植物育种简史
Brief History of Plant Breeding

育种 3.0：基因型选择的精确革命

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摘　要　育种 3.0 是一种基于精确基因型选择以及遗传和基因组数据的育种阶段，它代表了植物育种领域的一次重要技术转变，将传统的性状表现选择转变为基因型选择，以提高选择效率和准确性。育种 3.0 的起步可以追溯到约 1995 年，当时开始利用分子标记和基因组数据来补充表型数据。标志性的学术成果，如水稻的饱和性连锁图谱和全基因组测序突破，标志着育种 3.0 的开始阶段。育种 3.0 的方法包括辅助标记回交和家系确认、利用连锁图谱解析复杂性状和高通量基因分型技术的应用。整合遗传和基因组数据使得育种 3.0 具备了精准性和效率方面的优势。基于基因型选择的育种方法为改良植物品种提供了新的途径，而全基因组选择使得解析复杂的数量性状成为可能。

关键词　育种 3.0; 基因型选择; 遗传和基因组数据; 分子标记辅助育种

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 using genetic and genomic data, represents a significant technological shift in the field of plant breeding, replacing traditional phenotypic selection with genotype selection to enhance selection efficiency and accuracy. The inception of Breeding 3.0 can be traced back to approximately 1995 when molecular markers and genomic data began complementing phenotypic data. Landmark 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

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).

育种一直是农业领域的重要工作，旨在改良植物品种，提高农作物的产量、抗性和品质。随着科学技术的不断进步，育种方法也在不断演变。育种 2.0 阶段以常规育种为主，基于孟德尔的遗传定律和数量遗传学理论，通过创建变异群体和应用表型选择来改良植物品种。然而，在育种 2.0 中，仍然存在一些局限性，如选择效率的限制和复杂性状的解析困难(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.

约 30 年前，我们进入了育种 3.0 阶段，这是育种方法的一次重大转变。育种 3.0 通过整合遗传和基因组数据，以基因型选择为基础，对育种进行精确的革命性改进(Wallace et al., 2018)。这一阶段的出现标志着育种方法的进一步优化和提升。

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.

在育种 3.0 中，辅助标记回交和家系确认等技术的引入使得育种工作更加精确和高效(Fang et al., 2001)。同时，连锁图谱的应用使得解析复杂性状变得更加可行，而高通量基因分型的发展则扩展了数量遗传学的工具包，通过全基因组关联分析和基因组选择，可以更准确地估计育种值和选择植物品种。

1 The Evolution of Breeding 3.0

1.1 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.

1 育种 3.0 的演进

1.1 育种 3.0 的开端和标志性成果

大约 30 年前，育种 3.0 的开端标志着遗传和基因组数据开始与表型数据相结合。其中一项标志性成果是首张饱和的水稻分子遗传图谱的构建(Causse et al., 1994)。通过该图谱，研究人员能够准确地定位和关联水稻基因组上的重要农艺性状(Causse et al., 1994)。这一研究利用了分子标记技术，如限制性片段长度多态性(RFLP)和简单序列重复(SSR)，通过分析遗传标记与表型之间的关联，实现了对重要农艺性状的精确定位。随后，随着分子标记技术的进一步发展，更多的分子标记，如单核苷酸多态性(SNP)和单碱基扩增片段长

度多态性(CAPS)，被应用于育种 3.0 中。这些分子标记具有高度多态性和高通量分型的优势，使得研究人员能够更快速、更精确地进行遗传分析和基因定位。

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).

此外，水稻全基因组测序也是育种 3.0 的重要突破之一。通过对水稻基因组的全面测序，我们揭示了水稻基因组的组成和功能，为育种工作提供了更深入的理解(International Rice Genome Sequencing Project and Sasaki, 2005)。

1.2 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).

1.2 技术转变与育种 3.0

育种 3.0 的演进是由技术的转变推动的。最初，辅助标记回交和家系确认被广泛应用于育种 3.0 的起步阶段(Hospital and Charcosset, 1997)。这一技术利用分子标记辅助选择具有目标性状的后代，从而提高了选择效率(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).

通过分子标记的应用，研究人员能够准确地追踪和识别重要农艺性状的遗传基础。例如，分子标记辅助选择在育种中的应用可以加速选育进程，提高选育效率。通过分析与目标性状密切相关的分子标记，研究人员可以在早期选择阶段排除不带目标基因的后代，从而减少选育周期和成本(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).

随后，连锁图谱的应用成为育种 3.0 中解析复杂性状的关键方法。通过构建连锁图谱，我们能够揭示复杂性状的遗传基础，为育种工作提供了重要线索(Ming et al., 2002; Paterson, 2019)。此外，水稻全基因组测序的突破也推动了育种 3.0 的发展。全基因组测序揭示了与重要农艺性状相关的基因，为育种工作提供了宝贵的资源(Yu et al., 2002)。

1.3 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).

1.3 高通量基因分型与育种 3.0

高通量基因分型是育种 3.0 的重要工具之一。通过高通量基因分型，研究人员能够对自然群体的变异进行解析，从而识别与农艺性状相关的基因(例如，全基因组关联分析)。此外，基于基因组估计的育种值(例如，基因组选择)也成为育种 3.0 的重要方法。通过利用基因组信息预测个体的育种价值，基因组选择能够加速育种进程，提高选择效率(Resende 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.

综上所述，育种 3.0 的演进是由技术的转变推动的，包括辅助标记回交、连锁图谱构建和全基因组测序等。这些技术的应用为育种工作提供了更准确、更高效的方法，使我们能够更深入地理解植物性状的遗传基础。高通量基因分型和基于基因组的育种值估计等方法在育种 3.0 中发挥着重要作用，进一步提升了育种 3.0 的效率和精确性。为育种工作带来了新的机遇和挑战。随着技术的不断进步和创新，育种 3.0 将继续推动植物育种领域的发展和进步。

2 Methodology of Breeding 3.0

2.1 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.

2 育种 3.0 的方法论

2.1 辅助标记回交和家系确认的优化

在育种 3.0 中，辅助标记回交和家系确认技术得到了进一步优化和应用。辅助标记回交通过利用分子标记筛选具有目标性状的后代，加速了育种进程。在育种 3.0 中，我们采用更精确的分子标记，如 SNP 和 SSR，以提高选择效率和准确性。同时，家系确认技术在育种 3.0 中也得到了广泛应用。通过家系确认，我们可以追踪目标性状的遗传背景，并选择出最优质的后代作为育种材料。

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).

例如，在大麦育种中，"Advanced backcross QTL analysis in barley (*Hordeum vulgare* L.)"这篇论文展示了如何利用辅助标记回交技术将来自野生大麦的产量相关的 QTL 从供体转移到优良受体中(Pillen et al., 2003)。此外，"Population structure and breeding patterns of 145 US rice cultivars based on SSR marker analysis"这项研究使用 SSR 分子标记技术对 145 个美国水稻种质资源进行家系确认，为育种工作提供了准确的遗传背景信息(Lu et al., 2005)。

2.2 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.

2.2 连锁图谱在解析复杂性状中的应用

育种 3.0 中连锁图谱的应用对于解析复杂性状起着关键作用。通过构建连锁图谱，我们能够揭示性状与基因座之间的关联关系，并确定控制性状的关键基因。这种基因-性状关联的解析对于育种目标的选择和优化至关重要。在育种 3.0 中，我们采用更高分辨率的连锁图谱技术，如高密度 SNP 芯片和基因组测序，从而更准确地定位和识别与复杂性状相关的基因。

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).
"Dissection of complex traits in crop plants: A plea for multiparental populations " (Plant, Cell & Environment, 2004)这篇论文提出了使用多亲本群体构建连锁图谱来解析作物植物的复杂性状的重要性(Lander and Schork, 2006)。在玉米育种中，"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)"这项研究使用高密度 SNP 标记在玉米中进行了全基因组关联研究，展示了 17 种农艺性状的遗传结构(Yang et al., 2014)。

2.3 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.

2.3 高通量基因分型的技术进展与应用

高通量基因分型技术在育种 3.0 中取得了显著的进展和应用。通过高通量基因分型技术，我们能够快速、准确地分析大规模的遗传变异。这些技术包括 SNP 芯片、全基因组关联分析和全基因组测序等。通过这些技术，我们可以在自然群体中筛选出与农艺性状相关的候选基因，并加快育种进程。高通量基因分型的技术进展为育种工作提供了更全面、更深入的遗传信息，从而提高了育种的准确性和效率。

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).
例如，"The 3000 Rice Genomes Project" (GigaScience, 2014)这个项目利用高通量基因分型技术对 3 000 个水稻基因组进行了全面测序，揭示了水稻基因组的多样性和遗传变异。在小麦育种中，"Genome-Wide Association Study Reveals Novel Genes Associated with Culm Cellulose Content in Bread Wheat (*Triticum aestivum* L.) (BMC Plant Biology, 2017)"这项研究通过对 288 种不同小麦品种的茎秆纤维素含量进行分析，并进行全基因组关联研究(GWAS)，揭示了与小麦茎秆纤维素含量相关的新基因。另一篇论文“Genome-wide association mapping of black point reaction in common wheat (*Triticum aestivum* L.) (BMC Plant Biology, 2017)”，通过高密度小麦 90 K 和 660 K 单核苷酸多态性(SNP)分析，对小麦黑点反应进行了全基因组关联研究(GWAS)。在五个环境中评估了 166 种精英小麦品种的黑点反应，鉴定了 25 个独特位点，这些位点分布在多个染色体上，解释了 7.9%至 18.0%的表型变异(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.
综上所述，育种 3.0 的方法论包括优化的辅助标记回交和家系确认技术，连锁图谱的应用以解析复杂性状，以及高通量基因分型技术的技术进展与应用。这些方法的发展使我们能够更准确地选择和优化育种材料，为植物育种提供更多的遗传信息和工具。

3 The Advantages and Applications of Breeding 3.0

3.1 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).

3 育种 3.0 的优势和应用

3.1 整合遗传和基因组数据的精准性和效率

育种 3.0 的一个显著优势是能够整合遗传和基因组数据，从而提高育种的精准性和效率。例如，在番茄育

种中，"Efficiency of genomic selection for tomato fruit quality (Molecular Breeding, 2016)这项研究表明通过交叉验证评估基因组选择对多种代谢和品质特性的准确性，并估计不同因素对其准确性的影响。结果表明，预测表型值的准确性与特性的遗传率密切相关。训练群体的大小增加了预测的准确性。使用 122 个品种和 5995 个单核苷酸多态性(SNP)标记是最优条件(Duangjit et al., 2016)。显然，通过整合遗传和基因组数据，可以显著提高对番茄果实品质性状的预测准确性。在柑橘育种中，Genome wide selection in Citrus breeding (Genetics and Molecular Research, 2016)，这项研究评估了基因组广泛选择(GWS)在柑橘种群中的效率，并将其与基于表型数据的选择进行了比较。研究表明，GWS 可以准确地预测表型，并缩短选择周期。这表明基因组选择在柑橘育种中是有用的，因为它可以早期并准确地预测表型(Gois et al., 2016)。类似地，在玉米育种中，"Genome Wide Association Study for Drought, Aflatoxin Resistance, and Important Agronomic Traits of Maize Hybrids in the Sub-Tropics" (The Plos One, 2015)，这项研究使用了一个由温带、亚热带和热带地区的 346 个玉米自交系组成的多样性面板，进行了全基因组关联分析。研究发现了 10 个与粮食产量、植株和穗高、开花时间等重要农艺性状相关的数量性状变异。这些发现证明了基因组关联研究在识别影响数量和复杂性状(如干旱条件下的产量)的主要变异方面的潜力(Farfan et al., 2015)。同样在水稻育种中，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)，这项研究评估了基因组选择(GS)在水稻育种中的有效性。研究发现，基因组预测模型在所有三个性状(包括粮食产量和开花时间)上都优于仅基于谱系记录的预测。研究还表明，使用每 0.2 cM 一个标记的子集进行基因组选择在这些水稻育种材料中是足够的(Spindel et al., 2015)。

3.2 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).

3.2 基于基因型选择的改良植物品种

育种 3.0 的另一个重要应用是基于基因型选择改良植物品种。通过利用基因组信息和基因型选择技术，育种 3.0 能够更准确地选择具有目标性状的植物个体，加速育种进程。例如，在小麦育种中，"Genomic selection for yield and yield-related traits in durum wheat" (Molecular Breeding, 2018)这项研究评估了单性状(ST)和多性状(MT)基因组预测模型在硬粒小麦产量和质量性状上的潜力。研究使用了 170 个品种和先进育种系的育种群体(BP)以及 154 个双单倍体(DH)系。这两个群体都进行了 Infinium iSelect 90K SNP 芯片基因分型和多种

性状表型。研究应用了六种 ST-GS 模型和三种 MT 预测方法，预测产量、蛋白质含量、麸质指数和面团特性。ST 预测准确率在不同性状和模型之间变化在 0.5 到 0.8 之间，除了 BayesA 和 BayesB 在 DH 群体中更好地预测了麸质指数、韧性和强度外，大多数性状在两个群体中的预测准确率相当(Haile et al., 2018)。这项研究表明，基于基因型选择可以显著提高硬粒小麦产量和相关性状的选择效率。在木薯育种中，"Genome-wide association and prediction reveals the genetic architecture of cassava mosaic disease resistance and prospects for rapid genetic improvement" (The Plant Geneme, 2015)这个研究是首次对 6 128 个非洲木薯育种系进行的全基因组关联映射研究，旨在识别与木薯花叶病抗性相关的基因。研究发现，第 8 号染色体上的一个区域是主要的抗性区域，但也识别出了 13 个小效应区域。此外，研究还评估了基因组选择对 CMD 抗性的准确性(Wolfe et al., 2015)。

3.3 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).

3.3 全基因组选择对数量性状解析的贡献

育种 3.0 中的全基因组选择技术对于解析数量性状起到了重要作用。通过全基因组选择，我们能够精确地解析数量性状的遗传基础，并识别出与这些性状相关的关键基因。例如，在水稻育种中，"Genome-wide association mapping for yield and other agronomic traits in an elite breeding population of tropical rice (*Oryza sativa*)" (PLoS One, 2015)这项研究利用全基因组关联分析技术，成功地识别出了 11 个农艺性状的 52 个 QTL，包括开花时间和粮食长度/粮食宽度/粮食长度宽度比的大效应 QTL。研究还发现了可以用于选择矮秆、早开花和高产量植株的单倍型(Begum et al., 2015)。类似地，在苹果育种中，"Genome-wide association mapping of flowering and ripening periods in apple" (Front. Plant Sci., 2017)这项研究通过在欧洲范围内使用 1,168 种不同苹果基因型的关联面板，对这些表型特征进行了大规模的基因组关联研究(GWAS)。研究发现了影响花期和成熟期的关键 SNPs，并探讨了这些基因组区域的候选基因(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.

育种 3.0 通过整合遗传和基因组数据提高了育种的精准性和效率，基于基因型选择改良植物品种，并且全基因组选择对数量性状解析起到了重要的贡献。这些应用的例子充分展示了育种 3.0 在植物育种中的潜力和实际应用的重要性。

4 Challenges and Future Prospects

4.1 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.

4 挑战和未来展望

4.1 育种 3.0 面临的技术和方法上的挑战

尽管育种 3.0 带来了许多革新，但它仍然面临着一些技术和方法上的挑战。首先，育种 3.0 需要大规模的遗传和基因组数据，这对于资源有限的育种项目可能是一个挑战。获取和分析大规模的遗传和基因组数据需要高昂的成本和复杂的技术，这可能限制了育种 3.0 在一些地区和作物上的应用。

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.

育种 3.0 需要先进的计算和信息处理系统来解释和利用大量的遗传和基因组数据。处理和解释如此庞大的数据量需要高度专业化的技能和强大的计算能力，这可能限制了育种 3.0 在一些育种项目中的应用。

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.

育种 3.0 还需要克服与遗传和基因组数据相关的伦理和法律问题。例如，隐私和知识产权问题可能会对数据共享和合作造成困扰。此外，对于涉及基因编辑等新兴技术的应用，还需要制定相关的法规和伦理准则，以确保其安全和可持续性。

4.2 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.

4.2 育种 3.0 发展的未来方向与前景

育种 3.0 的发展前景广阔，有许多未来的方向可以探索。首先，随着技术的进步和成本的降低，育种 3.0 将更广泛地应用于各种作物和地区。这将有助于提高作物的适应性、产量和品质，并满足不断增长的全球粮食需求。

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.

育种 3.0 将进一步整合多种遗传和基因组数据，包括表型、基因组序列、转录组数据等，以更全面地了解和利用作物的遗传潜力。这将有助于发现更多与农艺性状相关的基因，并提高预测育种值的准确性。

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.

育种 3.0 将继续推动基因编辑和基因组改造技术的发展。随着基因编辑技术的成熟和应用的推广，我们将能够更精确地修改作物基因组，创造出更具有农艺价值的新品种。

4.3 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.

4.3 引入育种 4.0 的概念

育种 4.0 代表着育种领域的新一层次，即通过全基因组的能力将任何已知等位基因组合成理想的组合。我们现在正处于育种 4.0 的前沿，这一层次的育种能够比以往更快、更好地有目的地组合功能性遗传变异。这种育种水平的发展得益于遗传学和信息系统方面的重大技术进步。例如，基因组重测序研究的成本现在可以低于重复的产量试验，并且基因组编辑预计将使得每一代可以进行数百个位置(可能是数百个)的并行、精确修改。高通量表型测定可以以前所未有的时空分辨率测量众多性状，而机器学习方法使得农艺数据的处理和解释远远超出人类的能力。

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