Brief History of Plant Breeding Open Access

Breeding 3.0: The Precise Revolution of Genotype Selection

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Abstract Breeding 3.0, the stage of breeding based on precise genotype selection and genetic and genomic data, represents a significant technological shift in the field of plant breeding, transforming traditional phenotypic selection into genotype selection to enhance selection efficiency and accuracy. The beginning of Breeding 3.0 can be traced back to approximately 1995 when molecular markers and genomic data were used to supplement phenotype data. Iconic academic achievements, such as the construction of saturated linkage maps in rice and breakthroughs in rice whole genome sequencing, marked the early stages of Breeding 3.0. The methodological framework of Breeding 3.0 includes marker-assisted backcrossing and pedigree confirmation, the application of linkage maps in unraveling complex traits, and advancements in high-throughput genotyping. The integration of genetic and genomic data confers advantages in precision and efficiency to Breeding 3.0. Genotype-based breeding approaches provide new avenues for improving plant varieties, while genome-wide selection enables the analysis of complex quantitative traits.

Keywords Breeding 3.0; Genotype selection; Genetic and genomic data; Marker-assisted breeding

1 Introduction

Breeding has always been an important task in the field of agriculture, aimed at improving plant varieties, increasing crop yield, resistance and quality. With the continuous progress of science and technology, breeding methods are also constantly evolving. The Breeding 2.0 stage focuses on conventional breeding, based on Mendel's Law of Inheritance and Quantitative Genetics Theory, to improve plant varieties by creating mutant populations and applying phenotype selection. However, there are still some limitations in Breeding 2.0, such as limitations in selection efficiency and difficulties in analyzing complex traits (Fang, 2023).

About 30 years ago, we entered the Breeding 3.0 stage, which was a significant shift in breeding methods. Breeding 3.0 achieves precise and revolutionary improvements in breeding by integrating genetic and genomic data, based on genotype selection (Wallace et al., 2018). The emergence of this stage marks further optimization and improvement of breeding methods.

In Breeding 3.0, the introduction of techniques such as assisted-marker backcrossing and pedigree confirmation has made breeding work more precise and efficient (Fang et al., 2001). Meanwhile, the application of linkage maps has made it more feasible to analyze complex traits, while the development of high-throughput genotyping has expanded the toolkit of quantitative genetics. Through genome-wide association study and genome selection, breeding values can be more accurately estimated and plant variety can be more accurately selected.

2 The Evolution of Breeding 3.0

2.1 The beginning and iconic achievements of Breeding 3.0

About 30 years ago, the beginning of Breeding 3.0 marked the start of the integration of genetic and genomic data with phenotypic data. One of the iconic achievements is the construction of the first saturated molecular genetic map of rice (Causse et al., 1994). Through this map, researchers can accurately locate and associate important agronomic traits on the rice genome (Causse et al., 1994). This study utilized molecular marker techniques such as restriction fragment length polymorphism (RFLP) and simple sequence repeat (SSR) to accurately locate important agronomic traits by analyzing the association between genetic markers and phenotype. Subsequently, with the further development of molecular marker technology, more molecular markers such as single nucleotide polymorphism (SNP) and cleaved amplified polymorphic sequence (CAPS) were applied in Breeding 3.0. These molecular markers have the advantages of high polymorphism and high-throughput typing, enabling researchers to conduct genetic analysis and gene mapping more quickly and accurately.

In addition, whole genome sequencing of rice is also one of the important breakthroughs in Breeding 3.0. Through comprehensive sequencing of the rice genome, we have revealed the composition and function of the rice genome, providing a deeper understanding for breeding work (International Rice Genome Sequencing Project, and Sasaki, 2005).

2.2 Technological transformation and Breeding 3.0

The evolution of Breeding 3.0 is driven by technological changes. Initially, assisted-marker backcrossing and pedigree confirmation were widely used in the early stages of Breeding 3.0 (Hospital and Charcosset, 1997). This technology utilizes molecular markers to assist in selecting offspring with target traits, thereby improving selection efficiency (Hospital and Charcosset, 1997).

Through the application of molecular markers, researchers are able to accurately track and identify the genetic basis of important agronomic traits. For example, the use of molecular markers in breeding can expedite the selection process and enhance breeding efficiency. By analyzing molecular markers closely associated with target traits, researchers can exclude offspring without the target gene in the early selection stages, thereby reducing breeding cycles and costs (Xu and Crouch, 2008).

Subsequently, the application of linkage maps became a key method for analyzing complex traits in Breeding 3.0. By constructing a linkage map, we can reveal the genetic basis of complex traits, providing important clues for breeding work (Ming et al., 2002; Paterson, 2019). In addition, the breakthrough in whole genome sequencing of rice has also driven the development of Breeding 3.0. Whole genome sequencing reveals genes related to important agronomic traits, providing valuable resources for breeding work (Yu et al., 2002).

2.3 High-throughput genotyping and Breeding 3.0

High-throughput genotyping is one of the important tools for Breeding 3.0. Through high-throughput genotyping, researchers can analyze variations in natural populations and identify genes related to agronomic traits (such as genome-wide association study). In addition, breeding values based on genome estimation (such as genome selection) have also become an important method for Breeding 3.0. By utilizing genomic information to predict the breeding value of individuals, genomic selection can accelerate the breeding process and improve selection efficiency (Resinde et al., 2012).

In summary, the evolution of Breeding 3.0 is driven by technological advancements, including assisted-marker backcrossing, linkage map construction, and whole genome sequencing. The application of these technologies provides more accurate and efficient methods for breeding work, enabling us to have a deeper understanding of the genetic basis of plant traits. High-throughput genotyping and genome-based breeding value estimation methods play an important role in Breeding 3.0, further improving its efficiency and accuracy, and bringing new opportunities and challenges to breeding work. With the continuous progress and innovation of technology, Breeding 3.0 will continue to promote the development and progress of plant breeding.

3 Methodology of Breeding 3.0

3.1 Optimization of assisted-marker backcrossing and pedigree confirmation

In Breeding 3.0, assisted-marker backcrossing and pedigree confirmation technologies have been further optimized and applied. The use of molecular markers to screen offspring with target traits has accelerated the breeding process through the use of assisted markers. In Breeding 3.0, we use more precise molecular markers such as SNP and SSR to improve selection efficiency and accuracy. Meanwhile, pedigree confirmation technology has also been widely applied in Breeding 3.0. Through pedigree confirmation, we can track the genetic background of the target trait and select the highest quality offspring as breeding materials.

For example, in barley breeding, the paper "Advanced Backcross QTL Analysis in Barley (*Hordeum vulgare* L.)" demonstrated how to use assisted-marker backcrossing technology to transfer yield-related QTLs from wild barley donors to superior receptors (Pillen et al., 2003). In addition, the study "Population Structure and Breeding Patterns of 145 US Rice Cultivars Based on SSR Marker Analysis" used SSR molecular marker technology to confirm the lineage of 145 US rice germplasm resources, providing accurate genetic background information for breeding work (Lu et al., 2005).

3.2 Application of linkage maps in analyzing complex traits

The application of linkage maps in Breeding 3.0 plays a crucial role in analyzing complex traits. By constructing a linkage map, we can reveal the association between traits and loci, and identify key genes that control traits. The analysis of the gene-trait association is crucial for the selection and optimization of breeding objectives. In Breeding 3.0, we use higher resolution linkage mapping technologies such as high-density SNP chips and genome sequencing to more accurately locate and identify genes related to complex traits.

The paper "Dissection of Complex Traits in Crop Plants: A Plea for Multiparental Populations" (Plant, Cell&Environment, 2004) proposed the importance of using multi parent populations to construct linkage maps to analyze complex traits in crop plants (Lander and Schork, 2006). In maize breeding, the study "Genome Wide Association Studies Using a New Nonparametric Model Reveal the Genetic Architecture of 17 Agronomic Traits in an Enlarged Maize Association Panel" (Plos Genetics, 2014) conducted a genome-wide association study using high-density SNP markers in maize, showcasing the genetic structure of 17 agronomic traits (Yang et al., 2014).

3.3 Technological progress and application of high-throughput genotyping

High throughput genotyping technology has made significant progress and application in breeding 3.0. Through high-throughput genotyping technology, we can quickly and accurately analyze large-scale genetic variations. These technologies include SNP chips, genome-wide association study, and whole genome sequencing. Through these technologies, we can screen candidate genes related to agronomic traits in natural populations and accelerate the breeding process. The technological progress of high-throughput genotyping provides more comprehensive and in-depth genetic information for breeding work, thereby improving the accuracy and efficiency of breeding.

For example, the "The 3000 Rice Genomes Project" (GigaScience, 2014) used high-throughput genotyping technology to comprehensively sequence 3 000 rice genomes, revealing the diversity and genetic variation of the rice genome. In wheat breeding, the study "Genome-Wide Association Study Reveals Novel Genes Associated with Culm Cellulose Content in Bread Wheat (*Triticum aestivum* L.)" (BMC Plant Biology, 2017) analyzed the stem cellulose content of 288 different wheat varieties and conducted genome-wide association studies (GWAS), revealing new genes related to wheat stem cellulose content. Another paper, "Genome-wide Association Mapping of Black Point Reaction in Common Wheat (*Triticum aestivum* L.)" (BMC Plant Biology, 2017), conducted a genome-wide association study (GWAS) on black point of wheat through high-density 90 K and 660 K single nucleotide polymorphisms (SNP) analysis. The black points of 166 elite wheat varieties was evaluated in five environments, and 25 unique loci were identified, which were distributed on multiple chromosomes and explained 7.9% to 18.0% of phenotypic variations (Liu et al., 2017).

Based on the above statements, the methodology of Breeding 3.0 includes optimized assisted-marker backcrossing and pedigree confirmation technologies, the application of linkage maps to analyze complex traits, and the technological progress and application of high-throughput genotyping technology. The development of these methods enables us to select and optimize breeding materials more accurately, providing more genetic information and tools for plant breeding.

4 The Advantages and Applications of Breeding 3.0

4.1 Precision and efficiency in integrating genetic and genomic data

A significant advantage of Breeding 3.0 is its ability to integrate genetic and genomic data, thereby improving the accuracy and efficiency of breeding. For example, in tomato breeding, The study "Efficiency of Genomic Selection for Tomato Fruit Quality" (Molecular Breeding, 2016) demonstrated the accuracy of genome selection in evaluating multiple metabolic and quality characteristics through cross validation, and estimated the impact of different factors on its accuracy. The results indicated that the accuracy of predicting phenotype values is closely related to the heritability of traits. The size of the training population increases the accuracy of predictions. The optimal conditions were to use 122 varieties and 5 995 single nucleotide polymorphism (SNP) markers (Duangjit et al., 2016). Obviously, by integrating genetic and genomic data, the accuracy of predicting tomato fruit quality traits can be significantly improved. In citrus breeding, the study “Genome Wide Selection in Citrus Breeding” (Genetics and Molecular Research, 2016) evaluated the efficiency of genome-wide selection (GWS) in citrus populations and compared it with phenotypic selection. Research has shown that GWS can accurately predict phenotypes and shorten selection cycles. This indicated that genome selection is useful in citrus breeding as it can predict phenotypes early and accurately (Gois et al., 2016). Similarly, in maize breeding, the study “Genome Wide Association Study for Drought, Aflatoxin Resistance, and Important Agronomic Traits of Maize Hybrids in the Sub-Tropics” (The Plos One, 2015) used a diversity panel consisting of 346 maize inbred lines from temperate, subtropical, and tropical regions for genome-wide association analysis. The study found 10 quantitative trait variations related to important agronomic traits such as grain yield, plant and spike height, and flowering time. These findings demonstrated the potential of genomic association studies in identifying major variations that affect quantity and complex traits such as yield under drought conditions (Farfan et al., 2015). Similarly, in rice breeding, the study “Genomic Selection and Association Mapping in Rice (*Oryza sativa*): Effect of Trait Genetic Architecture, Training Population Composition, Marker Number and Statistical Model on Accuracy of Rice Genomic Selection in Elite, Tropical Rice Breeding Lines” (Plos Genetics, 2015) evaluated the effectiveness of genomic selection (GS) in rice breeding. Research has found that genome prediction models outperform predictions based solely on lineage records for all three traits, including grain yield and flowering time. The study also suggested that using a subset of markers every 0.2 cM for genome selection is sufficient in these rice breeding materials (Spindel et al., 2015).

4.2 Improving plant varieties based on genotype selection

Another important application of Breeding 3.0 is the improvement of plant varieties based on genotype selection. By utilizing genomic information and genotype selection technologies, Breeding 3.0 can more accurately select plant individuals with target traits, accelerating the breeding process. For example, in wheat breeding, the study “Genomic Selection for Yield and Yyield-related Traits in Durum Wheat” (Molecular Breeding, 2018) evaluated the potential of single trait (ST) and multi trait (MT) genomic prediction models for yield and quality traits in durum wheat. The study used a breeding population (BP) of 170 varieties and advanced breeding lines, as well as 154 double haploid (DH) lines. Both populations underwent Infinium iSelect 90K SNP chip genotyping and multiple trait phenotypes. The study applied six ST-GS models and three MT prediction methods to predict yield, protein content, gluten index, and dough characteristics. The accuracy of ST prediction varies between 0.5 and 0.8 for different traits and models. Except for BayesA and BayesB better predicting gluten index, toughness, and strength in DH populations, the prediction accuracy of most traits in both populations was comparable (Haile et al., 2018). This study indicated that genotype selection can significantly improve the selection efficiency of yield and related traits in durum wheat. In cassava breeding, the study “Genome-wide association and prediction reveals the genetic architecture of cassava mosaic disease resistance and prospects for rapid genetic improvement” (The Plant Geneme, 2015) was the first genome-wide association mapping study conducted on 6128 African cassava breeding lines, aimed at identifying genes related to cassava mosaic disease resistance. Research has found that a region on chromosome 8 is the main resistance region, but 13 small effect regions have also been identified. In addition, the study also evaluated the accuracy of genomic selection for CMD resistance (Wolfe et al., 2015).

4.3 Contribution of genome-wide selection to quantitative trait analysis

The genome-wide selection technology in Breeding 3.0 plays an important role in analyzing quantitative traits. Through genome-wide selection, we can accurately analyze the genetic basis of quantitative traits and identify key genes related to these traits. For example, in rice breeding, the study “Genome-wide association mapping for yield and other agronomic traits in an elite breeding population of tropical rice (*Oryza sativa*)” (PLoS One, 2015) successfully identified 52 QTLs for 11 agronomic traits by using genome-wide association analysis technology, including large effect QTLs for flowering time and grain length/grain width/grain length-width ratio. The study also found haplotypes that can be used to select dwarf, early flowering, and high-yield plants (Begum et al., 2015). Similarly, in apple breeding, the study “Genome-wide Association Mapping of Flowering and Ripening Periods in Apple” (Front. Plant Sci., 2017) conducted a large-scale genome-wide association study (GWAS) on these phenotypic characteristics by using association panels from 1 168 different apple genotypes across Europe. The study identified key SNPs that affect flowering and maturation stages, and explored candidate genes for these genomic regions (Urrestarazu et al., 2017).

Breeding 3.0 has improved the accuracy and efficiency of breeding by integrating genetic and genomic data, improving plant varieties based on genotype selection, and making important contributions to quantitative trait analysis through genome-wide selection. These examples of applications fully demonstrate the potential and practical importance of Breeding 3.0 in plant breeding.

5 Challenges and Future Prospects

5.1 Technical and methodological challenges faced by Breeding 3.0

Although Breeding 3.0 has brought many innovations, it still faces some technical and methodological challenges. Firstly, Breeding 3.0 requires large-scale genetic and genomic data, which may be a challenge for resource limited breeding projects. Obtaining and analyzing large-scale genetic and genomic data requires high costs and complex technologies, which may limit the application of Breeding 3.0 in some regions and crops.

Breeding 3.0 requires advanced computing and information processing systems to interpret and utilize a large amount of genetic and genomic data. Processing and interpreting such a large amount of data requires highly specialized skills and powerful computing power, which may limit the application of Breeding 3.0 in some breeding projects.

Breeding 3.0 also needs to overcome ethical and legal issues related to genetic and genomic data. For example, privacy and intellectual property issues may pose challenges to data sharing and collaboration. In addition, for applications involving emerging technologies such as gene editing, relevant regulations and ethical guidelines need to be established to ensure their safety and sustainability.

5.2 Future directions and prospects of breeding 3.0 development

The development prospects of Breeding 3.0 are broad, and there are many future directions to explore. Firstly, with the advancement of technology and the reduction of costs, Breeding 3.0 will be more widely applied to various crops and regions. This will help improve the adaptability, yield and quality of crops, and meet the growing global food demand.

Breeding 3.0 will further integrate multiple genetic and genomic data, including phenotype, genome sequence, transcriptome data, etc., to gain a more comprehensive understanding and utilization of the genetic potential of crops. This will help discover more genes related to agronomic traits and improve the accuracy of predicting breeding values.

Breeding 3.0 will continue to promote the development of gene editing and genome modification technologies. With the maturity and promotion of gene editing technology, we will be able to more accurately modify crop genomes and create new varieties with greater agronomic value.

5.3 The introduction of the concept of Breeding 4.0

Breeding 4.0 represents a new level in the field of breeding, which involves synthesizing any known allele genome into an ideal combination through the ability of the whole genome. We are currently at the forefront of Breeding 4.0, which can purposefully combine functional genetic variations faster and better than ever before. The development of this breeding level benefits from significant technological advancements in genetics and information systems. For example, the cost of genome resequencing research can now be lower than that of repeated yield trials, and genome editing is expected to enable parallel and precise modifications of hundreds (possibly hundreds) of positions per generation. High throughput phenotyping can measure numerous traits with unprecedented spatiotemporal resolution, and machine learning methods make the processing and interpretation of agronomic data far beyond human capabilities.

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