Effects of High Temperature Stress During Grain Filling on Wheat Grain Filling and Mitigation by Foliar Sprays: Postprint

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Abstract

To address the issue of high temperature during the grain filling stage affecting wheat grain filling and yield in the North China wheat region, this study was conducted during two wheat growing seasons (2013-2014 and 2014-2015) using natural warming with field plastic sheds. Four high temperature stress treatments at different time periods during the grain filling stage were established as main treatments: in the two years, high temperature treatments were applied during 12-25 d, 12-16 d, 15-20 d, and 20-25 d after anthesis, and during 8-21 d, 8-12 d, 14-20 d, and 16-21 d after anthesis, respectively. Natural temperature without shed coverage served as the control (designated as A1, A2, A3, A4, and A5, with A5 being the control). Four foliar spray treatments—0.2% potassium dihydrogen phosphate, 0.05% zinc sulfate, water, and no spray—were used as sub-treatments (designated as B1, B2, B3, and B4, respectively). The study investigated the effects of high temperature treatments at different periods during the grain filling stage on wheat grain filling, the mitigating effects of different foliar sprays on high temperature stress, and conducted quantitative analysis of wheat grain filling characteristics under different treatments. The results showed that: (1) High temperature at different periods during the wheat grain filling stage caused yield reduction compared with natural temperature, with yield reduction ranges of 12.64%-15.34% and 2.04%-9.41% in the two experimental years, respectively. Treatment A1, which had the longest high temperature stress duration and earliest treatment timing, showed the greatest yield reduction, reaching an extremely significant level compared with control A5. The direct causes of yield reduction under high temperature were decreased grains per spike and reduced thousand-grain weight. In the two experimental years, grains per spike decreased by 0.71-5.45 and 1.73-3.00, respectively, and thousand-grain weight decreased by 1.28-3.41 g and 0.84-4.27 g, respectively. Based on model-simulated grain filling characteristics in the 2013-2014 season, high temperature treatments at different periods caused wheat to reach the first and second inflection points earlier. For A1-A4, the first inflection point was advanced by 0.29-0.75 d and the second inflection point by 0.22-1.42 d compared with the control. Therefore, high temperature treatment shortened the grain filling duration and reduced the average grain filling rate, ultimately leading to lower thousand-grain weight. (2) Foliar sprays had a mitigating effect on high temperature stress. In the two experimental years, foliar sprays increased yield by 3.08%-7.05% and 2.09%-3.52% compared with the no-spray control, respectively, and could alleviate to some extent the adverse effects of high temperature on grains per spike and thousand-grain weight. In the two experimental years, foliar sprays increased grains per spike by 1.04-2.30 and 0.95-2.01, respectively, and increased thousand-grain weight by 1.10-1.42 g and 0.60-0.89 g, respectively, with B1 showing the best effect. Based on analysis of grain filling numerical characteristics, foliar sprays delayed the time to reach the first and second inflection points. Different sprays delayed the time to the first inflection point by 0.48-0.98 d and the second inflection point by 0.32-0.98 d, extended the grain filling duration, and increased the average grain filling rate by 0.01-0.04 mg · grain ^{1} · d ^{1}, with B1 (potassium dihydrogen phosphate) showing the best effect. Therefore, foliar sprays can extend the wheat grain filling period, increase grains per spike and thousand-grain weight to varying degrees, and represent one of the effective measures for yield increase and disaster mitigation.

Full Text

Impact of High Temperature Stress on Grain Filling and the Mitigative Effect of Foliar Sprays During the Grain-Filling Stage of Wheat

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Abstract

To address the problem of high temperatures during the grain-filling stage affecting wheat grain filling and yield in the North China Plain wheat region, this study was conducted over two wheat growing seasons (2013-2014 and 2014-2015). Using a split-plot design, four high-temperature stress treatments were applied as main plots during different periods of the grain-filling stage. In 2013-2014, treatments were applied at 12-25 d, 12-16 d, 15-20 d, and 20-25 d after anthesis, while in 2014-2015 they were applied at 8-21 d, 8-12 d, 14-20 d, and 16-21 d after anthesis. Natural temperature without plastic covering served as the control (A1, A2, A3, A4, and A5, with A5 as the control). Subplot treatments consisted of three foliar sprays: 0.2% potassium dihydrogen phosphate (B1), 0.05% zinc sulfate (B2), water (B3), and a no-spray control (B4). The effects of high-temperature stress during different grain-filling periods on wheat grain filling and the mitigative effects of different foliar sprays were investigated, with quantitative analysis of wheat grain-filling characteristics under various treatments.

The results showed that: (1) High temperature during different periods of the grain-filling stage reduced wheat yield compared with natural temperature, with yield reductions of 12.64%–15.34% and 2.04%–9.41% in the two experimental years, respectively. Treatment A1, which had the longest duration and earliest timing of high-temperature stress, showed the greatest yield reduction, reaching extremely significant levels compared with control A5. The direct causes of yield loss under high temperature were reduced grain number per spike and decreased thousand-grain weight. Across the two years, grain number per spike decreased by 0.71–5.45 and 1.73–3.00 grains, respectively, while thousand-grain weight decreased by 1.28–3.41 g and 0.84–4.27 g, respectively. Based on model-simulated grain-filling characteristics from 2013–2014, high-temperature treatments during different periods advanced the first and second inflection points by 0.29–0.75 d and 0.22–1.42 d, respectively, compared with the control. Consequently, high-temperature treatments shortened the grain-filling duration and reduced the average grain-filling rate, ultimately leading to lower thousand-grain weight.

(2) Foliar sprays mitigated high-temperature stress, increasing yield by 3.08%–7.05% and 2.09%–3.52% compared with the no-spray control in the two experimental years. The sprays partially alleviated the adverse effects of high temperature on grain number per spike and thousand-grain weight, increasing grain number per spike by 1.04–2.30 and 0.95–2.01 grains, and thousand-grain weight by 1.10–1.42 g and 0.60–0.89 g in the two years, respectively, with B1 showing the best effect. Analysis of grain-filling numerical characteristics revealed that foliar sprays delayed the timing of the first and second inflection points by 0.48–0.98 d and 0.32–0.98 d, respectively, extended the grain-filling duration, and increased the average grain-filling rate by 0.01–0.04 mg · grain ^{1} · d ^{1}, with B1 (potassium dihydrogen phosphate) demonstrating the best performance.

Therefore, foliar sprays can extend the wheat grain-filling period and increase grain number per spike and thousand-grain weight to varying degrees, representing an effective measure for yield increase and disaster mitigation.

Keywords: High temperature stress; Grain-filling characteristics; Logistic model; Foliar spray; Yield-increase mechanism; Wheat

Introduction

Wheat (*Triticum aestivum*) is a cool-season crop with an optimal grain-filling temperature of 20–24°C, and the grain-filling stage represents a critical period determining final wheat yield and quality [1]. However, in northern China, temperatures rise rapidly during the late growth stages of wheat, frequently resulting in high-temperature events. Particularly under dry conditions, high temperature combined with low humidity and strong winds creates typical dry-hot wind conditions that cause premature ripening, with yield losses reaching 10%–30%. This has become one of the most important limiting factors for wheat production in northern China [2–4]. With global climate warming, the risk of high-temperature damage during the late wheat growth stages will further intensify [5], making research on wheat heat tolerance and temperature stress critically important both theoretically and practically.

High temperatures during grain filling accelerate plant senescence and shorten the grain-filling duration, exerting extremely adverse effects on wheat grain yield and quality formation [6–8]. Jiang et al. [9] investigated the effects of high-temperature stress at different post-anthesis stages on membrane lipid peroxidation and protective enzyme activities in wheat flag leaves, finding that high-temperature treatment at 8–10 d after anthesis could effectively activate the reactive oxygen defense system in flag leaves, thereby reducing membrane lipid peroxidation, while mid-grain-filling stage high-temperature stress caused irreversible damage. Guo et al. [10] studied heat tolerance mechanisms in different wheat genotypes, demonstrating that high-temperature induction at 5–7 d after anthesis significantly extended plant heat-lethal time during late growth stages, conferring heat tolerance that persisted until maturity. Moreover, appropriate high-temperature acclimation after anthesis facilitated dry matter transport to grains [11–12]. Using ^{1} C tracer methods, Guo et al. [13] studied photosynthate translocation under 30°C and 40°C conditions during grain filling, revealing that high-temperature stress reduced photosynthetic assimilation efficiency in flag leaves, disrupted the dynamics of leaf photosynthate export, inhibited photosynthate accumulation in grains, and ultimately decreased thousand-grain weight. Wang et al. [14] employed artificial climate simulation to examine the effects of high temperature during grain filling on chlorophyll *a* fluorescence parameters in wheat flag leaves, showing that temperature stress reduced Fo, Fv, Fm, Fv/Fm, and Fv/Fo, thereby decreasing PSII potential activity and photochemical efficiency.

Regarding high-temperature and dry-hot wind prevention measures, Rehman et al. [15] used artificial warming methods to screen for heat-tolerant germplasm resources. Other measures such as spraying plant ash water and potassium dihydrogen phosphate at the jointing and booting stages, applying 0.1% acetic acid or 1:800 vinegar solution during grain filling, and spraying petroleum growth promoters during flowering and grain filling have been used to enhance wheat resistance to high temperature and dry-hot wind [16]. Appropriate application of regulators during grain filling can delay leaf senescence, coordinate source-sink relationships, and reduce damage from high-temperature stress [17-18].

Previous research has extensively investigated high-temperature effects during grain filling on wheat heat tolerance, yield, quality, photosynthetic mechanisms, and defense measures. Numerous studies have also modeled wheat grain-filling processes. However, few reports have analyzed grain-filling simulation and parameter characteristics following high-temperature stress and foliar spray mitigation, with most conducted under fixed temperature stress or greenhouse conditions. This study employed natural warming using plastic sheds under field conditions, with natural temperature without covering as the control, to impose high-temperature stress during different grain-filling periods while investigating the mitigative effects of different foliar regulators. By modeling the grain-filling process, this research reveals the mechanisms underlying yield impacts, providing data support for understanding high-temperature effects on yield and developing cultivation measures for yield increase in this region.

1.1 Experimental Overview

The experiment was conducted at the Dry-farming Water-saving Experiment Station of the Institute of Dry-land Farming, Hebei Academy of Agriculture and Forestry Sciences, during the 2013-2014 and 2014-2015 wheat growing seasons. The experimental soil was clay loam with the following pre-planting nutrient levels: organic matter 15.5 g · kg ^{1}, available phosphorus 33.3 mg · kg ^{1}, available potassium 126.2 mg · kg ^{1}, and alkaline-hydrolyzable nitrogen 84.7 mg · kg ^{1}.

In 2013-2014, wheat was sown on October 18, 2013, with three spring irrigations (March 25, April 25, and May 20) and harvested on June 9, 2014. In 2014-2015, wheat was sown on October 11, 2014, with freezing irrigation on November 15, 2014, three spring irrigations (March 25, April 26, and May 20), and harvested on June 11, 2015. Other management practices followed conventional field protocols. Rainfall during the wheat growth period was 136.4 mm and 143.9 mm in the two years, respectively (annual average rainfall 109 mm). The tested variety was 'Heng 4399'.

1.2.1 Experimental Design

A split-plot design was employed with four high-temperature treatments during different periods as main plots (designated A): In 2013-2014, treatments were applied during May 12-25 (A1, 12-25 d after anthesis), May 12-16 (A2, 12-16 d after anthesis), May 15-20 (A3, 15-20 d after anthesis), and May 20-25 (A4, 20-25 d after anthesis). In 2014-2015, treatments were applied during May 12-25 (A1, 8-21 d after anthesis), May 12-16 (A2, 8-12 d after anthesis), May 18-24 (A3, 14-20 d after anthesis), and May 20-25 (A4, 16-21 d after anthesis). Natural temperature without plastic covering served as the control (A5). Temperature treatments were achieved using plastic film sheds, with temperature and humidity inside and outside the sheds shown in Table 1 (monitored using JL-16 temperature and humidity recorders).

Subplot treatments consisted of foliar spray applications (designated B): 0.2% potassium dihydrogen phosphate (B1), 0.05% zinc sulfate (B2), water (B3), and no spray (B4). Sprays were applied twice at the booting stage (April 28) and early milk stage (May 7), with 450 kg · hm ^{2} of spray solution per application.

All treatments had three replications, with plot size of 31.5 m^2 (7 m × 4.5 m). Basal fertilizer consisted of 495 kg · hm ^{2} diammonium phosphate (containing 17% N, 47% P O) and 150 kg · hm ^{2} urea (containing 46% N), with an additional 375 kg · hm ^{2} urea applied with the first spring irrigation.

1.2.2 Measurement Indicators and Methods

Grain-filling rate: Before anthesis, spikes with uniform flowering were tagged in each plot. Measurements began 3 d after anthesis (anthesis date: May 1, 2013–2014; May 4, 2014–2015), with sampling every 3 d. Ten spikes were selected per plot, killed at 105°C, dried at 80°C to constant weight, and used to determine grain number per spike and grain dry weight for calculating individual grain weight.

Grain-filling model: The Logistic curve is widely used in agricultural research to describe grain weight increase [19]. The theoretical regression model Yt = k/(1 + e^(a+bt)) was used for simulation, where Yt is grain dry matter weight at time t (dry matter accumulation), t is days after grain filling began, and a, b, k are parameters. The theoretical grain weight is the Yt value when t approaches infinity. Taking the second derivative of the equation and setting it to zero yields the time to maximum grain-filling rate: tmax = ln(a)/b. Substituting into the first derivative equation gives the maximum grain-filling rate: Vmax = kb/4. The average grain-filling rate V = maximum dry matter accumulation (g)/growth duration (d). The equation curve has two inflection points dividing the growth/filling process into early, middle, and late stages, calculated as: t , = -ln[(4 ± 3.464)/2a]/b.

Yield and yield components: At maturity, three representative 1 m^2 samples (total 3 m^2) were harvested from the center of each plot for yield measurement and conversion to per-hectare yield. Forty representative spikes were randomly selected from each plot to determine grain number per spike (averaged). Thousand-grain weight was determined by weighing two 500-grain samples from air-dried plot samples, with the two sample weights differing by no more than 0.3 g; the sum of the two samples represented thousand-grain weight.

1.2.3 Data Processing Methods

The DPS data processing system developed by Tang Qiyu [20] was used for statistical analysis and grain-filling process model simulation, with Microsoft Excel software used for graphing and data analysis.

2.1 Effects of High-Temperature Treatments During Different Periods on Wheat Yield and Yield Components

Yield and yield components were analyzed using two-year results, while other findings primarily used the 2013-2014 growing season for analysis.

Yield results from different high-temperature treatments and the control (Table 2) showed consistent trends across both years. In 2013-2014 and 2014-2015, high-temperature treatments A1, A2, A3, and A4 reduced yield by 15.34%, 13.11%, 14.93%, 12.64% and 9.41%, 3.89%, 4.93%, 2.04% compared with control A5, respectively. In 2013-2014, differences between all high-temperature treatments and the control reached extremely significant levels, while differences among high-temperature treatments were not significant. In 2014-2015, treatment A1 differed extremely significantly from control A5 but not from A2, A3, or A4; treatment A3 differed significantly from A5, while A2 and A4 did not differ significantly from A5. These results indicate that high temperature during any period caused yield reduction, with greater yield losses under longer high-temperature stress.

Subplot treatments B1, B2, and B3 increased yield by 7.05%, 5.28%, 3.08% and 3.52%, 3.23%, 2.09% compared with control B4 in 2013-2014 and 2014-2015, respectively. In 2013-2014, B1 and B2 differed extremely significantly from B4, with no significant difference between B1 and B2, but B1 differed significantly from B3 (B2 and B3 did not differ significantly). In 2014-2015, B1, B2, and B3 differed significantly from B4, with B1 and B2 differing extremely significantly from B4, but no significant differences among B1, B2, and B3. Thus, foliar sprays increased yield.

Under different high-temperature periods in 2013-2014, B3, B2, and B1 increased yield by 3.73%-7.57%, 5.51%-7.99%, 0.76%-8.99%, and 1.32%-6.64% compared with B4 (yield increase under normal temperature was 2.73%-4.50%). Spray B1 showed the greatest yield-increasing effect, followed by B2 and B3, with A1B1 differing significantly from the control, while differences among other spray treatments during different periods were not significant. This indicates that B1 provided better yield-increasing effects under high-temperature stress. In 2014-2015, the yield-increasing effect of sprays during different periods was smaller than in the control field, possibly related to temperature differences and climatic year types between the two years.

High-temperature treatments during different periods reduced grain number per spike (Table 2). In 2013-2014, grain number per spike in A1, A2, A3, and A4 decreased by 5.45, 1.45, 0.87, and 0.71 grains compared with the control, with A1 and A2 differing extremely significantly from A5, A3 differing significantly, and A4 not differing significantly. Treatment A1 differed significantly from A2, A3, and A4, while no significant differences existed among A2, A3, and A4. In 2014–2015, grain number per spike decreased by 1.95, 2.30, 3.00, and 1.73 grains, with A1, A2, and A3 differing significantly from the control, but no significant differences among A1, A2, A3, and A4.

Foliar sprays increased grain number per spike. In 2013–2014, B1, B2, and B3 increased grain number by 2.30, 1.21, and 1.04 grains compared with B4, all reaching extremely significant differences. The grain-increasing effect of B1 was significant, differing extremely significantly from B2 and B3, while B2 and B3 did not differ significantly. In 2014–2015, B1, B2, and B3 increased grain number by 2.01, 2.75, and 0.95 grains, with B1 and B2 differing extremely significantly from the control. No significant differences existed between B1 and B2 or between B1 and B3, but B2 and B3 differed extremely significantly.

The effect of sprays on grain number per spike under different high-temperature periods varied between years. In 2013–2014, A1B1 and A1B2 showed good grain-increasing effects, differing significantly from the control, while differences among other spray treatments during different periods were not significant. In 2014–2015, A4B2 showed the best grain-increasing effect, while other period sprays increased grain number but without significant differences.

High temperature negatively affected thousand-grain weight. In 2013–2014 and 2014–2015, A1, A2, A3, and A4 reduced thousand-grain weight by 1.96 g, 3.41 g, 1.71 g, 1.28 g and 4.27 g, 0.84 g, 1.23 g, 2.19 g, respectively. In 2013–2014, all treatments differed significantly from the control, with A1, A2, and A3 differing extremely significantly. Treatment A2 differed extremely significantly from A1, A3, and A4, while no significant differences existed among A1, A3, and A4. In 2014–2015, A1 and A4 differed extremely significantly from the control, A3 differed significantly, and A2 did not differ significantly from the control, though no significant difference existed between A2 and A3.

Treatments B1 and B2 increased thousand-grain weight by 1.10 g and 1.42 g in 2013–2014 and by 0.89 g and 0.60 g in 2014–2015, with differences reaching extremely significant levels in 2013–2014. The effect of foliar sprays on grain weight under different high-temperature periods showed interannual variation. In 2013–2014, B1 and B2 increased grain weight by 1.52% and 3.01%, 3.04% and 5.96%, 2.52% and 2.37%, and 3.76% and 4.33% under high-temperature treatments A1, A2, A3, and A4, respectively, with no significant differences among treatments. Under normal temperature, A5B1 and A5B2 increased grain weight by 2.25% and 1.40%, respectively. This indicates that spraying B1 and B2 under high-temperature stress increased grain weight, though in 2014–2015 only A1B1 showed an extremely significant grain weight increase, with no significant effects in other periods.

These results demonstrate that yield reduction from high temperature during different periods primarily resulted from decreased grain number per spike or grain weight, influenced by both the timing and duration of stress. Treatment A1, with the longest high-temperature stress duration, showed the greatest reductions in grain number per spike and thousand-grain weight and the lowest average yield. Both B1 and B2 sprays increased grain number per spike, though their effects varied under different high-temperature periods. Longer high-temperature stress caused more significant grain number reduction, while grain weight was constrained by grain number, showing less clear patterns. Spray B1 demonstrated the best mitigation effect.

2.2 Effects of High-Temperature Treatments During Different Periods on Wheat Grain Weight

The grain-filling stage is critical for wheat yield formation, and grain weight is an important yield component. Grain weight observations were made on 10 tagged spikes with consistent growth, using a different method from yield structure determination but showing the same trends across treatments. As shown in Table 3 , grain weight increase followed a slow-fast-slow pattern. High-temperature stress treatments reduced final grain weight to varying degrees, with A1, A2, A3, and A4 decreasing by 2.44 mg, 3.72 mg, 1.98 mg, and 1.10 mg compared with control A5, with differences reaching significant levels. Foliar sprays mitigated these negative effects, with B1, B2, and B3 increasing grain weight by 1.73 mg, 1.48 mg, and 0.54 mg compared with B4, with B1 and B2 showing extremely significant differences.

2.3 Numerical Characteristics of High-Temperature Effects on Grain Filling

To further investigate the effects of high-temperature stress during grain filling on grain-filling patterns, the grain-filling processes under different high-temperature stress treatments were simulated using Logistic model regression, achieving satisfactory results with determination coefficients (R^2) above 0.99, reaching extremely significant levels (Table 4).

Wheat grain weight depends on grain-filling parameters such as rate and duration [21]. Table 5 lists the grain-filling characteristic parameters from fitted equations. Regarding grain-filling characteristic parameters (Table 6), high-temperature treatments A1, A2, A3, and A4 advanced the time to maximum grain-filling rate by 0.70 d, 1.09 d, 0.54 d, and 0.26 d, respectively, compared with control A5. The first inflection point occurred 0.48 d, 0.75 d, 0.46 d, and 0.29 d earlier, while the second inflection point occurred 0.92 d, 1.42 d, 0.61 d, and 0.22 d earlier. Maximum grain-filling rates decreased by 0.07 mg · grain ^{1} · d ^{1}, 0.11 mg · grain ^{1} · d ^{1}, 0.09 mg · grain ^{1} · d ^{1}, and 0.08 mg · grain ^{1} · d ^{1}, respectively, while average grain-filling rates decreased by 0.06 mg · grain ^{1} · d ^{1}, 0.10

mg·grain^{1}·d^{1}, 0.05 mg·grain^{1}·d^{1}, and 0.03 mg·grain^{1}·d^{1}, respectively. The rapid grain-filling periods for different high-temperature treatments were 13.63 d, 13.39 d, 13.91 d, 14.13 d, and 14.07 d. Treatments A1, A2, and A3 shortened the rapid grain-filling period by 0.44 d, 0.67 d, and 0.16 d compared with the field control, while late-grain-filling high-temperature treatment had no effect on the rapid increase period. These results demonstrate that high-temperature treatments during different periods affected grain-filling characteristic parameters by reducing maximum and average grain-filling rates, advancing the timing of the first and second inflection points, and shortening grain-filling duration, which were important causes of reduced grain weight and yield.

Overall, the main numerical characteristics of high-temperature stress effects on wheat grain filling were advancing the first and second inflection points and shortening the rapid grain-filling process, with greater advancement values when stress occurred earlier.

The numerical characteristic values from model fitting for each spray treatment are shown in Table 7 . Regarding the effects of foliar sprays, B1, B2, and B3 increased grain weight to varying degrees, with B1 showing the most pronounced weight increase. In terms of grain-filling parameters, B1, B2, and B3 delayed the timing of the first and second inflection points by 0.48 d, 0.98 d, 0.89 d and 0.98 d, 0.39 d, 0.32 d, respectively. The time to maximum grain-filling rate was delayed by 0.73 d, 0.69 d, and 0.61 d, respectively. Maximum grain-filling rates increased by 0.03 mg·grain^{1}·d^{1}, 0.16 mg·grain^{1}·d^{1}, and 0.11 mg·grain^{1}·d^{1}, while average grain-filling rates increased by 0.04 mg·grain^{1}·d^{1}, 0.03 mg·grain^{1}·d^{1}, and 0.01 mg·grain^{1}·d^{1}, respectively. Therefore, foliar sprays improved grain-filling characteristic parameters by delaying the first and second inflection points, extending grain-filling duration, and increasing average grain-filling rate, thereby increasing grain weight, with B1 showing the best effect.

Examining the buffering effects of foliar sprays under different high-temperature periods, B1 performed best. Under A1, A2, A3, and A4 treatments, B1 extended the rapid increase period by 0.58 d, 0.77 d, 0.69 d, and 0.33 d compared with respective unsprayed treatments, while under normal temperature, B1 extended the rapid increase period by 0.21 d compared with no spray. Thus, spraying foliar spray B1 under high-temperature conditions provided effective yield-increasing benefits.

High temperature accelerates crop development and shortens the growth period [22]. Most wheat grain yield originates from photosynthates accumulated after anthesis, which account for approximately half of total photosynthetic production [23]. High-temperature stress inhibits wheat canopy carbon assimilation [24], disrupts the dynamics of leaf photosynthate export, shortens the photosynthetic duration, reduces source supply, and inhibits photosynthate accumulation in grains [13], thereby decreasing grain weight and yield [25–28]. This study showed that high temperature during different periods affected yield to varying degrees, with treatment A1 (longest stress duration) causing the greatest yield reduction, followed by A2. Yield components showed reduced grain number per spike and grain weight. The grain-filling model effectively simulated the grain-filling process, with determination coefficients above 0.99. Grain-filling characteristic parameters showed that high-temperature treatments advanced the first and second inflection points, shortened grain-filling duration, and reduced average and maximum grain-filling rates, consistent with previous research [29-31].

This study demonstrated that foliar fertilization increased yield by increasing grain number per spike or grain weight to varying degrees. Grain-filling process modeling revealed that, contrary to high-temperature stress effects, foliar sprays delayed the first and second inflection points, extended grain-filling duration, and increased average and maximum grain-filling rates, indicating that foliar sprays can delay leaf senescence and promote photosynthesis [32-34]. Among the buffering effects of different sprays under various high-temperature stress periods, B1 performed best by extending the rapid grain-filling period and increasing grain weight, representing an important measure for wheat yield increase and disaster mitigation [35-37].

Wheat can acquire heat tolerance, which decreases with post-anthesis developmental progression. High-temperature stress during earlier stages can more effectively activate the reactive oxygen defense system in flag leaves, while damage during later stages is irreversible [9]. High-temperature treatment at 20-22 d after anthesis has the greatest impact on wheat grain development and weight [38]. In this study, late-grain-filling high-temperature treatment A4 (20-25 d and 16-21 d after anthesis) caused the smallest yield reduction, while A3 (15-20 d and 14-20 d after anthesis) had relatively greater impact on yield. Grain weight was most affected at 12-16 d (2013-2014) and 16-21 d (2014-2015) after anthesis, while grain number per spike was most affected at 12-16 d (2013-2014) and 14-20 d (2014-2015) after anthesis. Differences in timing between years suggest that further research is needed on relationships between climatic year types, wheat stage-specific heat tolerance, and irrigation effects during the growth period.

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Note: Figure translations are in progress. See original paper for figures.