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Breeding by design for future rice: Genes and genome technologies

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1. Introduction

Rice is a staple food for 3.2 billion people. The food security threat that shook many Asian countries in 2008 still looms, because farmers are facing the challenge of producing more rice with fewer resources of water, land, and inputs. The targets of rice improvement have changed from high yield alone to the combined targets of high yield, good quality, balanced nutrition, health safety, and sustainable production, especially in China [1]. Breeding rice cultivars like green super rice (GSR) will meet such targets and increase the profit of rice production. The advances made in genetics, genomics and breeding technologies in recent decades [2], provide the opportunity of efficient development of future cultivars via breeding by design. In this special issue “Rice as a model crop: genetics, genomics, and breeding”, we invited 19 experts in various fields to review advances in rice genetics, genomics, and breeding technologies. There are four papers on abiotic stress tolerance, two on biotic stress resistance, four on agronomic traits, three on platforms for gene mining, one on genome selection, one on gene editing, two on genome-designed breeding, and two on rice heterosis. The aim of this special issue is to survey the major advances in rice genomics and molecular breeding technologies, especially in China. Here we summarize these papers according to the classification of topics, adding our perspectives.

2. Genes and molecular mechanisms determining response to abiotic stresses

Recent years have witnessed climate changes that bring high or low temperature extremes [3], and severe drought in rainfed lowlands, aggravating salinity damage due to accumulation of salt in the surface soil [4]. Rice production under these conditions is becoming increasingly vulnerable and unsustainable. Multiple abiotic stresses need to be addressed in breeding programs targeting these environments. Global warming has threatened food security. Rice is vulnerable to heat stress, especially at heading and grain-filling stages, resulting in severe yield reduction [5,6] and reduced milling quality [7]. In this special issue, Kan and Lin [8] review

putative mechanisms underlying high-temperature perception and response in plants. They describe how rice responds to heat stress at multiple cell-component and functional levels. The gene *TT1* (*Thermo-tolerance 1*) with heat tolerance at seedling and flowering stages, isolated from an African rice strain [5], can be used for developing heat-tolerant cultivars of rice and wheat. Chen et al. [9] review salinity tolerance in rice, including identified genes and QTL, major underlying molecular mechanisms, and limitations in breeding. As a major abiotic stress secondary to drought, salinity imposes constraints on plant growth and production [10]. Where it is difficult to increase rice yield per unit, it is advisable to increase total rice yield by extending planting to saline-alkaline soil. Although great efforts have been made to identify mechanisms of salinity tolerance in rice, there has been limited progress in salinity tolerance breeding. More efforts should be made to identify salt-responsive channels and transporter activities at tissue- and cell-specific levels before the relevant traits can be used for breeding. In breeding for salinity tolerance, much attention should be paid to identifying novel alleles from wild rice relatives [11,12], to recover salinity-tolerance traits lost during domestication.

Soil, the backbone of agriculture, is essential for human survival. With the rapid development of modern industry and intensive agricultural fertilizer application, soil pollution in rice fields, in particular of cadmium (Cd), is of concern, given that Cd accumulation in rice grain is harmful to human health. Luo and Zhang [13] review the genes and mechanisms underlying Cd accumulation and detoxification in plants. In contrast to physicochemical soil remediation, bioremediation methods offer promise for removing or reducing the bioavailability of Cd in soil by breeding. Some inbred and hybrid *indica* rice cultivars with low Cd accumulation in grain [14,15], can be used for planting in Cd-contaminated fields. Several major genes for Cd accumulation or tolerance have been identified in rice [16,17] and will be useful in breeding for low Cd accumulation or tolerance using marker-assisted selection (MAS).

Another soil problem is nitrogen (N) deficiency, occurring in more than 70% of moderate- and low-yielding fields in China, as the primary reason for the huge gap between experimental yield

in demonstration trials with high input (water and fertilizers) and average yield in farmers' fields nationwide [18]. Further increasing the productivity of irrigated rice requires the use of nutrient use-efficient cultivars, which are currently lacking. Nitrogen is the most important component of plant biomacromolecules such as proteins and nucleic acids. Nitrogen-use efficiency (NUE), and thus grain yield, could be increased by improving amino acid partitioning from source leaves to sink organs [19]. Guo et al. [20] summarize current understanding of amino acids in the rhizosphere and their metabolism and function as signal molecules in altering plant architecture, flowering time, and plant defense against both abiotic and biotic stresses. Natural variations identified in the promoter and coding regions of some amino acid transporters provide opportunities for improvement of rice grain yield, quality, and NUE by MAS and genetic manipulation.

3. Genes and molecular mechanisms for resistance to biotic stresses

Among rice diseases, rice blast, caused by *Magnaporthe oryzae*, is the severest threat to yield worldwide. Annually, blast disease is responsible for some 30% loss of rice production globally [21]. Understanding resistance mechanisms and breeding resistant cultivars are fundamental for disease control. In this section, Yin et al. [22] review recent advances in pathogen-associated molecular patterns in rice blast infection. Varieties with broad-spectrum resistance could be developed by pyramiding multiple *R* genes and by other strategies such as cross-species transformation, host-induced gene silencing, and gene editing. To coordinate the relationship between disease resistance and high yield, more resistance genes need to be cloned for characterizing the crosstalk between disease resistance and yield-associated physiological processes.

Wang et al. [23] describe the most recent research on rice anti-viruses and antiviral molecular mechanisms. Rice black-streaked dwarf virus disease [24] and rice stripe virus [25], with the small brown planthopper serving as vector, are two of the most destructive viral rice diseases. The first of these is relatively common in eastern China and other East Asian countries, resulting in severe yield losses [26,27]. Most currently cultivated rice cultivars are highly susceptible to virus infection. Besides development of virus-resistant cultivars by introgressing the favorable alleles of virus-resistance genes or QTL from resistant accessions, RNAi, and vector insect antiviral approaches are recommended as effective ways to control rice virus diseases in future.

4. Genes and molecular mechanisms controlling yield- and grain quality-related traits

Germplasm resources, especially landraces and wild rice relatives, are repositories of genes for improving agricultural crops. Genetic bottlenecks imposed on crop plants during domestication and modern plant breeding have rendered modern crop cultivars vulnerable to biotic and abiotic stresses [28]. Identifying genetic mechanisms of rice domestication is beneficial not only for understanding of rice domestication and genetic mechanisms controlling traits, but also for mining favorable alleles from wild rice. Xu and Sun [29] summarize current knowledge of the genetic mechanisms underlying various features of wild and cultivated rice. In comparison with wild rice, genetic diversity is much reduced in cultivated rice owing to domestication bottlenecks [30,31]. It is thus desirable to identify favorable genes and alleles from wild rice that were lost during domestication. Study of the mechanisms governing the domestication of African rice will identify novel genes and alleles from African rice for use in breeding.

Rice grain yield per plant is a complex trait determined mainly by kernel weight, kernel number per panicle, and productive panicle number per plant [32]. Coordination among source supply, sink capacity, and flow of photoassimilates is influenced by a series of “invisible” physiological factors including nutrient-use and photosynthetic efficiency [33,34]. Li et al. [35] review current understanding of mechanisms determining the three yield components and summarize progress in physiological traits such as NUE and photosynthetic efficiency. It is desirable to tune these invisible physiological traits for further improvement of rice yield by MAS, transgenic approaches, and genome editing. Li et al. [36] review the genetic regulatory networks governing panicle architecture including panicle branch and lateral spikelets, multifloret spikelets, and panicle type. Rice breeding experience in past decades in China has shown that increase in grain yield is contributed largely by increased kernel number per panicle [37,38]. Elucidating the genetic mechanism determining this yield component will thus provide useful information for further yield improvement. Given that genes for panicle architecture show different effects on kernel number and kernel weight, it is proposed to develop high-yielding rice cultivars by pyramiding favorable alleles with synergistic effects on these traits using MAS or gene editing with our increased understanding of the mechanisms involved.

Grain quality of rice includes traits associated with cooking, eating, appearance, milling, and nutrition. Health or functional foods with nutritional quality are receiving increasing attention owing to the improvement of people's living standards in recent years [39]. Black rice has drawn breeders' interest [40]. Anthocyanins, a major subclass of flavonoids controlling the color of black rice, have diverse biological functions and benefits to human health owing to their high antioxidant activities [41]. In this special issue, Xia et al. [42] summarize recent advances in rice anthocyanin research, including genes, biosynthetic pathways, and domestication processes. Rice cultivars with high grain anthocyanin [43] have been developed by genetic engineering. Particularly sought are cultivars with high endosperm anthocyanin [44], which will not be removed by polishing [45].

5. High-throughput genomics platforms

With the release of the first draft rice genome sequences followed by multiple genome sequences and wide application of high-throughput sequencing and multi-omics technologies, great progress has been made in rice structural and functional genomics [46,47]. In this special issue, Jia et al. [48] review progress in rice genome sequencing and multi-omics and describe bioinformatics databases and tools applicable to rice genome resources and breeding. Future bioinformatics faces challenges: how to integrate various databases for more efficient use and how to integrate multi-omics data with phenotypic data to guide genomic selection, particularly for rice yield and quality. Sequencing multiple rice genomes also makes it possible to construct comprehensive rice pan-genomes, which includes core genes present in all accessions and dispensable genes present only in a subset of accessions. Huang et al. [49] summarize current research on pan-genomes for the genus *Oryza*. They emphasize the importance of integration of multiple genome sequences to construct as complete a pan-genome as possible for providing comprehensive genomic information for rice breeding programs [50,51].

Although high-throughput genome sequence data have emerged at unexpected speed in recent years, they have not been adequately exploited for investigating the genetic mechanisms of complex traits, owing to a lack of sufficient and accurate phenotypic data [52]. High-throughput precise phenotyping has already become a major bottleneck restricting the identification of genes

and QTL underlying agronomic traits, hindering crop breeding and functional genomics research [53]. Two research groups [54] collaboratively summarize crop phenomics research at various technological and platform levels and its recent applications in abiotic and biotic stresses and yield assessment. They compare the advantages and disadvantages of various phenotyping platforms and emphasize that future phenomics research should focus on developing platforms with more artificial-intelligence support, high flexibility, and low cost.

6. Genome-based breeding technologies

QTL mapping of complex quantitative traits in plants has been popular in the past few decades, with thousands of QTL affecting agronomic traits identified in rice [2]. However, cultivar improvement based on QTL mapping results seems seldom to have been successful, owing largely to the separation of theoretical research in QTL discovery from breeding programs [55,56]. In this special issue, Zhang et al. [57] provide an overview of a breeding strategy by selective introgression for simultaneous genetic dissection and improvement of complex traits. The strategy consists of three components: a molecular breeding material platform developed from selected introgression lines, an information platform for breeding by design via QTL detection and allele mining for target traits, and breeding by design by pyramiding multiple favorable alleles in selected introgression lines. The strategy is demonstrated by improvement of single, two and multiple complex traits, and by dissection of QTL networks underlying tolerances to drought, submergence, cold, and salinity. In the post-genomics era, it is possible to realize breeding by design via development of single-segment substitution lines and genomic information acquired continuously. Zhang [58] systematically introduces the concept and strategy, describing his results in rice using a platform developed from the cultivar HJX74.

Conventional plant breeding creates genetic variation by allele recombination among loci from different parents, followed by selection of favorable variations [59]. In comparison with visual phenotypic selection, genomic selection (GS) holds great potential to accelerate breeding progress and permits cost reduction by early selection prior to phenotyping [60]. Two groups of scientists summarize the major genetical and statistical factors affecting predictive performance as well as current progress in the application of GS to rice breeding [61]. They also describe powerful strategies to increase the predictive ability of models and propose a further solution to improve efficiency while reducing cost by integrating GS with high-throughput phenotyping platforms.

Unlike GS for efficient selection of favorable variations throughout the genome, CRISPR/Cas-based techniques have been successfully used since their discovery in 2012 [62] to generate targeted variations by gene editing in a variety of species because of their simplicity, efficiency and versatility. Huang et al. [63] review recent applications of CRISPR/Cas technologies in improvement of rice traits, including grain yield and quality and resistance to herbicide, disease, and pests, and in exploiting heterosis. Wang et al. [64] have opened the door to fixing hybrid vigor in rice by simultaneously editing meiosis genes (*REC8*, *PAIR1*, *OSD1*) and a fertilization gene (*MTL*). Gene editing offers great potential in molecular breeding and functional genomics research, particularly in rice.

7. Exploitation of rice heterosis

Hybrid rice, referred to as the second Green Revolution with yield increases of around 20% over inbred rice, has contributed to food security worldwide [65]. The veil hiding the genetic mecha-

nisms of heterosis, or hybrid vigor, has been gradually lifted with the rapid development of plant genomics and quantitative genetics. A collaborative report [66] describes advances in the study of the genetic basis of grain yield heterosis and presents potential future approaches for genetic studies and hybrid breeding. Many heterosis-associated genes or favorable alleles have been identified [67] and could be applied for breeding indica-japonica hybrid rice using MAS. It is advisable to accurately assess heterotic effects by constructing near-isogenic lines containing single heterosis-associated alleles.

Despite our imperfect understanding of heterosis, exploitation of rice heterosis has been a great success in China and many other countries. Hybrid breeding and large-scale application of hybrid rice has contributed greatly to food security in China [65]. Considering the advantages and disadvantages of three-line and two-line hybrid systems, referred to respectively as first- and second-generation hybrid rice technologies, Liao et al. [68] introduce third-generation hybrid rice technology, realized by transforming an expression vector containing the fertility restoration gene *OsCYP703A3*, the pollen lethality gene *orfH79*, and the seed marker gene *DsRed2* into a *CYP703A3*-deficient recessive genic male-sterility line to generate a new maintainer line. Self-pollination of the maintainer line produces half male-sterile non-transgenic seeds as the sterile line and half red transgenic seeds as a maintainer line. After seed sorting by color, non-transgenic male-sterile seeds can be used for hybrid seed production. The authors also discuss the establishment of the third-generation hybrid rice technology and envisage further innovation and fixation of heterosis by apomixis.

8. Summary and perspectives

In recent decades, breeding has accounted for a greater than 50% increase in world food crop production [69]. However, it will be a great challenge to ensure food and nutrition security for an ever-increasing population based on limited resources under a climate-change scenario, in the face of heat, drought, salinity, and other abiotic stresses together with a surge of new biotic stresses. Future breeding to improve the rice productivity of existing arable land will emphasize highly efficient use of resources in an environmentally sustainable manner [1]. To reach this goal, rice breeding requires intensive and integrated deployment of a wide range of gene resources, and the adoption of multi-omics approaches combining high-throughput phenotyping and physiological understanding of the crop with molecular tools and approaches (such as MAS, GS, and gene editing) with the support of advanced data analysis and management.

Thousands of genes for agronomic traits such as yield, and mechanisms of various abiotic and biotic stress tolerances, have been identified in rice using map-based cloning and reverse-genetics approaches [2]. Future studies should focus on diversity of available genetic resources and, in particular, wild rice relatives, to recover traits lost during domestication [28]. Owing to the independent domestication of the wild species *O. rufipogon* for Asian cultivated rice (*O. sativa*) and *O. barthii* for African cultivated rice (*O. glaberrima*), some unique genes and alleles could be identified and introgressed from African to Asian rice for cultivar improvement. For exploiting genomic variation, comprehensive *Oryza* pan-genomes should be constructed from as many cultivated and wild AA rice genomes as possible to identify unique genes and alleles affecting agronomic traits that are not present in Nipponbare or other genomes [70]. To date, there has been very slow progress in improvement of complex quantitative traits, and only very few cloned genes have been successfully deployed in rice molecular breeding. Using the same population for both gene and QTL mapping and breeding and enriching novel alleles across associated loci

will facilitate molecular breeding in rice improvement. Breeding using the selective introgression strategy can integrate QTL mapping and allele mining with QTL-based breeding by design using trait-specific introgression lines, which are developed from the same elite genetic background by crossing with a set of diverse donors [18,55]. In the near future, great efforts should be made in identifying novel alleles for all cloned genes by evaluating target traits among accessions with diverse haplotypes, collected worldwide [71], providing abundant favorable alleles for efficient breeding. Supplementing this allele information with a quantitative genomics map and the navigation system, referred to as RiceNavi, developed recently by Wei et al. [72], will bridge rice genomic knowledge and quantitative-trait improvement.

Conventional rice breeding in the past has depended mostly on selection of morphological traits, almost ignoring the effects of physiological traits influencing sinks, sources, and yield. Disharmony between yield-related traits and physiological traits such as nutrient-use and photosynthetic efficiencies can limit increases in rice yield [73,74]. Optimized coordination of N- and carbon-partitioning processes is also critical for improving rice yield and nitrogen use efficiency [75]. Molecular understanding of physiological traits and their interaction with yield-related traits, and identification of key genes such as *NRT1.1B* that increase source strength for N and thereby increases grain yield will lead to the further improvement of rice yield [76]. For abiotic stress tolerance in rice, stress-response channels and transporter activities at tissue- and cell-specific levels await discovery. Understanding of function, networks, and crosstalk between genes and pathways regulating abiotic and biotic stress tolerances in rice at the molecular level would provide valuable information for precision breeding of stress tolerance in rice. The tradeoff between abiotic or biotic stress tolerance and grain yield must be addressed for simultaneous improvements in stress tolerance and grain yield, probably by spatial redistribution of cytokinins [77] or regulation of brassinosteroid [78].

There are still few studies applying GS to rice breeding, in contrast to maize [79]. To further accelerate the breeding process and reduce the breeding cost, GS should be integrated with other advanced breeding technologies and platforms. To this end, high-throughput phenotyping capacities should be established in multiple rice ecological regions for large-scale precision phenotyping of agronomic traits. Because predictive ability is much affected by population structure, relatedness, and linkage disequilibrium between training and test populations, it is challenging to balance and optimize the relationship between the two types of population in a self-pollinated crop such as rice. This challenge can be well addressed by molecular recurrent selection (MRS) mediated by a dominant male-sterile gene [55]. In this system, a breeding population can be established using a dominant male sterile line in an elite background to cross as a female with a set of diverse germplasm accessions or selected introgression lines in the same genetic background, each carrying multiple favorable alleles for one or more target traits. Half fertile and half sterile plants will appear at each round of recurrent population developed from the outcrossed seeds from male-sterile plants in the previous round. After three cycles of recombination, seeds randomly harvested from fertile plants will be planted to form a training population for genotyping and target trait evaluation, while seeds from sterile plants will be used for continuous recurrent selection. In this manner, in subsequent cycles of MRS, desirable multi-locus recombinants with improved target traits will be identified by marker-based GS. Owing to the similarity of population structure between the training and test populations, predictive ability will be much improved in the MRS system.

With the rapid development in rice genome technologies and functional genomics, it can be expected that many new genes

and innovative genome-assisted breeding strategies will emerge. We regret that this special issue lacks the space to cover all the traits and topics that are important for rice molecular breeding. We hope that more critical review papers on rice genome and molecular breeding will be published in coming regular issues of The Crop Journal.

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