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Key Genetic Markers Discovered through GWAS in Leguminous Crops and Their Application in Molecular Breeding

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Abstract The application of genome-wide association studies (GWAS) in molecular breeding of leguminous crops has shown great potential, despite technical and methodological challenges. These challenges include the need to process and analyze large-scale genetic data, the difficulty of ensuring high-quality genotypic and phenotypic data, and the complexity of controlling the effects of population structure and genetic background. Future development directions of this study may focus on developing more efficient data analysis algorithms, utilizing machine learning and artificial intelligence technologies, developing high-throughput phenotyping technologies, and integrating multi-omics data to reveal deeper molecular mechanisms of trait formation. Elaborate. It aims to discover that advances in GWAS and molecular breeding technologies are of great significance for increasing global food production and promoting agricultural sustainability, especially in improving leguminous crop yields, disease resistance and adaptability. The development of these technologies not only accelerates the cultivation of new varieties, but also helps reduce the use of chemical fertilizers and pesticides and promotes the process of ecological agriculture.

Keywords Genome-wide association studies (GWAS); Leguminous crops; Molecular breeding; Technical challenges; Agricultural sustainability

Legume crops are widely grown and consumed around the world, and they play a vital role in maintaining global food security, ecological balance, and economic development. As an important source of protein and other key nutrients, leguminous crops not only provide essential food resources for humans but also improve soil fertility through nitrogen fixation, thereby supporting sustainable agriculture and ecosystem health. In addition, leguminous crops also occupy an important position in the global trade market and have a significant impact on the economies of many countries.

However, with the growth of global population and the impact of climate change, leguminous crop production faces multiple challenges, including insufficient yields, pests and diseases, and vulnerability to adversities (e.g., drought, salinized soils). In this context, the development of molecular breeding technology provides new opportunities for the improvement of leguminous crops. Molecular breeding uses molecular biology tools, especially molecular markers, to select and breed crop varieties with superior traits. This method can significantly improve the efficiency and accuracy of breeding and help breed new varieties with high yield, strong disease resistance and wide adaptability (Sallam et al., 2016).

Genome -wide association studies (GWAS) are an important technique in molecular breeding, which identify genetic markers associated with specific traits by statistically analyzing the association between genomic data and phenotypic data. The advantage of GWAS is its ability to explore trait-related genetic variation across the entire genome, without being limited to known genes or markers, making it a powerful tool for discovering crop genetic diversity and the potential for trait improvement. Through GWAS, researchers can reveal the genetic basis that affects important agronomic traits in leguminous crops, such as yield, quality, stress resistance, etc., thereby guiding molecular breeding practices (Dhaliwal et al., 2022).

In recent years, the application of GWAS in genetic research and breeding of leguminous crops has achieved remarkable results. For example, through GWAS analysis, researchers successfully identified multiple genetic loci in soybean (*Glycine max*) related to oil and protein content, disease resistance, and tolerance to drought and saline-alkali environments (Korte and Farlow, 2013).

These findings not only enrich our understanding of soybean genetic diversity, but also provide valuable genetic markers for molecular-assisted selection, further promoting the progress of soybean breeding.

Although GWAS has shown great advantages in revealing the potential of crop genetic traits, it also faces some challenges in practical applications, such as the genetic background of complex traits, statistical analysis problems of high-dimensional data, and the management and management of large-scale genomic data. Explanation etc. Therefore, future research needs to continue to optimize GWAS analysis methods and improve its accuracy and efficiency in analyzing complex traits .

1 Application Cases of GWAS in Leguminous Crop Research

1.1 GWAS methodology

GWAS is a important technique in modern genetic research, which allows researchers to identify genetic variants associated with specific phenotypes or traits across the entire genome. In the study of leguminous crops, GWAS has become a powerful tool for discovering new genetic markers and understanding the genetic basis of traits. GWAS provide a powerful platform for identifying genetic markers associated with important traits in leguminous crops. Through the above methodological steps, GWAS can explore the genetic basis of traits across the entire genome, providing valuable resources for genetic improvement and molecular breeding of crops.

The first step in GWAS is to collect a sufficient number of study samples with sufficient genetic diversity and phenotypic data on the studied traits. In the study of leguminous crops, this often means selecting a broad variety or natural group for analysis. Subsequently, the samples are genotyped using high-throughput sequencing technologies , such as single nucleotide polymorphism (SNP) chips or whole-genome sequencing , to obtain genetic marker information for the entire genome (Hoyos-Villegas et al., 2015).

The collection of phenotypic data is another critical step in GWAS studies. This includes precise measurements of specific traits in leguminous crops, such as yield, disease resistance, stress tolerance, etc. The quality of phenotypic data directly affects the accuracy and reliability of GWAS analysis. Therefore, standardized measurement methods and repeated measurements across multiple environments or growing seasons are needed to ensure data stability and repeatability.

With genotypic and phenotypic data in hand, the next step is to perform association analysis using statistical methods. This often involves using multiple statistical models to detect correlations between variation in genotypic data and phenotypic traits. Commonly used statistical models include linear mixed models (LMM) and fixed and random effects mixed linear models (MLM), which can effectively identify genetic markers associated with traits while controlling the effects of population structure and kinship (Wen et al., 2018).

After the GWAS analysis is completed, the association signal needs to be interpreted, which includes identifying genetic markers and potential candidate genes that are significantly associated with the trait. Through further bioinformatics analysis and functional studies, such as gene expression analysis and gene function verification experiments, the mechanism of action of these candidate genes in trait formation can be deeply understood.

Functional verification of candidate genes is carried out through genetic transformation, gene editing or other molecular biology techniques to confirm that these genes indeed play a key role in the trait expression of leguminous crops. This step is of crucial significance for ultimately determining the molecular basis of the trait and applying GWAS results to molecular breeding of leguminous crops.

1.2 Discovery of key genetic markers

GWAS has achieved remarkable results in genetic research in leguminous crops, especially in identifying key genetic markers associated with important traits such as yield, disease resistance, and stress tolerance. Below are some specific examples of important genetic markers discovered through GWAS in leguminous crops, which demonstrate the scope and potential of GWAS technology in crop improvement research.

GWAS studies successfully identified multiple genetic markers associated with yield-related traits such as seed size, pod number, and seed number. For example, Zhang et al. (2016) discovered several SNP markers related to soybean seed size and yield through GWAS analysis, which provides valuable genetic resources for molecular breeding of soybean yield traits.

In pea (*Pisum sativum*), GWAS study reveals association with resistance to *Fusarium oxysporum* associated genetic markers. Kumar et al. (2015) reported that several SNP markers were significantly associated with Fusariu m wilt resistance in pea, and these findings can help improve disease resistance in pea through molecular marker-assisted selection (MAS).

In chickpea (*Cicer arietinum*), GWAS analysis identified key genetic markers associated with salt tolerance. Varshney et al. (2019) conducted GWAS analysis on chickpea varieties under salt stress conditions and identified multiple SNP markers related to salt tolerance. These findings provide a molecular basis for improving the stress tolerance of chickpea.

Root traits are key factors in the adaptation of leguminous crops to drought and low-fertilizer conditions. In a study of faba beans (*Vicia faba*), a GWAS study identified genetic markers associated with root depth and branch number, which are important for breeding crops adapted to drought conditions. Broad bean varieties are of great significance (Webb et al., 2016).

The above examples demonstrate the application of GWAS in genetic research of leguminous crops. By identifying genetic markers related to key agronomic traits, GWAS provides a powerful tool for genetic improvement and molecular breeding of crops. These research results not only deepen our understanding of the genetic basis of leguminous crop traits, but also point the way for future breeding efforts, especially in improving crop yield, disease resistance and stress tolerance.

1.3 Related case analysis

Genome-wide association analysis (GWAS) has achieved remarkable results in genetic research in leguminous crops, especially in identifying key genetic markers associated with important traits such as yield, disease resistance, and stress tolerance.

In Adzuki Bean , the author assembled a high-quality adzuki bean genome, covering almost the entire genome sequence of adzuki bean. At the same time, the author also combined the genome with genetic linkage groups for GWAS analysis and identified more than 300 potentially important genomic loci.

Aleena et al. (2022) performed single-molecule real-time (SMRT) long-read genome sequencing on the high-yielding Indian adzuki bean variety VRB3 , and assembled 1287 C ontig, with an N50 of 1.71 Mb and a total length of 605.22 Mb. The authors also used optical map data (589.03 Gb) and Hi-C library sequencing data (145.40 Gb) to correct these contigs. Illumina short read (186.45 Gb) corrects bases and fills gaps. The authors also anchored the assembled scaffold through an ultra-high-density genetic linkage map (containing 25 633 SNPs). With the help of this genetic linkage map, the authors constructed 11 chromosomes with a total chromosome length of 619.01 Mb (Figure 1). The genome covers almost 99.5% of the estimated genome length and is the largest chromosome-level genome of the genus Cowpea to date. The authors also generated VRB3 transcriptome data through the Iso-Seq method, generating a total of 33 004 transcripts with a total length of 94.43 Mb. The genome sequence after masking of repetitive sequences was used to annotate non-redundant and high-confidence genes, and 37 489 protein-coding genes were finally identified. BUSCO analysis also showed that the adzuki bean genome assembly was almost complete.

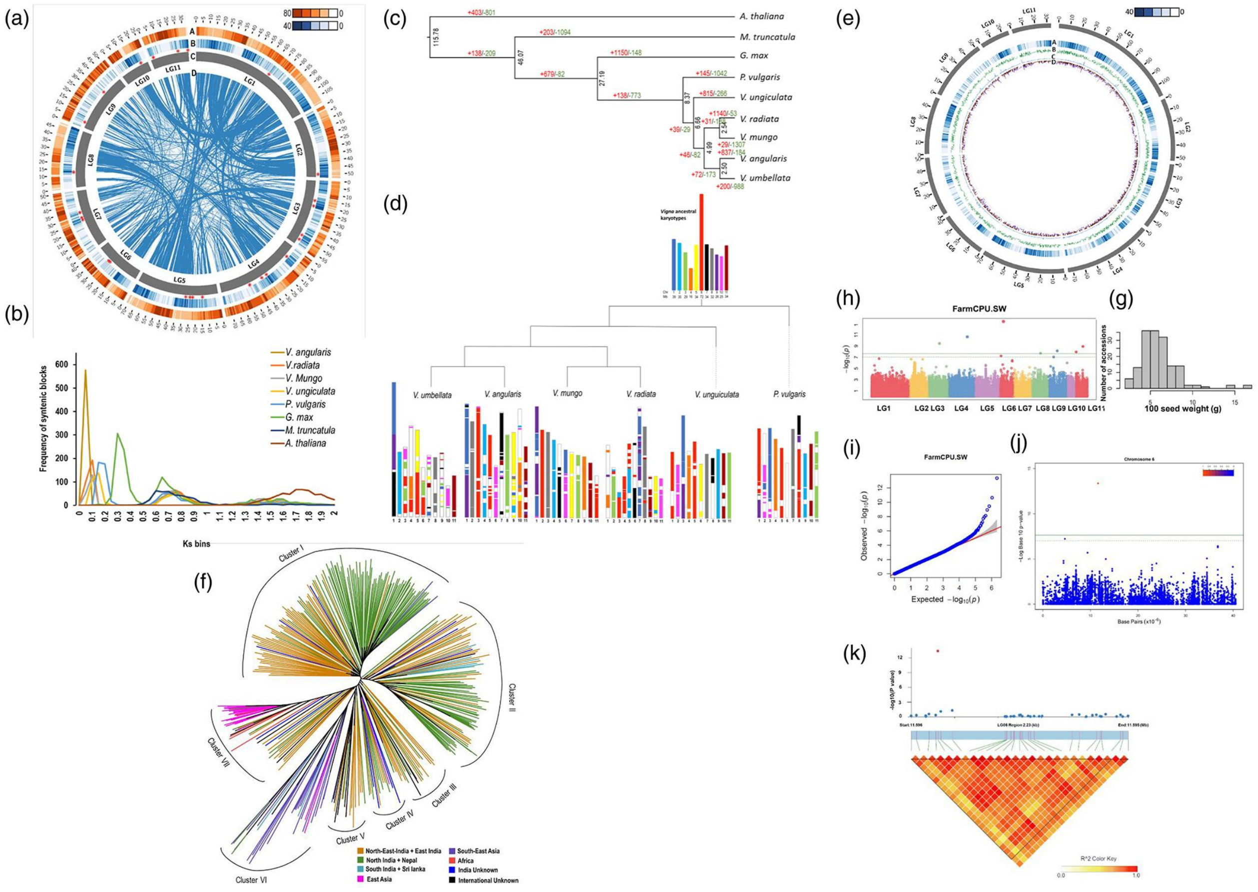

Figure 1 Multiple genetic characteristics of the adzuki bean genome (Aleena et al., 2022)

In order to analyze the genetic network behind soybean agronomic traits using genome-wide association studies, the research team conducted GWAS on 84 traits based on more than 4 million markers (with minor allele frequency [MAF]≥0.05] SNPs), 809 accessions were genotyped by MLM implemented in Efficient Mixed-Model Association eXped ited (EMMAX). Kinship relationships were used to define the variance structure of random variables for the total genetic effects of 809 accessions. No inflated P values were found, and the majority of markers (99%) exhibited P values equal to those expected under the null hypothesis, indicating that MLM controls group structure and cryptic relationships well. To control for false positives and false negatives, we also performed permutation testing by randomly shuffling phenotypes to break their relationship with genotypes, thereby deriving genome-wide thresholds (Figure 2). By using empirical thresholds, we identified 150 SALs that were significantly associated with 57 of the 4 traits using all 809 accessions (Figure 2) (Fang et al., 2022).

Kim et al. (2021) used the high-precision soybean genome reference sequence to conduct GWAS analysis on the protein and oil phenotypes of soybean seeds during the soybean domestication process. Many nearly identical materials were eliminated from the 116 soybean population. Then, using 36 of the SoySNP50K data 489 SNP pairs 8 844 non-redundant soybean materials were conducted 4 467 134 SNP genotype analysis, 3 082 234 SNPs were used for GWAS, and the median Beagle R2 after filtering was 0.95. As expected, main peaks appeared for both seed oil and protein. Interestingly, more than 10 new minor significant peaks appeared in both oil and protein GWAS, mainly located on chromosomes 2, 4, and 10. Deleterious mutation patterns during soybean domestication were used to construct a high-quality soybean SNP variation map, which can be used as a reference map to improve genotype assignment by GWAS for oil and protein traits. In addition to those unique genomic variation characteristics due to selfing, the author believes that the soybean variation map and method developed by him can be directly used for rapid and accurate mining of genetic variation in soybean (Figure 3).

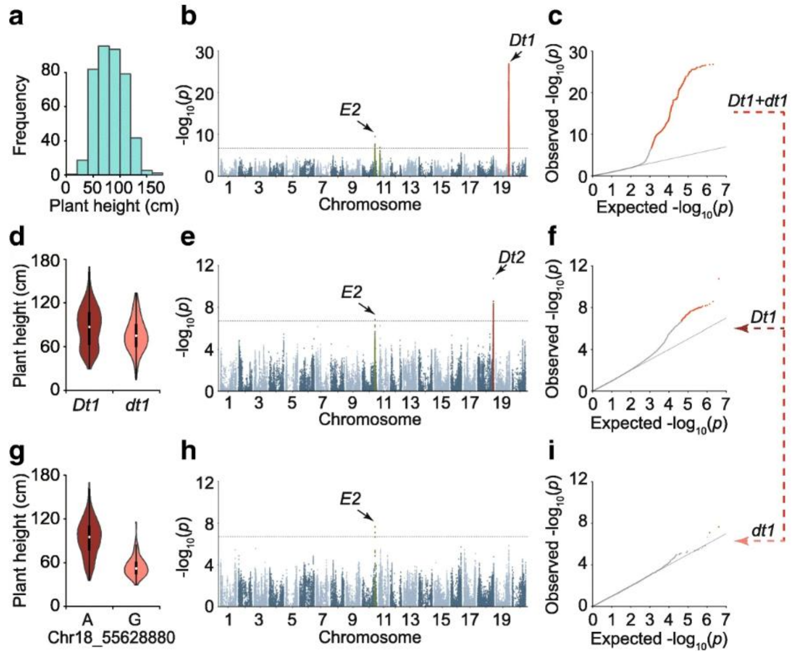

Figure 2 GWAS of the soybean plant height (Fang et al., 2022)

Note: a: Distribution of the plant height values across all of the 809 soybean accessions; b: GWAS result from all accessions. In the GWAS result, both known genes Dt1 and E2 are identified; c: Quantile–quantile plot for plant height; d: The plant height variation between different Dt1 alleles in all 809 accessions; e: The GWAS result of plant height using the accessions from the Dt1 subgroup; f: Quantile–quantile plot for plant height of Dt1 subgroup; G: Plant height variation between different Dt2 genotypes in the Dt1 subgroup; h: The GWAS result of plant height using the accessions from the dt1 subgroup; i: Quantile–quantile plot for plant height of dt1 subgroup (Fang et al., 2022)

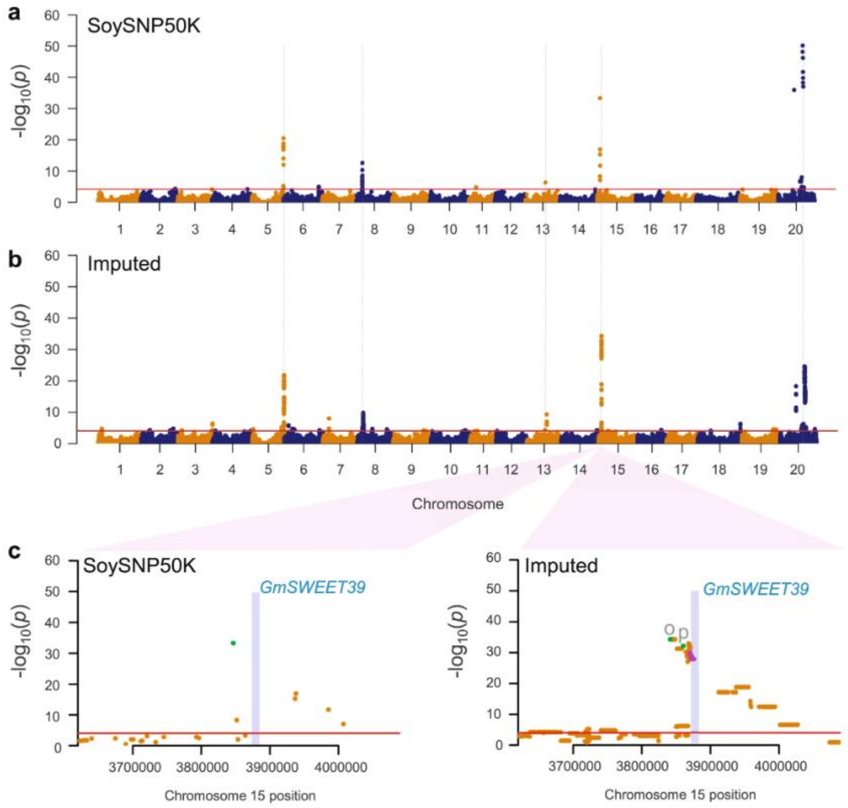

Figure 3 Comparison of mvMLM-based GWAS for oil and protein contents using unimputed and imputed genotype data (Kim et al., 2022)

These research results not only deepen our understanding of the genetic basis of leguminous crop traits, but also point the way for future breeding efforts, especially in improving crop yield, disease resistance and stress tolerance.

2 Application of Genetic Markers in Molecular Breeding

2.1 Genetic marker assisted selection (MAS)

Assisted Selection (MAS) is an important means in modern molecular breeding technology, which mainly uses molecular markers to assist traditional breeding. In MAS, by identifying molecular markers that are closely associated with target traits, breeders can more accurately and efficiently select plants with desired traits, thus accelerating the breeding process and improving the accuracy of breeding.

Genetic markers refer to specific sites in DNA sequences that exhibit polymorphism in different individuals or populations, that is, there are sequence variations. These polymorphic sites can serve as "markers" to help scientists track specific genetic material. In breeding, genetic markers usually have a genetic linkage relationship with important agronomic traits, such as yield, disease resistance, drought resistance, etc. By analyzing the genetic markers of plants, breeders can predict their phenotypic traits, that is, they can know what traits they will show without waiting for the plant to fully grow and develop (Izquierdo et al., 2023).

Legume crops, including soybeans, peas, lentils, etc., are important global food and feed crops and are of great significance for improving food security and agricultural sustainability. Many leguminous crops are susceptible to various diseases, such as soybean verticillium wilt, pea brown spot, etc. MAS can be used to identify plants carrying specific disease resistance genes, thereby effectively breeding more disease-resistant varieties. By identifying genetic markers associated with high-yielding traits via MAS, breeders can select plants that are more likely to exhibit high-yielding traits for hybridization and propagation, accelerating the development of high-yielding varieties. The quality of leguminous crops, such as protein content, oil content, etc., has a direct impact on their market value. MAS allows breeders to select for these specific quality traits and improve the overall quality of crops (Erdogmus et al., 2022).

Although MAS offers great potential in leguminous crop breeding, its implementation also faces several challenges, including the need for extensive preliminary studies to identify markers associated with important traits, relatively high costs, and complex technical requirements. However, with the continuous advancement of molecular biology technology and the gradual reduction of costs, the application scope of MAS is continuously expanding, and its role in precision breeding is becoming more and more important.

Genetic marker-assisted selection technology plays a key role in the molecular breeding of leguminous crops. It accelerates the breeding process and improves breeding efficiency by efficiently and accurately selecting individuals with desired traits. With the discovery of more genetic markers and the improvement of MAS technology, it is expected that greater progress will be made in increasing crop yields, improving quality, and enhancing stress resistance in the future.

2.2 Enhanced molecular breeding strategies

The discovery of genetic markers has provided powerful tools for molecular breeding, especially in the improvement of leguminous crops, and the application of these markers has greatly enhanced the efficiency and accuracy of breeding strategies. Below are several ways to enhance molecular breeding strategies by utilizing genetic markers.

Molecular marker-assisted selection (MAS) is a method that uses genetic markers that are closely associated with important agronomic traits to guide breeding selection. Genetic markers identified through GWAS can be used to directly select individuals with desired traits without having to wait until the crop matures to evaluate its traits. This method is particularly suitable for difficult-to-measure traits such as disease resistance and stress tolerance, as well as those that are less affected by the environment. MAS not only improves the accuracy of selection, but also significantly shortens the breeding cycle.

Genomic selection (GS) is a more comprehensive approach than MAS that uses genetic marker information across the entire genome to predict an individual's breeding value. Unlike MAS, GS does not rely on the association of specific genetic markers with traits, but rather considers the cumulative effect of all markers. This method is particularly suitable for the improvement of complex traits, such as yield and quality traits, because these traits are usually controlled by multiple genes (Cichy et al., 2015).

Gene editing technology, especially the CRISPR/Cas9 system, provides the possibility to precisely modify crop genomes. Using the genetic markers discovered by GWAS, researchers can design specific gene editing tools to precisely knock out or modify genes that affect key traits. This strategy allows breeding not only to select for naturally occurring genetic variations, but also to create new genetic variations, further expanding the breeding possibilities.

For some traits that are difficult to improve through traditional breeding methods, transgenic technology provides an effective solution. By introducing key genes identified in GWAS studies into crops, the performance of crop traits can be directly changed. This method has shown great potential in improving crop disease resistance and adaptability (Kamfwa et al., 2014).

In actual molecular breeding processes, the above methods are often not used in isolation. In order to achieve the best improvement effect, breeders can comprehensively apply MAS, GS, gene editing, transgenic and other technologies according to specific circumstances. Through such an integrated strategy, genetic markers can be effectively utilized to improve the yield, quality, disease resistance, and environmental adaptability of leguminous crops.

The application of genetic markers in molecular breeding has greatly enhanced the efficiency and precision of leguminous crop improvement. With the continuous advancement of genomic information and molecular biology technology, these strategies will be further optimized and expanded to provide strong support for global food security and sustainable agricultural development. Molecular breeding using genetic markers not only accelerates the process of crop improvement, but also provides new solutions to challenges encountered in traditional breeding.

2.3 Successful cases of application of genetic markers in molecular breeding

Rajendran et al. (2021) have promoted the expansion of genomic resources of leguminous food crops such as peas. In particular, by using genome sequencing (GBS) technology, researchers can quickly and cost-effectively screen germplasm resources, discover genome-wide single nucleotide polymorphisms (SNPs), develop high-density linkage maps, and evaluate species. Genetic diversity in quality collections. This provides an important basis for molecular breeding of leguminous crops such as peas (Figure 4).

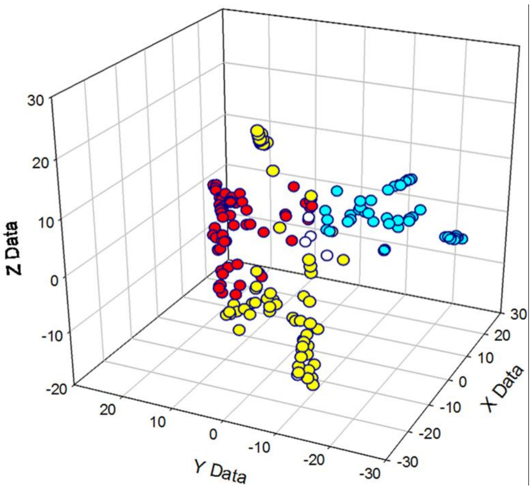

Figure 4 Principal component analysis of 176 lentil accessions with K = 3 based on SNP genotyping (Rajendran et al., 2021)

In alfalfa (*Medicago truncatula*): A study identified candidate genes associated with improved seed size and composition via GWAS. This work used two different models for genomic association prediction, including a single-locus mixed linear model and a multi-locus model. Through these analyses, researchers clearly identified quantitative trait nucleotides (QTNs) that are highly correlated with seed size and composition , providing powerful genetic markers for the improvement of seed traits (Chen et al., 2021) (Figure 5).

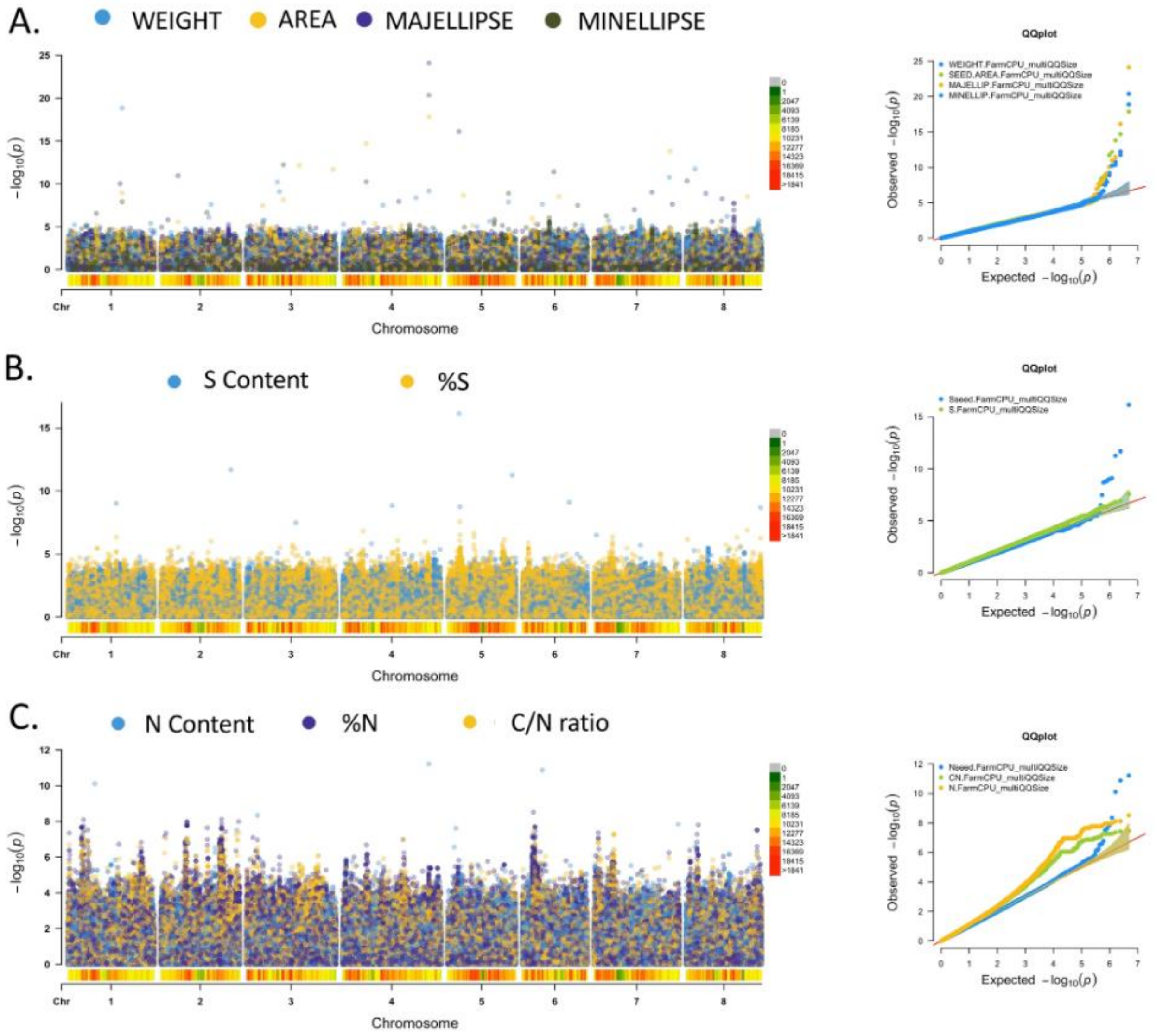

Figure 5 Genome wide association study between alfalfa seed traits and Manhattan and QQ maps obtained from FarmCPU

Note: A: Combination of studies on the correlation between seed size (weight, area, majellipse, minellipse); B: A combination of studies on the correlation between seed sulfur content (mg/seed) and sulfur concentration (%, w/w); C: Combination of correlation studies on seed protein content (nitrogen content (mg/seed); Nitrogen concentration (%, w/w); Carbon/nitrogen ratio (Chen et al., 2021)

These cases demonstrate the potential of GWAS technology in identifying genetic markers associated with important agronomic traits. By using these genetic markers, researchers can make more accurate breeding selections and speed up the process of improving leguminous crop varieties. These studies not only deepen our understanding of the genetic basis of crops, but also provide important tools and resources for achieving the breeding goals of high-yielding, high-resistant, and high-quality leguminous crops.

3 Challenges and Prospects

Genome-wide association studies (GWAS) is a technology widely used in plant genetics and breeding research, especially in leguminous crops. It has brought many breakthroughs, but it also faces a series of technical and methodological challenges. At the same time, with the advancement of science and technology and the deepening of research, GWAS and its application prospects in leguminous crop breeding are still very broad, and are of great significance for increasing global food production and agricultural sustainability.

The big data generated by GWAS requires powerful computing power for processing and analysis, which is a big challenge for research institutions with limited resources. With the development of sequencing technology, the amount of data has increased dramatically, and how to effectively store, manage and analyze these data has become an urgent problem that needs to be solved (Sonah et al., 2015).

High-quality genotypic and phenotypic data are the key to successful GWAS studies. However, the accurate recording of phenotypic data is greatly affected by environmental factors, which may lead to instability and poor reproducibility of research results. The genetic background of leguminous crops is diverse, and population structure and genetic relationships may have a significant impact on GWAS analysis, increasing the risk of false-positive results. More sophisticated statistical models need to be developed to control these confounding factors. Future research needs to develop more efficient algorithms and statistical models to handle big data problems in GWAS and improve the accuracy and efficiency of analysis. The introduction of machine learning and artificial intelligence technologies may provide new ideas for solving these problems (Cichy et al., 2015).

The development of high-throughput and automated phenotypic collection technologies will help improve the quality and quantification of phenotypic data, allowing GWAS to more accurately associate specific genetic variants. By integrating multi-omics data such as transcriptomics, proteomics, and metabolomics, GWAS can reveal the molecular mechanisms of trait formation at a deeper level and provide more comprehensive genetic information for breeding.

GWAS and molecular breeding technologies are of great significance in addressing global food security challenges by improving crop yield, resistance and adaptability. The application of GWAS technology in leguminous crops can not only accelerate the breeding of new varieties, but also improve the efficiency and sustainability of agricultural production. By precisely improving crop traits and reducing the use of chemical fertilizers and pesticides, molecular breeding technology can help promote the development of ecological agriculture and protect biodiversity.

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