

Feature Review

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Engineering Anthocyanin Biosynthesis for Purple Rice Development

Yanfu Wang, Danyan Ding 

Institute of Life Sciences, Jiyang College of Zhejiang A&F University, Zhejiang, China

 Corresponding email: danyan.ding@jicat.org

Rice Genomics and Genetics, 2025, Vol.16, No.6 doi: [10.5376/rgg.2025.16.0030](https://doi.org/10.5376/rgg.2025.16.0030)

Received: 30 Oct., 2025

Accepted: 15 Dec., 2025

Published: 28 Dec., 2025

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Preferred citation for this article:

Wang Y.F., and Ding D.Y., 2025, Engineering anthocyanin biosynthesis for purple rice development, *Rice Genomics and Genetics*, 16(6): 330-338 (doi: [10.5376/rgg.2025.16.0030](https://doi.org/10.5376/rgg.2025.16.0030))

Abstract Purple rice is increasingly attracting attention due to its rich anthocyanin content, which has significant nutritional and health benefits. Modifying the biosynthesis of engineered anthocyanins through synthetic pathways offers a promising strategy for developing rice varieties with health care functions to meet the growing market demand for healthy foods. This study reviews the molecular basis of anthocyanin biosynthesis in rice, with a focus on key structural genes (such as CHS, DFR, ANS and UFGT) as well as regulatory factors including MYB, bHLH and WD40. Meanwhile, the role of the MYB-bHLH-WD40 complex and its transcriptional regulatory network in tissue-specific expression were explored. Further, various synthetic biology strategies promoting anthocyanin accumulation were analyzed, including heterologous gene introduction, gene stacking, and endogenous pathway editing mediated by the CRISPR/Cas system. This study also lists typical cases from India, South Korea and China, demonstrating the practical exploration and achievements in the development of purple rice. This study aims to establish a research framework integrating synthetic pathway modification, functional verification and field application, in order to promote the commercial development of high anthocyanin rice.

Keywords Purple rice; Anthocyanin synthesis; Synthetic biology; Genetic engineering; Functional rice breeding

1 Introduction

Purple rice has been quite popular in recent years. The first thing that catches people's eyes might still be that touch of purple-red. But what lies behind the color, such as the antioxidant effect of anthocyanins and their potential health benefits, is the real reason why it has been pushed to the center stage of "functional food" (Yamuangmorn and Prom-U-Thai, 2021). Ultimately, what people want is not just good looks; they care more about whether the food is nutritious and beneficial to their health. Especially in today's era when functional foods are becoming increasingly popular, the development of purple rice has become a new hot spot for both breeding and nutrition fields to make joint efforts.

Of course, not all colored rice is rich in nutrition, but purple rice is an exception. It is not only rich in anthocyanins, but also contains trace nutrients such as zinc. Anthocyanins have more than one function. Besides their antioxidant properties, they are also associated with anti-inflammatory responses and metabolic regulation and other health mechanisms. This gives rice, which was originally just a staple food, the potential to "enhance human body functions" - and this is precisely where the market space of purple rice lies (Utasee et al., 2022). However, to make rice truly "purple" stably and have a high anthocyanin content, it is necessary to start from the plant's own synthetic mechanism. The synthesis pathway of anthocyanins is not short, involving multiple enzymes and regulatory factors, along with tissue-specific expression, which makes the matter even more complicated. Even for areas that originally do not accumulate pigments, such as endosperm, there are ways to "switch on" these pathways through genetic engineering. In the past few years, scientists have introduced structural genes and regulatory factors into rice through transgenic superposition technology, which has indeed enabled the endosperm to synthesize anthocyanins. This practice of "reactivating" the silent path has gradually solved the problems of low synthesis efficiency and instability (Qiao et al., 2020; Meng et al., 2021; Zeng et al., 2024).

This study reviews the current understanding of the anthocyanin biosynthesis pathways in rice, as well as the genetic and biotechnological strategies for breeding purple rice varieties. It summarizes the nutritional value and

market potential of purple rice, elaborates in detail the molecular mechanisms and regulatory networks that control anthocyanin production, and focuses on introducing the breakthroughs in anthocyanin biosynthesis engineering in recent years. Its significance lies in providing a comprehensive framework for future research and breeding projects that focus on enhancing the health benefits of rice, thereby contributing to food security and the improvement of human nutrition.

2 Molecular Basis of Anthocyanin Biosynthesis in Rice

2.1 Key enzyme genes in the anthocyanin biosynthetic pathway (e.g., CHS, DFR, ANS, UFGT)

The conversion of phenylalanine into anthocyanins through a series of reactions may sound like a smooth path, but in fact, it relies on many key enzymes to maintain the process. CHS, DFR, ANS and UFGT are indispensable steps in rice. Like OsDFR, it is responsible for reducing dihydroflavonoids to colorless anthocyanins. If this step is interrupted, the entire pigment chain will get stuck. As for the final step, UFGT adds sugar to the anthocyanin to help it stabilize; otherwise, it won't be able to stay. Although these structural genes are widely present, their expression is limited by tissue type. That is to say, the presence of pigments is not everywhere (Yang et al., 2019; Meng et al., 2021; Zhu et al., 2024).

2.2 Regulatory factors of anthocyanin biosynthesis

Ultimately, no matter how many synthases there are, without regulation, they are just "roaring". In rice, the MYB-bHLH-WD40 complex is the overall commander coordinating the expression of these enzymes. MYB proteins like OsMYB3, OsC1, and OsPL work together with bHLH partners (such as OsB1 and OsB2) and WD40 (OsTTG1) to activate structural genes. This process is not a one-off deal. There are multiple layers of control within the complex. For instance, the S1 of bHLH can also boost the expression of MYB and WD40. It should be noted that this regulation is not consistent - changes in external temperature and light can also be involved to regulate the activities of these factors, thereby affecting the generation level of anthocyanins (Yang et al., 2021; Zheng et al., 2021; Sun et al., 2022; Youdaoplaceholder0 et al., 2025).

2.3 Molecular mechanisms underlying the lack of pigmentation in conventional rice varieties

Not all rice varieties are purple. Many common varieties have white peels and leaves all over. Ultimately, this is closely related to problems with the regulatory genes. The familiar faces such as OsC1, OsRb and OsDFR, once mutated, the MBW complex cannot be formed and the structural genes naturally stop working. Sometimes, it is not the entire complex that malfunctions, but rather the issue of the regulatory region. For instance, genes like OsPa and OsPs, which control the pigment in the stigma and apause, once they malfunction, those areas will no longer show color (Zhou, 2025). In fact, this is not all bad. These variations provide potential targets for subsequent breeding - if you want to restore pigmentation or enhance it, you will know where to start (Zheng et al., 2019; Qiao et al., 2020).

3 Regulatory Networks and Transcriptional Control of Anthocyanin Biosynthesis

3.1 Role of the MYB-bHLH-WD40 (MBW) complex

In plants such as rice, some core factors that regulate anthocyanin synthesis do not operate in isolation. The MBW complex is a typical example, which is a combination of three types of proteins: MYB, bHLH and WD40. When it comes to the mechanism of action, it is actually not complicated. The MYB protein is mainly responsible for recognizing target genes (such as DFR, ANS, UFGT, etc.), while bHLH and WD40 play a stabilizing and enhancing role. Such as OsMYB3, OsC1, OsTTG1, these are the already identified participants in rice (Karppinen et al., 2021; Lee et al., 2024). However, the environment is not a completely static variable. External factors such as light exposure and hormonal changes can also be integrated into the regulation of this complex, thereby dynamically adjusting the accumulation of anthocyanins.

3.2 Synergistic regulation and feedback among various transcriptional factors

Not all regulation can be accomplished by the MBW complex alone. In the path of anthocyanin synthesis, there are still many regulatory factors working in coordination, and sometimes they even restrict each other. For instance, some MYB activators, in addition to activating target genes, can also promote the expression of other

regulatory factors, forming a positive feedback loop. In contrast, inhibitory factors like R3-MYB often compete with these activators for positions, blocking the formation of complexes and playing a negative regulatory role. Meanwhile, hormone pathways within plants, such as brassinosteroid signaling and various stress response pathways, also regulate the expression level or activity status of MBW components to ensure that this regulatory system responds to both growth and development and external changes (Figure 1) (Albert et al., 2014; Yang et al., 2022; Lee et al., 2024).

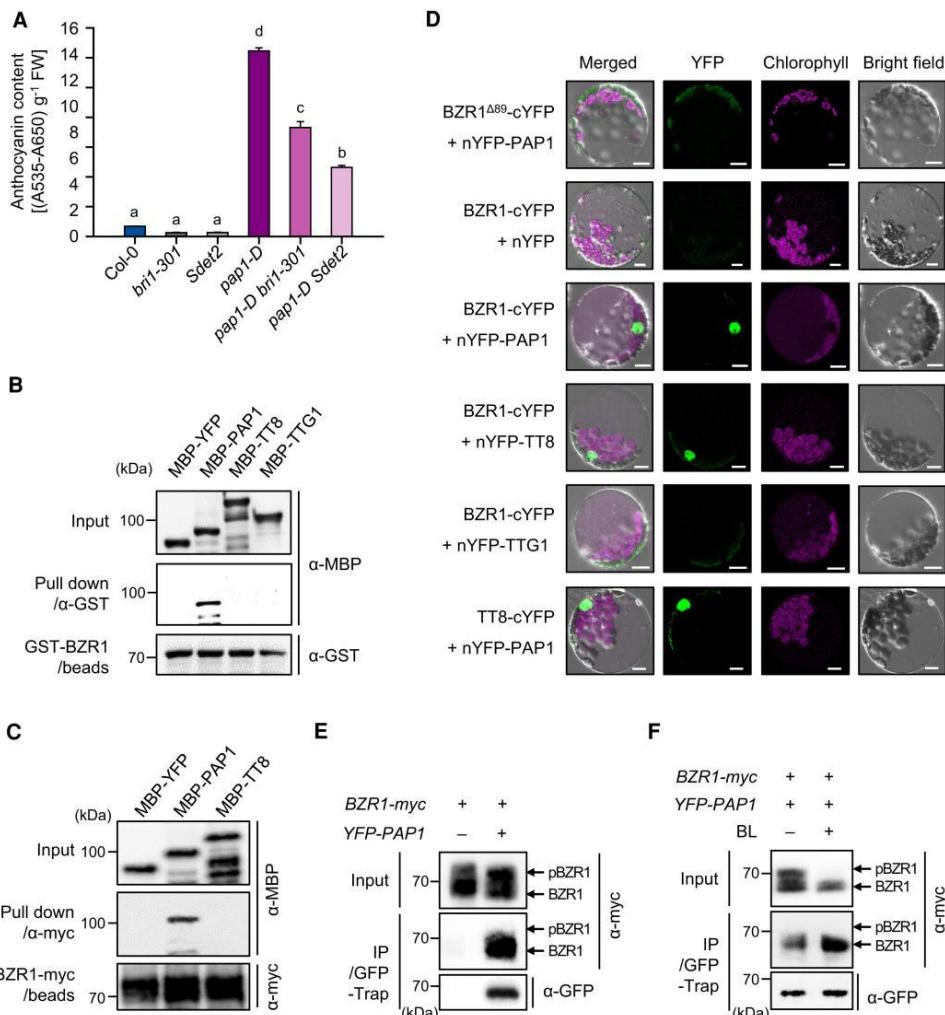


Figure 1 BZR1 interacts with PAP1 in vitro and *in vivo* (Adopted from Lee et al., 2024)

3.3 Tissue-specific and developmental stage-specific expression

Not all tissues accumulate anthocyanins, and the main factor behind this is the spatial and temporal expression patterns of regulatory factors. In crops such as rice, anthocyanins often only appear in specific parts, such as the pericarp, leaf sheaths or spike tips, which indicates that the expression of regulatory factors in different tissues is highly specific. In terms of developmental rhythm, many anthocyanin synthesis-related genes are activated only in the later stage of seed development or during intense light exposure (Karppinen et al., 2021; Yan et al., 2021; Yang et al., 2021). This regulatory approach is crucial in transgenic purple rice breeding - it not only determines the location of pigment deposition but also avoids negative effects in non-target tissues.

4 Engineering Strategies and Pathway Optimization for Anthocyanin Production

4.1 Introduction of heterologous genes and reconstruction of biosynthetic pathways

Sometimes, for plants or microorganisms to synthesize anthocyanins, relying solely on the original endogenous pathways is not sufficient or the efficiency is too low. In many cases, it is necessary to "transplant" in and use those key synthases from other species, such as CHS, DFR, ANS and UFGT, as well as regulatory proteins. The

genes of model plants such as pygmy and *Arabidopsis thaliana* have been attempted to be co-expressed in microorganisms, and eventually cornillin-3-O-glucoside can also be synthesized, which confirms that the exogenous gene recombination pathway is feasible (Cress et al., 2017; Zha and Koffas, 2017). In plant systems, a more common approach to this strategy is the superposition introduction of multiple genes, which simultaneously initiates multiple synthetic processes through transgenic means, avoiding issues such as pathway interruption or asynchronous expression, thereby achieving stable synthesis.

4.2 Gene stacking and multi-gene co-expression systems

The regulation of a single gene is far from sufficient, especially when the target is a synthetic pathway. Anthocyanin synthesis involves multiple steps. It is difficult for a single promoter or an exogenous gene alone to drive the entire pathway to operate efficiently. Therefore, one approach is to conduct gene stacking, package the related genes into an expression module, and then combine them with tissue-specific promoters for concentrated expression. For example, previously, a team introduced eight anthocyanin synthesization-related genes into rice endosperm and bred a variety with purple endosperm. Similar schemes also exist in microorganisms, but in slightly different ways. For example, by constructing synthetic microbiota, different enzymes are assigned to different strains respectively to share the metabolic load, and finally synthesis is completed in the co-culture system.

4.3 CRISPR/cas-based editing to optimize endogenous pathways

Not all anthocyanin synthesis-related genes need to be imported from the outside, especially when the goal is to optimize the existing synthetic pathways, the CRISPR/Cas tool comes in handy. It can precisely knock out some inhibitory factors or interfere with competitive pathways, indirectly enhancing the accumulation of target metabolites. In *Escherichia coli*, studies have used CRISPRi to inhibit the expression of MetJ, a repressor protein. As a result, the content of SAM precursor substances increased, and the production of O-methylated anthocyanins also rose accordingly (Cress et al., 2017). In plants, using CRISPR technology to activate synthetic genes that are not originally expressed or to delete some transcriptional repressor elements can also achieve the goal of enhancing pigment accumulation without introducing exogenous DNA. Compared with traditional transgenic methods, this approach is more refined, has fewer off-targets, and is more suitable for the precise breeding of functional crops such as purple rice in the future (Cress et al., 2017).

5 Trait Evaluation and Quality Assessment of Purple Rice

5.1 Quantitative analysis and component profiling of anthocyanins (e.g., HPLC)

How much anthocyanin is there in different varieties of purple rice and what are the differences in their components? It's hard to guess just by looking at the appearance. You still need to use an instrument. Chromatographic analysis methods like HPLC have long been used to determine exactly what anthocyanins are in purple rice and what proportions they account for. It can not only quantify but also analyze the types of components. Some varieties do have a high anthocyanin content. Due to different genetic backgrounds and environmental interference, the differences are also considerable. Selecting materials in this way is more reliable than relying solely on phenotypes, and it can also be seen which varieties can still stably "color" under different cultivation conditions (Fongfon et al., 2021; Zhang et al., 2022).

5.2 Evaluation of grain appearance, nutritional indicators, and sensory properties

When it comes to taste and appearance, purple rice and ordinary white rice are quite different in the eyes of consumers. Visible features such as the depth of color and the length of the grains often first influence people's willingness to purchase. Some experiments also found that the milling indicators of purple rice, such as the whole polished rice rate and the brown rice rate, showed quite significant differences. But when it comes to nutritional value, purple rice is no less impressive. Its protein and amino acid content is generally higher than that of white rice. However, in terms of sensory evaluation, some people think it has a rather hard texture, and acceptance varies from person to person. One more point, the yield performance of some purple varieties is not very ideal, which poses a balance problem for breeding (Ji et al., 2012; Peng et al., 2020; 2021).

5.3 Preliminary assessment of antioxidant capacity, biological activity, and health benefits

The "health label" of purple rice is mainly supported by anthocyanins. Its antioxidant capacity has performed outstandingly in many in vitro experiments and also has a certain alleviating effect on oxidative stress indicators. Although such health benefits are still in the initial verification stage, there are more and more voices supporting it as a functional food. Not only are the ingredients good-looking, but the physiological activity is also quite substantial. It can be said to be a dual boost in nutrition and functionality. These studies provide a good entry point for the subsequent inclusion of purple rice in more systematic health-oriented breeding (Peng et al., 2020; Fongfon et al., 2021).

6 Case Studies: Practical Development of Functional Purple Rice

6.1 Study on the natural anthocyanin accumulation mechanism in indian purple rice Kala Namak

Not all purple rice is developed through genetic modification; some varieties inherently carry "color genes". For instance, Kala Namak from India, this kind of purple rice is not artificially modified later. Instead, it naturally accumulates a relatively high level of anthocyanins in the peel and Aladdin layer. Research has found that its anthocyanin level is not solely determined by genotype; environmental conditions such as light intensity and soil nutrients also play a role. Moreover, the responses at different growth stages are also different. Sometimes, changes in cultivation methods are even more effective than genetic modification (Figure 2). The analysis of such natural accumulation mechanisms provides many ideas for those who do not want to touch transgenic improvement directions (Yamuangmorn and Prom-U-Thai, 2021).

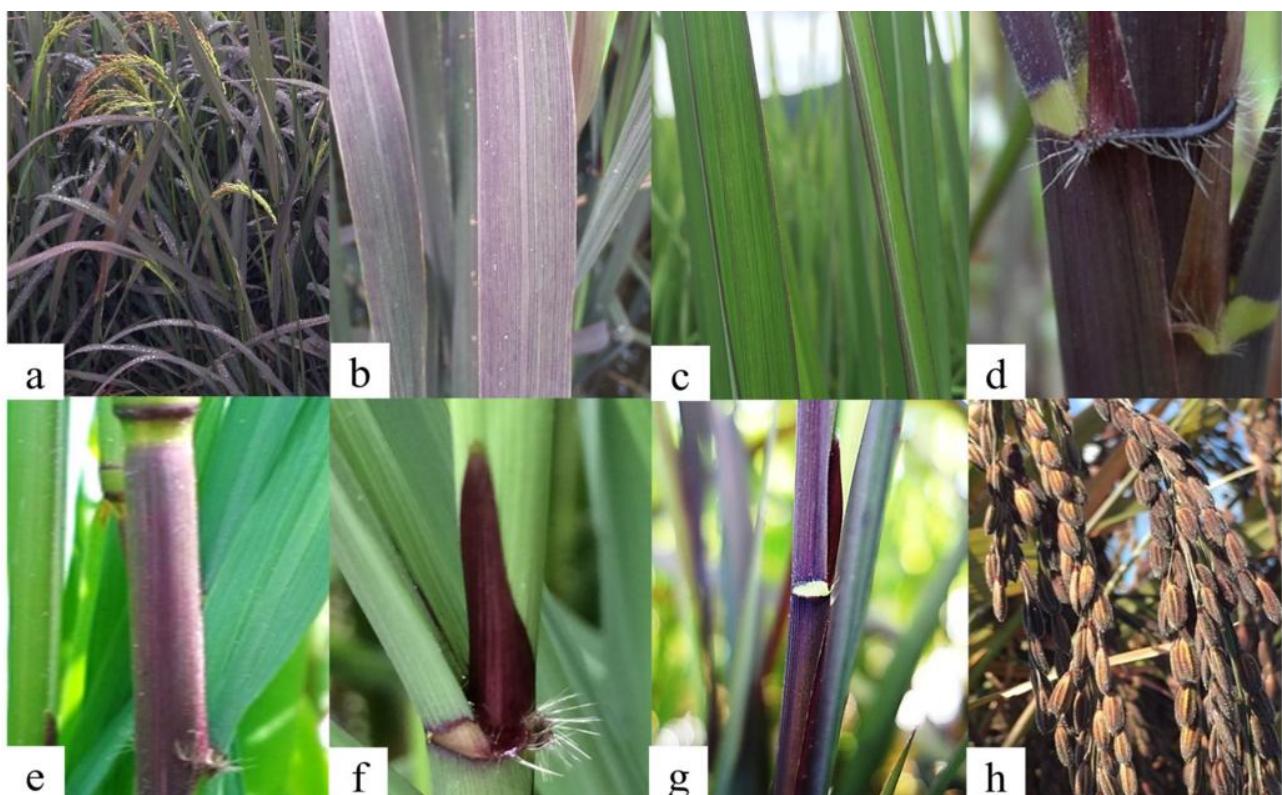


Figure 2 Anthocyanin pigmentation in the different plant parts. (a) Whole rice plant, (b) fully purple leaf blade, (c) margin purple leaf blade, (d) auricle, (e) node and internode, (f) ligule, (g) leaf sheath and (h) husk (Adopted from Yamuangmorn and Prom-U-Thai, 2021)

6.2 Biosynthetic pathway reconstruction in transgenic purple rice cultivars in Korea

In contrast, the South Korean research team has taken a different path. Instead of waiting for plants to be "gifted", they directly used synthetic biology methods to package several key genes from corn and colander and introduce them into the endosperm of rice. Among these genes, some are structural genes and some are regulatory factors. When they work together, they not only activate the originally "dormant" endogenous synthetic pathways in the

endosperm of rice, but also significantly increase the total amount of anthocyanins and their antioxidant capacity. The final produced "purple endosperm rice" not only has a distinct color but also has outstanding nutritional indicators. This path reconstruction strategy fully demonstrates the potential of modern gene overlay and pathway design in the development of functional rice.

6.3 Gene introduction strategies for high-anthocyanin rice by chinese research teams

Let's take a look at the attempts made in China. They are quite different from the previous two. They place more emphasis on making "additions" on the existing purple rice. For instance, in strains where anthocyanins have already accumulated to a certain extent, functional genes related to giant embryos and yellow endosperm were further introduced, and at the same time, molecular marker-assisted selection was used to cultivate a new type of purple rice that not only has a high yield but also is nutritionally fortified. That is to say, the Chinese team is more inclined to "optimize and upgrade" the existing resources rather than build the synthetic path from scratch. This method that combines functional genomics and conventional breeding, although it may not seem so "hardcore", is actually more down-to-earth and suitable for promotion and application (Wu et al., 2022).

7 Technical Challenges and Risk Assessment

7.1 Stability of exogenous gene expression and metabolic load concerns

It sounds easy to keep purple rice consistently and stably synthesizing anthocyanins, but it is not so simple to actually achieve. Once exogenous genes enter a plant, their expression is often not very controllable - even for the same construct, the expression level may vary greatly depending on the location. Not only that, sometimes environmental conditions and epigenetic changes can also play a role, causing the synthesis of pigments to fluctuate. Another easily overlooked issue is that if the anthocyanin synthesis pathway is always kept at "full capacity", plants may not be able to cope. With a heavy metabolic burden, the primary metabolism side will be squeezed out instead, and problems such as slower growth and reduced yield are not uncommon. To deal with these situations, many studies suggest starting from construction optimization, such as selecting promoters more appropriately or stacking multiple key genes reasonably, in an effort to enable the plant to stably synthesize the target pigment without "squeezing dry" it.

7.2 Potential impact of anthocyanin accumulation on yield and other agronomic traits

It's not the case that the more anthocyanins, the better. This may sound a bit harsh, but it is indeed the case. In some experimental materials, while the anthocyanin level increased, the grain yield often decreased, and even the taste and grain structure shifted. Some studies suggest that it might be that plants have devoted too many resources to the synthesis of these "secondary metabolites", sacrificing the parts originally intended for growth and development. However, not all varieties will experience this situation. The underlying regulatory mechanisms and interactions between genes still need to be further clarified. For breeding, this reminds us not only to focus on anthocyanin indicators, but also to comprehensively consider agronomic traits and figure out which combination schemes can preserve anthocyanins without affecting field performance.

7.3 Biosafety and regulatory considerations for transgenic and non-transgenic breeding approaches

Once engineered purple rice involves genetically modified elements, the risk assessment is an unavoidable hurdle. Although genetically modified technology is mature, its social acceptance and regulatory requirements remain high. Not only food safety needs to be evaluated, but also issues such as gene drift and environmental spread need to be taken into account. Conversely, although non-GMO methods such as genome editing and marker-assisted selection face less "pressure" at the legal level, this does not mean that they can completely bypass review, especially before being promoted to large-scale production. From the perspective of promotion, the public's trust in new breeding technologies and the compatibility of policies among various countries determine the speed at which purple rice leaves the laboratory. Therefore, scientific evidence alone is not sufficient. Safety assessment, compliance procedures and social communication are all indispensable.

8 Conclusion and Future Perspectives

Regarding purple rice, we have now gained a thorough understanding of the synthesis mechanism of anthocyanins - whether it's the regulatory network or the key genes, the pathways that need to be dismantled have been basically clarified. Through genetic engineering or molecular breeding methods, scientists have indeed enabled these pigment-related genes to stably "land" in rice, and to a certain extent, can even solve the problems that previously troubled people, such as unstable pigments and difficulty in coordinating agronomic traits (such as low yield and poor adaptability). This series of advancements has basically laid the technical foundation for new functional rice varieties that are both delicious and nutritious.

But what to do next might not be so "linear". To further increase the anthocyanin content of purple rice without causing the plants to grow too vigorously, it is necessary to control the expression of related genes more precisely. This involves promoter selection, stacking multiple target genes, and even directly using gene editing tools for "point-to-point" regulation. At the same time, it is also crucial to use systems biology methods to identify those latent metabolic bottlenecks or feedback inhibition links - often, the problem does not lie in insufficient synthetic capacity, but rather in being "restricted" by the system itself. Of course, there are still some overlooked but very important parts. For instance, is the stability of anthocyanins in purple rice consistent in different environments? Is the influence at the epigenetic level significant? These seemingly "secondary" issues actually largely determine whether new varieties can be truly promoted, especially how they perform under different climatic and soil conditions.

Looking at the market, the prospects for purple rice are quite bright. Consumers' demand for "functional and truly healthy" food is on the rise. Rice rich in anthocyanins not only has antioxidant and anti-inflammatory properties but also has considerable room for nutritional promotion. From an economic perspective, such varieties may open up new income channels for growers and enterprises, especially in the main rice-producing areas. In addition, it may also play a role in the two aspects of "nutritional intervention" and "food security". To truly transform these scientific achievements into commercial products, interdisciplinary collaboration is still necessary. Breeding, biotechnology, nutrition, and market research all need to be involved - only then is there a chance for purple rice to truly move from experimental fields into the staple food system.

Acknowledgments

We are grateful to Dr. W. Zhang for this assistance with the serious reading and helpful discussions during the course of this work.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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