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Adjusting the sowing date of fresh maize to promote grain filling, key starch synthesis enzymes, and yield

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Abstract: Clarifying the effects of meteorological factors on the growth and development of fresh maize after delayed sowing is important for selecting appropriate sowing dates and improving yield. Six sowing dates (B1 (March 10); B2 (March 20); B3 (March 30); B4 (April 9); B5 (April 19), and B6 (April 29)) and three fresh maize cultivars (A1 (Wan Nuo 2000); A2 (Nongke Nuo 336), and A3 (Caitian Nuo 6)) were chosen for experiments conducted between 2021 and 2022 in Guiyang, Qingzhen City, China. The results showed that the whole growth period and sowing-silking period were significantly reduced with delayed sowing, while the grain-filling period was relatively stable. Delayed sowing was beneficial in increasing the number of endosperm cells and the weight of the hundred kernels. The graining filling rate and the activities of four key starch synthesis enzymes (sucrose synthase, ADP-glucose pyrophosphorylase, starch branching enzyme, and starch debranching enzyme) were significantly influenced by light, temperature, and precipitation, and they mainly affected the hundred kernel weight. The yield tended to increase with delayed sowing, and the correlation analysis between precipitation and yield at different sowing periods showed a significant effect of precipitation on yield. Delaying the sowing to mid-early April was more favourable for grain filling, enhanced key enzyme activity, and increased the kernel weight and yield. These results highlight the importance of choosing excellent cultivars and matching them with the most suitable sowing date to fully exploit climatic resources and achieve high-yield and high-efficiency cultivation of fresh maize.

Keywords: sweet-waxy maize; climate change; *Zea mays* L.; grain filling characteristics; enzymatic activity

Fresh maize is rich in nutrients, widely used, and favoured by an increasing number of consumers. Fresh maize is the type of maize that is harvested at milk maturity for consumption and processing, mainly including sweet maize (*Zea mays* L. *saccharata* Sturt), waxy maize (*Zea mays* L. *sinensis* Kulesh) and sweet-waxy maize. With the adjustment of agricultural planting structure and the change in dietary structure, fresh corn has been widely planted worldwide (Mut et al. 2022, Kumar et al. 2023). Especially in China, the rapid development of fresh maize in the past two decades, the introduction of new cultivars,

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and the continuous improvement of the production level have become the main base of the international fresh maize industry and research (Hu et al. 2021). To meet the market demand and promote economic development, the comprehensive production capacity of fresh maize must be increased. The grain-filling period is critical for maize yield, and the accumulation of dry matter (DM) is mainly determined by the rate and duration of grain filling (Li et al. 2020). The characteristics of grain filling directly affect the yield of maize, and suitable filling conditions can help to achieve the coordination of the number of ears, kernel number, and kernel weight (KW) and improve yield (Wang et al. 2021a). Previous studies have found that maize KW is determined by both reservoir size and reservoir fullness and synergistically regulated by filling characteristics and cell expansion, with the number of endosperm cells determining the reservoir size and the filling characteristics reflecting the degree of kernel fullness (Ji et al. 2022, Sun and Zhang 2023). Starch is the main storage material in maize kernels (Zhang et al. 2022), and the filling process of fresh corn kernels depends mainly on the synthesis and accumulation of starch, which varies at different ambient temperatures (Wang et al. 2021b). Starch synthesis is regulated by several starch synthesis-related enzymes; sucrose is the carbon source for starch synthesis in the endosperm (Zhang et al. 2007a), with sucrose synthase (SS) being the first enzyme to convert sucrose to starch (Zhang et al. 2021). ADP-glucose pyrophosphorylase (AGPase) is the main rate-limiting enzyme for the production of adenosine diphosphate glucose (ADPG), a substrate for starch synthesis (Wang et al. 2021b). Starch branching enzyme (SBE) and starch debranching enzyme (DBE) are key enzymes that coordinate and control the synthesis of branched starch in kernels (Guo et al. 2006). The precise mechanism of starch biosynthesis in grains is complex, and the activity of different starch synthesis-related enzymes and the coordination between them require further research (Mu-Forster et al. 1996, Zhang et al. 2007b).

Light, temperature, and precipitation are the key ecological factors that affect crop production (He et al. 2020). Light, temperature, and precipitation signals are coordinated to control crop growth and development; several studies have shown that different climate resources can have important effects on crop filling characteristics and final yield (Li et al. 2003, He et al. 2020, Chen et al. 2020). Appropriately adjusting the sowing date is an important cultivation measure for improving the yield and quality of maize (Bonelli et al. 2016, Lv et al. 2020); additionally, it can optimise the allocation of the growth period and natural climate resources, thereby improving the utilisation efficiency of climate resources (He et al. 2020). The effect of sowing date on the grain filling rate is mainly achieved through changes in climatic conditions, with light acting indirectly on the average grain filling rate by affecting the grain plumpness and temperature acting on the average grain filling rate by affecting the speed of the filling process (Yang et al. 2014). Plants can automatically adjust their developmental processes to adapt to new ecological conditions by sensing changes in light and temperature on different sowing dates (Li et al. 2022). Maize growth requires a large amount of water, and an appropriate sowing date is conducive to achieving an effective match between precipitation and growth stages that require more water (Peng et al. 2022). The number of sunshine hours and temperature during the filling period on different sowing dates are the main factors affecting maize yield in different latitudinal ecological zones (Li et al. 2003). In contrast, under specific ecological conditions, changes in environmental conditions, such as temperature and solar radiation, due to a different sowing date can significantly affect the rate and duration of maize germination and ultimately impact the KW and yield (Li et al. 2003, Zhou et al. 2017). Similarly, precipitation conditions during the silking and filling periods also significantly impact maize yield but can be alleviated by irrigation (Chen and Zhou 2022). Changes in the sowing date can alter the growth rate and length of the phenological period of the crop, and late sowing of maize can cause insufficient grain filling due to a decrease in solar radiation and temperature during the reproductive period, resulting in a decrease in KW and subsequent yield reduction (Bonelli et al. 2016). Enzyme activities in organisms are also affected by temperature, and heat stress reduces the activity of enzymes involved in starch metabolism in fresh maize (Yang et al. 2018). Starch biosynthesis-related enzymes vary significantly between seasons (Iqbal et al. 2021). Climate change in recent years has undoubtedly led to a certain degree of decline in maize yield (Lv et al. 2020); however, reasonable sowing date adjustments can improve the adaptability of fresh maize to climate change and ensure higher yields.

In practice, it is difficult to artificially control climatic characteristics in the field, however, crop growth and development under suitable meteorological factors can be achieved by sowing adjust-

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ments. As fresh maize has a relatively short growth period compared with common maize, differences in weather conditions during the filling period are bound to have an important impact on yield. Previous studies have provided a theoretical basis for improving the yield and quality of maize by adjusting the sowing date, thereby laying the foundation for the efficient utilisation of natural ecological resources. However, few studies have analysed the effect of different sowing dates on kernel establishment from the microscopic perspective of endosperm cells or clarified the effects of sowing-related meteorological factors on grain filling, key starch synthesis enzymes, and yield formation. Here, we aimed to quantify the regulatory effects of sowing date on grain filling, key starch synthesis enzymes, KW, and yield by conducting 2-year sowing date experiments on different cultivars of fresh maize. The effects of light, temperature, and precipitation at different sowing dates on the kernel establishment and yield of fresh maize were analysed. The planting area of fresh maize in Guizhou has been increasing year by year, this is the first study to investigate the impact of sowing date on the production of fresh maize in Guiyang City, and it can provide scientific theoretical guidance for suitable sowing, high yield, and efficient cultivation of fresh maize.

MATERIAL AND METHODS

Experimental materials and location. Three common local fresh maize cultivars that present wide adaptability and high and stable yields were used as the test material: Wan Nuo 2000, bred by the Hebei Huasui Kernels Company; Nongke Nuo 336, bred by the Maize Research Center of Beijing Academy of Agricultural and Forestry Sciences; and Caitian Nuo 6, bred by the Jingzhou District Hengfeng Kernels Development Center. These three cultivars are classic cultivars widely planted in southern China. Among them, Wan Nuo 2000 is waxy maize, Nongke Nuo 336 and Caitian Nuo 6 are sweet-waxy maize.

This experiment was conducted at Anliu Town, Guiyang Qingzhen City, China (26°8'10"N, 106°3'48"E) from 2021–2022. The average elevation of the experimental field was 1 189 m a.s.l., and the area is characterised by a subtropical monsoonal humid climate. A high-performance small automatic weather station (WS-GP2) was installed in the field to monitor precipitation and temperature during the reproductive period of fresh maize, as shown in Figure 1. The soil texture at the experimental site is loam by the WRB system (IUSS Working Group WRB 2006), with a composition of 40% sand, 44% silt, and 16% clay. The soil (0–20 cm soil layer) contained a pH of 6.4, 12.43 g/kg of organic carbon, 2.19 g/kg of total nitrogen, 0.74 g/kg of total phosphorous, 11.03 g/kg of total potassium, 185.76 mg/kg of hydrolysable nitrogen, 7.82 mg/kg of available phosphorus (P_{Olsen}), and 85.33 mg/kg of available potassium (K_{NH_4OAc}), respectively.

Experimental design. A two-factor split-zone design was adopted, with the main zone being the sowing date. Six sowing dates were set: B1 – March 10;

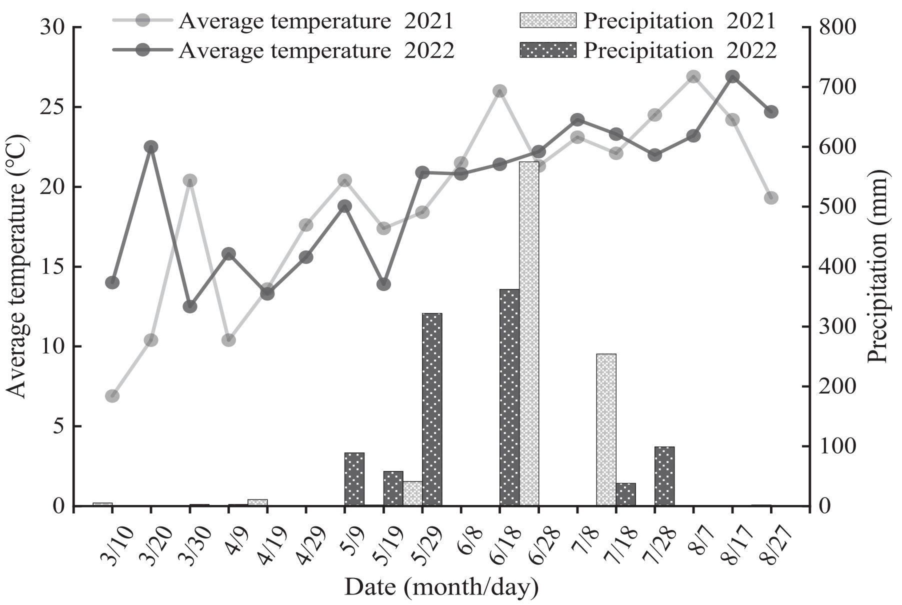

Figure 1. Average daily temperature and precipitation during the growth period

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B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19, and B6 – April 29. The secondary zone was the maize cultivars: A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; and A3 – Caitian Nuo 6. A wide spacing of 0.8 m was set between rows, and a narrow spacing of 0.6 m was set between plants. The plot area was 21 m^2 (6 × 3.5 m), and the planting density was 47 622 plants/ha. We applied 750 kg/ha of compound fertiliser (N:P:K = 15:15:15) as the base fertiliser and 300 kg/ha of urea as a follow-up fertiliser at the jointing and flare opening stages. Three replications were performed. Other cultivation measures were consistent with local practices.

Projects and measurement methods

Investigation of growth processes, effective accumulated temperature, and light use efficiency. The sowing, silking, and harvest dates of each sowing date were recorded using the method described by Peng et al. (2022) and Lu et al. (2015).

The effective accumulated temperature (GDD) of each growth stage was calculated using the method described by Yu et al. (2013).

$$GDD\ (°C \times d) = \sum_i^n [((T_{max} + T_{min})/2) - T_{base}]$$

T_{max} and T_{min} are the maximum and minimum temperatures on day *i*, and T_{base}= 10 °C.

The light use efficiency (LUE) for the whole growth period was calculated using the method described by Huang et al. (2018).

LUE (%) = (dry weight of kernels per unit area × × maize DM calorific value 18 070/total light radiation during the same period) × 100%

Number of endosperm cells. After silking, three ears were randomly selected from each plot every 5 days and brought back to the laboratory at low temperatures in ice boxes. Fifteen middle kernels were collected from each ear, immediately fixed in Carnoy's fluid, and stored at 22–24 °C. Endosperm cells were counted as described by Ren et al. (2016). The kernels were first washed with water for de-ethanolisation, treated with 1 mol/L HCl for approximately 1 h, placed in Markov reagents for 1–2 h, sealed in the dark, centrifuged, and filtered. The samples were then digested with 1 mL of 0.5% cellulase (pH = 5.5, prepared with 0.1 mol/L acetate buffer) at 40 °C for approximately 4 h. The digestion solution was diluted to 100 mL, and 5 mL was aspirated and filtered by extraction using a 0.45 μm microporous membrane. Finally, the cells were observed under a 10-objective optical microscope, and the number of red-stained nuclei was used to count the endosperm cells. The number of endosperm cells was calculated using the following equation:

Number of endosperm cells = (average number of cells in the field of view × (area of the filter membrane/field of view) × (volume of the digestion solution/volume of suspension cytosol used for extraction))/number of digested kernels = (average number of cells in the field of view × 3 125)/number of digested kernels.

Grain filling parameters. After the kernel DM was weighted, the grain filling process was fitted with Richards' equation based on the method of Fu et al. (2020), with the number of days after silking as the independent variable and KW as the dependent variable, and the grain filling model and related characteristic parameters were obtained.

$$W\ (g) = A / (1 + Be^{-Kt})^{1/N} \quad (1)$$

Where: W – KW; A – theoretical maximum kernel dry weight; t – number of days after silking, and B, N, K – equation parameters.

The first-order derivative of Eq. (1) gives the grain filling rate equation.

$$V\ (g/d) = AKBe^{-Kt} / [N(1 + Be^{-Kt})^{(1 + 1/N)}] \quad (2)$$

The second-order derivation of Eq. (2) gives the time when the kernels reach their maximum filling rate.

$$T_{max}\ (d) = (\ln B - \ln N)/K \quad (3)$$

Substituting Eq. (3) into Eq. (2) gives the maximum filling rate.

$$V_{max}\ (g/d) = AK\ (1 + N)^{-(1 + N)/N} \quad (4)$$

Substituting Eq. (4) into Eq. (1) gives the DM accumulation at the maximum grain filling rate.

$$W_{max}(g) = A(1 + N)^{-1/N} \quad (5)$$

Integrating Eq. (2) gives the average grain filling rate:

$$V_a\ (g/d) = AK/[2(N + 2)] \quad (6)$$

The active growth period D is the ratio of the theoretical maximum kernel dry weight to the average grain filling rate.

$$D\ (d) = A/ V_a = [2(N + 2)]/K \quad (7)$$

Enzyme assay. After silking, three ears were randomly collected from each plot every 5 days, brought back to the laboratory at low temperature in ice boxes, and stored in an ultra-low temperature refrigerator at –80 °C. The middle kernels were collected, and

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the activities of sucrose synthase (SS), ADP-glucose pyrophosphorylase (AGPase), starch branching enzyme (SBE), and starch debranching enzyme (DBE) were determined.

In 2021, the four enzymes were assessed as follows: 0.1 g of the sample was weighed, 1 mL of extraction solution was added, the solution was homogenised in an ice bath and centrifuged at 4 °C for 10 min at 12 000 × *g*, and the supernatant was collected as the crude enzyme solution and placed on ice until measurement. The activities of the four enzymes were determined using a commercial kit (Beijing Box Bio, Beijing, China).

In 2022, the four enzymes were assessed by the preparation of chemical reagent: 0.5 g of the sample was weighed, 2 mL of the extract (containing 50 mmol/L Hepes-NaOH, 5 mmol/L EDTA, 1 mmol/L DTT, 2 mmol/L KCl, 1% polyvinylpyrrolidone at pH = 7.5) was added, the solution was homogenised in an ice bath; the homogenate was then poured into a 10 mL centrifugal tube, the mortar was rinsed twice with 6 mL of extraction solution, the rinsing solution was poured into the centrifuge tube and centrifuged for 15 min at 15 000 × *g* at 4 °C, and the supernatant was used as the crude enzyme solution and placed on ice until measurement. The activities of the four enzymes were determined according to the method described by Nakamura et al. (1989).

Hundred kernel weight. After silking, three ears were randomly taken from each plot every 5 days and brought back to the laboratory at low temperatures in ice boxes. The dry weight was determined by taking a hundred randomly selected kernels after killing them out at 105 °C for 30 min and drying them at 80 °C for 48 h to constant weight; the average value of three determinations was taken.

Yield. During the suitable harvesting period of fresh maize (about 24 days after silking) (Lu et al. 2015), the fresh ears were harvested and weighed in plots, and then the yield per hectare was calculated according to the plot yield.

Statistical analyses. All analyses were conducted by using Microsoft Excel 2016 (Redmond, USA), analysis of variance and correlation tests were performed using IBM SPSS Statistics 22.0 (SPSS Inc., Chicago, USA), the Richards model of Curve Expert 1.4 (Boster Inc., Beijing, China) was used to fit the grain filling process and each grain filling parameter was calculated, and figures were drafted by Origin 2021 (Origin Software, Inc., Northampton, USA).

Table 1. Growth period and meteorological conditions at different sowing dates

Year	Treatment	Ds	Df	Dh	Te	LUE	ST	TA	SL	RA	SR
			(days)		(°C × d)	(%)	(°C × d)	(°C)	(h)	($MJ/m^2/d$)	(mm)
2021	B1	83^{a}	27^{a}	110^{a}	840.20^{c}	23.57^{c}	321.60^{a}	21.93^{d}	97.30^{a}	12.17^{b}	134.87^{a}
	B2	83^{a}	25^{a}	108^{a}	888.13^{b}	22.61^{c}	327.17^{a}	23.08^{c}	60.23^{c}	13.62^{a}	160.70^{a}
	B3	76^{b}	24^{a}	100^{b}	817.50^{c}	25.01^{bc}	314.80^{a}	23.30^{bc}	57.90^{c}	13.24^{a}	140.13^{a}
	B4	69^{c}	25^{a}	94^{c}	910.00^{b}	29.69^{a}	331.70^{a}	23.46^{b}	82.73^{b}	11.57^{c}	133.50^{a}
	B5	62^{d}	24^{a}	86^{d}	918.50^{b}	30.19^{a}	325.50^{a}	23.56^{ab}	82.10^{b}	11.37^{c}	133.00^{a}
	B6	60^{d}	25^{a}	85^{d}	967.03^{a}	28.34^{ab}	341.53^{a}	23.85^{a}	98.73^{a}	11.92^{bc}	175.13^{a}
2022	B1	87^{a}	25^{a}	112^{a}	831.67^{d}	22.51^{d}	296.67^{c}	21.71^{d}	46.83^{c}	10.22^{d}	117.43^{a}
	B2	81^{b}	25^{a}	106^{b}	799.63^{d}	25.63^{c}	307.87^{c}	22.16^{d}	68.03^{c}	11.75^{c}	98.10^{ab}
	B3	78^{c}	25^{a}	103^{c}	852.73^{cd}	25.73^{bc}	333.83^{b}	23.35^{c}	102.13^{b}	14.31^{b}	79.73^{b}
	B4	73^{d}	24^{ab}	97^{d}	913.43^{b}	28.18^{ab}	351.13^{ab}	24.42^{b}	136.50^{a}	16.65^{a}	45.07^{c}
	B5	66^{e}	23^{b}	89^{e}	905.70^{bc}	28.73^{a}	336.50^{b}	24.67^{ab}	149.10^{a}	17.99^{a}	32.40^{c}
	B6	68^{e}	24^{ab}	92^{e}	$1\,013.77^{a}$	26.67^{abc}	369.67^{a}	25.24^{a}	158.67^{a}	17.96^{a}	82.10^{b}

Ds – days of the sowing-silking period; Df – days of grain filling period; Dh – days of the whole growth period; Te – effective cumulative temperature of the whole growth period; LUE – light energy utilisation during the whole growth period; ST – effective cumulative temperature; TA – average temperature; SL – sunshine hours; RA – average daily radiation; SR – precipitation in the grain filling period. The values of the growth period and meteorological factors were analysed based on the average of three cultivars. Within a year means not sharing a common letter is significantly different among sowing dates at $P < 0.05$. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29

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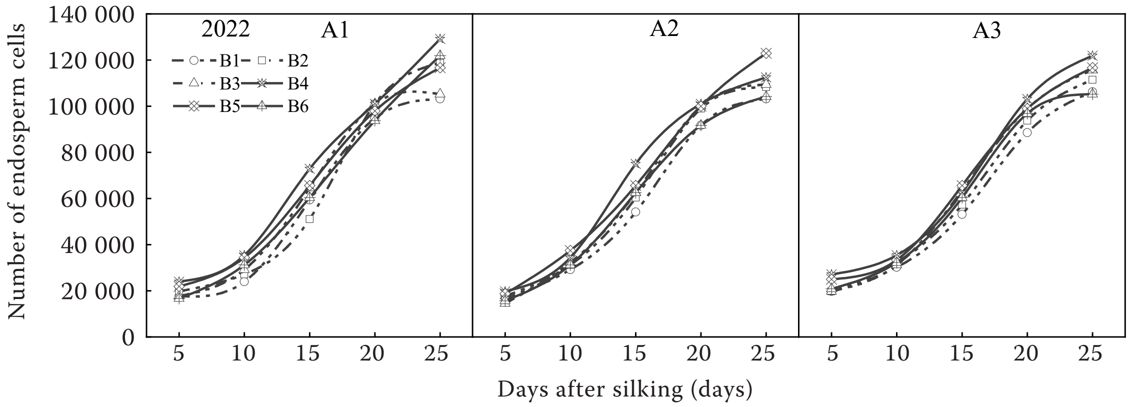

Figure 2. Proliferation of endosperm cells at different sowing dates and cultivars. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

RESULTS

Growth period and meteorological conditions. The growth period and meteorological conditions of fresh maize differed significantly between sowing dates (Table 1). Except for the B6 in 2022, Ds and Dh showed a shortening trend with a delay in the sowing date. This indicates that an appropriate delay in sowing is beneficial for accelerating the vegetative stages of growth in fresh maize, which may be related to the fact that Te, LUE, and TA gradually increase with a delay in the sowing date. In different years, precipitation and sowing dates showed irregularities; the difference in SR in 2021 was not significant and was higher than that in 2022 for all treatments. However, except for the B1, the SL and TA values in 2021 were lower than those in 2022, which was possibly caused by the higher SR in 2021. In 2022, except for B1 and B2, the Te, ST, and RA values were higher than those in 2021. The Ds and Dh values in 2022 were generally higher than those in 2021, whereas the Df value was generally lower than in 2021. This suggests that the growth process of fresh maize was significantly affected by the sowing date, and the effect varied over the years.

Number of endosperm cells. Endosperm cells showed slow-fast-slow "S"-shaped growth dynamics with an increase in the number of days after silking (Figure 2). At 5–10 days after silking, the difference in the number of endosperm cells between sowing dates was not obvious, although with a continuous increase in the number of days after silking, the difference in the number of endosperm cells gradually increased. At 25 days after silking, cultivars A1 and A3 had the highest number of endosperm cells for B4, at 129 166.67 and 121 875.00, which were 25.25% and 15.84% higher than those of the lowest sowing dates, respectively. Cultivar A2 had the highest number of endosperm cells for B5, at 122 916.67, which was 19.19% higher than the lowest sowing date. This revealed that the proliferation of endosperm cells was affected by sowing date and cultivar. All three fresh maize cultivars exhibited more endosperm cells at B4 and B5, whereas a decreasing trend was observed at B6, indicating that an appropriate delay in sowing date was beneficial to the proliferation of endosperm cells; however, the opposite effect occurred when sowing occurred too late.

Grain filling rate. The dynamics of the grain filling rate fitted by the Richards model displayed a single-peaked trend with an initial increase and then decreased for all treatments; however, differences were observed in the peak values under different sowing dates (Figure 3). In 2021, the grain filling rates of A1, A2, and A3 peaked at B1, B6, and B1, which were 109.96, 65.08, and 45.94% higher than those of the lowest sowing dates, respectively. In 2022, the grain filling rates of A1, A2, and A3 peaked at B1, B5, and B5, which were 66.33, 44.21, and 70.03% higher than those of the lowest sowing dates, respectively. The average grain filling rates of cultivars A1 and A3 were higher than those of cultivar A2. The difference in the grain filling rate of all cultivars was not obvious at 5–15 days after silking, whereas it showed apparent diversity and reached a maximum at 15–25 days after silking at different sowing dates.

Key starch synthesis enzyme activities. Both SS (Figure 4A) and AGPase (Figure 4B) showed a single-peak variation with grain filling, and both reached

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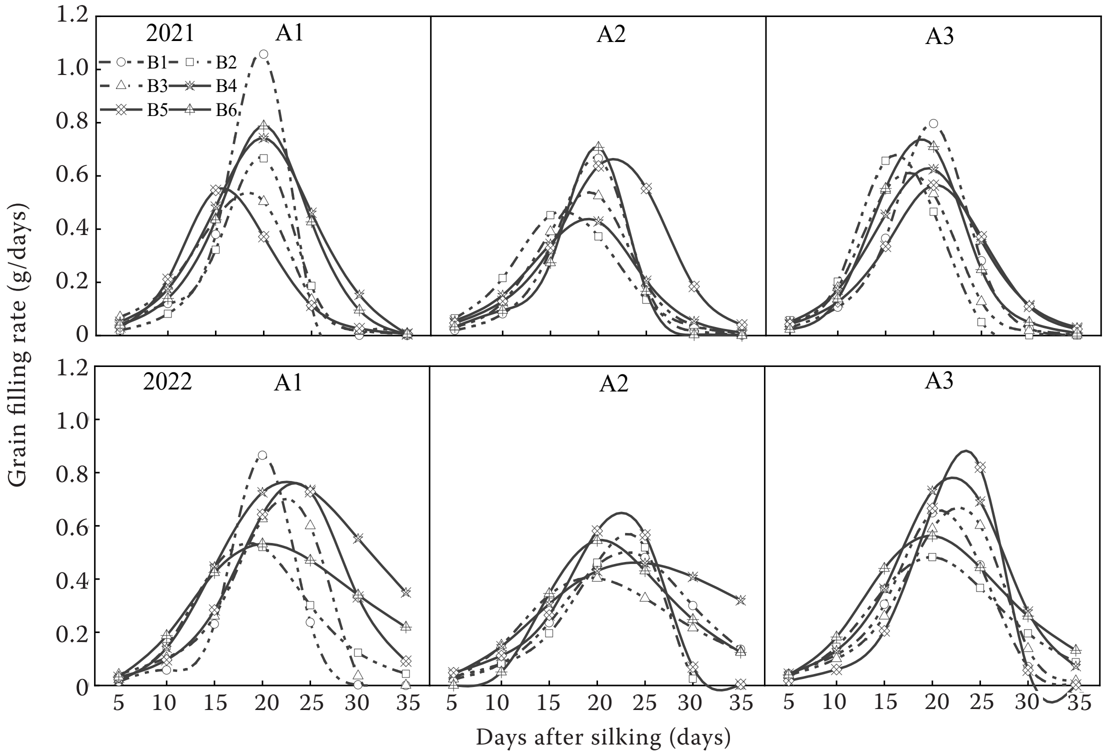

Figure 3. Grain filling rate at different sowing dates and cultivars. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

their peaks 20 days after silking. The SS activity in 2021 was significantly lower than that in 2022, whereas the gap in AGPase activity between the two years was not significant. The SS and AGPase of A3 were slightly higher than those of A1 and A2. The AGPase of A1, A2, and A3 peaked at B1, B6, and B6 in 2021, which were 34.48, 7.67, and 15.02% higher than those of the lowest sowing dates, respectively. The AGPase of cultivars A1, A2, and A3 peaked at B4, B5, and B6 in 2022, and the values were 17.33, 19.17, and 11.58% higher than those of the lowest sowing dates, respectively. The SS of A1, A2, and A3 peaked at B6, B5, and B5 in 2021, and the values were 36.94, 18.01, and 18.83% higher than those of the lowest sowing dates, respectively. The SS of A1, A2, and A3 peaked at B2, B3, and B2 in 2022, and the values were 38.82, 46.09, and 37.13% higher than those of the lowest sowing dates, respectively.

SBE (Figure 4C) and DBE (Figure 4D) generally showed single-peaked curves, although the peak time was not the same. SBE activity peaked at 15–20 days after silking, and discrepancies were observed between the different cultivars and sowing dates. Except for B1 in 2022, the SBE of A3 peaked 20 days after silking. The SBE of A1, A2, and A3 peaked at B6, B5, and B5 in 2021, and the values were 7.68, 20.31, and 6.03% higher than those of the lowest sowing dates, respectively. The SBE of A1, A2, and A3 peaked at B1, B5, and B5 in 2022, and the values were 14.43, 15.30, and 6.10% higher than those of the lowest sowing dates, respectively. The DBE was significantly higher in 2021 than in 2022, and the peak DBE in 2021 (10–15 days after silking) was earlier than that in 2022 (20 days after silking). In 2021, the DBE of A1, A2, and A3 peaked at B4, B1, and B3, and the values were 57.77, 56.97, and 30.28% higher than those of the lowest sowing dates, respectively. The DBE of A1, A2, and A3 peaked at B4, B2, and B5 in 2022, which were 25.71, 27.44, and 20.41% higher than those of the lowest sowing date, respectively.

Further analysis of the activities of different enzymes (Table 2) indicated that the main factors affecting the activities of the four enzymes were different. SS and DBE were mainly affected by cultivar and year in a highly significant way; AGPase only showed significant differences based on year, while SBE was significantly influenced by sowing date, cultivar, and year.

Hundred kernels weight. The dynamics of DM accumulation in the kernels showed a slow-fast-slow "S"-shaped trend and a continuous increase in DM was observed after silking (Figure 5). At 5–15 days

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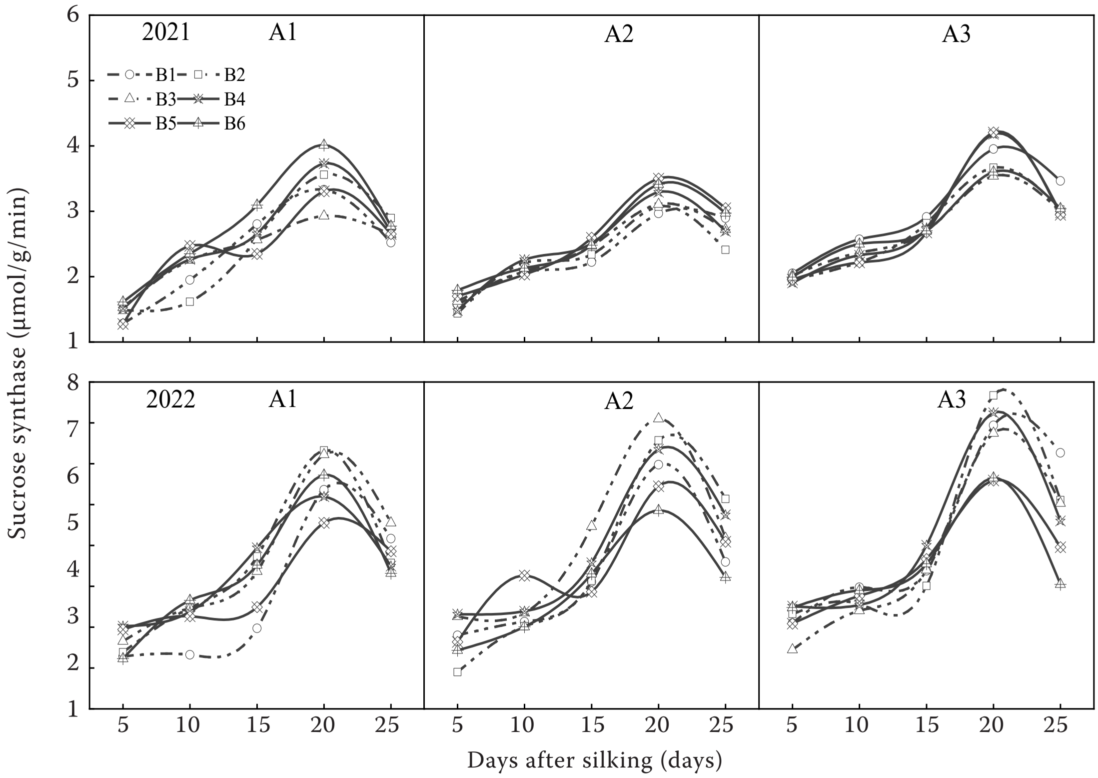

Figure 4A. Changes of sucrose synthase at different sowing dates and cultivars. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

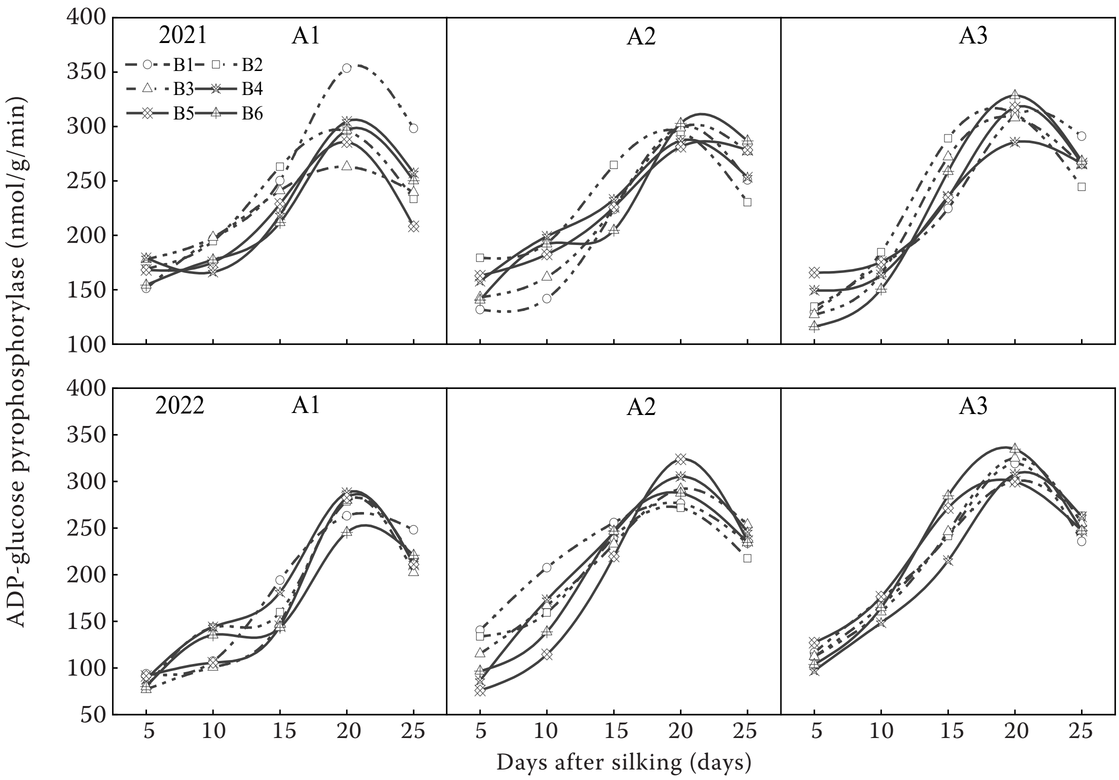

Figure 4B. Changes of ADP-glucose pyrophosphorylase (AGPase) at different sowing dates and cultivars. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

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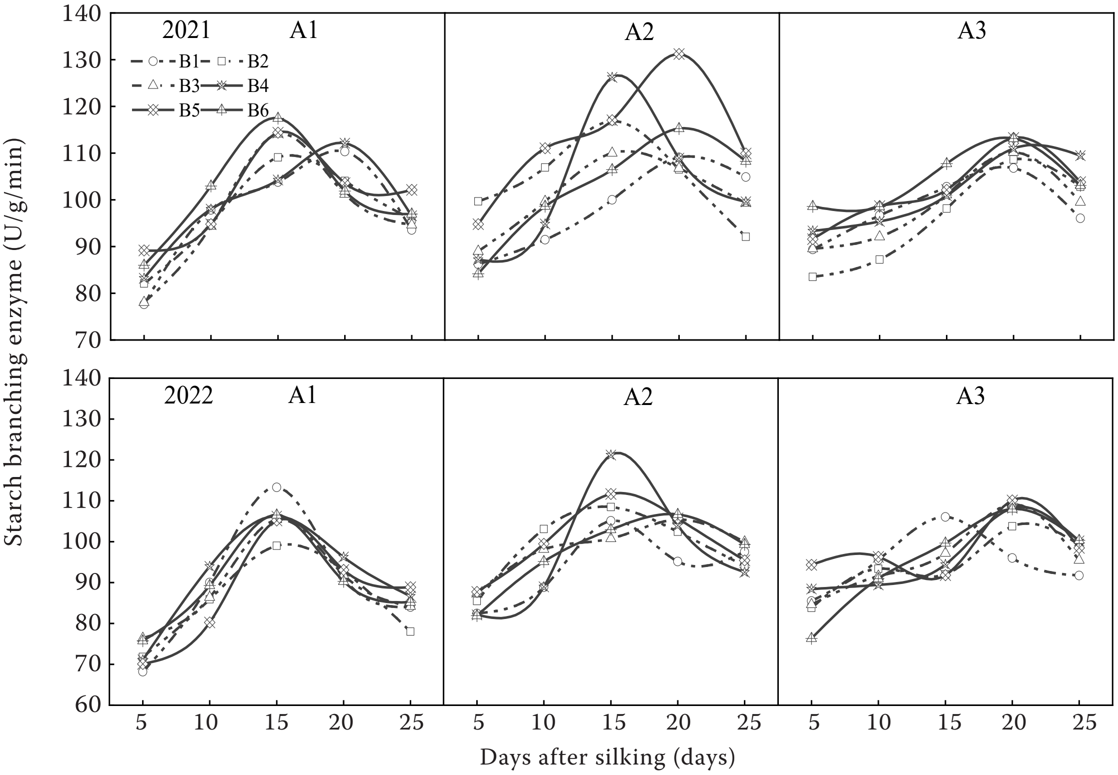

Figure 4C. Changes of starch branching enzyme (SBE) at different sowing dates and cultivars. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

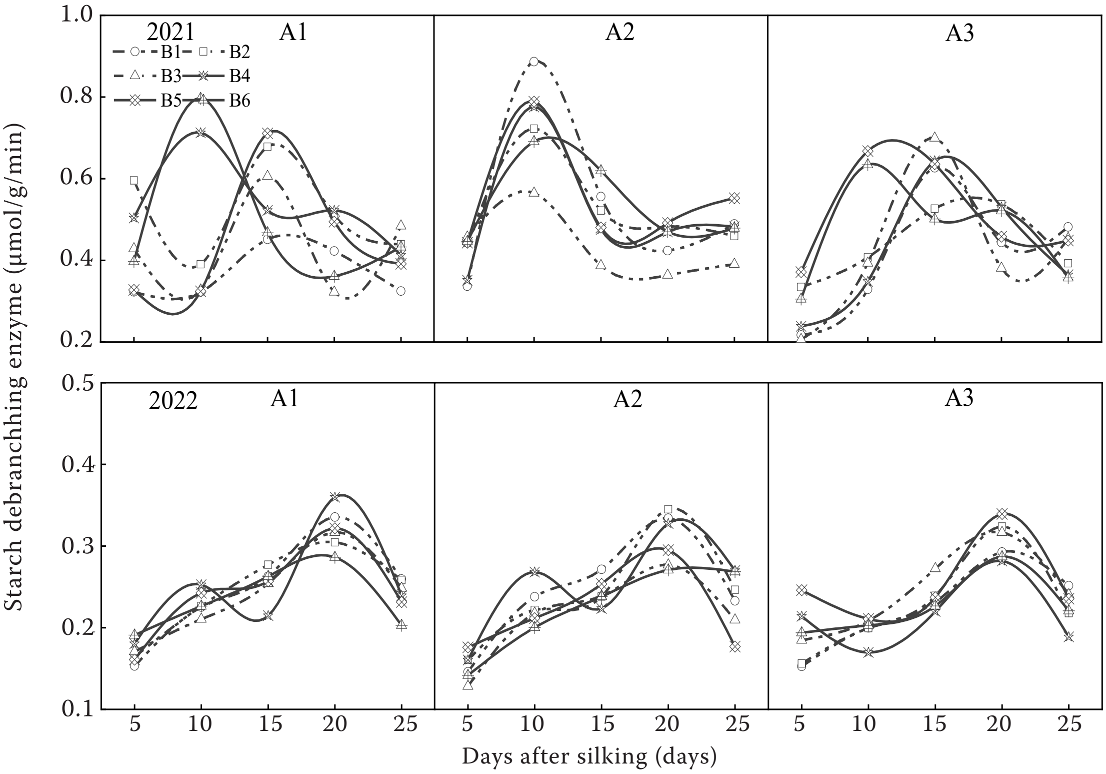

Figure 4D. Changes of starch debranchhing enzyme (SBE) at different sowing dates and cultivars. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

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Table 2. Variance analysis of different enzyme activities

Source of variation	SS	AGPase	SBE	DBE
Sowing date	ns	ns	**	ns
Cultivar	**	ns	**	**
Year	**	**	**	**
Sowing date × cultivar	ns	ns	ns	ns
Sowing date × year	ns	ns	ns	ns
Cultivar × year	**	ns	*	ns

SS – sucrose synthase; AGPase – ADP-glucose pyrophosphorylase; SBE – starch branching enzyme; DBE – starch debranching enzyme; *$P < 0.05$; **$P < 0.01$; ns – not significant

after silking, the accumulation of DM was slow and mainly focused on the formation of kernels. At 15–25 days after silking, the DM increased sharply, which corresponded to the stage with significant increases in KW. At 25–35 days after silking, the increase in DM slowly stabilised. At 35 days after silking, the highest KW values of A1, A2, and A3 in 2021 were 61.51, 51.23, and 23.45% higher than those of the lowest sowing dates, respectively, while the highest KW of A1, A2, and A3 in 2022 were 53.18, 38.64, and 40.01% higher than the lowest sowing dates, respectively. The KW of A1 and A3 was higher than that of A2. All cultivars showed maximum KW in B4, B5, and B6, indicating that a delayed sowing date is beneficial for the accumulation of DM in the kernels.

Yield. Varying degrees of yield gaps were observed between the different sowing dates and cultivars (Figure 6). There was a significant difference in yield between A2 and A3 in 2021, while there was a significant difference between A2 and A1 and A2 and A3 in 2022. The yields of all cultivars for B4, B5, and B6 in 2021 were significantly higher than those in the previous three sowing dates. However, the difference in the yield of each cultivar for B4, B5, and B6 was not significant. In 2021, the highest yield of A1 was 23 642.34 kg/ha at B6, while those of A2 and A3 were 25 765.46 kg/ha and 26 326.66 kg/ha at B5, respectively. In 2022, the highest yield of A2 was 17 785.88 kg/ha at B4, while those of A1 and A3 were 18 804.72 kg/ha and 18 788.07 kg/ha at B2, respectively; however, significant differences were not observed compared to that at B4, B5, and B6. The yields of B4, B5, and B6 in 2022 were significantly lower than those in 2021, possibly due to the

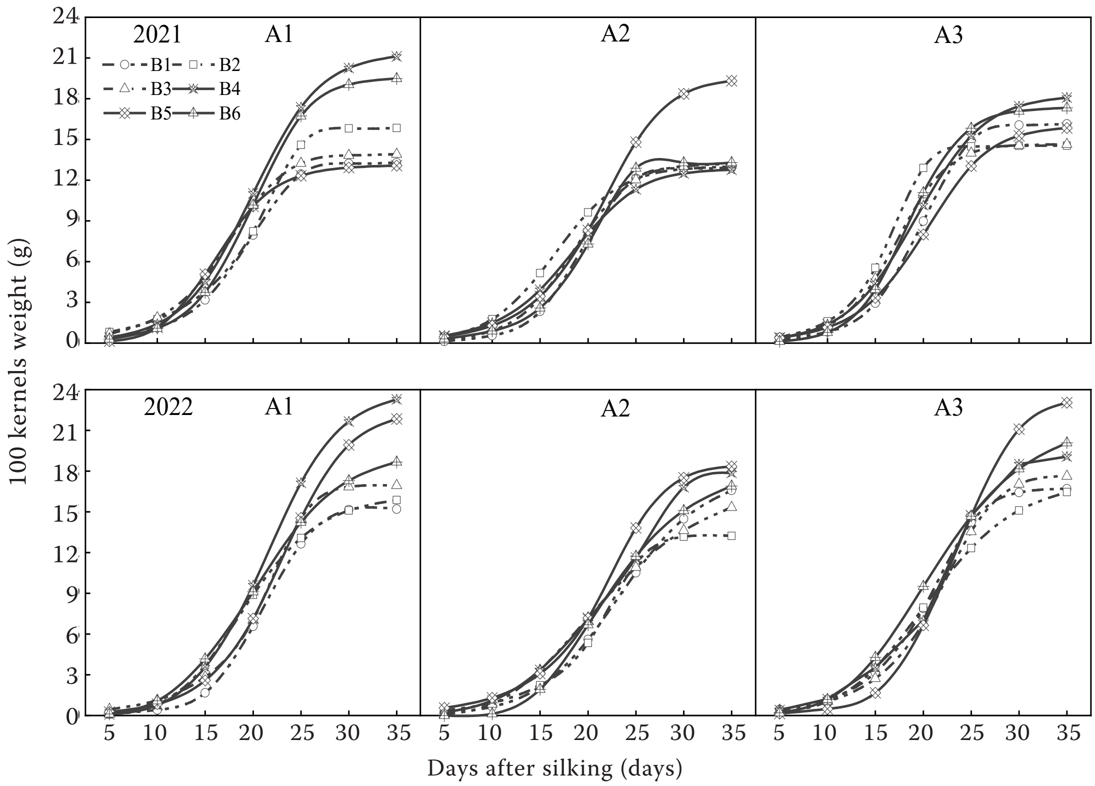

Figure 5. Hundred kernels weight (dry weight) at different sowing dates and cultivars. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

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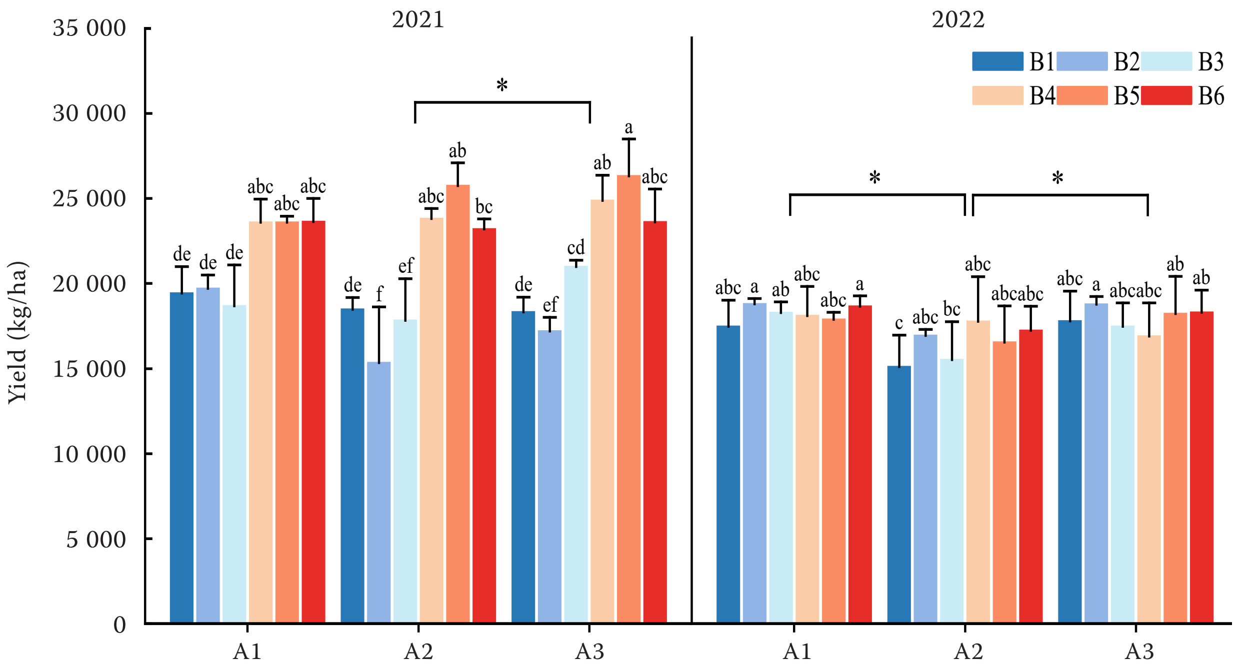

Figure 6. Fresh maize yield at different sowing dates and cultivars. Within a year, bars with different letters significantly differ at $P < 0.05$; $^*P < 0.05$. B1 – March 10; B2 – March 20; B3 – March 30; B4 – April 9; B5 – April 19; B6 – April 29; A1 – Wan Nuo 2000; A2 – Nongke Nuo 336; A3 – Caitian Nuo 6

higher TA and SL and lower SR of the three sowing dates in 2022. This implies that interannual climatic conditions also play an important regulatory role in the final yield.

Relationships among yield, grain filling characteristics, enzyme activities and meteorological conditions. The correlations among yield, grain filling characteristics, enzyme activities and meteorological conditions are shown in Figure 7. Yield was not significantly correlated with ST, TA, or SL but was highly significantly positively correlated with SR and significantly negatively correlated with RA; this implies that light, precipitation, and enzyme activities are important factors for yield. A highly significant positive correlation was observed between the number of endosperm cells and KW, ST, TA, SL, and RA, although the correlation with SR was not significant. The KW was significantly positively correlated with V_a and V_{max}, significantly positively correlated with SS, and significantly negatively correlated with AGPase and DBE levels. This suggests that KW is mainly determined by the grain filling rate and regulated by starch synthesis enzymes. V_a and V_{max} were significantly positively correlated with SL and RA, whereas D was significantly negatively correlated with SR. This indicates that the effect of light on the grain filling rate was more significant than that of temperature and precipitation, and precipitation was the main factor affecting the duration of grain filling. V_a and V_{max} showed highly significant negative correlations with D, indicating that an increase in the grain filling rate shortened the grain filling duration. AGPase and DBE were significantly negatively correlated with SL and RA, SS was significantly negatively correlated with SR, and SBE and DBE were significantly positively correlated with SR. D was significantly positively correlated with SS and negatively correlated with DBE, indicating that starch synthesis enzymes mainly regulate grain filling duration. The correlations between the four key enzymes reached significance or were highly significant. SS was negatively correlated with the other three enzymes, while AGPase, SBE, and DBE were positively correlated.

DISCUSSION

Effect of sowing date on the grain filling and key enzyme activities of starch synthesis. Meteorological conditions at different sowing dates prominently affect photosynthetic characteristics and grain filling, and suitable sowing adjustments can regulate the allocation of light, temperature, and precipitation resources during the crop growth period to a great

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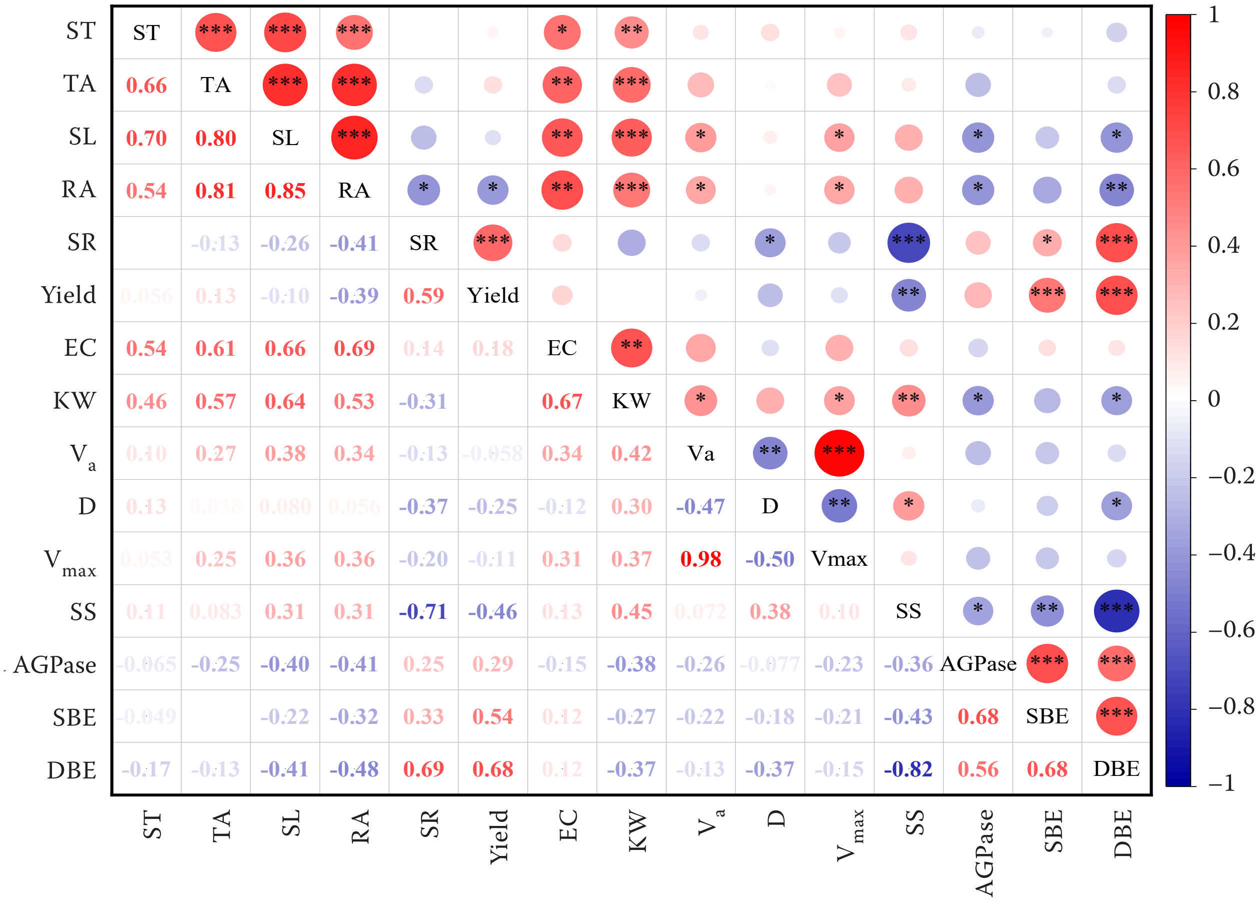

Figure 7. Correlation analysis of yield, grain-filling characteristics, enzyme activities and meteorological conditions during the grain-filling period. ST – effective cumulative temperature; TA – average temperature; SL – sunshine hours; RA – average daily radiation; SR – precipitation in the grain filling period; EC – number of endosperm cells; KW – hundred kernel weight; V_a – average grain filling rate; D – active growth period; V_{max} – maximum filling rate; SS – sucrose synthase; AGPase – ADP-glucose pyrophosphorylase; SBE – starch branching enzyme; DBE – starch debranching enzyme. The enzyme activity value was analysed based on the average of five sampling dates. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

extent and promote synergistic improvements in crop yield potential and resource use efficiency (Chen et al. 2020). Maize is a short-day crop, and delayed sowing accelerates plant development and shortens growth (Peng et al. 2022). Our results found that delayed sowing significantly shortened the Dh of fresh maize, and the difference in Dh between sowing dates was up to 25 days and 23 days in 2021 and 2022, respectively. However, delayed sowing had little effect on Df, which indicated that delayed sowing accelerated the vegetative stage of fresh maize. The maize kernel endosperm consists of a large number of endosperm cells, which is the most important grain component for determining grain yield (Guo et al. 2021); it accounts for 80–85% of the KW (Ren et al. 2016). Furthermore, the number of endosperm cells was significantly correlated with kernel size and KW. Endosperm cell proliferation increases the storage capacity of the kernels and directly determines the ability of endosperm to accumulate DM (Ren et al. 2016, Sun and Zhang 2023). Delayed sowing increased the proliferation of endosperm cells, and the number of endosperm cells was significantly positively correlated with KW, with a correlation coefficient of 0.674. This is consistent with the results of previous studies and may be related to the ability of endosperm cells to increase the uptake and transformation of photosynthetic products by increasing the capacity of the kernel reservoir. Additionally, delayed sowing accelerated the grain filling rate in our experiment; although the highest grain filling rate was observed for A1 at B1, it was more stable at B4, B5, and B6 for all cultivars. The maximum grain filling rate differed depending on the cultivar, indicating that

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various characteristics also affected the grain filling of fresh maize. SL and RA were significantly positively correlated with V_a and V_{max}, whereas SR was significantly negatively correlated with D, indicating that discrepancies in meteorological conditions were the main factors affecting grain filling.

Starch content is a primary determinant of yield in major cereal crops, such as rice, maize, and wheat (Ahmed 2008), and starch accumulation during the grain-filling period is highly dependent on the activities and synergistic effects of key starch synthesis enzymes, such as SS, AGPase, SBE, and DBE (Wang et al. 2014, Iqbal et al. 2021). An in-depth investigation of the effects of light and temperature resources on the activities of enzymes related to carbon assimilation at different sowing dates can aid in crop enzymatic regulation and genetic improvement. The enhanced activity of SS can effectively increase reservoir capacity and is a good predictor of reservoir strength (Iqbal et al. 2021, Zhang et al. 2021). AGPase is generally considered to be the rate-limiting enzyme in kernel starch synthesis (Maddelein et al. 1994, Zhang et al. 2007b), and its activity is related to the rate and final content of starch synthesis. Furthermore, SBE and DBE mainly affect starch quality (Wang et al. 2014). Unsuitable climatic conditions, such as low temperature (Yang et al. 2021), low light (Sun and Zhang 2023), and drought (Guo et al. 2021), can reduce the activity of starch synthesis enzymes during the grain-filling period to varying degrees, thereby limiting the accumulation of kernel starch and eventually affecting the grain filling and yield formation of fresh maize (Guo et al. 2021, Sun and Zhang 2023). AGPase and DBE were significantly negatively correlated with SL and RA; SS was highly significantly negatively correlated with SR; and SBE and DBE were significantly positively correlated with SR, thus demonstrating that light and precipitation during the grain filling period significantly affected the activities of key starch synthesis enzymes. SBE activity showed highly significant diversity between sowing dates, whereas all four enzyme activities showed highly significant diversity between years, which may be because the climatic differences between years were greater than those between sowing dates. SBE activity could be greater at higher temperatures during grain filling (Wang et al. 2021b), which was supported by our findings. The high expression of starch synthesis genes during grain filling significantly enhances the activity of starch synthesis enzymes (Iqbal et al. 2021), and the different enzymes coordinate with each other and function as functional protein complexes in the process of kernel starch accumulation (Zhang et al. 2007b); this explains the highly significant positive correlation between the four enzymes. Different enzymes play distinctive roles in maize growth (Yang et al. 2001), resulting in various peak enzyme activities. SBE and DBE peaked at inconsistent times in different years and on different sowing dates, implying that these two enzymes are more susceptible to external meteorological factors change. Our study validated the important role of climatic research in regulating key starch synthesis enzymes and showed that a suitable sowing date is an important cultivation measure to ensure grain filling under the most optimal climatic conditions and maintain higher enzyme activities. The mechanisms of enzyme activity regulation by climatic conditions at different sowing dates are not fully understood, and to effectively improve the yield and quality of fresh maize, the environmental factors controlling the activities of various enzymes and the interactions between these enzymes need to be further determined.

Effect of sowing date on kernel weight and yield. Fluctuations in meteorological conditions are among the main factors affecting maize production, and climate change, with increasing temperature, decreasing solar radiation, and decreasing precipitation represent the main factors underlying decreases in maize yield (Huang et al. 2018, He et al. 2020). Adapting to and fully exploiting the climate conditions of different regions can increase crop yields and represent an important issue in current research (He et al. 2020). In rice, the distinct average daily temperature between sowing dates results in significant differences in yield and quality (Tu et al. 2022). The optimum average daily temperature for grain filling of maize is 22–24 °C, and unsuitable light and temperature conditions can also affect grain filling and yield (Yang et al. 2014, Peng et al. 2022). Rain-fed crops are highly sensitive to climate change. Precipitation during the growing season significantly affects maize yield, and interannual precipitation uncertainty is a serious problem threatening maize production (Abdisa et al. 2022). The TA and SL values at B4, B5, and B6 in 2022 were higher than those in 2021, and the SR value was lower than that in 2021, which may be the main meteorological reasons for the lower yield in the three sowing periods in 2022 compared with that in 2021. Research has shown that shortening the grain-filling period might lead to a decrease in

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yield, and the magnitude of the yield change was consistent with that of the grain-filling period (Lv et al. 2020). Other studies have suggested that grain filling duration is easily limited by local ecological conditions and planting density and showed that maximising the grain filling rate and accelerating the accumulation of assimilates in kernels have a more significant effect on yield improvement than other changes (Wang et al. 2021a). Our experiment found that delayed sowing significantly shortened the vegetative stages rather than the reproductive stages and revealed that the yield showed an increasing trend. This is probably because the meteorological conditions in the grain filling period after the appropriate delay in the sowing date were more favourable for the increase in grain filling and accumulation of KW. KW was significantly positively correlated with ST, TA, SL, and RA, and yield was significantly positively correlated with SR, further demonstrating the importance of meteorological factors. To effectively respond to climate change and make more efficient use of climatic resources for fresh maize production, the matching patterns between meteorological factors and fresh maize yield at different sowing dates should be further explored.

Adjusting the sowing date is an important cultivation measure, and previous studies have suggested that delaying sowing would expose the crop to unfavourable climatic conditions for grain filling, which would reduce the rate and intensity of graining and lead to lower KW and yield (Bonelli et al. 2016, Martínez et al. 2017). However, our findings are not consistent with these previous results, as they showed that delayed sowing increases KW and yield to varying degrees, which may be related to the climatic conditions in different regions. The diversity in maize KW and yield between different sowing treatments was mainly influenced by the grain filling rate (Peng et al. 2022). Our results also demonstrated a significant positive correlation between KW and V_a and V_{max}, with correlation coefficients of 0.423 and 0.369, respectively. However, the effect on yield was limited, and yield was mainly regulated by the activity of starch synthesis enzymes. Starch synthesis requires the participation of multiple enzymes, and a reasonable cultivation system can effectively coordinate the activities of various enzymes during the grain-filling period, promote the development of kernels and starch accumulation, and affect KW and yield. Some studies concluded that the main climatic factors that affect crop yield in different years and ecological regions are the daily temperature range and accumulated photosynthetically active radiation (Hou et al. 2021). Our investigation further indicates that implementing an appropriate sowing date can lead to superior light, temperature, and precipitation conditions for the growth and grain filling of fresh maize, which results in significant increases (7.61–67.90%) in the final yield. Therefore, high-quality crop cultivars should be selected according to local conditions and matched with the most suitable sowing dates, which will regulate the relationship between light and temperature resources and crop growth and development to a greater extent; moreover, these effective cultivation measures will promote the synergistic advancement of fresh maize yield and natural resource utilisation efficiency (Chen et al. 2020).

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