

The Genetic Basis of Nutritional Quality Traits in Maize: Insights from GWAS

Liang Li, Wenzhong Huang ✉

Hainan Key Laboratory of Crop Molecular Breeding, Sanya, 572000, Hainan, China

✉ Corresponding author: 3048511772@qq.com

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Abstract As a cornerstone of global food security, the nutritional quality traits of maize are crucial for enhancing food value and meeting the growing nutritional demands. This study utilized the Genome-Wide Association Study (GWAS) method to explore the genetic basis of maize nutritional quality traits, including protein content, oil content, and the content of vitamins and minerals. By analyzing a vast array of maize genetic resources and phenotypic data, we identified several genetic markers and candidate genes significantly associated with nutritional quality traits. These discoveries provide new insights into the genetic regulatory mechanisms of maize nutritional quality traits and offer valuable molecular markers for future maize improvement and breeding programs. In summary, this study not only enhances our understanding of the genetic foundations of maize nutritional quality traits but also demonstrates the potential application of GWAS in crop genetic research, with the expectation that these fundamental research outcomes will promote the improvement of maize varieties to meet global demands for healthy food.

Keywords Maize; Nutritional quality traits; Genetic basis; Genome-wide association study (GWAS); Candidate genes

Corn is not only the cornerstone of global food production but also an important source of feed for humans and livestock. As the global population grows and nutritional needs increase, the nutritional value of corn has received unprecedented attention (Wallace et al., 2014). The nutritional components of corn, including protein, oil, vitamins, minerals, etc., are of great significance for improving human nutrition and health. Therefore, improving the nutritional quality of corn has become an important goal of today's agricultural research and breeding efforts. In this context, it is particularly important to understand the genetic mechanisms affecting nutritional quality traits of maize. The nutritional quality traits of maize are controlled by multiple genes, and the genetic complexity of these traits poses breeding challenges.

In recent years, genome-wide association studies (GWAS) have become a powerful tool for analyzing the genetic basis of complex traits. GWAS can identify key genetic loci and candidate genes that affect traits by analyzing the association between genetic variation and trait variation. This method has been successfully applied in a variety of crops, revealing the genetic basis of many important traits and providing new strategies and targets for crop genetic improvement. However, although GWAS has made progress in maize genetic research (Prasanna et al., 2021), research on the genetic basis of nutritional quality traits still faces challenges. These challenges include the complexity of traits, the influence of environmental and genetic interactions, and the lack of efficient algorithms suitable for large-scale sample analysis.

This study aims to use the GWAS method to deeply explore the genetic basis of corn nutritional quality traits (Sun et al., 2011). Through genome-wide scanning of a large number of genetically diverse maize samples, this study identified key genetic loci and candidate genes associated with maize nutritional quality traits. The purpose of this work is not only to improve our understanding of the genetic regulation mechanism of corn nutritional quality, but also to provide molecular markers for the improvement of corn nutritional quality, thereby promoting the breeding of high nutritional value corn varieties. We hope that these research results can support the direction of future corn breeding, especially in terms of improving global food security and nutrition, and providing corn with higher nutritional value for humans, livestock and poultry.

1 Nutritional Quality Traits of Corn

In today's world, as the population grows and living standards improve, the requirements for the nutritional value of food also increase. As one of the world's most important food crops, corn not only plays a key role in ensuring global food security, but the optimization of its nutritional components has also become a focus of research and breeding. The nutritional quality traits of corn, such as protein content, oil content, vitamin and mineral content, are directly related to its use value and market demand. These nutritional quality traits not only affect human health, but also have a significant impact on agricultural economy (Doebley et al., 2006).

1.1 Definition and classification

The nutritional quality traits of corn mainly include protein content, oil content, vitamin and mineral content. Protein is an indispensable component of living organisms and is related to the construction and repair of cells. The content and quality of protein in corn directly affect its nutritional value as food and feed. Oil is not only an important source of energy, but also contains a variety of unsaturated fatty acids, which are beneficial to human health. Although the content of vitamins and minerals in corn is not high, they play an important role in maintaining normal physiological functions of the human body and promoting health. Therefore, increasing the content of these nutrients in corn is of great significance to improving its overall nutritional value (Gibbon and Larkins, 2005).

1.2 Impact of nutritional quality traits on health and economy

The improvement of nutritional quality is directly related to consumers' health (Pixley et al., 2013). With the improvement of people's living standards, the nutritional demand for food is also increasing. Corn is a food crop with huge global consumption. Optimization of its nutritional components can effectively improve the nutritional intake of the population, especially in developing countries. Increasing the protein and vitamin content of corn (Dong et al., 2006) can help reduce the occurrence of malnutrition and related diseases. In addition, corn varieties rich in oil can provide the human body with more healthy fatty acids (Alrefai et al., 1995), such as omega-3 and omega-6 fatty acids, which have a positive effect on preventing cardiovascular diseases.

From an economic perspective, improving the nutritional quality traits of corn is of great significance to both agricultural producers and the processing industry. Corn varieties with high nutritional value usually have higher market demand and better price advantages, which can directly increase farmers' income and promote sustainable development of agriculture. At the same time, for the food and feed processing industry, high-quality corn raw materials can enhance the market competitiveness of final products and meet consumer demand for healthy food. In addition, with the development of biotechnology, corn varieties enriched in specific nutrients can also be used as raw materials for functional foods or biological products, opening up new economic growth points.

The nutritional quality traits of corn are not only related to human health, but also an important driving force for agricultural economic development. Through the advancement of scientific research and breeding technology, optimizing the nutritional composition of corn can improve human nutrition and health while ensuring global food security, and promote the economic development of the agriculture and food industries. Therefore, strengthening the research and improvement of corn nutritional quality traits is an important way to achieve dual security of food and health.

2 Overview of GWAS Technology

Genome-wide association studies (GWAS) are a research method used to find associations between specific traits and genetic markers in multiple genome data. In recent years, GWAS has become an important tool in genetic research, especially in crop genetic improvement and the discovery of disease-related genes.

2.1 Basic principles of GWAS

The basic principle of GWAS is to scan the entire genome to find the association between trait phenotype and genotype. This process usually involves the integrated analysis of large numbers of samples to ensure the reliability and accuracy of the research results. In GWAS, researchers examine thousands of single nucleotide polymorphisms (SNPs) markers spread across an individual's genome. By comparing the frequency of SNPs in

individuals with different phenotypes (e.g., corn varieties with different nutritional quality traits), genetic variants that are significantly associated with specific traits can be identified.

2.2 Methods of applying GWAS in corn genetic research

In corn genetic research, GWAS methods have been widely used to analyze the genetic basis of complex traits, such as yield, disease resistance, and nutritional quality (Dudley et al., 2007). Through GWAS, researchers can quickly identify key genes or genetic markers related to target traits in a large amount of genetic resources in maize (Figure 1) (Dudley et al., 2007). For example, in research on improving the nutritional quality of corn, GWAS can help scientists discover genetic loci that affect protein content, oil content, and vitamin content. This information not only helps to understand the genetic mechanism of traits, but also provides important molecular markers for molecular-assisted breeding of corn, thereby accelerating the selection of corn varieties with high nutritional value.

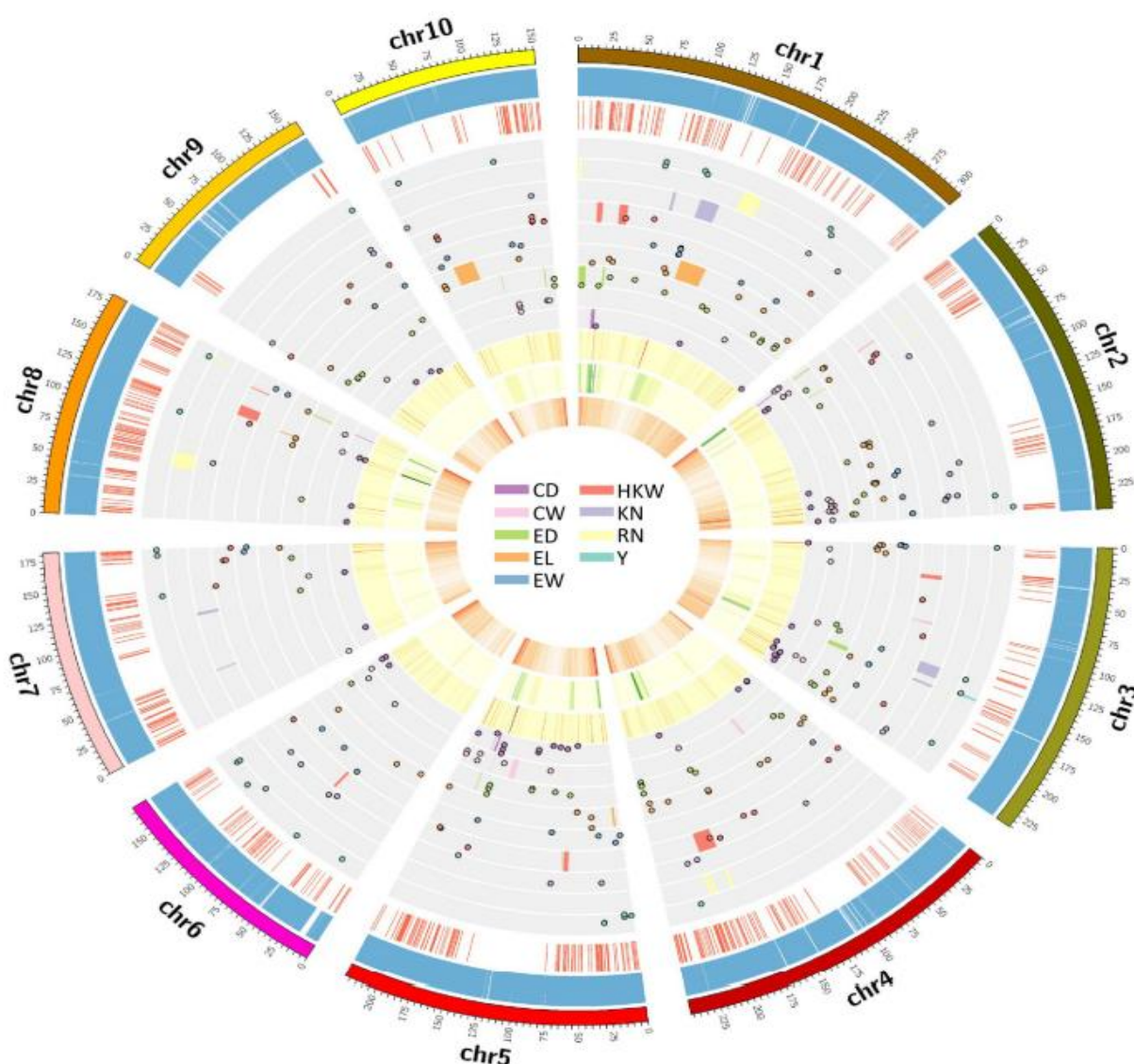


Figure 1 Distribution of genome-wide significant SNPs, QTL intervals, and related genomic features (Dudley et al., 2007)

2.3 GWAS data analysis and interpretation

The analysis and interpretation of GWAS data is a complex process involving a large amount of bioinformatics analysis. First, it is necessary to perform quality control on the large number of SNPs data generated by GWAS to exclude markers with unclear genetic information or high missing rates. Afterwards, statistical analysis methods, such as linear mixed models, are used to evaluate the strength of the association between each SNPs and the trait phenotype. Ultimately, significantly associated SNPs markers are further studied to determine whether they are

located near or within known functional genes that may directly or indirectly regulate the target trait. In addition, the interpretation of GWAS results also needs to consider the influence of population structure and genetic background to ensure the authenticity of the association results.

GWAS provides an efficient method for genetic research in crops such as corn, and can reveal the genetic basis of traits at the genome-wide level (Edwards et al., 1987). Through GWAS, we can not only discover the key genetic factors that affect the nutritional quality traits of corn (Table 1) (Chinthiya et al., 2019), but also use this knowledge to guide corn breeding (Liu, 2002), thereby breeding more adaptable Excellent variety for human needs. However, the analysis and interpretation of GWAS data requires complex statistical and bioinformatics methods, which requires researchers to have interdisciplinary knowledge and skills. With the continuous improvement of analysis tools and the improvement of computing power, the application of GWAS in genetic research of corn and other crops will be more extensive and in-depth in the future.

Table 1 Analysis of variance of parents and sweet corn hybrids for various biometrical and quality characters

Source of variance	Df	DFE	D50%T	D50%S	ASI	DM	CPH	PH	CL
Replication	1	0.1184	0.1184	0.18	1.0658	0.0202	313.229	11.9688	2.9962
Treatment	36	8.5366**	5.7799**	3.42**	2.6447**	19.7650**	356.25**	707.5577**	12.0902**
Error	36	1.9563	0.4911	0.6657	0.4712	7.9232	130.4861	206.7662	1.5691

Note: **: Significant at 0.01 level; *: Significant at 0.05 level; DFE: Days to first flowering; D50%T: Days to 50% tasseling; D50%S: Days to 50% silking; ASI: Anthesis silking interval; DM: Days to maturity; CPH: Cob placement height; PH: Plant height (Chinthiya et al., 2019)

3 Application of GWAS in the Study of Corn Nutritional Quality Traits

With the rapid development of molecular biology and genomics, genome-wide association studies (GWAS) have become a powerful tool to explore the genetic basis of crop nutritional quality traits. In the study of corn nutritional quality traits, GWAS methods have made a series of important discoveries. These results not only enrich our understanding of corn genetic diversity, but also provide scientific basis for the nutritional improvement of corn.

3.1 Important findings

Through GWAS methods, scientists have successfully identified multiple key genetic loci and genes related to corn nutritional quality traits. For example, when studying the genetic basis of corn oil content, researchers found that several SNPs located in specific regions of the corn genome were significantly related to oil content. The genes in these regions may be directly involved in the synthesis and regulation of oil in corn kernels (Liu et al., 2008). In terms of protein content, GWAS analysis also revealed some key genetic markers. The genes near these marker sites are involved in key pathways of nitrogen absorption and metabolism.

In addition to the above traits, GWAS has also been used to explore the genetic regulation mechanism of vitamin and mineral content in corn. For example, some studies have discovered genetic loci related to vitamin E content in corn through GWAS methods, which provides clues for further research on key genes in the vitamin E synthesis pathway. These findings not only enhance our understanding of the genetic basis of maize nutritional quality traits, but also provide the possibility for improving the nutritional quality of maize through molecular breeding methods in the future.

3.2 Case study

Taking a GWAS study on the genetic basis of corn protein content as an example, the research design included genotypic sequencing of thousands of corn varieties and phenotypic determination of protein content. By analyzing these data, the researchers successfully identified multiple SNPs that were significantly associated with protein content. Further gene annotation and functional analysis revealed that some genes near these SNPs are involved in nitrogen absorption and metabolism processes, which have a direct impact on the formation of corn protein content.

Another case is a GWAS study on the vitamin content of corn. The research design is also based on large-scale genotype and phenotype data sets. Through sophisticated statistical analysis, the research team discovered several

genetic markers related to vitamin content. The gene regions where these markers are located are closely related to vitamin biosynthetic pathways, providing important information for further research on key genes in these pathways (Wang, 2011, *Crop Journal*, 27(5): 8-12.).

These case studies demonstrate the application value of GWAS methods in the study of nutritional quality traits of corn. By revealing the association between traits and specific genetic loci, GWAS can not only help scientists understand the genetic mechanisms of complex traits, but also provide precise molecular markers for corn breeding, thereby accelerating the breeding process and developing new varieties of corn with more nutrients.

The application of GWAS in the study of corn nutritional quality traits provides us with a powerful tool (Figure 2) (Ruanjaichon et al., 2021), allowing us to deeply understand the genetic basis of traits from the genome level. These studies not only provide a new perspective for the scientific research of corn, but also provide a solid foundation for improving and optimizing the nutritional quality of corn. With the deepening of future research and technological advancement, GWAS will play a greater role in the genetic improvement and nutritional quality improvement of corn.

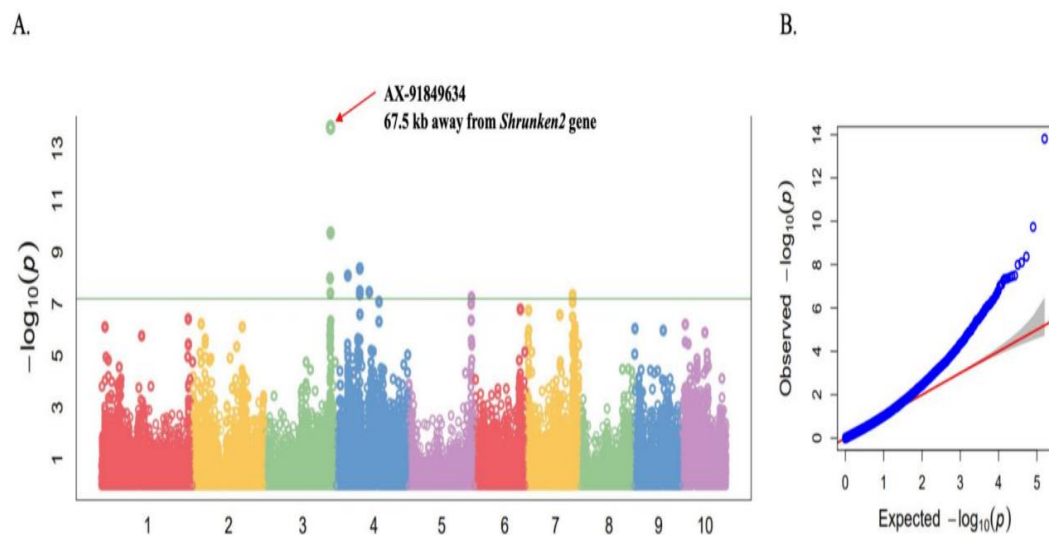


Figure 2 GWAS results for sweetness trait in 250 sweet- and waxy-corn inbred and recombinant inbred lines (RILs) (Ruanjaichon et al., 2021)

Note: A: Manhattan plots. Each dot represents a SNP. Bonferroni threshold of $-\log_{10} p\text{-value}=13.81$ is presented by a green line on Manhattan plots; Most associated SNP AX_91849634, located 67.5 kb on chromosome 3 near the Shrunken2 gene, is indicated by a red arrow; B: Quantile-quantile (Q-Q) plots; The plot shows the expected vs. observed- $\log_{10}(p)$ of each marker (blue dots); Red line is a guide for the perfect fit to expected- $\log_{10}(p)$; The gray shaded area shows the 95% confidence interval for the Q-Q plot under the null hypothesis of no association between the SNP and the trait

4 Challenges and Opportunities of GWAS Research

Genome-wide association studies (GWAS) play an important role in revealing the genetic basis of crop genetic traits and traits, especially in major food crops like corn. However, despite the great potential of GWAS, the method also faces various challenges during its application, while also bringing new opportunities.

4.1 Methodological challenges

The success of GWAS relies heavily on sufficient sample size and genetic diversity of the samples. In crop research, especially maize, it is challenging to collect representative collections of samples from a broad range of genetic backgrounds. Insufficient sample size or poor genetic diversity will limit the ability of GWAS to discover genetic markers associated with traits, reducing the accuracy and reliability of the study.

The population structure and complex genetic background of crops such as corn are also a major challenge in GWAS research (Li et al., 2009). Differences in population structure (i.e., genetic relatedness among individuals within a

population) and genetic background can lead to false-positive results, in which certain genetic markers are incorrectly associated with traits. This requires researchers to use complex statistical methods to correct the influence of this structure and background to ensure that the results of correlation analysis are accurate and reliable.

4.2 Solutions and technological advancements

With the development of bioinformatics and statistical methods, scientists have proposed and implemented multiple strategies to overcome these challenges in GWAS studies. For example, by increasing sample size and utilizing high-throughput sequencing technology, the resolution of GWAS and its ability to discover small effect sites can be improved. In addition, the use of advanced statistical models, such as mixed linear models (MLM) and principal component analysis (PCA), can effectively correct the effects of population structure and genetic background and reduce false positive results.

4.3 Combination of GWAS and other methods

GWAS are not the only tool for genetic research. In order to more comprehensively analyze the genetic basis of complex traits, combining GWAS with other methods has become a current research trend. For example, the combination of genomic selection (GS) and gene editing technologies (such as CRISPR-Cas9) with GWAS provides new strategies for improving crop traits.

Genomic selection uses all meaningful genetic markers discovered by GWAS to predict and select individuals with excellent traits, which can greatly speed up the breeding process. Gene editing technology can directly and accurately modify the key genes identified by GWAS in the crop genome, thereby directly affecting the target traits. This strategy of combining different methods can not only improve the efficiency and accuracy of crop trait improvement, but also provide new perspectives and tools for future crop genetic improvement (Hua et al., 2019).

5 Future Directions

With the widespread application of genome-wide association study (GWAS) technology in the field of crop science, it has shown great potential in corn nutritional improvement. In addition, international cooperation in interdisciplinary integrated research methods and data sharing also provides new perspectives and approaches for corn genetic improvement. Below is a detailed discussion of these future directions.

5.1 The potential of GWAS in corn nutritional improvement

GWAS technology has revealed many key genetic loci and genes that affect the nutritional quality traits of corn through association analysis. These findings provide the molecular basis for nutritional improvement of corn (Huang and Han, 2014). For example, genetic loci affecting protein content, oil content, and vitamin and mineral content discovered through GWAS can be used as molecular markers in corn breeding to selectively increase the content of these nutrients. As more and more genetic factors affecting the nutritional quality of corn are discovered, the application of GWAS technology in corn nutritional improvement will become more extensive and precise.

5.2 Interdisciplinary and integrated research methods

Research on corn nutritional improvement is not just a challenge of a single discipline, but requires the joint efforts of multiple disciplines such as botany, genetics, molecular biology, and bioinformatics (Buckler et al., 2009). Interdisciplinary integrated research methods will promote a deep understanding of the genetic basis of corn nutritional quality from different perspectives and discover new ways to improve it. For example, combining GWAS and transcriptomic analysis can help researchers not only discover genetic variants that affect nutritional quality, but also further explore how these variants affect gene expression. In addition, the application of bioinformatics tools to integrate and analyze large amounts of genetic and phenotypic data will accelerate the progress of corn nutritional improvement research.

5.3 Importance of data sharing and international cooperation

Globally, maize varieties from different regions exhibit rich genetic diversity. These diversity are indispensable resources for nutritional improvement of corn. Therefore, data sharing and international cooperation are particularly important in research on corn nutritional improvement (Morris et al., 2013). By sharing the large amounts of genetic and phenotypic data generated in GWAS studies, researchers can draw on a wider range of

samples for analysis, which helps improve the accuracy and reliability of their studies. At the same time, international cooperation can promote the exchange of research resources and technology, and accelerate the discovery and utilization of genetic factors that have an important impact on the nutritional quality of corn.

GWAS technology shows great potential in corn nutrition improvement, and international cooperation on interdisciplinary integrated research methods and data sharing will be an important direction for future research. Through these approaches and collaborations, we hope to unlock more secrets about the genetic basis of corn nutritional quality and use this knowledge to improve corn varieties to meet the world's growing nutritional needs.

6 Outlook

Genome-wide association study (GWAS), as an important technology in modern genetics and molecular biology, has important scientific value in revealing the genetic secrets of crops such as corn. Especially in understanding the genetic basis of maize nutritional quality traits (Tang et al., 2005), GWAS has made significant contributions. Future research and breeding strategies need to be further explored and optimized on this basis.

6.1 The contribution of GWAS to understanding the genetic basis of corn nutritional quality traits

Through GWAS, scientists have successfully identified multiple key genetic loci and genes related to corn nutritional quality traits, including genes affecting protein content, oil content, and vitamin and mineral content (Zhang et al., 2008). These findings not only provide molecular markers for nutritional improvement of corn, but also deepen our understanding of the formation mechanism of corn nutritional quality. For example, genes related to oil content discovered through GWAS revealed the complex network controlling oil synthesis and accumulation in corn. These research results provide the possibility to improve the nutritional quality of corn through molecular breeding or gene editing technology in the future.

6.2 Recommendations for future research and breeding strategies

Based on the important contribution of genome-wide association studies (GWAS) in the study of nutritional quality traits of corn, future research and breeding strategies will focus on several key directions. Considering the significant impact of environmental factors on crop trait performance, future research will strengthen GWAS research under a variety of environmental conditions. This method can help researchers more accurately identify genetic loci and genes related to specific traits, thereby improving the adaptability and stability of breeding. Using the genetic markers identified by GWAS, the breeding process of high nutritional value corn varieties will be accelerated through technologies such as molecular marker-assisted selection (MAS). For those key genes with known functions, gene editing technologies such as CRISPR can be used to precisely improve nutritional quality. In addition, research methods that integrate GWAS with transcriptomics, proteomics and other omics data will enable us to deeply understand the genetic regulation mechanism of corn nutritional quality traits from multiple levels and provide a more comprehensive scientific basis for breeding. Given the diversity of maize varieties and genetic resources, strengthening international cooperation and data sharing is of vital significance to accelerate the nutritional improvement of maize worldwide. This series of strategies and measures heralds a new direction in future research and practice on corn nutritional improvement, and is expected to push corn breeding to new heights.

The contribution of GWAS technology to the genetic basis research of corn nutritional quality traits is significant. Future research needs to continue to explore deeper genetic mechanisms based on existing results, and apply the research results to breeding practices to cultivate high-quality corn varieties that are more in line with human nutrition and health needs. Through continuous scientific exploration and technological innovation, we have reason to believe that more significant progress will be made in corn nutritional improvement in the future.

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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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