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Rice Functional Genomics Research: Past Decade and Future

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ABSTRACT

Rice (*Oryza sativa*) is a major staple food crop for more than 3.5 billion people worldwide. Understanding the regulatory mechanisms of complex agronomic traits in rice is critical for global food security. Rice is also a model plant for genomics research of monocotyledons. Thanks to the rapid development of functional genomic technologies, over 2000 genes controlling important agronomic traits have been cloned, and their molecular biological mechanisms have also been partially characterized. Here, we briefly review the advances in rice functional genomics research during the past 10 years, including a summary of functional genomics platforms, genes and molecular regulatory networks that regulate important agronomic traits, and newly developed tools for gene identification. These achievements made in functional genomics research will greatly facilitate the development of green super rice. We also discuss future challenges and prospects of rice functional genomics research.

Key words: functional genomics, gene identification, green super rice, *Oryza sativa*

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INTRODUCTION

Rice (*Oryza sativa*) has been recognized as a model for plant functional genomics research due to its small genome size, accurate genome sequences characterized by co-linearity with the sequences of other cereal crops, high-efficiency transformation technology, and abundant germplasm resources (Jiang et al., 2012). In the past decades, tremendous progress has been achieved in rice functional genomics research, which can be summarized into three aspects: (1) construction of technological and resource platforms for high-throughput gene identification; (2) functional genomic analysis of gene networks for important agronomic traits and biological processes; and (3) development of new tools for characterization of novel genes. In this article, we review the main progress achieved in the last 10 years. We also present our prospects for future studies of rice functional genomics research and possible challenges in applying the findings to the development of green super rice (GSR).

RECENT DEVELOPMENT OF PLATFORMS FOR RICE FUNCTIONAL GENOMICS RESEARCH

Since the completion of whole-genome sequencing in rice, various functional genomics platforms have been established in the past decade, including collection of germplasm resources and generation of mutant libraries, full-length cDNA libraries, gene expression microarrays, and RNA-sequencing (RNA-seq) technologies for expression profiling (Jiang et al., 2012; Yang et al., 2013b). Platforms of metabolomics, proteomics, and phenomics have also been gradually established and improved, and corresponding platforms of bioinformatics analysis and databases have also been set up in rice (Rajasundaram and Selbig, 2016).

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Germplasm Resources

Rice is rich in germplasm resources, including naturally occurring and artificially modified germplasms. The genus *Oryza* consists of 21 wild and two cultivated species, which are classified into 10 different genome types (Vaughan et al., 2003). The International Rice Research Institute (IRRI) maintained ~110 000 rice germplasm accessions, which is the world's largest and most diverse collection (http://irri.org/). To better understand the molecular basis of agronomically important traits, the genomes of many germplasms have been resequenced with the development of next-generation sequencing technologies (Xu et al., 2011). Recently, the Chinese Academy of Agriculture Science together with Huada Gene Research Institute (China) and IRRI performed deep resequencing of 3000 rice varieties (3,000 rice genomes project, 2014). Through alignment with the genome of Nipponbare, a total of 18.9 million single-nucleotide polymorphisms (SNPs) and insertions/deletions (InDels) were identified. Exploration of gene sequence variations from wild rice is also of great significance for genomic breeding. Some international peers have also explored the genomes of wild rice. For example, the Oryza Map Alignment Project (OMAP) was launched at the University of Arizona in 2005 (Wing et al., 2005).

Meanwhile, multiple rice mutant libraries generated by T-DNA insertion, *Ds*/*dSpm* tagging, *Tos17* tagging, and chemical/irradiation mutagenesis have been developed. A total of 246 566 flanking sequence tags from rice mutant libraries with T-DNA, *Ds*/*dSpm*, or *Tos17* insertion were obtained, targeting 211 470 unique sites (Yang et al., 2013b). Currently, 57% of non-transposable-element-related genes in rice have insertion tags (Jiang et al., 2012). Due to the non-random distribution of T-DNA and transposon insertions in the genome, it is almost impossible to make every coding gene contain at least one insertion tag. To generate mutations at the whole-genome level, fast-neutron irradiation has been used to generate a mutant library in rice variety Kitaake (Li et al., 2016a, 2017a). Genome-wide sequencing of 41 mutation lines reveled that 1284 genes were mutated and single base substitution was the most abundant mutant type (Li et al., 2016a, 2017a). Recently, a genome-wide mutant library has been generated using CRISPR/Cas9 (Lu et al., 2017a; Meng et al., 2017). Collectively, these mutant resources are of great value for both functional genomics and genetic improvement in rice.

Gene Expression Profiles

The Knowledge-Based Oryza Molecular Biological Encyclopedia (KOME) database collects information for about 38 000 full-length cDNAs of *japonica* cv. Nipponbare. The Rice *indica* cDNA Database (RICD) database (http://202.127.18.221/ricd/index.html) contains 10 081 and 12 727 full-length cDNA sequences from Gaungluai 4and Minghui 63, respectively. Affymetrix GeneChip Rice Genome Array was used for the analyses of specific expression profiles in various tissues under different stress conditions in elite hybrid rice Shanyou 63 and its parents Zhenshan 97 and Minghui 63, which were in the information platform of the Collection of Rice Expression Profiles (CREP) (http://crep.ncpgr.cn) (Wang et al., 2010). Gene expression microarrays were used to analyze and compare the transcriptomes of super hybrid rice LYP9 and its parental cultivars 93-11 and PA64s (Wei et al., 2009). Gene expression profiles of reproductive meristems in early inflorescences and the spatial and temporal transcription profiles during early embryogenesis were dissected by using a laser microdissection and RNA-seq approach (Harrop et al., 2016; Itoh et al., 2016). Wang et al. (2014c) used an Affymetrix GeneChip Rice Genome Array to analyze the expression quantitative trait loci (eQTLs) in rice seedlings and flag leaves during heading period from recombinant inbred lines (RILs) derived from a cross between Zhenshan 97 and Minghui 63. They found a large number of *cis*- and *trans*-eQTLs that regulate the expression of genes, leading to the construction of the regulatory network through gene coexpression analysis (Wang et al., 2014c). Further analysis of the flag leaves of 98 immortalized F2 (IMF2) identified many genomic loci that control the expression abundance of small RNAs (Wang et al., 2015a), providing new insight into the regulation of gene expression.

High-Throughput Phenotyping Facility

The construction of high-throughput and accurate phenomics platforms is becoming a new research area of rice functional genomics. CropDesign (Belgium) developed the TraitMill platform, which can be used to measure the traits such as aboveground biomass, plant height, total number of seeds, total number of filled seeds, total weight of seeds, and harvest index, which are useful for breeding applications (Reuzeau et al., 2010). LemnaTec Scanalyzer 3D enabled the fully automatic analysis of plant phenotypes. The Australian Plant Phenomics Facility has successfully applied this technology in the studies of salt stress (Rajendran et al., 2009), drought tolerance (Normanly, 2012), toxicity (boron) tolerance (Schnurbusch et al., 2010), as well as modeling and prediction of crop yield (Golzarian et al., 2011) and root development (Rahnama et al., 2011). In 2011, LemnaTec (Germany) and KeyGene (Netherlands) announced the commencement of commercial operation of a plant phenomics platform (PhenoFab), which has been officially applied in commercial crop breeding. Huazhong Agriculture University, in collaboration with Huazhong University of Science and Technology, developed a high-throughput rice phenotyping facility (HRPF), which allows the growing of 5472 pots of rice and can automatically monitor 15 important agronomic traits (Yang et al., 2013a, 2014). Currently, HRPF has been adapted for phenotyping other crops such as maize, rape, and cotton.

Epigenomics

Epigenomes are a collection of whole-genome chromatin profiles of cells under specific internal and environmental conditions, such as DNA methylation, histone modification, and arrangement of nucleosomes on genomic DNA. Epigenomes play important roles in gene expression reprogramming during cell differentiation, plant development and growth, and response to stress. DNA methylation widely occurs in the genomes of animals and plants, and plays important roles in inhibiting transposon activities, repressing gene expression and stabilizing the genomes. Compared with *Arabidopsis*, the features of DNA methylation in rice include the following. (1) The average methylation levels of CG, CHG, and CHH and the total cytosine methylation density in rice genome (44.46%, 20.14%, 4.02%, and 24.7%, respectively) are much higher. (2) The methylations of CG and CHG occur mainly in the heterochromatin regions, which modify the transposable elements and related genes. However, CHH methylation is distributed mainly in euchromatic regions and modifies certain transposable elements with shorter lengths, such as miniature

inverted-repeat transposable elements (MITEs) (Zemach et al., 2010; Tan et al., 2016). CHH methylation has a profound effect on gene expression in cereal crops (Wei et al., 2014; Tan et al., 2016). (3) Methylation in CHG and CHH sequences participates in inhibiting the expression of many functional genes in rice. (4) The methylation level of CG is relatively stable in various tissues during the development process but the levels of CHG and CHH increase with the development processes (Zemach et al., 2010).

In rice, research on histone modification has been mainly focused on the acetylation and methylation of histone lysine. H3K27ac and H3K9ac share similar distribution patterns in the genome, and mainly accumulate in the promoter region. H3K9ac and H3K27ac are highly correlated with gene transcription, suggesting the synergistic effects of the acetylation of different loci on gene expression (Du et al., 2013). H4K16ac and H3K23ac are enriched in genes with low expression and around the transcription start sites (Lu et al., 2015). Currently there are also studies of histone methylation on H3K4, H3K9, H3K27, and H3K36 in the rice genome. The distribution of H3K4me2/3 in the genome is similar to that of H3K9ac and H3K27ac modification, and is also located in euchromatin. The genes modified by H3K27me3 show dynamic variations in different tissues from callus, seedling, and shoot apical meristem to inflorescence meristem, and play important roles in maintaining the inhibition of genes (Liu et al., 2015b).

Epigenetic modifying factors regulate gene transcription through altering the chromatin states, affecting the growth and development and adaptation to the environments. For example, the H3K27 methyltransferase gene *SDG711* and the H3K4 demethylase gene *JMJ703* have agonistic functions in reprogramming the H3K27me3/H3K4me3 ratio and modulating gene expression in the inflorescence meristem (Liu et al., 2015b). Epigenetic modifications can also affect the expression patterns of genes in the hybrid progeny. Guo et al. (2015) found that the specific modification sites of H3K36me3 can enhance the expression of some specific alleles in F1 hybrids. A recent study showed that histone deacetylase OsSRT1 directly inhibits the metabolic pathways of glycolysis through mediating the deacetylation of the key enzyme in histone degradation and glycolysis, and affects starch accumulation and transposon repression to regulate normal seed development in rice (Fang et al., 2016).

Metabolomics

Plants can generate as many as 0.2–1 million metabolites (Dixon and Strack, 2003). In recent years, with the development of metabolomics analytical technologies, particularly the advance in metabolic profiling based on mass spectra and magnetic resonance imaging, the research fields of metabolomics have been continuously expanded (Saito et al., 2013). Progress has been made in the application of plant metabolomics to the identification of functional genes, dissection of metabolic pathways, and genetic analysis of natural variations through integration with other omics technologies (Kumar et al., 2017).

Traditional liquid chromatography-mass spectrometry (LC-MS) includes targeted and untargeted metabolomics. A platform of metabolomics based on broad-spectrum untargeted metabolomic analysis has been established, which can quantify more than 800 known and unknown metabolites within 30 min (Chen et al., 2014b). The metabolomic analysis of samples from 210 RILs derived from a cross between two elite indica rice varieties, Zhenshan 97 and Minghui 63, and detected approximately 1000 metabolites, which were resolved to over 2800 metabolic QTLs (Gong et al., 2013). Genome-wide association study (GWAS) was employed to identify several hundreds of loci/sites that control natural variations in metabolite contents (Chen et al., 2014b), and they annotated over 160 new metabolites, including flavonoids, vitamins, and terpenes.

Proteomics

Proteomics research focuses on protein identification, quantification, activity, stability, localization, and function, which play essential roles in cell signaling events (Wilkins et al., 1996). In the last decade great advances have been achieved in rice proteomics, which provide comprehensive snapshots on the understanding of rice development, stress tolerance, organelle, secretome, and protein post-translational modification (PTM). Proteomics studies in rice have been performed mostly using gel-based (1DE, 2DE, and 2DIGE) and gel-free (LC-MS/MS or MudPIT) approaches, and more recently iTRAQ (isobaric tags for relative and absolute quantitation) for protein quantitation based on MS/MS. Kim et al. (2014b) reviewed and summarized the progress in rice proteomics studies from 2010 to 2013, with major focus on rice under diverse abiotic and biotic stress conditions. More recently, an iTRAQ-labeling-based quantitative proteomics strategy was used to investigate the proteomes under high temperature in different rice cultivars. The results showed that high temperature stress induced small heat shock proteins, expansins, and lipid transfer proteins in high-temperature-resistant cultivars (Mu et al., 2017). Polyethylene glycol-simulated drought responsiveness in a time-dependent manner in root demonstrated that most of the differentially expressed proteins appeared to be involved in bioenergy and metabolism (Agrawal et al., 2016). By using polypeptides enriched and phosphorized by IMAC, 201 phosphopeptides showing pistil-specific expression were identified (Wang et al., 2014b). Protein phosphorylation is one of the most common post-translational modifications. It was speculated that the regulation of protein phosphorylation plays an important role in the growth and development of plants (Cabrillac et al., 2001). There are more than 1400 genes that encode protein kinases and 300 genes that encode phosphatases in rice (Dardick et al., 2007). Combination of PolyMAC and TiO_2 technologies has successfully identified 2000 phosphoproteins from mature stigma and embryonic tissues, which will greatly facilitate the studies of the development and pollination of rice stigma (Wang et al., 2014b). To further develop proteomics and integrate the available data, some databases of proteomics have been constructed, including Phospho*Rice*, a meta-predictor of rice-specific phosphorylation sites (http://bioinformatics.fafu.edu.cn/PhosphoRice; Que et al., 2012), Oryza PG-DB, a rice proteome database on shotgun proteogenomics (http://oryzapg.iab.keio.ac.jp/; Helmy et al., 2011), and PRIN, a predicted rice interactome network (http://bis.zju.edu.cn/prin/; Gu et al., 2011).

Future proteomics research should further refine routine and reliable methods for sample preparation, including tissue

Database	Description	Web site
IC4R	Comprehensive database	http://ic4r.org/
RiceGeneThresher	Comprehensive database	http://rice.kps.ku.ac.th/
MCDRP	Rice proteins database	http://www.genomeindia.org/biocuration/
PlantDHS	DNase I hypersensitive sites database	http://plantdhs.org/
RICD	Rice indica cDNA database	http://202.127.18.221/ricd/index.html
RiceFREND	Gene coexpression database	http://ricefrend.dna.affrc.go.jp/
BGI-RIS	Genome annotation	http://rise2.genomics.org.cn/
OGRO	Genome annotation	http://qtaro.abr.affrc.go.jp/ogro
RAP-DB	Genome annotation	http://rapdb.dna.affrc.go.jp/
RIGW	Genome annotation	http://rice.hzau.edu.cn/rice/
TIGR	Genome annotation	http://rice.plantbiology.msu.edu/
RiceNet	Genome-scale gene network	http://www.inetbio.org/ricenet/
IRRI	Germplasm and natural variation of rice	http://irri.org/
RiceCye	Information about metabolic pathways	http://pathway.gramene.org/gramene/ricecyc.shtml
PmiRKB	MiRNA databases	http://bis.zju.edu.cn/pmirkb/
Oryzabase	Phenotype description and classification of rice	http://shigen.nig.ac.jp/rice/oryzabase/
PRIN	Protein interaction databases	http://bis.zju.edu.cn/prin/
RKD	Protein kinase database	http://ricephylogenomics.ucdavis.edu/kinase/
RMG	Rice mitochondrial genome information	http://rmg.rice.dna.affrc.go.jp/
RiceXPro	Rice expression profile database	http://ricexpro.dna.affrc.go.jp/
ROAD	Rice expression profile database	http://www.ricearray.org/
CREP	Rice expression profile database	http://crep.ncpgr.cn/
RiceVarMap	Rice genomic variations database	http://ricevarmap.ncpgr.cn/
OryGenesDB	Rice mutant resource database	http://orygenesdb.cirad.fr/
POSTECH RISD	Rice mutant resource database	http://www.postech.ac.kr/life/pfg/risd/
RMD	Rice mutant resource database	http://rmd.ncpgr.cn/
RPAN	Rice Pan-genome database	http://cgm.sjtu.edu.cn/3kricedb/
RPD	Rice phylogenomics database	http://ricephylogenomics.ucdavis.edu/
Oryza PG-DB	Rice proteogenomics database	http://oryzapg.iab.keio.ac.jp/
Phospho Rice	Rice-specific phosphorylation sites	http://bioinformatics.fafu.edu.cn/PhosphoRice
HapRice	SNP haplotype database	http://qtaro.abr.affrc.go.jp/
RiTE-db	Transposons database	http://www.genome.arizona.edu/cgi-bin/rite/index.cgi

Table 1. Representative Bioinformatics Databases for Rice Functional Genomics Research.

harvesting and protein extraction, to systematically investigate the subcellular locations and post-translational modifications of proteins and clarify their biological functions. With the development of antibody immunoprotein technology, fabrication of protein microarrays can help to realize the high-throughput identification of the functional proteins in particular biological processes.

Bioinformatics and Datasets in Rice

Along with the advances in rice functional genomics research and the widespread application of various high-throughput technologies, there have been explosive increases in various kinds of omics datasets. A large number of bioinformatics databases have been constructed in rice, including the databases of genomes, transcriptomes, proteomes, and metabolomes. Table 1 lists some representative bioinformatics websites, which are widely accessible to the rice research community. These datasets can be classified into genome annotation databases, gene expression databases, gene function annotation databases, and some comprehensive databases, which would assist the dissection of the functional genes and regulatory mechanisms related to important agronomic traits in rice. For example, the RiceVarMap website provides comprehensive information of 6 551 358 SNPs and 1 214 627 (InDels) identified from sequencing data of 1479 rice accessions (Zhao et al., 2015a). The Rice Pan-genome Browser (RPAN) is a tool to search and visualize the pan-genome derived from the 3K rice genome project (Sun et al., 2016a).

NEWLY DEVELOPED TOOLS FOR GENE IDENTIFICATION

Genome-Editing Technology

The CRISPR/Cas9 system has become a prevalent tool for gene mutagenesis in rice functional genomic research. Feng et al. (2013) used the CRISPR/Cas9 system harboring single guide RNA driven by *OsU6-2* promoter for the disruption of genes *ROC5*, *SPP*, and *YSA* in rice. In the T_1 transgenic plants, the mutation rate of *SPP* was 5%, and that of *ROC5* and *YSA* was as high as 26%–84%. Miao et al. (2013) designed CRISPR/Cas9 system targeting either the *CAO1* or the *LAZY1* and observed the expected mutant phenotypes. Ma et al. (2015a, 2016) developed a robust CRISPR/Cas9 system for high-efficiency multiple genome editing in plants. With this system, an average mutation rate of 85.4% was obtained for the 46 target sites in rice. Currently, the CRISPR/Cas9 system can be used to knock out completely the functions of target genes for rice genetic improvement. It was reported that targeted mutation of *indica* rice allele *Sc-i* by CRISPR/Cas9 could improve male fertility in *japonica-indica* hybrids (Shen et al., 2017b). Recently, significant progress has been made in the generation of targeted point mutations in rice. By using the strategy of homology-directed repair-mediated targeted gene replacement, Sun et al. (2016b) introduced Cas9/guide RNA and repair templates simultaneously into rice and obtained multiple discrete point mutations in *ALS* gene. Li et al. (2016b) reported the use of a nicked Cas9 with only the D10A mutation (nCAS9) fused with a cytidine deaminase enzyme and the uracil glycosylase inhibitor to generate point mutations at a specific locus. Lu and Zhu. (2017b) developed a base-editing system in rice using rat APOBEC1, providing a simple and highly efficient base-replacement method for plant molecular breeding.

Genome-wide Association Studies

With the rapid development of high-throughput sequencing technologies, GWAS has become a new approach for dissecting important agronomic traits of rice. GWAS is a strategy to perform association analysis between agronomically important traits and whole-genome genotypes using genetically highly diverse germplasms. The genotypes commonly used in rice can be classified into SNP array genotypes and resequenced SNP genotypes.

Huang et al. (2010) identified ~3.6 million SNPs by sequencing 517 *japonica* and *indica* rice landraces and constructed a high-density haplotype map. GWAS for 14 agronomic traits revealed 37 associated loci, which could explain ~36% of the phenotypic variance. GWAS for the flowering time and grain-related traits was conducted with 950 varieties collected worldwide, resulting in the identification of 32 new loci (Huang et al., 2012). Large-scale GWAS on 38 agronomic traits identified 130 associated loci through developing an integrated genomic approach to construct a genome map for 1495 elite hybrid rice varieties and their inbred parental lines, which provided a global view of heterosis from a representative number of hybrid combinations (Huang et al., 2015b). A large number of GWAS peaks associated with panicle trait were identified through quantifying 49 panicle phenotypes in 242 tropical rice accessions with the imaging platform PANorama (Crowell et al., 2016). Yano et al. (2016) generated a set of 426 337 SNPs and 67 544 InDels by whole-genome sequencing of the 176 varieties, which identified four new genes associated with agronomic traits.

With the accumulation of genomic sequencing data, high-throughput phenotyping, and the perfection of various statistical methods, more and more loci related to agronomically important traits promise to be identified by GWAS. Combination of gene expression profiling, homologous gene analysis, mutant resources, and CRISPR/Cas9 technologies will facilitate the verification of more gene functions in rice.

GENES AND THEIR REGULATORY NETWORKS FOR IMPORTANT AGRONOMIC TRAITS

Rice functional genomics research is aimed at exploring the genes and molecular regulatory networks of agronomically important traits and applying them in varietal improvement, for traits like yield, quality, disease and pest resistance, nutrient-use efficiency (NUE), abiotic stress resistance, and reproductive development. At present, a total of 2294 rice functional genes have been identified (http://www.ricedata.cn/). To gain a glimpse of the newly cloned genes (in the period 2008–2017), we summarize the representative genes related to agronomically important traits in Table 2. Features for some of the genes will be discussed briefly, especially those showing potential applications in crop genetic improvement.

Yield

Rice grain yield is a complex trait determined by the number of panicles, number of grains per panicle, and grain weight. The formation of grain yield is mainly dependent on the genes that control tillering and panicle development. Xing and Zhang (2010) summarized the key genes that control rice yield trait cloned before 2010. *MOC1* encodes a plant-specific GRAS family protein, functioning to initiate axillary buds, and promotes tiller outgrowth in rice (Li et al., 2003). Some genes involved in the biosynthesis and signaling of strigolactones, such as *D3*, *D10*, and *D27*, also influence the tiller number of rice (Arite et al., 2007). A basic helix-loop-helix (bHLH) type transcription factor, *OsTB1*, negatively regulates the tiller number of rice (Choi et al., 2011). The number of grains per panicle is determined by length of panicle development and the rate of spikelet formation. For example, *LAX1*, *LAX2*, and *SPA* together enhance the formation of lateral meristems (Tabuchi et al., 2011), and *FZP* is required for the establishment of floral meristem identity by inhibiting the formation of axillary meristems (Komatsu, 2003). *APO1* positively regulates spikelet number by suppressing the precocious conversion of inflorescence meristems to spikelet meristems (Ikeda et al., 2007). The genes related to cytokinin, such as *Gn1a* and *LOG*, also influence the number of grains per panicle (Ashikari et al., 2005; Kurakawa et al., 2007). *Short panicle 1* (*SP1*) and *DENSE AND ERECT PANICLE1* (*DEP1*) control panicle size through enhancing meristem activity (Huang et al., 2009c; Li et al., 2009). *Ghd7* delays heading date through its enhanced expression under long-day conditions, resulting in increased plant height and panicle size (Xue et al., 2008).

It was shown that *TAD1*/*TE* controls rice tiller number by regulating the stability of MOC1 protein (Lin et al., 2012; Xu et al.,

Gene	Accession number	Functional annotation	Controlling trait	References
An-1	LOC_Os04g28280	Basic HLH protein	Yield	Luo et al., 2013b
BG1	LOC_Os03g07920	Primary auxin response gene	Yield	Liu et al., 2015a
D1	LOC_Os05g26890	G protein alpha subunit	Yield	Miura et al., 2009
D14	LOC_Os03g10620	Responser of SL signaling	Yield	Zhao et al., 2015b
D27	LOC_Os11g37600	Iron-containing protein	Yield	Lin et al., 2009
D53	LOC_Os11g01330	Substrate of the SCF^{D3} ubiquitination complex	Yield	Jiang et al., 2013; Zhou et al., 2013
DEP1	LOC_Os09g26999	PEBP-domain protein	Yield	Huang et al., 2009c
DEP2	LOC_Os07g42410	Plant-specific protein	Yield	Li et al., 2010a
DST	LOC_Os03g57240	ZFN transcription factor	Yield/abiotic stress	Li et al., 2013b; Huang et al., 2009b
ETR2	LOC_Os04g08740	Ethylene receptor protein	Yield	Wuriyanghan et al., 2009
GAD1	LOC_Os08g37890	Epidermal patterning factor like protein	Yield	Jin et al., 2016
Ghd7	LOC_Os07g15770	CCT domain protein	Yield	Xue et al., 2008
Ghd7.1	LOC_Os07g49460	Pseudo-response regulator	Yield	Yan et al., 2013
GIF1	LOC_Os04g33740	Cell-wall invertase	Yield	Wang et al., 2008a
GL2/OsGRF4	LOC_Os02g47280	Growth-regulating factor	Yield	Che et al., 2015; Duan et al., 2015
GL3.1	LOC_Os03g44500	Ser/Thr phosphatase	Yield/grain size	Qi et al., 2012
GS5	LOC_Os05g06660	Serine carboxypeptidase	Yield/grain size	Li et al., 2011b
GW2	LOC_Os02g14720	RING-type E3 ubiquitin ligase	Yield/grain size	Song et al., 2007
GW5	DQ991205	Calmodulin binding protein	Yield/grain size	Weng et al., 2008
GW7	LOC_Os07g41200	TONNEAU1-recruiting motif protein	Yield/grain size	Wang et al., 2015b
HAF1	LOC_Os04g55510	RING-type E3 ubiquitin ligase	Yield	Yang et al., 2015b
HOX12	LOC_Os03g10210	Homeodomain-leucine zipper transcription factor	Yield	Gao et al., 2016
LAX1	LOC_Os01g61480	bHLH transcription factor	Yield	Oikawa and Kyozuka, 2009
IPA1	LOC_Os08g39890	SPL family protein	Yield	Jiao et al., 2010; Zhang et al., 2017a
OsGA20ox2	LOC_Os01g66100	Gibberellin 20-oxidase	Yield	Lo et al., 2008
OsMADS57	LOC_Os02g49840	MADS-box gene	Yield	Guo et al., 2013
OsSPL13	LOC_Os07g32170	SPL family protein	Yield/grain size	Si et al., 2016
OsSPL16	LOC_Os08g41940	SPL family protein	Yield/grain size	Wang et al., 2012
PROG1	LOC_Os07g05900	ZFN transcription factor	Yield	Tan et al., 2008
RFL	LOC_Os04g51000	Rice LFY homolog protein	Yield	Rao et al., 2008
SCM2/APO1	LOC_Os06g45460	Ortholog of *Arabidopsis LEAFY*	Yield	Ookawa et al., 2010
SPIN1	LOC_Os03g60110	K homology domain protein	Yield	Vega-Sánchez et al., 2008
TAD1/TE	LOC_Os03g03150	Coactivator of APC/C	Yield	Lin et al., 2012; Xu et al., 2012
TGW6	LOC_Os06g41850	IAA-glucose hydrolase gene	Yield	Ishimaru et al., 2013
Badh2	LOC_Os08g32870	Betaine aldehyde dehydrogenase	Grain quality	Chen et al., 2008
Chalk5	LOC_Os05g06480	Vacuolar H^+-translocating pyrophosphatase	Grain quality	Li et al., 2014c

Table 2. Representative Genes Related to Agronomically Important Traits in Rice.

(Continued on next page)

Gene	Accession number	Functional annotation	Controlling trait	References
FLO2	LOC_Os04g55230	Tetratricopeptide repeat motif protein	Grain quality	She et al., 2010
GPA4	LOC_Os03g11100	Golgi transport	Grain quality	Wang et al., 2016b
OsPho1	LOC_Os03g55090	α-Glucan plastidial phosphorylase	Grain quality	Satoh et al., 2008
OsAAP6	LOC_Os01g65670	Amino acid permease	Grain quality	Peng et al., 2014
SSIIIa	LOC_Os08g09230	Starch synthase	Grain quality	Zhou et al., 2016
Waxy	LOC_Os06g04200	Granule-bound starch synthase	Grain quality	Tian et al., 2009
Bsr-d1	LOC_Os03g32230	ZFN transcription factor	Disease resistance	Li et al., 2017b
COPT1	LOC_Os01g56420	Copper transporter gene	Disease resistance	Yuan et al., 2010
COPT5	LOC_Os05g35050	Copper transporter gene	Disease resistance	Yuan et al., 2010
GH3-8	LOC_Os07g40290	IAA amino acid synthetase	Disease resistance	Ding et al., 2008
LHS1	LOC_Os03g11614	MADS-box gene	Disease resistance	Yi et al., 2009
OsBBI1	LOC_Os06g03580	RING-type E3 ubiquitin ligase	Disease resistance	Li et al., 2011a
OsCUL3a	LOC_Os02g51180	Cullin protein	Disease resistance	Liu et al., 2017b
OsRac1	LOC_Os01g12900	Small GTP-binding protein	Disease resistance	Nakashima et al., 2008
Pi21	LOC_Os04g32850	Proline-rich protein	Disease resistance	Fukuoka et al., 2009
PigmR/S	KU904633	*Pyricularia oryzae* resistance-gm	Disease resistance	Deng et al., 2017
Rac1-RbohB/H	LOC_Os01g25820	Respiratory burst oxidase homolog	Disease resistance	Nagano et al., 2016
RACK1	LOC_Os01g49290	Receptor for activated C kinase 1	Disease resistance	Nakashima et al., 2008
STV11	LOC_Os11g30910	Sulfotransferase	Disease resistance	Wang et al., 2014d
TIG1	EDK00306	HDAC transcriptional corepressor complex	Disease resistance	Ding et al., 2010
Tps1	LOC_Os08g34580	Trehalose-6-phosphate synthase gene	Disease resistance	Wilson et al., 2010
Xa10	LOC_Os11g37620	TAL effector-dependent R gene	Disease resistance	Tian et al., 2014
Xa21	LOC_Os11g35500	Receptor kinase-like protein	Disease resistance	Park and Ronald, 2012
Xa25	LOC_Os12g29220	MtN3/saliva family protein	Disease resistance	Richter et al., 2014
XB24	LOC_Os01g56470	ATPase	Disease resistance	Chen et al., 2010
BPH3	LOC_Os04g12580	Lectin receptor kinase 3	Resistance to Insects	Liu et al., 2015c
BPH9	LOC_Os12g37280/90	Leucine-rich repeat-containing/ NB-ARC protein	Resistance to insects	Zhao et al., 2016b
BPH14	LOC_Os03g63150	CC-NB-LRR protein	Resistance to insects	Du et al., 2009
COLD1	LOC_Os04g51180	Regulator of G-protein signaling	Abiotic stress	Ma et al., 2015b
CTB4a	LOC_Os04g04330	Leucine-rich repeat receptor-like kinase	Abiotic stress	Zhang et al., 2017c
DWA1	LOC_Os09g19900	G-beta repeat domain protein	Abiotic stress	Zhu and Xiong, 2013
ERECTA	LOC_Os06g10230	Receptor-like cytoplasmic kinase	Abiotic stress	Shen et al., 2015
MODD	LOC_Os03g11550	Mediator of OsbZIP46 deactivation and degradation	Abiotic stress	Tang et al., 2016
OsSKIPa	LOC_Os02g52250	SKIP/SNW domain protein	Abiotic stress	Hou et al., 2009
OsTT1	LOC_Os03g26970	α2 subunit of the 26S proteasome	Abiotic stress	Li et al., 2015
PYL9	LOC_Os06g36670	Pyrabactin resistance-like ABA receptor	Abiotic stress	Zhao et al., 2016a
qLTG3-1	LOC_Os03g01320	Low-temperature germinability QTL	Abiotic stress	Fujino et al., 2008
SIT1	LOC_Os02g42780	Receptor-like kinase	Abiotic stress	Li et al., 2014a
SLR1	LOC_Os03g49990	GRAS-domain protein	Abiotic stress	Fukao and Bailey-Serres, 2008

Table 2. *Continued*

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Gene	Accession number	Functional annotation	Controlling trait	References
SNORKEL1	AB510478	Ethylene response factor	Abiotic stress	Hattori et al., 2009
SNORKEL2	AB510479	Ethylene response factor	Abiotic stress	Hattori et al., 2009
SUB1A	LOC_Os09g15430	ERF transcriptional regulators	Abiotic stress	Singh and Sinha, 2016
CK2α3	LOC_Os03g10940	CK2 kinase	NUE	Chen et al., 2015
H^+-ATPase	LOC_Os12g44150	Plasma membrane ATPase	NUE	Wang et al., 2014a
HsfA4a	LOC_Os01g54550	Heat shock transcription factor	NUE	Shim et al., 2009
Lsi6	LOC_Os06g12310	Silicon influx transporter in rice	NUE	Yamaji et al., 2008
NRAT1	LOC_Os02g03900	Nramp aluminum transporter 1	NUE	Xia et al., 2010
NRT1.1B	LOC_Os10g40600	Nitrate-transporter gene	NUE	Hu et al., 2015a
OsAKT1	LOC_Os01g45990	Shaker K^+ channel	NUE	Li et al., 2014b
OsHKT2;4	LOC_Os06g48800	High-affinity potassium transporter	NUE	Lan et al., 2010
OsHMA4	LOC_Os02g10290	Cu-transporting ATPase gene	NUE	Huang et al., 2016
OsNAS3	LOC_Os07g48980	Nicotinamine synthase gene	NUE	Lee et al., 2009
OsNRT2.3b	LOC_Os01g50820	High-affinity nitrate transporter	NUE	Fan et al., 2016a
OsPTR9	LOC_Os06g49250	Peptide transporter	NUE	Fang et al., 2013
qNGR9	LOC_Os09g26999	PEBP domain protein	NUE	Sun et al., 2014
PSTOL1	BAK26566	Phosphorus-starvation tolerance	NUE	Gamuyao et al., 2012
SPX1	LOC_Os06g40120	SPX domain gene	NUE	Wang et al., 2014e
SPX4	LOC_Os03g61200	SPX domain gene	NUE	Lv et al., 2014
STAR1	LOC_Os06g48060	Bacterial-type ABC transporter	NUE	Huang et al., 2009a
STAR2	LOC_Os05g02750	Bacterial-type ABC transporter	NUE	Huang et al., 2009a
SPDT	LOC_Os06g05160	SULTR-like phosphorus distribution transporter	NUE	Yamaji et al., 2016
CSA	LOC_Os01g16810	R2R3-type MYB gene	Reproductive development	Zhang et al., 2010
CYP704B2	LOC_Os03g07250	Cytochrome P450 family member	Reproductive development	Li et al., 2010b
DPL1	LOC_Os01g15448	Paralogous hybrid incompatibility gene	Reproductive development	Mizuta et al., 2010
G1	LOC_Os07g04670	*Arabidopsis* LSH1 and Oryza G1	Reproductive development	Yoshida et al., 2009
NL1	LOC_Os05g50270	GATA type transcription factor	Reproductive development	Wang et al., 2009
OsGAmyb	LOC_Os01g59660	Gibberellin MYB gene	Reproductive development	Aya et al., 2009
OsMADS3	LOC_Os01g10504	MADS-box gene	Reproductive development	Hu et al., 2011
OsNP1	LOC_Os10g38050	Glucose methanol choline oxidoreductase	Reproductive development	Chang et al., 2016
PMS1T	DQ989628	PHAS locus	Reproductive development	Fan et al., 2016b
pms3	JQ317784/JQ317785	Photosensitive genic male sterility genes	Reproductive development	Ding et al., 2012
PTB1	LOC_Os05g05280	RING-type E3 ubiquitin ligase	Reproductive development	Li et al., 2013a
Rf3	JX131325	Pollen fertility restoration-3	Reproductive development	Luo et al., 2013a
Rf4	LOC_Os10g35240	Pentatricopeptide repeat protein	Reproductive development	Luo et al., 2013a
RF5	LOC_Os10g35436	Pentatricopeptide-repeat family protein	Reproductive development	Hu et al., 2012
RF6	LOC_Os08g01870	Pentatricopeptide-repeat family protein	Reproductive development	Huang et al., 2015a
S5-ORF3	LOC_Os06g10990	Wide compatibility gene	Reproductive development	Yang et al., 2012
S5-ORF4	LOC_Os06g11000	Wide compatibility gene	Reproductive development	Yang et al., 2012
S5-ORF5	LOC_Os06g11010	Wide compatibility gene	Reproductive development	Yang et al., 2012

Table 2. *Continued*

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Gene	Accession number	Functional annotation	Controlling trait	References
SaF	LOC_Os01g39670	F-box protein	Reproductive development	Long et al., 2008
SaM	LOC_Os01g39680	SUMO E3 ligase-like	Reproductive development	Long et al., 2008
UbL404	LOC_Os09g31031	Ubiquitin fusion ribosomal protein L40 gene	Reproductive development	Zhou et al., 2014

Table 2. ***Continued***

2012). *OsTB1* coupled with *OsMADS57* modulates rice tillering via *D14*, which participates in the strigolactone signaling pathway (Guo et al., 2013). Other genes such as *LAZY1*, *LPA1*, and *PROG1* participate in the regulation of rice tiller angle and influence rice plant architecture (Li et al., 2007; Jin et al., 2008; Wu et al., 2013). *SPL* family genes regulate the architecture of rice plants by inhibiting tillering and promoting panicle branching at optimal expression levels to increase grain number (Wang et al., 2015b; Wang and Zhang, 2017). *OsSPL14* (*IPA1*/*WFP*), which is one of the targets of *OsmiR156*, regulates rice plant architecture. *OsSPL14* directly binds to the promoter of rice *TEOSINTE BRANCHED1*, a negative regulator of tiller bud outgrowth, to suppress rice tillering (Jiao et al., 2010; Miura et al., 2010; Lu et al., 2013). Recent study shows that *OsSPL14* functions as a downstream transcription factor repressed by D53 in strigolactone signaling in rice (Song et al., 2017). In addition, *OsSPL14* can regulate panicle length and number of grains per panicle by directly mediating *DEP1*, a key gene for rice panicle architecture (Lu et al., 2013). The introduction of $OsSPL14^{ipa1}$ allele into Xiushui 11 (XS11) resulted in an approximately 11% increase of grain yield (Zhang et al., 2017a). Overexpression of *OsmiR397* led to a greater number of branches and grains per main panicle and substantially enhanced grain yield (Zhang et al., 2013b). Recent research demonstrated that repressed expression *FZP* could prolong the panicle branching period and increase grain yield (Bai et al., 2017). Huo et al. (2017) reported that *NUMBER OF GRAINS 1* (*NOG1*) encoding an enoyl-CoA hydratase can increase the grain yield by enhancing grain number per panicle.

Important progress has also been made in identification of genes related to grain size/weight. For example, *GS3* is a major QTL for grain length and weight (Fan et al., 2006; Mao et al., 2010). *GW2* encodes a RING-type protein with E3 ubiquitin ligase activity, controlling rice grain width and weight (Song et al., 2007). *GW5* functions in the ubiquitin–proteasome pathway to regulate cell division during seed development that affects grain width (Shomura et al., 2008; Weng et al., 2008). *GIF1* encodes a cell-wall invertase for increasing grain filling, which influences grain weight (Wang et al., 2008a). *DST* gene influences rice grain yield by controlling the biosynthesis of cytokinin (Li et al., 2013b). A dominant QTL, *GS2*/*OsGRF4*/*GL2*, which is regulated by *OsmiR396*, encodes a growth regulatory factor and controls grain size (Che et al., 2015; Duan et al., 2015; Hu et al., 2015b). In addition, blocking *OsmiR396* greatly increases grain yield by modulating development of auxiliary branches and spikelets through direct induction of *OsGRF6* (Gao et al., 2015).

Grain Quality

Rice grain quality is determined by four major factors, namely appearance, cooking, milling, and nutrition quality. Grain shape is a yield trait as well as a factor that determines the appearance quality of rice grains. Grain length gene *GS3* and width gene *GW5* are the major genes for grain shape, and play important roles in the regulation of the rate of head rice (Fan et al., 2006; Weng et al., 2008). *GS5* (Li et al., 2011b) is closely linked with *GW5*/*qSW5*, indicating that the region was selected during quality breeding (Shomura et al., 2008; Weng et al., 2008). The recently cloned gene *OsSPL13* can increase rice grain length (Si et al., 2016). Integration of elite genotypes (*gs3*, *GW7*, and *gw8*) can greatly enhance rice grain length but does not affect the grain yield, and thus can be applied to improve rice grain appearance (Wang et al., 2015c).

Grain chalkiness in rice is an undesirable trait that negatively affects the appearance, cooking, milling, and nutrition qualities as well as the head rice rate. *Chalk5* is a QTL that controls the chalkiness of rice grains (Li et al., 2014c), which encodes a pyrophosphatase that transports H^+ in vacuoles. *Chalk5* is a positive regulatory factor with specific expression in the endosperm, and its high expression and enzyme activity elevate H^+ concentration and increase the water loss in the vacuoles, resulting in the formation of chalky endosperm. Genes for grain shape also influence chalkiness. For example, *qTGW6* can enhance grain length/width ratio and at the same time remarkably decrease the rate of chalkiness in rice grains under high-temperature stress (Kim et al., 2014a). *OsSPL16*/*GW8* and *GW7* increase grain length and decrease grain width, and also significantly decrease chalkiness (Wang et al., 2012, 2015c).

Eating and cooking quality of rice grain is generally determined by three physicochemical indices: amylase content, gel consistency, and gelatinization temperature (GT). The *waxy* gene regulates the amylose content in the endosperm (Wang et al., 1995), and *ALK*/*SSIIa* and *RSR1* control the GT (Zhang et al., 2011). The rice grain fragrance is mainly controlled by *Badh2*, which encodes glycine betaine aldehyde dehydrogenase (Bradbury et al., 2005). In most fragrant rice varieties, there is an 8-bp deletion at the seventh exon in *Badh2* gene, causing the loss of function of *Badh2* and accumulation of its substrate 2-acetyl-1-pyrroline, resulting in fragrance (Chen et al., 2008).

Rice grain nutritional quality mainly comprises the grain protein content (GPC), and contents of fats, amino acids, vitamins, and other micronutrients. *qPC1*, encoding a putative amino acid transporter OsAAP6, accelerates the synthesis and accumulation of glutelins, prolamins, globulins, albumins, and starch, thus significantly enhancing the GPC (Peng et al., 2014).

Disease Resistance

A large number of pathogens, such as fungi (blast, false smut, sheath blight), bacteria (bacterial blight, bacterial stripe disease),

viruses (stripe virus disease, rice black-streaked dwarf disease), and nematodes, cause diseases in rice, resulting in serious yield losses worldwide. Functional genomics research of rice disease resistance has been mainly focused on the resistance against bacterial blight caused by the bacterial pathogen *Xanthomonas oryzae* pv. *oryzae* and blast caused by the fungal pathogen *Magnaporthe oryzae*.

Over 100 QTLs for rice blast resistance have been mapped, distributed on 11 of the chromosomes except for chromosome 3, and densely on chromosomes 6, 11, and 12. Twenty-seven genes have been cloned: *Pib*, *Pi-ta*, *Pi9*, *Pi2*, *Piz-t*, *Pi-d2*, *Pi33*, *Pii*, *Pi36*, *Pi37*, *Pikm*, *Pit*, *Pi5*, *Pid3*, *Pid3-A4*, *Pi54*, *Pish*, *Pik*, *Pik-p*, *Pi-CO39*, *Pi25*, *Pi1*, *Pb1*, *Pi64*, *LABR_64-1*, *LABR_64-2*, and *Pigm* (Liu et al., 2014; Deng et al., 2017). Most of the disease resistance genes (R genes) belong to NBS-LRR (nucleotide binding site and leucine-rich repeat) family. *Pigm* was recently found to be a gene cluster consisting of multiple NBS-LRR genes, and there are two functional proteins, namely PigmR and PigmS. PigmR confers broad-spectrum resistance, whereas PigmS competitively attenuates PigmR homodimerization to suppress the resistance (Deng et al., 2017). A single-nucleotide change in the promoter of the *bsr-d1* gene confers broad-spectrum blast resistance (Li et al., 2017c).

To date, at least 40 QTLs for bacterial blight resistance have been reported in rice. Eleven genes have been cloned, including seven dominant genes (*Xa1*, *Xa3/Xa26*, *Xa4*, *Xa10*, *Xa21*, *Xa23*, and *Xa27*) and four recessive genes (*xa5*, *xa13*, *xa25*, and *xa41*) (Zhang and Wang, 2013). These genes encode various types of proteins: *Xa1* is a member of the NBS-LRR class of plant disease-resistance genes; *Xa10* is localized on the endoplasmic reticulum and encodes a transcription activator-like (TAL) effector-dependent *R* gene for resistance to bacterial blight (Tian et al., 2014); *Xa23* encodes a 113-amino-acid transmembrane protein; *Xa3/Xa26* and *Xa21* encode LRR-kinase proteins; *xa5* provides race-specific resistance to *X. oryzae* pv. *oryzae*, and encodes the small subunit of transcription factor IIA; *xa13*, *xa25*, and *xa41* encode transmembrane proteins; *Xa4* encodes a cell wall-associated kinase and enhances resistance to bacterial infection by strengthening the cell wall (Hu et al., 2017a).

Five QTLs for stripe virus resistance have been reported in *indica* rice, including *Stv-bi*, $qSTV11^{IR24}$, $qSTV11^{TQ}$, $qSTV11^{KAS}$, and $qSTV11^{SG}$. All of them are located on chromosome 11. $qSTV11^{KAS}$ enhances resistance to stripe virus by catalyzing the conversion of salicylic acid into sulfonated SA (Wang et al., 2014d).

Resistance to Insect Pests

The major insect pests of rice include plant hoppers, leafhoppers, striped stem borer, yellow stem borer, leaf folders, and gall midge. A number of insect-resistant germplasms have been found from both cultivated and wild rice species. Great progress has been made in identifying resistance genes to brown planthopper (BPH), with 31 genes genetically mapped. Among these genes, *Bph3* (*Bph17*), *Bph14*, *Bph26* (*bph2*), and *bph29* have been cloned through map-based cloning. *Bph14* is the first cloned gene conferring resistance to BPH (Du et al., 2009; Hu et al., 2017b). It encodes a coiled-coil, nucleotide-binding, and leucine-rich repeat (CC-NB-LRR) protein. *Bph14* activates the salicylic acid signaling pathway and induces callose deposition in phloem cells and trypsin inhibitor production after planthopper infestation, thus conferring resistance to BPH. *BPH9* was identified from an *indica* rice variety Pokkali, encoding a CC-NB-LRR protein. Seven previously identified genes, *BPH1*, *BPH2*, *BPH7*, *BPH10*, *BPH18*, *BPH21*, and *BPH26*, are alleles of this locus (Zhao et al., 2016b). *BPH29* is a recessive gene derived from common wild rice RBPH54 with a conserved nucleic acid binding domain (Wang et al., 2015d). The locus of *Bph3* is a cluster of three genes encoding three plasma membrane-localized lectin receptor kinases (*OsLecRK1 OsLecRK3*). The cumulative effect of the three genes confers high BPH resistance in Rathu Heenati (Liu et al., 2015c).

Nine genes and some QTLs related to *Sogatella furcifera* resistance have been mapped. Genetic analysis identified 11 dominant genes and three recessive genes for resistance to *Empoasca flavescens* (Fab.) (*Glh1*, *Glh2*, *Glh3*, *Glh5*, *Glh6*, *Glh7*, *Glh9*, *Glh11*, *Glh12*, *Glh13*, *Glh14*, *glh4*, *glh8*, and *glh10*) (Du et al., 2016). Six major genes for rice leafhopper resistance have been mapped (Fujita et al., 2004). Although some germplasms of both wild and cultivated rice for leaf folder resistance have been reported (Rao et al., 2010), no major genes for resistance have been demonstrated.

Resistance to Abiotic Stress

In the past decades, more than 100 stress-responsive genes and QTLs have been identified in rice through either the forward or reverse genetics approach (Wang et al., 2016a).

Various protein kinases are involved in the mediation of abiotic stress responses. OsMAPK5 was functionally characterized as a stress-responsive MAPK (mitogen-activated protein kinase) that positively regulates the tolerance to abiotic stresses such as drought, salt, and cold but negatively regulates the tolerance to biotic stresses such as fungi and bacteria (Xiong and Yang, 2003).

Transcription factors also play important roles in regulating abiotic stress tolerance of rice. Overexpressing the members of bZIP, SKIP, and NAC transcription factor families could significantly enhance the drought tolerance of rice. For instance, the members of the NAC transcription factor family, *OsNAC6*, *OsNAC10*, *OsNAC9*, and *OsNAC5*, are involved in drought response, and constitutive activation of each of *OsbZIP16*, *OsbZIP23*, *OsbZIP46*, and *OsbZIP71* can also significantly increase drought tolerance (Fukao and Xiong, 2013). Transgenic rice overexpressing *OsSKIPa* exhibited significantly improved growth performance in the medium containing stress agents (Hou et al., 2009). Other transcription factors, such as *OsDREBE1*, *OsMYB3R-2*, and *OsZEP77*, were involved in the response to cold stress (Wang et al., 2008b; Ma et al., 2009).

COLD1, a QTL for chilling tolerance, was identified in *japonica* rice (Ma et al., 2015b). Overexpression of $COLD1^{jap}$ significantly enhances chilling tolerance in rice. *COLD1* encodes a regulator of G-protein signaling, and the *japonica* and *indica* varieties differ by an SNP. Li et al. (2015) identified a major QTL for thermotolerance in African rice (*Oryza glaberrima*), named

OgTT1 (*Thermo-Tolerance1*), encoding an α2 subunit of the 26S proteasome involved in the degradation of ubiquitinated proteins. Two genes for adaptation of rice to submergence, *SNORKEL* (*SK*) and *SUBMERGENCE-1* (*SUB1*), have been identified, conferring submergence escape and submergence tolerance, respectively (Xu et al., 2006; Hattori et al., 2009). Both of them encode tandem-repeated *ETHYLENE RESPONSIVE FACTOR* (*ERF*)-type transcription factors. Sub1A inhibits ethylene biosynthesis and the expression of cell-wall expansin proteins under submergence stress, resulting in submergence tolerance (Xu et al., 2006; Fukao and Bailey-Serres, 2008). Furthermore, SUB1A serves as a convergence point between submergence and drought response pathways, allowing rice plants to survive under drought tolerance (Fukao et al., 2011). Recently, it was reported that mitogen-activated protein kinase 3 (MPK3) regulates submergence escape through physically interacting with and phosphorylating SUB1A in a tolerant-allele-specific manner (Singh and Sinha, 2016). In addition, the ubiquitin E3 ligase OsHTAS has also been reported to enhance heat tolerance in rice (Liu et al., 2016).

Nutrient-Use Efficiency

To date, great progress has been achieved in uncovering the mechanisms of how rice senses and responds to external nutrients. Rice absorbs and transports ammonium nitrogen and nitrate nitrogen through ammonium transporters (AMTs) and nitrate transporters (NRTs), respectively. There are more than 80 NRT1/PTR, four NRT2, and two NAR2 members in rice (Li et al., 2017b; Xuan et al., 2017), but the functions for only a few of them have been clearly characterized. *OsNRT1* is a low-affinity nitrate transporter mediating nitrate uptake in roots (Lin et al., 2000; Leran et al., 2014). Overexpression of *OsPTR6* significantly improves rice growth but has little effect on nitrogen-use efficiency (Fan et al., 2014). Transgenic rice overexpressing *OsPTR9* also exhibited higher nitrogen-use efficiency and yields (Fang et al., 2013), but its ability to transport nitrate has not been confirmed. Variation in *NRT1.1B* contributes to the differences in higher nitrogen-use efficiency between *japonica* and *indica* rice. Introduction of *indica NRT1.1B* into *japonica* cultivars can potentially improve the higher nitrogen-use efficiency of *japonica* (Hu et al., 2015a). OsNRT2.1, OsNRT2.2, and OsNRT2.3a need to interact with OsNAR2.1 for nitrate uptake, while OsNRT2.3b and OsNRT2.4 can function independently of NAR2 (Yan et al., 2011). Ammonium is the major form of nitrogen source for rice. There are five subfamilies of ammonium transport proteins (OsAMT1–5) in rice. OsAMT1, OsAMT2, and OsAMT3 comprise three members each. OsAMT4 has only one member, and OsAMT5 includes two members. It was reported that OsAMT1;1, OsAMT1;2, OsAMT2;1, and OsAMT5;1 have the ability to transport ammonium. *OsAMT1;1* is a low-affinity ammonium transporter, and transgenic lines overexpressing *OsAMT1;1* exhibited symptoms of ammonium toxicity (Yang et al., 2015a). The transcription factor IDD10 (indeterminate domain 10) activates the transcription of *OsAMT1;2* to mediate the absorption of ammonium (Xuan et al., 2013). As for the nitrogen assimilation in rice, glutamine synthetase (GS), a key enzyme in nitrogen assimilation and remobilization, forms the GS-GOGAT cycle with glutamate synthase (GOGAT) to convert inorganic ammonium into glutamine. Two GS members (*OsGS1;1* and *OsGS1;2*) and two kinds of GOGAT (Fd-GOGAT and NADH-GOGAT) have been characterized in rice (Li et al., 2017b). Different *DEP1* alleles confer different nitrogen responses, and affect plant height and tiller number (Sun et al., 2014). A major QTL, *Tolerance of Nitrogen Deficiency 1* (*TOND1*), encodes a protein with thaumatin domain, conferring tolerance to nitrogen deficiency in the *indica* cultivar Teqing (Zhang et al., 2015).

Pup1 is a major QTL for phosphorus-deficiency tolerance (*PSTOL1*), which was identified from a traditional aus-type rice variety Kasalath. Overexpression of *PSTOL1* in modern rice varieties significantly enhances grain yield in phosphorus-deficient soil (Gamuyao et al., 2012). SULTR-like phosphorus distribution transporter (SPDT) controls the allocation of phosphorus to the grain. Knockout of *SPDT* decreased phosphorus content in the grains (Yamaji et al., 2016). PHR1 is a major regulatory factor of phosphate signaling in rice, and PHR2 enhances the expression of phosphate starvation-induced (PSI) genes via binding to its *cis*-regulatory elements (Lv et al., 2014). SPX4 negatively regulates phosphate signaling and homeostasis through interaction with PHR2. There has also been investigation of the regulatory mechanisms of potassium signaling in rice. It was reported that the Os-AKT1 channel is critical for K^+ uptake in rice roots (Li et al., 2014b).

Reproductive Development

Male sterility is a major subject of research on reproductive development in rice for both basic biology and breeding application. Zhang and Yuan (2014) summarized the relevant genes and molecular regulatory mechanism of microspore development in rice. Here, we provide a brief overview of the key genes identified in recent years that are relevant to hybrid rice breeding.

There are several major types of cytoplasmic male sterility (CMS): CMS-WA (wild abortive), CMS-HL (Honglian), and CMS-BT (Boro II) (Chen and Liu, 2014). Six CMS genes (*orf79*, *orfH79*, *WA352a*, *WA352b*, *WA352*/*WA352c*, and *WA314*) from the mitochondrial genome and four *Rf* genes (*Rf1a*/*Rf5*, *Rf1b*, *Rf4*, and *Rf6*) from the nuclear genome have been identified in CMS/*Rf* systems (Tang et al., 2017). Luo et al. (2013a) identified a CMS-WA gene *WA352*, which interacts with nuclear-encoded mitochondrial protein COX11 and thereby triggers pollen abortion, resulting in male sterility. Further study indicated that two fertility-restorer genes, *Rf3* and *Rf4*, restore the fertility through inhibiting the expression of *WA352* (Luo et al., 2013a). ORFH79 impairs mitochondrial function and then confers male sterility in CMS-HL (Wang et al., 2013). *RF5* encodes a pentatricopeptide repeat (PPR) protein in CMS-HL, which is identical to *Rf1A* in Boro II. The physical interaction between RF5 and GRP162 involves the processing of the CMS-associated transcript atp6-orfH79, and results in the restoration of fertility for CMS-HL (Hu et al., 2012). Another PPR protein RF6 interacts with OsHXK6, leading to rescue fertility for CMS-HL (Huang et al., 2015a).

Photoperiod-sensitive and thermosensitive genic male sterility (PGMS and TGMS) are the core components in two-line system breeding in rice. A long non-coding RNA, *pms3*, regulates PGMS (Ding et al., 2012). *p/tms12-1*, which shares the same locus with *pms3*, confers PGMS in the *japonica* rice line Nongken 58S and TGMS in the *indica* rice line Peiai 64S (Zhou et al., 2012). Another PGMS gene, *pms1*, produces a transcript

PMS1T targeted by miR2118 to generate 21-nt phasiRNAs. The abundance of the phasiRNAs is associated with the PGMS of Nongken 58S (Fan et al., 2016b). In TGMS line AnnongS-1, *tms5* causes the TGMS trait through a loss-of-function mutation in the gene coding for RNase Z^{S1} (Zhou et al., 2014). The aberrant transcripts of *Ugp1* undergo temperature-sensitive splicing in florets, leading to a novel TGMS (Chen et al., 2007). Rice *CARBON STARVED ANTHER* (*CSA*) encodes an R2R3-MYB transcription factor. Mutation in *CSA* results in male sterility under short-day conditions and normal fertility under long-day conditions (Zhang et al., 2013a).

Rice inter-subspecific hybrids are usually highly sterile. Genetic analyses of *indica–japonica* hybrids have identified a large number of loci conditioning hybrid sterility. *S5* is a major locus for hybrid sterility in rice that affects embryo sac fertility. A killer-protector system at the S5 locus encoded by three tightly linked genes regulates the fertility of *indica–japonica* hybrids (Yang et al., 2012). Rice pollen hybrid incompatibility genes, *DPL1* and *DPL2*, which encode highly conserved plant-specific small molecular proteins, play essential roles in the pollen germination of *indica–japonica* hybrids (Mizuta et al., 2010). Kubo et al. (2016) identified that the *hsa1* locus contains two interacting genes, *HSA1a* and *HSA1b*, which regulate the female gamete sterility of *indica–japonica* hybrids. Another locus for *japonica–indica* hybrid male sterility, *Sa*, also comprises two adjacent genes, *SaM* and *SaF*, encoding a small ubiquitin-like modifier E3 ligase-like protein and an F-box protein, respectively (Long et al., 2008). Recently, Shen et al. (2017a, 2017b) reported that genomic structural variation-mediated allelic suppression at *Sc* locus confer *japonica–indica* hybrid male sterility.

FROM FUNCTIONAL GENOMICS RESEARCH TO GREEN SUPER RICE BREEDING

To realize ''resource-saving and environment-friendly'' modern agriculture, a notion of green super rice (GSR) was proposed, such that the new rice varieties should possess resistances to multiple insects and diseases, high water and NUE, and high yield and good grain quality (Zhang, 2007). An international coordinated project named ''RICE2020'' in rice functional genomics research was proposed (Zhang et al., 2008), with the mission to decode the rice genome and apply the findings of functional genomics research to developing GSR.

Rice functional genomics research has provided abundant gene resources for developing GSR. For example, *Xa21* and *xa13* can be used to prevent rice bacterial leaf blight (Chu et al., 2006; Chen et al., 2010; Yuan et al., 2010). *Pigm* and *Bsr-d1* confer broad-spectrum resistance to rice blast and can be used in disease resistance breeding (Deng et al., 2017; Li et al., 2017c). Brown planthopper resistance gene *Bph14* was identified in *Oryza minuta* (Du et al., 2009), indicating that there are useful genes in wild rice. Other useful alleles, such as brown planthopper resistance gene *BPH3* (Liu et al., 2015c), salt tolerance gene *HKT2* (Lan et al., 2010), submerge tolerance gene *Sub1* (Singh and Sinha, 2016), and high-temperature tolerance gene *OsTT1* (Li et al., 2015), were identified from local varieties. These genes have great potentials to be used in rice breeding for stress tolerance. Genes for nitrogen-use efficiency *NRT1.1B* and *DEP1* (Sun et al., 2014; Hu et al., 2015a), and cold-tolerance gene *COLD1* (Ma et al., 2015b) have functional differentiations between *indica* and *japonica*, and can be applied to enhance the cold tolerance and nitrogen-use efficiency in rice breeding. Besides, photosensitive genic male sterility genes and thermosensitive sterility genes can be used in the breeding of two-line hybrids (Ding et al., 2012; Fan et al., 2016b). Genetic manipulation of wide compatibility locus *S5* (*ORF3*, *ORF4*, *ORF5*) would break down reproductive isolation and allow the hybridization between *indica* and *japonica* rice (Yang et al., 2012).

It is worth pointing out that the latest advances of the regulatory modules to improve important agronomic traits have been reported in rice. In the super rice Yongyou12, *ipa1-2D* locus is associated with reduced DNA methylation that attenuates the epigenetic repression of *IPA1* promoter and leads to increased yield in rice (Zhang et al., 2017a). Si et al. (2016) identified a tandem-repeat sequence in the 5′ UTR of *OsSPL13*, which alters its expression by affecting transcription and translation, and high expression level of *OsSPL13* is associated with large grains in tropical *japonica* rice. A translational repression mediated by a miniature inverted-repeat transposable element in the 3′ UTR of *Ghd2* affects important agronomic traits, including grain number, plant height, and heading date (Shen et al., 2017a). The *microRNA* regulatory module also plays an important role in the gene expression and regulating yield in rice. For example, a mutation of *GS2* affecting the binding site of *OsmiR396c* causes elevated expression of *GS2* and enhances grain weight and yield (Hu et al., 2015b). These findings presented a novel strategy for developing high-yield rice and improving the other important agronomic traits through manipulating the regulatory modules identified in rice, thus further contributing to the GSR breeding.

Genomic breeding chips facilitate the application of the findings from functional genomics research to the development of GSR. Genomic breeding chips can assist the accurate selection of the target genes and high-efficiency identification of genomic background, and thus enhance the efficiency of breeding. A number of genomic breeding chips have been developed globally in rice, such as the series of rice genome-wide breeding chips Rice6K and Rice60K. To date some useful markers of genes have been included in Rice6K, such as *IPA1* (plant architecture), *Sd-1* (plant height), *GS3* (grain length), *GW5* (grain width), and *Badh* (fragrance). RICE6K and RICE60K have been applied in the genotyping of germplasm resources and gene fingerprint identification of varieties (Chen et al., 2014a; Yu et al., 2014). With the progress in identification of agronomically important genes, more genes will be included in designing the chips to accelerate rice breeding.

CHALLENGES AND FUTURE PERSPECTIVES

Integration of the Resources and Datasets Generated by Various Platforms

Rice functional genomic research activities in the past decades have generated large resource, technological, and data

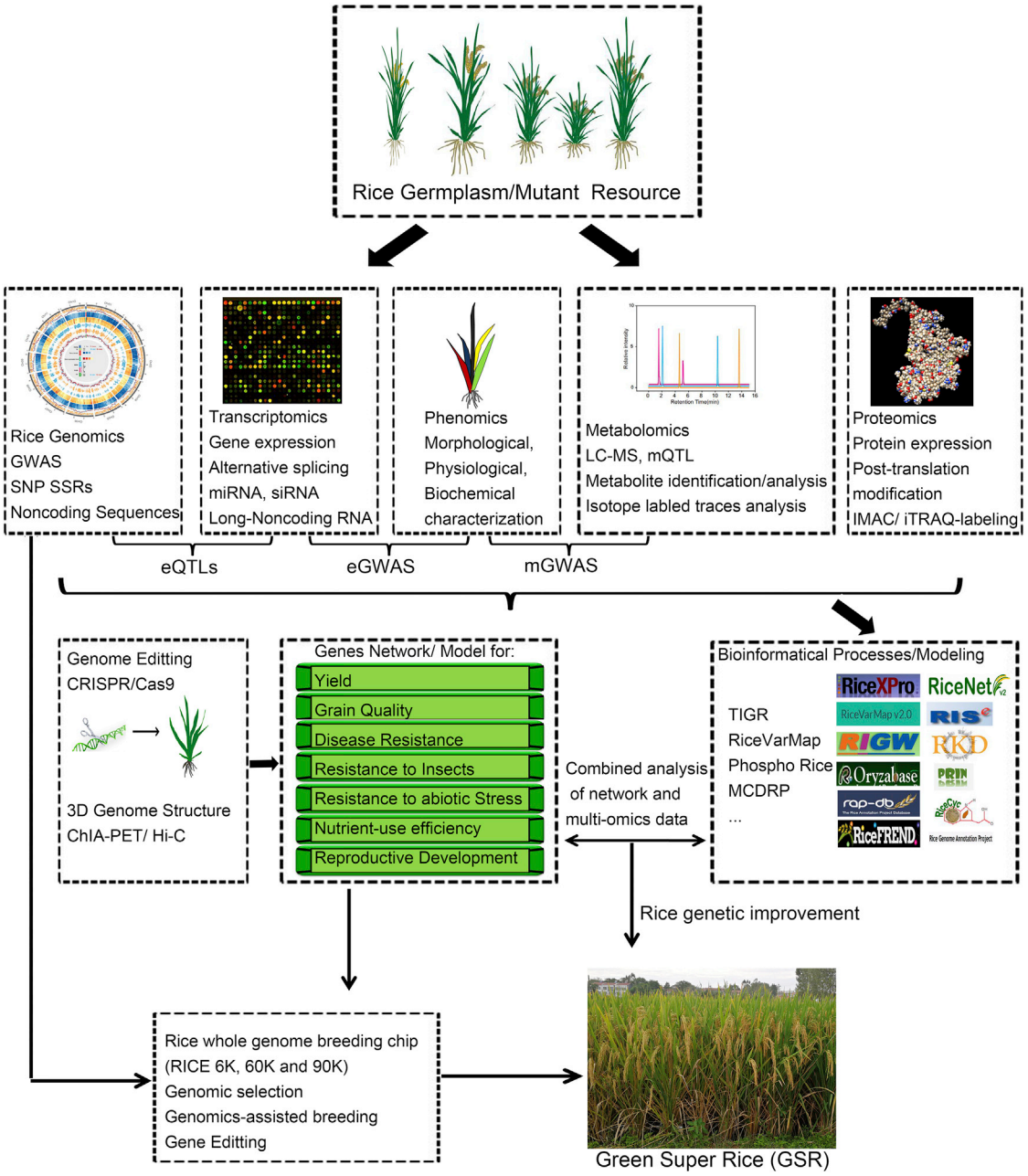

Figure 1. "Omics"-Based Approaches for Rice Functional Genomics Research and Their Integration to Develop Green Super Rice.
Flow of information from various "omics"-based platforms such as genomics, transcriptomics, metabolomics, proteomics, and phenomics needs to be integrated to understand complex traits net such as yield, grain quality, resistance, and NUE, toward the development of green super rice (GSR).

platforms, both in numbers and volumes as reviewed herein. Although collectively the amounts are huge, they are scattered as small pieces in may centers and small labs in many countries, and vary in format and quality. Extracting information for unified analysis and obtaining resources for joint studies by navigating these small databases and resource centers have been increasingly difficult and even prohibitive. Efforts should be made to consolidate these fragments into central/regional portals of data and resources to integrate them in specific order and classification to facilitate their utilization by the community. Such efforts may also help the development of Rice Systems Biology to understand the function of the rice genome.

Functional Analysis of Non-coding Sequences and Dispensable Genome Sequences

Non-coding sequences are prevalent in the genomes of eukaryotes, many of which are involved in complex and precise regulation of biological processes. Dispensable sequences are present in some individuals but not in others, and are believed to play important roles in phenotypic variation and genome evolution. Although

a specific dispensable sequence occurred only in a subset of the individuals in a given species, every individual carries certain dispensable sequences relative to others in the same species (Yao et al., 2015). Recently, high-quality genomes for *indica* rice of Zhenshan 97 and Minghui 63 (Zhang et al., 2016) and Shuhui 498 (Du et al., 2017) were obtained using third-generation sequencing technology, providing additional high-quality genomes for the discovery of genes and structure variations in rice. The recent availability of the 3K genome sequences together with the already large amounts of rice sequencing data have provided an almost unlimited data resource for the studies of (annotated) non-coding portions and dispensable portions of the genome (3,000 rice genomes project, 2014; Sun et al., 2016a). In addition, understanding of the dispensable portions may in turn help the determination of the indispensable genome, which may be used for conceiving (or constructing) an essential rice genome in questing a rice version of Synthetic Genome.

Decoding DNA Elements and Constructing 3D Genome Structure

The progress in the Human ENCODE (Encyclopedia of DNA Elements) Project has provided a model for studies of other organisms. Moreover, understanding how DNA is organized in three dimensions (3D) inside the cell nucleus can provide new insights into the mechanisms of gene regulation (The ENCODE Project Consortium, 2004, 2012).

Rice, with a relatively small genome size, accurate genome sequences of several varietal groups, considerable amounts of data for transcriptomes and epigenomes, and large number of characterized genes and informative genome annotation, is best positioned for studying DNA elements and 3D genome structure. Using a genome-wide chromatin conformation capture approach (Hi-C), Liu et al. (2017a) identified thousands of distinct topologically associated domains that cover about a quarter of the rice genome, which exhibited distinct structural features of chromatin organization at both chromosomal and local levels compared with *Arabidopsis thaliana*. In rice protoplast, Hi-C data showed high consistency with the whole-seedling Hi-C results, indicating that the chromatin contact pattern was not affected during the cell isolation process. Examinations of maize, tomato, sorghum, foxtail millet, and rice showed that different plants have their own complex and unique 3D chromatin architectures (Dong et al., 2017). In rice, long-term goals and strategies may be planned and designed with the help of the experience from Human ENCODE, to characterize the DNA elements and 3D genome of all organs and tissues, and further elucidate their biological functions.

Functional Genomics of Important Agronomic Traits

Functional genomic understanding of an agronomic trait refers to characterization of the genes (including non-coding sequences) and their regulatory networks, which collectively determine the formation and development of the trait. The formation of any trait involves a large array of genes, and the majority of the genes that participate in many processes thus affect the development of many traits (or pleiotropic effects). Data and literature accumulated to date have already clearly depicted such a ''net-like'' structure between genes and traits. In addition, formation and development of traits are greatly influenced by environmental conditions and also to some extent by field management practices. For functional genomic understanding of agronomic traits, a complex trait such as yield may be divided into subtraits, which in turn are subdivided into components and biological processes, which may be specified by pathways. Genes and regulatory networks then would be characterized for each component trait and process. Once the components are characterized, the genes and regulatory networks for the component traits and processes may then be assembled and integrated to form functional genomic understanding of the complex trait and applied to rice genomic breeding (Figure 1). Thus it is necessary to plan and pursue systematic efforts and strategies in future studies that are solidly based on the present findings, keeping in mind the net-like structure of the relationship between the genome and traits.

Designed Genomic Breeding Based on Functional Genomics Achievements

The ultimate goal of rice functional genomic research is for breeding application. The knowledge, genes, germplasms, and genomic data obtained presently are already sufficient to lead a revolutionary change in strategies and technologies in rice breeding, which can be termed ''designed genomic breeding.'' Such breeding may include the following components: (1) specifications of the traits (yield, quality, resistances to biotic and abiotic stresses, NUE) for cultivars adaptive to specific cropping systems, especially emphasizing resource saving and environment-friendly agriculture for green development; (2) lists of the genes and germplasms for the traits; (3) technologies for whole-genome selection and gene-specific introgression; (4) breeding programs for implementation. The progress in rice research may also provide models for other crops, thus transforming the norm of crop breeding.

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