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水稻花期高温热害耐性机制研究进展

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摘要 全球气候变暖背景下，高温热害发生频次呈增加趋势，对水稻生长发育以及产量和品质形成产生重要影响。水稻开花期遭遇高温热害会导致花粉不育，结实率下降，产量和品质受到影响。南方稻区是我国的主要粮食产区，该区水稻抽穗扬花期常遭遇高温热害，因此探究水稻花期高温热害耐性机制对于保障全球粮食安全具有重要意义。综合现有研究可知，水稻花期遭遇高温热害会引发水稻花粉活性丧失、颖花开放异常、花药开裂及花粉萌发率降低、花粉管发育受阻等生理与生殖障碍。对此，水稻将通过激活生理生化调节、启动热信号转导及调控耐热基因表达等机制抵御高温胁迫，且不同耐热性品种的响应存在显著差异。本文旨在深入阐明水稻花期高温的耐性机制，为水稻品种的耐性鉴定、抗逆新品种选育及配套栽培技术优化提供理论支撑。

关键词 水稻 花期 高温热害 耐性机制

近年来，由全球变暖引起的气候变化问题备受关注，IPCC（政府间气候变化专门委员会）第六次评估报告指出，2011—2020 年全球地表温度比 1850—1900 年升高 1.1℃，且随着全球变暖，未来中国极端天气事件如夏季高温等出现频率将增加[1]，这将对农业生产造成严重影响[2-3]。有研究预测，到 21 世纪中期中国的粮食作物产量可能因高温而减产 30%[4]。水稻作为我国主要粮食作物之一，占粮食种植总面积的 35%左右，我国约有 65%的人口以稻米为主食[5]，其中南方稻区是我国的主要粮食产区，在保障粮食安全生产方面占有极其重要的地位。

众所周知，高温热害对水稻的全生育期均可产生影响，其中抽穗扬花期是对高温热害最敏感的时期[6]。水稻花期临界高温为 37.2±0.2℃[7]，超过此温度将影响水稻的花粉发育、颖花开放、花药开裂、柱头花粉萌发及花粉管伸长，导致结实率下降，产量下降，

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严重时甚至绝收[8]，耐热性不同的水稻品种间存在一定差异[9-10]。已有研究发现[11]，水稻的高温抗性包括御热性、耐热性和避热性三种：御热性指水稻通过形态结构优化或即时生理响应（如表皮蜡质增厚、气孔动态调节等[12]）构建物理屏障，减少高温直接伤害；耐热性指水稻通过生理生化调节（如激素稳态[13-14]）适应高温并维持正常生长的能力；避热性则指通过某些方式（如提早开花、缩短开花历期等[15-16]）主动规避高温危害的生存策略。其中耐热性和避热性属于可遗传的内在抗高温机制，单纯依赖物理防御（御热性）或物候调整（避热性）难以应对长期胁迫，深入研究水稻内在耐热性是应对全球变暖的核心策略。不同耐热性水稻对花期高温的响应机制存在差异，主要体现在花器官发育特征及相关生理调控网络的特异性。

本文综述了花期高温胁迫下不同耐热性水稻品种在花粉发育、颖花开放、花药开裂、柱头花粉粒萌发及花粉管伸长方面的差异（图 1），并对不同耐热性水稻品种的耐热机制研究现状进行了分析，旨在进一步明确水稻花期的耐性机制，为南方水稻品种的耐性评定、新品种选育和栽培技术制订提供理论依据。

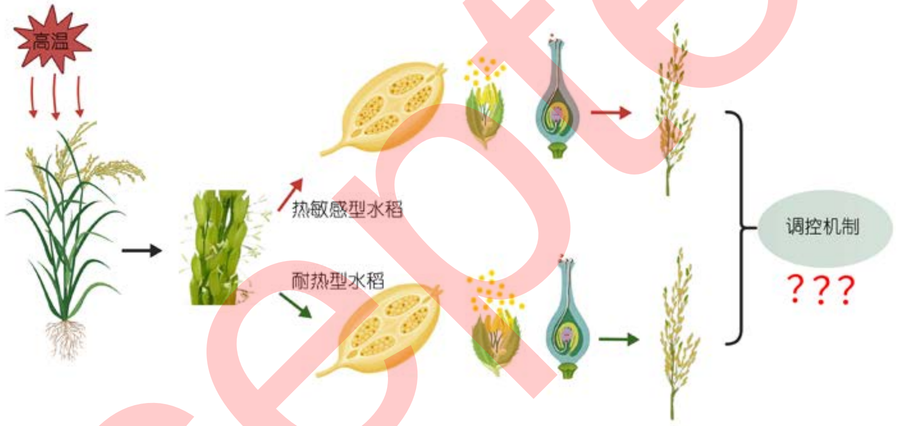

图 1 花期高温对不同耐热性水稻花器官的影响
Figure 1 Effect of high temperature during flowering on different heat-tolerant rice flower organs

1 花期高温对不同耐热性水稻花器官发育与功能的影响

1.1 花期高温对不同耐热性水稻花粉发育的影响

花期高温将干扰水稻花粉发育全过程，使花粉结构异常、活性丧失及受精失败[17]。花前高温破坏花粉壳开裂功能，花期高温损伤花粉膨胀能力，协同降低花粉活力[18]，同时高温还将扰乱花粉母细胞减数分裂进程，诱发染色体分离异常及淀粉代谢紊乱，导致败育[19-21]；短期高温则破坏渗透平衡，诱导活性氧（ROS）积累并触发绒毡层程序性死亡，抑制萌发与散粉[20,22-28]。但不同耐热性水稻品种间存在差异，花期高温下耐热型水稻花粉活力与萌发率降幅较小，花粉发育受高温危害程度较轻[29-30]，这一差异可能源于耐热品种中特异性基因的调控作用[31]。现有研究发现，热激蛋白基因（如 *OsHSP60-3B*）受热诱导表达后，可通过稳定花粉淀粉体发育、抑制 ROS 过度积累等机制维持花粉功能[32-33]；而 *UbL40* 基因的低表达也可能作为重要分子机制，增强花粉对高温的耐受性[34]。相比之下，热敏感型品种因缺乏上述高效调控机制，其花粉在高温下将遭遇结构损伤、代谢失衡、氧化应激等多重障碍，最终导致花粉败育率显著升高。此外，水稻花粉发育过程中积累的糖类可作为渗透物质提高花粉对胁迫的响应[35]，但相关研究尚未成系统。

1.2 花期高温对不同耐热性水稻颖花开放的影响

花期高温会破坏水稻颖花的水分平衡与生理代谢，导致其开放异常。高温大幅度提升颖花蒸腾速率，打破植株水势平衡，造成开闭节律紊乱、花时提前且分布离散[36-37]；同时通过抑制浆片可溶性糖、茉莉酸及其甲酯合成，缩短开颖时间、减小开颖角度并减少开放颖花数[38]，虽延长单日开花时间，但缩短整体开花历期并降低开花峰值。不同耐热性水稻品种间存在显著差异，耐热型水稻品种在高温下能维持较大开颖角度，结实率降幅较小，抽穗期高温对其颖花数影响

甚微[39]；而热敏感型水稻品种因高温下根系吸水能力锐减，伴随颖花内可溶性蛋白、糖及脯氨酸等渗透调节物质含量骤降[40-42]，导致颖花开放异常加剧并显著减产[13,43-44]。进一步研究发现，水稻颖花开放受qHTC2、qHTH4等耐热QTL[45]及*Hd1*、*OsPRR37*、*OsRHS*等基因调控。其中，*OsPRR37*通过“高温促开花”机制帮助水稻躲避花期高温热害，*OsRHS*在耐热型水稻品种中高温表达量更高[46-47]，其与热激蛋白cHSP70-4的互作研究表明，敲除*cHSP70-4*可增强开花期耐热性[48]，而QTL累加效应能有效提升株系的耐热性。

1.3 花期高温对不同耐热性水稻花药开裂的影响

花期高温会导致水稻花药发育与开裂过程受阻[49]。高温条件下花药内花粉粒黏结削弱膨胀能力，降低散粉效率[50]；诱导ROS积累，引发内皮层细胞次生壁异常加厚，阻碍开裂[51]；干扰生理代谢，致抗氧化酶活性、可溶性糖及热稳定蛋白含量下降，苯丙素合成途径受抑，削弱花药结构稳定性[52]。但不同耐热性水稻品种间存在显著差异，耐热型水稻品种在花期高温下能维持花粉粒的持续膨胀，通过保持高超氧化物歧化酶、过氧化物酶活性调控ROS稳态，积累更多可溶性糖与热稳定蛋白，并维持高赤霉素（GA3）、吲哚乙酸（IAA）及低脱落酸（ABA）水平延缓花药衰老，其开裂率显著高于热敏感品种；而热敏感型水稻品种随高温胁迫时间延长，花粉粒膨胀幅度急剧下降，抗氧化酶活性与渗透物质含量骤降，GA3、IAA含量锐减且ABA水平升高，导致花药开裂动力不足[53-54]。此外，研究发现，水稻花药开裂受OsTIE1-OsTCP1转录模块（调控茉莉素合成）、热激蛋白（HSPs）基因（如18个高温诱导上调基因）及激素网络（GA3、IAA、ABA与茉莉素）共同调控。其中，OsTIE1突变体因茉莉素异常积累导致花药早裂，耐热型水稻品种中*HSPs*基因上调幅度更高以强化蛋白保护机制以抵御高温损伤，而激素则通过协同调控内皮层发育与花药开裂动力影响高温响应[55-59]。

1.4 花期高温对不同耐热性水稻柱头花粉萌发的影响

花期高温会导致水稻花粉萌发率下降[24,51,60]，主要受三方面因素影响，高温破坏花粉与柱头的水合作用[61]；抑制花粉内蔗糖水解及转运，降低果糖激酶、己糖激酶活性，减少可溶性糖供给[23,62]；并可能引发花粉细胞壁变性，影响花粉在柱头的识别与附着[63-65]。但不同耐热性水稻品种间存在差异，耐热型水稻品种在高温条件下会维持更高的柱头着粉数和花粉萌发率，花粉对高温耐受性更强；而热敏感型水稻品种则可能出现花粉育性、柱头花粉数及花粉萌发率显著降低的情况[66-67]。进一步研究发现，水稻柱头花粉萌发过程中不同耐热性品种受蛋白稳定性及热激蛋白等共同调控。如温敏基因*OsMS1wenmin1*编码的蛋白在高温下稳定性降低，影响其与转录因子TDR互作及下游育性基因表达，最终影响花粉在柱头上的萌发能力；过表达*OsHSP60-3B*可抑制ROS积累和细胞凋亡，保障高温下花粉正常萌发[33,68]。

1.5 花期高温对不同耐热性水稻雌蕊花粉管生长的影响

花期高温会导致水稻花粉管萌发与伸长受阻，使花粉管尖端膨大、胼胝质过量累积、线粒体紊乱及能量失调，并干扰雌蕊生长素代谢，最终引发小穗败育[8,69]。不同耐热性水稻品种间存在差异：耐热型水稻品种在花期高温条件下能维持花柱、柱头和子房的ROS稳态，其胚珠内仍可见花粉管伸长；而热敏感型水稻品种则表现为ROS水平显著升高打破氧化还原平衡，胚珠内未见花粉管伸长[67,70]。进一步研究发现，耐热型水稻品种在花期高温条件下，通过稳定表达*OsMTD2*基因维持花粉管内ROS稳态，避免因ROS积累不足导致的细胞壁异常及尖端破裂，保障花粉管正常伸长[71]；同时，其TT2等位变异可减弱钙信号响应，持续激活蜡质合成转录因子OsWR2的表达，通过强化花粉管细胞壁蜡质层的完整性，使花粉管免受高温损伤[72]。

2 花期高温条件下水稻不同耐性品种的耐性机制

2.1 生理生化调控机制

水稻花期遭遇高温胁迫时，其生理生化系统通过一系列主动保护机制调控抗逆过程。激素稳态调控是核心机制之一，通过维持IAA、GA、Z+ZR等促进型激素与ABA之间的动态平衡来响应胁迫[73-74]。多胺代谢作为关键保护途径，其合成酶活性（如

SAMDc）维持腐胺和亚精胺的正常水平，对花粉发育至关重要[75]。渗透调节保护则依赖于积累游离脯氨酸和特定蛋白质来维持细胞渗透压，增强细胞持水能力以抵抗花粉脱水[76]。在抗氧化防御方面，超氧化物歧化酶等抗氧化酶系统迅速启动，清除高温诱导产生的过量 ROS，抑制膜脂过氧化，构成抵御氧化损伤的关键防线[77]。同时，糖代谢稳态维持机制通过保障蔗糖合酶和酸性转化酶等酶的活性，维持花粉粒淀粉含量和可溶性糖水平，为花粉管萌发和伸长提供持续能量供应[78-81]。值得注意的是，耐热品种能更有效地执行这些保护机制，其体内维持更高水平的 IAA、GA 和多胺含量[73-75]；抗氧化系统对 ROS 的清除效率显著提升[77]；尤其在配子体发育期能积累更丰富的可溶性糖与淀粉[78,80]。此外，保持一氧化氮（NO）适量产生、赤霉素合成通路顺畅以及胞内 Ca^{2+}浓度稳定，也被认为是支持雌雄蕊正常互作的重要保护因素[8,82-83]。这些协同作用的生理生化机制，特别是 ROS 动态平衡与糖代谢稳态的精密调控，构成了水稻品种间耐热性差异的生理基础，并为未来解析与提升耐热性指明了关键研究方向。

2.2 分子调控机制

2.2.1 热信号转导

水稻对热应激的感知依赖于热信号传感系统，而细胞壁作为植物抵御热胁迫的第一道物理屏障，是热信号的初始感知位点。高温诱导细胞壁发生结构性重塑，通过果胶甲酯酶（PMEs）的激活引发果胶去甲基化，伴随质外体 Ca^{2+}释放，形成初始信号触发机制[84]。质膜环核苷酸门控离子通道(CNGCs)家族成员，特别是 OsCNGC14 和 OsCNGC16，在钙信号起始过程中起着关键作用。这些通道蛋白被激活后可引起胞内 Ca^{2+}浓度快速升高，进而通过钙调蛋白如 OsCaM1-1 传递信号[85]。同时，表观遗传调控机制也参与温度感知，组蛋白变体 H2A.Z 被证实通过核小体定位变化来感知环境温度变化，其在染色质上的解离行为是植物温度感知的重要分子开关[86]。在信号转导过程中，热激转录因子发挥着核心调控作用。研究发现 OsHSFA1 家族成员能够通过形成异源三聚体，特异性地识别并结合热休克蛋白基因启动子中的热休克元件(HSE)，从而激活下游靶基因表达[87]。耐热品种表现出更高效的分子伴侣网络，其中 HSP70 和 HSP90 家族蛋白通过维持蛋白质稳态和防止蛋白错误折叠来增强热耐受性[88]。此外，非编码 RNA 通过转录后调控机制参与热应激反应，如某些 miRNAs 可通过调控热响应因子的表达来影响植物的耐热性[89-91]。值得注意的是，植物激素信号通路与热信号通路存在广泛的交叉对话。脱落酸(ABA)和茉莉酸(JA)信号通路被证实参与热耐受性的调节，这些激素通过与热激转录因子互作来协同调控热响应基因的表达[92]。

2.1.2 关键耐热基因的鉴定与表达

不同耐热性水稻品种的遗传差异由多基因协同调控网络决定，其关键基因的鉴定与表达差异成为解析耐热机制的核心（表 1）。目前全基因组研究已定位到分布于所有染色体的耐热相关 QTL，在功能基因层面，耐热品种中 *OsABA8ox3* 受热诱导显著上调，推测其通过脱落酸代谢参与耐热调控网络；细胞色素 P450 家族基因在耐热品种中特异性高表达，可能通过次生代谢增强高温适应性[101]。$TT1^{CG14}$ 基因通过强化蛋白酶体对毒性蛋白的清除效率，维持花粉细胞蛋白质稳态，在耐热品种中表达量显著高于热敏感型[102]。钙信号通路中，热敏感型品种依赖 $TT2^{HJX}$ 维持胞内钙信号正常传导，而高温通过 SCT1/2-CaM 互作下调 *OSWR2* 表达，导致蜡质合成受阻；耐热型品种因 $TT2^{HPS32}$ 功能缺失，可缓解 *OSWR2* 的表达抑制，维持蜡质含量以保护花粉管[103]。类受体激酶 ERECTA 在耐热型品种细胞膜上过表达，通过减轻细胞损伤增强高温适应性[104]。此外，首个调控产量的主效基因 *QT12* 在耐热水稻中克隆，CRISPR 编辑的突变株系在高温下产量显著提升[105]。值得注意的是，耐热型水稻品种中上述基因的表达调控呈现协同效应，如 *qHTT8* 与 *OsABA8ox3* 的共表达可增强细胞壁木质素合成，而 $TT2^{HPS32}$ 与 ERECTA 的互作强化了细胞膜稳定性；相比之下，热敏感型水稻品种因关键基因（如 $TT2^{HJX}$、*OSWR2*）的表达缺陷，无法建立有效的高温防御网络。

表 1 水稻花期关键耐热基因

Table1 Key heat-tolerant genes during the flowering period of rice

基因名称 Genes	功能 Function	参考文献 Reference
OsHsfA2e	增强花序茎和种子的热耐受性，调控热激蛋白表达	Yokotani, 2008[93]
TT1	DEAD-box RNA 解旋酶，调控穗发育与花期耐热性，突变体高温下育性显著下降	Li,2015[94]
OsHTAS	调控活性氧清除，增强花期耐热性与结实率	Liu, 2016[95]
OsMDHAR4	负调控花期耐热性，通过抑制 H2O2 诱导的气孔关闭增强高温适应性	Liu , 2018[96]
OsWR2、*OsTT2*	强化花粉管细胞壁蜡质层完整性	Muhlemann,2018[103]
OsPRR37	调控颖花开放，通过“高温促开花”躲避高温热害	Shim,2020[47]
UbL40	低表达可增强花粉对高温的耐受性	Wang, 2021[34]
OsMTD2	维持花粉管内 ROS 稳态，避免细胞壁异常及尖端破裂，保障花粉管伸长	Kim,2021[71]
HTH5	调控磷酸吡哆醛稳态，减少活性氧积累，增强花粉耐热性	Cao,2022[97]
OsHSP60-3B	受热诱导表达，稳定花粉淀粉体发育、抑制 ROS 过度积累，维持花粉功能	Lin, 2023[33]
qHTT4.2	受热诱导表达，参与高温下细胞稳态维持	Pan,2023[98]
ATT2	精准调控赤霉素水平，平衡活性氧与组蛋白甲基化，增强半矮秆水稻花期耐热性	Ling, 2025[99]
OsRHS	与 OsRHS 互作，敲除可增强开花期耐热性	Mao,2025[48]
OsNRAMP7	调控核糖体相关通路，维持高温下蛋白质合成系统稳定性，增强生殖期耐热性	Dong,2025[100]

3 结论与展望

现有研究表明，花期高温对不同耐热性水稻花器官发育与功能影响各异，其耐受机制也表现出多方面的分化特征：（1）在花粉发育中，高温通过干扰减数分裂、诱发淀粉代谢紊乱与 ROS 积累导致花粉败育，而耐热型品种可通过调控热激蛋白基因稳定淀粉体发育、抑制 ROS 积累，并以部分基因低表达增强耐受性，维持花粉活力；（2）颖花开放时，高温破坏水分与渗透物质的合成，导致开闭异常，耐热型品种依赖 qHTC2 等耐热 QTL 及“高温促开花”机制维持开颖能力，热敏感型品种则因根系吸水衰退、渗透物质耗竭加剧导致开放异常；（3）花药开裂环节，高温诱导花粉粒黏结、内皮层次生壁异常及抗氧化酶活性下降，耐热型品种通过维持 ROS 稳态、积累可溶性糖及调控激素平衡以延缓花药衰老，开裂率受基因协同调控，而热敏感型品种 GA3、IAA 含量锐减且 ABA 水平升高，导致花药开裂动力不足；（4）柱

头花粉萌发阶段，高温干扰水合作用、糖代谢及细胞壁识别，耐热型品种通过维持花粉内蛋白稳定并及时清除 ROS 保障萌发能力；（5）花粉管生长时，高温引发尖端膨大与能量失调，耐热型品种可通过基因调控维持 ROS 稳态、强化蜡质层合成以保障伸长。从本质上看，耐热型水稻品种通过基因表达网络的系统性重构、关键代谢通路的优化调控以及信号传导通路的协同作用，构建包含细胞壁与质膜结构保护、生理生化动态平衡维持及特异性基因模块激活的多层次高温胁迫防御体系。与之形成鲜明对比的是，热敏感型品种因缺乏上述多维度调控机制，在高温胁迫条件下，其花器官发育的全过程均出现显著的结构性损伤与功能性障碍，最终导致结实率大幅度降低。这种差异源于不同耐热性水稻品种在长期进化过程中形成的适应性策略分化：耐热型品种通过整合基因调控网络、代谢途径优化及信号响应机制，实现了对花期高温胁迫的系统性抵御；而热敏感型品种因调控网络存在缺陷，无法有效应对花期高温环境，进而引发生殖发育进程的功能性障碍。

尽管水稻花期高温热害耐性机制研究已取得阶段性进展（图 2），但不同耐热性水稻花器官发育与耐性机制方面的差异仍不明晰，一是在物质代谢层面，花粉的糖类代谢网络在高温下的动态变化及其对花粉活力的调控机制尚未明确，关键基因功能及品种间差异有待深入分析；二是在调控网络层面，关键基因互作模式、激素与 ROS 平衡对花药发育的调控路径，以及细胞壁组分协同作用机制未明晰；三是在生理调控层面，柱头花粉萌发阶段的花粉-柱头识别机制、水合作用的分子基础，以及花粉管伸长中 Ca^{2+}浓度梯度与微丝骨架的协同调控模式亟待揭示，尤其缺乏对耐热品种中维持花粉管生长的 Ca^{2+}传感器与信号通路的动态解析。未来研究可以代谢-调控-生理的逻辑开展研究，通过代谢组学与功能基因组学结合，解析花粉糖代谢关键基因的耐热调控功能；利用多组学整合与 CRISPR 技术，构建基因-激素-代谢物的互作网络；借助活体成像技术，实时追踪花粉管萌发过程中 Ca^{2+}信号与微丝骨架的动态关联，最终形成从分子机制到生理响应的完整研究体系，为水稻耐热品种的分子设计提供理论支撑。

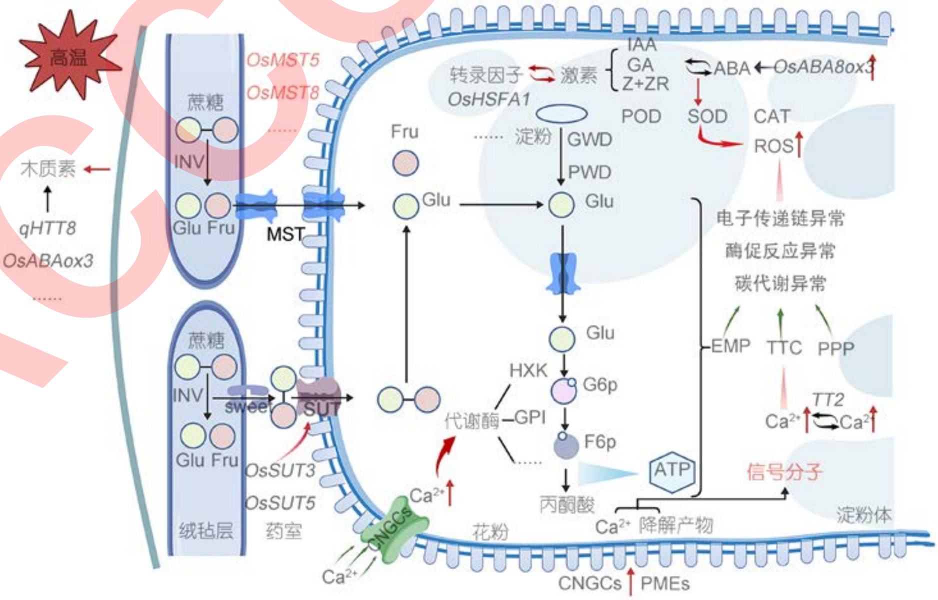

图 2 花期高温下水稻花器官的关键耐性机制. INV:蔗糖转化酶; MST:单糖转运蛋白; SUT:蔗糖转运蛋白; Glc:葡萄糖; Fru:果糖; GWD:α-葡聚糖水合二激酶; PWD:磷酸葡聚糖水合二激酶; HXK:己糖激酶; GPI:糖基磷脂酰肌醇; G6p:葡萄糖-6-磷酸; IAA:吲哚-3-乙酸; GA:赤霉素; Z+ZR:细胞分裂素,玉米素与玉米素核苷; ABA:脱落酸; POD:过氧化物酶; SOD:超氧化物歧化酶; CAT:过氧化氢酶; ROS:活性氧; EMP:糖酵解途径; TCA:三羧酸循环; PPP:磷酸戊糖途径; PMEs:果胶甲酯酶; CNGCs:环核苷酸门控离子通道.

Figure 2 Key tolerance mechanism of rice flower organs under high temperature during flowering period. INV: Invertase; MST:Monosaccharide Transporter; SUT:Sucrose Transporter; Glc:Glucose;Fru:Fructose; GWD:α-Glucan Water Dikinase; PWD:Phosphoglucan Water Dikinase; HXK:Hexokinase; GPI:Glycosylphosphatidylinositol; G6p:Glucose-6-phosphate; IAA:Indole-3-acetic acid; GA:Gibberellins; Z+ZR:Cytokinins,Zeatin and Zeatin riboside;

ABA:Abscisic acid; POD:Peroxidase; SOD:Superoxide Dismutase; CAT:Catalase; ROS:Reactive Oxygen Species; EMP:Embden-Meyerhof-Parnas pathway; TCA:Tricarboxylic Acid Cycle; PPP:Pentose Phosphate Pathway; PMEs:Pectin Methylesterases; CNGCs:Cyclic Nucleotide-Gated Channels.

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 (in Chinese). Cambridge: Cambridge University Press, 2021: 1-41 [IPCC.气候变化 2021: 自然科学基础. 第一工作组对政府间气候变化专门委员会第六次评估报告的贡献. 剑桥: 剑桥大学出版社, 2021: 1-41]

2 Matsui T, Omasa K, Horie T. The difference in sterility due to high temperatures during the flowering period among japonica-rice varieties[J]. Plant Production Science, 2001, 4(2): 90-93

3 Shah F, Huang J, Cui K, et al. Impact of high-temperature stress on rice plant and its traits related to tolerance[J]. The Journal of Agricultural Science, 2011, 149(5): 545-556

4 Zhang G L, Chen L Y, Lei D Y, et al. Research advances in heat tolerance of rice (in Chinese). Hybrid Rice, 2005, 20(1): 1-5 [张桂莲, 陈立云, 雷东阳, 等. 水稻耐热性研究进展. 杂交水稻, 2005, 20(1): 1-5]

5 National Bureau of Statistics of China. China Statistical Yearbook 2018 (in Chinese). Beijing: China Statistics Press, 2018 [中华人民共和国国家统计局. 中国统计年鉴 2018. 北京: 中国统计出版社, 2018]

6 Liu Q, Yang T, Yu T, et al. Integrating small RNA sequencing with QTL mapping for identification of miRNAs and their target genes associated with heat tolerance at the flowering stage in rice[J]. Frontiers in Plant Science, 2017, 8: 43

7 Liu M, Zhou Y, Sun J, et al. From the floret to the canopy: High temperature tolerance during flowering[J]. Plant Communications, 2023, 4(6)

8 Zhang C, Li G, Chen T, et al. Heat stress induces spikelet sterility in rice at anthesis through inhibition of pollen tube elongation interfering with auxin homeostasis in pollinated pistils[J]. Rice, 2018, 11: 1-12

9 Kovi M R, Bai X, Mao D, et al. Impact of seasonal changes on spikelets per panicle, panicle length and plant height in rice (Oryza sativa L.)[J]. Euphytica, 2011, 179: 319-331

10 Wang Y L, Zhang Y P, Zeng Y H, et al. Effect of high temperature at panicle differentiation stage on differentiation and degeneration of spikelets in rice (in Chinese). Chin J Agrometeorol, 2015, 36(6): 724-731 [王亚梁, 张玉屏, 曾研华, 等. 水稻穗分化期高温对颖花分化及退化的影响. 中国农业气象, 2015, 36(6): 724-731]

11 Jagadish S V K, Murty M V R, Quick W P. Rice responses to rising temperatures – challenges, perspectives and future directions[J]. Plant, cell & environment, 2015, 38(9): 1686-1698

12 Lu H P, Liu X H, Wang M J, et al. The NAT1–bHLH110–CER1/CER1L module regulates heat stress tolerance in rice[J]. Nature Genetics, 2025, 57(2): 427-440

13 Wu C, Cui K, Wang W, et al. Heat-induced phytohormone changes are associated with disrupted early reproductive development and reduced yield in rice[J]. Scientific Reports, 2016, 6(1): 34978

14 Wu C, Cui K, Wang W, et al. 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

15 Coast O, Ellis R H, Murdoch A J, et al. High night temperature induces contrasting responses for spikelet fertility, spikelet tissue temperature, flowering characteristics and grain quality in rice[J]. Functional Plant Biology, 2014, 42(2): 149-161

16 Ishimaru T, Hirabayashi H, Ida M, et al. A genetic resource for early-morning flowering trait of wild rice Oryza officinalis to mitigate high temperature-induced spikelet sterility at anthesis[J]. Annals of botany, 2010, 106(3): 515-520

17 Li Y, Tang Y, Wu Y F, et al. Research progress on response mechanism and defense measures of rice to high temperature stress (in Chinese). Chin Agric Sci Bull, 2024, 40(33): 1-10 [李渊, 唐洋, 吴云飞, 等. 水稻对高温逆境的响应机制及防御措施研究进展. 中国农学通报, 2024, 40(33): 1-10]

18 Matsui T, Omasa K, Horie T. High temperature at flowering inhibits swelling of pollen grains, a driving force for thecae dehiscence in rice (Oryza sativa L.)[J]. Plant Production Science, 2000, 3(4): 430-434

19 Francis K E, Lam S Y, Harrison B D, et al. Pollen tetrad-based visual assay for meiotic recombination in Arabidopsis[J]. Proceedings of the national academy of sciences, 2007, 104(10): 3913-3918

20 De Storme N, Geelen D. The impact of environmental stress on male reproductive development in plants: biological processes and molecular mechanisms[J]. Plant, cell & environment, 2014, 37(1): 1-18

21 Draeger T, Moore G. Short periods of high temperature during meiosis prevent normal meiotic progression and reduce grain number in hexaploid wheat (Triticum aestivum L.)[J]. Theoretical and Applied Genetics, 2017, 130: 1785-1800

22 Jain M, Chourey P S, Boote K J, et al. Short-term high temperature growth conditions during vegetative-to-reproductive phase transition irreversibly compromise cell wall invertase-mediated sucrose catalysis and microspore meiosis in grain sorghum (Sorghum bicolor)[J]. Journal of Plant Physiology, 2010, 167(7): 578-582

23 Das S, Krishnan P, Nayak M, et al. High temperature stress effects on pollens of rice (Oryza sativa L.) genotypes[J]. Environmental and Experimental Botany, 2014, 101: 36-46

24 Coast O, Murdoch A J, Ellis R H, et al. Resilience of rice (Oryza spp.) pollen germination and tube growth to temperature stress[J]. Plant, cell & environment, 2016, 39(1): 26-37

25 Djanaguiraman M, Perumal R, Jagadish S V K, et al. Sensitivity of sorghum pollen and pistil to high‐temperature stress[J]. Plant, Cell & Environment, 2018, 41(5): 1065-1082

26 Li N, Zhang D S, Liu H S, et al. The rice tapetum degeneration retardation gene is required for tapetum degradation and anther development[J]. The Plant Cell, 2006, 18(11): 2999-3014

27 Sato S, Peet M M, Thomas J F. Determining critical pre-and post-anthesis periods and physiological processes in Lycopersicon esculentum Mill. exposed to moderately elevated temperatures[J]. Journal of Experimental Botany, 2002, 53(371): 1187-1195

28 Parish R W, Phan H A, Iacuone S, et al. Tapetal development and abiotic stress: a centre of vulnerability[J]. Functional Plant Biology, 2012, 39(7): 553-559

29 Xie X J, Li B B, Shen S H, et al. Effects of high temperature stress during heading stage on pollen vitality and seed-setting rate in rice (in Chinese). Jiangsu J Agric Sci, 2009, 25(2): 238-241 [谢晓金, 李秉柏, 申双和, 等. 抽穗期高温胁迫对水稻花粉活力与结实率的影响. 江苏农业学报, 2009, 25(2): 238-241]

30 Li J C. Screening and identification of heat-tolerant and strong ratooning rice varieties and their physiological mechanisms (in Chinese). Changchun: Jilin Agricultural University, 2023 [李俊材. 耐热及强再生力水稻品种筛选鉴定及其生理机理研究. 长春: 吉林农业大学, 2023]

31 Mittler R, Finka A, Goloubinoff P. How do plants feel the heat?[J]. Trends in biochemical sciences, 2012, 37(3): 118-125

32 Burke J J, Chen J. Enhancement of reproductive heat tolerance in plants[J]. PLoS One, 2015, 10(4): e0122933

33 Lin S, Liu Z, Sun S, et al. Rice HEAT SHOCK PROTEIN60-3B maintains male fertility under high temperature by starch granule biogenesis[J]. Plant Physiology, 2023, 192(3): 2301-2317

34 Wang S Y, Tian Q Y, Zhang L A, et al. Comparative study on differences of pollen fertility tolerance to high temperature in different rice varieties (in Chinese). Life Sci Res, 2021, 25(5): 400-405 [王思瑶，田清源，张林安，等．不同水稻花粉育性耐高温的差异比较研究．生命科学研究, 2021, 25(5): 400-405]

35 Yang H, Liu C, Wang Z F, et al. Research advances in the mechanism of crop pollen response to high temperature (in Chinese). Chin Bull Bot, 2019, 54(2): 157-167 [杨浩，刘晨，王志飞，等．作物花粉高温应答机制研究进展．植物学报，2019, 54(2): 157-167]

36 Wang W, Cui K, Hu Q, et al. Response of spikelet water status to high temperature and its relationship with heat tolerance in rice[J]. The Crop Journal, 2021, 9(6): 1344-1356

37 Zhou J X, Zhang Y P, Zhu D F, et al. Effect of postponing high temperature on spikelet sterility in rice (in Chinese). Chin J Agrometeorol, 2014, 35(5): 544-548 [周建霞，张玉屏，朱德峰，等．高温后移对水稻颖花败育的影响．中国农业气象，2014, 35(5): 544-548]

38 Chen J, Xu Y, Fei K, et al. Physiological mechanism underlying the effect of high temperature during anthesis on spikelet-opening of photo-thermo-sensitive genic male sterile rice lines[J]. Scientific Reports, 2020, 10(1): 2210

39 Peng M, Su R, Tang R, et al. Effects of high temperature stress on flowering habits and seed-setting rate of Zhuoliangyou 141 and Wangliangyou 091 (in Chinese). Hybrid Rice, 2023, 38(4): 29-35 [彭敏，苏锐，唐睿，等．高温胁迫对卓两优 141 和望两优 091 开花习性与结实率的影响．杂交水稻，2023, 38(4): 29-35]

40 Tao L X, Tan H J, Wang X, et al. Physiological effects of high temperature stress during flowering and early grain filling on seed setting of Guodao 6 (in Chinese). Acta Agron Sin, 2009, 35(1): 110-117 [陶龙兴，谈惠娟，王熹，等．开花和灌浆初期高温胁迫对国稻 6 号结实的生理影响．作物学报, 2009, 35(1): 110-117]

41 Xu P, He Y Z, Huang Y R, et al. Effects of short-term high temperature at flowering stage on floret opening dynamics and yield of different rice varieties (in Chinese). Chin J Agrometeorol, 2023, 44(1): 25-35 [徐鹏，贺一哲，黄亚茹，等．花期短时高温对不同品种水稻颖花开放动态及产量的影响．中国农业气象, 2023, 44(1): 25-35]

42 Xu P, He Y Z, You C C, et al. Mechanism of high temperature stress leading to spikelet sterility in rice and its defense measures: a review (in Chinese). Jiangsu J Agric Sci, 2023, 39(1): 255-265 [徐鹏，贺一哲，尤翠翠，等．高温胁迫导致水稻颖花败育的机理及其防御措施研究进展．江苏农业学报，2023, 39(1): 255-265]

43 Wang M N, Xie K R, Gao T, et al. Effects of high temperature from panicle differentiation to heading stage on grain morphology and plumpness and their relationship with grain weight in rice (in Chinese). Acta Agron Sin, 1-17 [王梦宁，谢可冉，高逖，等．水稻幼穗分化期至抽穗期高温对籽粒形态和充实的影响及其与粒重的关系．作物学报, 1-17]

44 Hu Q, Yan N, Cui K, et al. 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

45 Liu J, Zhou H Y, Ma X D, et al. Mapping QTLs for heat tolerance at heading date in rice based on a high-density genetic map (in Chinese). J Plant Genet Resour, 1-11 [刘进，周慧颖，马小定，等．基于高密度遗传图谱定位水稻抽穗期耐热性 QTL．植物遗传资源学报, 1-11]

46 Guo T, Mu Q, Wang J, et al. Dynamic effects of interacting genes underlying rice flowering-time phenotypic plasticity and global adaptation[J]. Genome Research, 2020, 30(5): 673-683

47 Shim J S, Jang G. Environmental signal-dependent regulation of flowering time in rice[J]. International Journal of Molecular Sciences, 2020, 21(17): 6155

48 Mao X, Yu H, Xue J, et al. OsRHS Negatively Regulates Rice Heat Tolerance at the Flowering Stage by Interacting With the HSP Protein cHSP70‐4[J]. Plant, Cell & Environment, 2025, 48(1): 350-364

49 Zhang W Y, Bai T, He D, et al. Effects of high temperature stress at heading stage on anther, pollen and photosynthetic characteristics of rice (in Chinese). J Hunan Agric Univ (Nat Sci Ed), 2022, 48(4): 379-385 [张文怡，白涛，何东，等．抽穗期高温胁迫对水稻花药花粉和光合特性的影响．湖南农业大学学报(自然科学版), 2022, 48(4): 379-385]

50 Wu Q, Liu X, Yin D, et al. Constitutive expression of OsDof4, encoding a C2-C2 zinc finger transcription factor, confesses its distinct flowering effects under long-and short-day photoperiods in rice (Oryza sativa L.)[J]. BMC Plant Biology, 2017, 17: 1-13

51 Jagadish S V K, Muthurajan R, Oane R, et al. Physiological and proteomic approaches to address heat tolerance during anthesis in rice (Oryza sativa L.)[J]. Journal of experimental botany, 2010, 61(1): 143-156

52 Zhang G L, Zhao R, Liu Y T, et al. Analysis of differential proteins in anthers of rice with different heat tolerance based on iTRAQ technology (in Chinese). J Nucl Agric Sci, 2019, 33(4): 671-679 [张桂莲，赵瑞，刘逸童，等．基于 iTRAQ 技术的不同耐热性水稻花药差异蛋白分析．核农学报，2019, 33(4): 671-679]

53 Zhang G L, Zhang S T, Xiao L T, et al. Effects of high temperature stress during heading and flowering stages on physiological characteristics of anther, pollen and stigma in rice (in Chinese). Chin J Rice Sci, 2014, 28(2): 155-166 [张桂莲，张顺堂，肖浪涛，等．抽穗开花期高温胁迫对水稻花药、花粉粒及柱头生理特性的影响．中国水稻科学, 2014, 28(2): 155-166]

54 Zhang G L, Zhang S T, Xiao L T, et al. Physiological responses of rice anther to high temperature stress (in Chinese). Plant Physiol J, 2013, 49(9): 923-928 [张桂莲，张顺堂，萧浪涛，等．水稻花药对高温胁迫的生理响应．植物生理学报, 2013, 49(9): 923-928]

55 Fang Q, Pan X, Wu Z, et al. The LoMYB26/LoJAZ4-LoCOMT module regulates anther dehiscence via Jasmonic acid-mediated endothecium lignification in lily[J]. Journal of Advanced Research, 2025

56 Ding W, Gou Y, Li Y, et al. A jasmonate‐mediated regulatory network modulates diurnal floret opening time in rice[J]. New Phytologist, 2024, 244(1): 176-191

57 Fang Y, Guo D, Wang Y, et al. Rice transcriptional repressor OsTIE1 controls anther dehiscence and male sterility by regulating JA biosynthesis[J]. The Plant Cell, 2024, 36(5): 1697-1717

58 González-Schain N, Dreni L, Lawas L M F, et al. Genome-wide transcriptome analysis during anthesis reveals new insights into the molecular basis of heat stress responses in tolerant and sensitive rice varieties[J]. Plant and Cell Physiology, 2016, 57(1): 57-68

59 Zou J, Liu C, Liu A, et al. Overexpression of OsHsp17. 0 and OsHsp23. 7 enhances drought and salt tolerance in rice[J]. Journal of plant physiology, 2012, 169(6): 628-635

60 Li X, Lawas L M F, Malo R, et al. Metabolic and transcriptomic signatures of rice floral organs reveal sugar starvation as a factor in reproductive failure under heat and drought stress[J]. Plant, Cell & Environment, 2015, 38(10): 2171-2192

61 Pacini E, Dolferus R. Pollen developmental arrest: maintaining pollen fertility in a world with a changing climate[J]. Frontiers in Plant Science, 2019, 10: 679

62 Luo H B, Ma L, Duan W, et al. Effects of high temperature stress on photosynthesis of Cabernet Sauvignon grape (in Chinese). Sci Agric Sin, 2010, 43(13): 2744-2750 [罗海波，马苓，段伟，等．高温胁迫对赤霞珠葡萄光合作用的影响．中国农业科学，2010, 43(13): 2744-2750]

63 Ahmed F E, Hall A E, DeMason D A. Heat injury during floral development in cowpea (Vigna unguiculata, Fabaceae)[J]. American Journal of Botany, 1992, 79(7): 784-791

64 Porch T G, Jahn M. Effects of high‐temperature stress on

microsporogenesis in heat - sensitive and heat - tolerant genotypes of Phaseolus vulgaris[J]. Plant, Cell & Environment, 2001, 24(7): 723-731

65 Prasad P V V, Djanaguiraman M. Response of floret fertility and individual grain weight of wheat to high temperature stress: sensitive stages and thresholds for temperature and duration[J]. Functional Plant Biology, 2014, 41(12): 1261-1269

66 Liu L, Zou Z, Qian K, et al. Jasmonic acid deficiency leads to scattered floret opening time in cytoplasmic male sterile rice Zhenshan 97A[J]. Journal of Experimental Botany, 2017, 68(16): 4613-4625

67 Lin J. Mechanism of acetic acid affecting heat tolerance at flowering stage in rice (in Chinese). Changchun: Jilin Agricultural University, 2022 [林洁. 乙酸影响水稻花期耐热性机理研究. 长春: 吉林农业大学, 2022]

68 Wu L, Jing X, Zhang B, et al. A natural allele of OsMS1 responds to temperature changes and confers thermosensitive genic male sterility[J]. Nature communications, 2022, 13(1): 2055

69 Chen S Q, Wang Z, Liu M X, et al. Dynamics of pollen germination and pollen tube growth in rice (in Chinese). Chin J Rice Sci, 2007, 21(5): 513-517 [陈士强, 王忠, 刘满希, 等. 水稻花粉萌发及花粉管生长动态. 中国水稻科学, 2007, 21(5): 513-517]

70 Cui J, You C, Zhu E, et al. Feedback regulation of DYT1 by interactions with downstream bHLH factors promotes DYT1 nuclear localization and anther development[J]. The Plant Cell, 2016, 28(5): 1078-1093

71 Kim Y J, Kim M H, Hong W J, et al. OsMTD2-mediated reactive oxygen species (ROS) balance is essential for intact pollen-tube elongation in rice [J]. The Plant Journal, 2021, 107(4): 1131-1147

72 Kan Y, Mu X R, Zhang H, et al. TT2 controls rice thermotolerance through SCT1-dependent alteration of wax biosynthesis [J]. Nat Plants, 2022, 8: 53-67

73 Tang R S, Zheng J C, Jin Z Q, et al. Possible correlation between high temperature-induced floret sterility and endogenous levels of IAA, GAs and ABA in rice (Oryza sativa L.)[J]. Plant Growth Regulation, 2008, 54: 37-43

74 Cao Y Y, Chen Y H, Li W Z, et al. Responses of hormones, polyamines and proteins in young panicles of rice to high temperature at meiotic stage (in Chinese). Plant Physiol J, 2015, 51(10): 1687-1696 [曹云英, 陈艳红, 李卫振, 等. 水稻减数分裂期幼穗激素、多胺和蛋白质对高温的响应. 植物生理学报, 2015, 51(10): 1687-1696]

75 Falasca G, Franceschetti M, Bagni N, et al. Polyamine biosynthesis and control of the development of functional pollen in kiwifruit[J]. Plant Physiology and Biochemistry, 2010, 48(7): 565-573

76 Xie X J, Li B B, Li Y X, et al. Preliminary study on high temperature damage during flowering stage of rice in the Yangtze River Basin in recent 55 years (in Chinese). Jiangsu J Agric Sci, 2009, 25(1): 28-32 [谢晓金, 李秉柏, 李映雪, 等. 长江流域近 55 年水稻花期高温热害初探. 江苏农业学报, 2009, 25(1): 28-32]

77 Zhao Q, Zhou L, Liu J, et al. Involvement of CAT in the detoxification of HT-induced ROS burst in rice anther and its relation to pollen fertility[J]. Plant Cell Reports, 2018, 37: 741-757

78 Yaliang W, Yikai Z, Qinghua S, et al. Decrement of sugar consumption in rice young panicle under high temperature aggravates spikelet number reduction[J]. Rice Science, 2020, 27(1): 44-55

79 Lee S K, Lee J, Jo M, et al. Exploration of sugar and starch metabolic pathway crucial for pollen fertility in rice[J]. International Journal of Molecular Sciences, 2022, 23(22): 14091

80 Rieu I, Twell D, Firon N. Pollen development at high temperature: from acclimation to collapse[J]. Plant physiology, 2017, 173(4): 1967-1976

81 Kumar N, Kumar N, Shukla A, et al. Impact of terminal heat stress on pollen viability and yield attributes of rice (Oryza sativa L.)[J]. Cereal Research Communications, 2015, 43: 616-626

82 Fábián A, Sáfrán E, Szabó-Eitel G, et al. Stigma functionality and fertility are reduced by heat and drought co-stress in wheat[J]. Frontiers in Plant Science, 2019, 10: 244

83 Snider J L, Oosterhuis D M. How does timing, duration, and severity of heat stress influence pollen-pistil interactions in angiosperms?[J]. Plant signaling & behavior, 2011, 6(7): 930-933

84 Wu H C, Bulgakov V P, Jinn T L. Pectin methylesterases: cell wall remodeling proteins are required for plant response to heat stress[J]. Frontiers in plant science, 2018, 9: 1612

85 Cui Y, Lu S, Li Z, et al. CYCLIC NUCLEOTIDE-GATED ION CHANNELs 14 and 16 promote tolerance to heat and chilling in rice[J]. Plant Physiology, 2020, 183(4): 1794-1808

86 Cortijo S, Charoensawan V, Brestovitsky A, et al. Transcriptional regulation of the ambient temperature response by H2A. Z nucleosomes and HSF1 transcription factors in Arabidopsis[J]. Molecular plant, 2017, 10(10): 1258-1273

87 Yoshida T, Ohama N, Nakajima J, et al. Arabidopsis HsfA1 transcription factors function as the main positive regulators in heat shock-responsive gene expression[J]. Molecular Genetics and Genomics, 2011, 286(5): 321-332

88 Murthy V S, Ravishankar K V. Molecular mechanisms of heat shock proteins and thermotolerance in plants[M]//Abiotic stress physiology of horticultural crops. New Delhi: Springer India, 2016: 71-83

89 Li J, Cao Y, Zhang J, et al. The miR165/166-PHABULOSA module promotes thermotolerance by transcriptionally and posttranslationally regulating HSFA1[J]. The Plant Cell, 2023, 35(8): 2952-2971

90 Cao Y, Zhang J, Zhao Z, et al. Heat stress triggers enhanced nuclear localization of HYL1 to regulate miRNA biogenesis and thermotolerance in plants[J]. The Plant cell, 2025

91 Guan Q, Lu X, Zeng H, et al. Heat stress induction of mi R 398 triggers a regulatory loop that is critical for thermotolerance in Arabidopsis[J]. The Plant Journal, 2013, 74(5): 840-851

92 Prerostova S, Vankova R. Phytohormone-mediated regulation of heat stress response in plants[M]//Plant hormones and climate change. Singapore: Springer Nature Singapore, 2023: 167-206

93 Yokotani N, Ichikawa T, Kondou Y, et al. Expression of rice heat stress transcription factor OsHsfA2e enhances tolerance to environmental stresses in transgenic Arabidopsis[J]. Planta, 2008, 227(5): 957-967

94 Li X M, Chao D Y, Wu Y, et al. Natural alleles of a proteasome α 2 subunit gene contribute to thermotolerance and adaptation of African rice[J]. Nature genetics, 2015, 47(7): 827-833

95 Liu J, Zhang C, Wei C, et al. The RING finger ubiquitin E3 ligase OsHTAS enhances heat tolerance by promoting H2O2-induced stomatal closure in rice[J]. Plant physiology, 2016, 170(1): 429-443

96 Liu J, Sun X, Xu F, et al. Suppression of OsMDHAR4 enhances heat tolerance by mediating H2O2-induced stomatal closure in rice plants[J]. Rice, 2018, 11(1): 38

97 Cao Z, Tang H, Cai Y, et al. Natural variation of HTH5 from wild rice, Oryza rufipogon Griff., is involved in conferring high-temperature tolerance at the heading stage[J]. Plant Biotechnology Journal, 2022, 20(8): 1591-1605

98 Pan Y H, Chen L, Zhu X Y, et al. Utilization of natural alleles for heat adaptability QTLs at the flowering stage in rice[J]. BMC Plant Biology, 2023, 23(1): 256

99 Ling H, Wang Y, Li D, et al. Precise regulation of gibberellin to intermediate levels enhances rice alkali-thermal tolerance and yield. Nature. 2025, 633(7604): 645-652

100 Dong J, Chen K, Chen L, et al. OsNRAMP7 positively regulates heat tolerance at seedling and reproductive stages in rice[J]. Plant Stress, 2025: 100870

101 Zhou J, Peng Y, Chen X B. Analysis of differentially expressed genes in rice varieties with different heat tolerance under high

temperature stress (in Chinese). J Hunan Agric Univ (Nat Sci Ed), 2022, 48(5): 536-542 [周佳，彭艳，陈信波. 高温胁迫下不同耐热性水稻品种的差异表达基因分析. 湖南农业大学学报(自然科学版), 2022, 48(5): 536-542]
102 Li X M, Chao D Y, Wu Y, et al. Natural alleles of a proteasome α 2 subunit gene contribute to thermotolerance and adaptation of African rice[J]. Nature genetics, 2015, 47(7): 827-833
103 Muhlemann J K, Younts T L B, Muday G K. Flavonols control pollen tube growth and integrity by regulating ROS homeostasis during high-temperature stress[J]. Proceedings of the National Academy of Sciences, 2018, 115(47): E11188-E11197
104 Shen H, Zhong X, Zhao F, et al. Overexpression of receptor-like kinase ERECTA improves thermotolerance in rice and tomato[J]. Nature biotechnology, 2015, 33(9): 996-1003
105 Li W, Yang K, Hu C, et al. A natural gene on-off system confers field thermotolerance for grain quality and yield in rice[J]. Cell, 2025

Research progress on heat stress tolerance mechanisms in rice during flowering stage

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Against the backdrop of global climate warming, the frequency of high-temperature damage is on the rise, exerting a significant impact on rice growth and development, as well as yield and quality formation. Exposure to high-temperature damage during the rice flowering stage results in pollen sterility and reduced seed setting rate, consequently affecting yield and quality. The southern rice regions, as major grain-producing areas in China, frequently experience high-temperature damage during the heading and flowering stages of rice. Therefore, investigating the mechanisms underlying rice tolerance to high-temperature damage during the flowering stage holds great significance for ensuring global food security.Based on comprehensive existing studies, when rice is exposed to high temperatures during the flowering stage, it induces a series of physiological and reproductive disorders, including loss of pollen viability, abnormal spikelet opening, impaired anther dehiscence, reduced pollen germination rate, and inhibited pollen tube development. In response, rice copes with high-temperature stress through mechanisms such as activating physiological and biochemical regulation, initiating heat signal transduction, and regulating the expression of heat-tolerant genes. Furthermore, there are significant differences in the responses among rice varieties with varying heat tolerance.This study aims to elucidate in depth the heat tolerance mechanisms of rice during the flowering stage, thereby providing theoretical support for the identification of heat tolerance in rice varieties, the breeding of new stress-resistant varieties, and the optimization of supporting cultivation techniques.

rice, flowering stage, high-temperature heat stress, tolerance mechanism