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Review and Progress **Open Access**

Functional Genomics of Rice: Recent Discoveries and Future Prospects

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Abstract Rice (*Oryza sativa* L.) serves as a crucial staple food for over half of the global population and stands as a model organism for monocotyledon genomics research. Recent advancements in functional genomics have significantly enhanced the understanding of the genetic and molecular mechanisms underlying key agronomic traits in rice. Over the past decade, more than 2 000 genes associated with important traits such as yield, stress resistance, and nutrient use efficiency have been cloned and characterized. The development of comprehensive genomic resources, including large mutant libraries, global expression profiles, and extensive resequencing data, has accelerated gene discovery and functional analysis. The integration of these resources into platforms like the funRiceGenes database has facilitated the systematic characterization of rice genes, enabling more targeted breeding strategies. Furthermore, innovative tools such as the CRISPR Applicable Functional Redundancy Inspector (CAFRI-Rice) are addressing challenges like functional redundancy, thereby streamlining functional genomics research. The focus will be on leveraging these genomic insights to develop Green Super Rice varieties that combine high yield with sustainability, addressing the pressing need for increased food production in the face of global challenges.

Keywords Rice (*Oryza sativa* L.); Functional genomics; Gene cloning; Agronomic traits; Genomic resources

1 Introduction

Rice (*Oryza sativa* L.) is not only the staple food of more than half of the world's population, but also one of the most widely used research objects in plant science. Why study rice? In addition to its economic value, it is also because, as a representative of monocotyledons, it has rich genetic resources and clear genomic information. In the past decade, there has been a lot of research in this area. As soon as high-throughput sequencing technology came on the stage, researchers had new tools to explore genes related to key agronomic traits such as yield, stress resistance, and nutrient absorption. Now, more than 2 000 such genes have been identified (Jiang et al., 2012; Li et al., 2018).

Of course, genetic information alone is not enough. What really drives progress is the accumulation of resources and the maturity of technical means. For example, various large mutant libraries, full-length cDNA sequences, and expression profile data of different tissues and developmental stages have been established, which directly accelerated the pace of gene cloning and functional verification. The emergence of projects such as RICE2020 shows the extensive international cooperation in promoting rice genetic research (Zhang et al., 2008).

With the support of these technologies and resources, functional genomics has begun to play an increasingly important role in rice breeding. After all, the purpose is still the same - to select key genes that can improve rice yield, quality or environmental adaptability and turn them into usable tools. Here, high-throughput phenotyping platforms and mutagenesis technologies (such as T-DNA insertion or activation tagging) are particularly important because they directly connect the "causal chain" between genes and traits (Yang et al., 2013; Moin et al., 2017). This understanding not only stays in the laboratory, but also begins to truly serve breeding practice, such as developing new rice varieties that are more efficient, resistant to stress and suitable for sustainable agriculture (Huang et al., 2013).

This review focuses on the development of rice functional genomics in recent years, including both technical and resource aspects and exploration of practical applications. At the same time, we have to mention the problems that still exist in the research, such as the unclear functions of some genes, or the limitations of high-throughput technology in certain situations. What is the future direction? I am afraid that it is inseparable from international cooperation and multidisciplinary integration. Only in this way can we further understand the "full picture" of the rice genome and face the pressure of global food security with more confidence.

2 Progress in Rice Functional Genomics

2.1 High-throughput sequencing technology and its impact

In 2002, the advent of the draft of the rice genome was regarded as a major breakthrough, but that was just the beginning. Later, the addition of next-generation sequencing (NGS) technology suddenly accelerated the research progress of the rice genome. Compared with earlier methods, NGS has a wider coverage and is much faster, allowing researchers to quickly obtain genetic information of different germplasms and different strains, making it easier to analyze complex traits (Guo et al., 2014). However, the significance of this technology is not just in terms of sequencing speed. It has also greatly promoted molecular breeding, especially in terms of gene design. For example, the large number of SNP markers obtained through NGS are not only large in number, but also easy to call, suitable for high-throughput genotyping (Thomson, 2014). The relationship between genes and traits has also become clearer because of the accumulation of these data. Studies such as genome-wide association studies (GWAS) have developed rapidly relying on these marker resources.

It is worth mentioning that this wave of technological innovation relies not only on sequencing platforms, but also on practical analysis tools. Friendly software such as NGSEP has lowered the threshold for data processing, and many non-professional experimenters can also analyze gene variations (Duitama et al., 2014). From this perspective, the role of NGS is far more than "sequencing" in the laboratory.

Of course, even though NGS is already very mature, researchers still look to a more advanced solution - the third-generation sequencing technology. New technologies such as single-molecule real-time sequencing have longer read lengths and are more accurate. Especially when dealing with complex repetitive regions and identifying structural variations, its advantages are more obvious (Dijk et al., 2014). No PCR amplification is required, which means that there is less human interference during sequencing, making it closer to the real DNA sequence. This is a good tool for in-depth exploration of gene regulatory elements and new functional genes.

2.2 Genome databases and functional genomic resources

Current research cannot be separated from data, and rice genome data is particularly large. In this case, who will organize and how to organize it is particularly important. The value of the database is clearly reflected here. For example, the RICE2020 project attempts to find functional annotations for every gene in rice. It not only relies on sequencing data, but also integrates various phenotypic information (Yang et al., 2013). This kind of integration can help researchers see more quickly what traits a gene affects, and it is also convenient for subsequent verification.

As for the issue of data sharing, online platforms such as RAP-DB are very mature. It not only provides basic information about rice genes, but also expression conditions, functional predictions, and so on. Researchers do not need to look up information from scratch, they can use it by opening the webpage, which is very helpful for designing experiments. Although these platforms are already quite comprehensive, they are not static. As new data is added, they are also constantly updated. Only in this way can researchers get the latest information at any time and use it without being "outdated".

3 Discovery of Key Genes and Pathways in Rice Functional Genomics

3.1 Genes regulating stress resistance

Rice is not naturally able to easily resist drought, salinity or high temperature. Stress resistance itself is a multi-gene, multi-link trait, involving many regulatory pathways. For example, *OsPYL9*, an ABA receptor gene, was knocked out by researchers using CRISPR/Cas9 technology, and it was found that the mutant performed better under drought: ABA accumulation increased, antioxidant capacity increased, and yield did not drop (Usman et al., 2020). This is a bit unexpected.

But *OsPYL9* is just an example. In fact, drought resistance involves more than just the ABA pathway. Many quantitative trait loci (QTLs) have also been found, such as ABI5 and GBF4, which are genes that "show up" in drought response (Selamat and Nadarajah, 2021). These genes themselves may not be so "hot", but they are very active under stress.

Of course, not all relevant studies focus on ABA or transcription factors. Lenka et al. (2011) used transcriptome comparison to find that some genes involved in carbon fixation and flavonoid synthesis are also critical in drought-resistant genotypes. Although these genes seem a bit far from the word "drought resistance", they obviously play a role in maintaining basal metabolism and anti-oxidation. Similar situations also occur in salt and heat stress. For example, the *OsCDPK7* gene, which encodes a calcium-dependent protein kinase, performs well in regulating salt stress response. After overexpression, it can drive a group of stress-related genes to upregulate (Saijo et al., 2000). In other words, the presence of this gene can help rice maintain its position in harsh environments.

GWAS research is also not idle. In the study of salt tolerance at the seedling stage, the QTL qDTS1-2 is considered to be closely related to salt tolerance, and OsMYB48 may be a key regulatory factor, not only in salt tolerance, but also in drought tolerance (Kim and Kim, 2023). As for heat tolerance, meta-QTL analysis found genes such as OsBiP2 and OsWRKY10, which mainly play a role in heat stress of reproductive organs (Raza et al., 2020), which is particularly important for rice during the flowering and fruiting period.

3.2 Genes related to yield improvement

The study of stress resistance cannot avoid yield. Like *OsPYL9*, in addition to being able to withstand drought, it can also increase grain yield-regardless of whether it is adequately watered (Usman et al., 2020). This gene obviously takes care of both ends.

What factors affect yield? Grain development, panicle shape, and grain filling process are all considered. QTL analysis has pointed out that some regions contain genes related to starch and sucrose metabolism. These metabolic pathways directly determine whether the grains can be filled and how much they can be filled (Figure 1) (Qin et al., 2021; Selamat and Nadarajah, 2021). This is not only a problem of stress resistance, but also a matter of whether the grain can fill the pockets. In addition to the grain itself, the biomass and tiller number of the whole plant cannot be ignored. Lenka et al. (2011) pointed out that some genes related to carbon fixation and sugar metabolism are quite active in regulating these traits. More interestingly, genes such as *OsAAP7A* and *OsAMT2;1*, which are involved in nutrient absorption and tillering regulation, were screened out through QTL merging analysis (Raza et al., 2020), which can be said to be "behind-the-scenes heroes".

3.3 Genes related to quality

Yield is not the only indicator, and quality is also receiving more and more attention. Taste and nutritional content directly affect the commercial value and nutritional value of rice. Lenka et al. (2011) mentioned that some genes involved in flavonoid biosynthesis were identified in comparative transcriptomes. Such substances are usually classified as "secondary metabolites", but they do help improve the nutritional value of grains.

There are also many genes involved in the regulation of texture, especially those related to starch and sucrose metabolism. These genes affect the hardness, stickiness and taste of the grains (Selamat and Nadarajah, 2021), and have actually been repeatedly screened in variety improvement. As for aroma and flavor, the "protagonist" genes responsible for this aspect have not yet been clearly found, but many studies believe that pathways such as flavonoid metabolism may "assist" in it and indirectly affect the smell (Buti et al., 2019; Selamat and Nadarajah, 2021). To find out which genes are really responsible for flavor, we have to wait for further positioning research.

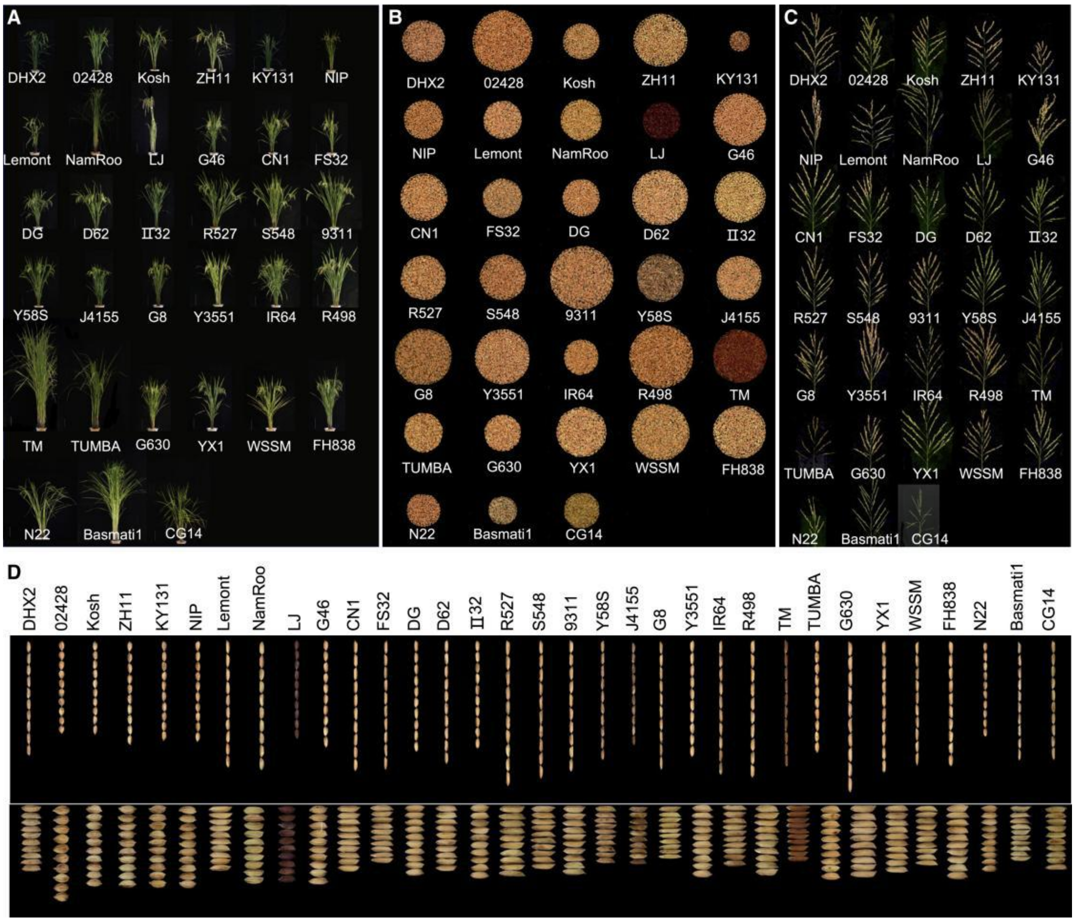

Figure 1 Diverse agronomic phenotypes for genetically diverse rice accessions (Adopted from Qin et al., 2021)

Image caption: A-D: The highly diverse agronomic phenotypes among 33 accessions, including plant height and architecture (A), grain number per panicle (B), panicle architecture (C), and grain width and length (D). These 33 accessions covered all known subpopulations of *O. sativa* and one *O. glaberrima* accessions (CG14) and encompassed 89.05% (MAF >0.05) of the SNPs present in the 3K-RG accessions (Adopted from Qin et al., 2021)

3.4 Disease resistance genes

Growing rice not only needs to prevent drought, salt, and heat, but also disease. Old problems such as rice blast and bacterial streak have always plagued farmers. Selamat and Nadarajah (2021) summarized multiple QTL analyses and found that some key genes contained in some QTLs are involved in the ABA and jasmonic acid pathways, which are related to the plant's "defense system".

In addition to these signaling pathways, there are also some specific transcription factors that are worth noting. For example, OsWRKY10 and OsWRKY21 can mobilize the expression of downstream defense-related genes under stress and enhance disease resistance (Raza et al., 2020). However, to achieve effective defense effects, these alone are not enough, and the regulation level of endogenous ABA and the coordination of various transcription factors must also be in place (Buti et al., 2019).

4 Functional Genomics Technology and Its Application in Rice

4.1 RNA-Seq and transcriptomics

Rice has to deal with problems such as drought, disease, and abnormal development, and there are complex genetic activities behind them, and RNA-Seq is a good tool to study these activities. It is not a recently popular technology, but it is still very practical in revealing how genes "change faces" under different environmental conditions. Even if it is just to find some new transcripts that are not often noticed, or to figure out who is connected to whom between genes, RNA-Seq can come in handy. With these data, researchers can draw a more complete "molecular activity map" of rice, and have a better sense of direction for breeding and improvement.

4.2 CRISPR-Cas9 and gene editing technology

Not all technologies are like CRISPR-Cas9, which can "rewrite the fate of genes as soon as they are used." It relies on a small piece of RNA (guide RNA) carrying the "scissor" protein Cas9, and directly "cuts" after finding the target site. How to repair it next is left to the cells to handle. This method has been widely used in rice, especially in improving yield, disease resistance and stress resistance (Xie and Yang, 2013; Zhang et al., 2014; Arora and Narula, 2017). Although the technology is not complicated, the key is to choose the right target gene, otherwise it will be useless no matter how accurate it is.

4.3 Proteomics and metabolomics methods

The transcriptome talks about information, while the proteome and metabolome talk about "execution". Many times, transcriptional changes are only superficial, and what really affects the state of rice is the underlying protein network and metabolite activity. For example, which protein is activated at which time point, and which metabolic pathway is accelerated due to external stimuli, all of these can be figured out through these technologies. Especially when studying rice modified by CRISPR, if you don't look at protein expression and metabolic reactions, you may miss some key changes (Liao et al., 2019; Usman et al., 2020).

4.4 Case study: application of CRISPR-Cas9 in improving drought resistance

In some agricultural areas that rely on the weather for food, drought occurs almost every year, and it is a luxury to talk about increasing production at this time. Therefore, instead of blindly pursuing high yields, it is better to make rice able to withstand drought first. Such traits are difficult to obtain through traditional breeding. Not only is the cycle long, but the effect is often limited. The emergence of CRISPR-Cas9 has given researchers a faster way: find genes involved in drought resistance and edit them directly. *OsPYL9* is a target that has been targeted. It is related to the ABA (abscisic acid) response and controls some physiological processes that are helpful for drought. Studies have shown that after mutating this gene, the survival rate of rice under drought can be significantly improved, and the antioxidant capacity can also be enhanced (Usman et al., 2020). However, not all gene editing will bring such obvious positive effects. After some changes, the performance becomes worse.

Another example is *OsSAP*, which plays a "boosting" role in drought response. Through gene editing, it was found that it can participate in regulating the removal of ROS (reactive oxygen species), which is particularly important for drought resistance (Figure 2) (Park et al., 2022). Of course, whether it is suitable for use as a breeding target depends on its actual performance. In general, research on genes such as *OsPYL9* and *OsSAP* is promoting the transformation of rice from "unable to withstand" to "able to withstand". Although the application of CRISPR-Cas9 technology cannot solve all problems, it does bring us one step closer to developing more drought-resistant varieties and brings hope for food stability in arid areas.

5 Multi-omics Integration: A Different Way to Look at Rice Traits

In the past, rice traits were often studied by looking at a certain type of data, such as only looking at the transcriptome, or only analyzing the phenotype. This approach can easily miss the complex connections behind it. The emergence of multi-omics integration has broken this limitation. Now, scientists can consider different types of data such as genome, transcriptome, proteome, metabolome and phenotype at the same time. This "puzzle-like" research method allows us to understand some complex traits in rice more systematically and specifically.

5.1 Look not only at genes, but also at performance-from "reading DNA" to "seeing how rice grows"

In the past, manual analysis of rice phenotypes was not only slow, but also prone to human errors. The emergence of high-throughput phenotyping platforms has solved this long-standing problem. Most of these systems use imaging, optics and other technologies to quickly and stably measure the external traits of a large number of rice plants, which is very helpful for subsequent data integration (Yang et al., 2013).

But sometimes, even if we knock out a gene, there is no obvious change in rice. This does not mean that the gene is not important, but it may be because of functional redundancy, that is, other genes quietly "fill in the gap". Tools like CAFRI-Rice are designed for this situation. It can predict which genes may be redundant based on phylogenetic clues, so as to help us more accurately select targets suitable for CRISPR/Cas9 knockout (Hong et al., 2020).

And databases like funRiceGenes connect various types of omics data and build a large and comprehensive rice gene archive. It not only lists the functions of various genes, but also integrates their interaction networks, allowing researchers to see which biological processes a gene is involved in and what "chain reactions" may occur (Yao et al., 2017).

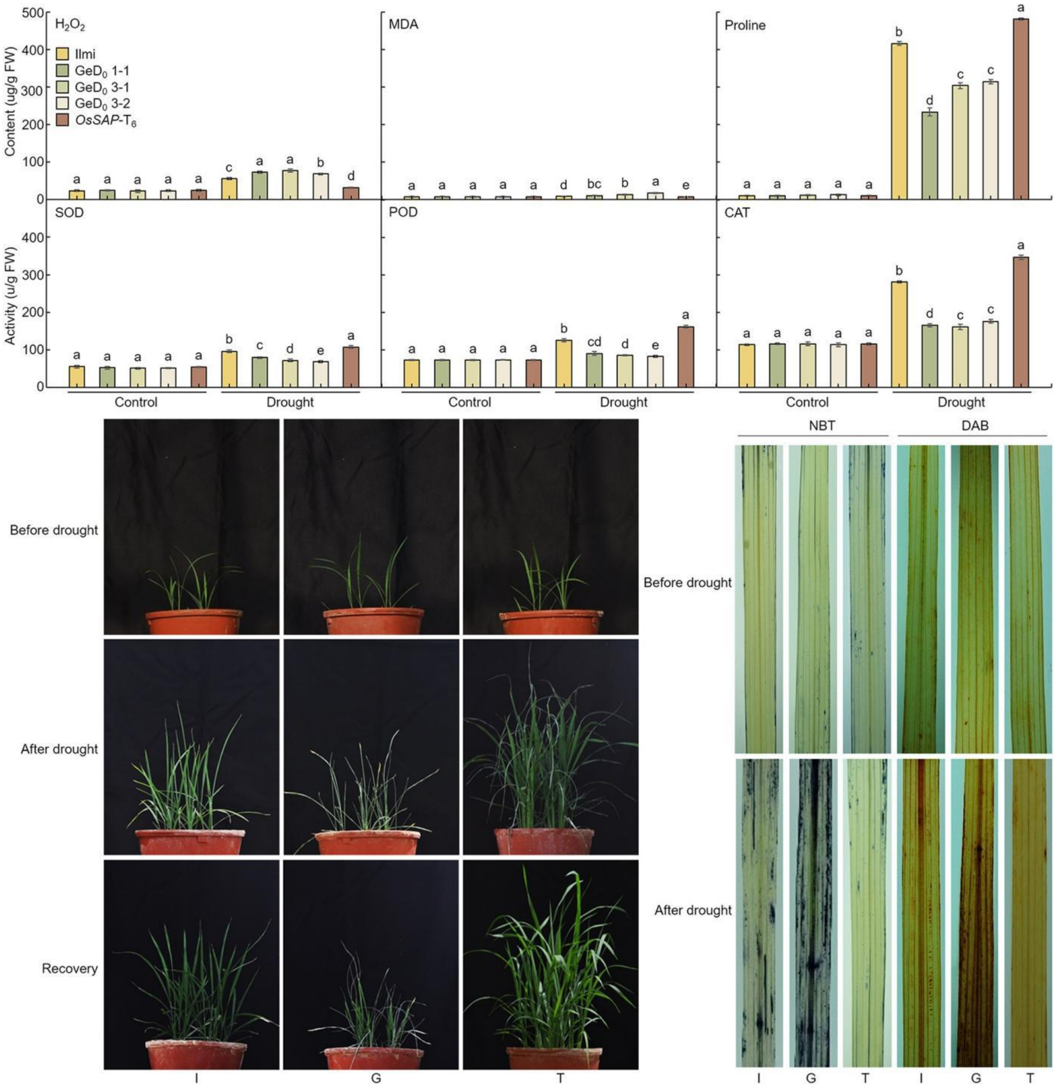

Figure 2 Effects of *OsSAP* on cellular antioxidants and reactive oxygen species (ROS) levels in Ilmi, GeD, and *OsSAP*-T$_6$ lines under normal and drought conditions (Adopted from Park et al., 2022)

Image caption: Under drought conditions, the effects of *OsSAP* on the level of endogenous hydrogen peroxide (H_2O_2), the accumulation of malondialdehyde (MDA), the accumulation of proline (proline), the activity of superoxide dismutase (SOD), the activity of peroxidase (POD), and the activity of catalase (CAT). Data presented are expressed as mean ± SD from five independent biological experiments per line. Bars represent means ± SE. Means denoted by the same letter are not significantly different ($P< 0.05$) as evaluated by Duncan's multiple range test. The GeD lines showed reduced drought tolerance, whereas the *OsSAP*-T$_6$ lines showed increased drought tolerance before drought stress, and 20 days after germination. Drought stress treatment; phenotypic changes at 20% soil moisture content. Phenotypes after 7 days of recovery achieved by watering (recovery from 20% soil moisture content). Phenotypes of 3,3-diaminobenzidine (DAB) and nitro blue tetrazolium (NBT) staining when the soil moisture content was 20%. After drought stress treatment, H_2O_2 was visualized as brown spots by DAB, and O_2^- as blue spots by NBT. The picture presented is the most representative of five independent biological experiments per each line. I: Ilmi. G: GeD$_0$ 1-1. T: *OsSAP*-T$_6$. Different letters on columns represent significant ($P < 0.05$) difference between rice lines based on Duncan's test (Adopted from Park et al., 2022)

5.2 Networks, pathways and databases: rice research also talks about "relationship diagrams"

In rice functional genomics, analyzing a single gene often does not show the whole picture. Genes cooperate and regulate each other to form complex life activities. As a result, the focus of research has gradually shifted to the analysis of networks and pathways. For example, OryzaExpress is a typical example. It integrates gene expression data and omics annotations to form expression networks (GENs). Researchers can use it to see which genes behave similarly in expression and then infer whether they are involved in the same biological process (Hamada et al., 2010).

Another example is the CARMO platform, which not only integrates multiple types of data such as transcriptomes, SNPs, and epigenetic modifications, but also groups them into gene modules to facilitate comparisons between different experiments or studies. This approach allows us to extract more general rules from "point" information (Wang et al., 2015). MBKbase goes a step further and not only integrates genomic data, but also takes phenotypic information into account. It provides a number of practical tools, such as directly searching for specific genotypes or visualizing the relationship between genotypes and phenotypes, which is particularly suitable for molecular breeding and functional research (Peng et al., 2019).

6 Outlook and Challenges: The Future of Rice Functional Genomics

6.1 Emerging technologies

In recent years, new technologies such as single-cell sequencing and synthetic biology have begun to appear frequently in rice research. They are potential not only because they are "new", but also because they can solve some problems that are difficult to handle with old methods. For example, single-cell sequencing can clearly see the differences between different cells, instead of just looking at the overall average level. This can provide more detailed clues for studying gene expression in rice development and adversity response (Lu et al., 2010). Of course, this technology itself also has problems such as complex data and high cost, and it may not be widely popularized in a short period of time. On the other hand, synthetic biology gives scientists greater freedom to combine or regulate genes like building blocks, and in theory, it can design higher-yield, disease-resistant, and stress-resistant rice varieties (Li et al., 2018). If combined with a high-throughput phenotyping platform, the speed of functional annotation can be even faster. And these advances, in the final analysis, are paving the way for the realization of "green super rice" (Yang et al., 2013).

6.2 Challenges and opportunities in translational functional genomics

The current problem is not that we don’t know which genes may be important, but that we know too much and cannot verify them all. The number of genes identified by high-throughput sequencing and various mutagenesis methods is huge, but it is only the tip of the iceberg to really figure out what they do in rice. Although many mutant resource libraries have been established, such as T-DNA insertion libraries, the functional verification of these materials is still time-consuming and laborious (Jiang et al., 2012; Lo et al., 2016). In addition, traditional phenotypic observation relies on manual judgment, which is inevitably subjective and slow. If we really want to transform genetic research into actual results in breeding, we must have supporting automated phenotyping technology (Yang et al., 2013). However, from another perspective, it is these limitations that have promoted cross-disciplinary collaboration. Integrating genomics, phenomics and informatics may be the key to improving efficiency, especially when dealing with complex crops such as rice (Delseny et al., 2001; Guo et al., 2014).

6.3 Precision breeding and the potential of sustainable agriculture

Precision breeding sounds like a technical issue, but it is more of a choice issue. Researchers can already find "good" genes related to yield, resistance, and nutrient absorption efficiency at the genomic level (Jiang et al., 2012; Li et al., 2018). Using this information to guide breeding can not only avoid detours, but also greatly shorten the research and development cycle of new rice varieties. However, it should be noted that the implementation of precision breeding is not achieved overnight, it requires long-term technical accumulation and data support. On the other hand, sustainable agriculture is no longer a slogan, especially in the context of climate change and resource constraints. For rice to be "sustainable", it must not only produce more, but also eat less and be able to withstand it. This requires us to truly understand the genetic mechanisms that control these traits, and functional genomics can fill this gap (Huang et al., 2013; Li et al., 2018).

7 Conclusion

Rice functional genomics has been developing rapidly in recent years, but looking back, what is truly valuable is not only the progress of technology, but also our understanding of the mechanisms behind some key agronomic traits, which is much clearer than before. For long-standing problems such as yield, quality, and stress resistance, thousands of related genes have been cloned and partially annotated, relying on the genetic resources that have been established one after another, such as T-DNA insertion mutants and various mutant libraries. These resources actually laid the foundation as early as the last decade, and later promoted high-throughput research methods, allowing people to systematically see what each gene in the rice genome does.

Of course, not all genes are easy to study. The functions of some genes are still vague, especially those without obvious phenotypes. However, with functional databases such as funRiceGenes, the currently known gene functions and the relationship network between them have been clarified, and subsequent research has a handle. Now even gene editing tools like CRISPR, or AI technologies like deep neural networks that were originally used for image recognition, have been used in rice research. They make the positioning of regulatory elements faster and more accurate, which was unthinkable before.

As for where to go next, the research community actually has some consensus. For example, a large project like RICE2020 aims to figure out the function of every gene in the rice genome. It sounds like a science fiction goal, but the technical conditions are gradually maturing. The key is how to turn these research results into real-world traits that can be used, such as new varieties that are more drought-resistant, higher-yielding, or less prone to pests and diseases - these are what farmers care about most.

Another point that is easily overlooked is the "black box" behind gene regulation - that is, epigenetics. It does not directly rewrite the DNA sequence, but it has a great impact on how plants develop and how they respond to stress. Incorporating this part of the research in the future may help us design breeding strategies more carefully, and even change the logic of traditional breeding. These advances ultimately depend on the continuous upgrading of functional genomics tools.

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Conflict of Interest Disclosure

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