

水稻分蘖期干旱锻炼对幼穗分化期高温下穗发育和产量形成的影响

赵艺婷 谢可冉 高逖 崔克辉*

(作物遗传改良国家重点实验室/农业农村部长江中游作物生理生态与耕作重点实验室/华中农业大学 植物科学技术学院, 武汉 430070; *通信联系人, email: cuikeshui@mail.hzau.edu.cn)

Effects of Drought Priming During Tillering Stage on Panicle Development and Yield Formation Under High Temperature During Panicle Initiation Stage in Rice

ZHAO Yiting, XIE Keran, GAO Ti, CUI Kehui*

(National Key Laboratory of Crop Genetic Improvement/Ministry of Agriculture Key Laboratory of Crop Ecophysiology and Farming System in the Middle Reaches of the Yangtze River/College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, China; *Corresponding author, email: cuikeshui@mail.hzau.edu.cn)

Abstract: 【Objective】 The aim of this study was to investigate the impact of drought priming during the tillering stage on rice panicle development and yield formation under high temperatures during the panicle initiation stage, along with the underlying physiological mechanisms. 【Method】 Two rice varieties, Liangyoupeijiu (heat-sensitive) and Shanyou 63 (heat-tolerant), were chosen for the study. A pot experiment was conducted with two water treatments (flooding irrigation and drought priming during tillering stage) and two temperature treatments (normal temperature and high temperature during panicle initiation stage). The effects of drought priming on spikelet differentiation and degradation, pollen viability, spikelet fertility, spikelet size, grain yield, and underlying physiological characteristics were evaluated. 【Result】 Under normal temperature treatment, there was no significant difference in grain yield between flooding irrigation and drought priming for both varieties. However, under high temperature treatment, drought priming led to a significant increase in seed setting rate and 1000-grain weight, resulting in a 54.0% increase in grain yield for Liangyoupeijiu and a 20.1% increase for Shanyou 63 compared to flooding irrigation. Drought priming also resulted in the significant increases in the activities of peroxidase and superoxide dismutase and significant decrease in malondialdehyde content of spikelet, and significant increase in the pollen viability by 26.0%, and in spikelet fertility by 39.0% in Liangyoupeijiu under high temperature treatment. Under flooding irrigation, high temperature treatment resulted in significant reductions in spikelet size and differentiated spikelet number for both varieties compared to normal temperature treatment. However, under high temperature treatment, drought priming led to significant increases in the contents of panicle non-structural carbohydrates and spikelet cytokinins (trans-zeatin and trans-zeatin-riboside), as well as increases in spikelet length, width, and differentiated spikelet number across both varieties. 【Conclusion】 Drought priming during the tillering stage effectively mitigated the negative effects of high temperature stress on spikelet development and fertility by enhancing antioxidant enzyme activities, cytokinin content in spikelets, and non-structural carbohydrate levels in panicles. This resulted in improved rice yield formation under high temperature stress conditions, offering insights for rice production in regions prone to high temperature stress.

Key words: drought priming; high temperature during panicle initiation stage; spikelet fertility; spikelet development; grain yield

摘 要: 【目的】明确分蘖期干旱锻炼对幼穗分化期高温下水稻穗发育和产量形成的影响,并探究其生理机理。【方法】以两优培九(热敏感型)和汕优 63(耐热型)为材料,在盆栽条件下设置全生育期淹灌和分蘖期干旱锻

炼、幼穗分化期适温和高温共四种水分和温度处理组合,研究干旱锻炼对高温胁迫下水稻颖花分化与退化、花粉活力、颖花育性、颖花大小、产量及穗生理特性的影响。【结果】与淹灌相比,在适温下干旱锻炼对两个品种产量无显著影响,但高温下干旱锻炼后两优培九和汕优 63 的产量分别显著提高了 54.0%和 20.1%,这主要是因为结实率和千粒重显著提高。与淹灌相比,幼穗分化期高温下,分蘖期干旱锻炼显著增强两优培九颖花过氧化物酶和超氧化物歧化酶活性,降低了丙二醛含量,其花粉活力和颖花育性分别显著提高了 26.0%和 39.0%。与适温相比,全生育期淹灌下,高温显著降低了两个品种的颖花大小和总颖花分化数。与淹灌相比,分蘖期干旱锻炼显著提高了幼穗分化期高温下两品种穗非结构性碳水化合物含量和颖花细胞分裂素(反式玉米素+反式玉米素核苷)含量,两个品种颖花长、颖花宽和总颖花分化数平均显著增加了 3.2%、4.4%和 15.0%。

【结论】分蘖期干旱锻炼可通过增加抗氧化酶活性、非结构性碳水化合物和细胞分裂素含量来促进颖花发育和提高颖花育性,进而缓解幼穗分化期高温对水稻产量的不利影响,研究结果可为高温热害频发地区的水稻生产实践提供理论指导。

关键词: 干旱锻炼; 幼穗分化期高温; 颖花育性; 颖花发育; 产量

随着全球工业化的加剧,2011—2020 年间全球地表温度比 1850—1900 年间升高 1.09℃,并预测在 21 世纪内超过 1.5℃和 2℃,因此极端高温天气将更频繁更剧烈地发生^[1]。连续 3 d 最高温度 $\geq 38^{\circ}\text{C}$ 或日平均温度 $\geq 33^{\circ}\text{C}$,并且每天持续时间 $\geq 5\text{ h}$ 是判断中稻幼穗分化期至抽穗开花期遭受高温热害的温度指标^[2]。水稻幼穗分化期是对高温最敏感的时期之一,该时期遭受高温胁迫会降低每穗颖花数、颖花大小、花粉活力和颖花育性^[3-4]。高温下幼穗生长发育受阻与幼穗糖代谢、活性氧代谢和激素代谢等生理过程紊乱有关^[5-6]。

糖类物质为幼穗的生长发育提供结构物质和能量来源^[7]。高温下叶片净光合速率略有增加,而高温通过抑制同化物向穗部分配来降低穗干质量和非结构性碳水化合物含量(non-structural carbohydrates, NSC),进而导致产量下降^[8-9]。正常环境下幼穗中活性氧的产生和清除处于平衡状态,并作为信号分子参与调控绒毡层细胞的程序化死亡和降解^[10]。高温下活性氧在幼穗和花药中过量积累从而导致枝梗和颖花退化、花粉败育^[11-12]。酶促抗氧化系统是植物体内清除活性氧的特定机制之一,包括超氧化物歧化酶(superoxide dismutase, SOD)、过氧化氢酶(catalase, CAT)、过氧化物酶(peroxidase, POD)等^[13]。幼穗分化期高温导致颖花 SOD、POD 和 CAT 活性降低和细胞膜受损加剧,花药开裂和柱头花粉萌发受阻^[14]。幼穗中细胞分裂素氧化酶活性在高温下增强,细胞分裂素含量降低,导致每穗颖花数和产量显著降低^[15-16]。这些研究表明高温通过影响水稻植株的生理生化 and 生长发育过程来影响产量的形成。

逆境锻炼是指植株经历一种逆境胁迫后,可以提高植株应对后续发生的逆境胁迫的抗性^[17]。前人研究表明,干旱锻炼提高了大豆植株的干旱抗性,也增强了高羊茅和拟南芥植株的高温抗性^[18-19]。干

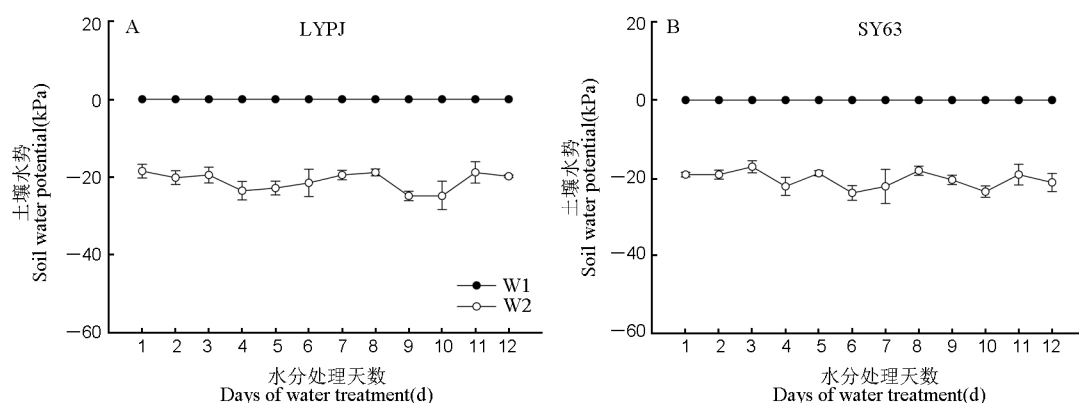
旱锻炼对作物产量的影响不一致^[20-22],其差异可能与土壤落干程度、干旱处理时穗和籽粒发育进程等密切相关。干旱胁迫对水稻影响的相关研究多集中在特定时期的干旱胁迫对其生长发育和产量的影响;然而,面对频发的高温天气,水稻干旱锻炼对其高温敏感时期高温下穗发育和产量形成的影响有待进一步研究。因此,本研究选用抗热性有差异的两个杂交籼稻品种两优培九和汕优 63,研究水稻分蘖期干旱锻炼对幼穗分化期高温下穗发育和产量形成的影响,以期对高温下水稻生产实践提供理论指导。

1 材料与方法

1.1 试验设计

本研究于 2022 年水稻生长季在华中农业大学玻璃温室和棚栽场进行。水稻材料为两优培九(热敏感型)和汕优 63(耐热型)。室外湿润育秧至三叶一心时移栽至盆栽桶内(直径 24.4 cm \times 高 25.5 cm,盆内装粉碎过筛的风干稻田土 10 kg),每盆 3 株水稻均匀分布。两优培九于 6 月 26 日移栽,汕优 63 于 6 月 30 日移栽。全生育期施过磷酸钙(折合纯磷)1.5 g/盆,氯化钾(折合纯钾)1.5 g/盆,尿素(折合纯氮)2.0 g/盆,磷肥和钾肥全部作为基肥施入,氮肥按 $m_{\text{基肥}}:m_{\text{分蘖肥}}:m_{\text{穗肥}}=4:3:3$ 的比例施用。每个品种均包含四个处理,分别是全生育期淹灌-适温处理(W1T1)、全生育期淹灌-高温处理(W1T2)、分蘖期干旱锻炼-适温处理(W2T1)、分蘖期干旱锻炼-高温处理(W2T2)。每个处理 3 个重复,每个重复 15 盆。

在 2021 年试验中,两个品种从三叶一心到开始幼穗分化间隔约 40 d。为保证水稻植株有充足的有效分蘖数,在分蘖后期进行干旱锻炼。因



数据为均值 \pm 标准误 ($n=3$)。LYPJ: 两优培九; SY63: 汕优 63。W1: 淹灌; W2: 干旱锻炼。下同。

Data are shown as mean \pm SE ($n=3$). LYPJ, Liangyoupeijiu; SY63, Shanyou 63. W1, Flooding irrigation; W2, Drought priming. The same as below.

图 1 干旱锻炼处理期间的土壤水势

Fig. 1. Soil water potential during drought priming treatment

此, 在 2022 年试验中两个品种均于移栽后 28 d 开始为期 12 d 的干旱锻炼。干旱锻炼前后所有植株均正常淹灌, 干旱锻炼期间保持土层表面下方 15 cm 处土壤水势为-20 kPa(田间晒田复水前其土层表面下方 15 cm 处土壤水势均值为-12 kPa)。采用张力计监测土壤水势, 其陶瓷探头固定安装在土层表面下方 15 cm 处, 当土壤水势值低于设定值, 单盆加水 0.7 L。在分蘖期干旱锻炼期间两个供试水稻品种的土壤水势均围绕预设水势(-20 kPa)波动(图 1)。在干旱锻炼的 12 d 里, 两优培九土壤水势均值为-20.8 kPa(图 1-A), 汕优 63 土壤水势均值为-20.3 kPa(图 1-B)。

干旱锻炼结束后复水, 剥穗观察幼穗发育进程, 在幼穗长 1~2 mm 时开始温度处理, 20 d 后结束。两个品种各使用一间适温温室和一间高温温室, 每间温室中淹灌和干旱锻炼处理的植株各占一半。温室(长 4 m \times 宽 4 m \times 高 4.5 m)内有 1 台空调, 1 台除湿机, 1 个时控开关, 2 个环流风机, 6 个 LED 投光灯, 1 个 HOBO 温湿度自动记录仪。白天高温处理各时段具体温度设置: 7:00—9:00, 29 $^{\circ}$ C; 9:00—11:00, 33 $^{\circ}$ C; 11:00—15:00, 36 $^{\circ}$ C; 15:00—17:00, 33 $^{\circ}$ C; 17:00—19:00, 29 $^{\circ}$ C; 19:00—次日 7:00, 27 $^{\circ}$ C; 适温处理各时段具体温度设置: 7:00—9:00, 28 $^{\circ}$ C; 9:00—11:00, 29 $^{\circ}$ C; 11:00—15:00, 31 $^{\circ}$ C; 15:00—17:00, 29 $^{\circ}$ C; 17:00—19:00, 28 $^{\circ}$ C; 19:00—次日 7:00, 27 $^{\circ}$ C。相对湿度设置均为 80%, 光照时间设置为 7:00—19:00。从两个适温温室的平均值看, 适温处理下的白天最高温度 33.5 $^{\circ}$ C, 最低温度 25.7 $^{\circ}$ C, 平均温度 30.0 $^{\circ}$ C(图 2-A)。两间高温温室的平均值为白天最

高温度 40.6 $^{\circ}$ C, 最低温度 28.2 $^{\circ}$ C, 平均温度 35.5 $^{\circ}$ C(图 2-A)。适温和高温温室的平均湿度分别为 76.6%和 80.0%(图 2-B)。

1.2 测定方法

1.2.1 产量和颖花育性的测定

在水稻完熟后每个处理取 9 株长势一致的植株, 每株单独脱粒计产。单穗饱粒数 ≥ 5 粒则记为有效穗, 分离的籽粒先后用水选法和风选法区分开饱粒、半饱粒和瘪粒; 初步筛选出的瘪粒还需人工按压, 打开内外稃观察, 如果受精则为半饱粒。产量即每株饱粒重, 并计算出每穗粒数、千粒重和结实率。颖花育性=(饱粒数+半饱粒数)/(饱粒数+半饱粒数+瘪粒数) $\times 100\%$ 。

1.2.2 花粉活力的测定

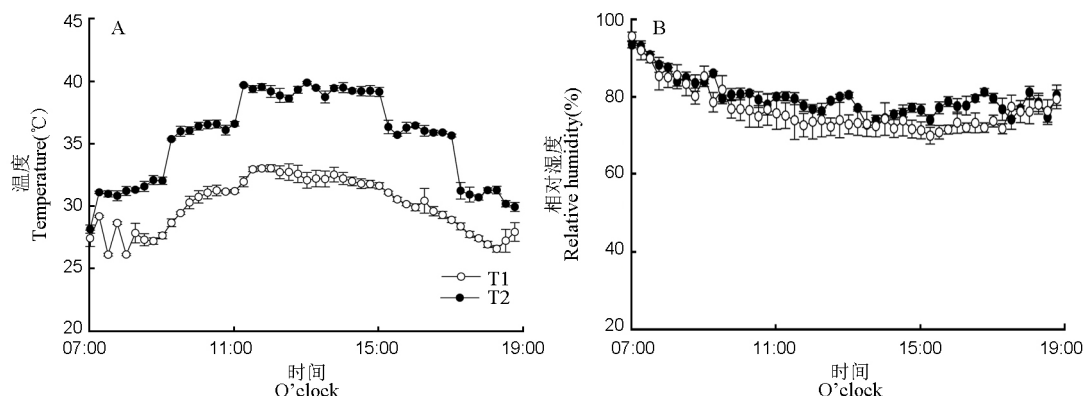
在抽穗初期每个处理取 9 个即将抽穗开花的穗, 每穗选取中上部共 8 个颖花用于花粉活力测定。参考 Gunawardena 等^[23]用 1% I_2 -KI 溶液对花粉粒进行染色, 在倒置荧光显微镜(Ti-SR, Nikon, 日本)的 10 倍镜下拍照观察, 每个重复观察 5 个视野。花粉粒着色呈深蓝色且为饱满圆球者为可育花粉, 其余均为败育花粉。花粉育性(%)=可育花粉粒数/(可育花粉粒数+败育花粉粒数) $\times 100\%$ 。

1.2.3 颖花和籽粒大小的测定

在抽穗初期每个处理随机选取 90 粒即将开花的颖花, 用累积法测定颖花长和颖花宽。在成熟期随机选取 150~200 粒饱粒用大米外观品质检测仪(杭州万深检测科技有限公司)扫描测定粒长和粒宽, 每个处理测定 15 次。

1.2.4 穗部结构的测定

在抽穗初期主茎穗抽出 1/2~3/4 时, 每个处理



数值为高温处理期间各时间点的均值 \pm 标准误 ($n=4$)。T1: 适温处理; T2: 高温处理。

The data at each point-in-time are the average values over the duration of the high temperature treatment \pm SE ($n=4$). T1, Normal temperature; T2, High temperature.

图 2 高温处理期间温室的平均温度和湿度

Fig. 2. Average daytime temperature and relative humidity in the greenhouse during high temperature treatment

取 9 个主茎穗观察每穗枝梗及颖花的分化与退化。参考王亚梁等^[24]的方法统计每穗一次和二次枝梗现存数、一次和二次颖花现存数、一次和二次枝梗退化数、一次和二次颖花退化数,并计算一次和二次枝梗分化数、一次和二次颖花分化数。总枝梗分化数=一次枝梗分化数+二次枝梗分化数,总颖花分化数=一次颖花分化数+二次颖花分化数。

1.2.5 穗部非结构性碳水化合物含量的测定

在幼穗分化期高温处理 15 d 后,每个处理取 3 株水稻,剥离幼穗烘干至恒重,然后粉碎过 100 目筛。取 0.1 g 过筛后样品,用蒽酮比色法分别测定可溶性糖含量和淀粉含量^[25-26],参照 Li 等^[27]用间苯二酚法测定蔗糖含量(mg/g)。非结构性碳水化合物含量是可溶性糖含量和淀粉含量的总和(mg/g)。

1.2.6 颖花丙二醛含量和抗氧化酶活性的测定

在幼穗分化期高温处理 15 d 后,每个处理取 9 个发育进程一致的幼穗,并于液氮中剥取颖花。研磨后取 0.08~0.1 g 鲜样测定丙二醛含量(malondialdehyde, MDA)和抗氧化酶活性。参考 Heath 和 Packer^[28]用硫代巴比妥酸显色法测定 MDA 含量。参照 Dhindsa 和 Matowe^[29]用氮蓝四唑光还原法测定超氧化物歧化酶活性(SOD),以抑制氮蓝四唑光还原的 50%为一个酶活性单位(U)。参照 Maehly 和 Chance^[30]用 H_2O_2 -愈创木酚法测定过氧化物酶活性(POD)。参照 Aebi^[31]用紫外吸收法测定过氧化氢酶活性(CAT)。酶提取液中总蛋白质含量采用考马斯亮蓝染色法测定^[32]。

1.2.7 颖花细胞分裂素含量的测定

样品来源与 1.2.6 相同,取 0.1~0.12 g 样品,参照何爱斌^[33]的方法使用岛津高效液相色谱仪

LC-30A 与三重四级杆质谱仪 LCMS-8050 系统测定颖花各种细胞分裂素含量(ng/g)。活性细胞分裂素总量为反式玉米素型细胞分裂素含量(反式玉米素、反式玉米素核苷)和异戊烯腺嘌呤型细胞分裂素含量(异戊烯腺嘌呤、异戊烯腺苷、异戊烯腺苷磷酸)之和。

1.2.8 统计分析

采用 Excel 软件进行数据统计,利用 Statistix 9.0 软件进行方差分析,运用 LSD 法进行多重比较,使用 Sigmaplot 10.0 进行作图。

2 结果与分析

2.1 产量及其构成因素

方差分析表明温度和水分处理互作显著影响产量、结实率和千粒重(表 1)。全生育期淹灌下,与适温相比,高温处理导致汕优 63 产量显著降低了 26.9%,两优培九产量显著下降了 36.9%;高温胁迫下两优培九结实率和千粒重分别显著降低了 29.7%和 5.9%,汕优 63 千粒重降幅为 11.8%,结实率无显著差异。高温胁迫对两个品种穗数和每穗粒数无显著影响。与淹灌相比,干旱锻炼对适温下水稻产量无显著影响;然而,在高温胁迫下,干旱锻炼后两优培九和汕优 63 的产量比淹灌处理分别显著提高了 54.0%和 20.1%。与淹灌相比,干旱锻炼后高温下两优培九的结实率和千粒重分别显著提高了 36.5%和 4.6%,汕优 63 的千粒重显著提高了 4.1%,结实率无显著差异。

2.2 花粉活力和颖花育性

方差分析表明温度和水分处理互作显著影响

表 1 干旱锻炼对幼穗分化期高温下水稻产量的影响

Table 1. Effects of drought priming on rice yield under high temperature during panicle initiation stage

| 品种 Variety | 处理 Treatment | 产量 Yield(g/plant) | 单株穗数 Panicles per plant | 每穗粒数 Grains per panicle | 结实率 Seed setting rate(%) | 千粒重 1000-grain weight(g) |
|------------------------|-----------------|----------------------|----------------------------|----------------------------|-----------------------------|-----------------------------|
| 两优培九 Liangyoupeiuiu | W1T1 | 24.6±0.1 a | 11.4±0.6 a | 133.7±2.8 a | 69.0±1.7 a | 23.6±0.1 a |
| | W2T1 | 24.4±1.0 a | 11.9±0.5 a | 133.2±2.0 a | 64.7±2.1 a | 23.9±0.3 a |
| | W1T2 | 15.5±1.1 b | 11.0±0.2 a | 131.6±5.6 a | 48.5±3.1 b | 22.3±0.2 b |
| | W2T2 | 23.9±1.6 a | 12.0±0.7 a | 131.9±11.6 a | 66.2±1.8 a | 23.3±0.3 a |
| 汕优 63 Shanyou 63 | W1T1 | 35.5±0.4 a* | 12.3±0.4 a | 133.9±5.8 ab | 84.6±3.5 a* | 25.6±0.1 a* |
| | W2T1 | 34.6±1.9 a* | 13.3±0.2 a | 142.5±8.3 a | 73.4±1.5 b* | 25.2±0.1 a* |
| | W1T2 | 25.9±1.2 b* | 12.3±0.4 a | 119.7±3.1 b | 78.7±3.5 ab* | 22.6±0.1 c |
| | W2T2 | 31.2±1.2 a* | 13.4±0.6 a | 128.1±2.3 ab | 78.4±1.4 ab* | 23.5±0.2 b |
| ANOVA | | | | | | |
| 品种 Variety(V) | | ++ | ns | ns | ++ | ++ |
| 温度 Temperature(T) | | ++ | ns | ns | ns | ++ |
| 水分 Water content(W) | | + | ++ | ns | ns | + |
| V×T | | ns | ns | ns | ns | ++ |
| V×W | | ns | ns | ns | ++ | ns |
| T×W | | ++ | ns | ns | ++ | + |
| V×T×W | | ns | ns | ns | ns | ns |

数据为均值 ± 标准误(n=3)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD 法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。+和++分别表示在 $P < 0.05$ 和 $P < 0.01$ 水平下差异显著，ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温，W2T1 表示干旱锻炼和适温，W1T2 表示淹灌和高温，W2T2 表示干旱锻炼和高温。

Data are shown as mean ± SE (n=3). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations for the same variety at $P < 0.05$ (LSD test). * indicates significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. + and ++ indicate significant difference at $P < 0.05$ and $P < 0.01$, respectively, while ns indicates no significant difference at $P < 0.05$. W1T1, Flooded irrigation and normal temperature; W2T1, Drought priming and normal temperature; W1T2, Flooded irrigation and high temperature; W2T2, Drought priming and high temperature.

花粉活力和颖花育性(图 3)。在全生育期淹灌下，与适温处理相比，高温处理导致两优培九的花粉活力和颖花育性显著降低 23.5%和 26.6%(图 3-A 和图 3-B)，高温胁迫对汕优 63 的这两个性状无显著影响。与淹灌相比，干旱锻炼显著增强了高温下两优培九的花粉活力和颖花育性，增幅分别为 26.0%和 39.0%，而对汕优 63 的花粉活力和颖花育性无显著影响。在淹灌和高温处理下，汕优 63 这二个性状均显著高于两优培九，干旱锻炼和高温处理下两品种花粉活力没有显著差异，而汕优 63 的颖花育性显著高于两优培九。

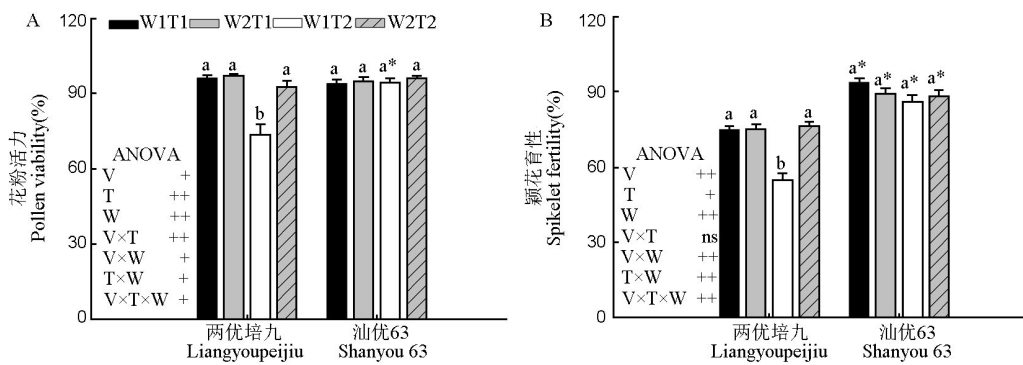
2.3 颖花和籽粒大小

方差分析表明温度和水分处理交互显著影响颖花长、颖花宽和籽粒宽，对籽粒长影响不显著(表 2)。干旱锻炼和高温胁迫对两个品种颖花和籽粒宽的影响均大于粒长。在淹灌下，与适温处理相比，幼穗分化期高温导致抽穗时两优培九的颖花长和宽分别显著降低了 3.3%和 5.9%，汕优 63 显著降低了 5.0%和 9.5%，成熟时两优培九的籽粒

长和宽分别显著下降了 1.5%和 2.9%，汕优 63 显著下降了 3.5%和 5.8%。在高温处理下，与淹灌处理相比，干旱锻炼导致两优培九颖花长和颖花宽分别显著提高了 2.7%和 4.7%，籽粒宽显著提高了 3.6%；而在汕优 63 中，颖花长和颖花宽分别提高了 3.8%和 4.1%，籽粒长和籽粒宽分别显著提高了 2.1%和 3.2%。

2.4 穗部枝梗和颖花分化

淹灌处理和干旱锻炼两种处理下，与适温处理相比，高温处理对两品种总枝梗分化数、一次和二次枝梗分化数、一次和二次枝梗退化数均无显著影响(表 3)。方差分析表明温度和水分处理交互显著影响总颖花分化数和二次颖花分化数，对一次颖花分化数、一次和二次颖花退化数的影响不显著(表 4)。在淹灌处理下，高温处理下两品种的总颖花分化数和二次颖花分化数显著低于适温处理，二次颖花退化数显著高于适温处理。其中，两优培九的总颖花分化数和二次颖花分化数降幅分别为 14.3%和 19.6%，每穗二次颖花退化数



数据为均值 ± 标准误 (n=3)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。V 表示品种, T 表示温度, W 表示水分。+和++分别表示在 $P < 0.05$ 和 $P < 0.01$ 水平下差异显著, ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温, W2T1 表示干旱锻炼和适温, W1T2 表示淹灌和高温, W2T2 表示干旱锻炼和高温。

Data are shown as mean ± SE (n=3). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations for the same variety at $P < 0.05$ (LSD test). * indicates the significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. V indicates variety, T indicates temperature, and W indicates water. + and ++ indicate significant difference at $P < 0.05$ and $P < 0.01$, respectively, while ns indicates no significant difference at $P < 0.05$. W1T1 indicates flooded irrigation and normal temperature, W2T1 indicates drought priming and normal temperature, W1T2 indicates flooded irrigation and high temperature, and W2T2 indicates drought priming and high temperature.

图 3 干旱锻炼对幼穗分化期高温下水稻花粉活力和颖花育性的影响
Fig. 3. Effects of drought priming on rice pollen viability and spikelet fertility under high temperature during panicle initiation stage

表 2 干旱锻炼对幼穗分化期高温下颖花大小和籽粒大小的影响
Table 2. Effects of drought priming on rice spikelet size and grain size under high temperature during panicle initiation stage

| 品种 Variety | 处理 Treatment | 抽穗期 Heading stage | | 成熟期 Mature stage | |
|------------------------|-----------------|----------------------------|---------------------------|-------------------------|------------------------|
| | | 颖花长 Spikelet length(mm) | 颖花宽 Spikelet width(mm) | 籽粒长 Grain length(mm) | 籽粒宽 Grain width(mm) |
| | | | | | |
| 两优培九 Liangyoupeiiju | W1T1 | 9.07±0.02 a* | 3.00±0.03 a | 8.85±0.05 a* | 2.62±0.05 b |
| | W2T1 | 8.97±0.00 a* | 2.98±0.04 a | 8.82±0.02 ab* | 2.69±0.02 a |
| | W1T2 | 8.77±0.07 b* | 2.82±0.02 b | 8.72±0.03 b* | 2.54±0.03 c |
| | W2T2 | 9.00±0.13 a* | 2.96±0.07 a | 8.80±0.08 ab* | 2.63±0.02 b |
| 汕优 63 Shanyou 63 | W1T1 | 8.40±0.11 a | 3.28±0.04 a* | 8.44±0.06 a | 2.96±0.00 a* |
| | W2T1 | 8.37±0.02 a | 3.22±0.01 a* | 8.48±0.04 a | 2.94±0.02 a* |
| | W1T2 | 7.98±0.01 b | 2.97±0.02 c* | 8.15±0.07 c | 2.78±0.01 c* |
| | W2T2 | 8.28±0.03 a | 3.09±0.01 b* | 8.32±0.09 b | 2.87±0.01 b* |
| ANOVA | | | | | |
| 品种 Variety(V) | | ++ | ++ | ++ | ++ |
| 温度 Temperature(T) | | + | ++ | + | + |
| 水分 Water content(W) | | ns | ns | ns | ++ |
| V×T | | ns | ns | ns | ns |
| V×W | | ns | ns | ns | + |
| T×W | | + | + | ns | ++ |
| V×T×W | | ns | ns | ns | + |

数据为均值 ± 标准误(n=3)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。+和++分别表示在 $P < 0.05$ 和 $P < 0.01$ 水平下差异显著, ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温, W2T1 表示干旱锻炼和适温, W1T2 表示淹灌和高温, W2T2 表示干旱锻炼和高温。

Data are shown as mean ± SE (n=3). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations in the same variety at $P < 0.05$ (LSD test). * indicates the significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. + and ++ indicate significant difference at $P < 0.05$ and $P < 0.01$, respectively, while ns indicates no significant difference at $P < 0.05$. W1T1 indicates flooded irrigation and normal temperature, W2T1 indicates drought priming and normal temperature, W1T2 indicates flooded irrigation and high temperature, and W2T2 indicates drought priming and high temperature.

表 3 干旱锻炼对幼穗分化期高温下每穗枝梗数的影响

Table 3. Effects of drought priming on the number of rachis branches per panicle under high temperature during panicle initiation stage

| 品种 Variety | 处理 Treatment | 总枝梗分化数 NBD (No./panicle) | 一次枝梗分化数 NPBD (No./panicle) | 二次枝梗分化数 NSBD (No./panicle) | 一次枝梗退化数 NPBG (No./panicle) | 二次枝梗退化数 NSBG (No./panicle) |
|------------------------|-----------------|--------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|
| 两优培九 Liangyoupeijiu | W1T1 | 73.7±2.3 a | 12.8±0.4 a | 60.9±1.9 a | 0.0±0.0 a | 22.3±2.3 ab |
| | W2T1 | 68.0±1.6 a | 12.3±0.2 a | 55.7±1.5 a | 0.0±0.0 a | 18.9±1.6 ab |
| | W1T2 | 66.8±1.5 a | 12.1±0.1 a | 54.7±1.4 a | 0.0±0.0 a | 23.8±1.7 a |
| | W2T2 | 68.0±1.9 a | 12.2±0.1 a | 55.8±1.8 a | 0.0±0.0 a | 18.6±1.1 b |
| 汕优 63 Shanyou 63 | W1T1 | 67.3±0.7 a | 14.0±0.3 a | 53.3±1.0 a* | 0.0±0.0 a | 17.7±1.2 a |
| | W2T1 | 67.0±2.1 a | 13.2±0.7 a | 53.8±1.5 a | 0.0±0.0 a | 17.2±3.6 a |
| | W1T2 | 64.4±0.2 a | 13.4±0.1 a* | 51.0±0.3 a | 0.0±0.0 a | 22.4±1.3 a |
| | W2T2 | 65.8±1.0 a | 13.1±0.1 a* | 52.7±1.1 a | 0.0±0.0 a | 17.9±0.9 a |
| ANOVA | | | | | | |
| 品种 Variety(V) | | ns | ns | + | ns | ns |
| 温度 Temperature(T) | | + | ns | + | ns | ns |
| 水分 Water content(W) | | ns | ns | ns | ns | ns |
| V×T | | ns | ns | ns | ns | ns |
| V×W | | ns | ns | ns | ns | ns |
| T×W | | ns | ns | ns | ns | ns |
| V×T×W | | ns | ns | ns | ns | ns |

数据为均值 ± 标准误(n=3)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD 法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。+表示在 $P < 0.05$ 水平下差异显著，ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温，W2T1 表示干旱锻炼和适温，W1T2 表示淹灌和高温，W2T2 表示干旱锻炼和高温。

Data are shown as mean ± SE (n=3). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations for the same variety at $P < 0.05$ (LSD test). * indicates significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. + indicates significant difference at $P < 0.05$, and ns indicates no significant difference at $P < 0.05$. W1T1 indicates flooded irrigation and normal temperature, W2T1 indicates drought priming and normal temperature, W1T2 indicates flooded irrigation and high temperature, and W2T2 indicates drought priming and high temperature. NBD, Total number of differentiated rachis branches; NPBD, Number of differentiated primary rachis branches; NSBD, Number of differentiated secondary rachis branches; NPBG, Number of degenerated primary rachis branches; NSBG, Number of degenerated secondary rachis branches.

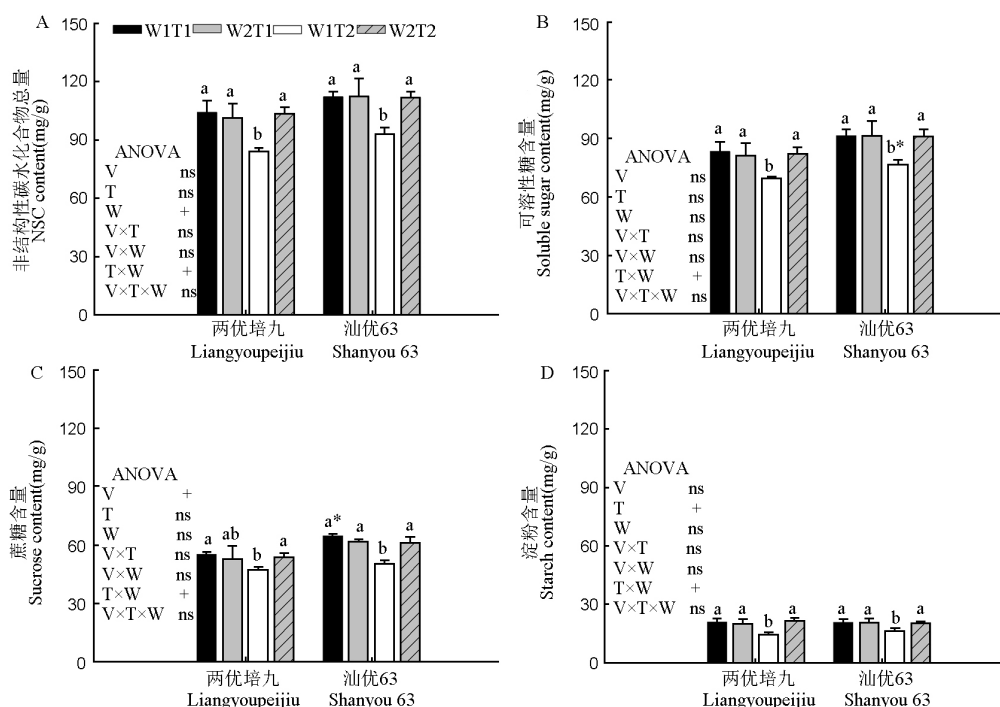
表 4 干旱锻炼对幼穗分化期高温下每穗颖花数的影响

Table 4. Effects of drought priming on spikelets per panicle under high temperature during panicle initiation stage

| 品种 Variety | 处理 Treatment | 总颖花分化数 NSD (No./panicle) | 一次颖花分化数 NPSD (No./panicle) | 二次颖花分化数 NSSD (No./panicle) | 一次颖花退化数 NPSG (No./panicle) | 二次颖花退化数 NSSG (No./panicle) |
|------------------------|-----------------|--------------------------------|----------------------------------|----------------------------------|----------------------------------|----------------------------------|
| 两优培九 Liangyoupeijiu | W1T1 | 189.4±5.5 a | 69.6±2.9 a | 119.9±4.1 a | 0.0±0.0 a | 7.4±0.9 b* |
| | W2T1 | 187.7±1.3 a | 69.6±1.7 a | 118.1±2.1 a | 0.0±0.0 a | 7.6±3.9 b |
| | W1T2 | 162.3±1.9 b | 66.0±0.8 a | 96.3±2.2 b* | 0.1±0.1 a | 16.4±3.5 a* |
| | W2T2 | 182.9±3.2 a | 67.0±1.3 a | 115.9±2.5 a | 0.1±0.1 a | 8.0±1.8 b |
| 汕优 63 Shanyou 63 | W1T1 | 197.0±5.3 a | 80.7±3.3 a | 116.3±7.3 a | 0.1±0.1 a | 3.0±1.0 b |
| | W2T1 | 193.2±0.8 a | 80.6±3.6 a | 112.7±3.8 a | 0.0±0.0 a | 3.4±0.7 b |
| | W1T2 | 160.3±3.7 b | 74.0±2.0 a* | 86.3±2.8 b | 0.3±0.3 a | 8.0±1.0 a |
| | W2T2 | 188.2±4.0 a | 75.3±1.8 a* | 112.9±5.1 a | 0.0±0.0 a | 4.7±0.9 ab |
| ANOVA | | | | | | |
| 品种 Variety (V) | | ns | ns | + | ns | ns |
| 温度 Temperature (T) | | ++ | ns | ++ | ns | + |
| 水分 Water content (W) | | ++ | ns | ++ | ns | ns |
| V×T | | ns | ns | ns | ns | ns |
| V×W | | ns | ns | ns | ns | ns |
| T×W | | ++ | ns | ++ | ns | ns |
| V×T×W | | ns | ns | ns | ns | ns |

数据为均值 ± 标准误(n=3)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD 法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。+和++分别表示在 $P < 0.05$ 和 $P < 0.01$ 水平下差异显著，ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温，W2T1 表示干旱锻炼和适温，W1T2 表示淹灌和高温，W2T2 表示干旱锻炼和高温。

Data are shown as mean ± SE (n=3). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations for the same variety at $P < 0.05$ (LSD test). * indicates the significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. + and ++ indicate significant difference at $P < 0.05$ and $P < 0.01$, respectively, while ns indicates no significant difference at $P < 0.05$. W1T1 indicates flooded irrigation and normal temperature, W2T1 indicates drought priming and normal temperature, W1T2 indicates flooded irrigation and high temperature, and W2T2 indicates drought priming and high temperature. NSD, Total number of differentiated spikelets; NPSD, Number of differentiated spikelets on primary rachis branches; NSSD, Number of differentiated spikelets on secondary rachis branches; NPSG, Number of degenerated spikelets on primary rachis branches; NSSG, Number of degenerated spikelets on secondary rachis branches.



数据为均值±标准误($n=3$)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD 法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。V 表示品种, T 表示温度, W 表示水分。+表示在 $P < 0.05$ 水平下差异显著, ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温, W2T1 表示干旱锻炼和适温, W1T2 表示淹灌和高温, W2T2 表示干旱锻炼和高温。Data are shown as mean \pm SE ($n=3$). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations for the same variety at $P < 0.05$ (LSD test). * indicates significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. V indicates variety, T indicates temperature, and W indicates water. + indicates significant difference at $P < 0.05$, and ns indicates no significant difference at $P < 0.05$. W1T1 indicates flooded irrigation and normal temperature, W2T1 indicates drought priming and normal temperature, W1T2 indicates flooded irrigation and high temperature, and W2T2 indicates drought priming and high temperature.

图 4 干旱锻炼对幼穗分化期高温下穗部非结构性碳水化合物含量的影响

Fig. 4. Effects of drought priming on non-structural carbohydrate contents in panicle under high temperature during panicle initiation stage

增加 9.0 粒; 汕优 63 降幅为 18.6%和 25.8%, 每穗二次颖花退化数增加 5.0 粒。在适温处理下, 与淹灌处理相比, 干旱锻炼对两个品种总颖花分化数无显著影响; 然而, 在高温处理下, 相较于淹灌处理, 干旱锻炼导致两优培九总颖花分化数和二次颖花分化数分别显著提高了 12.7%和 20.3%, 汕优 63 分别显著提高了 17.4%和 30.8%。此外, 干旱锻炼导致两优培九的二次颖花退化数减少 8.4 粒, 对汕优 63 的二次颖花退化数无显著影响。

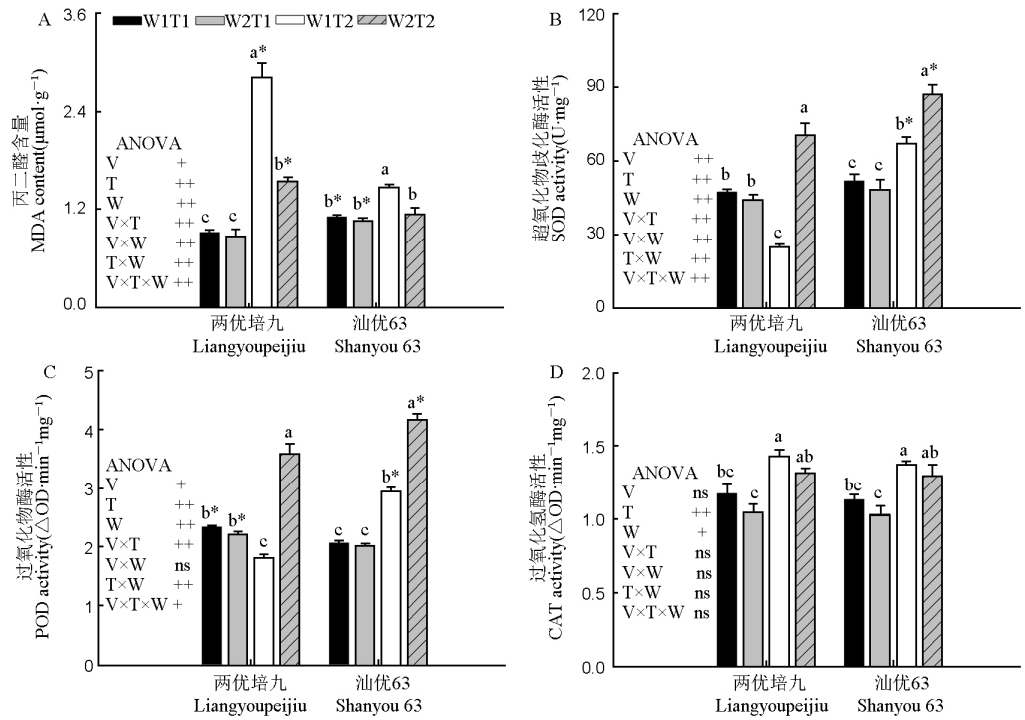
2.5 穗部非结构性碳水化合物含量

方差分析表明温度和水分处理互作显著影响穗部 NSC、可溶性糖、蔗糖和淀粉含量(图 4)。在淹灌处理下, 与适温相比, 高温胁迫导致两优培九和汕优 63 穗部 NSC 含量分别显著降低了 19.3%和 17.1%(图 4-A), 两个品种穗部可溶性糖含量降幅一致(16.4%和 16.3%) (图 4-B), 两优培九的蔗糖含量降幅(14.1%)比汕优 63(21.8%)少 7.7 个百分点(图 4-C), 淀粉含量降幅(30.7%)比汕优

63(20.5%)多 10.2 个百分点(图 4-D)。在高温处理下, 干旱锻炼后两优培九和汕优 63 的穗部 NSC 含量比淹灌处理下显著增长了 23.2%和 20.0%, 两优培九可溶性糖、蔗糖和淀粉含量分别显著提高了 17.8%、13.4%和 48.9%, 汕优 63 分别显著提高了 18.9%、21.0%和 25.1%。

2.6 颖花抗氧化能力

方差分析表明温度和水分处理互作显著影响颖花 MDA 含量、超氧化物歧化酶和过氧化物酶活性, 对过氧化氢酶活性无显著影响(图 5)。在淹灌和干旱锻炼两个处理下, 高温胁迫时两优培九的颖花 MDA 含量显著高于汕优 63(图 5-A), SOD 和 POD 活性显著低于汕优 63(图 5-B 和图 5-C), CAT 活性无显著差异(图 5-D)。淹灌条件下, 高温下两优培九和汕优 63 的颖花 MDA 含量比在适温下分别显著增加 2.1 倍和 0.3 倍, 两优培九颖花 SOD 和 POD 活性分别显著降低了 47.2%和 22.3%, 汕优 63 中这两种抗氧化酶活性分别显著



数据为均值 ± 标准误 (n=3)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD 法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。V 表示品种, T 表示温度, W 表示水分。+和++分别表示在 $P < 0.05$ 和 $P < 0.01$ 水平下差异显著, ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温, W2T1 表示干旱锻炼和适温, W1T2 表示淹灌和高温, W2T2 表示干旱锻炼和高温。

Data are shown as mean ± SE (n=3). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations for the same variety at $P < 0.05$ (LSD test). * indicates significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. V indicates variety, T indicates temperature, and W indicates water. + and ++ indicate significant difference at $P < 0.05$ and $P < 0.01$, respectively, while ns indicates no significant difference at $P < 0.05$. W1T1 indicates flooded irrigation and normal temperature, W2T1 indicates drought priming and normal temperature, W1T2 indicates flooded irrigation and high temperature, and W2T2 indicates drought priming and high temperature.

图 5 干旱锻炼对幼穗分化期高温下颖花丙二醛含量和抗氧化酶活性的影响
Fig. 5. Effects of drought priming on MDA content and antioxidant enzyme activities in spikelet under high temperature during panicle initiation stage

增加了 29.5%和 42.5%, 两个品种的 CAT 活性均显著增加 0.2 倍。高温胁迫下, 干旱锻炼过的两个品种颖花 MDA 含量显著低于淹灌处理的植株, 颖花 SOD 和 POD 活性显著高于淹灌处理的植株, 具体表现为两优培九颖花 MDA 含量显著降低了 44.9%, SOD 和 POD 活性分别显著增加 1.8 倍和 1.0 倍, 汕优 63 颖花 MDA 含量显著降低了 22.4%, SOD 和 POD 活性分别显著增加 0.3 倍和 0.4 倍。干旱锻炼后两品种颖花 CAT 活性无显著差异。

2.7 颖花细胞分裂素含量

方差分析表明温度和水分处理互作显著影响颖花 tZR 含量, 而对其他激素含量影响不显著(表 5)。适温处理下, 两种水分处理对两个品种颖花各种细胞分裂素含量无显著影响。淹灌下, 与适

温相比, 高温处理显著降低了两优培九颖花活性细胞分裂素含量(22.4%), tZ、tZR 和 iPMP 含量分别显著降低了 84.4%、50.7%和 22.5%, 对汕优 63 颖花活性细胞分裂素、tZ 和 iPMP 含量无显著影响, tZR 含量显著降低了 20.3%。高温处理下, 与淹灌相比, 干旱锻炼处理显著增加汕优 63 颖花 tZR 含量(20.9%), 两优培九的颖花 tZR 含量(103.0%)和 tZ 含量(38.9%), 而对两品种中其他激素含量无显著影响。

3 讨论

3.1 干旱锻炼对高温下水稻产量形成的影响

本研究发现幼穗分化期高温通过降低结实率和千粒重来降低两个品种的籽粒产量, 而分蘖期干旱

表 5 干旱锻炼对幼穗分化期高温下颖花细胞分裂素含量的影响

Table 5. Effects of drought priming on cytokinin contents in spikelet under high temperature during panicle initiation stage

| 品种 Variety | 处理 Treatment | 活性细胞 分裂素总量 aCTKs(ng/g) | 反式玉米素含量 tZ(ng/g) | 反式玉米素 核苷含量 tZR(ng/g) | 异戊烯腺嘌呤含量 iP(ng/g) | 异戊烯腺苷含量 iPA(ng/g) | 异戊烯腺苷 磷酸含量 iPMP(ng/g) |
|------------------------|-----------------|------------------------------|---------------------|----------------------------|----------------------|----------------------|-----------------------------|
| 两优培九 Liangyoupeijiu | W1T1 | 19.38±0.97 a | 0.70±0.01 a | 1.41±0.08 a | 1.90±0.09 a | 1.32±0.06 a* | 14.05±1.11 a |
| | W2T1 | 19.54±1.34 a | 0.69±0.02 a | 1.55±0.09 a | 1.74±0.07 a* | 1.23±0.06 a* | 14.33±1.16 a |
| | W1T2 | 15.05±0.53 c | 0.11±0.00 c | 0.69±0.02 b | 2.01±0.06 a* | 1.35±0.08 a | 10.89±0.44 b |
| | W2T2 | 17.18±0.95 b | 0.15±0.00 b | 1.41±0.06 a | 1.89±0.08 a | 1.33±0.11 a | 12.40±0.82 ab |
| 汕优 63 Shanyou 63 | W1T1 | 19.43±0.73 a | 0.64±0.06 a | 1.71±0.14 a* | 1.70±0.21 a | 1.17±0.08 a | 14.23±0.27 a |
| | W2T1 | 19.56±0.97 a | 0.65±0.07 a | 1.69±0.11 a | 1.58±0.07 a | 1.09±0.08 a | 14.54±0.77 a |
| | W1T2 | 18.59±0.65 a* | 0.64±0.02 a* | 1.36±0.03 b* | 1.80±0.06 a | 1.29±0.05 a | 13.50±0.63 a* |
| | W2T2 | 19.29±1.12 a* | 0.71±0.03 a* | 1.65±0.07 a* | 1.80±0.01 a | 1.30±0.10 a | 13.84±1.03 a |
| ANOVA | | | | | | | |
| 品种 Variety(V) | | + | ++ | ns | + | ns | ns |
| 温度 Temperature(T) | | + | ++ | ++ | ns | ns | ns |
| 水分 Water content(W) | | ns | ns | ++ | ns | ns | ns |
| V×T | | ns | ++ | ns | ns | ns | ns |
| V×W | | ns | ns | ++ | ns | ns | ns |
| T×W | | ns | ns | ++ | ns | ns | ns |
| V×T×W | | ns | ns | ns | ns | ns | ns |

数据为均值 ± 标准误(n=3)。不同小写字母表示同一品种在不同水分和温度处理组合下同一性状在 $P < 0.05$ 水平下差异显著(LSD 法)。*表示相同水分与温度处理组合下两个品种间同一性状在 $P < 0.05$ 水平下差异显著。+和++分别表示在 $P < 0.05$ 和 $P < 0.01$ 水平下差异显著，ns 表示在 $P < 0.05$ 水平下差异不显著。W1T1 表示淹灌和适温，W2T1 表示干旱锻炼和适温，W1T2 表示淹灌和高温，W2T2 表示干旱锻炼和高温。

Data are shown as mean ± SE (n=3). Different lowercase letters indicate significant difference for a given trait among the four water and temperature treatment combinations for the same variety at $P < 0.05$ (LSD test). * indicates significant difference for a given trait between two varieties in the same combination of water and temperature treatment at $P < 0.05$. + and ++ indicate significant difference at $P < 0.05$ and $P < 0.01$, respectively, while ns indicates no significant difference at $P < 0.05$. W1T1 indicates flooded irrigation and normal temperature, W2T1 indicates drought priming and normal temperature, W1T2 indicates flooded irrigation and high temperature, and W2T2 indicates drought priming and high temperature. aCTKs indicates active cytokinins; tZ indicates trans-zeatin; tZR indicates trans-zeatin-riboside; iP indicates N6-isopentenyl adenine; iPA indicates N6-isopentenyl adenosine riboside; iPMP indicates N6-isopentenyl adenosine-5'-monophosphate.

锻炼提高这两个产量构成来缓解高温对水稻产量的不利影响(表 1)。类似地，Liu 等^[21]也观察到适度干旱锻炼提高了高温胁迫下的作物产量。水稻粒重由粒径大小和籽粒充实度决定^[34]，干旱锻炼提高粒重的途径可能有二种：一是 Zhang 等^[20]发现干旱锻炼促进了灌浆期高温胁迫下小麦叶片光合作用，增加籽粒充实度和千粒重；二是本研究发现的干旱锻炼缓解了高温下颖花和籽粒大小的下降(表 2)。颖花育性对高温响应非常敏感，高温下颖花育性大幅下降是水稻热敏感品种结实率下降并减产的主要原因^[4, 35]。在本研究中，分蘖期干旱锻炼则提高了高温下两优培九的颖花育性(图 3)。因此，干旱锻炼通过促进颖花发育和提高颖花育性来缓解高温对产量的不利影响。

3.2 干旱锻炼提高高温下的颖花育性

水稻幼穗分化期高温下花粉活力降低导致颖花不育^[36]。本研究也发现了同样的结果，而干旱锻炼能缓解幼穗分化期高温下两优培九花粉活力的下降(图 3)。类似地，Saini 等^[37]发现鹰嘴豆营养生长期的干旱锻炼提高了开花期低温胁迫下的花粉活力。高温胁迫下过量活性氧积累使绒毡层

降解异常和膜脂过氧化，导致花粉败育^[38-39]。在本研究中，高温显著增加了两优培九颖花丙二醛含量，而干旱锻炼能降低幼穗分化期高温下其含量(图 5)；类似地，前人研究也发现营养生长期的干旱锻炼可以减少花后干旱胁迫下叶片丙二醛含量^[40]。这些结果表明干旱锻炼可以提高植株抗氧化能力。酶促抗氧化系统是植物解毒活性氧的机制之一，在植物耐热性中发挥着重要作用^[11]。在本研究中干旱锻炼通过提高 SOD 和 POD 活性来增强两优培九颖花的抗氧化胁迫能力(图 5)。Ru 等^[41]也发现干旱锻炼可以通过激活根系抗氧化酶活性来降低干旱胁迫下玉米根系丙二醛含量。Saini 等^[42]发现干旱锻炼后植株在后续低温胁迫下 SOD 和 POD 的基因表达上调。另外，Fe、Cu、Zn 等微量营养元素作为抗氧化酶的辅因子在抵抗氧化胁迫上发挥作用^[43]。Ru 等^[44]认为干旱锻炼可能通过促进根系对微量营养元素的吸收而增加抗氧化酶基因的转录和表达。因此，分蘖期干旱锻炼下颖花抗氧化能力的增强可能是水稻幼穗分化期高温下的花粉活力和颖花育性高的生理原因之一。

3.3 干旱锻炼促进高温下的颖花发育

Abid 等^[45]发现干旱锻炼可以促进颖花发育, 提高花后干旱胁迫下的籽粒大小和粒重。本研究发现分蘖期干旱锻炼能缓解幼穗分化期高温对颖花大小和总颖花分化数的不利影响(表 2 和表 4)。幼穗分化期高温导致同化物向穗部供应不足, 制约颖花的生长和分化, 导致总颖花分化数和颖花大小下降^[46]。在本研究也发现穗部非结构性碳水化合物含量与颖花宽($r=0.69$, $P<0.001$)和总颖花分化数($r=0.60$, $P<0.01$)紧密相关, 而分蘖期干旱锻炼缓解了幼穗分化期高温下穗部碳水化合物含量的下降(图 4)。同样地, 干旱锻炼提高了温度和干旱胁迫下植株可溶性糖和淀粉含量^[37, 44]。究其原因, 干旱锻炼增加叶片叶绿素和 Rubisco 蛋白含量, 这有利于提高光合速率并促进同化物积累^[40]; 另外, Bahuguna 等^[47]发现水稻花前干旱锻炼提高了干旱胁迫下颖花细胞壁转化酶活性, 从而增强了库活性。这表明分蘖期干旱锻炼可以通过增加穗部非结构性碳水化合物含量来促进水稻幼穗分化期高温下的颖花发育和缓解产量下降。

幼穗分化期高温下穗部反式玉米素和反式玉米素核苷含量的下降也导致了总颖花分化数下降和籽粒减小^[48]。本研究发现分蘖期干旱锻炼提高了幼穗分化期高温下两个品种反式玉米素类细胞分裂素含量(表 5); 类似地, 旱后复水提高了玉米叶片玉米素核苷含量^[49]。Hirose 等^[50]发现反式玉米素类细胞分裂素主要在根系产生并运输到地上部发挥作用。适度干旱胁迫可促进根系生长^[51], 这可能有利于根细胞分裂素合成; Wu 等^[48]发现高温下较多的根细胞分裂素向颖花运输来促进颖花分化是抗性品种耐高温的原因之一。另外, 颖花原基分化期到雌雄蕊形成期根系和穗部高的玉米素和玉米素核苷含量有利于超高产杂交稻大穗形成^[52]。因此, 分蘖期干旱锻炼可能促进根系细胞分裂素合成并增加向地上部的分配, 从而提高颖花细胞分裂素含量, 促进水稻幼穗分化期高温下颖花发育和缓解产量下降。

3.4 不同品种对高温胁迫和干旱锻炼的响应

比较高温下结实率和产量表现, 两优培九表现出高温敏感性, 汕优 63 具有高的耐高温抗性(表 1), 这与 Wu 等^[48]研究一致。因此, 低结实率是制约高温下热敏感品种产量的主要原因。与两优培九相比, 汕优 63 通过高抗氧化酶活性缓解了高温对花粉活力的不利影响, 在高温下维持高颖花育性和结实率(表 1, 图 3, 图 5), 这与 Zhao 等^[11]

的研究结果类似。本研究发现适温下两品种的穗部淀粉含量相当, 然而高温下汕优 63 穗部淀粉含量降幅小于两优培九(图 4), 因此汕优 63 花粉中高的淀粉含量有利于其高温下花粉发育和活力。高温下分蘖期干旱锻炼后两优培九颖花 SOD 和 POD 活性增幅均高于汕优 63, 进而维持了两优培九高温下的高花粉活力和颖花育性(图 3, 图 5)。高温下分蘖期干旱锻炼后两优培九产量、结实率和千粒重的增幅均大于汕优 63(表 1), 这与 Abid 等^[45]的研究结果类似。因此, 这些研究表明干旱锻炼对热敏感型品种高温伤害的缓解作用更大。

4 结论

水稻分蘖期干旱锻炼缓解了幼穗分化期高温对水稻穗发育和产量的不利影响, 这主要是因为干旱锻炼增强了高温下颖花 SOD 和 POD 活性, 减轻了颖花氧化胁迫, 提高花粉活力和颖花育性; 促进了穗部非结构性碳水化合物和颖花反式玉米素类细胞分裂素积累, 增加颖花大小和数量。因此, 适当的干旱锻炼可提高水稻植株的耐热性。本研究为盆栽试验, 因田间生长环境(如光照、温度、天气)复杂, 大田条件下干旱锻炼对高温伤害的缓解作用需进一步研究。

参考文献:

- [1] IPCC. Climate change 2021: The Physical Science Basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press, 2021: 3949.
- [2] 中华人民共和国农业行业标准. NY/T 2915-2016. 水稻高温热害鉴定与分级[S]. 北京: 中国农业出版社, 2016. Agricultural Industry Standard of the People's Republic of China. NY/T 2915 — 2016. Identification and classification of heat injury of rice[S]. Beijing: China Agriculture Press, 2016. (in Chinese with English abstract)
- [3] Iovane M, Aronne G. High temperatures during microsporogenesis fatally shorten pollen lifespan[J]. *Plant Reproduction*, 2022, 35(1): 9-17.
- [4] 谢可冉, 高逖, 崔克辉. 高温下钾肥调控水稻产量的研究进展[J]. *作物杂志*, 2024(1): 8-15. Xie K Z, Gao T, Cui K H. Research progress of potassium fertilizer controlling rice yield under high temperature[J]. *Crops*, 2024(1): 8-15. (in Chinese with English abstract)
- [5] Wang Z Q, Zhang W Y, Yang J C. Physiological mechanism underlying spikelet degeneration in rice[J]. *Journal of Integrative Agriculture*, 2018, 17(7): 1475-1481.

- [6] Liu X L, Ji P, Yang H T, Jiang C J, Liang Z W, Chen Q Z, Lu F, Chen X, Yang Y Y, Zhang X B. Priming effect of exogenous ABA on heat stress tolerance in rice seedlings is associated with the upregulation of antioxidative defense capability and heat shock-related genes[J]. *Plant Growth Regulation*, 2022, 98(1): 23-38.
- [7] Kumar S, Thakur M, Mitra R, Basu S, Anand A. Sugar metabolism during pre- and post-fertilization events in plants under high temperature stress[J]. *Plant Cell Reports*, 2022, 41(3): 655-673.
- [8] 王亚梁, 张玉屏, 朱德峰, 向镜, 陈惠哲, 张义凯. 水稻器官形态和干物质积累对穗分化不同时期高温的响应[J]. *中国水稻科学*, 2016, 30(2): 161-169.
Wang Y L, Zhang Y P, Zhu D F, Xiang J, Chen H Z, Zhang Y K. Response of rice organ morphology and dry matter accumulation to high temperature at different panicle initiation stages[J]. *Chinese Journal of Rice Science*, 2016, 30(2): 161-169. (in Chinese with English abstract)
- [9] Zhang C X, Feng B H, Chen T T, Fu W M, Li H B, Li G Y, Jin Q Y, Tao L X, Fu G F. Heat stress-reduced kernel weight in rice at anthesis is associated with impaired source-sink relationship and sugars allocation[J]. *Environmental and Experimental Botany*, 2018, 155: 718-733.
- [10] Yi J, Moon S, Lee Y S, Zhu L, Liang W, Zhang D, Jung K H, An G. Defective Tapetum Cell Death 1 (*DTC1*) regulates ROS levels by binding to metallothionein during tapetum degeneration[J]. *Plant Physiology*, 2016, 170(3): 1611-1623.
- [11] Zhao Q, Zhou L J, Liu J C, Du X X, Asad M A U, Huang F D, Pan G, Cheng F M. Relationship of ROS accumulation and superoxide dismutase isozymes in developing anther with floret fertility of rice under heat stress[J]. *Plant Physiology and Biochemistry*, 2018, 122: 90-101.
- [12] Zhang C X, Feng B H, Chen T T, Zhang X F, Tao L X, Fu G F. Sugars, antioxidant enzymes and IAA mediate salicylic acid to prevent rice spikelet degeneration caused by heat stress[J]. *Plant Growth Regulation*, 2017, 83(2): 313-323.
- [13] Gill S S, Tuteja N. Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants[J]. *Plant Physiology and Biochemistry*, 2010, 48(12): 909-930.
- [14] Zhang C X, Fu G F, Yang X Q, Yang Y J, Zhao X, Chen T T, Zhang X F, Jin Q Y, Tao L X. Heat stress effects are stronger on spikelets than on flag leaves in rice due to differences in dissipation capacity[J]. *Journal of Agronomy and Crop Science*, 2016, 202(5): 394-408.
- [15] Kurakawa T, Ueda N, Maekawa M, Kobayashi K, Kojima M, Nagato Y, Sakakibara H, Kozuka J. Direct control of shoot meristem activity by a cytokinin-activating enzyme[J]. *Nature*, 2007, 445(7128): 652-655.
- [16] Wu C, Cui K H, Wang W C, Li Q, Fahad S, Hu Q Q, Huang J L, Nie L X, Mohapatra P K, Peng S B. Heat-induced cytokinin transportation and degradation are associated with reduced panicle cytokinin expression and fewer spikelets per panicle in rice[J]. *Frontiers in Plant Science*, 2017, 8: 371.
- [17] Bruce T J A, Matthes M C, Napier J A, Pickett J A. Stressful “memories” of plants: Evidence and possible mechanisms[J]. *Plant Science*, 2007, 173(6): 603-608.
- [18] Zhang X X, Wang X Y, Zhuang L L, Gao Y L, Huang B R. Abscissic acid mediation of drought priming-enhanced heat tolerance in tall fescue (*Festuca arundinacea*) and *Arabidopsis*[J]. *Physiologia Plantarum*, 2019, 167(4): 488-501.
- [19] Sintaha M, Man C K, Yung W S, Duan S, Li M W, Lam H M. Drought stress priming improved the drought tolerance of soybean[J]. *Plants-Basel*, 2022, 11(21): 2954.
- [20] Zhang X X, Wang X L, Zhong J W, Zhou Q, Wang X, Cai J, Dai T B, Cao W X, Jiang D. Drought priming induces thermo-tolerance to post-anthesis high-temperature in offspring of winter wheat[J]. *Environmental and Experimental Botany*, 2016, 127: 26-36.
- [21] Liu S, Li X, Larsen D H, Zhu X, Song F, Liu F. Drought priming at vegetative growth stage enhances nitrogen-use efficiency under post-anthesis drought and heat stress in wheat[J]. *Journal of Agronomy and Crop Science*, 2017, 203(1): 29-40.
- [22] Tankari M, Wang C, Ma H Y, Li X N, Li L, Sothar R K, Cui N B, Zaman-Allah M, Hao W P, Liu F L, Wang Y S. Drought priming improved water status, photosynthesis and water productivity of cowpea during post-anthesis drought stress[J]. *Agricultural Water Management*, 2021, 245: 106565.
- [23] Gunawardena T A, Fukai S, Blamey F P C. Low temperature induced spikelet sterility in rice: I. Nitrogen fertilisation and sensitive reproductive period[J]. *Australian Journal of Agricultural Research*, 2003, 54(10): 937-946.
- [24] 王亚梁, 张玉屏, 曾研华, 武辉, 向镜, 陈惠哲, 张义凯, 朱德峰. 水稻穗分化期高温对颖花分化及退化的影响[J]. *中国农业气象*, 2015, 36(6): 724-731.
Wang Y L, Zhang Y P, Zeng Y H, Wu H, Xiang J, Chen H Z, Zhang Y K, Zhu D F. Effect of high temperature stress on rice spikelet differentiation and degeneration during panicle initiation stage[J]. *Chinese Journal of Agrometeorology*, 2015, 36(6): 724-731. (in Chinese with English abstract)
- [25] Cock J H, Yoshida S. Accumulation of ¹⁴C-labelled carbohydrate before flowering and its subsequent redistribution and respiration in the rice plant[J]. *Japanese Journal of Crop Science*, 1972, 41(2): 226-234.
- [26] Pucher G W, Leavenworth C S, Vickery H B. Determination of starch in plant tissues[J]. *Analytical Chemistry*, 1948, 20: 850-853.
- [27] Li G H, Pan J F, Cui K H, Yuan M S, Hu Q Q, Wang W C, Mohapatra P K, Nie L X, Huang J L, Peng S B. Limitation of unloading in the developing grains is a possible cause responsible for low stem non-structural carbohydrate translocation and poor grain yield formation in rice through verification of recombinant inbred lines[J]. *Frontiers Plant Science*, 2017, 8: 1369.
- [28] Heath R L, Packer L. Photoperoxidation in isolated chloroplasts I. kinetics and stoichiometry of fatty acid peroxidation[J]. *Archives Biochemistry Biophysics*, 1968,

- 125(1): 189-198.
- [29] Dhindsa R S, Matowe W. Drought tolerance in two mosses: correlated with enzymatic defence against lipid peroxidation[J]. *Journal of Experimental Botany*, 1981, 32(1): 79-91.
- [30] Maehly A C, Chance B. The assay of catalases and peroxidases[J]. *Methods of Biochemical Analysis*, 1954, 1: 357-424.
- [31] Aebi H. Catalase in vitro[J]. *Methods in Enzymology*, 1984, 105: 121-126.
- [32] Bradford M M. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding[J]. *Analytical Biochemistry*, 1976, 72(1-2): 248-254.
- [33] 何爱斌. 头季源库调节对再生稻再生力的影响及其机理探究 [D]. 武汉: 华中农业大学图书馆, 2022.
He A B. Effect of source-sink regulation at main season on the regeneration ability of ratoon rice and its mechanism[D]. Wuhan: Huazhong Agricultural University, 2022. (in Chinese with English abstract)
- [34] Wu C, Cui K H, Fahad S. Heat stress decreases rice grain weight: Evidence and physiological mechanisms of heat effects prior to flowering[J]. *International Journal of Molecular Sciences*, 2022, 23(18): 10922.
- [35] Jagadish S V K, Craufurd P Q, Wheeler T R. Phenotyping parents of mapping populations of rice for heat tolerance during anthesis[J]. *Crop Science*, 2008, 48(3): 1140-1146.
- [36] Cheabu S, Panichawong N, Rattanamettha P, Wasuri B, Kasemsap P, Arikrit S, Vanavichit A, Malumpong C. Screening for spikelet fertility and validation of heat tolerance in a large rice mutant population[J]. *Rice Science*, 2019, 26(4): 229-238.
- [37] Saini R, Das R, Adhikary A, Kumar R, Singh I, Nayyar H, Kumar S. Drought priming induces chilling tolerance and improves reproductive functioning in chickpea (*Cicer arietinum* L.) [J]. *Plant Cell Reports*, 2022, 41(10): 2005-2022.
- [38] Giorno F, Wolters-Arts M, Mariani C, Rieu I. Ensuring reproduction at high temperatures: the heat stress response during anther and pollen development[J]. *Plants*, 2013, 2(3): 489-506.
- [39] Hasanuzzaman M, Nahar K, Alam M M, Fujita M. Modulation of antioxidant machinery and the methylglyoxal detoxification system in selenium-supplemented *Brassica napus* seedlings confers tolerance to high temperature stress[J]. *Biological Trace Element Research*, 2014, 161(3): 297-307.
- [40] Abid M, Tian Z W, Ata-Ul-Karim S T, Liu Y, Cui Y K, Zahoor R, Jiang D, Dai T B. Improved tolerance to post-anthesis drought stress by pre-drought priming at vegetative stages in drought-tolerant and -sensitive wheat cultivars[J]. *Plant Physiology and Biochemistry*, 2016, 106: 218-227.
- [41] Ru C, Hu X T, Chen D Y, Wang W E. Droughts and thermo-priming enhance acclimation to later drought and heat stress in maize seedlings by improving leaf physiological activity[J]. *Agronomy*, 2023, 13(4): 1124.
- [42] Saini R, Adhikary A, Juneja S, Kumar R, Singh I, Nayyar H, Kumar S. Drought priming triggers diverse metabolic adjustments and induces chilling tolerance in chickpea (*Cicer arietinum* L.) [J]. *Plant Physiology and Biochemistry*, 2023, 194: 418-439.
- [43] Banerjee A, Roychoudhury A. Dissecting the phytohormonal, genomic and proteomic regulation of micronutrient deficiency during abiotic stresses in plants[J]. *Biologia*, 2022, 77(11): 3037-3058.
- [44] Ru C, Hu X T, Chen D Y, Wang W, Song T Y. Heat and drought priming induce tolerance to subsequent heat and drought stress by regulating leaf photosynthesis, root morphology, and antioxidant defense in maize seedlings[J]. *Environmental and Experimental Botany*, 2022, 202: 105010.
- [45] Abid M, Shao Y H, Liu S X, Wang F, Gao J W, Jiang D, Tian Z W, Dai T B. Pre-drought priming sustains grain development under post-anthesis drought stress by regulating the growth hormones in winter wheat (*Triticum aestivum* L.) [J]. *Planta*, 2017, 246(3): 509-524.
- [46] Wang Y L, Zhang K, Shi Q H, Chen H Z, Xiang J, Hu G H, Chen Y H, Wang X D, Wang J K, Yi Z H, Zhu D F, Zhang Y P. Decrement of sugar consumption in rice young panicle under high temperature aggravates spikelet number reduction[J]. *Rice Science*, 2020, 27(1): 44-45.
- [47] Bahuguna R N, Tamilselvan A, Muthurajan R, Solis C A, Jagadish S V K. Mild preflowering drought priming improves stress defences, assimilation and sink strength in rice under severe terminal drought[J]. *Functional Plant Biology*, 2018, 45(8): 27-839.
- [48] Wu C, Cui K H, Wang W C, Li Q, Fahad S, Hu Q Q, Huang J L, Nie L X, Peng S B. Heat-induced phytohormone changes are associated with disrupted early reproductive development and reduced yield in rice[J]. *Scientific Reports*, 2016, 6: 34978.
- [49] Wang X L, Wang J J, Sun R H, Hou X G, Zhao W, Shi J, Zhang Y F, Qi L, Li X L, Dong P H, Zhang L X, Xu G W, Gan H B. Correlation of the corn compensatory growth mechanism after post-drought rewatering with cytokinin induced by root nitrate absorption[J]. *Agricultural Water Management*, 2016, 166: 77-85.
- [50] Hirose N, Take K, Kuroha T, Kamada-Nobusada T, Hayashi H, Sakakibara H. Regulation of cytokinin biosynthesis, compartmentalization and translocation[J]. *Journal of experimental Botany*, 2008, 59(1): 75-83.
- [51] Zhang Y J, Du H, Gui Y, Xu F Y, Liu J P, Zhang J H, Xu W F. Moderate water stress in rice induces rhizosheath formation associated with abscisic acid and auxin responses[J]. *Journal of Experimental Botany*, 2020, 71(9): 2740-2751.
- [52] Liu K, Li T T, Chen Y, Huang J, Qiu Y Y, Li S Y, Wang H, Zhu A, Zhuo X X, Yu F, Zhang H, Gu J F, Liu L J, Yang J C. Effects of root morphology and physiology on the formation and regulation of large panicles in rice[J]. *Field Crops Research*, 2020, 258: 107946.