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Identification of QTLs Associated with Silk Emergence Time Under Heat Stress

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Abstract The Silk Emergence Time (SET) is a critical period for the formation of corn (*Zea mays* L.) grains. Especially under high-temperature stress conditions, its coordination is of great significance for successful pollination and stable yield. High temperatures often lead to delayed filaments and failed pollination, seriously affecting the final yield. This study, with QTL mapping at its core, systematically analyzed the genetic and physiological mechanisms affecting the silk production period under high-temperature stress, providing theoretical support and genetic resources for the molecular breeding of heat-tolerant corn. Analyze the genetic regulatory mechanism of SET and the role of hormone signaling pathways in the heat hypochondrium response; Evaluate the effects of agronomic factors such as plant height and ASI on SET variations; Precise QTL localization is carried out by using the combined method of genomics and transcriptomics. Screen key candidate genes and conduct functional verification; Compare the differences and stability of QTLS in different thermal ecological zones through regional cases; And explore the practical application paths of QTL in heat-resistant breeding. This study reveals the genetic basis for the regulation of the silk production period of corn under high-temperature stress, providing potential targets for marker-assisted selection (MAS) and genomic selection (GS), and is conducive to the breeding of corn varieties with strong high-temperature adaptability and high yield stability.

Keywords *Zea mays* L.; Silk emergence time; Heat stress; Quantitative trait loci (QTL) mapping; Stress-resilient breeding

1 Introduction

Whether the yield of corn is high or not often depends on whether the filaments can emerge in time. The seed setting rate is closely related to the appearance of filaments, especially during the pollination period. Although we often use the "flower-silk interval (ASI)" to measure the synchronization degree of pollen and filaments, once this indicator becomes longer, pollination is prone to problems, resulting in less grain production and a decline in yield, especially under adverse conditions such as heat and drought (Dong et al., 2023). However, not all traits can be so clearly associated. For instance, filaments acceptability, pollen viability and ASI, although all are linked to yield, are greatly influenced by the environment in actual field performance, and sometimes there are exceptions.

During the flowering period when heat waves hit, it's very easy for the stamens and pollen to "not match". If the filaments fail to develop, the pollen matures slowly, lacks vitality, and the condition of the filaments deteriorates, the entire pollination process may be disrupted, ultimately resulting in fewer grains and reduced yields. Some literatures even point out that during severe high temperatures, the yield loss can exceed 70% (Wang et al., 2019; 2020; 2022). Moreover, the most vulnerable period is the first few days after the silk production ends, when the plants are the most vulnerable. When high temperatures rise, reactive oxygen species (ROS) accumulate in the filaments, preventing the pollen tubes from continuing to grow and even directly leading to infertility (Gong et al., 2024). This kind of heat sensitivity during the reproductive stage is ultimately closely related to the genetic basis. Heat tolerance is not determined by one or two genes, but is a complex trait controlled by multiple genes. Therefore, it is a crucial step to identify the quantitative trait loci (QTLS) that can affect filaments appearance, ASI, and even yield performance. In recent years, many QTL mapping and GWAS studies have identified relevant genomic regions and candidate genes. These achievements not only broaden our understanding of heat stress responses but also provide underlying resources for future marker-assisted breeding and the development of more heat-resistant corn varieties.

This study aims to identify QTLS related to the occurrence time of filaments under high-temperature stress, thereby clarifying the genetic structure of this key trait. By combining phenotypic assessment and high-resolution genotyping under controlled high-temperature stress conditions, a QTL map related to filaments appearance and related reproductive traits is drawn. These QTLS are verified in different genetic backgrounds and environments. Provide reliable markers for breeding projects targeting heat resistance. This research is expected to promote strategic breeding of corn varieties, enabling them to better withstand rising temperatures and ensure stable yield formation in the context of climate change.

2 Genetic Regulation and Environmental Response Mechanisms of Silk Emergence

2.1 Genetic basis and major gene regulatory models for silk emergence

Corn spinning is not something that can be determined by a single gene. According to current research, the regulatory mechanism involves both cis and trans elements, and the situation is not always simply linear. Transcription factors like MYB do play a key role in regulating the development, metabolism and response to environmental stress of filaments (Wang et al., 2024). However, there are also significant differences among different inbred lines. Some genes are highly expressed in one material but show mediocre performance in others. eQTL analysis has identified a large number of filament-specific expression genes, especially trans eQTL is more active in regulating these genes (McNinch et al., 2020; Chu et al., 2024). However, the time and intensity of filamentary expression are likely related to environmental conditions and the way genotypes are combined, and its dynamic changes also add a lot of difficulty to precise breeding.

2.2 Disruptive mechanisms of heat stress on flowering coordination and reproductive physiology

Whether the filaments can come out on time often determines whether powder can be applied in the end. It is precisely when the temperature is high that this matter is most likely to go wrong. When the filaments are late and the pollen Withers early, the elongation of ASI naturally leads to a decline in fertilization efficiency. However, the problem is not limited to the filaments. The anthers do not crack, the pollen is inactive, and the fine structure is damaged at high temperatures. These factors are often brought down together (Wang et al., 2019). From a molecular mechanism perspective, the accumulation of ROS within filamentous cells is a major problem, as it can cause cell death and block the development of pollen tubes. Many genes related to hormones, ROS clearance and stress response pathways become unstable in expression at high temperatures (Gong et al., 2024). The time when problems are most likely to occur is not before the flowering period, but at the moment when silk production just begins and pollination is underway (Begcy et al., 2019).

2.3 Role of hormones (e.g., GA, ABA) and ROS signaling in silk emergence response

When it comes to filaments and high temperatures, it is impossible to avoid plant hormones, especially GA and ABA. GA is the "engine" that drives cell elongation and pulls filaments to grow out. ABA is more like a "brake" or "regulator", and it has regulatory effects on both flowering rhythm and stress response (Waadt et al., 2022; Shah et al., 2023). However, the relationship between the two is not always opposing. Under some conditions, the delicate balance between them is the key to the smooth appearance of filaments. In addition, high-temperature stress often induces a large accumulation of ROS. Although ROS itself is a signaling molecule, once it is excessive, it is easy to cause harm. ROS and hormone signals can "crosstalk" and jointly affect gene expression and cell state (Xia et al., 2015). So, whether silk spinning can be successfully completed is not merely a matter of genes; the regulatory network behind it is much more complex.

3 Key Agronomic Factors Influencing Silk Emergence Under Heat Stress

3.1 Correlation analysis between plant height and silk elongation

Under the background of high-temperature stress, the reduction of plant height is actually not uncommon, and in research, it is often accompanied by the phenomenon of delayed filaments. But whether there is always a direct connection between the two actually depends on the specific situation. For instance, the differences in expression among different genotypes are quite obvious: in some varieties, the plant height has significantly decreased, but the spikelets have not been much affected and can still extend normally. That is to say, these genotypes may have some kind of "compensation mechanism" that enables them to maintain a certain reproductive capacity even when the plants become shorter. Although the overall trend is that plant height and panicle height decrease simultaneously under heat stress, ASI is elongated, and the growth rhythm is disrupted, it cannot be generalized (Turc et al., 2016; Hosamani et al., 2020; Bista et al., 2022). This complexity also reminds us that we cannot judge the heat tolerance level merely by the height of the plant. Some materials with medium plant types actually show a good ability to develop filaments.

3.2 Anthesis-silking interval (ASI) as an indicator of heat tolerance

When it comes to heat resistance or not, many people's first reaction is to look at ASI. Indeed, on hot days, the filaments often come out later than the pollen, and the ASI suddenly elongates. This "asynchronization" is the key factor leading to failed pollination and reduced yields. However, there are exceptions. Some materials can maintain a relatively short ASI even at high temperatures, thus ensuring the success rate of fertilization. Compared with other phenotypes, ASI appears more intuitive and easier to measure. Especially now that the automated platform can monitor the flowering period and silk production in real time, the breeding work has become much more efficient than before (Figure 1) (Zhuang et al., 2024). However, short ASI does not mean everything is good. It is necessary to consider factors such as the activity of the filaments and the pollination environment together.

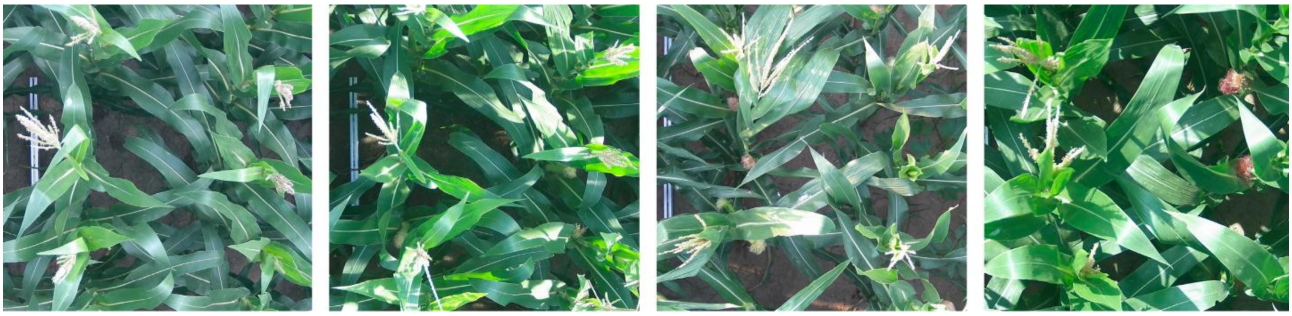

Figure 1 Partial images of the dataset created (Adopted from Zhuang et al., 2024)

3.3 Agronomic management (planting density, irrigation) modulating silk emergence under stress

Breeding is of course important, but sometimes, management methods can also be a "rescue". Before the arrival of high temperatures, it is not new but often overlooked to appropriately reduce the density, avoid planting too densely, and keep up with the watering. In fact, when the density is relatively high, the competition among plants intensifies, and the already fragile filaments become even more strained for development. Water is equally crucial. Once the soil moisture level fails to keep up, the "dual pressure" of high temperature and drought will significantly delay silk spinning. In addition, strategies such as adjusting the sowing period to avoid the peak of high temperatures and choosing hybrid varieties that are more suitable for the local climate are also quite practical at the farmer level. These practices, in combination with genetic resistance, are often more reliable than going it alone (Borras and Vitantono-Mazzini, 2018; Dong et al., 2021).

4 Application of Multi-Omics Approaches in Fine Mapping of QTLs Under Heat Stress

4.1 Integrative genomic and transcriptomic analysis for candidate region identification

Relying solely on a single omics approach to locate QTLS, especially under the multi-factor interference of high-temperature stress, is often hard to convince people. Nowadays, an increasing number of studies tend to combine genomic and transcriptomic data, especially when looking for candidate genes related to filaments. This joint strategy is not new, but it does improve the accuracy of positioning. Once information such as GWAS, linkage maps, and transcriptome expression is integrated, many key genes and QTL regions can emerge relatively clearly, especially when dealing with flowering regulation and stress response (Longmei et al., 2021). However, differential expression alone is not enough; some regulatory sites only function in specific circumstances. At this point, the eQTL map can make up for the deficiency. It can further refine the localization of the regulatory region, especially being very helpful when dealing with changes in expression patterns at high temperatures.

4.2 Construction of co-expression networks linking gene expression and phenotypes

Not all genes with upregulated expression are important; the key lies in identifying those that act in unison. This is why co-expression network analysis is receiving increasing attention in stress research. Through these networks, the gene modules that "advance and retreat simultaneously" during high-temperature stress and filaments development can be extracted and then connected with phenotypic data, which basically can narrow down the candidate range. Many studies have proved that such networks can locate some regulatory centers. For instance, certain core transcription factors are often found at the "crossroads" of these networks, and they have a significant impact on flowering time and adaptability to adverse conditions (Schaefer et al., 2017; Zhou and Liang, 2024). Once these networks are linked to eQTL or phenotypic QTL data, it becomes more confident to identify those genes and regulatory relationships that play key roles.

4.3 Predictive models based on genomic selection (GS) and machine learning

When dealing with complex traits, traditional models often "neglect one aspect for another". But now, genomic selection (GS) and machine learning (ML) are gradually becoming powerful tools to address this challenge. They can not only model with whole-genome marker data, but also introduce transcriptome and epigenome data to improve prediction accuracy. Especially for traits like silk spinning time that are influenced by multiple factors, they show obvious nonlinearity at high temperatures. At this time, deep learning or random forests can come in play and perform more stably than linear models. However, these models are not a universal template, provided that the quality of the omics data is good enough. Overall, once multi-omics information can be smoothly embedded into GS and ML systems, it will be a considerable boost for the rapid screening of high-potential genotypes and the improvement of heat-resistant breeding efficiency.

5 Functional Validation and Molecular Mechanism of Key Candidate Genes

5.1 Screening and annotation of candidate genes within QTL regions

Identifying candidate genes that affect silk spinning under high-temperature stress, relying solely on QTL mapping is clearly insufficient. Usually, methods such as GWAS, linkage mapping and meta-QTL need to be used in combination in order to screen out those truly potentially useful genes from the huge data, especially those that are actively expressed during the flowering stage (Longmei et al., 2021; Djaloviac et al., 2023). Members like ZmBAG-8 and ZmBAG-11 in the BAG family, as well as ZmLACS9 in the LACS family, have drawn attention due to their active performance under high-temperature conditions. They are not only significantly upregulated under stress, but have also been found to be involved in processes such as protein folding, lipid metabolism and ROS clearance. The annotation results also suggest that they possess typical stress response regulatory motifs. However, not all candidate genes have the same high "appearance rate" as them, and the screening process always involves many trade-offs.

5.2 Functional validation via expression profiling and transgenic approaches

Whether the candidate genes are "really working" or not needs to be proved by experiments. qPCR and RNA-seq are conventional methods for initial analysis, but to really get to the bottom of it, one still has to resort to genetically modified organisms. Take ZmBAG-8 and ZmBAG-11 for example. The expression levels of these two significantly increased after stress in heat-resistant strains and their F1, but decreased when in heat-sensitive materials, indicating that they are indeed related to heat resistance (Farid et al., 2025). The situation of ZmLACS9 was similar. When mutant experiments were conducted, it was found that it was prone to damage chloroplasts and increased ROS accumulation under heat stress, and its performance was worse than that of the wild type (Wang et al., 2023). Some protein-protein interaction network analyses have even pushed these genes to the "central position" of regulation. When these results are combined, it can basically be said that these genes are involved in regulating the heat resistance response during silk spinning.

5.3 Regulatory network construction and integration with signaling pathways

The matter is not as simple as "a certain gene is upregulated under stress". Many candidate genes are actually located in a very complex signaling pathway. To understand their roles, we need to take the regulatory network out and look at it together. For instance, tools such as co-expression analysis and eQTL networks have revealed that some genes with silk priority expression are actually remotely regulated by trans-factors, not just by their own "rotation". Interestingly, genes such as ZmHsftf13 or Bx10 are not only related to heat stress, but also involved in hormone signaling and defense metabolism (Long et al., 2022; Wang et al., 2024). This network framework, in other words, describes how environmental signals are ultimately transmitted to affect silk spinning and reproductive success, providing a complete set of ideas for subsequent heat-tolerant breeding.

6 Case Studies: QTL Divergence and Commonality Across Heat-Stressed Ecological Zones

6.1 Comparative analysis of QTLs in the North China Plain and Southeast Asia

The expression of QTL varies in different ecological environments, which is particularly evident in the comparison between the North China Plain and Southeast Asia. In the North China Plain, studies on the recombinant inbred line (RIL) population have shown that there are hotspots on chromosomes 3, 8, 9 and 10 that control the number of days of silk production (DTS), the number of days of flowering (DTA) and ASI. Some regions, such as 118 MB-125 Mb on chromosome 8, Still stable under different stresses (Leng et al., 2022). However, when it comes to Southeast Asia, the situation is quite different. GWAS analysis revealed that although SNPS related to ASI, plant height and yield under high-temperature stress could also be detected, these markers often did not overlap much with those under normal conditions, and the environmental influence was significant (Longmei et al., 2021). That is to say, some QTLS are indeed highly adaptable, while others may only "work" in specific regions.

6.2 Validation of QTL stability in heat-sensitive and heat-tolerant varieties

Not all QTLS can "stand firm" under all conditions. Often, stability is the key to whether they can be truly utilized by breeders. Some QTLS, such as mQTL2.2, mQTL6.1, mQTL7.5 and mQTL9.2, were repeatedly detected in the integrated analysis of 18 maize populations, and were all associated with yield and ASI, whether under water stress or adequate water conditions. However, such QTLS are only in the minority. The majority are either only effective under specific treatments or are significantly influenced by genetic background. Therefore, those loci that can maintain stable expression in both heat-sensitive and heat-tolerant varieties are more worthy of devoting efforts to MAS (Leng et al., 2022).

6.3 Environmental adaptation and breeding utility of precise QTLs across regions

A QTL that can perform stably in different ecological zones is often the truly useful one. Meta-QTL and GWAS techniques can now compress the QTL region to a smaller size and directly identify core candidate genes including transcription factors and stress regulators, which is of great reference value for breeding in tropical and temperate regions (Figure 2) (Longmei et al., 2021; Djalovic et al., 2023). However, when using these QTLS, MAS and GS must also be combined to stably introduce heat-resistant alleles into superior materials, thereby maintaining yield performance under high-temperature conditions (Leng et al., 2022). It is worth noting that the trait of heat tolerance is inherently complex, with many genes involved and is also susceptible to environmental interference. Therefore, even if the QTL is precise, it still needs to be continuously verified and optimized in various regions.

7 Prospects and Strategies for QTL Application in Heat-Tolerant Breeding

7.1 Interaction mechanisms between key QTLs and traits such as yield and flowering time

Some QTLS related to silk spinning under high-temperature stress are also frequently found in studies that control yield or flowering time. For instance, QTLS that affect ASI and DTA were simultaneously located on chromosomes 3, 8, and 9, and they manifested under both normal and stressful conditions (Zhang and Xu, 2024). This "overlap" may be due to pleiotropy or simply a chain relationship. In any case, they offer an opportunity to simultaneously regulate multiple important traits. But things are not that simple. Some QTL effects are indeed stable and applicable to multiple environments, while others are highly sensitive to the environment and change their appearance when conditions are altered. This is also why breeding programs are more inclined towards QTLS that have "stood firm" in multi-year trials in multiple locations (Du et al., 2021; Longmei et al., 2021). Stability might be more important than the size of the effect value.

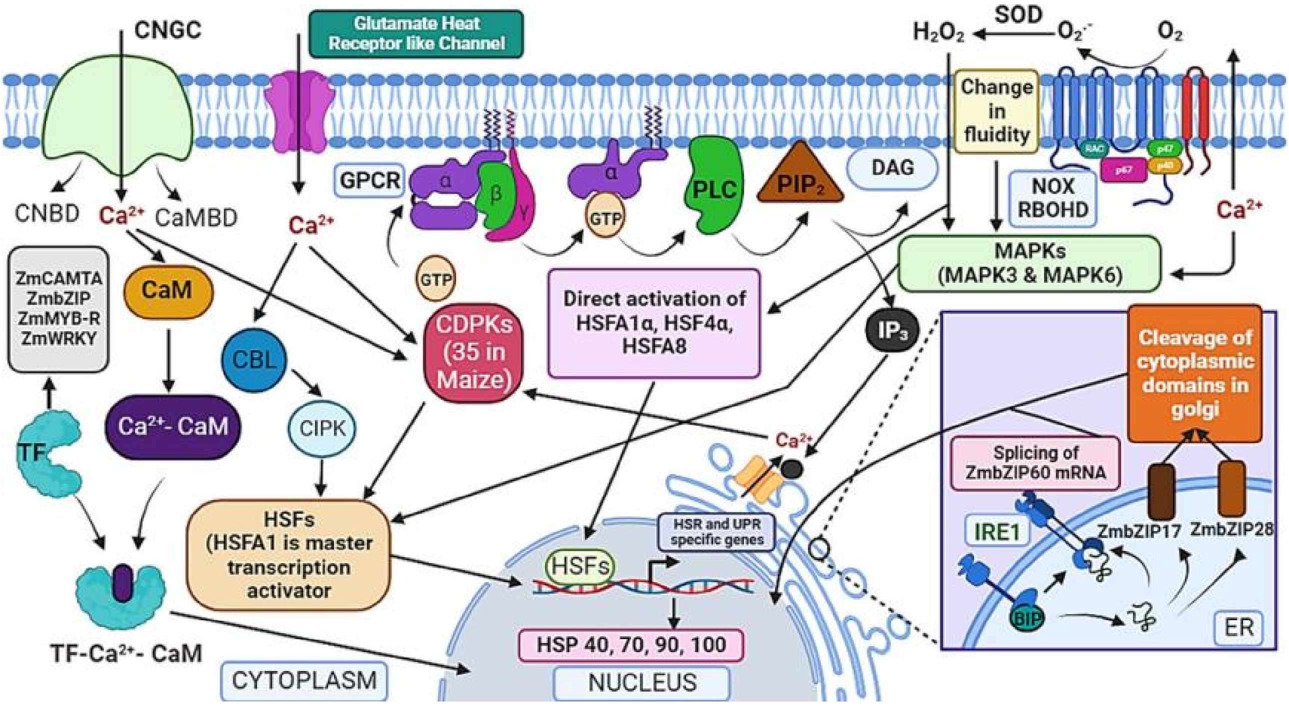

Figure 2 Schematic diagram showing heat stress response in maize at the cellular level (Adopted from Djalović et al., 2023)

7.2 Integration of MAS, GS, and gene editing for improved silk emergence

To make good use of these sites in actual breeding, it depends on whether the tools at hand are precise enough. MAS is still quite useful in the early stage, especially for those major QTLS with obvious additive effects, which can be easily introduced into strains. However, traits like the filament stage are often not explained by just one or two large QTLS, but rather by the combined effect of many small effect sites. At this point, GS comes in handy - it can integrate these scattered genetic effects and enhance the predictive ability (Budhlakoti et al., 2022). As for gene editing, it is no longer just a theory now. Tools like CRISPR/Cas9 have been able to directly target QTL regions for modification. Some teams have even begun to attempt multi-gene editing, targeting the entire gene network to improve the overall expression of complex traits. MAS, GS and gene editing - none of these three tools can be lacking. A combination of them is the key to success.

7.3 Establishing genetic improvement models for heat-adapted silk emergence traits

Breeding cannot be accomplished merely by relying on a single good QTL; a model is needed to connect these scattered pieces of information. To construct an improved strategy adapted to heat stress, it is necessary to consider the relationship among genes, phenotypes and the environment simultaneously. For instance, MAS can focus on major loci, but GS models have more advantages in multi-environment predictions, especially for those traits that are greatly influenced by the environment (Cerrudo et al., 2018). Nowadays, many teams are beginning to attempt to combine the two, along with high-throughput phenotyping and genotyping technologies, to increase the "hit rate" of selection. The ultimate goal is to establish a continuously operating breeding pipeline: in the early stage, breakthroughs are sought through QTL localization; in the middle stage, multi-site combinations are predicted by GS; and in the later stage, details are corrected by gene editing (Leng et al., 2022). The climate is becoming increasingly uncontrollable, and the window of opportunity for breeders to make mistakes is getting smaller and smaller.

8 Conclusion and Future Perspectives

Some QTLS related to the occurrence time of filaments under high-temperature stress, although often regarded as having the potential to improve the adaptability of corn to rising temperatures, have not always been smoothly applied in practice. Meta-QTL analysis has indeed screened out some regions and candidate genes that are relatively stable in multiple environments, among which there are no shortage of transcription factor families involved in stress responses (which can be used for marker-assisted selection and functional studies), but the "implementation" of these achievements in breeding often still needs to overcome several practical problems. For instance, the phenotypic effects of these QTLS are mostly small, the genotype-environment interaction is complex, and their expression in different contexts is often unstable. Not to mention that some seemingly "useful" heat tolerance loci, once lacking verification or not superimposed with other key stress resistance genes, are difficult to support genetic gain in actual breeding work.

If only traditional field screening is relied upon, these problems may be magnified. But now, the combination approach integrating high-throughput phenotypic platforms, quantification of environmental factors, and genomic data is helping researchers more accurately locate the key sites that control filaments development and the flower-filament interval (ASI) under high-temperature stress. Especially on the basis of multi-environment trials, precise measurements of traits such as ASI and flowering period can enable GWAS and genomic selection techniques to more accurately infer the action regions and genetic contributions of QTLS. It should be noted that when environmental data is used alone, it is of little help in yield prediction. However, once it is linked with phenotypic and genomic data, it often significantly improves the accuracy of climate adaptability prediction.

There is still a long way to go from discovery to actual application. The implementation of heat-resistant breeding achievements does not rely on breakthroughs in a single discipline, but rather on the joint efforts of various experts. Whether they are geneticists, breeding experts, physiological researchers, data analysis teams or field managers, collaboration is the key. At present, molecular tools such as double haploid and gene editing, in combination with precise phenotypic platforms, have been gradually integrated into some national and international cooperation projects, accelerating the promotion of climate-adapted corn in high-risk areas. However, to truly establish an efficient and sustainable climate breeding system, investment, data sharing mechanisms and regional capacity building remain indispensable fundamental conditions.

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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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