

外源 6-BA 缓解孕穗期低温胁迫对小麦光合性能、 灌浆特性和产量的影响

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摘要: 【目的】探究外源 6-BA 对孕穗期低温胁迫后小麦光合性能及产量下降的缓解效果。【方法】选用低温迟钝型品种烟农 19 和低温敏感型品种皖麦 52 进行盆栽试验。每盆装入 0—20 cm 大田耕层土壤, 然后将盆栽埋置于试验田内。于孕穗期, 将盆栽小麦移入人工生长室内进行低温胁迫处理, 设置两个处理温度: -2°C 、 0°C , 低温处理时间为 18:00—6:00, 其余时段 (6:00—18:00) 温度均为 5°C , 处理周期为 24 h, 处理结束后移回大田。设置 4 个 6-BA 溶液喷施浓度处理: 0 (CK)、10、20、30 mg/L, 低温处理后 1 天进行喷施。在抽穗期、灌浆期和成熟期, 取小麦旗叶样品, 测定 SPAD 值、光合性能指标、光合相关酶活性。开花后 10 天起, 取籽粒样品, 测定灌浆特性、产量及其构成因素。【结果】与 CK 相比, 喷施 6-BA 均提高了两个低温胁迫小麦旗叶 SPAD 值、净光合速率 (P_n)、气孔导度 (G_s)、蒸腾速率 (T_r) 以及最大光化学效率 (F_v/F_m); 喷施 6-BA 处理的小麦旗叶 RuBP 羧化酶活性在花后 10 天提高 12.72%~53.64%, PEP 羧化酶活性提高 6.40%~44.17%。低温胁迫处理后, 外源 6-BA 溶液提高了籽粒千粒重和灌浆速率。与对照相比, 烟农 19 喷施 6-BA 处理的灌浆平均速率和千粒重分别提高 1.12%~25.00% 和 1.32%~20.84%, 皖麦 52 分别提高了 2.75%~28.42% 和 6.26%~27.67%。外源 6-BA 对低温敏感的小麦皖麦 52 产量的修复效果优于对低温迟钝型小麦品种烟农 19。【结论】外源 6-BA 能够显著改善孕穗期低温后小麦旗叶的光合特性, 提高小麦籽粒灌浆能力, 减轻低温胁迫造成的减产。在本试验条件下, 20 mg/L 的外源 6-BA 缓解低温胁迫的效果最好。

关键词: 小麦; 孕穗期低温; 光合特性; 灌浆特性; 产量

Effects of exogenous 6-BA on alleviating the impacts of low-temperature stress during booting stage on photosynthetic performance, grain-filling characteristics, and yield of wheat

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Abstract: 【Objectives】We explored the alleviation effect of exogenous 6-benzylaminoadenine (6-BA) on the decline of photosynthetic performance and yield of wheat after low temperature (LT) stress at booting stage, and the appropriate spray concentration. 【Methods】A low temperature insensitive wheat variety ‘Yannong 19’ and a sensitive wheat variety ‘Wanmai 52’ were selected as the test materials in a pot experiment. The wheat pots were filled with the 0–20 cm layer soil, and then the potted plants were buried into soil during the wheat growing periods. At the booting stage, wheat pots were dug out and subjected to low temperature stress in a growing chamber for one day. The designed low temperatures were -2°C , and 0°C during 18:00–6:00, and 5°C during 6:00–18:00. Then the wheat pots were moved back to the field and sprayed with 10, 20 and 30 mg/L 6-BA solution, and the same amount of distilled water as control, respectively. At the booting, grain filling and maturing

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stage of wheat, the flag leaf samples were collected for the measurements of SPAD, photosynthetic parameters and relative enzyme activities. Grain samples were collected since the 10th day of anthesis for the determination of grain filling rate, at maturing stage, yield and 1000-grain weight were investigated. 【 **Results** 】 Compared with the control group, spraying 6-BA increased the SPAD value, net photosynthetic rate (P_n), stomatal conductance (G_s), transpiration rate (T_r) and maximum photochemical efficiency (F_v/F_m) of flag leaves of wheat subjected to low temperature stress, and increased the RuBP carboxylase activity by 12.72%–53.64% and the PEP carboxylase activity by 6.40%–44.17%. Compared with the control, spraying 6-BA increased the average grain filling rate and 1000-grain weight of Yannong 19 by 1.12%–25.00% and 1.32%–20.84%, respectively, and increased the average grain filling rate and 1000-grain weight of Wanmai 52 by 2.75%–28.42% and 6.26%–27.67%, respectively. The recovery effect of exogenous 6-BA on the yield of sensitive wheat variety ‘Wanmai 52’ was superior to that on the low temperature insensitive wheat variety ‘Yannong 19’. 【 **Conclusions** 】 Spraying 6-BA at booting stage can significantly improve the photosynthetic characteristics of wheat flag leaves after low temperature stress, speed up the grain filling rate and enhance the 1000-grain weight of wheat, thus reduce the yield loss caused by low temperature stress. In this experiment, 20 mg/L 6-BA solution shows the best mitigation effect on the effects of low temperature stress.

Key words: wheat; low temperature at booting; photosynthetic characteristics; grain filling characteristics; yield

春季低温严重影响着小麦的高产稳产^[1–4], 我国长江中下游地区春季低温常发生在3月底和4月初小麦孕穗期, 对小麦花粉母细胞发育产生严重不良影响^[5–6]。低温胁迫还会导致小麦旗叶受损, 使旗叶RuBP羧化酶和PEP羧化酶活性下降^[7–8], 降低光合速率和光化学效率^[9–10], 进而影响籽粒灌浆能力, 最终导致小麦减产^[11–12]。

6-苊氨基腺嘌呤(6-BA)是一种人工合成的细胞分裂素, 可以促进细胞分裂, 改善农作物生长, 提高作物对环境胁迫的抵抗能力^[13–16]。研究表明, 外源6-BA具有维持叶绿体结构稳定, 延缓叶绿素降解, 缓解叶片衰老的功能^[17–18]。喷施6-BA可以提高小麦RuBP羧化酶活性, 进而增强光合能力, 缓解逆境胁迫的影响^[19]。Wang等^[20]研究发现, 涝渍前喷施6-BA溶液能够使旗叶保持较高的光合速率, 从而减缓籽粒产量的损失。此外, 喷施6-BA可以增加基部和中部小穗的可育小花数量, 进而增加穗粒数, 也可以提高小麦平均灌浆速率和最大灌浆速率, 使籽粒更加饱满, 进而增加千粒重, 最终提高产量^[21–23]。Yang等^[17]在小麦开花期喷施6-BA溶液, 显著提高籽粒灌浆速率, 增加粒重, 有效缓解了高温胁迫造成的小麦减产。水稻孕穗期低温处理直接影响了花粉育性和籽粒结实率^[24–25]。而Wang等^[26]发现, 6-BA通过提高水稻穗粒数和粒重来提高产量, 且对低温敏感型水稻品种的缓解效果比对低温迟钝型品种更好。

6-BA已被证明能调节植物的生长, 有效缓解多种非生物胁迫, 如涝渍^[27]、干旱^[28]和盐胁迫^[29]。我们

前期研究发现, 外源6-BA可以有效缓解小麦孕穗期低温对旗叶光合能力及产量的损伤, 但其作用机理尚不清晰。本研究旨在分析低温胁迫后不同浓度的6-BA对小麦光合能力、灌浆特性和产量的影响, 探究外源6-BA缓解小麦低温胁迫伤害的生理基础, 为小麦减灾调控措施提供理论依据。

1 材料与方法

1.1 试验材料

选用低温迟钝型品种‘烟农19’(山东省烟台市农业科学研究院选育)和低温敏感型品种‘皖麦52’(安徽省宿州市种子公司选育)为试验材料。

1.2 试验设计

试验于2021年11月—2023年6月在安徽农业大学校内试验基地农萃园(31.83°N, 117.24°E)进行。土壤类型为黄棕壤, 其有机质含量为14.21 g/kg, 全氮含量为1.04 g/kg, 速效氮含量为149.61 mg/kg, pH为7.25。盆栽试验采用聚乙烯塑料桶, 高30 cm、直径30 cm, 桶底中央有6个排水孔。每盆装0—20 cm大田耕作层土壤9 kg, 将盆栽埋于试验田中, 盆栽顶部边缘与盆外土壤高度持平。小麦播种前每盆施入有机肥75.00 g、N 2.23 g、P₂O₅ 1.70 g、K₂O 2.12 g, 播种后再覆0.9 kg沙土。于拔节期, 每盆追施N 2.07 g, 待盆栽齐苗后间苗, 每盆留苗10株。

分别于2022年3月18日和2023年3月21日小麦幼穗发育至药隔期, 将盆栽小麦移入人工气候室

内进行低温处理, 处理时间为当天 18:00 至次日早上 6:00。设置-2℃、0℃ 两个低温处理, 处理期间相对湿度 70%、光照强度 0 lx; 次日早上 6:00 至 18:00, 温度设为 5℃, 相对湿度 70%, 光照强度 12000 lx。处理 24 h 结束后移回大田, 一天后分别喷施浓度为 10、20 及 30 mg/L 的 6-BA 溶液 (记为 B₁、B₂、B₃), 以喷施等量蒸馏水 (CK) 作为对照, 每个浓度总喷施量为 1.5 L, 每个处理 20 盆, 直至叶片正反两面均湿润为止。

1.3 测定项目与方法

在小麦抽穗期、开花期和灌浆期, 每个处理分别选取 10 盆生长发育一致的小麦, 于天气晴朗的上午 9:00—11:00 测定旗叶 SPAD 值、光合参数和最大光化学效率。在小麦开花期选取同一天开花并且长势一致的小麦穗挂牌标记。从开花后第 10 天开始, 每 5 天随机从标记的小麦中挑选出大小一致的 10 片旗叶和 10 个麦穗样品, 将旗叶样品放到液氮 (-80℃) 中速冻保存, 用于光合相关酶活性的测定。剥出麦穗样品中的籽粒, 105℃ 下杀青 30 min 后烘干 (烘箱 75℃), 用于灌浆特性的测定。

每个处理预留出 6 盆小麦, 不对其进行破坏性取样, 用于后续产量的测定。

1.3.1 光合参数测定 旗叶 SPAD 值采用叶绿素含量测定仪 (SPAD-502 Konica Minolta, Japan) 测定, 分别在小麦抽穗期、开花期、灌浆期, 每个叶片的上中下位置测 3 点, 然后取平均值, 同一处理重复 10 次。

光合效率指标分别在小麦抽穗期、开花期、灌浆期测定。选择标记的小麦旗叶, 用带有 2 cm×3 cm 标准叶室的光合作用-荧光系统 (Li-6400XT, Li-Cor Inc, USA), 测定旗叶的最大光化学效率 (F_v/F_m) 和净光合速率 (P_n)、气孔导度 (G_s)、蒸腾速率 (T_r)。

1.3.2 RuBP 羧化酶和 PEP 羧化酶活性测定 称取 0.1 g 旗叶鲜样在冷冻研磨机上充分研磨, 再加入 1 mL pH 7.4 的 PBS 缓冲液, 震荡后以 4℃ 8000 r/min 离心 30 min, 取上清液, 暂存于 4℃ 冰箱。RuBP 羧化酶活性参考裴建峰等^[30]方法测定, PEP 羧化酶活性参考 Behera 等^[31]的方法测定。

1.3.3 灌浆特性测定 开花后 10 天开始取样, 每 5 天在每个处理中随机取出籽粒, 籽粒杀青后称重计算千粒重。用 Logistic 方程拟合灌浆过程: $Y=K/(1+e^{a-bt})$, 其中 Y 为籽粒千粒重 (g), K 为拟合的最大千粒重, t 为花后天数, a 和 b 为参数, e (2.71828)

为自然对数的底数, 即可推导出下列参数。

灌浆持续天数 (T):

$$T = \left(\ln \frac{1}{9} - a \right) / b$$

平均灌浆速率 (R):

$$R = K/T$$

最大灌浆速率 ($R_{\max}$):

$$R_{\max} = -Kb/4$$

灌浆渐增期持续时间 (T_1):

$$T_1 = (a - 1.317)/b$$

灌浆快增期持续时间 (T_2):

$$T_2 = (a + 1.317)/b - (a - 1.317)b$$

灌浆缓增期持续时间 (T_3):

$$T_3 = T - T_1 - T_2$$

籽粒最大灌浆速率出现的时间 ($T_{\max}$):

$$T_{\max} = -a/b$$

1.3.4 产量及产量构成因素测定 待成熟期, 测定提前预留的小麦的单株穗数、穗粒数、千粒重, 并计算单盆产量。

1.4 数据分析

光合特性数据采用 SPSS 26.0 软件作统计分析, 采用 LSD 法检验差异显著性。酶活性采用 Origin 2018 作图。

2 结果与分析

2.1 6-BA 对孕穗期低温胁迫后小麦旗叶光合特性的影响

2.1.1 SPAD 值 由图 1 可知, 喷施 6-BA 提高了小麦旗叶 SPAD 值。低温-2℃ 和 0℃ 处理下, B₂ 处理对 SPAD 值的提升最显著, 两年试验结果一致。以 2023 年开花期为例, -2℃ 低温胁迫后烟农 19 和皖麦 52 的 SPAD 值较对照分别提高了 5.13%~9.89% 和 8.31%~11.52%, 0℃ 低温胁迫后提升幅度分别是 1.99%~5.61% 和 2.60%~6.59%。-2℃ 低温处理后, 喷施 6-BA 的处理效果更为显著, 且低温敏感型品种皖麦 52 旗叶 SPAD 值更高。

2.1.2 最大光化学效率 (F_v/F_m) 由图 2 可知, 喷施 6-BA 溶液显著提高了低温胁迫后小麦旗叶的 F_v/F_m 。低温胁迫后, B₂ 处理的 F_v/F_m 显著高于 B₁ 和 B₃ 处理, B₁、B₃ 处理间差异不显著 (除皖麦 52 灌浆期外)。以开花期 B₂ 处理为例, -2℃ 低温胁迫后烟农

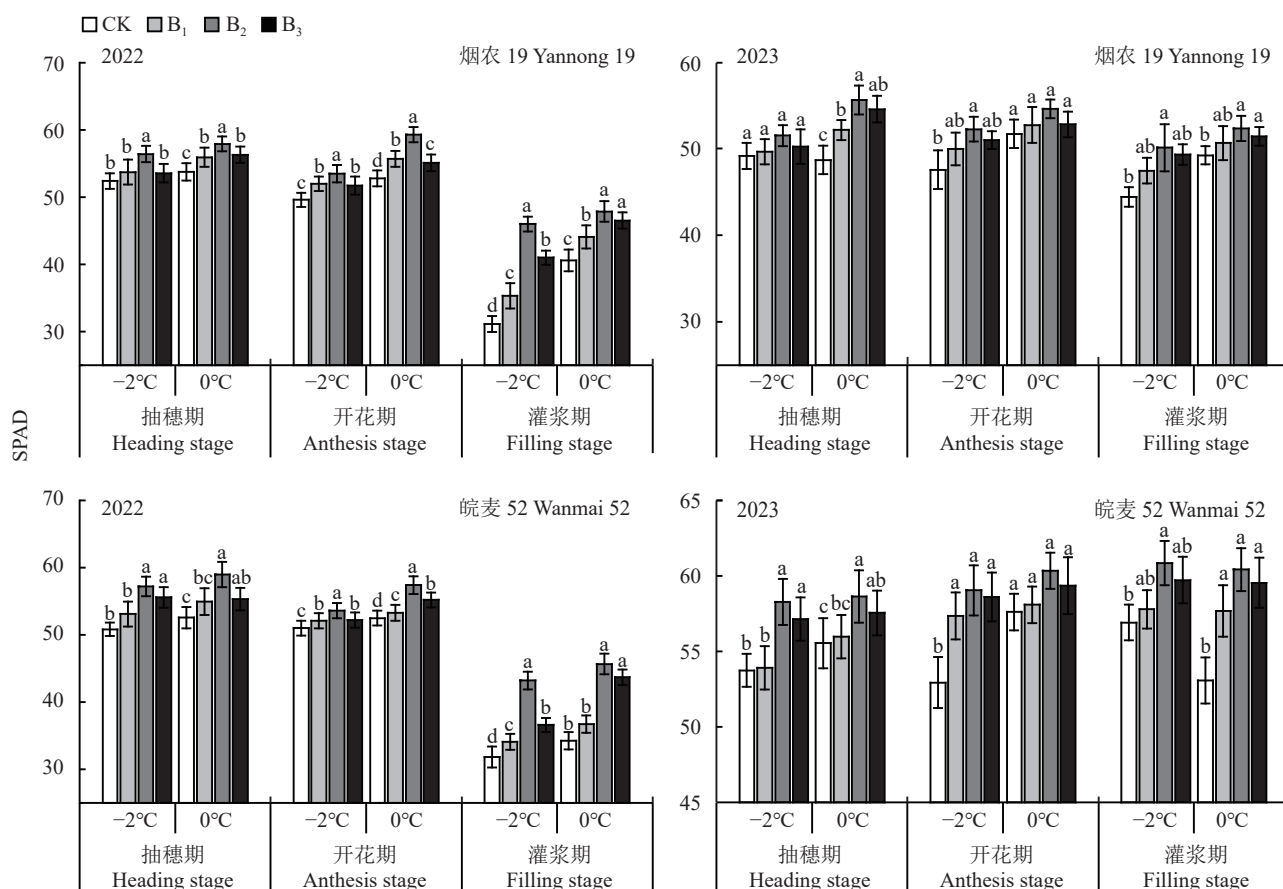


图 1 6-BA 对孕穗期低温胁迫后小麦旗叶 SPAD 值的影响

Fig. 1 Effects of 6-BA on SPAD values of wheat flag leaves after low temperature stress at booting stage

注: CK 为蒸馏水对照, B₁、B₂、B₃ 分别为 6-BA 溶液喷施浓度 10、20、30 mg/L。柱上不同小写字母表示同一时期同一温度不同处理间差异显著 ($P < 0.05$)。

Note: CK is distilled water control, and the spraying concentration of 6-BA in B₁, B₂ and B₃ are 10, 20, and 30 mg/L, respectively. Different small letters above the bars indicate significant difference among treatments under the same stage and temperature ($P < 0.05$).

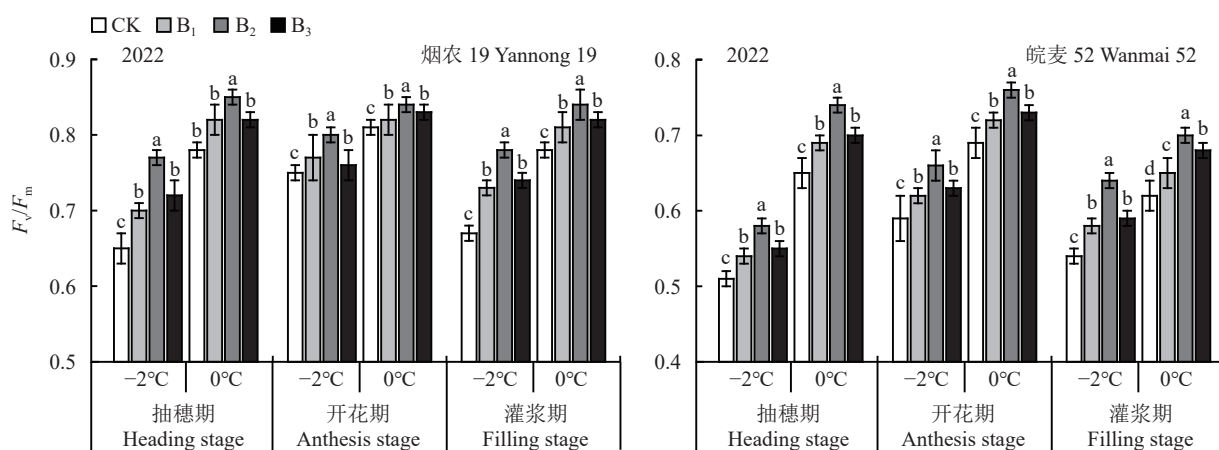


图 2 6-BA 对孕穗期低温胁迫后小麦旗叶最大光化学效率 (F_v/F_m) 的影响

Fig. 2 Effects of 6-BA on maximum photochemical efficiency (F_v/F_m) of wheat flag leaves after low temperature stress at booting stage

注: CK 为喷施蒸馏水, B₁、B₂、B₃ 分别为 6-BA 溶液喷施浓度 10、20、30 mg/L。柱上不同小写字母表示同一时期同一温度不同处理间差异显著 ($P < 0.05$)。

Note: Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B₁, B₂ and B₃ are 10, 20, and 30 mg/L, respectively. Different small letters above the bars indicate significant difference among treatments under the same stage and temperature ($P < 0.05$).

表 1 6-BA 对孕穗期低温胁迫后小麦旗叶光合参数的影响
Table 1 Effects of 6-BA on photosynthetic parameters of wheat flag leaves after low temperature stress at booting stage

年份 Year	品种 Cultivar	温度 Temperature (°C)	处理 Treatment	抽穗期 Heading stage			开花期 Anthesis stage			灌浆期 Grain filling stage		
				P_n μmol/(m ² ·s)	G_s mol/(m ² ·s)	T_r mmol/(m ² ·s)	P_n μmol/(m ² ·s)	G_s mol/(m ² ·s)	T_r mmol/(m ² ·s)	P_n μmol/(m ² ·s)	G_s mol/(m ² ·s)	T_r mmol/(m ² ·s)
2022	烟农19 Yannong 19	0	CK	14.66±2.28 b	0.17±0.01 c	3.48±0.10 c	14.25±0.86 b	0.15±0.01 c	4.42±0.03 c	10.92±0.53 c	0.10±0.00 b	3.04±0.08 c
			B ₁	17.36±0.99 a	0.18±0.01 bc	4.56±0.17 b	14.83±1.12 b	0.18±0.01 b	4.71±0.22 bc	11.14±0.53 bc	0.14±0.00 ab	3.43±0.03 b
			B ₂	21.70±0.74 a	0.22±0.01 a	5.62±0.05 a	20.05±1.39 a	0.22±0.01 a	5.75±0.20 a	13.89±0.14 a	0.18±0.02 a	4.07±0.06 a
			B ₃	19.26±0.14 a	0.21±0.02 ab	5.08±0.16 b	19.98±0.72 ab	0.21±0.01 ab	5.20±0.21 ab	12.76±0.18 ab	0.15±0.02 a	3.57±0.07 b
		-2	CK	10.41±0.28 c	0.12±0.01 b	3.12±0.10 c	9.50±1.35 c	0.12±0.01 b	3.47±0.19 d	8.84±0.64 c	0.08±0.02 b	2.36±0.04 c
			B ₁	12.02±0.31 bc	0.13±0.02 ab	3.69±0.10 bc	10.03±0.16 bc	0.13±0.01 b	4.38±0.11 c	9.20±1.02 bc	0.11±0.01 ab	2.63±0.17 c
			B ₂	14.49±0.86 a	0.16±0.01 a	4.43±0.26 a	14.06±1.48 a	0.16±0.01 a	5.85±0.19 a	12.06±0.74 a	0.14±0.01 a	3.95±0.09 a
			B ₃	12.31±0.42 b	0.14±0.01 ab	4.10±0.24 ab	13.29±0.66 ab	0.15±0.01 a	4.94±0.31 b	11.20±0.18 ab	0.12±0.00 a	3.37±0.04 b
		0	CK	14.36±1.10 b	0.13±0.01 c	3.33±0.10 c	13.17±0.19 b	0.13±0.00 c	4.07±0.17 c	9.67±0.32 c	0.10±0.01 b	2.51±0.09 c
			B ₁	16.57±1.68 a	0.14±0.02 c	4.19±0.25 b	15.49±0.39 b	0.15±0.01 b	4.52±0.16 bc	10.31±0.27 bc	0.11±0.01 ab	3.01±0.32 b
			B ₂	18.84±0.53 a	0.23±0.01 a	5.10±0.13 a	17.43±0.04 a	0.21±0.00 a	5.64±0.24 a	12.29±0.69 a	0.15±0.01 a	4.68±0.20 a
			B ₃	17.66±0.20 a	0.20±0.01 b	4.66±0.36 b	16.31±1.47 ab	0.18±0.01 ab	5.06±0.25 ab	11.97±0.69 ab	0.14±0.00 a	3.78±0.02 b
	皖麦52 Wanmai 52	-2	CK	12.33±1.05 c	0.12±0.01 b	2.97±0.10 c	11.74±0.83 c	0.12±0.01 b	3.16±0.24 d	7.30±0.31 c	0.08±0.01 b	2.07±0.04 d
			B ₁	12.91±0.65 bc	0.13±0.01 b	3.47±0.27 bc	12.19±0.08 bc	0.12±0.01 b	4.14±0.09 c	8.81±0.96 bc	0.11±0.00 ab	2.51±0.10 c
			B ₂	15.50±0.69 a	0.19±0.01 a	4.24±0.08 a	14.90±1.60 a	0.18±0.02 a	5.54±0.17 a	11.91±0.59 a	0.14±0.00 a	3.86±0.01 a
			B ₃	14.49±2.00 a	0.18±0.01 a	3.51±0.23 ab	13.64±1.09 ab	0.17±0.01 a	4.66±0.14 b	10.08±0.36 ab	0.13±0.01 a	3.14±0.09 b

续表 1 Table 1 continued

年份 Year	品种 Cultivar	温度 Temperature (°C)	处理 Treatment	抽穗期 Heading stage			开花期 Anthesis stage			灌浆期 Grain filling stage		
				P_n μmol/(m ² ·s)	G_s mol/(m ² ·s)	T_r mmol/(m ² ·s)	P_n μmol/(m ² ·s)	G_s mol/(m ² ·s)	T_r mmol/(m ² ·s)	P_n μmol/(m ² ·s)	G_s mol/(m ² ·s)	T_r mmol/(m ² ·s)
2023	烟农19 Yannong 19	0	CK	13.39±2.50 b	0.15±0.00 c	2.13±0.31 c	12.41±0.46 b	0.14±0.00 c	3.02±0.19 c	9.83±1.01 c	0.09±0.01 b	1.64±0.10 c
			B ₁	16.50±1.11 a	0.18±0.01 bc	2.84±0.24 b	14.01±0.90 b	0.15±0.01 bc	3.67±0.18 bc	10.14±0.28 bc	0.12±0.01 ab	1.95±0.03 b
			B ₂	19.74±0.63 a	0.21±0.01 a	3.95±0.02 a	18.61±0.04 a	0.18±0.01 a	4.59±0.18 a	14.55±0.94 a	0.15±0.02 a	2.98±0.01 a
			B ₃	16.45±2.24 a	0.19±0.00 ab	3.11±0.30 b	17.70±0.53 ab	0.17±0.01 ab	4.16±0.12 ab	12.63±0.41 ab	0.13±0.01 a	2.47±0.08 b
			-2	12.78±1.41 c	0.13±0.01 c	2.27±0.20 c	9.54±0.21 c	0.12±0.01 b	2.85±0.07 d	7.01±0.54 c	0.07±0.00 b	1.27±0.05 d
			B ₁	13.89±0.20 bc	0.15±0.02 bc	2.65±0.26 bc	14.44±0.39 bc	0.13±0.01 b	3.25±0.02 c	8.64±0.64 bc	0.08±0.01 ab	1.83±0.02 c
			B ₂	17.78±0.03 a	0.19±0.01 a	3.64±0.21 a	16.65±0.48 a	0.17±0.00 a	4.80±0.02 a	11.43±0.95 a	0.14±0.00 a	2.46±0.09 a
			B ₃	16.09±0.88 a	0.17±0.01 ab	3.22±0.39 ab	15.87±0.79 ab	0.16±0.01 a	4.05±0.12 b	10.17±0.35 ab	0.13±0.01 a	2.05±0.03 b
			0	9.88±0.35 b	0.12±0.01 c	2.02±0.35 c	9.17±0.39 b	0.11±0.01 c	2.98±0.05 c	7.08±0.05 c	0.08±0.01 b	1.38±0.09 c
			B ₁	12.57±0.67 a	0.15±0.01 bc	2.56±0.13 b	10.12±0.32 b	0.14±0.02 b	3.26±0.03 bc	8.28±0.63 bc	0.10±0.01 ab	1.86±0.09 b
皖麦52 Wanmai 52			B ₂	14.94±0.46 a	0.18±0.01 a	3.76±0.18 a	13.72±1.44 a	0.16±0.01 a	4.39±0.18 a	11.66±0.47 a	0.13±0.02 a	2.80±0.02 a
			B ₃	13.19±0.60 a	0.16±0.00 ab	2.83±0.19 b	12.23±0.83 ab	0.15±0.01 ab	3.91±0.17 ab	10.12±0.52 ab	0.12±0.01 a	2.06±0.08 b
			-2	8.24±1.21 c	0.11±0.00 b	1.85±0.21 c	8.06±0.40 c	0.10±0.01 b	2.03±0.12 d	6.03±0.04 c	0.07±0.01 b	1.42±0.01 c
			B ₁	9.51±0.14 bc	0.13±0.01 ab	2.10±0.04 bc	9.10±0.51 bc	0.11±0.00 b	3.14±0.04 c	6.21±0.87 bc	0.08±0.01 ab	1.53±0.06 c
			B ₂	12.26±0.63 a	0.16±0.02 a	3.22±0.06 a	11.62±1.28 a	0.15±0.01 a	4.42±0.14 a	10.20±0.35 a	0.12±0.01 a	2.46±0.08 a
			B ₃	11.55±0.51 ab	0.14±0.00 ab	2.61±0.09 ab	11.01±0.97 ab	0.14±0.01 a	3.94±0.10 b	9.75±0.65 ab	0.11±0.01 a	1.88±0.08 b

注: P_n —净光合速率; G_s —气孔导度; T_r —蒸腾速率。CK为喷施蒸馏水, B₁、B₂、B₃分别为6-BA溶液喷施浓度10、20、30 mg/L。同列数据后不同小写字母表示同一品种同一温度不同处理间差异显著($P<0.05$)。
Note: P_n —Net photosynthetic rate; G_s —Stomatal conductance; T_r —Transpiration rate. Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B₁, B₂ and B₃ are 10, 20, and 30 mg/L, respectively. Different lowercase letters after data in the same column indicate significant difference among treatments under the same stage and temperature ($P<0.05$).

19 和皖麦 52 的 F_v/F_m 较对照分别提升了 6.67% 和 11.86%, 0℃ 低温胁迫后, 分别提升了 3.70% 和 10.14%。在 -2℃ 低温胁迫下, 6-BA 的处理效果更为显著, 尤其是在低温敏感型品种皖麦 52 上, 其 F_v/F_m 的提升幅度高于低温迟钝型品种烟农 19。

2.1.3 光合参数 由表 1 可知, 随着生育时期的推移, 旗叶的净光合速率 (P_n) 和气孔导度 (G_s) 逐渐降低, 蒸腾速率 (T_r) 先上升后下降, 在开花期达到峰值。外源喷施不同浓度的 6-BA 溶液均能提高小麦旗叶的 P_n 、 G_s 、 T_r , 以 B_2 处理的提升效果最为显著, 且对低温敏感型小麦品种皖麦 52 的修复效果更为明显, 两年试验变化一致。以 2022 年开花期 B_2 处理为例, -2℃ 低温处理下, 烟农 19 的 P_n 、 G_s 、 T_r 较对照分别提高了 27.24%、33.33%、68.59%, 皖麦 52 分别提升了 38.73%、50.00%、75.32%; 0℃ 低温处理下, 烟农 19 的 P_n 、 G_s 、 T_r 较对照分别提高了 19.65%、26.67%、30.09%; 皖麦 52 分别提升了 32.35%、38.46%、38.57%。

2.1.4 RuBP 羧化酶活性 由图 3 可知, 小麦旗叶

光合相关酶 RuBP 羧化酶活性在开花后逐渐下降, 喷施 6-BA 溶液显著提高其活性 ($P<0.05$)。低温胁迫后, B_2 处理的 RuBP 羧化酶活性显著高于 B_3 处理, B_1 处理最低 (0℃ 处理烟农 19 在开花后 20~25 天、-2℃ 处理烟农 19 在开花后 25 天、0℃ 处理皖麦 52 在开花后 25 天除外)。以 B_2 处理花后 10 天为例, -2℃ 低温胁迫后, 烟农 19 和皖麦 52 的旗叶 RuBP 羧化酶活性较对照分别提高了 43.61% 和 53.64%; 0℃ 低温胁迫后, 分别提高了 36.57% 和 43.58%。综合来看, 花后 10 天喷施 6-BA 溶液可以使小麦旗叶 RuBP 羧化酶活性较对照提高 12.72%~53.64%。喷施 6-BA 后 -2℃ 低温处理下旗叶 RuBP 羧化酶活性的提升幅度更高, 且皖麦 52 的 RuBP 羧化酶活性更高。

2.1.5 PEP 羧化酶活性 由图 4 可知, 小麦旗叶光合相关酶 PEP 羧化酶活性在开花后呈下降趋势, 而 6-BA 喷施显著提高了 PEP 羧化酶活性 ($P<0.05$)。低温处理后, B_2 处理的 PEP 羧化酶活性显著高于 B_3 处理, B_1 处理最低 (-2℃ 处理烟农 19 在开花后 25 天除外)。6-BA 在 -2℃ 低温处理后对旗叶 PEP 羧化酶

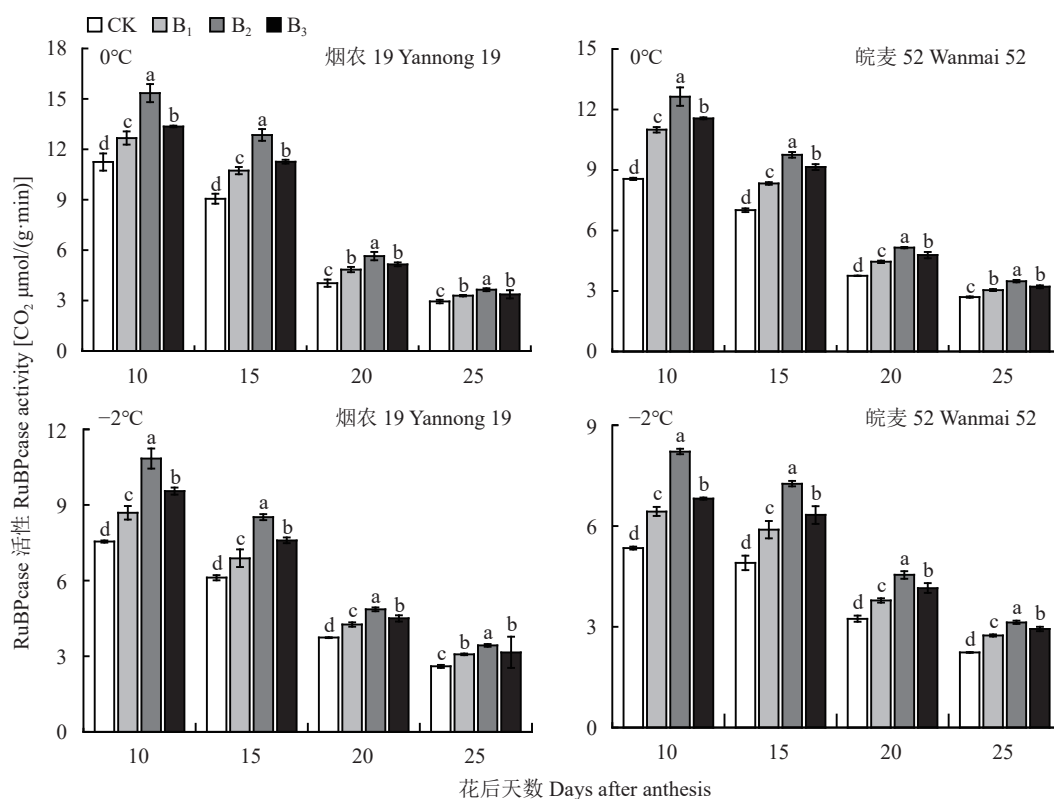


图 3 6-BA 对孕穗期低温胁迫后小麦旗叶 RuBP 羧化酶活性的影响

Fig. 3 Effects of 6-BA on RuBPcase activity in flag leaves of wheat after low temperature stress at booting stage

注: CK 为喷施蒸馏水, B_1 、 B_2 、 B_3 分别为 6-BA 溶液喷施浓度 10、20、30 mg/L。柱上不同小写字母表示同一天处理间差异显著 ($P<0.05$)。

Note: Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B_1 , B_2 and B_3 are 10, 20, and 30 mg/L, respectively. Different small letters above the bars indicate significant difference among treatments on the same day ($P<0.05$).

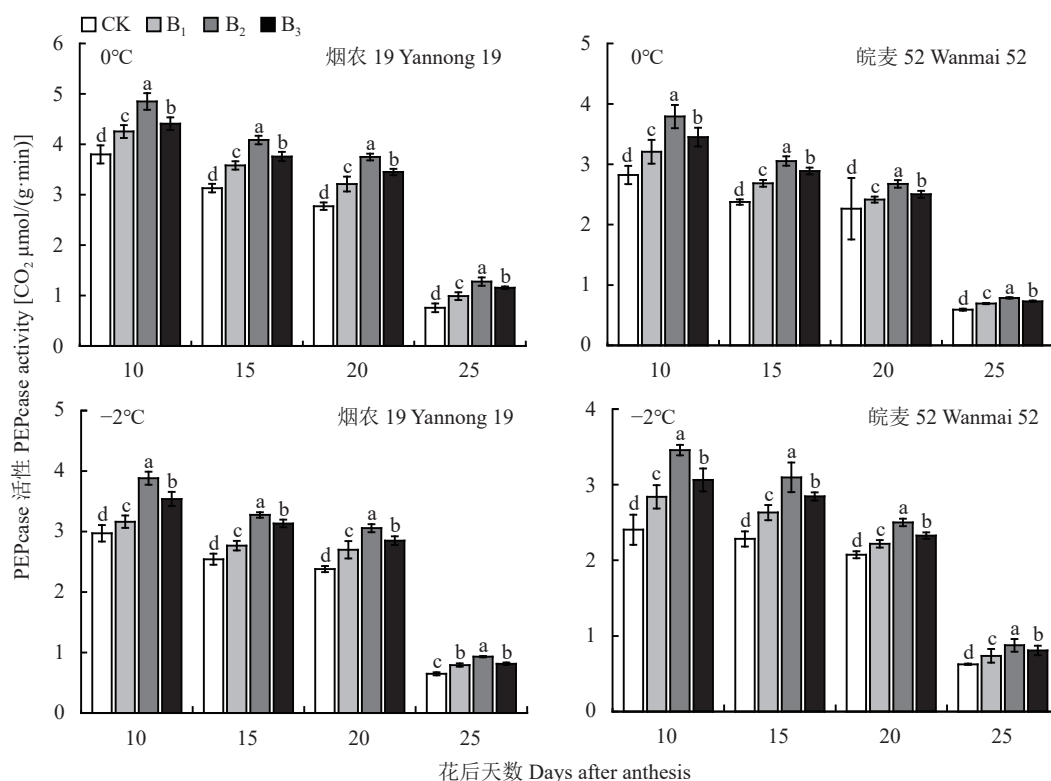


图4 6-BA对孕穗期低温胁迫后小麦旗叶PEP羧化酶活性的影响

Fig. 4 Effect of 6-BA on PEP carboxylase activity in flag leaves of wheat after low temperature stress at booting stage

注: CK为喷施蒸馏水, B₁、B₂、B₃分别为6-BA溶液喷施浓度10、20、30 mg/L。柱上不同小写字母表示同一天处理间差异显著($P < 0.05$)。

Note: Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B₁, B₂ and B₃ are 10, 20, and 30 mg/L, respectively. Different lowercase letters above the bars indicate significant difference among treatments on the same day ($P < 0.05$).

活性的提升效果更为显著,且皖麦52喷施6-BA后PEP羧化酶活性高于烟农19。以B₂处理花后10天为例,−2℃低温胁迫后,烟农19和皖麦52旗叶PEP羧化酶活性较对照分别提高了30.64%和44.17%;0℃低温胁迫后,烟农19和皖麦52分别提高了27.63%和34.40%。综合来看,花后10天喷施6-BA溶液可以使小麦旗叶PEP羧化酶活性较对照提高6.40%~44.17%。

2.2 6-BA对孕穗期低温胁迫后小麦灌浆特性的影响

由图5可知,两年试验变化趋势相同,千粒重呈“S”形曲线增长。开花后10~15天烟农19各处理间千粒重无显著差异(2023年0℃处理花后15天除外),B₂、B₃处理下皖麦52的千粒重显著高于B₁,B₂、B₃处理间无显著差异;开花后20~30天两品种B₂处理的千粒重显著高于B₁、B₃处理(2023年烟农19花后20天除外);开花后35天两品种B₂、B₃处理的千粒重均显著高于B₁处理,B₂、B₃处理间无显著差异(0℃处理烟农19和皖麦52除外)。以2022年

开花后25天B₂处理为例,−2℃低温处理后,烟农19和皖麦52的千粒重较对照分别提高了21.18%和24.64%;0℃低温处理后,分别提高了16.00%和23.20%。

由图6可知,籽粒灌浆速率呈先增加后下降的趋势。开花后10~15天烟农19各处理间的灌浆速率无显著差异(0℃处理花后15天除外),B₂、B₃处理的皖麦52灌浆速率显著高于B₁处理,B₂、B₃处理间无显著差异(0℃处理花后10天除外);开花后20~30天两品种B₂处理的灌浆速率显著高于B₁、B₃处理(2023年−2℃处理皖麦52除外);开花后35天两品种B₂、B₃处理的灌浆速率显著高于B₁处理,B₂、B₃处理间无显著差异(0℃处理烟农19和皖麦52除外)。以2022年开花后25天B₂处理为例,−2℃低温处理后,烟农19和皖麦52的灌浆速率较对照分别提高了12.50%和20.00%;0℃低温处理后,分别提高了12.31%和16.39%。综合来看,喷施6-BA溶液可以使烟农19小麦籽粒灌浆速率较对照提高1.12%~25.00%,皖麦52小麦籽粒灌浆速率

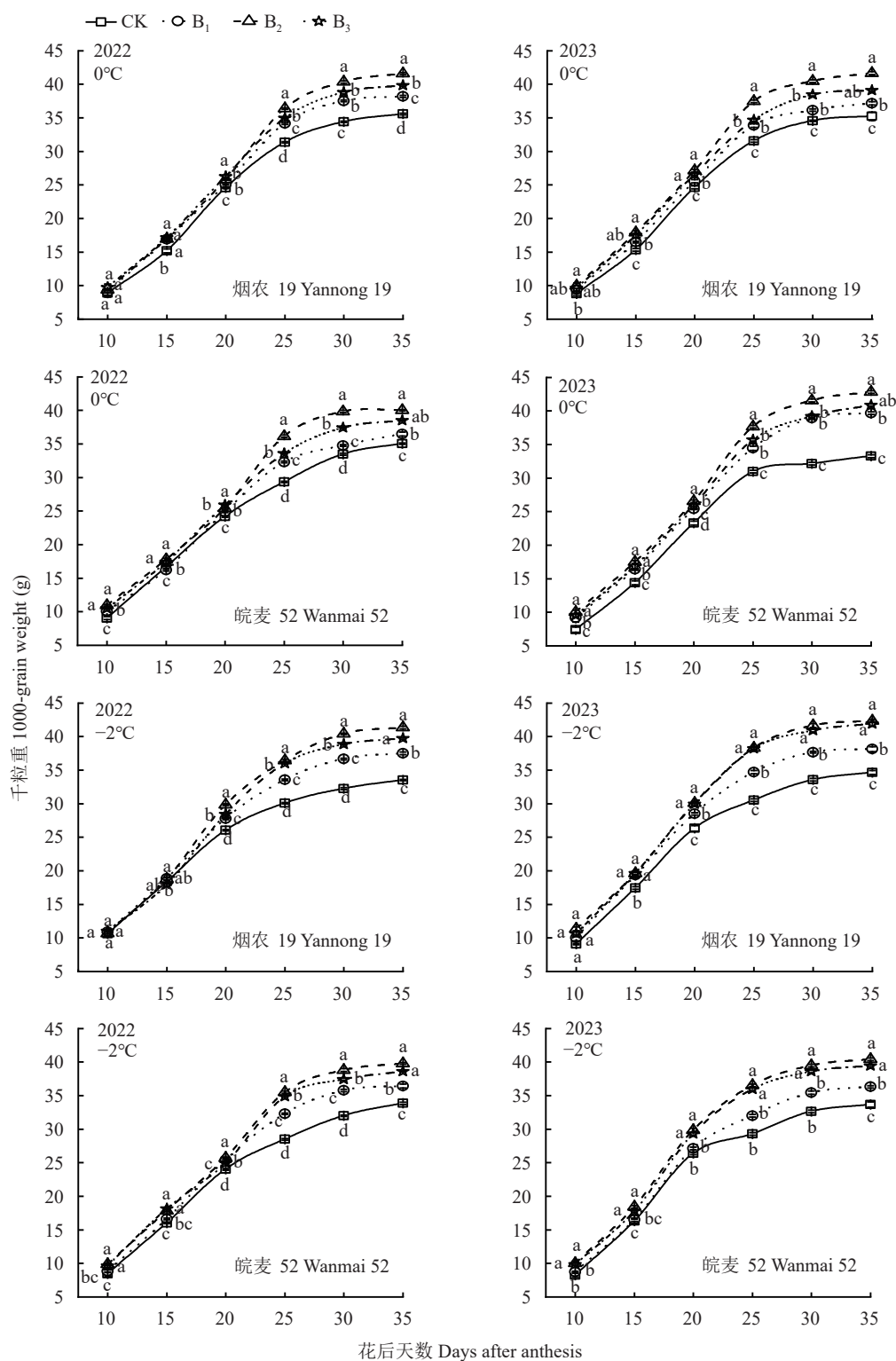


图 5 6-BA 喷施对孕穗期低温胁迫后灌浆期小麦籽粒千粒重的影响

Fig. 5 Effects of 6-BA on 1000-grain weight of wheat at grain-filling stage after low temperature stress at booting stage

注: CK 为喷施蒸馏水, B₁、B₂、B₃ 分别为 6-BA 溶液喷施浓度 10、20、30 mg/L。图中不同小写字母表示同一天处理间差异显著 ($P < 0.05$)。

Note: Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B₁, B₂ and B₃ are 10, 20, and 30 mg/L, respectively. Different lowercase letters beside the lines in the figure indicate significant differences among treatments on the same day ($P < 0.05$).

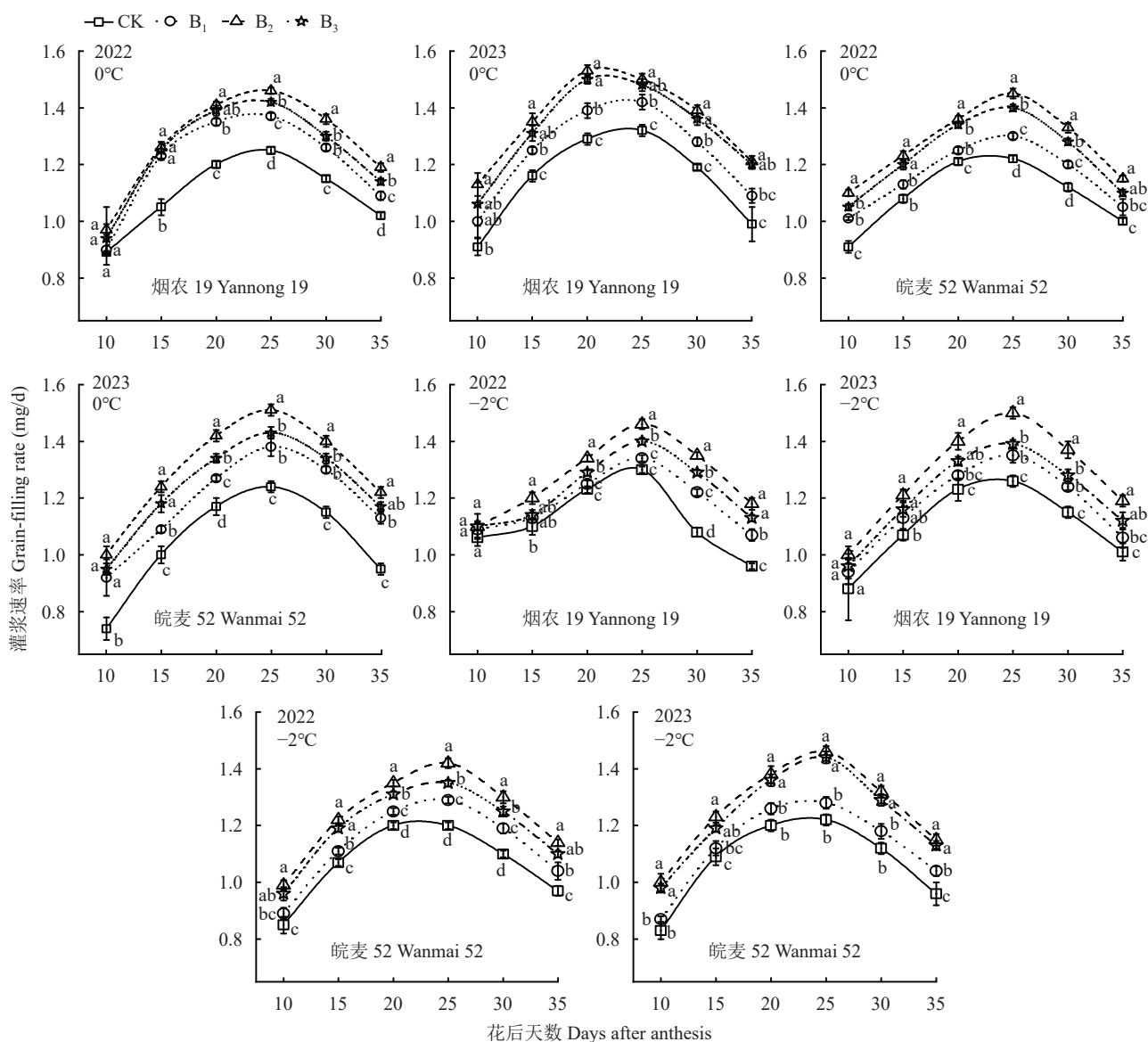


图 6 6-BA 对孕穗期低温胁迫后小麦籽粒灌浆速率的影响

Fig. 6 Effects of 6-BA on grain-filling rate of wheat after low temperature stress at booting stage

注: CK 为喷施蒸馏水, B_1 、 B_2 、 B_3 分别为 6-BA 溶液喷施浓度 10、20、30 mg/L。图中不同小写字母表示同一天处理间差异显著 ($P < 0.05$)。

Note: Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B_1 , B_2 and B_3 are 10, 20, and 30 mg/L, respectively. Different lowercase letters beside the lines in the figure indicate significant differences among treatments on the same day ($P < 0.05$).

较对照提高 2.75%~28.42%。

由表 2 可知, 用 Logistic 方程拟合籽粒千粒重, 决定系数均高于 0.98。两年试验中均表现为快增期 (T_3) 最长, 缓增期 (T_2) 次之, 渐增期 (T_1) 最短。喷施 6-BA 溶液延长了小麦籽粒的灌浆持续期 (T)、 T_2 和 T_3 , 提高了灌浆平均速率 (R) 与最大灌浆速率 ($R_{\max}$) ($P < 0.05$)。其中, B_2 处理对小麦籽粒灌浆影响最大, 尤其在 -2°C 低温处理后, 6-BA 的处理效果更为显著。以 2022 年 B_2 处理的烟农 19 为例, -2°C 低温处理后烟农 19 的 T 、 R 和 $R_{\max}$ 较对照分别增加了

13.87%、16.36% 和 12.22%。

2.3 产量及产量构成因素

由表 3 可知, 喷施 6-BA 溶液提高了低温处理后小麦单株穗数、穗粒数、千粒重和单盆产量。 B_2 处理在穗粒数、千粒重和单盆产量方面显著高于 B_3 处理, B_1 处理最低 (2022 年 0°C 处理烟农 19 的千粒重和单盆产量除外)。烟农 19 各处理间的单株穗数多无显著差异, B_2 处理下皖麦 52 的单株穗数显著高于 B_1 、 B_3 处理, B_1 、 B_3 处理间无显著差异 (2023 年 0°C 处理除外)。6-BA 处理对低温敏感型品种皖麦

表 2 6-BA 对孕穗期低温胁迫后小麦灌浆特性的影响

Table 2 Effects of 6-BA on wheat filling characteristics after low temperature stress at booting stage

品种 Cultivar	温度 (°C) Temperature	处理 Treatment	拟合方程 Fitting equation	R^2	T (d)	T_1 (d)	T_2 (d)	T_3 (d)	$R_{\max}$	R
2022										
烟农19 Yannong 19	0	CK	$Y=36.8682/(1+e^{3.1753-0.1931t})$	0.998	40.26	9.63	13.65	16.98	1.78	0.91
		B ₁	$Y=40.0769/(1+e^{3.1864-0.1904t})$	0.996	40.87	9.82	13.83	17.22	1.91	0.98
		B ₂	$Y=43.9529/(1+e^{3.2330-0.1849t})$	0.996	42.34	10.36	14.24	17.73	2.03	1.04
		B ₃	$Y=41.7903/(1+e^{3.1128-0.1850t})$	0.994	41.66	9.71	14.23	17.72	1.96	1.01
	-2	CK	$Y=33.8962/(1+e^{2.7298-0.1942t})$	0.999	37.72	7.27	13.56	16.88	1.65	0.90
		B ₁	$Y=39.0050/(1+e^{2.7668-0.1800t})$	0.999	40.90	8.05	14.63	18.21	1.76	0.95
		B ₂	$Y=43.7776/(1+e^{2.9300-0.1752t})$	0.996	42.95	9.21	15.03	18.71	1.92	1.01
		B ₃	$Y=41.8057/(1+e^{2.9443-0.1811t})$	0.994	41.63	8.98	14.54	18.10	1.89	1.00
皖麦52 Wanmai 52	0	CK	$Y=36.2853/(1+e^{2.8937-0.1809t})$	0.999	41.40	8.71	14.56	18.12	1.64	0.88
		B ₁	$Y=38.1406/(1+e^{2.8977-0.1782t})$	0.997	42.05	8.87	14.78	18.39	1.70	0.91
		B ₂	$Y=43.2076/(1+e^{2.9095-0.1719t})$	0.988	43.66	9.26	15.32	19.07	1.86	0.99
		B ₃	$Y=40.7062/(1+e^{2.8528-0.1732t})$	0.998	43.00	8.87	15.21	18.93	1.76	0.95
	-2	CK	$Y=34.3716/(1+e^{3.0997-0.1977t})$	0.999	38.92	9.02	13.32	16.58	1.70	0.88
		B ₁	$Y=37.7547/(1+e^{3.1721-0.1961t})$	0.999	39.61	9.46	13.43	16.72	1.85	0.95
		B ₂	$Y=41.9431/(1+e^{3.0384-0.1814t})$	0.995	42.08	9.49	14.52	18.07	1.90	1.00
		B ₃	$Y=40.4914/(1+e^{3.0002-0.1821t})$	0.992	41.71	9.24	14.46	18.00	1.84	0.97
2023										
烟农19 Yannong 19	0	CK	$Y=36.5861/(1+e^{3.2287-0.1982t})$	0.998	39.47	9.64	13.29	16.54	1.81	0.93
		B ₁	$Y=38.6148/(1+e^{3.1796-0.1959t})$	0.997	39.69	9.51	13.44	16.73	1.89	0.97
		B ₂	$Y=43.8315/(1+e^{3.1750-0.1871t})$	0.999	41.53	9.93	14.08	17.52	2.05	1.05
		B ₃	$Y=40.6464/(1+e^{3.1677-0.1944t})$	0.989	39.93	9.52	13.55	16.86	1.97	1.02
	-2	CK	$Y=35.0024/(1+e^{3.1250-0.2085t})$	0.997	37.03	8.67	12.63	15.72	1.82	0.94
		B ₁	$Y=39.0273/(1+e^{3.1505-0.2085t})$	0.999	37.15	8.79	12.63	15.72	2.03	1.05
		B ₂	$Y=43.9980/(1+e^{3.0699-0.1936t})$	0.992	38.46	8.79	13.22	16.45	2.19	1.14
		B ₃	$Y=43.1653/(1+e^{3.1953-0.2027t})$	0.997	38.43	9.27	12.99	16.17	2.19	1.12
皖麦52 Wanmai 52	0	CK	$Y=33.8227/(1+e^{3.6821-0.2286t})$	0.994	36.21	10.35	11.52	14.34	1.93	0.93
		B ₁	$Y=41.9173/(1+e^{3.2020-0.1853t})$	0.992	42.08	10.17	14.21	17.69	1.94	1.00
		B ₂	$Y=45.3649/(1+e^{3.1914-0.1828t})$	0.984	42.59	10.25	14.41	17.93	2.07	1.06
		B ₃	$Y=42.8722/(1+e^{3.1761-0.1843t})$	0.985	42.19	10.09	14.30	17.80	1.97	1.02
	-2	CK	$Y=33.9618/(1+e^{3.2405-0.2117t})$	0.983	37.01	9.08	12.44	15.48	1.80	0.92
		B ₁	$Y=37.4071/(1+e^{3.2003-0.1987t})$	0.983	39.23	9.48	13.26	16.50	1.86	0.95
		B ₂	$Y=42.3934/(1+e^{3.0831-0.1868t})$	0.990	41.10	9.45	14.10	17.55	1.98	1.03
		B ₃	$Y=41.2833/(1+e^{3.1384-0.1910t})$	0.980	40.49	9.54	13.79	17.16	1.97	1.02

注: CK为喷施蒸馏水, B₁、B₂、B₃分别为6-BA溶液喷施浓度10、20、30 mg/L。方程中Y为千粒重, t 为开花后天数, e (2.71828)为自然对数的底数。 T 为灌浆持续期; T_1 、 T_2 、 T_3 分别为灌浆渐增期、灌浆缓增期、灌浆快增期; $R_{\max}$ 为籽粒灌浆最大速率(mg/d); R 为籽粒灌浆平均速率(mg/d)。

Note: Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B₁, B₂ and B₃ were 10, 20, and 30 mg/L, respectively. In the fitting equation, Y is 1000-grain weight, t is the days after anthesis, e (2.71828) is the base of the natural logarithm. T is duration of grouting; T_1 , T_2 , T_3 are gradually increasing, slow increasing and fast increasing stages of grouting, respectively; $R_{\max}$ is maximum grain filling rate (mg/d); R is mean grain filling rate (mg/d).

表 3 6-BA 对孕穗期低温胁迫后小麦产量及其构成因素的影响
Table 3 Effects of 6-BA on wheat yield and its components after low temperature stress at booting stage

年份 Year	品种 Cultivar	温度 (°C) Temperature	处理 Treatment	单株穗数 Spikes per plant	千粒重 (g) 1000-grain weight	穗粒数 Grain number per spike	产量 (g/pot) Yield
2022	烟农19 Yannong 19	0	CK	21.23±0.13 c	36.26±0.68 c	35.50±0.70 c	27.20±0.94 c
			B ₁	22.57±0.32 b	40.04±0.50 b	37.50±1.08 b	33.89±1.10 b
			B ₂	23.60±0.15 a	41.85±0.07 a	39.50±0.67 a	39.01±0.66 a
			B ₃	23.03±0.04 ab	40.42±0.52 b	37.67±1.01 b	35.07±0.55 b
		-2	CK	20.23±0.25 c	33.97±0.31 c	31.50±1.08 c	21.65±1.17 d
			B ₁	22.64±0.27 b	34.42±0.28 c	33.00±0.50 b	25.72±0.43 c
			B ₂	24.32±0.14 a	39.71±0.27 a	37.83±0.68 a	36.53±1.06 a
			B ₃	23.62±0.31 a	35.96±0.31 b	34.67±0.94 b	29.45±0.76 b
	皖麦52 Wanmai 52	0	CK	20.81±0.09 c	35.61±0.25 d	27.54±0.54 c	20.41±0.29 d
			B ₁	22.67±0.50 b	37.84±0.31 c	29.22±0.38 b	25.07±1.00 c
			B ₂	24.37±0.26 a	41.55±0.22 a	34.57±0.71 a	35.00±0.82 a
			B ₃	23.33±0.20 b	39.83±0.20 b	31.35±0.50 b	29.13±0.74 b
		-2	CK	20.23±0.23 c	34.19±0.54 d	21.68±1.23 c	15.00±1.14 d
			B ₁	20.74±0.21 b	37.63±0.25 c	24.94±0.42 b	19.46±0.45 c
			B ₂	22.03±0.18 a	41.27±0.22 a	29.46±0.69 a	26.78±1.03 a
			B ₃	21.30±0.12 b	39.79±0.17 b	25.07±0.15 b	21.25±0.51 b
2023	烟农19 Yannong 19	0	CK	22.33±0.38 a	36.25±0.15 d	31.47±0.70 c	25.47±0.61 d
			B ₁	22.68±0.22 a	38.30±0.24 c	33.53±0.71 b	29.13±0.90 c
			B ₂	23.10±0.41 a	41.89±0.47 a	36.47±0.18 a	35.29±0.66 a
			B ₃	22.86±0.55 a	39.66±0.16 b	34.60±0.12 b	31.37±0.84 b
		-2	CK	20.17±0.26 c	34.88±0.35 d	26.87±0.85 c	18.90±0.27 d
			B ₁	21.29±0.06 b	38.92±0.05 c	28.65±0.13 b	23.74±0.09 c
			B ₂	22.34±0.25 a	42.15±0.19 a	32.27±0.24 a	30.39±0.27 a
			B ₃	21.96±0.22 ab	40.81±0.15 b	31.31±0.15 b	26.78±0.53 b
	皖麦52 Wanmai52	0	CK	19.45±0.20 d	33.54±0.22 d	25.80±0.72 d	16.82±0.37 d
			B ₁	20.23±0.30 c	39.97±0.16 c	27.13±0.37 c	21.94±0.44 c
			B ₂	21.87±0.22 a	42.82±0.24 a	30.27±0.18 a	28.34±0.19 a
			B ₃	21.14±0.16 b	41.13±0.21 b	29.33±0.18 b	25.50±0.31 b
		-2	CK	19.33±0.34 c	34.51±0.27 d	23.73±0.35 d	15.83±0.40 d
			B ₁	20.37±0.23 b	37.53±0.16 c	26.67±0.70 c	20.08±0.80 c
			B ₂	21.92±0.37 a	40.44±0.26 a	33.33±0.24 a	29.54±0.21 a
			B ₃	21.19±0.23 b	39.45±0.11 b	30.33±0.07 b	25.35±0.26 b

注：CK为喷施蒸馏水，B₁、B₂、B₃分别为6-BA溶液喷施浓度 10、20、30 mg/L。同列数据后不同小写字母表示同一品种同一温度处理不同 6-BA处理间差异显著($P<0.05$)。

Note: Distilled water is sprayed in CK, and the spraying concentration of 6-BA in B₁, B₂ and B₃ are 10, 20, and 30 mg/L, respectively. Different lowercase letters after data in the same column indicate significant difference among 6-BA treatments for the same cultivar under the same temperature treatment ($P<0.05$).

52 的产量修复效果优于对低温迟钝型品种烟农 19。以 2023 年-2℃ 低温处理后 B₂ 处理为例，烟农 19 和皖麦 52 的单盆产量较对照分别增加了 60.79% 和 86.61%，千粒重分别增加了 20.84% 和 17.18%，单株穗数分别增加了 10.76% 和 13.40%，穗粒数分别增加了 20.10% 和 40.46%。综合来看，与对照相比，烟

农 19 喷施 6-BA 处理的单盆产量、千粒重、单株穗数、穗粒数分别提高 14.37%~68.73%、1.32%~20.84%、1.57%~20.22%、4.76%~20.10%; 皖麦 52 喷施 6-BA 处理的单盆产量、千粒重、单株穗数、穗粒数分别提高 22.83%~86.61%、6.26%~27.67%、2.52%~17.11%、5.16%~40.46%。

3 讨论

3.1 6-BA 对孕穗期低温胁迫后小麦光合特性的影响

低温胁迫对小麦旗叶光合作用的抑制主要体现在光合同化能力下降, 表现为 SPAD 值、 P_n 、 T_r 和 G_s 降低, 从而加速旗叶衰老^[32-34]。这一现象可能与部分气孔关闭导致的 CO_2 供应减少 (气孔限制) 和 RuBP 羧化酶活性受限导致的 CO_2 利用受阻 (非气孔限制) 有关^[35]。叶绿素荧光参数, 尤其是 F_v/F_m , 是评估光合作用中化学反应变化的重要指标^[36-37]。低温胁迫还会降低小麦旗叶 F_v/F_m ^[38], 表明光系统 II (PS II) 的完整性受损。前人研究表明, 低温胁迫后, 外源施用水杨酸^[39]、褪黑素^[40]、海藻糖^[41]等植物生长调节剂能够提高冬小麦的光合作用。本研究发现, 6-BA 的应用显著减轻了低温胁迫带来的负面影响, 提高了旗叶的 SPAD 值, 缓解了 P_n 、 G_s 和 T_r 的降低。这可能与 6-BA 促进叶绿素前体 δ -氨基乙酰丙酸的合成, 维持植物叶绿体结构的稳定有关。此外, 6-BA 通过增加内部叶片 CO_2 浓度和 G_s , 促进 CO_2 的固定, 增加光合产物的积累, 从而减轻了低温胁迫对植物光合能力的抑制。本研究还发现 6-BA 能提高小麦旗叶的 F_v/F_m , 说明 6-BA 能有效减轻低温胁迫对小麦叶片 PSII 造成的损伤, 增强叶片中电子传递速率, 从而维持光合作用的正常运行, 这与吴雪霞等^[42]研究结果相似。喷施 6-BA 显著减轻低温诱导的 PSII 损伤, 通过提高叶绿素含量, 增强叶绿体对光的吸收和利用能力, 进而缓解低温胁迫对植物光合作用的破坏, 提高了植株的抗寒能力。

RuBP 羧化酶和 PEP 羧化酶是参与碳代谢的关键酶, 能够改善植物光合作用^[43]。研究表明, 低温胁迫通过抑制 RuBP 羧化酶活性和 PEP 羧化酶活性, 降低小麦旗叶的光合能力, 最终导致产量降低^[44-45]。小麦叶片 RuBP 羧化酶活性的增加有利于植物在逆境条件下生存^[46]。本研究结果表明, 6-BA 能够提高孕穗期低温胁迫后小麦旗叶中 RuBP 羧化酶和 PEP 羧化酶活性, 从而有效改善光合作用。6-BA 的应用可能通过减轻类囊体膜损伤和促进 ATP 合成来提高

RuBP 羧化酶活性。另有研究发现, 喷施 6-BA 可以提高小麦叶片 RuBP 羧化酶和 PEP 羧化酶活性, 缓解产量损失^[47]。Hu 等^[48]在涝渍胁迫下喷施 6-BA, 缓解了玉米叶片 PEP 羧化酶与 RuBP 羧化酶活性的下降。本试验中喷施 6-BA 显著提高了小麦叶片 RuBP 羧化酶和 PEP 羧化酶活性, 增加了叶片 G_s , 促进了光合 CO_2 同化, 保护了 PSII 反应中心和光合暗反应, 从而促进卡尔文循环。另外, 低温胁迫后, 6-BA 对低温敏感型品种皖麦 52 的光合缓解效果优于对低温迟钝型品种烟农 19, 这可能是因为低温敏感型小麦的抗逆性较弱, 外源 6-BA 的喷施可以通过促进小麦的细胞分裂和修复过程, 增强其恢复能力。以上结果表明, 外源喷施 6-BA 能够通过提高旗叶的 SPAD 值与 RuBP 羧化酶和 PEP 羧化酶的活性, 缓解 P_n 、 G_s 和 T_r 的降低, 从而减轻低温胁迫对小麦旗叶光合作用的抑制, 有利于减少产量损失。

综上所述, 6-BA 在提高小麦光合作用和抗逆性中具有重要作用。通过提高关键光合作用酶的活性, 6-BA 增强了小麦在低温胁迫下的光合作用, 从而提高了产量。此外, 6-BA 的应用效果在不同品种间存在差异, 这一发现为小麦品种改良和逆境管理提供了新的策略和依据。

3.2 6-BA 对孕穗期低温胁迫后小麦灌浆特性及产量的影响

籽粒灌浆是决定小麦产量形成的重要过程, 与最终产量密切相关。灌浆速率与持续天数决定了籽粒充实程度^[49-50]。研究表明, 开花前温度胁迫对小麦粒重有显著影响^[51], 尤其在孕穗期, 小麦对温度异常敏感^[52]。孕穗期低温胁迫会导致花粉母细胞发育不良和花粉不育, 从而造成小麦严重减产^[7]。在逆境条件下, 植物生长调节剂能够调节小麦生理反应以适应不利环境^[53-56]。6-BA 作为一种有效的植物生长调节剂, 已被证实能够缓解非生物胁迫对作物生长发育的抑制作用^[27, 57-58]。本研究发现, 小麦经孕穗期低温处理后, 喷施 6-BA 溶液提高了籽粒的灌浆速率, 延长了籽粒灌浆持续时间, 千粒重增加, 产量较对照得以提高。这一结果与 Zhang 等^[59]的研究结果相似。表明 6-BA 能够改善低温胁迫后小麦产量相关特性。也有研究在其他逆境胁迫中发现了 6-BA 缓解植物逆境胁迫的效果。Yang 等^[60]在热胁迫下发现, 6-BA 能够提高籽粒灌浆速率, 增加粒重和产量。Zhang 等^[61]在渍水条件下发现, 外源喷施 6-BA 能够提高小麦籽粒灌浆的持续时间和速率, 增加淀粉积累量, 减轻

渍水对小麦产量的不利影响。此外, 6-BA 会影响光合产物的积累或运输^[61]。水稻、玉米等作物的灌浆特性也受到 6-BA 的调控^[62-63]。本研究进一步证实, 6-BA 能够促进小麦旗叶的光合作用, 缓解低温胁迫对籽粒灌浆的抑制作用, 增加千粒重, 减少产量损失。这可能是由于 6-BA 通过提高小麦的光合能力, 维持光合产物的形成与转运能力, 从而提高籽粒灌浆速率, 延长灌浆天数, 使千粒重增加, 最终缓解低温胁迫对产量的抑制作用。因此, 6-BA 的应用是提高低温胁迫后小麦产量的一种有效手段。

在实际生产中, 应根据小麦的生长阶段和环境条件, 合理搭配 6-BA 与正常肥料的使用, 以实现最佳的产量和品质。

4 结论

孕穗期低温胁迫后喷施 6-BA 可以显著改善小麦旗叶的光合作用, 增强光合作用相关酶活性, 有效减轻低温对光合系统的损害。同时, 外源 6-BA 增加了孕穗期低温后小麦籽粒平均灌浆速率和最大灌浆速率, 延长了籽粒灌浆活跃期, 增加穗粒数与千粒重, 降低了低温对产量的影响。6-BA 喷施浓度为 20 mg/L 时缓解低温胁迫的效果最好。

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