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Rice breeding in the post-genomics era: from concept to practice

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Future world food security requires continued and sustainable increase in rice production. Much of this increase has to come from new high yielding cultivars with resistances to multiple stresses. While future rice breeding in the post-genomics era has to build upon the progress in rice functional genomics research, great challenges remain in understanding the genetic/molecular systems underlying complex traits and linking the tremendous genome sequence diversity in the rice germplasm collections to the phenotypic variation of important traits. To meet the challenges in future rice improvement, a molecular breeding (MB) strategy has been practiced in China with significant progress in establishing the MB material and information platforms in the process of breeding, and in developing new varieties through two novel MB schemes. However, full implementation of this strategy requires tremendous investment to build capacities in high-throughput genotyping, reliable/precision phenotyping and in developing and adopting new genomics/genetic information-based analytic/application breeding tools, which are not in place in most of the public rice breeding institutions. Nevertheless, future advances and developments in these areas are expected to generate enormous knowledge of rice traits and application tools that enable breeders to deploy more efficient and effective breeding strategies to maximize rice productivity and resource use efficiencies in various ecosystems.

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Rice is the staple food for half of the world population. Rice (*Oryza sativa* L.) is also the model species of monocot plants for genomic research. During the past two decades, tremendous advances have been made in the rice genetic and genomic research since the rice genome was completely sequenced [1]. These include cloning and characterization of more than 600 rice genes, genetic mapping of huge numbers of genes/QTL that control many important traits [2••]. While these advances have tremendously enhanced our knowledge of rice, many challenges remain to turn this huge source of genomic/genetic information into more efficient and effective breeding strategies for future rice improvement. In this article, we briefly review the current status of rice breeding with focuses on how the recent advances in the rice genetic and genomic research may affect the future rice improvement in the post-genomics era.

A major shift of breeding goals for achieving sustainable yield improvement of rice

Extensive breeding efforts with the primary goal for high yield in past decades, particularly since the 'green revolution' (GR) in 1960s, have more than doubled rice productivity under the modern high-input agricultural conditions [3]. The successful commercialization of hybrid rice in China since late 1970s resulted in a second leap in rice productivity [4]. However, the world rice production has to be doubled again by 2030 to meet the projected demand of the increasing world population [5] and much of this increase has to come from improved rice cultivars. Thus, further improving yield potential has been the highest priority in almost all the rice breeding programs worldwide. Progress, though slow, has been made in further raising rice yields through developing 'super inbred and hybrid rice' cultivars by 'ideotype' breeding [6,7] and by exploiting inter-subspecific heterosis [4]. Unfortunately, most 'super rice' or 'super hybrid rice' cultivars require very high inputs to realize their yield potentials. In China, pursuing high yields of these super rice cultivars has been accompanied with excess uses of chemical fertilizers and pesticides in rice production, resulting in serious environmental pollutions and related problems [8]. Nevertheless, modern semidwarf rice cultivars have rarely achieved their yield potentials in farmers' fields because of many abiotic and biotic stresses. Meanwhile, rice farmers in ~35% rainfed systems of the world rice lands have not benefited from GR, because most high yielding semidwarf rice cultivars are sensitive to abiotic stresses (drought, problem soils, low and high temperatures, submergence, alkalinity, salinity, and so on) in the rainfed environments [9,10]. To reverse the trend and achieve sustainable yield increases of rice, there has been a call for developing 'green super rice' (GSR) cultivars that can produce high and stable yields under lesser inputs [8]. In addition, high nutritional values such as high iron and zinc contents have become important objectives in many breeding programs for specific groups of poor people in the developing world [11]. Translating these shifts into breeding means that future rice breeding would require breeders that improve many 'green' traits in addition to high yield potential and desirable quality.

Challenges in post-genomic era rice breeding

There is no doubt that future rice breeding will be increasingly based on the accumulated information from rice genomics research and should have the following 5 components [2••]: (1) the population structure that can make maximum use of the solar energy in given ecological conditions; (2), the plant architecture (ideotypes) to realize the population structure; (3) the traits to make up ideotypes and to achieve high quality, resistances to multiple biotic and abiotic stresses, and high nutrient use efficiency, and so on; (4) the genes and their regulatory networks to produce the traits; and (5) the genomic technology to assemble the genes. Of these, components (1)–(3) are related to breeding objectives, which may have different trait combinations and genetic contexts in specific target environments to be clearly defined. Component (4) refers specific combination(s) of genes or multi-locus genotype(s) that constitute the phenotypes or trait combinations that can reach the maximum yield and desirable quality in different target environments, which requires complete genetic information and knowledge of rice traits and trait combinations. Component (5) refers to novel molecular breeding (MB) technology/strategies to achieve (1)–(3) based on (4) in two key steps of the breeding process: first, to identify the best parents and simplest crossing scheme(s) that can produce, through recombination, desirable target multi-locus genotype(s) in breeding populations; and second, the most efficient and effective selection scheme(s) that lead to the quickest identification and fixation of the targeted genotype(s) from breeding populations.

Building the rice breeding information platform

The rich genetic diversity in the worldwide rice germplasm collections has been the driving engine for rice improvement in the past, and will be so for the future. Rice breeding in the post-genomics era requires a comprehensive information platform that contains at least two key components. The first is a permanent breeder-use-friendly database that links most sequence diversity in the rice germplasm collections to the phenotypic variation of all traits interesting to breeders. Ideally, this database should contain at least three types of well integrated information: first, comprehensively annotated/analyzed genome sequences of all potential rice breeding parents (commercial varieties, hybrid parents and the rice core germplasm collection accessions); second, high density SNPs between any pair of these lines; and third, alleles (haplotypes) at each of the functional loci contributing to the phenotypic variation of all target traits, and their molecular functions in specific signaling pathways. The second component should contain various analytic/application tools that can continuously build up, manage and upgrade the database from the worldwide rice research, and allow various applications of the information to various decision making processes in specific rice breeding programs to achieve the highest efficiency and effectiveness.

Unfortunately, the current genetic/molecular information on rice traits generated from past research is far from the requirements. For example, a significant portion of the 600+ cloned rice genes are induced deleterious mutants [2••]. The phenotypic effects of different alleles in rice germplam accessions at these cloned rice genes and their values in rice breeding remain largely unknown, making it difficult to use them in breeding. In addition, while huge numbers of genes/QTL have been identified and mapped to the rice genome (URL: http://www.gramene.org/), most QTL information is not directly useful to breeders because of two major reasons. First, epistasis, particularly high order epistasis affecting complex traits, has not been addressed in most QTL mapping studies which are important based on available evidence [12–17,18•]. Second, most QTL were identified from populations involving few parents independent of breeding. Thus, phenotypic effects of most mapped and cloned rice genes/QTL are largely unpredictable in new genetic backgrounds and target environments in the presence of epistasis and genotype by environment interaction [19,20]. Recent genome-wide association studies (GWAS) can resolve some cloned QTL into a few candidate loci [21••], but the current GWAS methodology has low efficiency and power in detecting QTL than the normal linkage analyses for the same population size and is unable to detect epistasis or differentiate phenotypic effects to multiple alleles in a diverse panel of rice germplasm accessions.

To resolve the problem in characterizing epistasis, a new molecular quantitative genetics model was developed [22••], which formulates two important concepts, the functional genetic units (FGU) and the principle of hierarchy, based on two commonest types of functional relationships between genes. Hierarchy reflects the one-way functional dependency (FD) of genes in downstream metabolic pathways on their upstream regulators. FGU represents the mutual FD among a group of genes at each level of signaling pathways, which affect phenotype(s) in a manner of complementarity. Epistasis normally results from these two types of FD between loci within a signaling pathway [22••].

The new theory has two major advances over the classical quantitative genetic theory. First, it provides powerful ways to characterize genetic networks controlling complex traits by characterizing high order epistasis. In these cases, the presence of high order epistasis can be inferred and quantified based on QTL main effects and related digenic epistasis parameters. Second, the nature of QTL