

高温对水稻粒重形成的影响及其栽培调控研究进展

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Research Progress on Effects of High Temperature on Rice Grain Weight Formation and Cultivation Strategies

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Abstract: Frequent extreme heat events pose a serious threat to rice production due to global warming. As a component of rice yield, increased grain weight is beneficial for further improvement of rice production. Grain weight exhibits high genetic stability; however, it often varies significantly in the same rice variety under different environmental and cultivation conditions, such as high temperature, fertilizer, and water management. Therefore, the increase and stability of grain weight are closely associated with stable rice production under extreme high temperatures. This work briefly describes the formation and regulation of rice grain weight, and reviews the underlying mechanisms of high-temperature-induced reduction in grain weight from the perspective of physiological and biochemical processes, including assimilate translocation, sugar metabolism, and hormonal changes. Additionally, cultivation management measures for mitigating high-temperature damage are summarized. Based on current research, the work also suggests possible future research directions regarding the effects of high temperature on grain weight in rice.

Keywords: rice; high temperature; grain weight; grain size; grain filling; sugar metabolism; hormone; cultivation regulation

摘 要: 全球气候变暖使水稻生产持续面临极端高温威胁。粒重是水稻产量的重要构成因子, 增加粒重有利于水稻产量的进一步提升。粒重具有较高的遗传稳定性, 然而同一水稻品种粒重在高温、肥水管理等不同环境和栽培条件下具有较大差异。因此, 粒重的增加和稳定与极端高温下水稻稳产密切相关。本文简要叙述了水稻粒重的形成及其调控, 从同化物转运、糖代谢及激素变化等生理生化过程角度综述了不同时期高温导致水稻粒重降低的机理, 并概述了优化栽培调控措施对高温危害的缓解作用, 结合现有研究展望了未来高温影响水稻粒重的相关研究方向。

关键词: 水稻; 高温; 粒重; 籽粒大小; 灌浆充实; 糖代谢; 激素; 栽培调控

水稻是重要的粮食作物, 其安全生产关系着中国乃至全球的粮食安全。IPCC 第六次评估报告显示未来 20 年内全球升温将达到或超过 1.5℃, 水稻生产将持续面临极端高温威胁^[1]。抽穗开花期日最高温度连续三天超过 35℃可对水稻构成热胁迫^[2], 研究表明全球平均气温每升高 1℃可导致全球平均水稻产量下降 3.2%^[3], 当超过最适温度时白天温度升

高 1℃水稻产量降低 6%, 而夜间温度升高 1℃降低 7%^[4]。由此可见, 持续的全球变暖对水稻产量构成了重大挑战。

高温胁迫对水稻产量构成因子(穗数、每穗颖花数、结实率和粒重)等均有不同程度影响。高产大穗型水稻品种的增产主要通过稳定穗数和增加每穗颖花数^[5], 但在现有栽培管理条件下进一步增加水

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稻单位面积颖花数易造成群体质量恶化^[6]。除穗数和每穗颖花数外,水稻高产与粒重的增加密切相关,增加粒重有利于产量的进一步提升^[7-8]。此外,粒重还与稻米品质形成密切相关^[9]。一般认为粒重具有高遗传稳定性,目前关于粒重大小的相关研究主要集中于其遗传调控^[10-11];然而,同一水稻品种在不同栽培和环境(尤其是高温条件)下粒重存在较大差异^[12-13]。因此,阐明高温对水稻粒重的影响机理及栽培调控措施,对水稻高产稳产和栽培管理措施优化至关重要。

1 水稻粒重的形成和调控

水稻粒重由籽粒大小及其灌浆充实决定,颖壳和胚乳发育是籽粒大小的决定因素,籽粒灌浆与胚乳中淀粉积累紧密相关^[14-15]。目前发现了一些调控颖壳发育影响粒重的基因,如 *OsMADS56*、*TGW2*、*GW9* 和 *GSW3* 等^[16-18]。另一方面,植物激素参与调控水稻颖壳和胚乳发育。内源吲哚乙酸(IAA)、细胞分裂素(CTK)、赤霉素(GA)、油菜素内酯(BR)和乙烯(ETH)可通过促进颖壳细胞增殖和伸长^[19-25],脱落酸(ABA)可参与调节胚乳细胞化过程^[26],进而增加籽粒大小和粒重;ETH 还可与多胺互作调控籽粒大小,高乙烯/多胺比值与籽粒大小正相关^[27]。

水稻籽粒灌浆充实过程是籽粒中一系列酶将转运至胚乳中的蔗糖转化为淀粉并积累的过程^[28]。糖转运蛋白相关基因 *OsSUT1* 和 *OsSWEET4/11/14/15* 均在籽粒灌浆中发挥重要作用^[29-31]。淀粉合成相关酶,如腺苷二磷酸葡萄糖焦磷酸化酶(AGP)和颗粒结合淀粉合成酶(GBSS)等酶活性的提高及相关基因表达的上调均可促进籽粒灌浆^[32]。水稻籽粒中激素水平也可调控灌浆过程,IAA 可介导糖向胚乳转运和淀粉合成^[33-35];高水平的籽粒 CTK、ABA 含量可促进淀粉合成相关酶基因表达^[36-38],从而增加灌浆能力和粒重;然而,ETH、低 ABA/GA 比值可通过抑制淀粉合成相关酶的基因表达和酶活性,进而负向调控籽粒灌浆^[39-41]。

2 高温对籽粒大小和灌浆充实的影响及其与粒重的关系

2.1 幼穗分化期高温对籽粒大小、灌浆充实和粒重的影响

生殖生长早期高温是影响籽粒大小的重要环境因素^[42]。幼穗分化期高温降低了水稻颖壳长度和

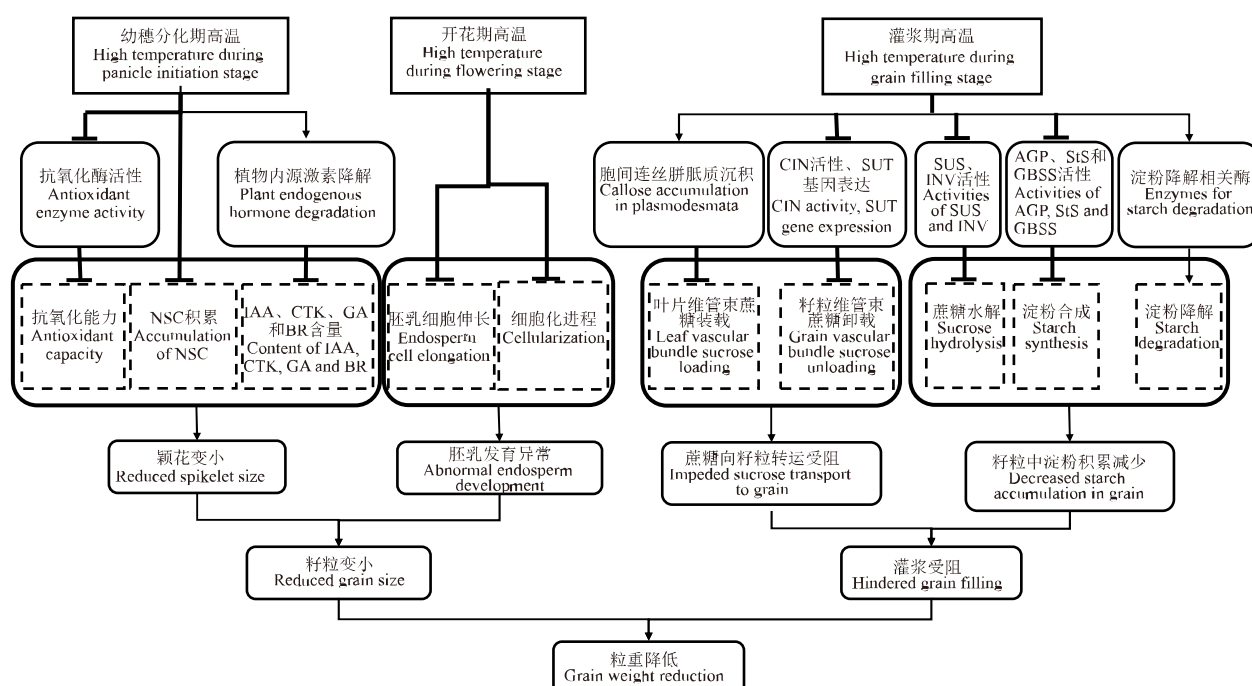
宽度,导致籽粒变小和粒重降低^[43]。曹云英等^[44]在江苏地区研究观察到减数分裂期高温仅显著降低了双桂 1 号的颖壳宽度,王亚梁等^[45]则报道在浙江地区幼穗分化期高温显著降低丰两优 6 号颖壳长度。这些研究表明水稻颖壳长度和宽度、粒重对高温的响应可能存在着品种和地区差异。

幼穗分化期高温通过多种途径来影响籽粒大小(图 1)。一是高温减少了穗部同化物供应和利用,幼穗分化早期高温降低了水稻叶片净光合速率,降低了幼穗中蔗糖转运蛋白相关基因 *OsSUT1*、*OsSUT2* 和 *OsSUT4* 表达量,导致穗部碳水化合物的供应和积累不足^[46-48];也降低穗部蔗糖合酶和可溶性酸性转化酶的活性,抑制糖酵解和三羧酸循环,从而阻断蔗糖水解和利用^[49]。二是高温导致水稻幼穗抗氧化酶活性降低即抗氧化能力降低,从而伤害颖花发育导致籽粒和粒重均变小^[50-51]。三是幼穗分化期高温导致幼穗中活性 CTK、IAA、GA₁ 和 BR 含量降低,抑制籽粒发育^[51-52]。高温导致水稻幼穗内源激素含量降低的可能原因是这些激素合成减少和降解增加。如陈燕华等^[47]发现幼穗分化期高温导致 *OsLOGL2* 和 *OsLOGL3* 基因表达下调、*OsCKX5* 和 *OsCKX9* 基因表达上调;另外, Wu 等^[13]发现幼穗分化期高温导致水稻植株根源 CTK 向穗部运输减少, Chen 等^[51]发现高温上调幼穗中与 BR、GA 降解相关基因的表达。因此,幼穗分化期高温可能通过减少幼穗同化物供应与利用、降低激素含量、增强颖花氧化损伤等途径抑制颖壳细胞发育,进而导致籽粒变小。然而颖壳细胞增殖和伸长对幼穗分化期高温的响应研究较少,颖壳糖代谢及激素变化与籽粒大小变化的内在联系有待于深入探究。

幼穗分化期高温也可影响籽粒灌浆充实进而影响粒重,如 Zhang 等^[42]研究表明湖南地区幼穗分化期高温抑制同化物向籽粒的转运,进而导致胚乳淀粉积累减少; Lin 等^[53]研究表明江苏地区一次枝梗分化期和雌雄蕊原基分化期高温导致胚乳直链淀粉积累量减少和粒重降低。此外, Zhen 等^[46]研究表明与抽穗期和灌浆期高温相比,江苏地区幼穗分化期高温对粒重的影响更严重, Wu 等^[13]在华中地区的五年定点试验也发现了这一现象。由此可见,幼穗分化期高温胁迫可能表现出调控粒重的后效应,然而对灌浆期淀粉积累影响的内在机理研究较少。

2.2 抽穗和灌浆期高温对籽粒大小、灌浆充实和粒重的影响

与幼穗分化期高温不同,抽穗期高温对籽粒大小的影响则更多与胚乳发育有关(图 1)。一方面,胚



图中→表示促进, —表示抑制。NSC, 非结构性碳水化合物; CIN, 细胞壁转化酶; SUS, 蔗糖合酶; INV, 蔗糖转化酶; AGP, 腺苷二磷酸葡萄糖糖基磷酸化酶; StS, 淀粉合成酶; GBSS, 颗粒结合淀粉合成酶。

→ indicates promotion effect in the figure, and — indicates inhibiting effect. NSC, Non-structural carbohydrates; CIN, Cell wall invertase; SUS, Sucrose synthase; INV, Sucrose invertase; AGP, Adenosine diphosphate glucose pyrophosphorylase; StS, Starch synthase; GBSS, Granule-bound starch synthase.

图 1 高温降低水稻粒重的机理

Fig. 1. Mechanism of the reduction of grain weight in rice under high temperature stress

乳细胞数量和大小受高温影响,如 Morita 等^[54]报道抽穗期夜间高温降低胚乳细胞大小; Wada 等^[55]研究表明抽穗后 5 d 夜间高温处理通过渗透调节抑制胚乳细胞伸长和降低粒宽。另一方面,胚乳细胞化提前或滞后不利于胚乳发育,水稻受精后中度高温胁迫上调 *OsFIE1* 基因表达引起胚乳细胞化提前^[56],重度高温胁迫则直接导致胚乳无法进行细胞化^[56],开花期高温胁迫下调 *OsMADS87* 基因表达,胚乳细胞化加快^[57],从而导致籽粒变小。因此,高温所致的胚乳细胞增殖、伸长及发育进程受阻可导致籽粒变小和粒重降低。

水稻灌浆期籽粒形成涉及源叶同化物供应、蔗糖的维管束转运(装载、运输和卸载)、籽粒中蔗糖水解和淀粉合成等生理生化过程,该时期高温常常导致籽粒灌浆受阻和粒重降低(图 1)。前人研究认为由于蒸腾降温的存在,白天高温对光合作用无显著影响,但呼吸作用增强导致同化物消耗增加抑制籽粒灌浆^[58];然而,Baruah 等^[59]研究表明灌浆期夜间高温可降低叶绿素荧光参数和光合速率。这表明光合作用对白天高温和夜间高温响应存在差异,但高温均可减少同化物供应,降低籽粒灌浆充实和粒重。

高温下粒重降低还与同化物向籽粒分配减少有关(图 1)。一方面,叶片蔗糖维管束装载受阻导致蔗糖向籽粒供应不足。高温增加了水稻叶片、叶鞘中编码葡聚糖合酶的基因 *OsGSL2*、*OsGSL4* 和 *OsGSL5* 的表达,导致胞间连丝胼胝质沉积,糖装载的共质体运输量降低^[60-61]。另一方面,高温导致同化物从茎鞘向穗部运输受阻,茎鞘大量积累同化物^[62]。第三,籽粒中蔗糖卸载受阻导致灌浆底物不足,如灌浆期高温降低细胞壁转化酶活性,下调编码蔗糖转运蛋白基因(*OsSUT1*、*OsSUT2* 和 *OsSUT4*)表达,抑制籽粒韧皮部蔗糖质外体卸载^[63-65]。此外,灌浆期高温可破坏水稻籽粒内源激素稳态,如高温显著降低籽粒 ABA/GA₄、ABA/(玉米素+玉米素核苷+IAA)比例可导致籽粒灌浆受阻、淀粉积累减少^[66-67]。

灌浆期高温可通过影响水稻籽粒中蔗糖-淀粉转化及淀粉积累进而影响粒重(图 1)。灌浆期持续 12 d 40℃ 高温或灌浆初期持续 15 d 夜间高温可降低日本晴高温敏感突变体、浙禾香 2 号籽粒中蔗糖合酶和酸性蔗糖转化酶活性,导致淀粉合成的前体物质供应不足^[61,65];另一方面,灌浆期高温也导致浙禾香 2 号和 IR64 籽粒中编码 AGP 和 GBSS 的基因表达下调和酶活性降低^[64,68],直接抑制淀粉合

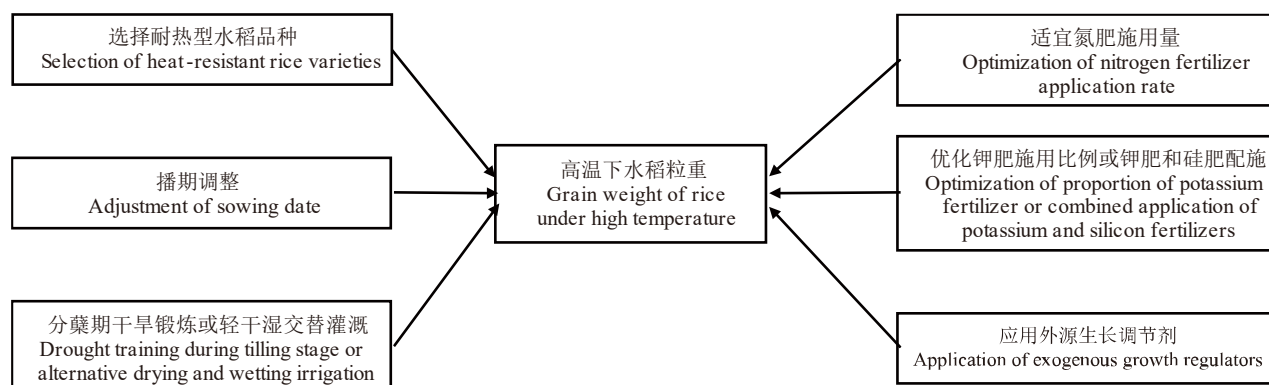


图 2 缓解高温胁迫下水稻粒重降低的措施

Fig. 2. Measures for mitigation of the decrease in rice grain weight under high temperature stresses

成。高温导致淀粉合成相关酶活性降低的可能原因是籽粒抗氧化酶活性降低导致抗氧化能力下降、ROS 积累增加^[69]；然而，Shao 等^[66]发现灌浆期 40℃ 高温下水稻湘早籼 45 籽粒 AGP、GBSS 等淀粉合成相关酶活性升高，而籽粒淀粉含量和产量降低，其可能原因是淀粉磷酸化酶和 α -葡萄糖苷酶活性升高。这些研究表明灌浆期高温调控淀粉积累的生理生化过程较为复杂，其高温响应也可能与水稻品种、高温强度和高温持续时间有关。

3 缓解高温胁迫下水稻粒重降低的栽培措施

3.1 选择耐热水稻品种

选择耐热型水稻品种是缓解高温下产量损失的重要措施(图 2)。Fukai 等^[70]研究表明，大气和水稻冠层之间的温差存在基因型变异，叶片和穗部保持较低温度的品种表现出更高的耐高温能力和籽粒饱满度。一些转录因子在水稻耐热中发挥重要作用，如 MYB、NAC、DST 等^[71-73]，例如，编码 MYB 转录因子的 *OsPL* 基因突变体具有比野生型植株高的耐热能力^[71]，敲除和过表达 *ONAC127* 和 *ONAC129* 植物均表现出耐热能力降低、籽粒灌浆不完全和籽粒皱缩^[72]，水稻 DST 转录因子通过 ROS 介导的气孔运动和热响应基因表达负向调节耐热性^[73]。这些基因型间差异和耐热基因的发现为耐热品质的培育提供了可能。

3.2 播期管理

根据水稻栽培地区气候和品种生育期适当调整播种期可缓解高温危害(图 2)。Mohapatra 等^[74]报道不同水稻品种对不同播期的响应差异与其对生殖生长期高温的耐受性有关，调整播期减少生殖生

长期与高温发生的重合时间，可以减轻高温对产量的影响。段里成等^[75]研究表明，与常规播期相比，适当提前早稻播种时间能显著缩短其生育期内遭遇高温的时间，提高粒重和产量；此外，Liu 等^[76]和 Zhang 等^[77]发现与 4 月底和 5 月初播种相比，华中地区中稻 5 月中下旬播种可降低热胁迫程度并获得较高的粒重和产量。因此，实际生产中应结合种植区温度变化特征，适当提前早稻播种时间或推迟中稻播种时间，避开水稻生殖生长期内高温或缩短高温时间，有利于缓解高温对水稻粒重和产量的不利影响。

3.3 优化肥料管理

研究发现高温下增施氮肥可影响水稻粒重，韩展誉等^[78]报道浙江地区与低氮相比，增施氮素穗肥显著增加了灌浆期高温下秀水 134 和秀水 09 的粒重和产量；Dou 等^[79]研究表明江苏地区增加全生育期氮肥施用量可缓解灌浆结实期高温危害，显著增加高温下武运粳 31 的粒重和产量。此外，高温下氮肥类型对粒重的影响存在差异，如在开花期全天高温下，施用铵态氮肥时耐热品系和热敏感品系的粒重提高了约 4.4%，施用 NH_4NO_3 时则提高了约 7.7%^[80]。钾肥施用可调控高温下水稻叶片气孔特征及同化物运输等^[81]，施用钾肥(如叶面喷施 KH_2PO_4)可缓解高温对粒重及产量的影响。在高温下，与钾肥仅作基肥相比，按照基肥：促花肥为 7：3 施用可显著提高旭粳 21 的粒重^[82]。此外，在四川地区水稻抽穗扬花期高温下，钾硅配施可提高旌优 127 粒重和产量^[83]。因此，优化施肥有利于增加高温下水稻粒重(图 2)，其可能原因包括：一是提高叶片抗氧化酶活性，减轻高温对叶片的伤害^[80]；二是调控气孔导度，提高叶片光合速率，保证籽粒灌浆所需的同化物供应^[78,81]；三是降低穗部温度，维持生殖

表 1 外源生长调节剂对高温下水稻粒重的影响

Table 1. Effect of exogenous growth regulators on grain weight of rice under high temperature

高温处理时间 High temperature treatment time	处理 Treatment	处理效果 Treatment effect	参考文献 Reference
拔节期全天高温处理 7 d Full day high temperature treatment for 7 days during the jointing stage	高温处理当天和次日叶面喷施 0.1 mmol·L ⁻¹ 茉莉酸甲酯 Apply 0.1 mmol·L ⁻¹ methyl jasmonate to the leaf surface on the day of high temperature treatment and on the second day	高温下喷施茉莉酸甲酯粒重提高 2.3% Spraying methyl jasmonate under high temperature increases grain weight by 2.3%	[50]
幼穗分化期白天高温 (持续 15 d) Daytime high temperature during the panicle initiation stage (lasting for 15 days)	高温处理前、后 2 d 每株茎上各喷施 20 mL 60 mg·L ⁻¹ 6-BA Spray 20 mL of 60 mg·L ⁻¹ 6-BA on each stem on the second day before and after high temperature treatment	高温胁迫下喷施 6-BA 粒重显著提高 7.8% Spraying 6-BA under high temperature stress significantly increased grain weight by 7.8%	[52]
幼穗分化期高温(持续 7 d) High temperature during the panicle initiation stage (lasting for 7 days)	每株喷施 37.5 mL 0.15 mg·L ⁻¹ EBR Each plant was sprayed with 37.5 mL of 0.15 mg·L ⁻¹ EBR	高温胁迫下喷施 EBR 后耐热品种粒重显著提高 3.6%，热敏感品种粒重显著提高 7.3% After spraying EBR under high temperature stress, the grain weight of heat-tolerant varieties significantly increased by 3.6%, while that of heat-sensitive varieties significantly increased by 7.3%	[51]
开花期高温 High temperature during flowering stage	每株穗部喷施 20~30 mL 浓度为 10 μmol·L ⁻¹ IAA 或 100 μmol·L ⁻¹ 萘乙酸 Each panicle was sprayed with 20-30 mL of 10 μmol·L ⁻¹ IAA or 100 μmol·L ⁻¹ naphthaleneacetic acid	高温下喷施 10 μmol·L ⁻¹ IAA 和 100 μmol·L ⁻¹ 萘乙酸后粒重分别增加 54.7%和 49.7% After spraying 10 μmol·L ⁻¹ IAA and 100 μmol·L ⁻¹ naphthaleneacetic acid under high temperature, the grain weight increased by 54.7% and 49.7%, respectively	[87]
开花期全天高温处理 8 d High temperature treatment throughout the flowering period for 8 days	孕穗末期叶面或穗部喷施 50 μmol·L ⁻¹ ABA、100 μmol·L ⁻¹ ABA 或 1%原花青素 Spraying 50 μmol·L ⁻¹ ABA, 100 μmol·L ⁻¹ ABA, or 1% procyanidins on the leaves or panicles at the late booting stage	高温下喷施 50 μmol·L ⁻¹ ABA、100 μmol·L ⁻¹ ABA 和喷施 1%原花青素后粒重分别增加 6.2%、7.2%和 5.2% After spraying 50 μmol·L ⁻¹ ABA, 100 μmol·L ⁻¹ ABA, and 1% procyanidins at high temperature, the grain weight increased by 6.2%, 7.2%, and 5.2%, respectively	[88]
授粉后 5 d 全天高温处理 5 d High temperature treatment for 5 days after pollination, starting from the 5th day	授粉 3 d 后连续 3 d 每穗每天喷施 4 mL 1.5 mmol·L ⁻¹ 亚精胺 After three days of pollination, spray 4 mL of 1.5 mmol·L ⁻¹ spermidine on each panicle every day for 3 consecutive days	高温下喷施亚精胺粒重提高 13.4% Spraying spermidine at high temperature increased grain weight by 13.4%	[89]
开花期白天高温处理 5 d High temperature treatment during the flowering period for 5 days	高温处理前 1 d 和处理后 3 d 喷施 500 μmol·L ⁻¹ 水杨酸 Spray 500 μmol·L ⁻¹ salicylic acid 1 day before high temperature treatment and 3 days after treatment	高温下喷施水杨酸显著提高粒重 Spraying salicylic acid under high temperature significantly increases grain weight	[77]

器官(花粉和花药)的正常发育^[79,84]。

3.4 水分调控

适宜水分管理可减轻水稻高温危害(图 2)。分蘖期干旱锻炼显著提高幼穗分化期高温下热敏感型品种的粒重^[85]；与保持 1~2 cm 浅水层和重干湿交替灌溉相比，轻度干湿交替灌溉显著提高抽穗灌浆期高温下热敏感型品种的粒重^[86]。适宜水分管理可缓解水稻高温伤害的可能原因包括：一轻干湿交替灌溉增加了茎鞘 α、β-淀粉酶等酶的活性^[86]，分蘖期干旱锻炼增加了颖花非结构性碳水化合物含量^[85]，促进同化物向籽粒转运；二增加了籽粒中多胺特别是亚精胺和精胺含量、玉米素和玉米素核苷含量，促进籽粒发育，进而增加粒重^[85-86]；三提高抗氧化能力，分蘖期干旱锻炼通过增加穗分化期高温下热敏感品种幼穗过氧化物酶和超氧化物歧化酶

活性，进而导致籽粒变大和粒重增加^[85]。

3.5 施用外源生长调节剂

外源施用生长调节剂可以缓解水稻高温伤害，增加高温下粒重，如 6-BA(6-苄氨基腺嘌呤)^[52]、EBR(2,4-表油菜素内酯)^[51]、茉莉酸甲酯^[50]、IAA 或萘乙酸^[87]、ABA^[88]、亚精胺^[89]、水杨酸^[77]等，其中幼穗分化期高温下喷施 6-BA、开花期高温下喷施 IAA 或萘乙酸效果更好(图 2)。高温发生时期和持续时间、调节剂种类和浓度、喷施位置和时间等均影响外源生长调节剂的调控效应(表 1)。施用外源生长调节剂提高高温下水稻粒重的可能原因包括：一提高光合速率，进而增加同化物向籽粒转运^[87]；二提高抗氧化能力，降低籽粒中过氧化物含量，进而减轻氧化损伤^[52,77,88]；三增加幼穗内源 BR、CTK 和 IAA 含量，缓解高温伤害^[51]。

4 展望

水稻籽粒大小和灌浆充实是决定粒重的关键因素。已有研究从颖壳发育、胚乳发育及灌浆充实等角度揭示了不同时期高温影响粒重形成的机制,但高温条件下颖壳和胚乳发育的调控网络不明确,及其对高温环境(如高温强度、持续时间与发生时期、环境湿度、水肥管理)的响应和基因型差异仍不清楚,未来应进一步利用多学科和多种技术手段,系统解析在不同高温环境条件下颖壳和胚乳发育的调控,阐明高温影响水稻籽粒大小和灌浆充实的分子机制。第二,提高水稻品种高温抗性是维持高温条件下水稻产量和粒重稳定的根本途径,通过基因编辑和分子标记辅助育种,加速耐高温水稻品种选育与应用。第三,栽培管理措施对减缓高温伤害有着重要调节作用,未来应进一步优化栽培管理技术(如播期调整、水肥调控)、研发与应用抗逆物化产品(如外源生长调节物质、抗氧化剂)。因此,应注重多学科交叉,利用分子生物学、遗传育种、作物生理学和作物栽培学的研究思路和技术手段,阐明高温下水稻产量和粒重形成调控机理,选育和应用耐高温品种,优化栽培管理技术,为实现高温胁迫下水稻高产稳产提供理论支撑、品种和技术保障。

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] Coast O, Ellis R H, Murdoch A J, Quiñones C, Jagadish K S V. High night temperature induces contrasting responses for spikelet fertility, spikelet tissue temperature, flowering characteristics and grain quality in rice[J]. *Functional Plant Biology*, 2015, 42(2): 149-161.
- [3] Zhao C, Liu B, Piao S L, Wang X H, Lobell D B, Huang Y, Huang M T, Yao Y T, Bassu S, Ciaia P, Durand J L, Elliott J, Ewert F, Janssens I A, Li T, Lin E, Liu Q, Martre P, Müller C, Peng S S, Peñuelas J, Ruane A C, Wallach D, Wang T, Wu D H, Liu Z, Zhu Y, Zhu Z C, Asseng S. Temperature increase reduces global yields of major crops in four independent estimates[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2017, 114(35): 9326-9331.
- [4] Su Q, Rohila J S, Ranganathan S, Karthikeyan R. Rice yield and quality in response to daytime and nighttime temperature increase: A meta-analysis perspective[J]. *Science of the Total Environment*, 2023, 898: 165256.
- [5] Li R H, Li M J, Ashraf U, Liu S W, Zhang J E. Exploring the relationships between yield and yield-related traits for rice varieties released in China from 1978 to 2017[J]. *Frontiers in Plant Science*, 2019, 10: 543.
- [6] 凌启鸿, 张洪程, 丁艳锋, 仲维功, 祝树德. 水稻丰产高效技术及理论[M]. 北京: 中国农业出版社, 2005: 29-30.
- [7] Ling Q H, Zhang H C, Ding Y F, Zhong W G, Zhu S D. High yield and high efficiency technology and theory of rice [M]. Beijing: China Agriculture Press, 2005: 29-30. (in Chinese)
- [7] 陶士宝, 柯健, 孙杰, 尹传俊, 朱铁忠, 陈婷婷, 何海兵, 尤翠翠, 郭爽爽, 武立权. 长江中下游地区不同穗型中籼杂交稻高产群体农艺特征[J]. 作物学报, 2023, 49(2): 511-525.
- [8] Tao S B, Ke J, Sun J, Yin C J, Zhu T Z, Chen T T, He H B, You C C, Guo S S, Wu L Q. High-yielding population agronomic characteristics of middle-season indica hybrid rice with different panicle sizes in the middle and lower reaches of the Yangtze River[J]. *Acta Agronomica Sinica*, 2023, 49(2): 511-525. (in Chinese with English abstract)
- [8] 朱德峰, 杨从党, 向镜, 陈惠哲, 张玉屏, 陈叶平, 王岳钧, 王亚梁, 张义凯. 水稻亩产千公斤品种产量潜力分析[J]. 中国稻米, 2020, 26(4): 7-9.
- [9] Zhu D F, Yang C D, Xiang J, Chen H Z, Zhang Y P, Chen Y P, Wang Y J, Wang Y L, Zhang Y K. Analysis of yield potential of rice varieties for 15 ton per hectare[J]. *China Rice*, 2020, 26(4): 7-9. (in Chinese with English abstract)
- [9] Guo E J, Wang L Z, Shi Y Y, Jiang S K, Cheng X, Chen X, Ma H Y, Wan N H, Bai F, Zhang Z T, Zhang T Y, Li T, Yang X G. Response of rice yield, grain quality to chilling at grain filling stages[J]. *Journal of the Science of Food and Agriculture*, 2024, 104(15): 9312-9323.
- [10] 程琴, 孔令汉, 王鹏, 黄涛, 吴光亮, 王燕宁, 刘睿琦, 何欣月, 贺浩华, 边建民. 水稻粒型、粒重和灌浆研究进展[J]. 分子植物育种, 2023, 21(4): 1196-1205.
- [11] Cheng Q, Kong L H, Wang P, Huang T, Wu G L, Wang Y N, Liu R Q, He X Y, He H H, Bian J M. Research progress of grain shape, grain weight and grain filling in rice(*Oryza sativa* L.)[J]. *Molecular Plant Breeding*, 2023, 21(4): 1196-1205. (in Chinese with English abstract)
- [11] Li L F, Li J J, Liu K K, Jiang C L, Jin W H, Ye J K, Qin T R, Luo B J, Chen Z Y, Li J Z, Lü F X, Li X J, Wang H P, Jin J H, Deng Q M, Wang S Q, Zhu J, Zou T, Liu H N, Li S C, Li P, Liang Y Y. *DGW1*, encoding an hnRNP-like RNA binding protein, positively regulates grain size and weight by interacting with *GW6* mRNA[J]. *Plant Biotechnology Journal*, 2024, 22(2): 512-526.
- [12] 吕川根, 宗寿余, 胡凝, 邹江石, 姚克敏, 唐卫亚. 两系杂交稻两优培九粒重因子的环境模型解析及生态特征分析[J]. 作物学报, 2008, 34(12): 2202-2209.
- [13] Lü C G, Zong S Y, Hu N, Zou J S, Yao K M, Tang W Y. Modeling with climatic factors and analysis on ecological characters for grain weight dissected factors of two-line hybrid rice, Liangyoupeijiu[J]. *Acta Agronomica Sinica*,

- 2008, 34(12): 2202-2209. (in Chinese with English abstract)
- [13] 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.
- [14] Li G M, Tang J Y, Zheng J K, Chu C C. Exploration of rice yield potential: Decoding agronomic and physiological traits[J]. *Crop Journal*, 2021, 9(3): 577-589.
- [15] Alam I, Batool K, Huang Y Y, Liu J J, Ge L F. Developing genetic engineering techniques for control of seed size and yield[J]. *International Journal of Molecular Sciences*, 2022, 23(21): 13256.
- [16] Ruan B P, Shang L G, Zhang B, Hu J, Wang Y X, Lin H, Zhang A P, Liu C L, Peng Y L, Zhu L, Ren D Y, Shen L, Dong G J, Zhang G H, Zeng D L, Guo L B, Qian Q, Gao Z Y. Natural variation in the promoter of *TGW2* determines grain width and weight in rice[J]. *New Phytologist*, 2020, 227(2): 629-640.
- [17] Bai F, Ma H J, Cai Y C, Shahid M Q, Zheng Y B, Lang C, Chen Z X, Wu J W, Liu X D, Wang L. Natural allelic variation in *grain size and weight 3* of wild rice regulates the grain size and weight[J]. *Plant Physiology*, 2023, 193(1): 502-518.
- [18] Wen Y, Hu P, Fang Y X, Tan Y Q, Wang Y Y, Wu H, Wang J G, Wu K X, Chai B Z, Zhu L, Zhang G H, Gao Z Y, Ren D Y, Zeng D L, Shen L, Dong G J, Zhang Q, Li Q, Xiong G S, Xue D W, Qian Q, Hu J. *GW9* determines grain size and floral organ identity in rice[J]. *Plant Biotechnology Journal*, 2024, 22(4): 915-928.
- [19] Guo T, Chen K, Dong N Q, Ye W W, Shan J X, Lin H X. *Tillering and small grain 1* dominates the tryptophan aminotransferase family required for local auxin biosynthesis in rice[J]. *Journal of Integrative Plant Biology*, 2020, 62(5): 581-600.
- [20] Panda B B, Sekhar S, Dash S K, Behera L, Shaw B P. Biochemical and molecular characterisation of exogenous cytokinin application on grain filling in rice[J]. *BMC Plant Biology*, 2018, 18(1): 89.
- [21] Zhang Y C, Gan L, Zhang Y J, Huang B S, Wan B L, Li J B, Tong L Q, Zhou X, Wei Z S, Li Y, Song Z J, Zhang X H, Cai D T, He Y C. OsCBL5-CIPK1-PP23 module enhances rice grain size and weight through the gibberellin pathway[J]. *The Plant Journal*, 2023, 115(4): 895-909.
- [22] Shi C L, Dong N Q, Guo T, Ye W W, Shan J X, Lin H X. A quantitative trait locus *GW6* controls rice grain size and yield through the gibberellin pathway[J]. *The Plant Journal*, 2020, 103(3): 1174-1188.
- [23] Li J, Zhang B L, Duan P G, Yan L, Yu H Y, Zhang L M, Li N, Zheng L Y, Chai T Y, Xu R, Li Y H. An endoplasmic reticulum-associated degradation-related E2-E3 enzyme pair controls grain size and weight through the brassinosteroid signaling pathway in rice[J]. *The Plant Cell*, 2023, 35(3): 1076-1091.
- [24] Tao Y J, Wang J, Miao J, Chen J, Wu S J, Zhu J Y, Zhang D P, Gu H W, Cui H, Shi S Y, Xu M Y, Yao Y L, Gong Z Y, Yang Z F, Gu M H, Zhou Y, Liang G H. The spermine synthase OsSPMS1 regulates seed germination, grain size, and yield[J]. *Plant Physiology*, 2018, 178(4): 1522-1536.
- [25] Liu C, Ma T, Yuan D Y, Zhou Y, Long Y, Li Z W, Dong Z Y, Duan M J, Yu D, Jing Y Z, Bai X Y, Wang Y B, Hou Q C, Liu S S, Zhang J S, Chen S Y, Li D Y, Liu X, Li Z K, Wang W S, Li J P, Wei X, Ma B, Wan X Y. The OsEIL1-OsERF115-target gene regulatory module controls grain size and weight in rice[J]. *Plant Biotechnology Journal*, 2022, 20(8): 1470-1486.
- [26] Zhang X F, Tong J H, Bai A N, Liu C M, Xiao L T, Xue H W. Phytohormone dynamics in developing endosperm influence rice grain shape and quality[J]. *Journal of Integrative Plant Biology*, 2020, 62(10): 1625-1637.
- [27] Hu W L, Wang R, Hao X H, Li S Z, Zhao X J, Xie Z J, Wu S, Huang L Q, Tan Y, Tian L F, Li D P. OsLCD3 interacts with OsSAMS1 to regulate grain size via ethylene/polyamine homeostasis control[J]. *The Plant Journal*, 2024, 119(2): 705-719.
- [28] Krishnan S, Dayanandan P. Structural and histochemical studies on grain-filling in the caryopsis of rice (*Oryza sativa* L.)[J]. *Journal of Biosciences*, 2003, 28(4): 455-469.
- [29] Yang J L, Luo D P, Yang B, Frommer W B, Eom J S. SWEET11 and 15 as key players in seed filling in rice[J]. *New Phytologist*, 2018, 218(2): 604-615.
- [30] Fei H H, Yang Z P, Lu Q T, Wen X G, Zhang Y, Zhang A H, Lu C M. OsSWEET14 cooperates with OsSWEET11 to contribute to grain filling in rice[J]. *Plant Science*, 2021, 306: 110851.
- [31] Li G H, Cui K H, Hu Q Q, Wang W C, Pan J F, Zhang G, Shi Y G, Nie L X, Huang J L, Peng S B. Phloem unloading in developing rice caryopses and its contribution to non-structural carbohydrate translocation from stems and grain yield formation[J]. *Plant & Cell Physiology*, 2022, 63(10): 1510-1525.
- [32] Huang L C, Tan H Y, Zhang C Q, Li Q F, Liu Q Q. Starch biosynthesis in cereal endosperms: An updated review over the last decade[J]. *Plant Communications*, 2021, 2(5): 100237.
- [33] Basunia M A, Nonhebel H M, Backhouse D, McMillan M. Localised expression of OsIAA29 suggests a key role for auxin in regulating development of the dorsal aleurone of early rice grains[J]. *Planta*, 2021, 254(2): 40.
- [34] Wu D X, Cao Y N, Wang D J, Zong G X N, Han K X, Zhang W, Qi Y H, Xu G H, Zhang Y L. Auxin receptor OsTIR1 mediates auxin signaling during seed filling in rice[J]. *Plant Physiology*, 2024, 194(4): 2434-2448.
- [35] Panda D, Mohanty S, Das S, Mishra B, Baig M J, Behera L. Light intensity-mediated auxin homeostasis in spikelets links carbohydrate metabolism enzymes with grain filling rate in rice[J]. *Protoplasma*, 2023, 260(4): 1233-1251.

- [36] Zhang D P, Zhang M Y, Zhou Y, Wang Y Z, Shen J Y, Chen H Y X, Zhang L, Lü B, Liang G H, Liang J S. The rice G protein γ subunit DEPI/qPE9-1 positively regulates grain-filling process by increasing auxin and cytokinin content in rice grains[J]. *Rice*, 2019, 12(1): 91.
- [37] Qin P, Zhang G H, Hu B H, Wu J, Chen W L, Ren Z J, Liu Y L, Xie J, Yuan H, Tu B, Ma B T, Wang Y P, Ye L M, Li L G, Xiang C B, Li S G. Leaf-derived ABA regulates rice seed development via a transporter-mediated and temperature-sensitive mechanism[J]. *Science Advances*, 2021, 7(3): eabc8873.
- [38] 唐塘, 谢红, 吕冰, 梁建生. 植物激素对杂交稻籽粒灌浆及蔗糖合酶活性的影响[J]. 中国水稻科学, 2011, 25(2): 182-188.
Tang T, Xie H, Lü B, Liang J S. Effects of plant hormones in regulating sucrose synthase activity and grain filling of rice[J]. *Chinese Journal of Rice Science*, 2011, 25(2): 182-188. (in Chinese with English abstract)
- [39] Shaw B P, Sekhar S, Panda B B, Sahu G, Chandra T, Parida A K. Grain filling in rice vis-a-vis ethylene production in the spikelets[J]. *Crop Science*, 2023, 63(2): 351-361.
- [40] Cui W W, Song Q H, Zuo B Y, Han Q F, Jia Z K. Effects of gibberellin (GA(4+7)) in grain filling, hormonal behavior, and antioxidants in high-density maize (*Zea mays* L.)[J]. *Plants*, 2020, 9(8): 978.
- [41] 杨建昌, 张建华. 促进稻麦同化物转运和籽粒灌浆的途径与机制[J]. 科学通报, 2018, 63: 2932-2943.
Yang J C, Zhang J H. Approach and mechanism in enhancing the remobilization of assimilates and grain-filling in rice and wheat[J]. *Chinese Science Bulletin*, 2018, 63: 2932-2943. (in Chinese with English abstract)
- [42] Zhang X Z, Zhang Q P, Yang J, Jin Y H, Wu J S, Xu H, Xiao Y, Lai Y S, Guo Z Q, Wang J L, Shi W J. Comparative effects of heat stress at booting and grain-filling stage on yield and grain quality of high-quality hybrid rice[J]. *Foods*, 2023, 12(22): 4093.
- [43] Zhen F X, Wang W, Wang H Y, Zhou J J, Liu B, Zhu Y, Liu L L, Cao W X, Tang L. Effects of short-term heat stress at booting stage on rice-grain quality[J]. *Crop & Pasture Science*, 2019, 70(6): 486-498.
- [44] 曹云英, 段骅, 杨立年, 王志琴, 周少川, 杨建昌. 减数分裂期高温胁迫对耐热性不同水稻品种产量的影响及其生理原因[J]. 作物学报, 2008, 34(12): 2134-2142.
Cao Y Y, Duan H, Yang L N, Wang Z Q, Zhou S C, Yang J C. Effect of heat-stress during meiosis on grain yield of rice cultivars differing in heat-tolerance and its physiological mechanism[J]. *Acta Agronomica Sinica*, 2008, 34(12): 2134-2142. (in Chinese with English abstract)
- [45] 王亚梁, 张玉屏, 朱德峰, 向镜, 武辉, 陈惠哲, 张义凯. 水稻穗分化期高温胁迫对颖花退化及籽粒充实的影响[J]. 作物学报, 2016, 42(9): 1402-1410.
Wang Y L, Zhang Y P, Zhu D F, Xiang J, Chen H Z, Zhang Y K. Effect of heat stress on spikelet degeneration and grain filling at panicle initiation period of rice[J]. *Acta Agronomica Sinica*, 2016, 42(9): 1402-1410. (in Chinese with English abstract)
- [46] Zhen F X, Zhou J J, Mahmood A, Wang W, Chang X N, Liu B, Liu L L, Cao W X, Zhu Y, Tang L. Quantifying the effects of short-term heat stress at booting stage on nonstructural carbohydrates remobilization in rice[J]. *Crop Journal*, 2020, 8(2): 194-212.
- [47] 陈燕华, 王亚梁, 朱德峰, 石庆华, 陈惠哲, 向镜, 张义凯, 张玉屏. 外源油菜素内酯缓解水稻穗分化期高温伤害的机理研究[J]. 中国水稻科学, 2019, 33(5): 457-466.
Chen Y H, Wang Y L, Zhu D F, Shi Q H, Chen H Z, Xiang J, Zhang Y K, Zhang Y P. Mechanism of exogenous brassinolide in alleviating high temperature injury at panicle initiation stage in rice[J]. *Chinese Journal of Rice Science*, 2019, 33(5): 457-466. (in Chinese with English abstract)
- [48] Ji D L, Xiao W H, Sun Z W, Liu L J, Gu J F, Zhang H, Harrison M T, Liu K, Wang Z Q, Wang W L, Yang J C. Translocation and distribution of carbon-nitrogen in relation to rice yield and grain quality as affected by high temperature at early panicle initiation stage[J]. *Rice Science*, 2023, 30(6): 598-612.
- [49] Jiang N, Yu P H, Fu W M, Li G Y, Feng B H, Chen T T, Li H B, Tao L X, Fu G F. Acid invertase confers heat tolerance in rice plants by maintaining energy homeostasis of spikelets[J]. *Plant, Cell & Environment*, 2020, 43(5): 1273-1287.
- [50] Tang S, Zhao Y F, Ran X, Guo H, Yin T Y, Shen Y Y, Liu W Z, Ding Y F. Exogenous application of methyl jasmonate at the booting stage improves rice's heat tolerance by enhancing antioxidant and photosynthetic activities[J]. *Agronomy*, 2022, 12(7): 1573.
- [51] Chen Y H, Wang Y L, Chen H Z, Xiang J, Zhang Y K, Wang Z G, Zhu D F, Zhang Y P. Brassinosteroids mediate endogenous phytohormone metabolism to alleviate high temperature injury at panicle initiation stage in rice[J]. *Rice Science*, 2023, 30(1): 70-86.
- [52] 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.
- [53] Lin G Q, Yang Y, Chen X Y, Yu X R, Wu Y F, Xiong F. Effects of high temperature during two growth stages on caryopsis development and physicochemical properties of starch in rice[J]. *International Journal of Biological Macromolecules*, 2020, 145: 301-310.
- [54] Morita S, Yonemaru J I, Takanashi J I. Grain growth and endosperm cell size under high night temperatures in rice (*Oryza sativa* L.)[J]. *Annals of Botany*, 2005, 95(4): 695-701.
- [55] Wada H, Chang F Y, Hatakeyama Y, Erra-Balsells R, Araki

- T, Nakano H, Nonami H. Endosperm cell size reduction caused by osmotic adjustment during nighttime warming in rice[J]. *Scientific Reports*, 2021, 11(1): 4447.
- [56] Folsom J J, Begcy K, Hao X J, Wang D, Walia H. Rice fertilization-Independent Endosperm1 regulates seed size under heat stress by controlling early endosperm development[J]. *Plant Physiology*, 2014, 165(1): 238-248.
- [57] Chen C, Begcy K, Liu K, Folsom J J, Wang Z, Zhang C, Walia H. Heat stress yields a unique MADS box transcription factor in determining seed size and thermal sensitivity[J]. *Plant Physiology*, 2016, 171(1): 606-622.
- [58] Li G Y, Chen T T, Feng B H, Peng S B, Tao L X, Fu G F. Respiration, rather than photosynthesis, determines rice yield loss under moderate high-temperature conditions[J]. *Frontiers in Plant Science*, 2021, 12: 678653.
- [59] Baruah U, Das S, Kalita P, Saikia M, Bhoulgal S, Pal S, Das R. High-night temperature-induced changes in chlorophyll fluorescence, gas exchange, and leaf anatomy determine grain yield in rice varieties[J]. *Journal of Plant Growth Regulation*, 2023, 42(9): 5538-5557.
- [60] Luan R W, Liu J Y, Tao L X, Fu G F, Zhang C X. Comparative transcriptome analysis reveals OsBGs and OsGSLs influence sugar transport through callose metabolism under heat stress in rice[J]. *International Journal of Molecular Sciences*, 2023, 24(4): 3175.
- [61] 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.
- [62] Sun T, Liu B, Hasegawa T, Liao Z Y, Tang L, Liu L L, Cao W X, Zhu Y. Sink-source unbalance leads to abnormal partitioning of biomass and nitrogen in rice under extreme heat stress: An experimental and modeling study[J]. *European Journal of Agronomy*, 2023, 142: 126678.
- [63] Bahuguna R N, Solis C A, Shi W J, Jagadish K S V. Post-flowering night respiration and altered sink activity account for high night temperature-induced grain yield and quality loss in rice (*Oryza sativa* L.)[J]. *Physiologia Plantarum*, 2017, 159(1): 59-73.
- [64] 王军可, 王亚梁, 陈惠哲, 向镜, 张义凯, 朱德峰, 张玉屏. 灌浆初期高温影响水稻籽粒碳氮代谢的机理[J]. 中国农业气象, 2020, 41(12): 774-784.
- Wang J K, Wang Y L, Chen H Z, Xiang J, Zhang Y K, Zhu D F, Zhang Y P. Mechanism of high temperature affecting carbon and nitrogen metabolism of rice grain at the early stage of grain filling[J]. *Chinese Journal of Agrometeorology*, 2020, 41(12): 774-784. (in Chinese with English abstract)
- [65] 张玉屏, 王军可, 王亚梁, 陈燕华, 朱德峰, 陈惠哲, 向镜, 张义凯, 刘小军, 朱艳, 曹卫星. 水稻淀粉合成对夜温变化的响应[J]. 中国水稻科学, 2020, 34(6): 525-538.
- Zhang Y P, Wang J K, Wang Y L, Chen Y H, Zhu D F, Chen H Z, Xiang J, Zhang Y K, Liu X J, Zhu Y, Cao W X. Response of rice starch synthesis to night temperature changes[J]. *Chinese Journal of Rice Science*, 2020, 34(6): 525-538. (in Chinese with English abstract)
- [66] Shao C, Shen L, Qiu C, Wang Y, Qian Y, Chen J, Ouyang Z, Zhang P, Guan X, Xie J, Liu G, Peng C. Characterizing the impact of high temperature during grain filling on phytohormone levels, enzyme activity and metabolic profiles of an early indica rice variety[J]. *Plant Biology*, 2021, 23(5): 806-818.
- [67] Cao Y Y, Chen Y H, Chen M X, Wang Z Q, Wu C F, Bian X C, Yang J C, Zhang J H. Growth characteristics and endosperm structure of superior and inferior spikelets of *indica* rice under high-temperature stress[J]. *Biologia Plantarum*, 2016, 60(3): 532-542.
- [68] Shi W J, Yin X Y, Struik P C, Solis C, Xie F M, Schmidt R C, Huang M, Zou Y B, Ye C R, Krishna Jagadish S V. High day- and night-time temperatures affect grain growth dynamics in contrasting rice genotypes[J]. *Journal of Experimental Botany*, 2017, 68(18): 5233-5245.
- [69] Liu X L, Zhong X, Liao J P, Ji P, Yang J S, Cao Z R, Duan X M, Xiong J R, Wang Y, Xu C, Yang H T, Peng B, Jiang K. Exogenous abscisic acid improves grain filling capacity under heat stress by enhancing antioxidative defense capability in rice[J]. *BMC Plant Biology*, 2023, 23(1): 619.
- [70] Fukai S, Mitchell J. Role of canopy temperature depression in rice[J]. *Crop and Environment*, 2022, 1(3): 198-213.
- [71] Akhter D, Qin R, Nath U K, Eshag J, Jin X L, Shi C H. A rice gene, *OsPL*, encoding a MYB family transcription factor confers anthocyanin synthesis, heat stress response and hormonal signaling[J]. *Gene*, 2019, 699: 62-72.
- [72] Ren Y, Huang Z Q, Jiang H, Wang Z, Wu F S, Xiong Y F, Yao J L. A heat stress responsive NAC transcription factor heterodimer plays key roles in rice grain filling[J]. *Journal of Experimental Botany*, 2021, 72(8): 2947-2964.
- [73] Ding Y F, Zhou M, Wang K, Qu A L, Hu S S, Jiang Q, Yi K K, Wang F J, Cai C, Zhu C, Chen Z X. Rice DST transcription factor negatively regulates heat tolerance through ROS-mediated stomatal movement and heat-responsive gene expression[J]. *Frontiers in Plant Science*, 2023, 14: 1068296.
- [74] Mohapatra S, Tripathy S K, Mohanty A K, Tripathy S. Effect of heat stress on yield and economics of rice (*Oryza sativa* L.) cultivars under different sowing dates[J]. *Journal of Agrometeorology*, 2021, 23(1): 38-45.
- [75] 段里成, 郭瑞鸽, 蔡哲, 杨军, 龚琦, 张崇华. 不同播期下高温对江西早稻灌浆结实及产量的影响[J]. 中国农业气象, 2024, 45(6): 584-593.
- Duan L C, Guo R G, Cai Z, Yang J, Gong Q, Zhang C H. Effects of high temperature on grain filling and yield of early season rice under different sowing dates in Jiangxi[J]. *Chinese Journal of Agrometeorology*, 2024,

- 45(6): 584-593. (in Chinese with English abstract)
- [76] Liu K W, Song C Y, Ye P, Liu H, Xia Z H, Waseem H, Deng Y J, Liu Z X, Wang L, Wang B, Yang X H, Zhu J Q. Optimizing rice sowing dates for high yield and climate adaptation in Central China[J]. *Agronomy*, 2023, 13(5): 1339.
- [77] Zhang M, Li Z, Feng K X, Ji Y L, Xu Y Z, Tu D B, Teng B, Liu Q M, Liu J W, Zhou Y J, Wu W E. Strategies for indica rice adapted to high-temperature stress in the middle and lower reaches of the Yangtze River[J]. *Frontiers in Plant Science*, 2022, 13: 1081807.
- [78] 韩展誉, 吴春艳, 许艳秋, 黄福灯, 熊义勤, 管弦悦, 周庐建, 潘刚, 程方民. 不同施氮水平下灌浆期高温对水稻贮藏蛋白积累及其合成代谢影响[J]. *中国农业科学*, 2021, 54(7): 1439-1454.
Han Z Y, Wu C Y, Xu Y Q, Huang F D, Xiong Y Q, Guan X Y, Zhou L J, Pan G, Cheng F M. Effects of high-temperature at filling stage on grain storage protein accumulation and its biosynthesis metabolism for rice plants under different nitrogen application levels[J]. *Scientia Agricultura Sinica*, 2021, 54(7): 1439-1454. (in Chinese with English abstract)
- [79] Dou Z, Zhou Y C, Zhang Y Y, Guo W, Xu Q, Gao H. Influence of nitrogen applications during grain-filling stage on rice (*Oryza sativa* L.) yield and grain quality under high temperature[J]. *Agronomy*, 2024, 14(1): 216.
- [80] You C C, Xu P, He Y Z, Wang H Y, Ke J, He H B, Wu L Q. The application of mixed nitrogen increases photosynthetic and antioxidant capacity in rice (*Oryza sativa*) under heat stress at flowering stage[J]. *Acta Physiologiae Plantarum*, 2023, 45: 100.
- [81] 谢可冉, 高遯, 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 R, 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)
- [82] 李友发, 孙源泽, 董俊杰, 富昊伟, 张馨月. 水稻灌浆期高温下钾肥运筹对籽粒灌浆及垩白的影响[J]. *浙江农业科学*, 2024, 65(1): 16-21.
Li Y F, Sun Y Z, Dong J J, Fu H W, Zhang X Y. Effects of potassium fertilizer management on grain filling and chalkiness of rice under high temperature during grain filling stage[J]. *Zhejiang Agricultural Sciences*, 2024, 65(1): 16-21. (in Chinese with English abstract)
- [83] 何巧林. 钾硅配施对水稻抽穗扬花期耐高温能力及抗倒伏性的影响[D]. 成都: 四川农业大学, 2017.
He Q L. Effects of combined application of potassium and silicon on high temperature resistance and lodging resistance of rice at heading and flowering stage [D]. Chengdu: Sichuan Agricultural University, 2017. (in Chinese with English abstract)
- [84] Hu Q Q, Yan N, Cui K H, Li G H, Wang W C, Huang J L, Peng S B. Increased panicle nitrogen application improves rice yield by alleviating high-temperature damage during panicle initiation to anther development[J]. *Physiologia Plantarum*, 2024, 176(2): e14230.
- [85] 赵艺婷, 谢可冉, 高遯, 崔克辉. 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[J]. *中国水稻科学*, 2024, 38(3): 277-289.
Zhao Y T, Xie K R, Gao T, Cui K H. Effects of drought priming during tillering stage on panicle development and yield formation under high temperature during panicle initiation stage in rice[J]. *Chinese Journal of Rice Science*, 2024, 38(3): 277-289. (in Chinese with English abstract)
- [86] 段骅, 俞正华, 徐云姬, 王志琴, 刘立军, 杨建昌. 灌溉方式对减轻水稻高温危害的作用[J]. *作物学报*, 2012, 38(1): 107-120.
Duan H, Yu Z H, Xu Y J, Wang Z Q, Liu L J, Yang J C. Role of irrigation patterns in reducing harms of high temperature to rice[J]. *Acta Agronomica Sinica*, 2012, 38(1): 107-120. (in Chinese with English abstract)
- [87] Aryan S, Gulab G, Kakar K, Habibi N, Amin M W, Sadat M I, Zahid T, Durani A, Baber B M, Safi Z, Zerak A. Auxin application at the flowering stage of rice alleviates the negative impact of heat stress on spikelet fertility and yield attributes[J]. *Agriculture*, 2023, 13(4): 866.
- [88] 刘晓龙, 季平, 杨洪涛, 丁永电, 付佳玲, 梁江霞, 余聪聪. 脱落酸对水稻抽穗开花期高温胁迫的诱抗效应[J]. *植物学报*, 2022, 57(5): 596-610.
Liu X L, Ji P, Yang H T, Ding Y D, Fu J L, Liang J X, Yu C C. Priming effect of abscisic acid on high temperature stress during rice heading-flowering stage[J]. *Chinese Bulletin of Botany*, 2022, 57(5): 596-610. (in Chinese with English abstract)
- [89] Chen M, Fu Y Y, Mou Q S, An J Y, Zhu X B, Ahmed T, Zhang S, Basit F, Hu J, Guan Y J. Spermidine induces expression of stress associated proteins (SAPs) genes and protects rice seed from heat stress-induced damage during grain-filling[J]. *Antioxidants*, 2021, 10(10): 1544.