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Research Progress on Heat-resistant Breeding of Fresh-eating Corn: Screening and Utilization of Heat-resistant Germplasm Resources

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Abstract Fresh corn is favored by consumers for its soft and sticky taste, unique flavor and rich nutrition. Breeding high-yield, high-quality and stress-resistant glutinous corn varieties has become an important goal. Global warming has brought severe challenges to corn production, especially high temperature stress has a significant impact on corn flowering and pollination and grain filling stages, resulting in a decrease in yield. In recent years, the advancement of molecular breeding technology and the application of methods such as genome-wide association analysis (GWAS) have promoted the discovery of heat-resistant gene markers and quantitative trait loci (QTLs), laying a solid genetic foundation for heat-resistant corn breeding. At the same time, the rich genetic diversity in local varieties and wild corn resources provides an important resource for exploring heat-resistant genes. Heat shock proteins (HSPs) and heat shock factors (HSFs) play a key role in the heat resistance mechanism of corn. Transgenic technology also provides a new direction for breeding heat-resistant corn. In current breeding practice, many heat-resistant related traits are not included in the selection indicators, mainly because their determination is complex and costly. Therefore, the development of low-cost and easy-to-operate phenotypic identification methods, combined with genomic technology, can accelerate the breeding of heat-resistant corn and enhance the sustainable development capacity of agriculture.

Keywords Fresh corn; High temperature stress; Molecular breeding; Heat shock protein; Phenotypic identification

1 Introduction

As a new type of food, glutinous corn is loved by more and more consumers because of its soft taste, unique flavor and rich in various nutrients necessary for the human body. Breeding glutinous corn varieties with high and stable yield, good quality and outstanding flavor has always been an important goal of breeders. Since my country officially included fresh glutinous corn in the corn variety management system in 2000, various regions have continued to strengthen breeding research and promotion and application, effectively promoting the breeding process of new varieties.

As global temperatures continue to rise, climate change has posed a severe challenge to corn production, especially in terms of crop growth and yield. As an important food crop, corn is extremely sensitive to high temperature stress, especially in key growth stages such as the reproductive period and the early stage of grain filling. High temperature can easily lead to reduced pollen vitality, obstructed pollination and fertilization, and ultimately lead to a decrease in yield (Hussain et al., 2006). In addition, high temperature stress is often accompanied by changes in humidity and insufficient soil moisture, making it a complex and difficult agronomic problem to solve (Djalović et al., 2023).

In recent years, the continuous advancement of molecular breeding technology and the application of methods such as genome-wide association analysis (GWAS) have greatly promoted the discovery of genetic markers and quantitative trait loci (QTLs) related to heat stress tolerance (Djalović et al., 2023; Yang et al., 2024), providing a solid genetic foundation for the breeding of heat-resistant corn hybrids.

At the same time, the rich genetic diversity in local varieties and wild corn resources provides an important resource for exploring new heat-resistant genes. These excellent genes can be used to improve existing cultivated varieties and enhance their adaptability to high temperature environments (Djalović et al., 2023). In addition, studies have also found that heat shock proteins (HSPs) and heat shock factors (HSFs) play an important role in the heat resistance mechanism of corn, and transgenic technology has also provided a new direction for the construction of high-temperature tolerant corn (Xue et al., 2024). It can be seen that strengthening corn heat-resistant breeding is an effective way to cope with global warming. By integrating genetic resources and advanced breeding technologies, the construction of high-yield, stable-yield and high-temperature resistant corn varieties will provide strong support for the sustainable development of agriculture in the future.

Therefore, breeding heat-resistant corn is a key measure to ensure sustained yields, improve resource utilization efficiency, and cope with future climate change. Breeding heat-resistant varieties can help reduce irrigation needs and improve yield stability in high temperature environments. However, in current breeding practices, many important traits related to heat resistance are not included in selection indicators. The main reason is that the measurement process of such "secondary traits" is complex, costly, and dependent on precision equipment. Therefore, it is urgent to explore cost-effective and easy-to-operate phenotypic identification methods. At the same time, combined with advanced genomic technology, the breeding process of new "climate-adaptive" varieties can be accelerated.

2 Current Status of Fresh Corn

2.1 Current status of research on heat-resistant breeding of fresh corn

With the increasing trend of global warming, high temperature stress has become an important limiting factor affecting the yield and quality of fresh corn. Fresh corn (including glutinous corn and sweet corn) is extremely sensitive to high temperature, especially during the flowering and pollination period and the grain filling period, which is prone to problems such as decreased pollen vitality, blocked pollination and poor grain development, which seriously affect the quality of commodities and economic benefits (Park et al., 2024). Therefore, heat-resistant breeding has become an important direction for the current breeding of fresh corn.

The current research progress of heat-resistant breeding of fresh corn is mainly focused on phenotypic screening and the establishment of an evaluation index system. The traditional heat resistance evaluation method mainly relies on field trials, which are comprehensively evaluated by indicators such as flowering duration, silking interval, fruiting rate, and leaf burn index. However, it is greatly affected by environmental variation, and has high labor intensity and a long cycle. Some studies have tried to introduce high-throughput phenotyping technologies, such as image recognition and sensor monitoring, to improve screening efficiency and accuracy.

In-depth research is also needed on genetic resource mining and germplasm innovation. In recent years, researchers have begun to pay attention to the mining of heat-resistant genes in local varieties, wild species and tropical germplasm resources, and to improve germplasm by combining molecular marker-assisted selection (MAS) with conventional breeding. Some excellent gene loci (such as genes related to heat shock proteins and heat shock transcription factors) have been gradually identified, providing a theoretical basis for genetic improvement of heat resistance (Saluci et al., 2024).

At the same time, molecular breeding techniques such as genomic selection (GS), genome-wide association analysis (GWAS), and QTL positioning have also been gradually introduced into fresh corn breeding. These methods help to reveal the genetic mechanism of heat resistance traits and shorten the breeding cycle. For example, researchers have located multiple SNP loci related to heat resistance through the GWAS method and conducted candidate gene verification studies (Longmei et al., 2021).

It can be seen that the breeding of heat resistance in fresh corn not only focuses on stress resistance, but also must take into account commodity traits such as yield, taste, and flavor. Therefore, breeders need to balance the synergistic improvement of various traits in multi-target selection, and improve breeding efficiency and selection accuracy through multi-trait index selection models. High temperature stress often interacts with other environmental factors such as drought and humidity. In recent years, some studies have attempted to construct a multi-environment breeding model that considers genotype×environment interaction (G×E) to improve the accuracy of heat resistance trait prediction (Jarquín et al., 2014).

2.2 Current status of fresh corn production

Fresh corn is a type of corn that is harvested at the milky stage and can be eaten directly or after simple processing. It mainly includes two categories: glutinous corn and sweet corn. my country is the origin of glutinous corn, so glutinous corn is often called "Chinese glutinous corn" internationally. As early as 1908, American scholar Collins introduced glutinous corn to the United States, and then gradually spread to all parts of the world. In 1944, Wallace, the founder of Pioneer Seed Company and then vice president of the United States, introduced China's rich glutinous corn germplasm resources on a large scale during his visit to China, further promoting the development of global glutinous corn breeding (Bernardo et al., 2021).

Although my country has rich glutinous corn germplasm resources, related research and development started relatively late. It was not until the 1970s that systematic glutinous corn breeding was officially carried out, and a number of excellent inbred lines and hybrid varieties were successively bred, such as 'Zhongnuo No. 1', 'Zhongnuo No. 2', 'Yannuo No. 5', 'Jiongnuo No. 6', 'Lunuoyu No. 1', 'Zhongnuo 301', 'Kennian No. 1', 'Xixing Nuoyu No. 1', etc. Although these varieties have made progress in quality, the scale of cultivation is still small, mainly for picking fresh ears for consumption, and fresh consumption is still the mainstream application direction. Industrial utilization is not yet widespread, and it is only used in green consumption, quick freezing and other fields (Devasirvatham et al., 2016).

Sweet corn originated in America. It can be divided into three main types according to different sweet genes: ordinary sweet type, super sweet type and enhanced sweet type. Sweet corn was commercially cultivated in the early 20th century, with the United States becoming the world's largest producer and exporter of sweet corn. Since the 1940s, the area of sweet corn cultivation in the United States has continued to expand, doubling almost every five years. Data show that by 1999, the global sweet corn planting area had reached 667 000 hectares, of which the United States had a planting area of 315 000 hectares, about 7% of the output was used for fresh consumption, and about one-third of its processed products were exported to the international market. In addition, Japan, South Korea and Taiwan also have high consumption and planting demand for sweet corn.

In my country, although sweet corn breeding started early, dating back to the 1950s, its promotion and application in actual production lagged behind. It was not until the past decade that the development of sweet corn has accelerated significantly, especially in Guangdong Province, where the annual planting area has reached about 67 000 hectares, becoming one of the main areas for the development of my country's sweet corn industry.

2.3 Improvement of fresh corn quality

According to the variety approval data, all regions of the country have made certain improvements in the quality of glutinous corn, and the appearance, flavor and tenderness of fresh glutinous corn are generally on the rise. Most varieties have reached the national second-level fresh glutinous corn standard, although there are no varieties that have reached the first-level standard. Breeding improvements in recent years have mainly focused on optimizing appearance traits, improving flavor, softening taste, and reducing pericarp thickness (Qureeshi et al., 2020). For example, compared with 2005, the sensory scores, flavor performance and tenderness of the varieties approved in 2009 have been improved to varying degrees, while the pericarp thickness has decreased, reflecting that the breeding direction is steadily moving towards the goal of improving the quality of fresh food.

However, in terms of core quality characteristics such as smell, color and glutinousness, the overall performance has been stable since 2006, with no significant breakthroughs, and some traits have even declined slightly. This phenomenon may be related to the current insufficient utilization of germplasm resources and the fact that some breeding projects still use the "glutinous quality" improvement method of ordinary corn, which limits the space for quality improvement (Chen et al., 2023). Therefore, although the yield and quality of glutinous corn breeding have improved in recent years, in order to achieve the leap from "meeting the standard" to "high quality", it is necessary to more efficiently integrate excellent germplasm resources, optimize breeding technology routes, and promote the development of glutinous corn breeding in the direction of high quality and diversification.

3 Heat-Resistant Breeding Strategies

3.1 Conventional breeding methods

As one of the most important food crops in the world, the yield and quality of corn are often seriously affected by high temperature stress. Against the background of the increasingly intensified trend of global warming, heat-resistant breeding has become an important direction to ensure stable and high yields of corn. Conventional breeding methods, as the basic means of corn improvement, still play an irreplaceable role in the current breeding system, especially in the selection of heat-resistant varieties, which have wide application value (Dowd and Johnson, 2018).

Hybrid breeding is the most widely used method in conventional heat-resistant breeding. This strategy uses hybrid vigor to select hybrids that perform well under high temperature conditions by hybridizing inbred lines with strong heat resistance with inbred lines with high yield, good quality but poor heat resistance. Studies have shown that hybrids are usually more heat-resistant than their parents because most heat stress-related traits are controlled by dominant genes. Therefore, hybrid breeding not only helps to improve heat resistance, but also enhances the adaptability of varieties while ensuring yield and quality (El-Sappah et al., 2022). However, this method also has certain limitations, such as a long combining ability screening cycle, a large workload of field trials, and strong dependence on environmental conditions.

Pedigree selection is also a common heat-resistant breeding method. This method accumulates heat-resistant genes from generation to generation through continuous self-pollination and systematic selection, thereby cultivating heat-resistant strains with stable genetic backgrounds. This method is of great significance in breeding basic parent materials, but because heat stress traits are controlled by multiple genes and are easily affected by the environment, pure phenotypic selection is often inefficient and the improvement progress is relatively slow (Mukaro et al., 2023).

Backcross breeding has also gradually shown its application prospects in improving maize heat resistance. This method uses excellent main varieties as receptors to introduce excellent genes from heat-resistant donors into target strains to achieve precise transfer of heat-resistant genes. Backcross breeding improves its adaptability to high temperature environments while maintaining the excellent traits of the original varieties. However, since heat stress-related traits often involve multiple gene loci, the introduction of a single gene is difficult to obtain significant improvement effects, and the background recovery process is relatively complicated (Prasanna et al., 2021; Hill and Li, 2022).

Although conventional breeding methods have a solid foundation and broad application prospects in corn heat-resistant breeding, they also face problems such as low genetic improvement efficiency, long cycle, and great environmental interference. Therefore, in future research, in heat-resistant breeding work, we should integrate modern technical means such as molecular marker-assisted selection (MAS), genome-wide association analysis (GWAS) and genomic selection (GS) on the basis of conventional methods, build a "conventional+molecular" collaborative breeding system, and promote corn heat-resistant breeding towards high efficiency, precision and intelligence.

3.2 Utilizing the genetic diversity of local varieties and wild germplasm resources

In the current corn breeding system, improving the stress resistance and adaptability of crops has become a research focus. As a rich genetic diversity pool, local varieties and wild germplasm resources provide an important foundation for modern corn genetic improvement. Compared with modern cultivated varieties, these resources have accumulated unique stress resistance traits under long-term natural selection and farmer selection, especially in terms of heat resistance, drought resistance, disease and insect resistance.

Wild corn (such as Mexican wild corn Teosinte) is considered to be an important ancestor of modern corn. During the evolution process, it has retained a large number of genes that have not been used by modern breeding, especially in terms of genes related to environmental stress response, which has potential utilization value. Studies have shown that some wild corn germplasms have important genetic diversity in terms of heat resistance, root system structure, nutritional efficiency, etc. In recent years, with the development of genomics technology, more and more studies have begun to focus on identifying QTL loci and functional genes related to heat resistance traits in wild species through genome comparative analysis and association studies.

A key way to utilize local and wild germplasm resources is to build a genetic diversity evaluation system and a core germplasm bank. On this basis, modern breeding technologies such as molecular marker-assisted selection (MAS) and genome-wide association analysis (GWAS) are used to carry out targeted transfer and gene integration of target genes to improve breeding efficiency. For example, the research team of the Chinese Academy of Agricultural Sciences has constructed a genetic diversity pedigree map based on local germplasm and wild germplasm, providing important support for the discovery of heat-resistant genes in maize.

3.3 Molecular breeding technology

Molecular marker-assisted selection (MAS) plays an important role in improving the heat tolerance of maize. By selecting specific genetic markers associated with heat tolerance traits, breeders can quickly identify and screen target traits at the molecular level, thereby accelerating the breeding process. MAS technology has helped locate key genomic regions and candidate genes associated with heat tolerance in multiple studies, providing technical support for the development of heat-resistant maize varieties.

With the continuous development of molecular breeding technology, researchers have gradually revealed a number of important genes related to heat tolerance and their regulatory pathways. Genome-wide association analysis (GWAS) has been widely used to identify important SNP sites and candidate genes associated with heat stress resistance. For example, studies have found that heat shock transcription factors (Hsfs) and heat shock proteins (Hsps) play a key role in the heat tolerance response of sweet corn. In addition, the study also accurately located the genomic regions associated with heat stress resistance, providing a theoretical basis for the implementation of marker-assisted backcrossing and whole-genome selection in the future (Seetharam et al., 2021).

4 Molecular Marker-Assisted Breeding Technology

4.1 Study on the physiological mechanism and genetic improvement strategy of heat tolerance traits in maize

With the increasing trend of global warming, high temperature stress has become one of the key factors restricting maize yield and production stability. The main impact of high temperature on maize is the destruction of photosynthesis and reproductive mechanisms, which in turn leads to a significant decrease in grain yield. Studies have shown that high temperature stress not only causes morphological changes such as slowing down the overall growth rate of maize, leaf burns, and reduced plant height, but also causes physiological disorders such as early flowering, prolonged pollen-silk interval (ASI), and decreased pollen vitality, which seriously affect pollination and fruiting rate (Alam et al., 2017; Hussain et al., 2019).

In breeding practice, heat tolerance has become an important goal of maize genetic improvement. Studies have shown that high temperature stress mainly reduces the number of grains and fruiting rate by weakening pollen vitality, among which the silking time is relatively stable, but the fertilization ability of silking may be delayed due to high temperature. Therefore, improving the pollen viability and fertilization ability of maize under high temperature conditions is the core direction of improving heat tolerance.

In recent years, the combination of molecular physiology and quantitative genetics has provided a theoretical basis for precision breeding of heat-resistant traits. For example, studies conducted under controlled environments revealed the molecular response mechanism of maize seedlings under heat stress, and subsequent phenotypic studies under field conditions further clarified the effects of heat stress on key agronomic traits.

Frey et al. (2021) developed a heat sensitivity index to evaluate the response of different segregating families in temperate maize populations to heat stress, and located multiple important QTL loci related to heat tolerance on chromosomes 2 and 3. It is worth noting that the QTL on chromosome 3 is highly consistent with the region associated with pollen viability found in previous studies. In addition, heat-sensitive QTL hotspots associated with leaf burn severity and plant height changes were also found on chromosome 9 (Inghelandt et al., 2019), further enriching the genetic basis map of maize heat tolerance traits.

4.2 Core germplasm pool and allele mining based on molecular markers

Molecular marker technology provides a powerful tool for the efficient utilization and genetic improvement of crop germplasm resources. Through molecular marker-assisted analysis, researchers can systematically and accurately screen representative core germplasm subsets from a large number of breeding materials and germplasm resource pools to maximize the retention of genetic diversity. These core germplasm pools are not only of great value in germplasm resource management, but also provide a basis for subsequent allele mining and target trait improvement (Naveed et al., 2016). In recent years, several international projects, including the Global Crop Generation Challenge Program (GCP), have established micro-core germplasm pools for a number of major food crops, and combined molecular and phenotypic methods to conduct in-depth analysis, aiming to discover new functional genes and genetic variations with potential application value.

In corn, based on high-throughput molecular markers and whole genome resequencing technology, researchers have identified a large number of SNP sites and haplotypes associated with key agronomic traits. These genomic information provides data support for gene positioning, allele mining and subsequent molecular breeding. For example, association maps and genome-wide association analysis (GWAS) methods can not only locate QTL regions associated with target traits, but also further identify excellent alleles with breeding potential (Nelimor et al., 2019). By analyzing the "haplotype" structure, single feature polymorphism (SFP) and near alleles (NIP) between different inbred lines, we can have a deeper understanding of the functional diversity and evolutionary laws of the maize genome.

At present, allele mining is mainly determined by genome resequencing and ecological planting screening, and gene-based resequencing methods are more widely used in maize. Through whole genome genotyping, not only can sequence variations be detected, but also functional association analysis can be performed in combination with phenotypic data to determine whether new alleles have beneficial effects on specific traits (Driedonks et al., 2016). Studies have also shown that the function and application value of alleles can be further confirmed through marker-assisted backcrossing (MABC), genetic transformation, transient expression analysis and association verification between different germplasms.

4.3 Challenges and prospects of integrating genomic data into breeding programs

Although genomic data has broad application prospects in breeding, there are still many challenges in the actual integration process, such as the high demand for large-scale, accurate phenotypic data to support the population, and the need for extensive testing under multiple environmental conditions (Miedaner et al., 2020). In addition, heat stress tolerance, as a typical quantitative trait, is greatly affected by the interaction between genotype and environment, which also increases the difficulty of accurately predicting breeding values.

However, with the continuous advancement of molecular tools and technologies, such as the development of low-cost marker detection technology and in-depth mining of candidate genes, these problems are gradually being overcome (Jagtap et al., 2020; Tyagi et al., 2021). Future research should focus on optimizing genomic selection models and strengthening multi-omics data integration to further improve the accuracy and efficiency of heat-tolerant maize breeding programs.

5 Case Studies

5.1 CIMMYT and GWAS studies promote progress in heat-tolerant maize breeding

Against the backdrop of increasingly severe global climate change, maize yield stability under heat stress has become a focus of breeding research. The International Maize and Wheat Improvement Center (CIMMYT), in collaboration with Purdue University and partners from the South Asian National Agricultural Research System (NARS), conducted a large-scale genome-wide association study (GWAS) to analyze the genetic basis of maize yield and related traits under heat stress. The study included more than 500 testcross lines of maize lines with different genetic backgrounds, aiming to identify key genomic regions associated with heat tolerance traits.

The study achieved remarkable results, identifying five haplotype regions and eight important SNP variant sites that are closely associated with maize yield under heat stress. In addition, the CIMMYT Asia research team validated the above GWAS results in an independent biparental breeding population and confirmed 22 genomic regions associated with maize yield and related secondary agronomic traits under heat stress (Kamweru et al., 2022). These validation results not only enhance the reliability of GWAS results, but also provide actionable molecular marker resources for heat-resistant breeding.

Through integrated analysis of multiple genetic background populations, the study further identified three major QTL intervals with significant effects in a variety of high-temperature-related traits. These QTL regions can be used as priority genetic resources in future breeding programs and have good breeding application prospects.

It is worth mentioning that CIMMYT's research has also expanded to lipid-related traits and field phenotypic performance under high temperature and non-stress conditions. The study found 78 significant SNP associations at 40 loci, involving 53 candidate genes, which further enriched the genetic map of heat-resistant traits and strengthened the association basis between phenotype and genotype.

The joint study clearly revealed the multi-gene control characteristics of maize yield traits under high temperature or combined stress (such as drought+high temperature) conditions. The research team pointed out that in this complex genetic control background, the use of whole genome prediction (genomic prediction, GP) will be the best way to improve yield performance and breeding efficiency (Kamweru et al., 2022). By integrating GWAS data with GP models, we can not only improve the accuracy of selection, but also accelerate the breeding of heat-resistant varieties, providing scientific and technological support for coping with future climate uncertainties.

5.2 ZmHSF20 regulatory network analyzes the molecular mechanism of heat tolerance in maize

Against the background of climate warming and increasing frequency of high temperature stress, analyzing the molecular regulatory mechanism of crop heat tolerance has become an important topic in maize genetic improvement research. The team of Zhang Mei, a researcher at the Institute of Botany, Chinese Academy of Sciences, conducted research on the "functional mechanism of core transcription factors of maize heat tolerance", constructed a systematic high temperature stress transcriptome map, and successfully identified the key regulatory factor-heat shock transcription factor ZmHSF20 through co-expression network analysis (Li et al., 2024).

The results of co-expression analysis showed that the ZmHSF family and the ethylene response factor (ERF) family were highly enriched in the "heat response" module, among which ZmHSF20 was confirmed as the core regulatory factor. In order to verify its function, the researchers constructed Zmhsf20 deletion mutants and ZmHSF20 overexpression lines. Phenotypic analysis results showed that ZmHSF20 overexpressing plants were more sensitive to high temperature stress, while the heat tolerance of Zmhsf20 mutants was significantly enhanced, clarifying the function of ZmHSF20 as a negative regulatory factor in corn to inhibit heat tolerance (Figure 1) (Li et al., 2024).

In-depth mechanism studies found that ZmHSF20 affects the heat tolerance of plants by downregulating the expression of target genes *ZmCesA2* (cellulose synthase) and ZmHSF4 (another heat shock transcription factor). Experiments have confirmed that ZmHSF4 has the function of transcriptionally activating ZmCesA2, and overexpression of *ZmCesA2* and *ZmHSF4* can improve the heat tolerance of corn (Li et al., 2024). Zmhsf4 mutants are more sensitive to heat stress, further verifying the positive role of ZmHSF4 in heat tolerance regulation. The constructed Zmhsf20-1Zmhsf4-1 double mutant further proved the downstream position of ZmHSF4 in the ZmHSF20 regulatory pathway.

In addition, ultrastructural observations showed that the Zmhsf20 mutant and the ZmHSF4 overexpression strain had a more stable cell wall structure under high temperature. The study also found that ZmHSF20 regulates *ZmCesA2*, thereby affecting the expression of cell wall-related genes such as *ZmPAL1*, participating in the cell wall construction process, and further improving the stability of cell structure under heat stress.

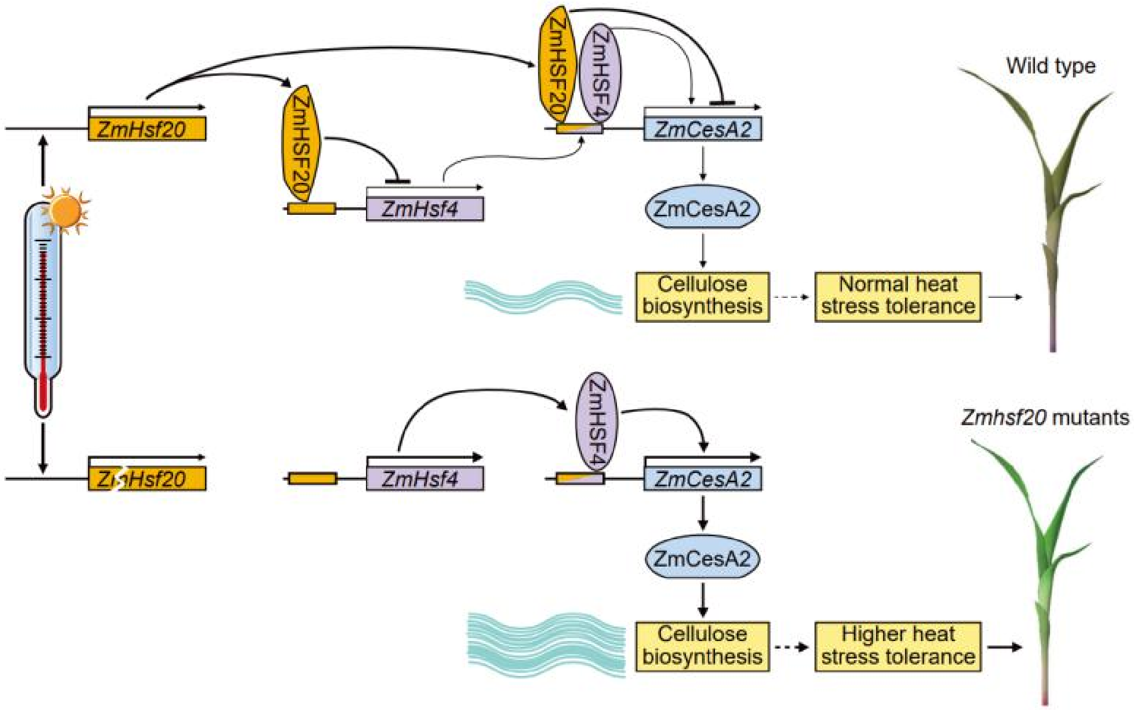

Figure 1 Proposed model of ZmHSF20 function in conferring tolerance to heat stress in maize (Adopted from Li et al., 2024)

Image caption: Under heat stress, *ZmHSF20* transcripts and ZmHSF20 protein accumulate, leading to the direct transcriptional repression of *ZmHSF4* and *ZmCesA2* expression. In parallel, ZmHSF4 normally promotes the expression of *ZmCesAs*, such that heat treatment further decreases cellulose content in a ZmHSF20- and ZmHSF4-dependent manner (Adopted from Li et al., 2024)

Based on the above research results, the research team proposed a maize high temperature stress response model with ZmHSF20 as the core: in the Zmhsf20 mutant, the expression levels of *ZmHSF4* and *ZmCesA2* increased, and ZmHSF4 further activated the expression of *ZmCesA2*, enhancing cellulose synthesis and cell wall-related gene expression, thereby improving cell wall stability and overall heat resistance (Li et al., 2024).

This study not only reveals the key role of the ZmHSF20-ZmHSF4-ZmCesA2 regulatory network in maize heat tolerance, but also for the first time clarifies the function of cellulose synthesis in the heat tolerance mechanism, providing a new perspective for high temperature stress response. More importantly, this research result provides valuable genetic resources and theoretical basis for molecular breeding of heat-resistant maize varieties, and expands the technical path for improving crop heat tolerance.

6 Summary

Under the background of global warming, heat-resistant breeding of fresh corn has become a key direction to ensure the sustainable development of agriculture. High temperature stress not only affects the normal growth and development of corn, especially causing serious losses in pollen vitality and fruiting rate, but also seriously restricts the stable improvement of fresh food quality and economic benefits. Therefore, it has become an urgent need in current scientific research and production practice to cultivate high-yield, high-quality and heat-resistant corn varieties through systematic breeding methods.

At present, the work of heat-resistant breeding of fresh corn has made initial progress. Breeders not only continuously optimize parent combinations through conventional hybridization and pedigree selection methods, but also begin to pay attention to the genetic potential of local varieties and wild germplasm resources in heat-resistant traits. At the same time, the construction of an efficient phenotypic screening system and the introduction of high-throughput screening technology have greatly improved the breeding efficiency. Especially in terms of germplasm innovation, local varieties and wild resources are regarded as an important treasure house for mining new heat-resistant genes, and their genetic diversity provides a solid foundation for improving the current breeding population.

The development of molecular breeding technology has further promoted the in-depth analysis of the genetic basis of heat resistance. MAS, GWAS, QTL positioning and GS have not only improved the accuracy of breeding, but also greatly shortened the variety selection cycle. In particular, the strategy of building a core germplasm bank and allele mining allows researchers to more efficiently use key gene sites for aggregation and improvement, forming a new path for heat-resistant breeding with multi-gene coordinated regulation as the core. At the same time, the integration of genomic data has also laid a technical foundation for the establishment of a three-dimensional selection model of "phenotype-genotype-environment interaction".

CIMMYT's joint GWAS research and ZmHSF20 regulatory network research fully demonstrated the cutting-edge achievements of modern heat-resistant breeding in genetic resource utilization and regulatory mechanism research. The former revealed the multi-gene control characteristics of yield and heat resistance traits and their stable inheritance laws among multiple breeding populations, while the latter clarified the core role of the ZmHSF20-ZmHSF4-ZmCesA2 pathway in cell wall stability and heat resistance formation. These studies not only provide specific molecular targets for the selection of heat-resistant varieties, but also provide technical support and theoretical guidance for the construction of an intelligent and precise corn breeding system. In the future, integrating traditional and modern breeding methods and exploring and utilizing genetic diversity will be important directions to promote the sustainable development of heat-resistant breeding of fresh-eating corn.

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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.

References

Alam M., Seetharam K., Zaidi P., Dinesh A., Vinayan M., and Nath U., 2017, Dissecting heat stress tolerance in tropical maize (*Zea mays* L.), Field Crops Research, 204: 110-119.
https://doi.org/10.1016/J.FCR.2017.01.006

Bernardo P., Frey T.S, Barriball K., Paul P.A., and Redinbaugh M., 2021, Detection of diverse maize chlorotic mottle virus isolates in maize seed, Plant Disease, 105(6): 1596-1601.
https://doi.org/10.1094/PDIS-07-20-1446-SR

Chen Y., Du T., Zhang J., Chen S., Fu J., Li H., and Yang Q., 2023, Genes and pathways correlated with heat stress responses and heat tolerance in maize kernels, Frontiers in Plant Science, 14: 1228213.
https://doi.org/10.3389/fpls.2023.1228213

Devasirvatham V., Tan D., and Trethowan R., 2016, Breeding strategies for enhanced plant tolerance to heat stress, Advances in Plant Breeding Strategies: Agronomic, Abiotic and Biotic Stress Traits, 12: 447-469.
https://doi.org/10.1007/978-3-319-22518-0_12

Djalović I., Kundu S., Bahuguna R., Pareek A., Raza A., Singla-Pareek S., Prasad P., and Varshney R., 2023, Maize and heat stress: physiological, genetic, and molecular insights, The Plant Genome, 17(1): e20378.
https://doi.org/10.1002/tpg2.20378

Dowd P., and Johnson E., 2018, Insect damage influences heat and water stress resistance gene expression in field-grown popcorn: implications in developing crop varieties adapted to climate change, Mitigation and Adaptation Strategies for Global Change, 23: 1063-1081.
https://doi.org/10.1007/s11027-017-9772-x

Driedonks N., Rieu I., and Vriezen W., 2016, Breeding for plant heat tolerance at vegetative and reproductive stages, Plant Reproduction, 29: 67-79.
https://doi.org/10.1007/s00497-016-0275-9

El-Sappah A., Rather S., Wani S., Elrys A., Bilal M., Huang Q., Dar Z., Elashtokhy M., Soaud N., Koul M., Mir R., Yan K., Li J., El-Tarabily K., and Abbas M., 2022, Heat stress-mediated constraints in maize (*Zea mays*) production: challenges and solutions, Frontiers in Plant Science, 13: 879366.
https://doi.org/10.3389/fpls.2022.879366

Hill C., and Li C., 2022, Genetic improvement of heat stress tolerance in cereal crops, Agronomy, 12(5): 1205.
https://doi.org/10.3390/agronomy12051205

Jagtap A., Vikal Y., and Johal G., 2020, Genome-wide development and validation of cost-effective KASP marker assays for genetic dissection of heat stress tolerance in maize, International Journal of Molecular Sciences, 21(19): 7386.
https://doi.org/10.3390/ijms21197386

Jarquín D., De Leon N., Romay C., Bohn M., Buckler E.S., Ciampitti I., Edwards J., Ertl D., Flint-Garcia S., Gore M.A., Graham C., Hirsch C.N., Holland J.B., Hooker D., Kaeppler S.M., Knoll J., Lee E.C., Lawrence-Dill C.J., Lynch J.P., and Moose S.P., 2021, Utility of climatic information via combining ability models to improve genomic prediction for yield within the genomes to fields maize project, Frontiers in Genetics, 11: 592769.
https://doi.org/10.3389/fgene.2020.592769

Kamweru I., Anani B.Y., Beyene Y., Makumbi D., Adetimirin V.O., and Prasanna B.M., 2022, Genomic analysis of resistance to fall armyworm (*Spodoptera frugiperda*) in CIMMYT maize lines, Genes, 13(2): 251.
https://doi.org/10.3390/genes13020251

Li Z., Li Z., Ji Y., Wang C., Wang S., Shi Y., Le J., and Zhang M., 2024, The ZmHSF20-ZmHSF4-ZmCesA2 module regulates heat stress tolerance in maize, bioRxiv, 581499: 1-46.
https://doi.org/10.1101/2024.02.21.581499

Longmei N., Gill G., Zaidi P., Kumar R., Nair S., Hindu V., Vinayan M., and Vikal Y., 2021, Genome wide association mapping for heat tolerance in sub-tropical maize, BMC Genomics, 22: 154.
https://doi.org/10.1186/s12864-021-07463-y

Miedaner T., Boeven A., Gaikpa D., Kistner M., and Grote C., 2020, Genomics-assisted breeding for quantitative disease resistances in small-grain cereals and maize, International Journal of Molecular Sciences, 21(24): 9717.
https://doi.org/10.3390/ijms21249717

Mukaro R., Kamutando C., Magorokosho C., Mutari B., Zaidi P., Kutywayo D., and Sibiya J., 2023, Genetic potential of tropically adapted exotic maize (*Zea mays* L.) heat-tolerant donor lines in sub-tropical breeding programs, Agronomy, 13(8): 2050.
https://doi.org/10.3390/agronomy13082050

Naveed M., Ahsan M., Akram H., Aslam M., and Ahmed N., 2016, Genetic effects conferring heat tolerance in a cross of tolerant×susceptible maize (*Zea mays* L.) genotypes, Frontiers in Plant Science, 7: 729.
https://doi.org/10.3389/fpls.2016.00729

Nelimor C., Badu-Apraku B., Tetteh A., and N'guetta A., 2019, Assessment of genetic diversity for drought, heat and combined drought and heat stress tolerance in early maturing maize landraces, Plants, 8(11): 518.
https://doi.org/10.3390/plants8110518

Park T., Wang S., Kang J., Kang M., Chung J., and So Y., 2024, Digital Image analysis of low-temperature responses in sweet corn hybrid seedlings, Agriculture, 14(3): 360.
https://doi.org/10.3390/agriculture14030360

Prasanna B., Cairns J., Zaidi P., Beyene Y., Makumbi D., Gowda M., Magorokosho C., Zaman-Allah M., Olsen M., Das A., Worku M., Gethi J., Vivek B., Nair S., Rashid Z., Vinayan M., Issa A., Vicente S., Dhliwayo, T., and Zhang X., 2021, Beat the stress: breeding for climate resilience in maize for the tropical rainfed environments, Theoretical and Applied Genetics, 134: 1729-1752.
https://doi.org/10.1007/s00122-021-03773-7

Qureeshi M., Hussain F., Noorka I., and Rauf S., 2020, Screening of spring wheat (*Triticum aestivum* L.) germplasm against drought and heat stress, Cereal Research Communications, 49: 365-374.
https://doi.org/10.1007/s42976-020-00110-4

Saluci J., Vivas M., De Almeida R., Vasconcelos L., Valadares F., De Andrade Junior M., Santos J., Mussi-Dias V., Da Silveira S., and Amaral Júnior A., 2024, Evaluation and selection of sources of resistance in popcorn to southern corn leaf blight, Plant Pathology, 73(8): 2147-2156.
https://doi.org/10.1111/ppa.13957

Seetharam K., Kuchanur P., Koirala K., Tripathi M., Patil A., Sudarsanam V., Das R., Chaurasia R., Pandey K., Vemuri H., Vinayan M., Nair S., Babu R., and Zaidi P., 2021, Genomic regions associated with heat stress tolerance in tropical maize (*Zea mays* L.), Scientific Reports, 11: 13730.
https://doi.org/10.1038/s41598-021-93061-7

Tyagi S., Kumar A., Gautam T., Pandey R., Rustgi S., and Mir R., 2021, Development and use of miRNA-derived SSR markers for the study of genetic diversity, population structure, and characterization of genotypes for breeding heat tolerant wheat varieties, PLoS ONE, 16(2): e0231063.
https://doi.org/10.1371/journal.pone.0231063

Xue M., Han X., Zhang L., and Chen S., 2024, Heat-resistant inbred lines coordinate the heat response gene expression remarkably in maize (*Zea mays* L.), Genes, 15(3): 289.
https://doi.org/10.3390/genes15030289

Yang Q., Guo Z., Zhang J., Wang Y., Xu Y., and Nian H., 2024, Genome-wide association study reveals marker-trait associations for heat-stress tolerance in sweet corn, Agronomy, 14(9): 2171.
https://doi.org/10.3390/agronomy14092171