kovach MJ, Calingacion MN, Fitzgerald MA, McCouch SR (2009) The origin and evolution of fragrance in rice (*Oryza sativa* L.). Proc Natl Acad Sci USA 106:14444–14449

Kowittaya C, Lumdubwong N (2014) Molecular weight, chain profile of rice amylopectin and starch pasting properties. Carbohydr Polym 108:216–223

Krishnan SG, Waters DLE, Henry RJ (2014) Australian wild rice reveals pre-domestication origin of polymorphism deserts in rice genome. PLoS One 9:e98843

Kwak HS, Ahn BH, Lee Y, Kreger J, Lee S-Y (2013) Correlation of liking and disliking measurements in consumer acceptance tests. Food Qual Prefer 30:86–92

Kwon S-W, Cho Y-C, Lee J-H, Suh J-P, Kim J-J, Kim M-K, Choi I-S, Hwang H-G, Koh H-J, Kim Y-G (2011) Identification of quantitative trait loci associated with rice eating quality traits using a population of recombinant inbred lines derived from a cross between two temperate *japonica* cultivars. Mol Cells 31:437–445

Lanceras JC, Huang Z-L, Naivikul O, Vanavichit A, Ruanjaichon V, Tragoonrung S (2000) Mapping of genes for cooking and eating qualities in Thai jasmine rice (KDML105). DNA Res 7:93–101

Lapcharoensuk R, Sirisomboon P (2014) Eating quality of cooked rice determination using Fourier transform near infrared spectroscopy. J Innov Opt Health Sci 7(6):1450003. doi:10.1142/S1793545814500035

Leung H, Hettel GP, Cantrell RP (2002) International Rice Research Institute: roles and challenges as we enter the genomics era. Trends Plant Sci 7:139–142

Li JY, Wang J, Zeigler RS (2014) The 3000 rice genomes project: new opportunities and challenges for future rice research. Gigascience 3:8

Limpawattana M, Shewfelt RL (2010) Flavor lexicon for sensory descriptive profiling of different rice types. J Food Sci 75:S199–S205

Lisle AJ, Martin M, Fitzgerald MA (2000) Chalky and translucent rice grains differ in starch composition and structure and cooking properties. Cereal Chem 77:627–632

Liu G (2011) Detection of chalk degree of rice based on image processing. In: Proceedings of the 2011 International Conference on Intelligence Science and Information Engineering. IEEE Computer Society, pp 515–518

Liu X, Wan X, Ma X, Wan J (2011) Dissecting the genetic basis for the effect of rice chalkiness, amylose content, protein content, and rapid viscosity analyzer profile characteristics on the eating quality of cooked rice using the chromosome segment substitution line population across eight environments. Genome 54:64–80

Liu L, Waters DLE, Rose TJ, Bao J, King GJ (2013) Phospholipids in rice: significance in grain quality and health benefits: a review. Food Chem 139:1133–1145

Lorieux M, Petrov M, Huang N, Guiderdoni E, Ghesquiere A (1996) Aroma in rice: genetic analysis of a quantitative trait. Theor Appl Genet 93:1145–1151

Luo W, Guo T, Yang Q, Wang H, Liu Y, Zhu X, Chen Z (2014) Stacking of five favorable alleles for amylase content, fragrance and disease resistance into elite lines in rice (*Oryza sativa*) by using four HRM-based markers and a linked gel-based marker. Mol Breed 34:805–815

Mahattanatawee K, Rouseff RL (2014) Comparison of aroma active and sulfur volatiles in three fragrant rice cultivars using GC-Olfactometry and GC-PFPD. Food Chem 154:1–6

Manzanilla DO, Paris TR, Tatlonghari GT, Tobias AM, Chi TTN, Phuong NT, Siliphouthone I, Chamarerk V, Bhekasut P, Gandasoemita R (2013) Social and gender perspectives in rice breeding for submergence tolerance in Southeast Asia. Exp Agric 50:191–215

Maraval I, Mestres C, Pernin K, Ribeyre F, Boulanger R, Guichard E, Gunata Z (2008) Odor-active compounds in cooked rice cultivars from Camargue (France) analyzed by GC-O and GC-MS. J Agric Food Chem 56:5291–5298

Mariotti M, Fongaro L, Catenacci F (2010) Alkali spreading value and image analysis. J Cereal Sci 52:227–235

Mathure SV, Jawali N, Thengane RJ, Nadaf AB (2014) Comparative quantitative analysis of headspace volatiles and their association with *BADH2* marker in non-basmati scented, basmati, and non-scented rice (*Oryza sativa* L.) cultivars of India. Food Chem 142:383–391

Matsuda F, Okazaki Y, Oikawa A, Kusano M, Nakabayashi R, Kikuchi J, J-i Yonemaru, Ebana K, Yano M, Saito K (2012) Dissection of genotype–phenotype associations in rice grains using metabolome quantitative trait loci analysis. Plant J 70:624–636

Matthews JP, Gemme S, Huebschmann HJ, Llorente C, Jimenez R, Sreenivasulu N (2014) Thermo Sci Appl 10419:1–9

Meilgaard MC, Civille GV, Carr BT (2007) Sensory evaluation techniques, 4th edn. CRC Press, Boca Raton

Mestres C, Ribeyre F, Pons B, Fallet V, Matencio F (2011) Sensory texture of cooked rice is rather linked to chemical than to physical characteristics of raw grain. J Cereal Sci 53:81–89

Meullenet J-FC, Marks BP, Hankins J-A, Griffin VK, Daniels MJ (2000) Sensory quality of cooked long-grain rice as affected by rough rice moisture content, storage temperature, and storage duration. Cereal Chem 77:259–263

Mingyin Y, Muhua L, Huadong Z (2010) Exterior quality inspection of rice based on computer vision. In: World Automation Congress (WAC), pp 369–374

Moretti D, Zimmermann MB, Muthayya S, Thankachan P, Lee T-C, Kurpad AV, Hurrell RF (2006) Extruded rice fortified with micronized ground ferric pyrophosphate reduces iron deficiency in Indian schoolchildren: a double-blind randomized controlled trial. Am J Clin Nutr 84:822–829

Myint KM, Courtois B, Risterucci A-M, Frouin J, Soe K, Thet KM, Vanavichit A, Glaszmann JC (2012) Specific patterns of genetic diversity among aromatic rice varieties in Myanmar. Rice 5:20

Nakamura Y, Francisco PB, Hosaka Y, Sato A, Sawada T, Kubo A, Fujita N (2005) Essential amino acids of starch synthase IIa differentiate amylopectin structure and starch quality between japonica and indica rice varieties. Plant Mol Biol 58:213–227

Niu X, Tang W, Huang W, Ren G, Wang Q, Luo D, Xiao Y, Yang S, Wang F, Lu B-R, Gao FY, Lu T, Liu Y (2008) RNAi-directed downregulation of *OsBADH2* results in aroma (2-acetyl-1-pyrroline) production in rice (*Oryza sativa* L.). BMC Plant Biol 8:100

Pandey MK, Rani NS, Madhav MS, Sundaram R, Varaprasad GS, Sivaranjani AKP, Bohra A, Kumar GR, Kumar A (2012) Different isoforms of starch-synthesizing enzymes controlling amylose and amylopectin content in rice (*Oryza sativa* L.). Biotechnol Adv 30:1697–1706

Peng SB, Khush GS, Virk P, Tang QY, Zou YB (2008) Progress in ideotype breeding to increase rice yield potential. Field Crop Res 108:32–38

Perez CM, Pascual CG, Juliano BO (1979) Eating quality indicators for waxy rices. Food Chem 4:179–184

Perez CM, Juliano BO, Bourne MC, Anzaldua-Morales A (1993) Hardness of cooked milled rice by instrumental and sensory methods. J Texture Stud 24:81–94

Ramesh M, Ali SZ, Bhattacharya KR (1999) Structure of rice starch and its relation to cooked-rice texture. Carbohydr Polym 38:337–347

Rao Y, Li Y, Qian Q (2014) Recent progress on molecular breeding of rice in China. Plant Cell Rep 33:551–564

Redestig H, Kusano M, Ebana K, Kobayashi M, Oikawa A, Okazaki Y, Matsuda F, Arita M, Fujita N, Saito K (2011) Exploring molecular backgrounds of quality traits in rice by predictive models based on high-coverage metabolomics. BMC Syst Biol 5:176

Ridout MJ, Parker ML, Hedley CL, Bogracheva TY, Morris VJ (2006) Atomic force microscopy of pea starch: granule architecture of the *rug3-a*, *rug4-b*, *rug5-a* and *lam-c* mutants. Carbohydr Polym 65:64–74

Sabouri A, Rabiei B, Toorchi M, Aharizad S, Moumeni A (2012) Mapping quantitative trait loci (QTL) associated with cooking quality in rice (*Oryza sativa* L.). Aust J Crop Sci 6:808–814

Septiningsih EM, Trijatmiko KR, Moeljopawiro S, McCouch SR (2003) Identification of quantitative trait loci for grain quality in an advanced backcross population derived from the *Oryza sativa* variety IR64 and the wild relative *O. rufipogon*. Theor Appl Genet 107:1433–1441

Septiningsih EM, Pamplona AM, Sanchez DL, Neeraja CN, Vergara GV, Heuer S, Ismail AM, Mackill DJ (2009) Development of submergence-tolerant rice cultivars: the Sub1 locus and beyond. Ann Bot 103:151–160

Shao G, Tang A, Tang S, Luo J, Jiao G, Wu J, Hu P (2011) A new deletion mutation of fragrant gene and the development of three molecular markers for fragrance in rice. Plant Breed 130:172–176

Shi W, Yang Y, Chen S, Xu M (2008) Discovery of a new fragrance allele and the development of functional markers for the breeding of fragrant rice varieties. Mol Breed 22:185–192

Shimada H, Tada Y, Kawasaki T, Fujimura T (1993) Antisense regulation of the rice waxy gene expression using a PCR-amplified fragment of therice genome reduces the amylose content in grain starch. Theor Appl Genet 86:665–672

Shrestha AK, Arcot J, Paterson JL (2003) Edible coating materials: their properties and use in the fortification of rice with folic acid. Food Res Int 36:921–928

Siebenmorgen TJ, Grigg BC, Lanning SB (2013) Impacts of preharvest factors during kernel development on rice quality and functionality. Annu Rev Food Sci Technol 4:101–115

Singh N, Kaur L, Sodhi NS, Sekhon KS (2005) Physicochemical, cooking and textural properties of milled rice from different Indian rice cultivars. Food Chem 89:253–259

Singh A, Singh P, Singh R, Pandit A, Mahato A, Gupta D, Tyagi K, Singh A, Singh NK, Sharma T (2010) SNP haplotypes of the *BADH1* gene and their association with aroma in rice (*Oryza sativa* L.). Mol Breed 26:325–338

Son J-S, Do VB, Kim K-O, Cho MS, Suwonsichon T, Valentin D (2014) Understanding the effect of culture on food representations using word associations: the case of "rice" and "good rice". Food Qual Prefer 31:38–48

Sowbhagya CM, Ramesh BS, Bhattacharya KR (1987) The relationship between cooked-rice texture and the physicochemical characteristics of rice. J Cereal Sci 5:287–297

Spindel J, Begum H, Akdemir D, Virk P, Collard B, Redoña E, Atlin G, Jannink JL, McCouch SR (2015) Genomic selection and association mapping in rice (*Oryza sativa*): effect of trait genetic architecture, training population composition, marker number and statistical model on accuracy of rice genomic selection in elite tropical rice breeding lines. PLoS Genet 11:e1004982

Sreenivasulu N, Butardo VM Jr, Misra G, Cuevas RP, Anacleto R, Kavi Kishor PB (2015) Designing climate-resilient rice with ideal grain quality suited for high-temperature stress. J Exp Bot 66:1737–1748

Stone H, Bleibaum RN, Thomas HA (2012) Sensory evaluation practices, 4th edn. Academic Press, San Diego

Su Y, Rao Y, Hu S, Yang Y, Gao Z, Zhang G, Liu J, Hu J, Yan M, Dong G, Li Z, Guo L, Qian Q, Zeng D (2011) Map-based cloning proves *qGC-6*, a major QTL for gel consistency of japonica/indica cross, responds by *Waxy* in rice (*Oryza sativa* L.). Theor Appl Genet 123:859–867

Subbaiyan GK, Waters DLE, Katiyar SK, Sadananda AR, Satyadev V, Henry R (2012) Genome-wide DNA polymorphisms in elite indica rice inbreds discovered by whole-genome sequencing. Plant Biotechnol J 10:623–634

Suwannaporn P, Linnemann A (2008) Rice-eating quality among consumers in different rice grain preference countries. J Sens Stud 23:1–13

Sun S-Y, Hao W, Lin H-X (2006) Identification of QTLs for cooking and eating quality of rice grain. Rice Sci 13:161–169

Tan YF, Li JX, Yu SB, Xing YZ, Xu CG, Zhang Q (1999) The three important traits for cooking and eating quality of rice grains are controlled by a single locus in an elite rice hybrid, Shanyou 63. Theor Appl Genet 99:642–648

Tang H, Mitsunaga T, Kawamura Y (2006) Molecular arrangement in blocklets and starch granule architecture. Carbohydr Polym 63:555–560

Thompson JL, Drake MA, Lopetcharat K, Yates MD (2004) Preference mapping of commercial chocolate milks. J Food Sci 69:S406–S413

Tomlins K, Manful JT, Gayin J, Kudjawu B, Tamakloe I (2007) Study of sensory evaluation, consumer acceptability, affordability and market price of rice. J Sci Food Agric 87:1564–1575

Tran N, Daygon VD, Resurreccion AP, Cuevas RP, Corpuz HM, Fitzgerald MA (2011) A single nucleotide polymorphism on the *Waxy* gene explains a significant component of gel consistency. Theor Appl Genet 123:519–525

Tsugawa H, Tsujimoto Y, Sugitate K, Sakui N, Nishiumi S, Bamba T, Fukusaki E (2014) Highly sensitive and selective analysis of widely targeted metabolomics using gas chromatography/triple-quadrupole mass spectrometry. J Biosci Bioeng 117:122–128

Tsugita T (1985) Aroma of cooked rice. Food Rev Int 1:497–520

Umemoto T, Aoki N, Lin H, Nakamura Y, Inouchi N, Sato Y, Yano M, Hirabayashi H, Maruyama S (2004) Natural variation in rice *starch synthase IIa* affects enzyme and starch properties. Funct Plant Biol 31:671–684

Varshney RK, Terauchi R, McCouch SR (2014) Harvesting the promising fruits of genomics: applying genome sequencing technologies to crop breeding. PLoS Biol 12:e1001883

Verma B (2010) Image processing techniques for grading and classification of rice. In: International conference on computer and communication technology (ICCCT), pp 220–223

Vilaplana F, Hasjim J, Gilbert RG (2012) Amylose content in starches: toward optimal definition and validating experimental methods. Carbohydr Polym 88:103–111

Wang K, Hasjim J, Wu AC, Henry RJ, Gilbert RG (2014) Variation in amylose fine structure of starches from different botanical sources. J Agric Food Chem 62:4443–4453

Waters DLE, Henry RJ, Reinke RF, Fitzgerald MA (2006) Gelatinization temperature of rice explained by polymorphisms in *starch synthase*. Plant Biotechnol J 4:115–122

Widjaja R, Craske JD, Wootton M (1996) Comparative studies on volatile components of non-fragrant and fragrant rices. J Sci Food Agric 70:151–161

Windham WR, Lyon BG, Champagne ET, Barton FE, Webb BD, McClung AM, Moldenhauer KA, Linscombe S, McKenzie KS (1997) Prediction of cooked rice texture quality using near-infrared reflectance analysis of whole-grain milled samples. Cereal Chem 74:626–632

Yang DS, Lee KS, Jeong OY, Kim KJ, Kays SJ (2008a) Characterization of volatile aroma compounds in cooked black rice. J Agric Food Chem 56:235–240

Yang DS, Shewfelt RL, Lee K-S, Kays SJ (2008b) Comparison of odor-active compounds from six distinctly different rice flavor types. J Agric Food Chem 56:2780–2787

Yau NJN, Huang JJ (1996) Sensory analysis of cooked rice. Food Qual Prefer 7:263–270

Zader A (2011) Understanding quality food through cultural economy: the "politics of quality" in China's northeast japonica rice. Agric Hum Values 29:53–63

Zheng X-Z, Lan Y-B, Zhu J-M, Westbrook J, Hoffmann WC, Lacey RE (2009) Rapid identification of rice samples using an electronic nose. J Bionic Eng 6:290–297