

· 特邀综述 ·

作物花粉高温应答机制研究进展

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摘要 随着全球气候变暖加剧, 农作物面临更加严峻的高温威胁。高温胁迫影响作物生长发育各个阶段, 其中花粉发育过程对高温胁迫最为敏感, 因此花粉高温应答机制成为当前植物学研究热点。研究表明, 花粉可以通过质膜上的钙离子通道、内质网中的未折叠蛋白反应、活性氧积累以及H2A.Z等机制感知高温胁迫, 并通过调控热激蛋白表达、糖代谢、激素水平及活性氧清除能力适应高温胁迫。该文从高温对花粉发育的影响、花粉高温胁迫应答机制以及花粉高温胁迫研究的实验设计等方面进行综述, 旨在为相关研究提供借鉴。

关键词 作物, 花粉, 高温, 应答机制

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随着全球气候逐渐变暖, 温度变化对生态环境的影响日益明显(Hansen, 2015)。IPCC (Intergovernmental Panel on Climate Change)研究报告指出, 相比20世纪末, 目前全球气温已经增加约4°C, 而温度升高将严重影响农作物生长, 威胁粮食安全(Lobell et al., 2011)。因此, 开展作物的高温胁迫研究具有重要意义。花粉作为一种具有特殊结构和功能的微小生命有机体, 包含父本基因组信息, 是种子植物有性生殖的重要调控者。由于花粉结构简单, 因此成为研究植物细胞极性、命运分化和发育的理想体系(鲁云龙等, 2014)。在生产实践中, 雄蕊产生有活性的花粉是作物形成种子和果实的前提。花粉发育过程对高温非常敏感, 高温导致花粉活性降低甚至失活, 使作物穗粒数和坐果率显著降低, 最终导致粮食减产。因此, 花粉高温应答机制研究成为植物学家关注的重点。

通常情况下, 在高于最适温度5°C以上的环境下, 花粉就会遭受高温伤害。许多重要作物如小麦(*Triticum aestivum*)、水稻(*Oryza sativa*)和玉米(*Zea mays*), 其开花期均集中在夏季, 极易遭遇连续或严重的高温天气, 从而导致花粉发育异常(Barnabás et al., 2008)。水稻散粉时环境温度通常在28°C以上, 温度每升高1°C, 就会造成水稻减产约8%。如果温度升高到33°C, 会导致花粉产量降低到13%; 而温度升高

到39°C, 就会导致花粉完全丧失活性, 落在柱头上的花粉无法萌发(Prasad et al., 2006; Endo et al., 2009)。高温对小麦影响更为严重, 在小孢子形成期, 环境温度达30°C时就会造成小孢子发育异常; 而在小花发育阶段, 长期温和高温(25°C, 白天)也会影响小麦的花粉发育(Farooq et al., 2011)。此外, 对玉米、高粱(*Sorghum bicolor*)和大麦(*Hordeum vulgare*)等的研究表明, 白天温度高于32°C会对花粉发育造成不同程度的影响(Lyakh et al., 1991; Liu et al., 2015)。

由于花粉取材相对困难, 因此针对花粉高温应答机制的研究相对较少。但随着分离技术的发展以及多种组学技术的应用, 人们对花粉的高温应答机制已有一定认识(Qin et al., 2008; Jagadish et al., 2010; Yang et al., 2015; González-Schain et al., 2016; Keller et al., 2017, 2018)。本文针对高温对作物花粉发育过程的影响、花粉高温胁迫应答机制, 以及花粉高温胁迫研究实验设计进行综述, 以期对相关研究提供借鉴。

1 高温对花粉发育的影响

花粉作为植物高度特化的雄配子体, 其发育过程既短

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暂又复杂(图1) (Twell, 2011)。位于花药内的花粉母细胞(pollen mother cells, PMC)经过1次减数分裂形成4个单倍体的小孢子(uninucleate microspore, UNM)。在中央大液泡的挤压下,小孢子细胞核发生极化,随后进行1次不对称有丝分裂(pollen mitosis I, PMI),产生1个大的营养细胞(vegetative cell, VC)和1个位于营养细胞内的较小的生殖细胞(generative cell, GC)。最后,生殖细胞再进行1次有丝分裂(pollen mitosis II, PMII)产生2个精细胞(sperm cell, SC)。精细胞携带父本信息,在营养细胞产生的花粉管帮助下被运输到胚囊中,分别与中央细胞和卵细胞融合完成双受精。

高温影响花粉发育全过程,导致花粉结构和发育异常,产生没有活性的花粉,并最终导致受精失败(Porch and Jahn, 2001; Sato et al., 2006; Pecrix et al., 2011)。其中,花粉母细胞减数分裂期到小孢子形成前期对高温最为敏感(图1)。高温影响花粉母细胞减数分裂进程,造成同源染色体交叉和重组频率增加、染色体分离异常,以及形成不完整的四分体和染色体倍性异常的小孢子等(Francis et al., 2007; De Storme and Geelen, 2014; Omid et al., 2014; Draeger and Moore, 2017)。对大麦的研究表明,高温诱导小孢子母细胞中减数分裂特异基因ASY1 (ASYNAPSIS1)上调表达,从而提高染色体交叉和重组频率(Oshino et al., 2007)。染色体倍性异常的小孢子,如二价体(diploid dyads)的产生则是由于高温导致维管骨架解聚以及纺锤体错误排列引起的(Francis et al., 2007; Pecrix et al., 2011; Wang et al., 2017)。已在拟南芥(*Arabidopsis thaliana*)中鉴定到3个调节减数分裂期纺锤丝定位的基因(*FORMIN14*、*JASON*和*PARALLEL SPINDLES 1*),推测高温影响这3个基因的表达,导致产生异常倍性的小孢子(De Storme and Geelen, 2014)。*FORMIN14*属于植物第二类形成素,通过调节微管和微丝骨架的形成和交联参与花粉母细胞减数分裂过程(Li et al., 2010b)。*jason*和*parallel spindles 1*产生二倍体小孢子是由于减数分裂II期纺锤体呈异常的平行排列,并且*PARALLEL SPINDLES 1*的表达受到*JASON*调控(d'Erfurth et al., 2008; De Storme and Geelen, 2011)。这种由于高温引起小孢子母细胞减数分裂异常,进而导致花粉多倍体化(polyploidization)的现象对植物进化具有重

要意义(Pecrix et al., 2011)。

高温还影响小孢子的发育。研究表明,蔗糖转化酶(invertases, INVs)在高温胁迫下小孢子发育过程中发挥重要作用。高温导致小孢子和花药中INVs基因表达量下降,从而影响蔗糖水解过程,造成小孢子中淀粉积累异常,产生没有活性的花粉(Jain et al., 2010)。在体外对分离的小孢子进行高温处理有助于诱导其形成胚胎,表明高温还影响小孢子细胞的分化(Ochatt et al., 2009)。

高温通过改变花粉和柱头细胞中生长素和糖类的平衡影响花粉管在柱头内的生长,表现出花粉萌发失败以及花粉管末端膨大、扭曲和破裂等现象,最终导致受精过程无法完成(Kakani et al., 2005; Snider et al., 2011; Snider and Oosterhuis, 2011; Song et al., 2015; Coast et al., 2016; Parrotta et al., 2016; Shi et al., 2018; Zhang et al., 2018)。对拟南芥的研究表明,高温下CLE45-SKM1/SKM2信号通路在确保花粉和柱头正常相互识别过程中发挥重要作用(Endo et al., 2013)。

高温还可以促进绒毡层细胞提前发生程序性死亡(programmed cell death, PCD),进而影响花粉发育、活性以及散粉过程(Sato et al., 2002; Parish et al., 2012; De Storme and Geelen, 2014)。绒毡层细胞提前发生程序性死亡,是由于高温导致更多的蛋白质折叠异常,超出内质网相关降解机制(ER-associated degradation machinery, ERAD)和未折叠蛋白响应机制(unfolded protein response, UPR)的修复能力(Li et al., 2006)。此外,绒毡层分泌的 β -1,3-葡聚糖酶对花粉细胞壁形成以及小孢子发育至关重要(Suzuki et al., 2001)。在水稻小孢子形成期,YY1和YY2等绒毡层特异表达的基因在高温胁迫下显著下调,可影响花粉在柱头上的吸附性,并最终导致萌发率降低(Endo et al., 2009; Müller and Rieu, 2016)。

2 花粉对高温胁迫的应答机制

2.1 花粉的高温胁迫感应

植物进化出完整而复杂的胁迫响应机制来适应高温并维持自身的生长发育(Kotak et al., 2007)。已有研究表明,花粉至少可以通过4种方式感知环境温度的变化,并通过诱导高温胁迫相关基因的表达来适应高

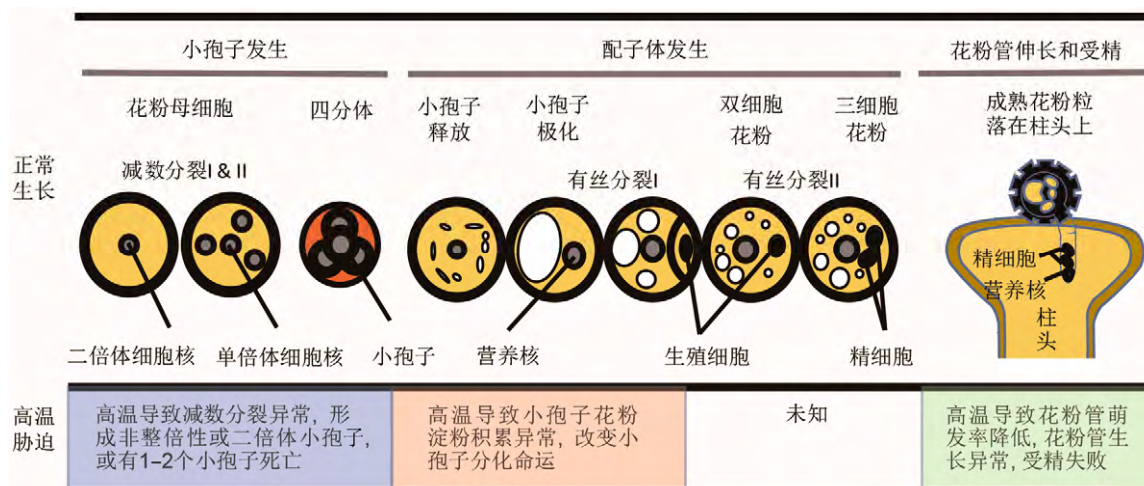


图1 花粉发育过程及高温对花粉发育的影响

Figure 1 Pollen development process and the influence of high temperature on pollen development

温环境(Mittler et al., 2012)。这4种方式分别为质膜上的钙离子通道、未折叠蛋白反应(unfolded protein response, UPR)、积累的活性氧(reactive oxygen species, ROS)以及含有组蛋白变体H2A.Z的核小体(Kumar and Wigge, 2010)。

质膜上的钙离子通道是植物细胞重要的高温感受器。电化学和生化等实验证实, 温度升高可以触发质膜上钙离子通道打开, 导致胞外钙离子内流, 使胞质内钙离子增加, 引起细胞产生热激反应(heat shock response, HSR) (Saidi et al., 2009)。拟南芥基因组编码40多个钙离子通道, 且大多数位于质膜上(作为高温感受器), 可以与钙调素蛋白AtCaM3结合, 通过激活WRKY39等因子参与热激反应(Ward et al., 2009; Zhang et al., 2009; Li et al., 2010a)。其中, 一类环腺苷酸门控离子通道(cyclic nucleotide gate channels, CNGCs)被证实参与拟南芥花粉的高温感应。环境温度升高后, 花粉中的cAMP含量升高并导致CNGC16通道打开, 使得胞外的 Ca^{2+} 内流, 而胞内积累的 Ca^{2+} 又可以进一步激活热激转录因子(heat shock transcription factors, HSFs) HsfA2和HsfB1, 从而参与高温胁迫应答(Gao et al., 2012; Tunc-Ozdemir et al., 2013)。最近, 研究者通过分析高温胁迫下cngc16突变体与野生型花粉的基因表达情况, 鉴定到至少有27个转录因子参与花粉的高温响应; 此外, 还鉴定到cngc16和野生型在高温胁迫下存在

192个差异表达基因, 其中突变体中的差异表达基因更多参与细胞生长和花粉发育过程, 并且缺少在野生型中表达的转录因子AGAMOUS-like 29, 暗示CNGC16在调控花粉的高温胁迫响应中具有一定的特异性(Rahmati Ishka et al., 2018)。

绒毡层或者花粉细胞内的UPR反应也可以感受高温胁迫, 并通过ER-UPR (内质网中未折叠蛋白反应)提高内质网对蛋白质的折叠能力, 降低未折叠蛋白质的数量, 从而提高花粉的胁迫耐受能力。一些转录因子和RNA剪切因子也参与ER-UPR, 并在花粉发育过程中发挥重要作用, 其中erdj2a、bip1/2/3和pod1等突变体均表现出花粉发育异常表型(Fragkostefanakis et al., 2016a)。而ER-UPR反应的重要组分IRE1 (Inositol Requiring Enzyme 1)可以利用其核糖核酸酶活性对bZIP60的mRNA进行剪切, 进而参与花粉的高温胁迫响应(Deng et al., 2016)。IRE1还可以影响HOP3 (HSP70-HSP90 organizing protein)蛋白的表达水平, 而后者通过与BiP (binding immunoglobulin protein)及TMS1 (THERMOSENSITIVE MALE STERILE 1)互作, 参与调控花粉在柱头上的萌发(Yang et al., 2009; Ma et al., 2015; Fernández-Bautista et al., 2017)。

ROS是一类化学性质活泼且具有较高氧化活性的分子, 高温胁迫会导致植物体内产生大量ROS。积累的ROS不仅会造成核酸和蛋白质等重要生物大分

子的氧化损伤,也可以作为信号分子激活植物体内的抗氧化系统,从而调控植物多个器官(包括花粉)响应高温胁迫。对小麦花粉进行高温处理(42°C, 2小时)后,发现花粉中ROS和超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)和过氧化氢酶(catalase, CAT)含量显著升高,同时伴随着热激蛋白(heat shock proteins, HSPs) HSP70、HSP90、HSP17和HSP26含量增加(Kumar et al., 2013)。番茄(*Lycopersicon esculentum*)和水稻花粉中也有类似机制(Frank et al., 2009; Zhao et al., 2018a)。水稻花粉中具有ROS清除能力的MT-1-4B蛋白表达量下调会导致花粉丧失育性,进一步证明ROS参与花粉的高温胁迫应答(Hu et al., 2011)。

H2A.Z是一种组蛋白变体,包含H2A.Z的核小体与DNA结合更加紧密。研究表明,高温处理可以减少含有H2A.Z的核小体在基因转录起始位点的占有率,从而调控相关基因的表达(Kumar and Wigge, 2010)。但目前关于H2A.Z参与花粉高温胁迫响应的研究非常有限。在二穗短柄草(*Brachypodium distachyum*)中,含有H2A.Z的核小体参与开花和种子形成期的高温感应,温度过高会破坏H2A.Z在染色体上的分布规律,最终导致二穗短柄草的结实率下降(Boden et al., 2013)。

2.2 花粉的高温胁迫应答

花粉感知环境中的高温信号后,通过信号转导引起代谢、转录甚至表观遗传水平的改变,从而实现对高温胁迫的响应。其中热激转录因子是高温胁迫应答网络中的关键组分,可以诱导高温胁迫应答重要效应物热激蛋白的表达,通过维持蛋白的构型稳定减少由高温导致的蛋白变性和聚集,从而提高植物耐热性。在烟草(*Nicotiana tabacum*)花粉发育过程中,高温诱导不同的HSPs表达(Volkov et al., 2005)。在番茄等植物的花粉中,高温可以诱导HSFA2、HSFA3、HSP100和HSP17等热激转录因子和热激蛋白基因的表达(Fragkostefanakis et al., 2016b; Kumar et al., 2016)。在番茄花粉发育过程中,抑制HSFA2的表达导致花粉小孢子发育异常(Frank et al., 2009; Giorno et al., 2010; Fragkostefanakis et al., 2016b)。在拟南芥花粉中,高温可以诱导HSFA2、HSFB1和HSFA7a基因表达,协同参与高温胁迫响应(Larkindale and

Vierling, 2008; Gao et al., 2012)。此外,HSFA5同源基因*AtREN1*突变体的花粉对高温非常敏感(Reňák et al., 2014)。HSP除了受到转录因子HSF的影响,可变剪切也可以通过调控HSPs基因的表达及多样性参与高温胁迫响应(Keller et al., 2017)。与营养器官相比,高温诱导花粉中产生的HSFs和HSPs种类和数量仍然很少,这也是花粉对高温更加敏感的原因之一。在拟南芥花粉中表达体细胞特异的*AtHSP101*可以有效提高花粉对高温的耐受能力(Burke and Chen, 2015)。

活性氧清除系统、激素以及糖类物质在花粉的高温应答中也发挥重要作用(Frank et al., 2009; Min et al., 2014)。花粉和绒毡层细胞含有大量线粒体,高出营养器官20倍以上。在高温条件下,线粒体会产生大量的ROS,从而给花粉带来严重的活性氧压力。这些ROS可以被SOD、CAT、抗坏血酸过氧化物酶(ascorbate peroxidase, APX)和谷胱甘肽过氧化物酶(glutathione peroxidase, GPX)等抗氧化系统清除(Kumar et al., 2014; Müller and Rieu, 2016; Zhao et al., 2018a, 2018b)。

高温胁迫下,植物体内的激素水平也会发生显著变化(Verma et al., 2016)。番茄花粉中乙烯合成基因(*SIACS3*和*SIACS11*)及其信号通路中的相关基因(*SIETR3*和*SICTR2*)受高温诱导表达(Jegadeesan et al., 2018)。对乙烯不敏感的番茄突变体花粉对高温非常敏感,但在高温处理前,外源施加乙烯可以显著提高花粉的耐热性(Firon et al., 2012),表明乙烯参与花粉的高温胁迫响应。此外,已有研究表明,生长素参与调控花粉母细胞的减数分裂和小孢子的有丝分裂进程。高温处理拟南芥和大麦花粉会降低花粉和绒毡层细胞中生长素合成基因(*YUC2*、*YUC6*和*TAA1/TIR2*)的表达,导致小孢子有丝分裂异常,产生败育的花粉,而外源施加生长素则可提高花粉的耐热性(Sakata et al., 2010; Firon et al., 2012; Higashitani, 2013)。研究表明,在棉花(*Gossypium hirsutum*)中,microRNA(miR157和miR160等)等可以通过调节生长素信号通路影响高温胁迫下的花粉活性(Ding et al., 2017)。研究还显示,赤霉素(GA)和脱落酸(ABA)也参与花粉热胁迫响应(Sakata et al., 2014)。ABA作为重要的植物胁迫响应激素,参与植物的多种非生物胁迫响应(Tang et al., 2008)。越来

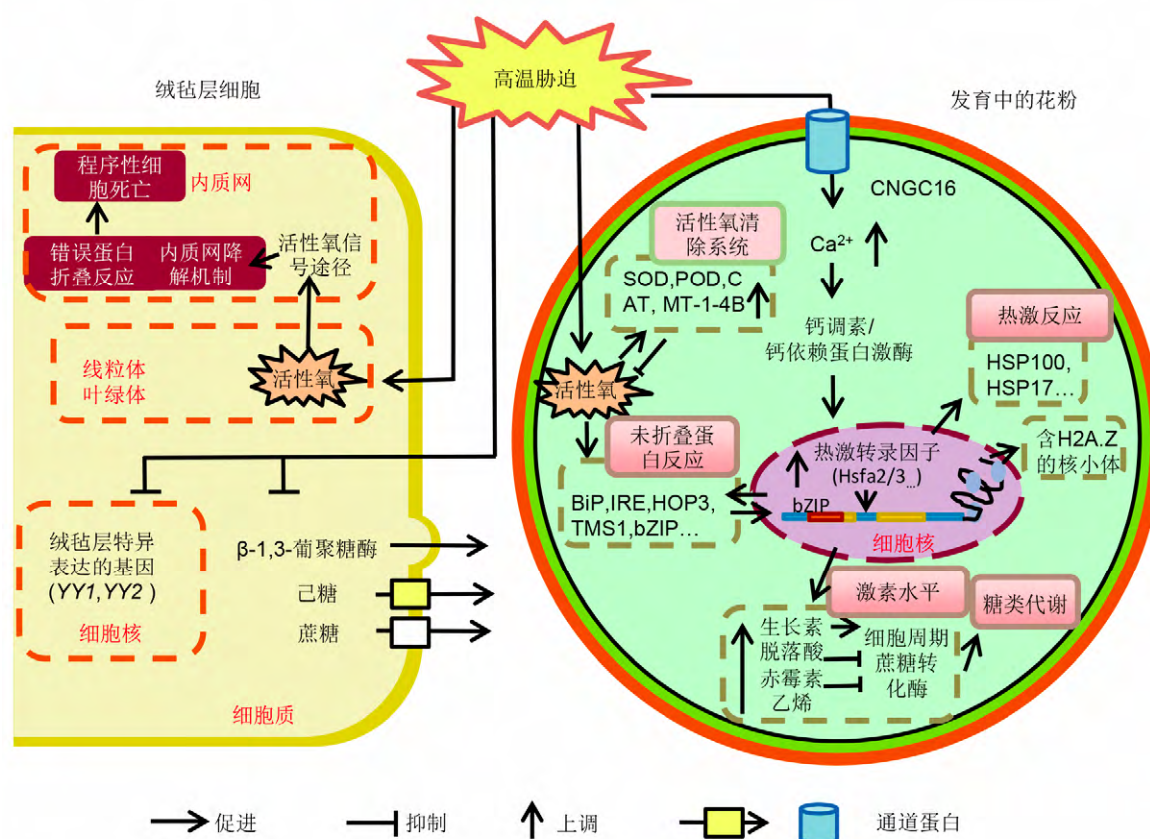


图2 花粉的高温应答机制

Figure 2 The mechanism of pollen response to high temperature stress

越多的证据表明, ABA可以通过与糖信号通路互作(如在胁迫下抑制INV活性)影响植物的胁迫响应(Oliver et al., 2007)。在小孢子母细胞减数分裂时期, 用外源ABA喷施水稻叶片可以提高蔗糖的转运效率并加速糖类代谢, 从而增强花粉对高温的耐受能力(Rezaul et al., 2018)。

花粉作为有性生殖过程中光合产物重要的“库”, 其淀粉含量通常在二细胞花粉期达到最高值, 而可溶性糖的含量在散粉期达到最高值。积累的糖类物质不仅为花粉发育和花粉管形成提供能量, 也可以作为渗透物质提高花粉对胁迫的响应。通过比较不同的番茄品种可以发现, 耐高温品种的花粉中含有更多的淀粉和可溶性糖(Pressman et al., 2002; Firon et al., 2006), 而其它渗透调节物质(如甜菜碱和脯氨酸)以及次生代谢产物等也会影响花粉对高温胁迫的应答(Sangu et al., 2015; Qi et al., 2018)。

综上, 在应对高温胁迫时, 花粉至少可以通过4种机制感受高温信号并利用多种机制响应胁迫, 这些机制和途径之间也存在“交叉对话”。例如, 内流的钙离子可以参与多个途径; ROS可以影响UPR; ABA则影响糖类代谢; 而糖信号通路又可以影响ROS的平衡。这些机制之间的相互作用也增加了花粉高温胁迫研究的复杂性(图2) (Couée et al., 2006; Kotak et al., 2007)。

3 花粉高温胁迫研究的实验设计

在进行花粉高温胁迫研究时, 需要考虑胁迫温度、处理方式以及花粉取材时期。首先需要选择合适的温度处理范围, 不同的温度处理会产生不同的结果。温和高温可以使植物获得高温耐受能力, 严重高温则直接破坏植物细胞, 导致植株不可逆损伤甚至死亡。通过

总结常见作物的花粉高温胁迫研究,发现常见作物的高温胁迫温度通常选择30–39°C。尽管番茄花粉高温胁迫研究也有选择45°C高温的情况,但处理时间相对较短(Zinn et al., 2010; Fragkostefanakis et al., 2015; Mesihovic et al., 2016; Arshad et al., 2017)。其次,还需考虑胁迫施加的方式(Mesihovic et al., 2016)。对植物直接施加高温(direct applied heat stress, DAHS),主要用来研究植物的基础高温胁迫耐受性(basal thermo tolerance, BTT)。如果在对植物施加高温处理前先预施加一个温和高温(pre-induction heat stress, PIHS),则主要用于研究植物获得性高温胁迫耐受性(acquired thermotolerance, ATT)。例如,在番茄花粉的ATT研究中,可以将花粉32°C预处理1小时,然后置于25°C恢复1小时,最后再于50°C的高温条件下进行处理。也可以利用温和高温(30–36°C)对植物处理几周甚至几个月,这种处理方式被称为温和的慢性高温处理(mild chronic heat stress, MCHS),可以引起植物产生温和高温胁迫耐受性(mild heat thermotolerance, MHTT)。由于MCHS处理方式可以更好地模拟大气环境中温度的变化并覆盖花粉整个发育阶段,更有利于人们对花粉发育的各个时期的发育状态和生理指标进行监测,因此已成为花粉高温处理的主要方式(Mesihovic et al., 2016)。

在设计花粉高温胁迫相关实验时,还需要考虑花粉所处的发育阶段。不同发育阶段的花粉对高温胁迫的敏感性和响应机制可能不同。在实际研究中,通常把花粉发育过程分为4个阶段:(1)花粉母细胞到四分体时期;(2)小孢子形成到早期的二细胞时期;(3)二细胞末期/三细胞期到成熟花粉期;(4)花粉萌发期。目前,可以通过一些形态指标对常见作物花粉发育阶段进行判断。例如,水稻花粉的发育阶段可以通过花芽长度进行判断;而玉米花粉的发育阶段则可以通过茎秆的叶领(leaf collar)数进行判断(Zhang et al., 2011; Begcy and Dresselhaus, 2017)。只有选择合适的花粉发育时期,采用合适的高温处理方式,才可以得到更加准确的实验结果。

4 总结与展望

研究作物花粉高温胁迫应答机制并提高作物花粉的高温耐受能力,对于稳定和提高作物产量具有重要意义。

目前,人们已对高温导致的花粉败育进行了系统的形态学观察和多种组学分析,并且已鉴定到一些参与花粉高温胁迫响应的因子,但对于花粉高温胁迫应答调控机制的认知仍然有限(De Storme and Geelen, 2014)。已知钙离子信号通路、激素水平、糖代谢以及活性氧压力都参与花粉的高温胁迫应答,并且它们之间存在相互作用。此外,表观遗传机制在植物高温胁迫响应过程中也发挥重要作用(Chen et al., 2016)。研究表明,高温胁迫可以引起花粉细胞热激蛋白编码基因甲基化水平的改变(Solís et al., 2012);染色质构型和各种sRNA的表达均参与花粉的高温胁迫响应(Pecinka and Scheid, 2012; Bokszyzanin et al., 2015; Chen et al., 2016)。但是对于表观机制具体如何调控花粉的高温胁迫响应,以及花粉是否可以将遭受的高温胁迫“表观印迹”传递到子代,目前仍有争议,需要深入研究(Lang-Mladek et al., 2010; Migicovsky et al., 2014)。

尽管目前对花粉高温胁迫响应机制认识有限,但是随着各种组学技术、全基因组关联分析(genome-wide association study, GWAS)和CRISPR-Cas9等基因编辑技术在花粉高温胁迫研究中的应用(Paupière et al., 2014; Xing et al., 2014; Chaturvedi et al., 2015; Kim et al., 2015; Xu et al., 2017),未来研究者们可以更好、更全面地解析高温胁迫下花粉生理生化及分子水平的变化,并从中选择重要的调节基因进行功能研究,最终为作物耐高温分子育种提供指导。

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Advances in the Regulatory Mechanisms of Pollen Response to Heat Stress in Crops

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Abstract As a consequence of global warming, crops face more acute and more frequent high-temperature stress. Heat threatens the whole plant development, especially pollen development, which seems to be the most sensitive process in the plant life cycle. Hence, the mechanism underlying the pollen response to heat stress has become a hot topic in the field of plant biology. Recent studies have revealed that pollen has at least 4 ways to perceive the heat stress signal: calcium channels, unfolded protein response, reactive oxygen species and H₂A.Z. Pollen responds to heat stress by regulating heat shock protein expression, glycol-metabolism and phytohormone level and enhancing reactive oxygen species scavenging capacity. In this review, we summarize pollen development defects under heat stress, the mechanism of pollen thermotolerance and discuss how to design the experiments to study pollen thermotolerance. The overview provides guidelines for the pollen heat response mechanism in crops.

Key words crop, pollen, heat, response mechanism

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