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高温和干旱对水稻的影响及其机制的研究进展

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Research Advances in the Effect of Heat and Drought on Rice and Its Mechanism

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Abstract: Heat and drought are two major environmental stresses that affect rice growth, productivity, and grain quality. a comprehensive understanding of which is critical to evaluate the impacts of climate change on crop production. We review the independent and combined effects of heat and drought on rice growth, yield, and grain quality, demonstrate the possible mechanisms involved from multiple perspectives, such as photosynthesis, antioxidant system, endogenous hormones, activities of the key enzymes involved in sucrose-to-starch conversion, and molecular profiling, proposes reasonable strategies to mitigate the stress of environmental heterogeneity, and provide considerable suggestions for future study.

Key words: rice; heat; drought; combined heat and drought; grain yield; quality; physiological mechanism

摘 要：高温和干旱是影响水稻生长、发育、产量和品质的两个最重要的环境因子，全面理解高温和干旱胁迫对评价气候变化对水稻生产的影响至关重要。概述了高温、干旱及其复合胁迫对水稻生长发育、产量形成和稻米品质的影响；从光合作用、抗氧化系统、内源激素、蔗糖-淀粉代谢途径关键酶活性、分子机制等方面阐述其生理机制；提出减轻水稻高温干旱胁迫的调控措施；对未来深入开展水稻高温干旱逆境的研究提出建议。

关键词：水稻；高温；干旱；高温干旱复合胁迫；产量；品质；生理机制
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气候变化是 21 世纪中国乃至全球农业面临的严峻挑战之一，对农业的影响直接关系到粮食安全和经济安全。水稻是我国最主要的粮食作物之一，生殖生长期遇 35℃以上的高温就会对水稻产生危害[1]。全球气候变化报告[2]指出，近 130 年(1880－2012 年)全球平均地表温度上升了 0.85℃，预计 2016－2035 年全球平均地表温度将继续升高 0.3℃~0.7℃，水稻遭受干旱胁迫的面积将扩大一倍。而气候变化造成粮食产量和品质的降低，主要原因在于高温和干旱胁迫[2]。近年来国内外学者针对高温或干旱单一因子影响水稻的特征和机理进行了大量研究，涉及生长发育[3-5]、生理生态[6, 7]、产量与品质[8, 9]等方面。但在大田生产中，高温和干旱同时发生的几率逐年增加[10]，加重了高温或干旱对水稻产量和品质形成的危害。笔者就高温和干旱对水稻产量和品质的影响及其生理机制进行综述，以期进一步认识高温和干旱与水稻产量和品质形成的关系，为指导水稻高温干旱育种、抗热节水栽培，保障我国粮食安全提供理论参考。

1 高温与干旱对水稻生长发育及产量和品质的影响

1.1 对生长发育的影响

在不同发育时期，水稻对高温的响应表现不同，敏感程度依次为抽穗开花期＞幼穗发育期＞灌浆期[11, 12]。在抽穗开花期遇到高温，能使开花期提前[13, 14]，致使花药开裂不良、花粉萌发率低和花粉活力下降，最终造成水稻籽粒败育[15-17]；幼穗发育期遇到高温，会抑制颖花分化，导致颖花退化；在灌浆期遇到高温，会缩短灌浆期，阻碍籽粒充实[18]。营养生长期遇到高温会促进水稻的生长，株高、茎

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蘖数、叶面积和地上部干物质量明显增加[19]。

水稻营养生长期遇到干旱胁迫，光合作用受到限制，叶面积减小、分蘖减少[20]，叶片易卷曲[21]；水稻生殖生长期对干旱胁迫高度敏感，干旱不仅导致叶面积减小，株高和收获指数降低，还会阻碍水稻的生殖器官发育，如降低可育花粉数量、延长开花期、致使花药异常开裂等[12, 22]；灌浆中后期干旱导致叶片早衰，灌浆持续时间缩短，同化物供应受限，粒重降低。

有关高温和干旱复合胁迫对水稻生长发育的影响，已有学者进行了初步研究[17, 23]。多数研究认为，大气温度和土壤温度的升高会提高作物蒸腾耗水量和农田蒸散量，增加作物总耗水量，造成干旱缺水或进一步加剧干旱胁迫的危害[24-26]，如 Lawas 等[10]发现，水稻抽穗灌浆期间，高温干旱复合胁迫显著降低株高和生物量；但 Rang 等[17]利用不同基因型水稻品种为材料，在开花期设置高温、干旱和高温干旱复合胁迫，通过花药开裂、花粉萌发和主穗结实率等指标，观察不同品种对高温、干旱的响应。结果表明，虽然高温、干旱和高温干旱双重胁迫均导致主穗败育，但高温胁迫造成的空粒率在不同处理中最高。高温干旱复合胁迫对主穗发育的影响并没有远大于高温或干旱单一胁迫的影响，这体现了高温和干旱复合胁迫的独特性和复杂性。

1.2 对产量及其构成因素的影响

水稻减数分裂期和抽穗开花期是对高温和水分胁迫最敏感的时期[27-29]。在水稻开花当日，如果田间遭遇高温或水分胁迫，就会导致花药异常开裂[30, 31]，传粉受阻[32, 33]和花粉发育异常[34]，造成小穗不育，易形成空秕粒，从而导致结实率和粒重降低，进而使水稻减产[35]。营养生长期高温或干旱影响分蘖发生，进而降低有效穗数[21, 36]。

现有较多报道证明[37-39]，水稻抽穗开花期高温干旱双重胁迫会导致产量下降，高温干旱双重胁迫的影响大于单一高温或干旱胁迫。在产量构成要素中，结实率降幅最为明显，而对于千粒重，则有不同的结论。多数研究认为[33, 37, 39]，高温干旱会显著降低千粒重，但也有研究发现[38]，在胁迫环境下光合产物集中供应少数籽粒，会引起千粒重在一定幅度上的增加，但粒重之增远不足以弥补结实率和实粒数之失，最终还是会导致产量大幅下降。

1.3 对稻米品质的影响

稻米品质形成是品种遗传特性和环境条件综合作用的结果[11]。在环境因子中，温度升高对稻米品质影响的研究和进展最多[11, 35, 40]。虽然对水稻品质的影响尚存在诸多不确定性，这可能与品质分析和研究比较复杂有关，但研究结果多为不利的影响。灌浆结实期是环境影响稻米品质的关键时期，特别是灌浆前、中期高温对品质的影响最大[41]。高温通过缩短灌浆持续期，降低光合产物积累和运转、籽粒中蔗糖-淀粉代谢酶活性以及胚乳细胞发育和淀粉体的充实等生理过程，造成整精米率降低和直链淀粉含量降低[42, 43]、垩白粒率和垩白度增加、蛋白质含量和糊化温度升高[11]，导致稻米品质变劣[11, 35, 44]。

干旱对稻米品质的影响与基因型和水分胁迫程度有关。结实期土壤适度干旱，可以显著提高籽粒内蔗糖-淀粉代谢途径中关键酶活性和灌浆速率，降低内源乙烯水平，显著提高稻米的最高黏度和崩解值，降低垩白度和消减值，改善品质，而重度干旱的结果则相反[45]。

关于高温干旱复合胁迫下稻米品质的变化，相关研究报道较少。笔者[33, 39]曾观察到，抽穗灌浆早期高温、干旱或高温干旱双重胁迫显著降低了稻米的精米率、整精米率和崩解值，增加了垩白米率、垩白度和消减值，但在品种间存在很大差异，高温及高温干旱双重胁迫对高温干旱敏感型品种的影响大于耐热耐旱型品种，稻米品质在高温干旱双重胁迫下变劣的幅度大于单一胁迫。高焕晔等[46]研究也表明，在相同胁迫时间内，高温干旱复合胁迫导致稻米直链淀粉含量降低和蛋白质含量增高的效应远大于单一高温胁迫和干旱胁迫。表 1 总结了高温和干旱对水稻不同生育阶段生长发育及产量和品质的影响。

2 高温与干旱影响水稻生长发育与产量形成的生理机制

2.1 光合作用

水稻遭遇高温或干旱单一胁迫会导致光合作用速率下降[35]，一种原因是气孔限制，即胁迫促使气孔关闭，降低气孔导度，导致 CO_2 供应受阻，进而降低光合作用和物质生产[54]；另一种是非气孔限制，即胁迫通过影响植株内 Rubisco 活性和光系统 PSⅡ结构而抑制光合作用[55]。现有研究均表明，水稻在高温干旱复合胁迫下光合作用速率较单一胁迫下大幅降低[56-60]。然而，水稻在高温干旱复合胁迫下光合作用速率降低的原因，究竟是由气孔因素还是非气孔因素引起，尚无定论。赵凤云等[60]认为，叶绿素含量及其比例是高温干旱复合胁迫下水稻光合作用降低的原因；刘照等[59]发现，气孔因素和

表 1　高温和干旱对水稻不同生育阶段生长发育及产量和品质的影响

Table 1. Effects of heat and drought on rice growth, yield, and quality at different growth stages.

生育期 Growth stage	高温 Heat	干旱 Drought
营养生长期 Vegetative	增加株高、分蘖数、叶面积和地上部干物质量[19]	降低光合作用和气孔导度[21]； 降低叶面积和叶片数[20]，叶片易卷曲[21]； 降低穗数和生物量[36]；
生殖生长期 Reproductive	花时提前[16, 47]；花峰集中[48]；缩短花期[23]； 降低花药开裂率、花粉萌发率和花粉活力[17]； 降低光合速率[49]； 降低结实率和产量[15-17]	延长花时[50]，延长花期[17]； 降低可育花粉数量，花药开裂异常[12, 22]； 降低光合速率[51]、叶面积、株高和收获指数[22, 52]； 降低结实率和产量[15-17]；
灌浆结实期 Grain-filling	增加灌浆速率，缩短灌浆持续时间，提前灌浆进程， 降低粒重，灌浆不充实[18]； 降低整精米率[42, 43]；增加垩白粒率和垩白度[11]	叶片早衰，缩短灌浆持续时间，限制同化物供应[21, 53]； 降低粒重[45]； 降低整精米率，增加垩白粒率和垩白度[21, 45]

非气孔因素均会导致高温干旱复合胁迫下水稻光合速率下降；高焕晔等[56]虽然比较了水稻在高温、干旱单一胁迫与双重胁迫间的光合生理差异，包括叶绿素含量和气孔导度等参数的变化，但是不同胁迫下影响光合作用的气孔限制与非气孔限制的比重如何，并未详细阐述；Perdomo 等[58]研究观察到，水稻在干旱下光合速率降低的原因是气孔因素，而在高温下以及在高温干旱复合胁迫下，光合降低的原因与水稻植株内 Rubisco 活性降低显著相关。

2.2　抗氧化系统

活性氧(reactive oxygen species，ROS)在调控生物进程(如生长、发育和响应逆境胁迫)中作为信号分子起关键作用[61]。在干旱或高温等逆境胁迫下，活性氧的积累会导致大量细胞氧化损伤，抑制水稻光合作用[62]。为防止植物体受损，活性氧会被抗氧化机制清除。植物内的抗氧化系统可分为酶促系统和非酶促系统两大类，酶促系统主要包括超氧化物歧化酶(SOD)、谷胱甘肽还原酶(GR)、过氧化物酶(POD)和过氧化氢酶(CAT)等，非酶促系统主要由抗坏血酸(ASA)和还原性谷胱甘肽(GSH)构成。抗氧化系统也会受到逆境胁迫的影响[61]。

现有研究均表明，高温胁迫或干旱胁迫下，水稻抗氧化酶活性下降，清除能力降低，活性氧积累增加，膜脂过氧化作用加剧，细胞膜结构和功能受到破坏，质膜透性增加，剑叶生理生化机能受到伤害，光合速率降低[21, 49, 63, 64]。而高温或干旱胁迫对抗氧化系统的影响程度因品种的耐热性不同而存在差别[52, 65]。最近，Lai 等[66]发现生物钟调控基因在昼夜节律条件下表现出特定的表达阶段，白天 ROS 清除系统的效率较高。Byeon 和 Back[67]观察到，夜间高温对水稻的影响与褪黑素的产生密切相关，褪黑素作为一种有效的抗氧化剂，能有效清除夜间高温下植物细胞中的 ROS。因此，夜间 ROS 清除系统效率较低可能是水稻生产对夜间温度升高更敏感的原因之一。

有研究报道[37, 68]，高温干旱复合胁迫下，水稻叶片中的抗氧化酶 SOD 和 POD 的活性降低，丙二醛、脯氨酸及超氧阴离子含量增加，降低了水稻的抗氧化能力；但也有研究发现[69]，在高温胁迫、干旱胁迫及高温与干旱的复合胁迫下，水稻叶片的 SOD、POD、CAT 的活性总体上均显著高于对照，但 SOD 在高温与严重干旱的长期复合胁迫下，其活性比对照显著下降。

2.3　内源激素

根据植物激素对植物生长发育的调控作用可以将其分为抑制型植物激素和促进型植物激素两类。通常将脱落酸(abscisic acid，ABA)和乙烯称为抑制型植物激素，将生长素(indole-3-acetic acid，IAA)、细胞分裂素(cytokinins，CTK)和赤霉素(gibberellin，GA)称为促进型植物激素。杨建昌等[70]研究表明，在减数分裂期遭受水分胁迫，颖花中 ABA、乙烯和 1-氨基环丙烷-1-羧酸(ACC)浓度显著增加。Yang 等[71]发现，结实期适度土壤干旱，导致水稻籽粒激素平衡发生改变，特别是赤霉素减少和 ABA 增加，促进了茎鞘中贮藏性 ^{14}C 的运转，加快了籽粒灌浆速率。还有一些研究表明，适度干旱后的复水灌溉可以显著提高叶片[72]和籽粒[73]中的 CTK 含量，这将有助于提高作物的光合能力和对氮素的吸收利用[74]，加速胚乳细胞增殖，提高籽粒产量[75]。Tang 等[76]发现，高温降低水稻花药中 IAA、赤霉素含量，但增加 ABA 含量。

植物体内的多胺，最常见的有腐胺(putrescine，Put)、亚精胺(spermidine，Spd)和精胺(spermine，Spm)，被普遍认为是生长调节物质或激素的第二信使，调节植物的生长、发育、形态建成和对环境逆境的响应[77-79]。曹云英等[3, 80]报道，灌浆期高温胁迫引起剑叶多胺积累，耐热性强的品种积累得更多，说明多胺积累能增强水稻对高温的适应性。

Yang 等[81]观察到，水稻具有较强的增强叶片多胺生物合成能力，以响应水分胁迫。多胺在植物防御水分胁迫中的作用因多胺形式和胁迫阶段而异。具有更高水平的游离型 Spd/Spm 和非溶性结合 Put 以及早期游离多胺积累的生理特性，对水稻适应干旱更有利。

李钰等[68]研究表明，高温干旱复合胁迫下，水稻内源激素中 IAA、玉米素(ZT)和 GA 含量下降，而 ABA 和水杨酸(SA)含量上升，但作者并未比较高温或干旱单一胁迫下的内源激素变化。高温干旱复合胁迫如何影响水稻籽粒内源激素和多胺水平，目前尚缺乏充分的试验证据。

2.4 蔗糖-淀粉代谢途径关键酶活性

稻米胚乳中的淀粉约占糙米质量的 90%以上[82]，籽粒灌浆实质上是淀粉合成与累积的过程。源器官光合同化物(含茎鞘储存的非结构性碳水化合物)以蔗糖的形式经韧皮部运输到籽粒，之后在一系列酶作用下形成淀粉[83, 84]。据报道[84]，水稻胚乳发育期参与籽粒蔗糖-淀粉代谢途径的酶有 33 种，但 5 种酶在其中起关键作用[84-86]。这些酶包括蔗糖合酶(sucrose synthase，EC 2.4.1.13，SuS)、腺苷二磷酸葡萄糖焦磷酸化酶(ADP glucose pyrophosphorylase, EC 2.7.7.27, AGP)、淀粉合酶(starch synthase，EC 2.4.1.21, StS)、淀粉分支酶(starch branching enzyme，EC 2.4.1.18, SBE)和淀粉脱支酶(starch debranching enzyme，EC 3.2.1.70, DBE)。其中，淀粉合酶又分为可溶性淀粉合酶(soluble starch synthase，EC 2.4.1.18, SSS)和颗粒结合型淀粉合酶(granule bound starch synthase, EC 2.4.1.242, GBSS)，每组酶有几种同工型[87]。在灌浆期水稻籽粒里，这 5 种酶活性与籽粒灌浆速率和淀粉积累速率正相关[83, 84, 88]。

高温胁迫会影响这些酶的活性，进而影响籽粒中淀粉的生成[43, 89]。Jiang 等[89]观察到，花后高温下 SBE 和 GBSS 活性降低，SSS 活性增加，导致支链淀粉的分支频率下降，从而导致胚乳支链淀粉长链的比例增加。Cheng 等[90]则发现，高温下 AGP 活性和蔗糖浓度增加，而淀粉积累和 SuS 活性降低。

Yang 等[88]研究表明，在适度土壤干旱条件下，水稻籽粒灌浆过程中 SuS、SSS 和 SBE 活性显著增强，与淀粉积累速率呈正相关。土壤干旱使 AGP 活性增强，但与淀粉积累速率相关性较小。GBSS 及酸性转化酶活性受土壤干旱的影响较小。结果表明，水稻在籽粒灌浆期遭遇土壤干旱，可以通过调节蔗糖-淀粉代谢途径关键酶活性增大库强，从而加快籽粒灌浆速率。

针对水稻抽穗开花期遭遇高温、干旱单因子胁迫影响籽粒淀粉积累和酶活性的研究已较多，但高温干旱复合胁迫研究较少。笔者[91]发现，水稻遭遇高温和干旱双重胁迫时，SuS、AGP、StS、SBE 和 DBE 活性降低，淀粉中长链比例上升，短链比例下降，说明高温干旱胁迫通过淀粉合成关键酶而影响籽粒淀粉的合成与积累，最终影响水稻品质。

2.5 分子机制

逆境胁迫会使植物改变自身的生理生化、分子细胞水平来顺应不利的生存环境。对不同逆境胁迫下植物的不同组织器官、不同生长发育阶段、不同环境胁迫因子响应时的差异表达的功能基因进行分析筛选，获取关键功能基因和抗性之间的联系，将有助于从转录水平上了解胁迫因子的伤害机理及植物适应逆境胁迫的分子机制[92]。

Shen 等[93]最近报道，类受体蛋白激酶 ERECTA 基因(简称“ER 基因”)可以通过调控细胞死亡，提高转基因作物的耐热性。研究还发现，ER 基因在水稻和番茄中也有相同的功能，它能使转基因植物在正常气温下保证不减产，高温条件下，产量优势明显。其主要原因在于 ER 基因能促进植物细胞数量增多，细胞体积增大，导致各器官与生物量的增大。Li 等[94]成功发掘出水稻抗热数量性状基因 *TT1* (Thermo-tolerance 1)，并揭示了作物抗热新机制，*TT1* 能增强包括水稻、草坪草和十字花科等在内的多种植物的抗热性，在水稻、小麦、玉米、大豆和蔬菜等作物抗热育种中有广泛的应用前景。Li 等[95]研究了耐热型水稻品种(N22)和热敏感品种(Moroberekan)的花药、授粉前雌蕊和授粉后雌蕊的代谢组学和转录组学变化，发现复合胁迫下 N22 编码糖转运蛋白基因(*MST8*)和细胞壁转化酶基因(*INV4*)的表达量增高，而敏感型品种表现出 *MST8* 和 *INV4* 基因表达量降低、CSA(Carbon Starved Anther)基因表达量增高。

近年来，水稻抗逆分子机制的研究主要集中在转录因子及其分子调控机制方面。在水稻中，目前研究较多的转录因子类型主要有 bZIP[96, 97]、MYB/MYC[98]、WRKY[99]、AP2/EREBP[100] 和 NAC[101]，它们的结构通常由 DNA 结合结构域、转录活化结构域、寡聚化位点和核定位信号组成[102]。例如，当 *OsbZIP23*、*OsbZIP46* 和 *OsbZIP71* 在水稻中过表达时，其通过调节脱水蛋白、膜转运蛋白的表达，增强水稻抗旱性[103-105]。*OsMYB55* 过表达能增强谷氨酰胺合成酶(*OsGS1/2*)、谷氨酰胺转移酶

(*GAT1*)和谷氨酸脱羧酶 3(*GAD3*)等靶基因的表达，并调节其他氨基酸代谢基因，从而提高水稻的耐热性[98]。如 *OsWRKY11* 受热处理诱导，在热激诱导启动子 *HSP101* 的驱动下，*OsWRKY11* 的超量表达显著提高转基因水稻幼苗的高温和干旱抗性[106]；*OsWRKY30* 被丝裂原活化蛋白激酶(MAP)激活，过量表达 *OsWRKY30* 显著提高水稻的耐旱性[107]。ERF 类转录因子 SUB1A 不仅能增强水稻的耐涝性，而且能提高水稻的抗旱性[108]。关于 DREB 类转录因子的研究报道较多，Chen 等[109]从水稻中分离到 3 个与拟南芥 *DREB* 同源的基因 *OsDREB1E*、*OsDREB1G* 和 *OsDREB2B*，其中过量表达 *OsDREB1G* 和 *OsDREB2B* 均可显著提高水稻耐旱性。同样，已证明 NAC 家族的转录因子在水稻的耐旱性中起关键作用，例如，*OsNAC6*、*OsNAC10*、*OsNAC9* 和 *OsNAC5* 的过表达通过增加水稻根数和直径来改善耐旱性[101, 110-113]。过表达 *SNAC1* 的转基因水稻通过调节气孔减少水分流失，在营养和生殖阶段均表现出抗旱性[114]。

3 减轻水稻高温干旱胁迫的调控措施

3.1 选育耐热耐旱新品种

现有研究已经明确，不同品种间耐热、耐旱的能力差异较大，选用耐高温和抗旱品种可在一定程度上减轻高温或干旱的危害。长期以来，我国的作物育种的方向以高产(含抗病虫)和优质为主，但未来应确立抗逆、广适性的育种目标，以此作为解决高温、干旱等非生物逆境胁迫的主要技术途径之一。由于耐热和耐旱性状是两个有区别但又密切相关的性状，至今虽已获得一批具有较强耐热或耐旱性的水稻品系，但既耐热、又耐旱、还高产的品系较少，且尚未获得商业用品种。因此，采用常规育种与分子育种紧密结合的技术路线可能是尽快获得可在大面积上应用的耐热耐旱新类型品种的一个关键环节。

3.2 应对高温干旱的栽培调控技术

利用耕作、栽培和化控技术减轻高温干旱等逆境对作物的伤害，特别是减少逆境对作物产量与品质的不利影响，是水稻生产主要的措施之一。如根据高温天气规律和水稻高温、干旱敏感期，通过调整播种期，使开花结实期避开高温和干旱，已经成为缓解开花期高温和干旱危害的主要对策之一[115]。

合理施肥和适宜的水分管理也可有效提高水稻的抗热抗旱能力。抽穗结实期遭受高温胁迫，在穗分化期[116]和开花期[117]适当施用氮肥，以及在抽穗期采用轻干湿交替灌溉[118]，可以提高根系性能和地上部植株生理活性，从而获得较高的产量和较好的稻米品质。也有研究报道，通过配合施用生物炭和磷肥，在高温胁迫发生时，可以减轻或减缓高温胁迫带来的产量损失[119]。

前人为了缓解逆境对水稻带来的不利影响，利用化控技术做了大量的尝试，如喷施维生素 C、维生素 E、油菜素内酯、茉莉酸甲酯、水杨酸等植物生长调节剂[120-122]，以及喷施吡唑醚菌酯[123]等化学制剂，都取得了较好的效果。今后在深入阐明水稻耐高温、耐干旱机理的基础上，需从多途径选择栽培调控措施，突出作物生理调控作用，即利用作物本身或给作物创造环境发挥作物对逆境的适应能力和抵抗能力，以促进不同技术途径的深入发展，在实际生产中得到更广泛的应用。

3.3 响应高温干旱的分子调控机制

随着基因工程的深入，筛选和培育耐热、耐旱新品种已从简单的生理生化研究拓展到分子生物学领域当中。目前可通过调节抗性蛋白表达、选择耐性基因载体和遗传改良等多种方法进一步提高植物的抗逆性。中国科学院遗传与发育生物学研究所薛勇彪研究组与程祝宽研究组合作，成功克隆了 1 个耐热基因 *TOGR1*(Thermotolerant Growth Required 1)。该基因编码细胞核定位的 DEAD-box RNA 解旋酶。*TOGR1* 作为 pre-rRNA 的分子伴侣保证了高温下细胞分裂所需的 rRNA 有效加工，从而增强了水稻的耐热能力[124]。该研究不仅阐明了水稻耐高温的分子机制，而且为分子培育耐高温水稻品种提供了基因资源。

随着分子生物学和生物化学的不断进步和完善，利用现代生物技术，诸如生物信息学分析、蛋白互作分析、组学分析、基因芯片技术、高通量 RNA 测序(RNA-Seq)技术以及全基因组关联分析(GWAS)技术等，对这些问题进行深入地探索与分析，有望全面系统地理解水稻逆境相关转录因子的详细调控机理，为水稻抗逆机理研究提供更多的理论依据。图 1 总结了高温干旱对水稻的影响及其调控模式。

4 展望

4.1 高温和干旱影响水稻体内生理代谢整体认识

水稻对高温和干旱胁迫的响应是一个复杂的、但又是有序的生理生化过程，这一过程涉及水稻逆

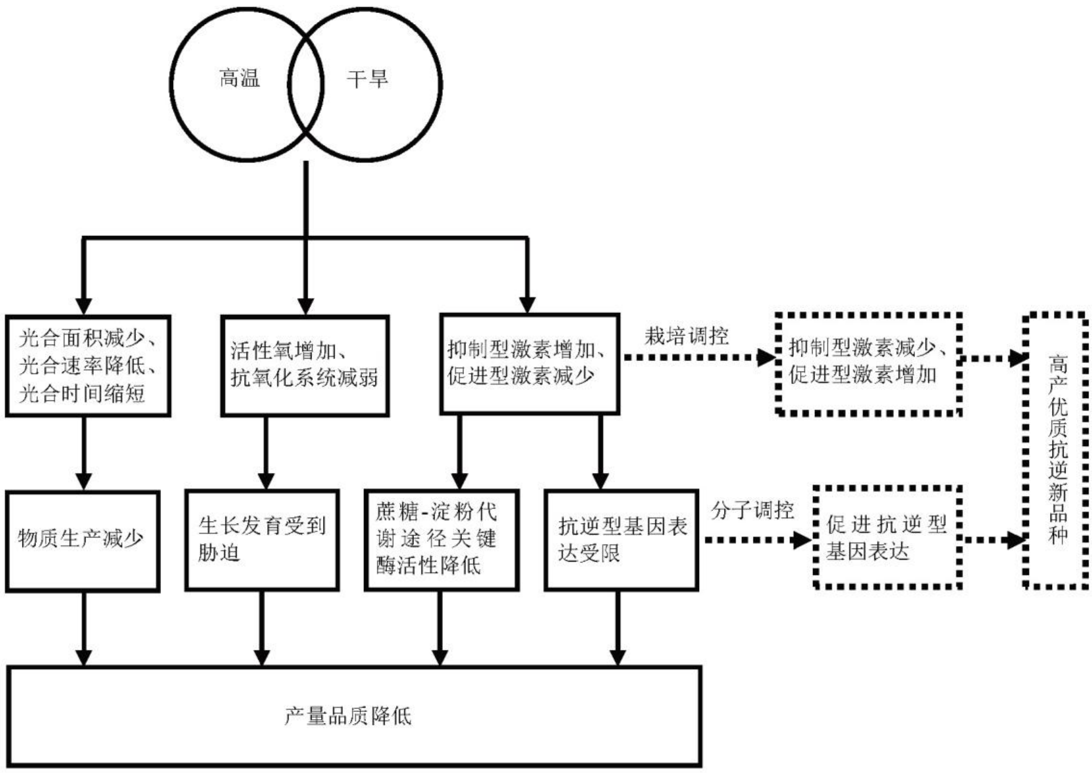

图 1　高温和干旱对水稻的影响及其调控模式
Fig. 1. Mode chart in the effect of heat and drought on rice and its regulation.

境下生长发育规律和养分吸收规律、根系形态建成和生理机制、酶学机制和激素机理、源库协调机制和物质运转分配机理、品质形成特点与机理。要充分认识其机理还要进行大量艰苦的工作。今后建议从群体、个体、组织、器官、细胞和分子等不同水平上研究水稻对高温和干旱及其复合胁迫的响应机制，揭示水稻对单一及复合胁迫响应和适应性机理；将水稻的产量和品质作为抗逆性的评定指标。研究并应用耕作、栽培、化控技术减轻高温和干旱对作物的伤害，特别是减少高温和干旱对作物产量与品质的不利影响。突出作物生理调控作用，即利用作物本身或给作物创造环境发挥作物对逆境的适应能力和抵抗能力。

4.2　多胁迫因子对水稻生长发育的交互影响

目前的研究多集中在高温或干旱单因子对水稻的影响，但双因子乃至高温、干旱、高 CO_2 浓度或高 O_3 浓度等多因子耦合作用的研究甚少。未来气候变化对水稻产量和品质的最终影响取决于所有环境因子间的协同作用，多因子的共同作用才能代表大田条件下水稻生长发育的真实情景。因此，水稻生殖生长期不同气候变化因子单独和耦合影响有待加强研究。另外，充分利用各种研究手段，如大田控制试验、遮雨棚、土培池、玻璃温室、人工气候室等模拟水稻的生长环境，综合分析温度、水分等多种环境因子的作用，是揭示水稻对高温、干旱等多重胁迫响应的基础。

4.3　水稻抗高温和干旱的分子设计育种与基因组编辑

近年来，我国在水稻生物学、进化与基因组学和激素生物学等领域表现尤为突出，并取得了许多突破性的研究成果[125, 126]，标志着中国在该领域居于引领地位。如李家洋团队率先提出并践行“分子设计育种”的理念，在系统研究作物产量、品质、耐逆性、营养高效、抗病虫等复杂农艺性状调控机理的基础上，挖掘关键基因的有利变异，通过品种设计进行多基因的配组优化，实现复杂性状的定向改良，达到综合性状优异的目标，为我国水稻分子设计育种与生产的跨越式发展奠定了开创性基础[127]。基因组编辑是近年来生命科学领域的突破性技术，能够精确改造生物基因组 DNA，从而在不改变其目标基因组整体稳定性的基础上直接对目的基因进行分子设计改良，其终产品无任何外源 DNA 成分，具有广阔的应用前景。我国科学家在作物基因组编辑技术领域取得多项突破性进展，使我国成为作物基因组编辑研究的国际领跑者[128, 129]。未来开展水稻高温、干旱抗性的改良研究，需要首先鉴定和了

解控制抵抗高温、干旱胁迫的关键基因，解析其表达调控机制、作用机理、信号途径和不同基因组合形成的调控网络。然后，根据需要改良的耐热、抗旱等农艺性状进行针对性的设计，选择最适宜的等位基因组，最终培育出抗高温、干旱以及高温干旱复合胁迫的水稻新品种，是水稻育种的发展方向。

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