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Molecular Breeding Strategies for Pyramiding Disease Resistance in Wheat

Jin Wang, Xing Zhao, Fumin Gao
Tropical Microbial Resources Research Center, Hainan Institute of Tropical Agricultural Resources, Sanya, 572025, Hainan, China
Corresponding email: fumin.gao@hitar.org

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Abstract Wheat is one of the most important food crops in the world, but its yield and quality are often seriously threatened by a variety of diseases such as rust, head blight and powdery mildew. Traditional single-gene disease resistance breeding faces huge challenges due to the rapid mutation of pathogen populations and the easy failure of resistance. In this context, the aggregation of multiple disease resistance genes through molecular breeding has become an effective strategy to improve wheat disease resistance. This study reviews the current research progress of wheat disease resistance genes, the application of molecular tools such as marker-assisted selection (MAS), genomic selection, and CRISPR gene editing, as well as the integration path of these technologies in the breeding of multi-resistant wheat varieties. Through actual cases such as the aggregation of rust resistance genes such as *Lr*, *Sr*, and *Yr*, and the combined application of *Fhb1* and *Fhb2* head blight resistance genes, the significant effect of gene aggregation in enhancing disease resistance was verified. At the same time, this study also analyzed the effects of aggregation on agronomic traits, explored the challenges faced by resistance persistence and gene interactions, and looked forward to the future direction of combining molecular breeding with sustainable agriculture, in order to achieve long-term control of wheat diseases and food security.

Keywords Wheat; Disease resistance gene aggregation; Marker-assisted selection; Genomic selection; Breeding strategy

1 Introduction

Wheat is an important guarantee for global food security and is the staple food for billions of people every day. It is highly adaptable and nutritious, so it is indispensable in many agricultural areas. Among all commercial crops, wheat has the largest planting area, especially in developing countries, where it is very important for food supply. Because it can adapt to a variety of climates and is the protagonist of people's diet, wheat has become a core crop in the global food system.

But there are also many problems. Wheat is often threatened by several major diseases during the planting process, such as rust, Fusarium head blight and powdery mildew. Once these diseases break out, they may cause a significant reduction in production and even affect the stability of food supply (Liu et al., 2000; 2020; Zhang et al., 2021; Luo et al., 2023). What's more troublesome is that pathogens change very quickly, and the effects of many disease-resistant genes are not long-lasting. This makes disease management more complicated. We urgently need some more reliable and long-lasting methods to solve these problems (Wang et al., 2022; Koller et al., 2023).

This study outlines the progress of major wheat diseases, molecular marker technology, and successful cases of gene aggregation through marker-assisted selection and transgenic methods in recent years. It also explores the molecular breeding strategy for wheat disease resistance gene aggregation, that is, integrating multiple resistance genes into a single variety to achieve broad-spectrum and lasting disease protection. The study emphasizes the integration of multiple resistance sites to cope with pathogen variation, so as to achieve long-term resistance to diseases and stable yield of wheat. This study hopes to aggregate disease resistance genes through molecular breeding methods to provide a powerful solution for achieving sustainable wheat production and global food security.

2 Major Wheat Diseases and Resistance Genes

2.1 Overview of key wheat diseases

Wheat is susceptible to a variety of diseases that affect yield and quality. The more common ones are leaf rust (*Puccinia triticina*), stripe rust (*Puccinia striiformis*) and stem rust (*Puccinia graminis*). These diseases occur in many countries and are prone to outbreaks (Ghimire et al., 2020; Ren et al., 2024). Powdery mildew is another common disease caused by *Blumeria graminearum*. This disease has always existed in many growing areas and is difficult to completely eliminate (Zou et al., 2018; Cai and Qian, 2024). Fusarium head blight (FHB) is also a serious disease caused by *Fusarium graminearum*. Not only will it reduce yields, but it may also cause food to be contaminated by mycotoxins, affecting food safety (Figure 1) (Ghimire et al., 2020). These diseases cause a lot of losses every year, so they are the focus of wheat breeding in various places (Mourad et al., 2024).

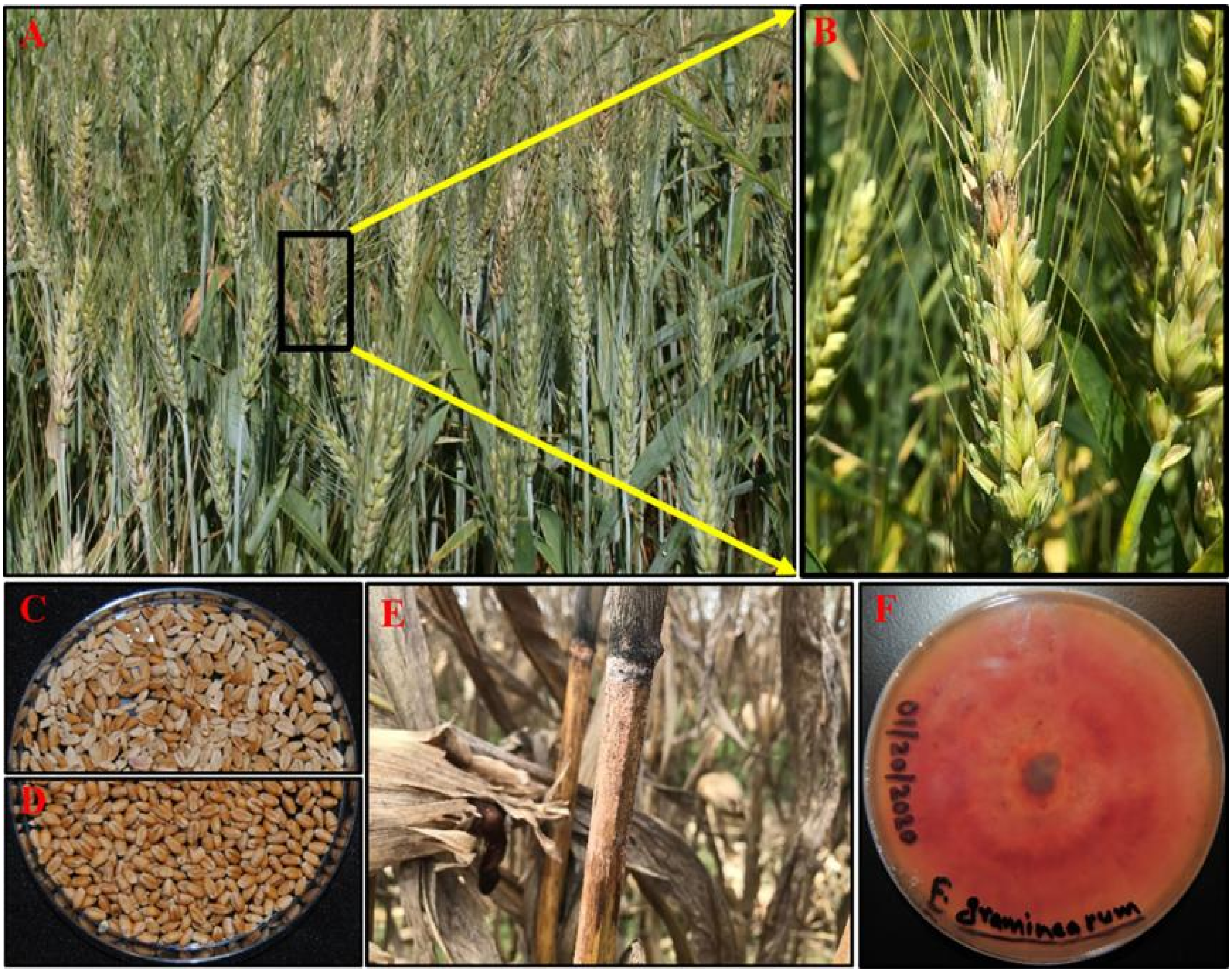

Figure 1 Fusarium head blight (FHB) symptom; FHB disease in the field used to assess FHB incidence (type I resistance) (A), infected spike with orange-colored sporodochia used to assess FHB severity (type II resistance) (B), infected seed used to assess *Fusarium*-damaged kernel (FDK) (type IV resistance) (C) compared to healthy seed lot (D), *F. graminearum* overwintering in corn stalk (E), and FHB isolate cultured in potato dextrose agar (PDA) plate showing characteristic pinkish-red colony (F). (Source: Figures 1A-F, B. Ghimire) (Adopted from Ghimire et al., 2020)

2.2 Resistance genes identified in wheat germplasm

Researchers have discovered many disease resistance genes in wheat and used them for breeding. There are many confirmed rust resistance genes, including 79 leaf rust resistance genes (*Lr*), 82 stripe rust resistance genes (Yr) and multiple stem rust resistance genes (*Sr*). Some of the common ones are *Lr13*, *Lr67*, *Yr27*, *Sr26*, *Sr61* and *Sr43* (Milne et al., 2018; Zhang et al., 2021; Athiyannan et al., 2022; Yu et al., 2023). For powdery mildew, genes such as *Pm21* and *Pm60* have been cloned and verified to have good resistance (Zou et al., 2018). *Fhb1* is the most commonly used Fusarium head blight resistance gene, and some QTLs have also been found to provide partial resistance (Ma et al., 2021). *Stb6* can help wheat resist leaf spot, and although *Lr34* and *Lr67* are not completely resistant, they can provide relatively stable, sustained, and effective partial resistance to multiple pathogens (Krattinger et al., 2016; Saintenac et al., 2018). These resistance genes were screened through traditional breeding, molecular mapping technology, and genomic methods developed in recent years (Juliana et al., 2018; Hafeez et al., 2021).

2.3 Limitations of single-gene resistance

Although a disease resistance gene can sometimes play a strong role in disease prevention, this effect generally does not last long. Because pathogens change very quickly, they may be able to break through the defense line of this gene within a few years (Hao et al., 2023; Waites et al., 2025). Many disease resistance genes are "race-specific", that is, they can only protect against a certain type of pathogen and are ineffective against other types. This makes their resistance range very limited and not stable enough (Hafeez et al., 2021). In contrast, to make resistance longer, it is usually necessary to combine several different disease resistance genes together. This combination is sometimes called a "gene pyramid". It uses major and minor effect genes together to allow plants to resist different types of diseases at the same time, and the defense line is stronger (Ghimire et al., 2020; Mourad et al., 2024). Therefore, although a single disease resistance gene is important, it is not enough to deal with the complex disease problems in reality. This is why current molecular breeding emphasizes combining multiple disease resistance genes to take the route of sustainable disease resistance.

3 Principles and Methods of Gene Pyramiding

3.1 Definition and theoretical basis of gene pyramiding

Gene aggregation is to combine multiple disease resistance genes into one wheat variety, so that it can produce long-term resistance to multiple diseases. The theoretical basis of this method is that different genes have different ways of disease resistance, and it will be more difficult for pathogens to break through all lines of defense at the same time. In this way, resistance is more stable and more effective (Dormatey et al., 2020). Now, scientists have also designed some mathematical models and family analysis tools to optimize hybridization plans and predict the possibility of successful combination of disease resistance genes (Servin et al., 2004).

3.2 Traditional breeding vs. molecular-assisted pyramiding

In the past, breeders mainly relied on phenotypic selection and repeated hybridization to aggregate disease resistance genes. This method is relatively slow, and if the disease resistance trait is not obvious or affected by the environment, it is difficult to accurately distinguish which materials carry the target gene (Servin et al., 2004; Sivasamy et al., 2017). Now, with molecular-assisted breeding methods, breeders can use DNA markers linked to disease resistance genes to screen individuals with multiple target genes early on. Technologies such as marker-assisted selection (MAS) and CRISPR/Cas9 gene editing have greatly accelerated breeding, allowing multiple resistance genes to be introduced and confirmed simultaneously in one generation (Laroche et al., 2019; Dormatey et al., 2020; Gautam et al., 2020; Luo et al., 2021; Li et al., 2022). Moreover, these new technologies can also help avoid "linkage burden", that is, not bringing in some unwanted traits together, while also combining genes from different sources.

3.3 Criteria for selecting resistance genes for combination

In order to make gene aggregation work, we must first select disease-resistant genes. When selecting genes, there are several aspects to pay attention to. It is best to choose genes with different disease resistance methods. For example, you can use both adult resistance genes and variety-specific resistance genes at the same time, so that the combination effect is better (Wang et al., 2022; Liu et al., 2020). You should also choose genes that are not alleles and are not linked. This can reduce the risk of losing the target gene during gene recombination (Laroche et al., 2019). The selected genes must be effective against common pathogens and also be able to prevent some emerging pathogens (Qie et al., 2019; Koller et al., 2023).

These genes cannot have a negative impact on other traits of wheat. For example, they cannot reduce yield and quality, and they must be compatible with the genetic background of good varieties (Tyagi et al., 2014; Gautam et al., 2020; Gupta et al., 2021). It is best if each gene has a corresponding molecular marker. This way, it can be more convenient to screen out during breeding. As long as genes are selected according to these standards, breeding work will be smoother and it will be easier to breed disease-resistant and high-yielding wheat varieties, which will be very helpful in achieving green agriculture and food security.

4 Molecular Tools and Strategies in Resistance Gene Pyramiding

4.1 Marker-assisted selection (MAS) and its application

Marker-assisted selection (MAS) is a technology used to track disease resistance genes. It uses DNA markers that are very close to resistance genes to help breeders find target genes in breeding populations. With MAS, breeders can select homozygous materials containing two or more disease resistance genes at an early stage. This not only combines resistance genes such as powdery mildew, rust, and nematodes, but also retains good agronomic traits and greatly accelerates the breeding process (Barloy et al., 2007; Wang et al., 2022; Jin et al., 2022). For example, through MAS, researchers successfully stacked gene combinations such as *Pm2+Pm4a* and *Pm2+Pm21* into wheat, improving resistance to powdery mildew. Rust resistance genes such as *Lr19*/*Sr25* and *Yr15* were also combined to obtain more resistant and durable varieties (Pal et al., 2020).

4.2 Genomic selection and high-throughput genotyping

Genomic selection (GS) is a method of predicting traits using whole genome data. This method can predict the breeding value of multiple complex traits, including disease resistance. With the development of next-generation sequencing (NGS) technology and the application of high-density SNP chips, researchers can build more detailed genetic maps, conduct GWAS analysis, and find QTLs that control disease resistance traits. These tools can help us select multiple resistance genes at the same time and speed up the selection of excellent wheat materials (Athiyannan et al., 2022; Melson et al., 2023). In addition, high-throughput genotyping technology can also quickly analyze large populations, save time, and improve efficiency. It is an important means to achieve precise disease resistance gene aggregation (Babu et al., 2020; Bariana et al., 2022).

4.3 CRISPR/Cas and gene editing for resistance stacking

CRISPR/Cas is a gene editing tool that can directly modify wheat genes. We can use it to insert new disease resistance genes, knock out genes that are sensitive to diseases, and even stack multiple resistance genes in one step. This method breaks through the limitations of traditional breeding and MAS, and can achieve the goal without backcrossing generations (Laroche et al., 2019; Luo et al., 2023). It can also quickly use disease resistance genes from wild relatives or newly discovered disease resistance genes in breeding, thereby expanding the source of wheat resistance. These gene editing tools allow us to modify wheat more specifically, improve its disease resistance, and make breeding faster and more precise, which is conducive to breeding stronger wheat varieties that are more suitable for sustainable agriculture.

5 Case Studies of Resistance Gene Pyramiding in Wheat

5.1 Pyramiding of *Lr*, *Sr*, and *Yr* genes for rust resistance

Combining resistance genes related to leaf rust (Lr), stem rust (Sr), and stripe rust (Yr) is an important method to improve wheat's resistance to rust. Many breeding projects have adopted a "pyramid" aggregation strategy. For example, the Indian wheat variety PBW343 initially introduced two leaf rust resistance genes, *Lr24* and *Lr28*, through marker-assisted selection. Later, multiple stripe rust resistance genes were added, including *Yr5*, *Yr10*, *Yr15*, *Yr17*, and *Yr70*. Later, researchers introduced exogenous genes *Lr37/Yr17/Sr38* and *Lr76/Yr70* through backcrossing.

The new variety PBW723 that was eventually bred showed stronger and more durable resistance to rust in the field (Figure 2) (Sivasamy et al., 2017; Gautam et al., 2020; Gupta et al., 2021; Sharma et al., 2021). There are also some typical examples, such as the combination of adult plant resistance genes *Yr18*, *Yr28* and *Yr36* in excellent wheat materials. These combinations enhance wheat's resistance to stripe rust throughout the growth period, further demonstrating the effect of multi-gene aggregation (Liu et al., 2020; Wang et al., 2022).

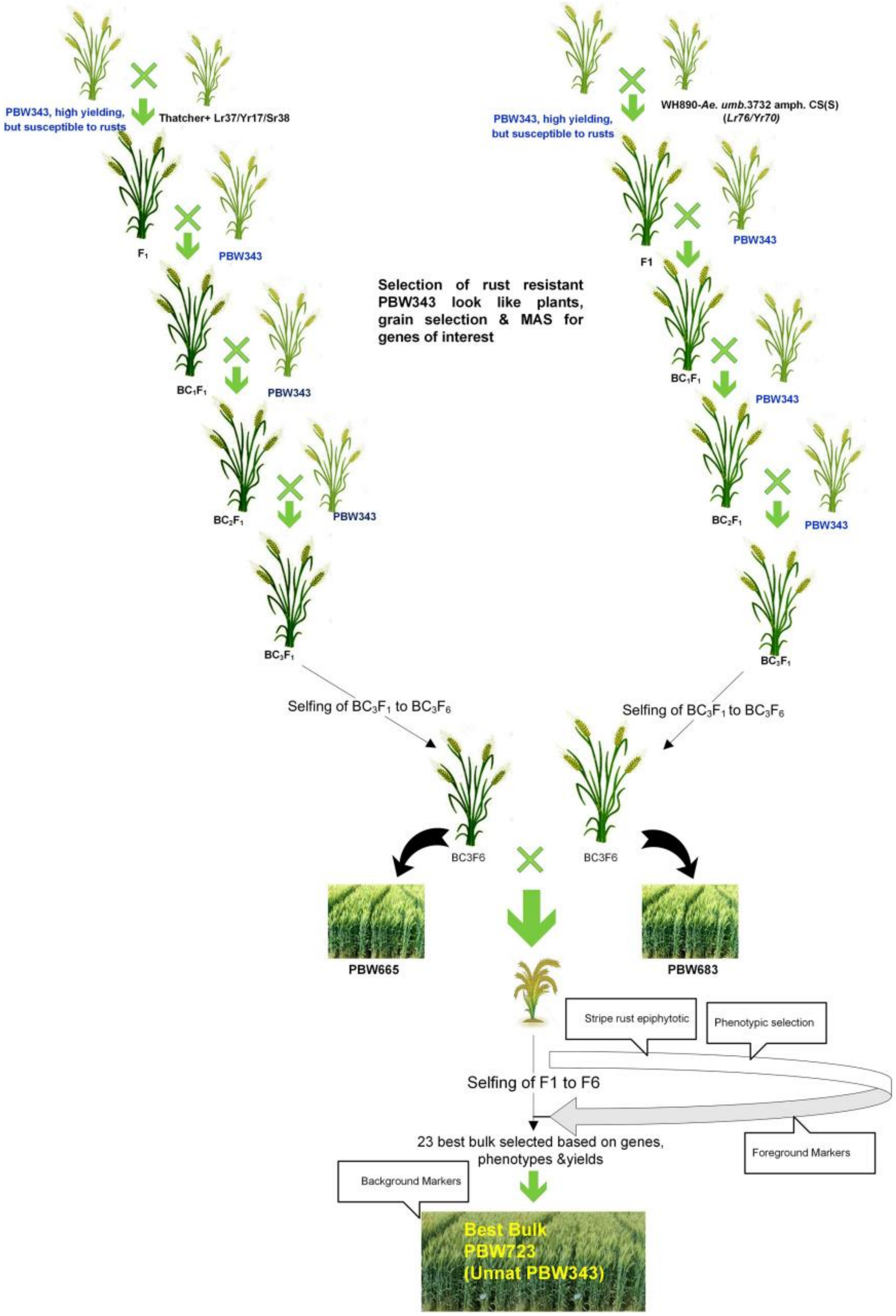

Figure 2 Schematic representation of the development of PBW723 alias *Unnat* PBW343 (Adopted from Sharma et al., 2021)

5.2 Deployment of *Fhb1* and *Fhb2* for Fusarium resistance

Fhb1 and *Fhb2* are two important QTLs that can improve wheat resistance to Fusarium head blight. When the researchers put these two genes together, they found that wheat was more resistant to the disease. Marker-assisted selection technology makes this gene combination possible. Experimental results show that wheat materials with both *Fhb1* and *Fhb2* have less severe diseases and better grain quality than those with only one gene. This shows that combining multiple disease resistance genes to deal with complex diseases such as Fusarium head blight is more effective (Laroche et al., 2019; Fedak et al., 2021).

5.3 Multi-locus stacking of genes using marker-assisted backcrossing

Marker-assisted backcrossing (MABC) is a very useful tool that can combine multiple disease resistance genes into a good variety. Now many studies have successfully achieved the aggregation of disease resistance genes using it. For example, some breeding efforts have integrated rust resistance genes such as *Yr36*, *Yr15*, *Lr24*, and *Sr24* into new varieties along with genes that improve grain quality. As a result, these new varieties not only have high yields and good protein content, but are also resistant to multiple rust diseases (Gautam et al., 2020; Gupta et al., 2021). Another example is the aggregation of powdery mildew resistance genes *Pm2*, *Pm4a*, and *Pm21*. Using molecular markers, researchers screened for double homozygotes carrying these genes. The resulting wheat varieties are both disease-resistant and maintain good agronomic traits (Liu et al., 2000). These examples show that with the help of molecular tools, gene aggregation has become faster and more accurate. This method can breed new wheat varieties that are resistant to multiple diseases and maintain good quality, and has a promising future.

6 Assessment of Resistance Effectiveness and Agronomic Traits

6.1 Evaluation of resistance spectrum under field conditions

Field trials are particularly important for judging the disease resistance of wheat varieties. Diseases such as rust and fusarium need to be tested under natural infection so that the results are more realistic. Studies have found that different wheat varieties (including local varieties and improved varieties) have very different disease resistance performance in the field, ranging from high resistance to susceptibility (Zhang et al., 2022; Maulenbay et al., 2023). For example, a study used field scoring to evaluate wheat resistance to stripe rust, found some strong genotypes (scored 0-TR), and identified some key disease resistance genes, such as *Yr-05*, *Yr-10* and *Yr-15* (Khan et al., 2025). In addition, multi-year trials in multiple locations can further confirm which varieties still maintain stable resistance in different locations and seasons (Megahed et al., 2022; Mulugeta et al., 2024).

6.2 Impact on yield, plant architecture, and grain quality

Combining multiple disease resistance genes not only enhances resistance, but may also affect yield and other agronomic traits. Some studies have found that certain disease resistance QTLs are linked to genes that control plant height, heading date, ear shape, and grain quality, so that disease resistance can be improved while yield and quality can be improved (Berraies et al., 2023; Xu et al., 2023). For example, the wheat variety Guinong No. 29 is a typical example. It has both disease resistance genes and excellent agronomic traits, is short, has good yield, and is suitable for baking. It can also resist a variety of diseases (Xiao et al., 2024). Now, through molecular marker-assisted selection, breeders have successfully bred a batch of new materials that are both disease-resistant and do not affect yield and quality (Bhatta et al., 2019; Zhang et al., 2022).

6.3 Stability of resistance under variable environments

A good disease-resistant wheat variety is not only disease-resistant in one environment, but also stable in various environments. Current studies have shown that some varieties perform well in different locations and years, and can maintain disease resistance and yield even under adverse conditions such as high temperature or drought (Li et al., 2019; Mulugeta et al., 2024). For example, some genotypes can stably resist stripe rust at different sowing times and in different fields, while maintaining high yields, which shows that they have strong adaptability. Materials like this are particularly suitable for breeding needs in the context of climate change (Megahed et al., 2022; Ogutu et al., 2024).

7 Challenges and Strategies

7.1 Gene interaction and epistatic effects

Putting multiple disease resistance genes together does not necessarily lead to stronger resistance every time. Sometimes, different genes will affect each other, for example, some effects will be superimposed, while others will interfere with each other. This "cooperation" between genes sometimes makes resistance stronger, but it may also weaken it. Not all resistance gene combinations will have an effect, and the specific performance is related to the genetic background of the plant. Some combinations may even bring unexpected results. Therefore, when breeding for resistance, we cannot only look at genes, but also analyze them together with trait performance to find the best combination (Mundt, 2018; Liu et al., 2020). In polyploid wheat, this interaction problem will be more complicated. Because they have many genes, their functions are sometimes repeated, and some genes are linked together, which increases the difficulty of breeding (Luo et al., 2021; Rajput et al., 2022).

7.2 Maintenance of resistance durability

Although combining multiple resistance genes is a promising approach, it is uncertain whether this combination will be effective for a long time. Some pathogens may evolve new abilities to overcome these resistances, especially when the same combination is widely used (Luo et al., 2023). Current studies have found that those combinations that can maintain resistance for a long time usually use the main resistance gene and the adult resistance gene together. However, there is not enough research on whether these combinations can be truly durable (Mundt, 2018). To maintain the long-term effectiveness of resistance, it is necessary to continuously monitor the changes in pathogens and continuously discover and introduce new disease resistance resources.

7.3 Integration with sustainable farming systems

Combining disease resistance gene aggregation with sustainable agriculture is a key approach to improving wheat health and yield. Current molecular breeding technologies, such as marker-assisted selection and gene editing, can not only reduce the use of pesticides, but also increase yields while protecting the environment (Laroche et al., 2019; Luo et al., 2023). However, there are still many challenges to adapt these disease-resistant wheats to various agricultural systems. We need to ensure that these varieties are not only disease-resistant, but also high-yielding and suitable for farmers to grow, and also retain other important traits (Luo et al., 2021). One future direction is to use more advanced genomic technologies to introduce new genes from wild wheat or closely related varieties, which can increase genetic diversity. At the same time, it is also necessary to develop breeding strategies that are more in line with sustainable development goals (Ceoloni et al., 2017; Dormatey et al., 2020; Zhang and He, 2024). Although gene aggregation technology has great potential in wheat disease resistance breeding, we also need to solve the problem of gene interactions to make resistance more stable. In this way, we can truly support the development of green agriculture.

8 Concluding Remarks

Molecular breeding techniques, such as marker-assisted selection (MAS), QTL mapping, genome-wide association studies (GWAS), and CRISPR/Cas gene editing, have greatly changed the way wheat is bred for disease resistance. These tools can help us find disease resistance genes more accurately and integrate good genes from wild wheat or old local varieties into existing excellent varieties. Breeding has also become faster through high-throughput genotyping and new molecular marker technologies. We can now combine multiple disease resistance genes more efficiently to breed wheat varieties that are resistant to multiple diseases and have longer-lasting resistance.

To truly achieve disease resistance and stability, we cannot rely on just one discipline. We need to combine molecular genetics, plant pathology, genomics, bioinformatics, and agronomy. For example, observing the disease in the field, diagnosing the disease with molecular methods, and combining genomic technology, can help us find useful disease resistance genes faster and use them in breeding. Cooperation between breeders, disease researchers, and molecular biologists is also particularly critical. They need to solve many problems together, such as the mutual influence between genes, different performances in different environments, and new challenges brought by the constant changes of pathogens.

Now these molecular breeding methods have given global wheat breeding a lot of hope. Disease-resistant varieties selected with these technologies can not only reduce the yield reduction caused by diseases, but also use less pesticides, which is more environmentally friendly and more suitable for green agriculture. However, the climate is changing, the pathogens are also changing, and the pressure on wheat production is increasing. Therefore, we need to breed multiple disease-resistant varieties faster and promote planting as soon as possible. Only in this way can we ensure production and ensure global food security. As long as various disciplines continue to collaborate, molecular breeding technology can play an increasingly important role in improving wheat, enhancing resistance, and keeping our jobs.

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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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