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小麦耐热性研究进展

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摘要:随着全球平均气温持续攀升,高温胁迫日益成为小麦生产的限制因素。综述了高温胁迫对小麦产量和品质的影响、高温胁迫下小麦生理生化的变化以及小麦耐热性的遗传研究。通过常规育种手段与高通量分子标记辅助选择等现代生物育种技术的融合,培育耐热、高产的小麦新品种,保障全球粮食安全。

关键词:小麦;高温胁迫;耐热性;生理生化;遗传研究

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小麦(*Triticum aestivum*)是全球范围重要的谷类作物,也是我国北方主要的食用细粮。伴随全球气候变暖的趋势,平均气温持续攀升,极端高温事件愈发频繁,这对小麦的生长构成了严峻挑战,高温胁迫正日益成为影响小麦生长发育的关键因素之一。小麦是喜凉的农作物,异常高温迫使小麦生长势减弱、育性降低并缩短籽粒灌浆时间,减少淀粉的积累,导致产量下降,品质变劣。据预测,平均气温每升高1℃,全球小麦将减产约6%^[1]。干热风是黄淮麦区频繁出现的农业气象灾害,主要发生在小麦籽粒灌浆时期,温度超过30℃是诱发干热风的主要因素。干热风对小麦各种生理功能造成损伤,降低产量,其危害面积可达小麦种植面积的2/3,导致减产10%~20%^[2]。可见,高温已成为我国小麦生产面临的重大气象灾害之一。因此,鉴定并筛选小麦耐热品种,发掘优异基因与等位变异,对培育小麦耐热品种具有重要理论和实际应用意义。

1 高温胁迫对小麦产量与品质的影响

高温胁迫影响小麦的整个生长发育阶段,小麦

在开花期和灌浆期等关键生育期对高温尤为敏感。据研究发现,当小麦分蘖期遭受高温时会降低分蘖数;拔节期遭受高温时会降低植株的株高,使得干物质的积累减少;开花期和灌浆期遭受高温会使小麦开花提前,减少单株穗数和穗粒数,缩短灌浆时间,降低粒质量,最终导致减产,品质下降^[3-5]。Wardlaw等研究发现,小麦灌浆期遭受高温,一定温度范围内,温度每升高1℃,其灌浆时间缩短约3.1 d,千粒质量下降2.8 g^[6]。Fischer等报道,利用小麦品种Yecora在拔节至开花期间进行高温处理,平均温度每升高1℃,籽粒产量下降3%~4%^[7]。封超年等研究发现,小麦灌浆期遭受高温使籽粒胚乳细胞分裂时间缩短,从而降低粒质量^[8]。郑飞等研究发现,高温能够抑制小麦灌浆期的光合作用以及同化物的转运、分配,导致小麦韧皮部和籽粒蔗糖积累减少,灌浆强度和千粒质量降低,最终产量下降^[9]。

高温胁迫对小麦品质相关指标的影响不同。李永庚等研究发现,小麦灌浆前期遭受高温使麦谷蛋白/醇溶蛋白的比值以及麦谷蛋白大聚合物(GMP)含量增加,其蛋白质和淀粉的膨胀势、高峰黏度、湿面筋含量和沉降值升高,中期下降,灌浆后期遭受高温影响淀粉的积累,使蛋白质相对含量提高^[10]。Hurkman等研究发现,高温胁迫能够提高小麦籽粒淀粉含量,影响面条的加工品质,并通过改变面筋蛋白的稳定性影响湿面条的质地结构^[11-12]。Sofield等研究表明,当小麦灌浆期的温度>30℃时,由于淀粉的合成对高温更加敏感,蛋白质相对含量提

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高,并且热敏感品种蛋白质含量增加的幅度显著高于耐热品种^[13]。闫素辉等研究发现,小麦花后遭受高温,其籽粒淀粉的含量、积累量及支链淀粉含量显著降低,由于支链淀粉的合成更易受高温抑制,其直链淀粉相对含量提高,直/支链淀粉含量的比例也相应提高^[14]。

2 小麦在高温胁迫下生理生化的响应

2.1 高温胁迫对光合作用的影响

光合作用是植物物质转换和能量代谢的关键,是植物产量形成的基础,它对高温极其敏感。在遭遇高温环境时,小麦的叶绿体结构及其光合系统各个组成部分的稳定性均会受到显著的影响,这直接关系到植物的光合作用效率和整体生长状况。随着叶绿体的降解,位于类囊体膜上的光系统 II (PS II) 酶的活性降低,导致光合作用速率降低,缩短生长周期,降低产量^[15]。研究发现,高温胁迫不仅会造成 PS II 损伤,也会抑制 PS II 的修复^[16],还会降低 Rubisco (核酮糖-1,5-二磷酸羧化酶/加氧酶)对 CO₂ 的亲和力以及使 PEP(磷酸烯醇式丙酮酸)羧化酶和丙酮酸羧激酶活性下降^[17];当小麦叶片处于约 40 °C 的高温环境时,无论昼夜,均会导致 Rubisco 及 Rubisco 活化酶发生显著的结构与功能变化^[18]。尤为关键的是,这些变化在黑暗条件下无法得到逆转,从而对光合作用的长期效能构成严重挑战^[19]。据报道,Rubisco 活化酶是小麦进行光合反应的关键酶,高温胁迫下其酶活性下降,导致小麦光合能力降低^[20]。高温刺激 Rubisco 活性抑制剂的合成,如 XuBP(木酮糖-1,5-二磷酸),它结合在 Rubisco 的催化位点并阻断该位点,而 Rubisco 激活酶是可从 Rubisco 催化位点去除紧密结合的抑制剂^[21]。在高温胁迫的环境下,尤其是在日间气孔趋于关闭的条件下,保持 RCA(核酮糖-1,5-二磷酸羧化酶/加氧酶活化酶)结构的稳定性和 Rubisco 的活性,可确保卡尔文循环正常运行,从而在不利的温度条件下维持植物的基本代谢活动^[22-23]。与耐热品种相比,热敏感品种因活性氧和丙二醛的积累,光合器官受损更为严重^[24]。

2.2 高温胁迫对呼吸作用的影响

呼吸作用是所有植物生命的基础,将碳水化合物和其他富含能量的有机物氧化,释放能量维持植物生长和输出细胞产物,同时为生物合成提供碳骨

架,维持细胞氧化还原平衡^[25]。在一定的温度范围内呼吸速率随着温度升高而加快,但当温度提高到阈值后,植物体内酶蛋白变性甚至失活,促使呼吸速率迅速下降,影响能量供应^[26]。对线粒体的超微结构观察发现,热胁迫导致抗逆性差的品种有更严重的嵴损伤和线粒体功能障碍^[27]。Almeselmani 等研究发现,高温胁迫下植物叶片呼吸速率提高,热敏感品种的呼吸速率明显高于耐热品种^[28]。呼吸作用能够通过降解和清除高温胁迫下积累在植物体内的一些有害物质,一定程度减轻高温给植物带来的危害^[29]。

2.3 高温对细胞膜透性的影响

细胞膜是一种具有选择透过性的半透膜,能选择性地控制透过细胞所需的各种物质进出,以此稳定细胞内环境的稳态^[30]。高温胁迫首先会破坏细胞膜的结构和功能,导致细胞膜的通透性增加,进而导致生物膜的疏水键断裂和膜选择性吸收功能丧失,使细胞内电解质大量泄露、细胞外溶液的电导率增加,通过电解质外渗量可直接测量相对电导率的变化从而判定生物膜受到的伤害^[31]。在高温胁迫环境下,那些能够保持其膜系统功能完整性的植物展现出了更强的高温适应能力^[32]。因此,植物对于高温胁迫的耐受性,在很大程度上取决于维持细胞膜结构完整性和功能效率的能力^[33]。在高温胁迫的作用下,膜的热稳定性发生改变,附着在膜上的酶的活性也随之受到影响,使呼吸作用、光合反应和光呼吸等依赖膜上酶催化的反应受到阻碍,影响植物的生长发育^[34]。若小麦籽粒灌浆发生在高温胁迫条件下,膜热稳定性高的品系比热稳定性低的品系产量更高^[35]。

2.4 高温对蒸腾作用的影响

蒸腾作用是植物对水分和无机盐等物质吸收的动力源泉,能维持植物进行光合作用的适宜温度,是植物重要的生理活动^[36]。温度是影响植物蒸腾速率的重要因素,一定的温度范围内,叶片气孔张开程度随着大气温度升高而变大,使蒸腾作用增强,加快水分子向外扩散的速率,起到降温的效果,防止叶片被灼伤^[37]。当温度对植物构成胁迫时,叶片气孔张开程度逐渐下降,蒸腾速率下降,影响植物水分和无机盐等物质运输,难以维持有利于生长的温度,从而影响植株的发育^[38]。研究表明,蒸腾作用与植物的耐热性具有一定的相关性,耐热品种在高温条件下维持较高的蒸腾速率^[39]。

2.5 高温下抗氧化防御系统的反应

植物在高温胁迫下为避免细胞受到伤害,植物会启动抗氧化防御系统,其中活性氧(ROS)单线态氧、超氧自由基和过氧化氢反应是热应激下细胞常见事件^[40]。在高温胁迫下,不同途径的抗氧化剂会积累于植物体内^[41]。小麦抗氧化防御系统主要分为酶和非酶2种类型^[42]。过氧化氢酶(CAT)、过氧化物酶(APX)、超氧化物歧化酶(SOD)、单脱氢抗坏血酸还原酶(MDHAR)、谷胱甘肽还原酶(GR)、脱氢抗坏血酸还原酶(DHAR)、谷胱甘肽-S-转移酶(GST)、愈创木酚过氧化物酶(GPX)构成酶抗氧化系统,而抗坏血酸(AsA)、谷胱甘肽(GSH)和生育酚构成非酶抗氧化系统^[43]。SOD是主要的抗氧化剂之一,有助于将抗氧化物转化为H₂O₂;另一方面,ROS的消除由APX、GPX和CAT控制^[44]。为了消除H₂O₂,APX需要AsA和通过AsA-谷胱甘肽循环产生的还原型谷胱甘肽(GSH),在AsA氧化成单脱氢抗坏血酸(MDHA)的帮助下将H₂O₂转化为H₂O,MDHA再次歧化为脱氢抗坏血酸(DHA)^[45]。高温胁迫下,耐热小麦品种的酶促抗氧化剂显著增加,过氧化氢酶和超氧化物歧化酶活性增加使小麦获得耐热性^[46-47]。也有研究证明,抗干热风的小麦品种以较强的活性氧清除能力来维持植株正常生长和代谢^[48]。

3 高温胁迫下热激转录因子的表达与调控

热激转录因子(Hsfs)广泛存在于植物中,对植物的生长发育调控、信号网络和非生物胁迫等过程发挥重要作用,是植物响应热应激中鉴定的主要转录因子之一^[49]。Hsfs通过与下游基因启动子中存在的热休克元件(HSE)结合,调节热激蛋白(HSP)基因的转录^[50]。Hsfs根据结构特征分为A、B和C类,其中A类结构的研究进展较多^[51]。在小麦耐热研究中,也存在众多热激转录因子,将基因转到拟南芥中进行高温处理并被诱导,维持植株体内稳定。*TaHSFA1*在高温条件下起作用,并与泛素结合蛋白相互作用改变*TaHSFA1*的活性^[52]。将*TaHsfA2d*和*TaHsfA6f*转到拟南芥中过表达,增加了植株对高温、干旱和盐胁迫的耐受性^[53]。在拟南芥中过表达*AtHsfA2*也显著增强植物对高温、氧化和盐胁迫的耐受性^[54]。*TaHsfA2e-5D*在拟南芥中的过表达也增加了耐热性和耐旱性,还有众多小麦热激转录因子*TaHsfA1-1*、*TaHsfA2-1*、*TaHsfA2-7*、*TaHsfA2-9*、

TaHsfA2-10、*TaHsfA2-12*和*TaHsfA2-13*在拟南芥中的过表达也增强了植物耐热性^[49,55-59]。研究证明,小麦的多数Hsf基因在拟南芥中高温处理,都能被诱导,并在耐热中发挥重要作用^[60]。

4 小麦耐热性遗传改良研究进展

运用遗传改良技术培育具备耐热特性的小麦品种,无疑是应对高温胁迫、保障作物产量与品质的有力策略。Sun等利用硬粒小麦(Langdon)进行耐热相关基因定位,用膜热稳定测定法在染色体3A、3B、4A、4B和5A定位到多个耐热位点^[61]。Mason等利用重组自交系(RIL)对热敏感指数进行遗传分析,得到5个分布在1A、2A、2B和3B上稳定表达的数量性状基因位点(QTL)^[62]。Yang等利用耐热品种(Ventnor)和热敏感品种(Karl92)构建的F_{2:3}家系,以灌浆持续时间为指标鉴定出2个QTL,解释了11%和12%的表型变异^[63]。Vijayalakshmi等以Ventnor和Karl92构建RIL群体,在2A、3A、3B、6A、6B和7A染色体上定位出与热胁迫下叶片持绿性相关基因^[64]。Paliwal等利用NW1014和HUW468构建RIL群体,鉴定到4个与耐热相关的QTL,分布在2B、7B和7D染色体上,能够解释7.21%~25.39%的表型变异^[65]。陈希勇等以中国春和小麦HOPE染色体代换系为材料,以膜热稳定性为指标,检测到HOPE在2A、3A、2B、3B和4B染色体上具有耐热相关基因位点,显著提高中国春的耐热性^[66]。李世平等以早选10号和鲁麦14为亲本,利用单倍体技术快速构建群体,在灌浆时期以生理性状和千粒质量耐热指数进行定位,检测到染色体1B、2D、5A、5B、6A、6B和7A中存在与灌浆期耐热相关的位点,其中有12个加性效应QTL表型变异贡献率为2.64%~11.41%,17对上位性效应QTL表型变异贡献率为2.45%~8.84%^[67]。Kumar等利用205个晚播小麦品种进行全基因组关联分析(GWAS),共鉴定出69个潜在热响应的QTL^[68]。Wang等用688份冬小麦材料,以千粒质量和热胁迫敏感指数为指标进行GWAS分析,发现在5A染色体存在同时调控粒质量和耐热性的优良等位基因^[69]。

在挖掘小麦耐热基因的同时,也有许多耐热基因通过转基因进行了验证。Xue等在小麦中过表达*TaHsfA6f*显著提高其耐热性^[70]。小麦耐热相关的基因*TaMBF1c*、*TaFER-5B*、*TaOEP16-2-5B*、*TaB2*和

TaGASR1在拟南芥中异源表达,可以提高拟南芥的耐热性^[71-75]。表1为经转基因研究证实耐热性中发挥作用的基因。通过对小麦耐热遗传研究,可为

小麦未来进行分子标记辅助选择提供基础,加快培育小麦耐热品种。

表1 通过转基因研究证实具有耐热功能的基因

基因	受体	功能	参考
TaHsfA6f	普通小麦	过表达 TaHsfA6f的转基因植物显示出更好的耐热性	Xue 等 ^[70]
TaFER-5B	普通小麦	转基因植物表现出增强的耐热性	Zang 等 ^[72]
TaGASR1	普通小麦	过表达 TaGASR1的植物提高了对热应激和氧化应激的耐受性	Zhang 等 ^[74]
TaHsfC2a	普通小麦	过表达 TaHsfC2a的小麦表现出更好的耐热性	Hu 等 ^[76]
TamiR159	水稻	相对于野生型,过表达 TamiR159的植株对热胁迫更敏感	Wang 等 ^[77]
TaMBF1c	水稻	过表达 TaMBF1c在幼苗和生殖阶段均表现出比对照植物更高的耐热性	Qin 等 ^[71]
TaOEP16-2-5B	拟南芥	过表达 TaOEP16-2-5B基因的转基因植物表现出更强的热胁迫耐受性	Zang 等 ^[73]
TaB2	拟南芥	拟南芥中过表达 TaB2增强对热应激的耐受性	Singh 等 ^[75]
TaWRKY33	拟南芥	TaWRKY33转基因株系对热应激的耐受性增强	He 等 ^[78]
TaNAC2L	拟南芥	过表达 TaNAC2L通过激活热相关基因的表达增强耐热性	Guo 等 ^[79]
TaHsfA2d	拟南芥	过表达 TaHsfA2d的转基因植物表现出更好的耐热性	Chauhan 等 ^[53]

5 总结与展望

高温胁迫已经成为限制小麦生产的重大灾害气候之一,选育耐热和高产的品种是有效提高我国小麦生产水平的重要途径。高温会破坏植物细胞膜的结构和功能,导致细胞膜的通透性增加,降低附在膜上的酶的活性,影响光合作用和呼吸作用,并缩短灌浆时间,从而影响小麦的产量。而耐热品种的膜热稳定性更高,能够快速启动抗氧化剂防御系统,显著提高酶促抗氧化剂;也能在高温条件下保持较高的蒸腾速率,从而增强小麦的耐热性,提高产量。

目前,已经挖掘了多个小麦耐热性位点或基因,并通过转基因方法在小麦和拟南芥中进行了验证,如现已发表关于小麦耐热相关的基因 TaMBF1c、TaFER-5B、TaOEP16-2-5B、TaB2和 TaGASR1异源表达可以提高拟南芥的耐热性,进而开发相应的分子标记^[69-73]。小麦在高温胁迫下的生理响应和耐热遗传方面的研究成果,以及基因芯片技术、转基因技术及基因编辑的开发和利用,为培育小麦耐热品种提供了相应的理论基础和参考依据。因此,确立小麦耐热性指标,建立小麦耐热性指标评价体系,筛选鉴定耐热性小麦种质资源,通过常规育种手段与高通量分子标记辅助选择等现代生物育种技术

的融合,选育耐热、高产小麦新品种,是应对全球气温变暖、保障全球粮食安全的重要举措之一。

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Research Progress in Heat Tolerance of Wheat

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Abstract: As the global average temperature continues to rise, heat stress has increasingly become a limiting factor for wheat production. The paper reviews the physiological and biochemical changes of wheat under heat stress, the impact of heat stress on the yield and quality of wheat, and the genetic research on heat tolerance of wheat. Integrating conventional breeding methods with modern biotechnological breeding techniques such as high-throughput molecular marker-assisted selection to cultivate new wheat varieties that are heat-tolerant and high-yield is an important measure to ensure global food security.

Key Words: Wheat; High-temperature stress; Heat tolerance; Physiology and biochemistry; Genetic research