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Regulation of Pollination Synchronization and Kernel Development in Glutinous Maize under Different Sowing Dates and Plant Densities

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Abstract This study mainly examined how pollination synchronization and kernel development of glutinous maize are regulated at different sowing times, and sorted out how changes in sowing time affect the growth rhythm, flowering time and pollination process of male and female ears, as well as the formation process of endosperm. The study also discussed the roles of hormone signals, carbon and nitrogen metabolism and some regulatory genes in pollination synchronization. It also analyzed whether choosing the right sowing time in different regions could help make the kernels plumper and the quality of the products better. This study hopes to provide some theoretical basis and practical suggestions for the planting management and high-yield and high-quality breeding of glutinous maize.

Keywords Glutinous maize; Sowing date; Pollination synchronization; Kernel development; Plant density

1 Introduction

Glutinous maize is an important food and economic crop. Its yield and quality largely depend on smooth pollination and normal kernel development. Pollination synchronization is extremely crucial. If the pollination time is inconsistent, some ovaries may be fertilized late or even not at all, which will result in fewer kernels and a decrease in yield. Research has found that simultaneous pollination can significantly increase the number of kernels and the maturity of kernels produced by each plant. This effect was obvious in different panicle positions and different hybrid varieties (Westgate et al., 2022). In addition, during the development of kernels, the accumulation of various substances is required, and they are also regulated by factors such as hormones and sugars (Doll et al., 2017; Dai et al., 2021).

The sowing time and planting density have a significant impact on the reproductive development and final yield of maize. If the density is too high, the filaments may appear relatively late, which can easily cause inconsistent flowering times of male and female flowers, affect pollination synchronization, and finally affect kernel development (Borrás and Vitantonio-Mazzini, 2018). If the sowing time and density are not well controlled, it will also aggravate environmental stress such as high temperature or drought, increase kernel miscarriage and lead to a decrease in yield (Guo et al., 2021; Niu et al., 2021). Reasonable arrangement of sowing time and density is conducive to better exposure of filaments during the pollination period, improving the success rate of pollination and yield stability.

This study analyzed the pollination synchronization and kernel development changes of glutinous maize under different sowing periods and densities, investigated the regulatory mechanisms between them, explored the relationship between pollination synchronization and kernel development and abortion, and found possible explanations at the physiological and molecular levels. This study hopes to provide some theoretical support and technical suggestions for improving the yield and quality of glutinous maize.

2 Phenological Responses of Glutinous Maize to Sowing Date and Density

2.1 Floral initiation and developmental timing affected by sowing date

The sowing time will directly affect when glutinous maize starts to flower and the development speed of the flowers. In hot or dry weather, the silk production time of female spikelets is often delayed, which easily leads to the problem of asynchronous male and female flowers, affecting the pollination effect and resulting in a decrease in seed setting rate (Borrás and Vitantonio-Mazzini, 2018). Studies have found that even a difference of 2 to 4 days in the time of silk spinning can significantly reduce the number of kernels produced, especially when planted densely or under environmental stress, the problem becomes more severe. If synchronous pollination can be achieved, it will increase the number of kernels and the seed setting rate, and to a certain extent, make up for the impact of delayed silk production. In addition, the sowing period also affects the temperature and light conditions in the field, thereby influencing the flowering time and development rate, as well as the duration and efficiency of kernel filling (Guo et al., 2021).

2.2 Vegetative-reproductive balance under different plant densities

The change in planting density also has a significant impact on the growth of glutinous maize. When the density is high, the plants compete for nutrients more fiercely, the biomass of individual plants decreases, the female spikelets receive less nutrients, the silk production is slower, and it is more likely to cause inconsistent flowering times (Borrás and Vitantonio-Mazzini, 2018). Under low-density conditions, the secondary female panicles can also bear fruit normally, and the number of kernels will increase. However, in high-density planting, basically only the main panicle can develop normally. Whether simultaneous pollination can be achieved has a significant impact on the number of kernels in the main panicle, with the maximum increase being 8% to 31%. The ideal glutinous maize variety should be able to maintain rapid growth of the female ears and timely silk production even when resources are limited, so as to produce as many kernels as possible.

2.3 Environmental sensitivity and genotype-dependent variation

Glutinous maize is highly sensitive to changes in temperature, light and moisture. Different varieties show different behaviors in terms of flowering period synchronization, female panicle growth and kernel development (Guo et al., 2021). Some varieties can maintain a relatively fast growth rate of spikelets and silk production even under adverse conditions, reduce delayed flowering and increase seed setting rate (Borrás and Vitantono-Mazzini, 2018). In addition, different genotypes also respond differently to high temperatures and drought. Heat-tolerant varieties can maintain a high supply of photosynthetic products and kernel filling rate at high temperatures, thereby reducing kernel failure (Guo et al., 2021; Niu et al., 2021). Therefore, in actual production, the arrangement of sowing time and density should be combined with the characteristics of different varieties to adjust the synchronization of flowering periods and ensure that the kernels can develop normally.

3 Pollination Synchronization: Mechanisms and Disruptions

3.1 Tassel and silk emergence coordination

Whether maize kernels can develop normally largely depends on whether the male ear (producing pollen) and the female ear (producing filaments) develop simultaneously. When planted too densely, the filaments tend to emerge later, but most of the filaments will still be exposed within five days after they are released. Pollination synchrony refers to the fact that these filaments receive pollen simultaneously within a short period of time, which is a key factor in enhancing seed setting rate and kernel count. Research has found that simultaneous pollination can significantly increase the number of kernels in both the main and secondary panicles. Especially when planted at low density, the number of kernels in the secondary panicles can increase by 39% to 535%. Even under high-density conditions, the kernel count of the main panicle can be increased by 8% to 31% (Westgate et al., 2022). In addition, synchronous pollination can also make the kernels of the upper and lower parts of the ear develop more uniformly, promoting the kernels of the entire ear to grow more evenly.

3.2 Asynchronous flowering: causes and agronomic consequences

Asynchronous pollen and filaments, that is, asynchronous flowering, are usually caused by environmental stress such as planting too densely, high temperature and drought, or the genetic characteristics of the variety itself. If the filaments emerge too late, or if some are too early and some too late, there may be a situation where all the pollen has fallen but the filaments have not yet come out. These filaments that are not pollinated in time cannot develop kernels and eventually affect the yield (Figure 1) (Shen et al., 2019; Shen et al., 2020). Research shows that if the pollination interval is 2 to 4 days, the number of kernels may drop sharply, by up to half. If synchronized pollination can be achieved, the impact caused by delayed filaments can be partially compensated for. Furthermore, asynchronous pollination can also cause the kernels on the same panicle to compete for nutrients, and some kernels may fail due to insufficient nutrient supply.

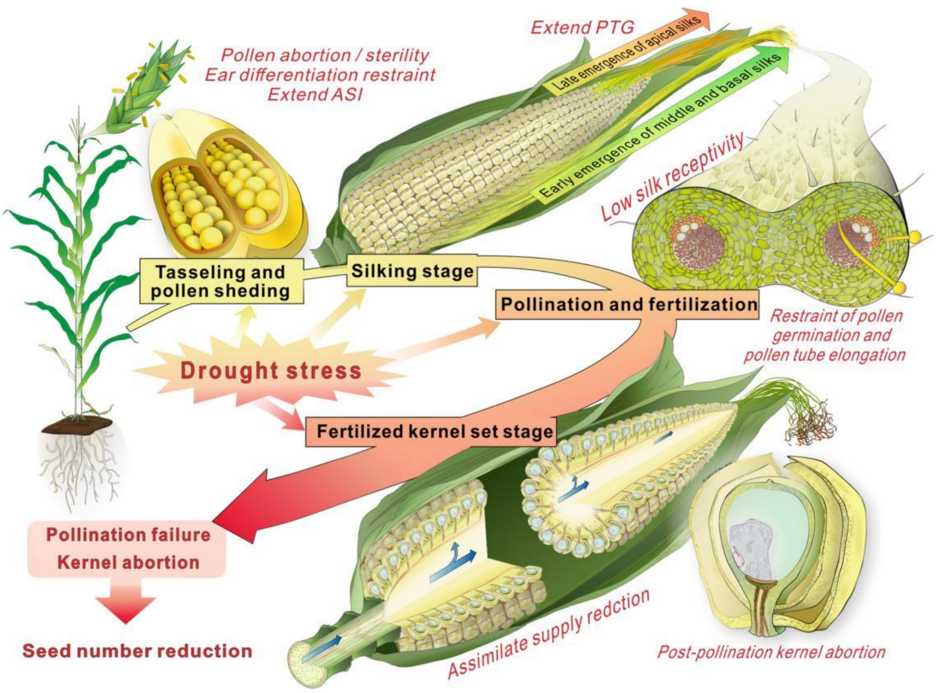

Figure 1 Multiple processes related to kernel set are affected by drought stress throughout the flowering stage (Adopted from Shen et al., 2019)

Image caption: At the tasseling stage, drought causes pollen abortion, limits ear differentiation, and extends the anthesis-silking interval (ASI), all of which are associated with kernel abortion. At the silking stage, drought can severely suppress silk elongation, widen the time intervals of early- and later-emerged silks, and extend the pollination time gaps (PTG) for ovaries within ear. Increased PTG is a factor known to induce kernel abortion. During the stage between pollination and fertilization, drought decreases silk receptivity and limits pollen germination and pollen tube elongation, leading to pollination failure or kernel abortion. After fertilization, kernel abortion may be induced by drought (Adopted from Shen et al., 2019)

3.3 Synchronization metrics and evaluation techniques

Pollination synchrony can be measured by several indicators, such as the distribution of filament exposure time, the length of pollination intervals, and the seed setting rate (for example, the number of kernels produced divided by the number of filaments involved in pollination). In the field, the effects of natural pollination and artificial synchronous pollination can be compared, and the impact of synchronous pollination can be evaluated by combining the changes in the number of kernels in the main and secondary panicles (Westgate et al., 2022). In addition, computational models can be used to simulate the process of pollen diffusion and pollen reception by filaments. Combined with the data measured in the field, pollination synchrony and its contribution to the final yield can be quantified more accurately (Kuo et al., 2021).

4 Effects of Sowing Date on Reproductive Timing and Fertility

4.1 Early vs. late sowing: thermal accumulation and developmental shifts

Early-sown maize usually grows better because it can utilize the temperature earlier and has a longer growth period. Thus, the plants grow vigorously, the kernel development time is sufficient, and the yield will naturally be higher (Tsafack et al., 2024). If sowing is too late, the vegetative growth period of the plants will be shortened. Although the reproductive period may be prolonged, the overall growth period is still shortened, the accumulated heat is reduced, and the kernel development will be affected (Cao et al., 2024). In the northern and northeastern regions of our country, early sowing can make full use of sunlight and temperature, which is conducive to increasing theoretical yields. If sown late, there will be less light and heat, and the yield is also prone to decline (Zhu et al., 2022; Wu et al., 2023). In tropical and subtropical regions, late sowing often causes maize to enter the reproductive period precisely at the hottest time, such as the V12 to R1 stage. This can easily lead to a reduction in kernels and a decrease in yield (Li et al., 2024).

4.2 Photoperiod sensitivity and stress susceptibility

Maize is very sensitive to changes in temperature and light. Early sowing can avoid high temperature and drought in the later stage, reduce heat damage during flowering and pollination, and make it easier to ensure kernel setting and quality (Cao et al., 2024; Li et al., 2024). Conversely, if sown late, maize may encounter problems such as high temperature and little rainfall during the reproductive period. As a result, pollen vitality decreases, filaments age faster, and eventually normal pollination is affected, and the seed setting rate is also low (Zhu et al., 2022). In addition, different sowing times will also affect the nutrition of the kernels. For example, the contents of protein and fiber will change accordingly (Liu et al., 2023).

4.3 Field observations on pollen viability and silk receptivity

The observations in the field also support these viewpoints. Appropriate sowing time can make pollen release and filamentous ejection more synchronous, which is conducive to improving pollination effect and seed setting rate. When sown early, both pollen vitality and filament state are relatively good, and it is less likely to have pollen death or pollination failure (Cao et al., 2024; Tsafack et al., 2024). Sowing too late can easily lead to poor pollen vitality and premature aging of filaments, thereby affecting normal pollination and kernel formation.

5 Plant Density and Reproductive Resource Allocation

5.1 Canopy structure and light penetration

Increasing the planting density will significantly change the canopy structure of maize. When the density is high, both the leaf area index (LAI) and the light energy received by the population (TPAR) will increase. However, if the density is too high, the lower leaves will be unable to carry out photosynthesis normally due to too weak light (Yang et al., 2021). Under high-density conditions, the area and Angle of the upper layer leaves become smaller, allowing the middle and lower layer leaves to receive more light, and the attenuation of light also becomes slower (the KL value decreases), which helps the entire maize plant to make better use of light energy (Tian et al., 2022). In addition, as long as the variety combination is reasonable and the planting density is properly controlled, dry matter accumulation and yield can also be increased.

5.2 Source-sink balance and nutrient partitioning to kernels

Planting density also directly affects the “source-reservoir relationship” of maize, that is, the way plants produce and transport nutrients. When the density is high, more dry matter and nitrogen can be accumulated per square meter, but the nutrients allocated to the roots and kernels per plant will decrease instead, the ratio of roots to stems will be lower, and the harvest index (HI) will also decline (Shao et al., 2024b). High density will concentrate more nutrients in the stems and leaves, resulting in less distribution to the kernels. Therefore, the number and weight of kernels per plant will decrease, but the overall population yield will still increase (Zhang et al., 2020). In this case, if nitrogen fertilizer is appropriately increased, it can help improve the efficiency of nitrogen transport from stems and leaves to kernels, and also enhance the utilization rate of nitrogen fertilizer (Duan et al., 2023; Shao et al., 2024a).

5.3 High-density stress effects on pollination efficiency

When the density is high, the competition for resources among plants will also be more intense. As a result, reproductive growth is prone to be affected. For example, the time for filaments to emerge becomes later, male and female are out of sync, pollination effect deteriorates, and eventually leads to a reduction in the number of kernels (Borrás and Vitantonio-Mazzini, 2018). Some varieties can enhance reproductive capacity at high density, such as growing multiple spikes, which can ensure yield as much as possible under the condition of limited nutrients (Ross et al., 2020). However, when the environmental stress is high, the nutrient distribution and filamentesis of the second spike (E2) are both restricted, which will affect its pollination and fruiting (D’Andrea et al., 2022; Parco et al., 2022). Therefore, to maintain synchronized pollination and healthy kernel development under high density, it is necessary to select the right variety, control the planting density well, and ensure the supply of nutrients during the critical period.

6 Interactions Between Sowing Date and Density

6.1 Synergistic and antagonistic effects on pollination window

The combination of sowing time and planting density will jointly affect the pollination synchronization of maize. Generally speaking, the higher the density, the later the filaments will appear. However, most of the filaments will still be fully exposed within five days after they are spun. If both the main spike and the secondary spike can successfully complete pollination during this period, it will significantly increase the number of fruiting kernels and the fruiting ratio of filaments per plant. In the fields where the seeds are planted relatively sparsely, the increase in the number of kernels in the secondary panicles is the most obvious. Under high density, the increase in kernels of the main panicle is more obvious. Synchronous pollination can alleviate the problems caused by the late appearance of filaments, make the coordination time between filaments and pollen more compact, and improve the pollination efficiency.

6.2 Combined influence on spikelet fertility and kernel set

The coordination of sowing time and density also affects the differentiation process of spikelets at the spike, whether they can be successfully pollinated, and whether kernels can be produced in the end. Late sowing combined with high density will result in less nutrient distribution from the plant to the spikelet, making it more difficult for the spikelet of the spikelet to grow well and reducing the proportion of exposed filaments. Eventually, the seed setting rate of the spikelet will decline. However, if the density is appropriate and the sowing time is also appropriate, the spikelets of the main spike and the secondary spike can grow more uniformly together, and the fruiting will be more stable (Parco et al., 2022). Moreover, the more synchronous the pollination is, the higher the seed setting rate and quantity will be, especially when the competition for nutrients is relatively intense (Rotili et al., 2022). If the sowing time and planting density can be properly adjusted, the kernel miscarriage caused by the asynchronous development of filaments can be reduced, and the overall fruiting efficiency can be improved (Shen et al., 2019).

6.3 Management strategies based on G × E × M interactions

There are significant differences among various maize varieties, climatic conditions and management methods (such as sowing time and planting density), so when planting, strategies can be adjusted according to the situation to make pollination more synchronized and the kernels grow better. For varieties that are prone to secondary panicles or have many tillers, if low density is used and the sowing time is appropriate, the secondary panicles can develop smoothly and produce seeds normally, which helps to improve the stability of yield (Rotili et al., 2022). However, if the density is too high or the resources in the environment are insufficient, the normal development and pollination of the main spike should be ensured first to avoid the secondary spike competing for nutrients (Parco et al., 2022). In addition, appropriately adjusting the pollination time, such as artificial synchronous pollination, can also increase the seed setting rate, especially when the density is high or the weather is bad (Westgate et al., 2022). Therefore, considering the variety characteristics, weather conditions and field management methods in combination, that is, the so-called G×E×M integrated management model, is the key to growing glutinous maize well and increasing yield and quality.

7 Physiological and Molecular Regulation of Kernel Development

7.1 Hormonal crosstalk during fertilization and early kernel growth

At the beginning of kernel development, some hormones, such as auxin (IAA), abscisic acid (ABA), salicylic acid and cytokinin, play a significant role and mainly affect the differentiation process of kernels after fertilization (Zhou and Hong, 2024). Auxin can help kernels with sugar metabolism and cell division, making them more active. ABA, on the other hand, is related to the early developmental competitiveness of kernels. Studies have found that IAA can promote the expression of genes related to sugar utilization, while inhibiting the synthesis and signal transduction of ABA, thereby helping kernels develop better (Du et al., 2023; Wang et al., 2023). The relationship between hormones and sugar is also very close. The level of sugar can affect auxin synthesis genes (such as *ZmYUC*), and thereby affect whether the kernels grow fast or not (Doll et al., 2017). Under stress conditions such as high temperature, the reactions of IAA, ABA and salicylic acid will also change, which is very crucial for kernel development (Figure 2) (Guo et al., 2021).

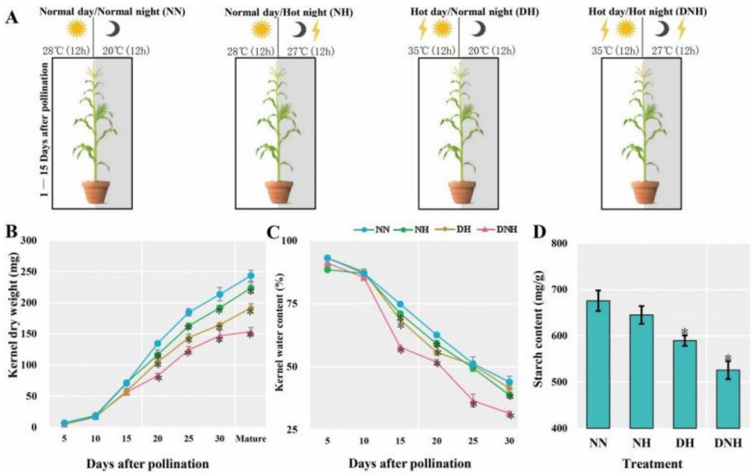

Figure 2 Effects of different high-temperature stress regimes on kernel characteristics of waxy maize (Adopted from Guo et al., 2021)
Image caption: (A) Schematic diagram of the different temperature treatments. NN, normal day/normal night; NH, normal day/hot night; DH, hot day/normal night; and DNH, hot day/hot night. The stress treatments were imposed during the period 1~15 d after pollination (DAP), and the plants were kept under NN conditions at all other times. (B) Changes in kernel dry weight and (C) and kernel water content with time. (D) Starch content of grains at maturity. Data are means (±SE) of n=3 replicates. Significant differences compared with the NN were determined using Student's t-test: *P<0.05 (Adopted from Guo et al., 2021)

7.2 Gene expression changes under different sowing-density scenarios

The changes in sowing time and planting density can affect whether pollen release is synchronized, whether nutrient distribution is balanced, and the distribution of hormones, all of which can influence the expression of genes related to kernel development. Multi-omics studies have found that the gene expression patterns of kernels vary greatly 10 and 25 days after pollination, involving functions such as starch synthesis, hormone signaling, and some transport proteins (Guo et al., 2021). At the junction of the kernel and the parent, some transcription factors, such as MADS-box, control the transport of sugar, amino acids and ions, thereby affecting whether the kernel can fill (He et al., 2024). In addition, an epigenetic modification called N^6-methyladenosine (m6A) can also affect the expression of genes related to kernel development, thereby influencing the size and quality of kernels (Wu et al., 2024).

7.3 Molecular markers related to pollination synchrony and kernel traits

Whether pollination is synchronized will directly determine the quantity of kernels and whether their development is uniform. From a molecular perspective, transcription factors of the BES1/BZR1 family (such as ZmBES1/BZR1-5) are related to kernel size and weight, and their SNP loci can also serve as molecular markers for improving kernel traits (Sun et al., 2020). In addition, the *KIL1* gene in the NAC family controls the senescence of filaments, affects the length of the pollination window, and thereby influences the seed setting rate (Ishka, 2022). During kernel development, genetic changes related to glucose metabolism, hormone signaling and transport proteins can also be used as molecular markers to help select high-yielding maize varieties with coordinated kernel development (He et al., 2024).

8 Case Study: Field-Based Evaluation of Sowing Date × Density on Glutinous Maize Yield

8.1 Site and hybrid description

In field trails, typical plots from different regions are usually selected and conducted together with multiple hybrid varieties of glutinous maize. There are obvious differences among different hybrids in terms of tillering ability, panicle position differentiation and kernel development. Some varieties have many tillers and panicles. These characteristics can help them maintain relatively stable yields in low-density or adverse environments (Parco et al., 2022; Rotili et al., 2022).

8.2 Experimental design and pollination synchronization results

In the experiment, different sowing times were set, such as early sowing, mid-sowing and late sowing. Several planting densities were also combined, such as 4 or 8 plants per square meter. The purpose of doing this is to observe the impact of these treatments on pollination synchrony and seed setting rate. High density will cause the filaments to emerge more slowly, but most of the filaments can still be exposed within five days after spinning. If all the filaments are pollinated at one time at this point in time, it is called "simultaneous pollination treatment". This approach significantly increased the number of kernels and the filigree setting index per plant. At low density, the number of kernels in the secondary panicles increases most significantly, with an increase ranging from 39% to 535%. At high density, mainly the number of kernels in the main panicle increased by 8% to 31% (Parco et al., 2022). In addition, the sowing time has little effect on the synchronization of the flower organs inside the spike, but there are significant differences among different varieties. Varieties with more tillers have more uniform development between spikes and less loss of flower organs at the spike tips.

8.3 Kernel yield, quality, and breeding implications

Simultaneous pollination can directly increase kernel count and yield, and the effect is particularly obvious in low-density planting and varieties with many tillers (Parco et al., 2022; Rotili et al., 2022). Under high density, some superior varieties can achieve faster kernel filling and higher yield by enhancing the "source-reservoir relationship", that is, improving photosynthesis and material transport efficiency (Ren et al., 2022). In addition, the combination of pollination synchronization with techniques such as male sterility and cross-pollination can further increase the kernel quantity, oil content and total yield, providing new management tools for growers (Westgate et al., 2022). When breeding, if the tillering ability, the synchrony of development between ears and the high-density adaptability can be taken into account, it will be easier to breed new varieties of glutinous maize with high and stable yields.

9 Challenges and Research Gaps

9.1 Climate variability and prediction models for flowering synchrony

The annual climate change and seasonal temperature difference have a significant impact on the flowering time and pollination synchronization of maize. These factors will eventually affect the kernel quantity and total yield (Amas et al., 2022). However, at present, few studies have incorporated these climate changes into pollination synchronization prediction models. Especially now that extreme weather is becoming increasingly common, we still lack flowering prediction tools that can cope with different sowing periods. Moreover, many studies have only focused on a certain region or a certain year, and the universality and adaptability of the models are not strong enough (Liu et al., 2023).

9.2 Limitations in density-specific breeding lines

Although increasing planting density can lead to a higher yield per mu, different maize varieties have different adaptations to density (Gheţe et al., 2021). At present, there are still relatively few specialized varieties that are highly adaptable to high-density or low-density environments. Especially for glutinous maize, the progress of genetic improvement in enhancing multi-spike ability and filamentary synchrony is still relatively slow (Omar et al., 2022; Parco et al., 2022). In addition, some breeding materials are very unstable at different densities and are not suitable for use in diverse planting methods.

9.3 Standardization of phenological measurement approaches

Nowadays, the standards used in observing pollination synchrony and kernel development vary from place to place. Some look at when the filaments emerge, some look at the flowering time, and some look at the number of kernels. The recorded time points are not uniform. This leads to the fact that the results of various experiments are difficult to compare directly and the research conclusions are not easy to generalize. Especially in maize with multiple panicles or tillers, the measurement criteria for main panicles and lateral panicles are currently unclear (Parco et al., 2022). In addition, there is no efficient automatic monitoring technology at present, which leads to relatively low data collection efficiency in large-scale trials (Omar et al., 2022).

10 Concluding Remarks

Whether pollination is synchronized will directly affect the seed setting rate and the number of maize kernels. If pollination can be synchronized, the number of kernels in both the main and secondary ears will increase significantly. Especially when the seeds are not planted so densely, the increase in the number of kernels in the secondary panicles is more obvious. When planted very densely, it is mainly due to an increase in the number of kernels in the main panicle. Planting density and nitrogen fertilizer levels can affect the growth of maize and the development of its reproductive organs. When the density is low, it is easier to grow multiple ears and also more conducive to maintaining the stability of the kernel quantity. During the development of kernels, they can also be affected by the competition among kernels on the same spike, hormonal levels (such as ethylene, polyamines, IAA, ABA), and changes in sugar metabolism. If environmental problems such as high temperature and drought occur, or certain hormones are applied, it may also affect the kernel filling and development process.

To achieve high maize yields, several models can be considered. If the seeds are not planted too densely and sown earlier, it can promote the development of secondary ears and make the yield more stable. This approach is suitable for areas with limited land but where a stable yield is desired. Under high density, to ensure that the main panicle also has a good seed setting rate, the yield can be increased through methods such as artificial synchronous pollination. The prerequisite for this is to select varieties with a high content of dry matter and high transportation efficiency. In terms of fertilization, if there is more nitrogen fertilizer, it will be beneficial to the development of secondary spikes. However, if there is insufficient nitrogen fertilizer or the plants are planted very densely, it is necessary to ensure the nutrient supply to the main panicles first. In addition, the combined use of artificial pollination, male sterility, and cross-pollination can further increase the number of kernels and yield. When encountering high temperatures or droughts, it is necessary to optimize the supply of sugar and hormone regulation in order to reduce the failure of kernel development and maintain the yield.

In the future, scientists will be able to use high-throughput phenotypic technology to monitor the kernel development process more precisely. Combined with molecular markers, key regulatory factors such as MADS-box transcription factors and m6A methylation can be identified, which is very helpful for a deeper understanding of kernel development. In terms of breeding, there is now an increasing emphasis on developing new glutinous maize varieties that are both high-yielding and stress-resistant by regulating gene expression and epigenetics. In the future, intelligent management can also be introduced, such as using environmental monitoring equipment, intelligent irrigation and precise pollination systems, etc., to dynamically regulate the kernel development process. This not only ensures stable yields but also improves quality. These technologies have made “precise phenotyping + intelligent breeding” a new direction for achieving efficient agriculture.

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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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