https://doi.org/10.17221/313/2023-PSE

Effects of spring low-temperature stress on winter wheat seed-setting characteristics of spike

*Xiang Chen[1], Lvzhou Liu[1], Hongmei Cai[1], Baoqiang Zheng[1], Jincai Li[1,2]**

[1]School of Agronomy, Anhui Agricultural University, Hefei, P.R. China
[2]Jiangsu Collaborative Innovation Centre for Modern Crop Production, Nanjing, P.R. China
**Corresponding author: lijincai@ahau.edu.cn*

Citation: Chen X., Liu L.Z., Cai H.M, Zheng B.Q., Li J.C. (2024): Effects of spring low-temperature stress on winter wheat seed-setting characteristics of spike. Plant Soil Environ., 70: 84–92.

Abstract: Global climate change leads to frequent occurrence of low-temperature stress (LTS), which poses a serious threat to global food security. Here, environment-control phytotron experiments were conducted on cold-responsive cv. XM26 and cold-tolerant cv. YN19 during the anther differentiation period. Six LTS levels (4, 2, 0, –2, –4, –6 °C) and a control treatment (10 °C) were set to study the effects of different levels of LTS on wheat seed-setting characteristics and yield. LTS significantly decreased grain number per spike, 1 000-grain weight, and grain yield per plant (GYPP) of the two wheat cultivars. Each spike's grain number and weight distribution showed a quadratic curve, and the near-medium dominance of grain development was not affected by temperature. The grain number percentage and grain weight of wheat at different grain positions were G2 (2^{nd} grain position) ≥ G1 (1^{st} grain position) > G3 (3^{rd} grain position) > G4 (4^{th} grain position), in which G3 and G4 grain positions were more sensitive to LTS. In summary, LTS during the anther differentiation in wheat mainly led to a decrease in GYPP by significantly reducing the number and weight of inferior grains. Improving wheat cultivation measures and promoting the development of inferior grains are significant ways to prevent disasters and increase wheat quality and productivity in the future.

Keywords: cereal; cold stress; *Triticum aestivum* L.; number of fertile grains; damage; global warming

Wheat (*Triticum aestivum* L.) is a significant food crop widely grown globally for adaptability (Hassan et al. 2021). Global wheat production was 761 million tons and 219 million hectares in 2020 (FAOSTAT 2022). The global mean surface temperature increased by 0.87 °C from 2006 to 2015 and is expected to rise by more than 1.5 °C by 2100 (Agnolucci et al. 2020). Global warming accelerated wheat fertility into the anther differentiation period, which was very sensitive to low temperatures (Xiao et al. 2018). If wheat is exposed to sudden spring cooling at this time, it may cause damage to young spikes and reduce grain yield. Recent data showed that a series of frost events from 1960 to 2013 resulted in a 2% annual reduction during wheat maturity in Australia (Crimp et al. 2016). Based on the projected climate for Europe in 2060, extreme frost damage is likely to reduce wheat yields by 1/3 or even 1/2 from current levels (Asseng et al. 2015). Huang-Huai wheat region is the leading wheat-producing area in China, where spring low-temperature stress (LTS) occurs to varying degrees almost every year (Xu et al. 2015b), the frequency of spring LTS is statistically 30% to 70% (Chen et al. 2020). The spring LTS has seriously reduced China's wheat yield, reaching 60% to 70% in the worst-hit areas (Assa et al. 2018). Therefore, spring LTS events caused by global warming pose a growing threat to global wheat production.

Supported by the Natural Science Foundation of Anhui Province, Project No. 2008085QC122; by the Major Science and Technology Special Project of Anhui Province, Project No. 202003b06020021, and by the Special Fund for Anhui Agriculture Research System, Project No. 340000222426000100009.

https://doi.org/10.17221/313/2023-PSE

The research on the effects of spring LTS on wheat's morphological, physiological, and biochemical characteristics has been widely carried out. LTS destroys the cellular structure of leaves and young spikes (Lorenzo et al. 2019), reduces the photosynthetic characteristics of major functional leaves (Xiao et al. 2022), and accumulates a large number of toxic substances such as reactive oxygen (Shah et al. 2019). This, in turn, reduces the number of grains and grain filling rate (Osman et al. 2020), ultimately leading to seed yield loss. Li et al. (2015) studied the effect of LTS on the photosynthetic physiology of wheat and found that spring LTS significantly decreased the gas exchange rate and maximum quantum efficiency of photosystem II in wheat leaves and, finally, led to a yield loss of 12% to 14%. Wang et al. (2021b) showed that LTS at the jointing stage significantly decreased the net photosynthetic rate, plant height, and biomass of wheat, resulting in a decrease in grain yield. Many studies have focused on spring LTS's effects on wheat physiology and yield (Vaitkevičiūtė et al. 2022). However, few studies have focused on the changes in grain weight and the number of grains per spike at different grain positions (Liu et al. 2019). There are significant differences in grain number and weight among different spikelets in wheat due to the comprehensive influence of genetic factors, nutrient supply level, and external climatic conditions (Ferrante et al. 2015). In previous studies, the spatial distribution of grain number and weight was found to exhibit parabolic changes, and the middle spikelets tend to have more and heavier grains than the basal and top spikelets (Bustos et al. 2013). In the same spikelet, well-developed G1 and G2 are considered superior grains, while dysplastic G3 and above grains are considered inferior grains (Luo et al. 2019). The filling rate of inferior grains was worse than that of superior grains, and the superior grains had a strong grain position of dry matter accumulation (Baillot et al. 2018). Therefore, the superior grains were heavier than the inferior grains, and the number of superior grains accounted for a higher proportion of the total grain (Feng et al. 2018).

This research used a smart climate box to test different cold-sensitive wheat cultivars during the anther differentiation period. This period is very sensitive to LTS, which may cause damage to young spikes and reduce grain yield (Wu et al. 2022). Our primary objective was to investigate the effects of different LTS on grain number and grain weight of wheat at different spikelet and grain positions. Quantifying yield losses caused by spring LTS can provide theoretical support for the prevention of reduction in wheat production.

MATERIAL AND METHODS

Plant material and experimental designs. The experiment was carried out from 2021 to 2022 in the Agricultural Extraction Garden of Anhui Agricultural University (31°86'N, 117°26'E; 30 m a.s.l.), which is in Hefei, Anhui Province, China. Through the pre-screening of the experimental team (Zheng et al. 2020), the main cultivars in Anhui Province were used as experimental materials. Two wheat cultivars (Table 1), Xinmai26 (cold-responsive cultivar, referred to as XM26) and Yannong19 (cold-tolerant cultivar, referred to as YN19), were sown in the test pots (30 cm diameter × 35 cm height; 3 drainage holes).

The pot soil was taken from the 0~20 cm tillage layer of the field soil (pH 6.5; organic carbon 9.45 g/kg; available nitrogen 112.2 mg/kg; available phosphorus 23.0 mg/kg; available potassium 161.6 mg/kg; yellow-brown soil.). Each pot was filled with 10 kg of the soil before sowing, and the wheat seeds were covered with 3 cm of the soil. 11.52 g of compound fertiliser (N:P:K = 15:15:15) was applied per pot before planting, and 0.87 g urea was applied to each pot during the wheat jointing stage. 18 seeds were planted in each pot, and 9 seedlings were maintained at the three-leaf stage. Then, all the potted plants were buried in the soil of the experimental field, and the

Table 1. Information about the two cultivars

Cultivar	Breeding unit	Certification unit	Information
XM26	Xinxiang Academy of Agricultural Sciences, Henan Province, China	China National Crop Variety Examination and Approving Committee	super stringy semi-winter wheat cultivar
YN19	Yantai Academy of Agricultural Sciences, Shandong Province, China	Shandong Provincial Crop Variety Certification Committee, China	medium-gluten winter wheat cultivar

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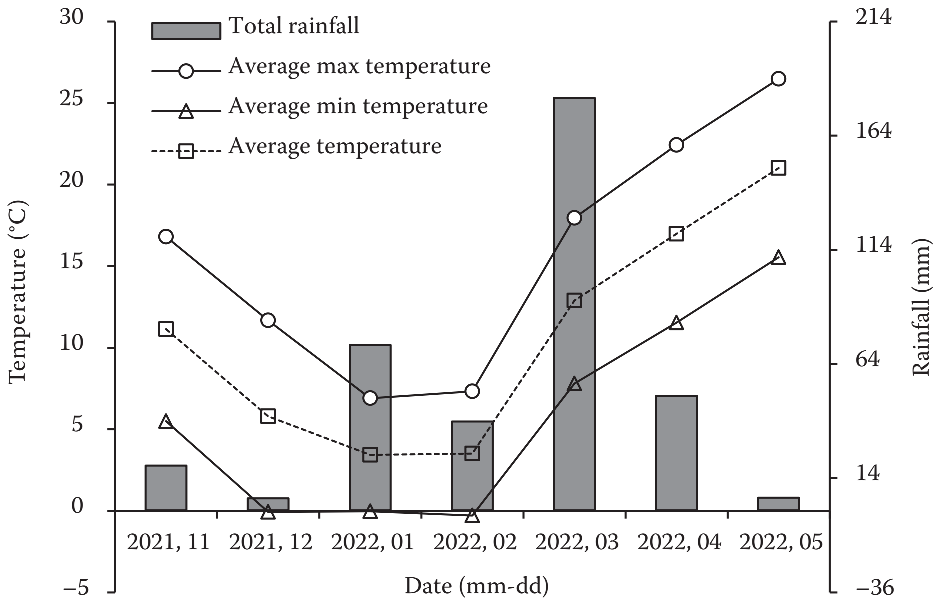

Figure 1. The weather conditions of wheat during the whole growth period

pots were kept at the same level as the ground. At the mature stage, a total of 56 pots of the two cultivars (4 pots for each treatment) were left for seed testing. The basic meteorological data for the entire growing season of this experiment is shown in Figure 1.

Based on previous experiments (Liu et al. 2023), six LTS levels of 4, 2, 0, –2, –4, –6 °C and a control CK (10 °C) were set. At the end of the regreening stage, three spikes were randomly selected daily to observe the differentiation process under a microscope (Olympus SZ2-ILST, Tokyo, Japan). When the young spikes reached the anther differentiation stage (50% of the wheat ears partly form a longitudinal split septum, dividing the anthers into four pollen bundles, 21 March 2022), all the pots were transferred to smart climate box (DGXM-1008; Ningbo Jiangnan Instrument Manufacturing Factory, Ningbo, China; 1 300 mm length × 630 mm width × 1 305 mm height) for LTS simulation experiment, with humidity 70% and light 17 000 LX during the day and 0 LX at night. The treatment time was 01:00 A.M. to 05:00 A.M., with continuous LTS treatment for 4 h (Figure 2). Immediately after the treatment, the pots were moved back to the field and continued to grow until maturity.

Grain yield and yield components. After the wheat reached maturity, ten wheat plants were randomly selected from each treatment to analyse the spike number per plant (SNPP), grain number per spike (GNPS), 1 000-grain weight (TGW), and the grain yield per plant (GYPP).

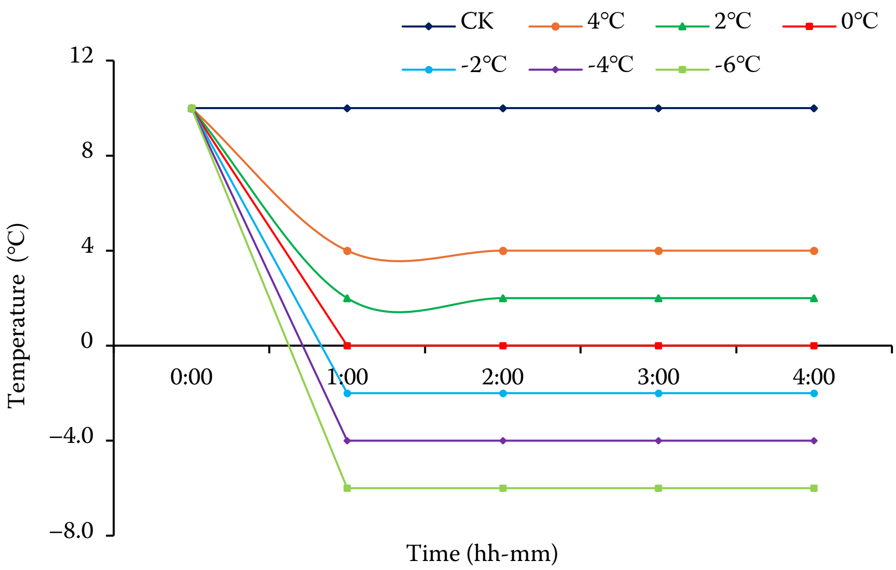

Figure 2. The temperature dynamics in the smart climate box during the low-temperature treatments

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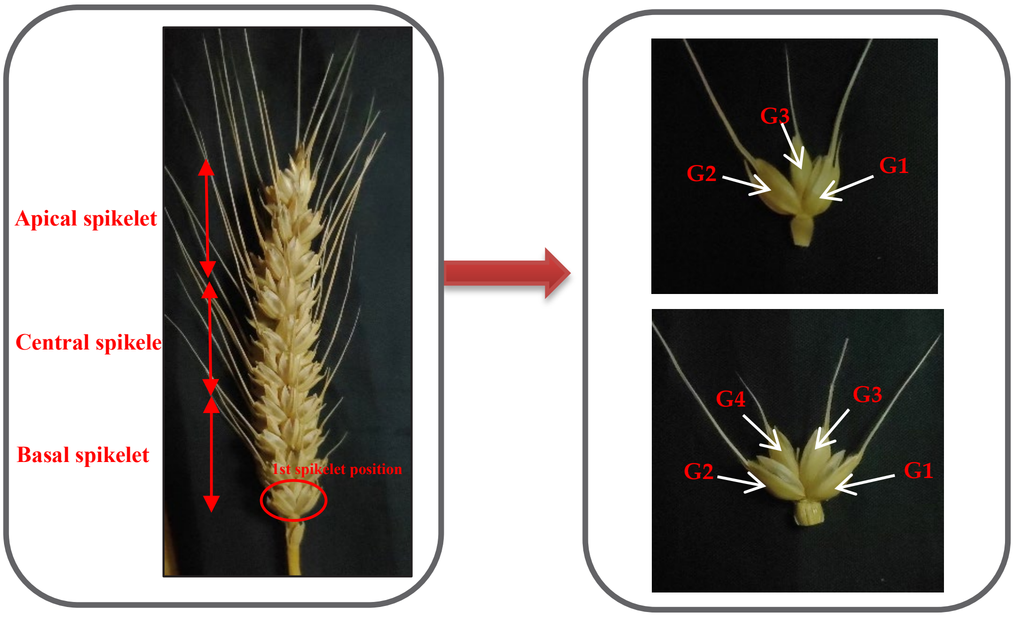

Figure 3. Diagram of different spikelet positions and grain positions in wheat. G2 – 2nd grain position; G1 – 1st grain position; G3 – 3rd grain position; G4 – 4th grain position

The spatial distribution of grain number and grain weight. Ten single-stem spikes were randomly selected from different pots to measure the grain number, average grain weight, and grain yield in different parts of spikelets. The grains of the different spikelet positions are bagged and counted (ten single-stemmed spikes were selected for each treatment, and the average was calculated), and the dry weight of the grains of each spikelet position was weighed separately and marked as G1, G2, G3, and G4 for position 1, 2, 3, and 4, respectively (Mirosavljević et al. 2021) (Figure 3).

Statistical analysis. Data were analysed by one-way ANOVA using SPSS 21.0 (SPSS Inc., Chicago, USA), and statistical divergence among treatments was determined using Tukey's honestly significant difference test. The data were expressed as mean ± standard error (SE) triplicates.

RESULTS

Effect of spring LTS on yield and its components. Different levels of LTS could significantly reduce wheat yield and its components in both cultivars (Table 2). When the temperature level decreased (from CK to −6 °C), SNPP, SSN, GNPS, and TGW yield components tended to decrease. LTS significantly reduced GYPP, GNPS and TGW in wheat, for GYPP, compared to CK cv. XM26 decreased by 27.15, 36.54, 39.66, 55.20, 66.59 and 80.89%, while cv. YN19 decreased by 20.78, 33.00, 37.44, 47.22, 62.44 and 75.44% at 4, 2, 0, −2, −4 and −6 °C, respectively. This showed that the effect of LTS on the yield of cv. XM26 was greater than that of cv. YN19. Table 1 also showed the effects of different cultivars (C), temperature (T), and their interaction (C × T) on SNPP, SSN, GNPS, TGW and GYPP. For SNPP, SSN, and GYPP, the effect of T reached a highly significant level ($P < 0.01$), while C and C × T did not affect them. For GNPS, the effects of C and T reached a highly significant level, while C × T had no effect. For TGW, the effects of C, T and C × T reached a highly significant level.

Effect of spring LTS on the spatial distribution of grain number at different spikelet positions. The number of grains per spikelet increased and then decreased from the bottom to the top spikelets, showing a quadratic curve trend (Figure 4). The results indicated that the quadratic equation could well reflect the change of grain number at the spikelet position. However, the spatial distribution of the grain number of the two wheat cultivars was not symmetrical. There was a linear increase in the grain number from the bottom to the middle of the spikelet and then a slow decrease from the middle to the top. Cv. XM26 had the highest number of grains at the 6–12 spikelet position, while cv. YN19 had the highest number of grains at the 5–11 spikelet position. This showed that both wheat cultivars had a higher grain number at the central spikelet position. In addition, spring LTS significantly reduced the grain number in different spikelet positions.

Effect of spring LTS on the spatial distribution of grain number at different grain positions. The

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Table 2. Effects of spring low-temperature stress (LTS) on grain yield and yield components during the anther differentiation period

Cultivar	Temperature (°C)	SNPP	SSN	GNPS	TGW (g)	GYPP (g/stem)	YRR (%)
XM26	CK	4.67 ± 0.33[a]	18.50 ± 0.87[a]	46.83 ± 1.17[a]	48.37 ± 2.12[a]	8.95 ± 0.56[a]	–
	4	4.33 ± 0.33[ab]	17.17 ± 0.60[ab]	41.75 ± 2.74[b]	46.34 ± 1.09[a]	6.52 ± 0.56[b]	27.15
	2	4.67 ± 0.33[a]	16.33 ± 0.33[ab]	37.50 ± 1.26[b]	38.22 ± 0.92[b]	5.68 ± 0.24[c]	36.54
	0	4.33 ± 0.17[ab]	16.17 ± 1.01[b]	38.00 ± 1.59[b]	38.05 ± 0.98[b]	5.40 ± 0.15[c]	39.66
	–2	4.33 ± 0.33[ab]	15.33 ± 0.83[b]	31.49 ± 1.00[c]	33.64 ± 5.22[c]	4.01 ± 0.47[d]	55.20
	–4	3.67 ± 0.33[ab]	13.00 ± 0.58[c]	30.83 ± 0.38[c]	30.74 ± 1.06[c]	2.99 ± 0.36[d]	66.59
	–6	3.33 ± 0.33[b]	12.00 ± 0.29[c]	22.00 ± 0.68[d]	29.30 ± 1.03[c]	1.71 ± 0.19[e]	80.89
YN19	CK	5.67 ± 0.38[a]	18.83 ± 0.17[a]	37.84 ± 0.73[a]	48.89 ± 0.43[a]	9.00 ± 0.52[a]	–
	4	4.67 ± 0.33[ab]	17.00 ± 0.58[a]	33.83 ± 0.73[b]	48.56 ± 0.37[a]	7.13 ± 0.57[b]	20.78
	2	4.33 ± 0.33[ab]	17.33 ± 0.83[a]	33.17 ± 0.60[b]	48.64 ± 0.89[a]	6.03 ± 0.49[b]	33.00
	0	4.67 ± 0.33[ab]	15.67 ± 0.44[ab]	29.84 ± 1.01[b]	44.74 ± 0.88[b]	5.63 ± 0.49[bc]	37.44
	–2	4.33 ± 0.67[ab]	12.83 ± 1.86[bc]	28.17 ± 1.17[b]	42.36 ± 0.39[c]	4.75 ± 0.88[bc]	47.22
	–4	4.00 ± 0.00[b]	12.00 ± 1.04[cd]	24.50 ± 2.47[c]	40.08 ± 0.50[c]	3.38 ± 0.36[cd]	62.44
	–6	3.33 ± 0.33[b]	9.33 ± 1.45[d]	20.33 ± 0.52[d]	37.39 ± 1.42[d]	2.21 ± 0.16[d]	75.44
ANOVA	cultivar (C)	1.563	3.967	55.479**	153.129**	0.518	–
	temperature (T)	5.313**	23.15**	53.778**	70.913**	34.83**	–
	C × T	0.688	1.07	2.327	8.205**	0.357	–

In each column, data represented mean ± standard error (n = 3). Different lowercase letters indicated a statistically significant difference (Tukey's test, $P \leq 0.05$) between different LTS treatments of two wheat cultivars. The value in the ANOVA row indicated the F-values. **indicated significance at the level of 0.01. SNPP – number of spikes per plant; SSN – number of fertile spikelets per spike; GNPS – grain number per spike; TGW – 1 000-grain weight; GYPP – grain yield per plant; YRR – yield reduction rate; CK – control

response of grain number percentage to spring LTS at different grain positions is shown in Figure 5. At the same temperature level, the percentage of grain number at different grain positions all showed a pattern of G2 ≥ G1 > G3 > G4. For cv. XM26, the spikelets treated with CK, 4 °C and 2 °C had G4

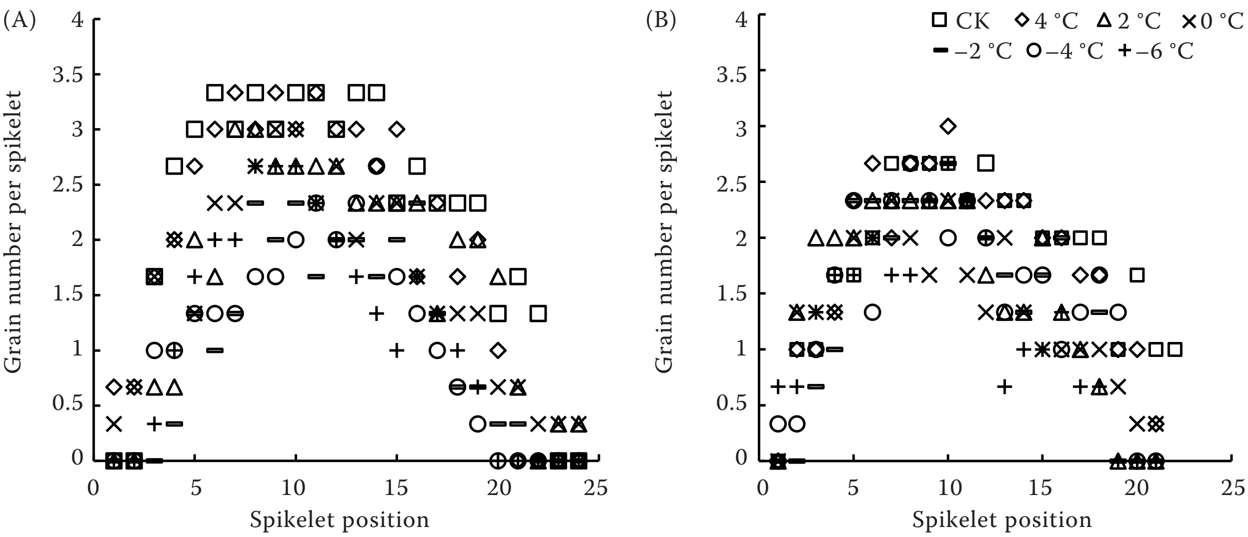

Figure 4. Effects of spring low-temperature stress on the spatial distribution of grain number at different spikelet positions in (A) cv. XM26 and (B) cv. YN19. The legend represents the mean (n = 3)

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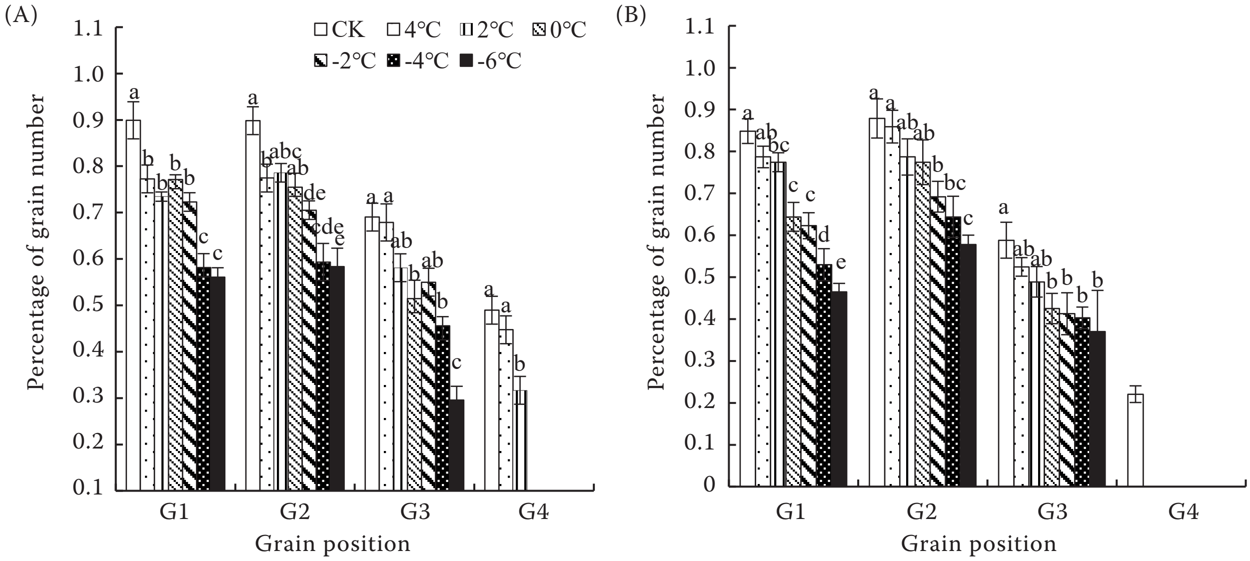

Figure 5. Effects of spring low-temperature stress on the percentage of grain number at different grain positions in (A) cv. XM26 and (B) cv. YN19. The same grain position on a spike is solid, and the percentage of grain in this grain position reaches 100%. The legend represents the mean ± standard error (n = 3). Different letters indicated significant differences (Tukey's test, $P \leq 0.05$). CK – control

grains, while other treatments only had grains at G1–G3 position. For cv. YN19, only the spikelets treated with CK had G4 grains. As the temperature level decreased, grain number percentage at different grain positions showed a decreased trend in both cultivars. In addition, the percentage reduction in grain number at different grain positions was higher in cv. XM26 than in cv. YN19 under different spring LTS, indicating that cv. XM26 was more sensitive to spring low-temperature stress.

Effects of spring LTS on the spatial distribution of average grain weight at different spikelet positions. Average grain weight per spikelet position varied parabolic trend from lower to upper spikelet position, first increasing and then decreasing (Figure 6). The results indicated that the spatial distribution of grain weight of the two wheat cultivars was not symmetrical. The grain weight increased linearly from the bottom to the middle of the spikelet and then decreased slightly from the middle to the top of the

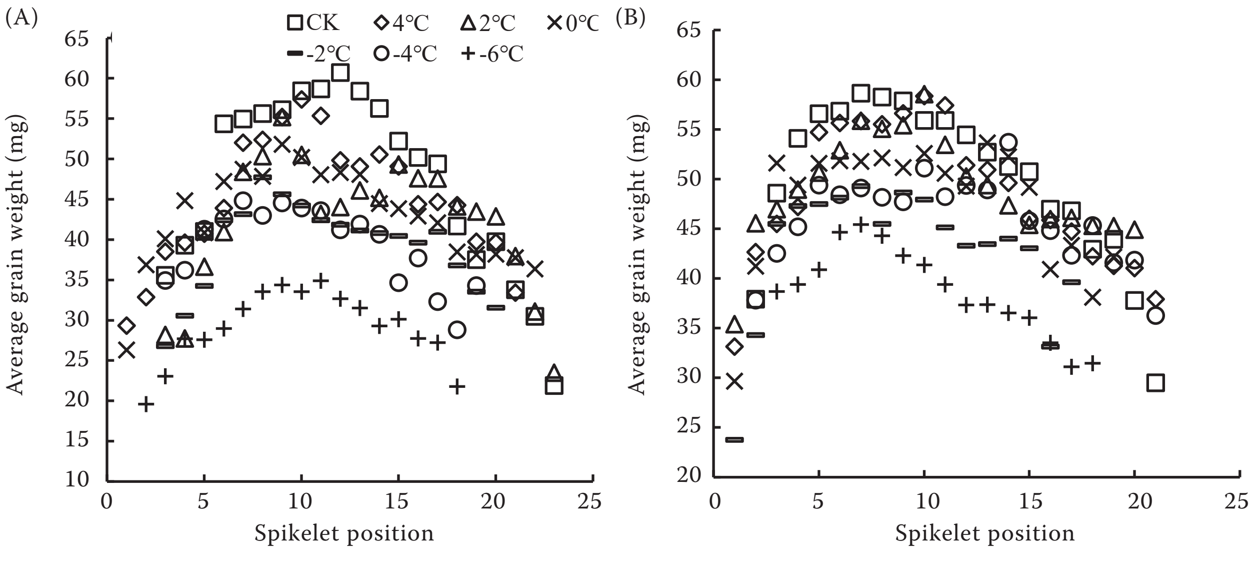

Figure 6. Effects of spring low-temperature stress on the spatial distribution of average grain weight at different spikelet positions in (A) cv. XM26 and (B) cv. YN19. The legend represents the mean (n = 3); CK – control

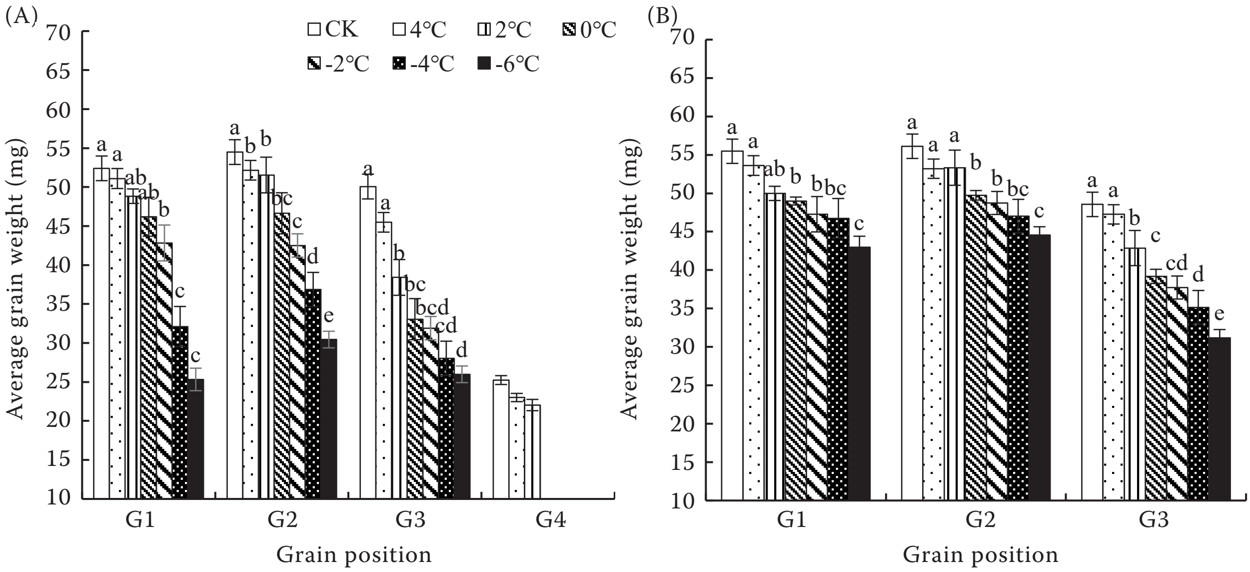

Figure 7. Effects of spring low-temperature stress (LTS) on average grain weight at different grain positions in (A) cv. XM26 and (B) cv. YN19. The legend represents the mean ± standard error (n = 3). Different letters indicated significant differences (Tukey's test, $P \leq 0.05$). CK – control

spikelet. The inflection points of the fitted equation indicated the maximum grain weight at the spikelet position. The maximum grain weight was found in cv. XM26 at the 7–11 spikelet position, whereas the highest grain weight was found in cv. YN19 at the 5–10 spikelet position. It can be seen that the central spikelet grain weights were higher in both wheat cultivars. In addition, average grain weight at different spikelet positions of cv. XM26 showed a greater decline under spring LTS compared to cv. YN19.

Effects of spring LTS on the spatial distribution of average grain weight at different grain positions. The average weight of the G1 and G2 grains was higher than that of the G3 and G4 grains (Figure 7). While the grain weight of G2 was the highest. Spring LTS could reduce the grain weight of different grain positions to various degrees. The sensitivity of two wheat cultivars' G3 and G4 grain weights to LTS was higher than that of other grain positions. Moreover, the reduction of grain weight at each grain position was significantly greater in cv. XM26 than in cv. YN19 under LTS, which indicated that the average grain weight of cv. XM26 was more sensitive.

DISCUSSION

The effect of LTS on yield has been widely reported. Previous studies have shown that spring LTS at jointing significantly reduced the number of spikes and grains per spike in wheat, resulting in 3.1–56.4% grain yield reduction (Ji et al. 2017). Nuttall et al. (2018) found that grain number and yield decreased by 8.8% and 7.2% for every 1 °C reduction in LTS treatment at anthesis. The results of this study indicated that LTS significantly reduced GNPS, TGW, and GYPP in both wheat cultivars. The GYPP of cv. XM26 and cv. YN19 showed the greatest decrease at –6 °C stress compared to CK, reaching 80.89% and 75.44%, respectively. It can be seen that cv. XM26 was more sensitive to spring low-temperature stress.

The number of spikelets depends on the fertility of the spikelets, while the grain number per spike is mainly related to the development of the florets (Bustos et al. 2013). The spikelets and florets of the wheat spike do not develop synchronously, with the central spikelets developing first, followed by the apical and basal spikelets (Li et al. 2013). Numerous studies have shown that the grain number of wheat tends to increase and then decrease as spikelet position rises (Mirosavljević et al. 2021). The results showed that the distribution of grain number at each spikelet showed a quadratic curve under different LTS. The inflexion points of grain number distribution of XM26 were at 6–12 spikelet positions in the central spikelet position, while cv. YN19 was at a 5–11 spikelet position. This study is consistent with the results of previous studies, showing near-medium dominance. This is because the apical and basal spikelets and florets develop later than the central spikelets and florets; they are more susceptible to LTS, leading to florets' abortion and

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degeneration (Liang et al. 2021). The grain number in different spikelets varies due to uneven distribution of anther development and nutrient supply. Previous studies showed that G1 and G2 accounted for a higher proportion of the total grains at different positions in the spikelet (Leske and Biddulp 2022). This study is consistent with the previous results; the percentage of grains at different grain positions showed a pattern of G2 ≥ G1 > G3 > G4 at the same temperature level. Among cultivars, cv. XM26 had a higher percentage drop in grain number at different grain positions than cv. YN19. Generally speaking, LTS reduced the grain number per spike in wheat mainly by reducing the grain number of G1 and G2 and that in the basal spikelet.

Grain weight is one of the important components of wheat grain yield, which depends on the matter accumulation in the spikelet. The lack of carbohydrate supply and the limitation of storage capacity resulted in differences in grain weight at different spikelet positions. In spikelets, the first and second well-developed grains are considered superior grains, while three or more maldeveloped grains are considered to be inferior grains (Wang et al. 2021a). The superior grains flowered early and were located in the middle of the spikelet, while the inferior grains flowered later and were mainly located at the bottom and top of the spikelet. Compared with inferior grains, superior grains usually have a greater filling rate and grain weight (Luo et al. 2019). In this study, the distribution of grain weight at different spikelet positions showed a quadratic curve under different LTS – the grain weight of cv. XM26 was the highest at 7–11 in the central spikelet position, while that of cv. YN19 was the highest at 5–10 spikelet position. It can be seen that the photosynthetic products of wheat under LTS are mainly transported to the central spikelets. The accumulation and transport of assimilates in wheat is the material basis for grain weight formation, and the position of wheat seeds determines the difference in the spatial distribution of grain transport processes and dry matter accumulation (Liu et al. 2016). In this experiment, the single grain weight in each spikelet was analysed, which showed that the grain weight of G1 and G2 was higher than that of G3 and G4, and G2 had the highest individual grain weight. Both wheat cultivars' G3 and G4 grain weights were more sensitive to LTS than other grain positions. In spring, LTS affects photosynthesis and assimilate transport to the grains in wheat, resulting in an uneven distribution of assimilates among the grains. This impediment limits the filling and enrichment of the inferior grains and, finally, affects the grain development of inferior grains (Xu et al. 2015a).

In conclusion, the results showed that LTS significantly decreased the two wheat cultivars' GNPS, TGW, and GYPP significantly. The distribution of grain number and grain weight at each spikelet position varied in a quadratic curve; the inflection point of both grain number and grain weight was at the central spikelet position. Within the same spikelet, the percentage of grain number and single grain weight at different grain positions were G2 ≥ G1 > G3 > G4. The grain positions of G3 and G4 showed higher sensitivity to LTS. Therefore, the grain yield can be increased by increasing the grain number and weight in G3 and G4 while maintaining the yield in G1 and G2.

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Received on: August 1, 2023
Accepted on: December 29, 2023
Published online: February 12, 2024