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MAPK 级联途径参与 ABA 信号转导调节的植物生长发育过程

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摘　要：植物激素 ABA 参与调控植物生长发育和生理代谢以及多种胁迫应答过程，促分裂原活化蛋白激酶(MAPK)级联途径应答于多种生物和非生物胁迫，广泛参与调控植物的生长发育。MAPK 级联途径与 ABA 信号转导协同作用参与调控植物种子萌发、气孔运动和生长发育，本文主要归纳了植物中受 ABA 调控激活的 MAPK 级联途径成员，阐述了它们参与 ABA 信号转导调控植物生理反应和生长发育的过程，并对 MAPK 级联途径与 ABA 信号转导的研究方向作出了展望，指出对 MAPK 下游底物的筛选是完善 MAPK 级联途径的重要组成部分。

关键词：促分裂原活化蛋白激酶(MAPK)级联途径；脱落酸(ABA)；信号转导；拟南芥

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Roles of Mitogen-activated Protein Kinase Cascades in ABA Signaling Regulation of Plant Development

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Abstract: The plant hormone abscisic acid (ABA) plays a pivotal role in a variety of developmental processes and adaptive stress responses to environmental stimuli in plants. Mitogen-activated protein kinase (MAPK) cascades are key signaling modules for responding to various biotic and abiotic stresses in plants. MAPK cascades are involved in ABA signaling in seed germination, stomatal movement, plant growth and development. We summarized the ABA-induced gene expressions and protein kinases activation of components in the MAPK cascades pathway, as well as the regulation of MAPK cascades implicated in ABA signaling. We also discuss research prospects of the roles played by MAPK cascades in ABA signaling, and the screening of MAPK substrates in the study of MAPK cascade responses to various stimuli.

Key words: MAPK cascade; Abscisic acid; Signaling transduction; *Arabidopsis thaliana*

促分裂原活化蛋白激酶(Mitogen-Activated Protein Kinase，MAPK)是一类广泛存在于真核生物中的丝氨酸/苏氨酸蛋白激酶。与动物和酵母中的 MAPK 类似，植物中的 MAPK 级联途径也是由 MAPKs、MAPKKs、MAPKKKs 三种类型的激酶组成；MAPKKKKs 存在于 MAPKKKs 上游，且能磷酸化激活 MAPKKKs，MAPK 家族成员的识别与分类主要取决于激酶的功能和进化关系。目前已经从植物中鉴定了一些 MAPKs、MAPKKs 和 MAPKKKs，它们广泛参与调节植物激素、生物胁迫及非生物胁迫过程的信号传导，存在于植物生长发育的各个时期。

为了响应发育周期和环境刺激的信号，植物基因组长期的进化产生了许多细胞内的信号转导途

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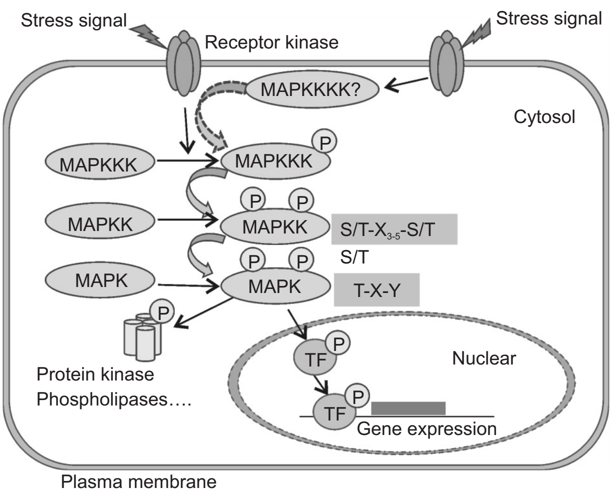
径，而磷酸化作为蛋白修饰的一种方式，是重要的信号转导模式，其中 MAPK 级联途径是高度保守的，是将信号传递到细胞内引起胞内应答反应的一种信号转导方式。拟南芥 MAPKKK-MAPKK-MAPK 信号级联途径的三个组分是由多个基因家族编码的，且许多基因的同源性较高，因此有些基因的功能是冗余性的，表现为一个 MAPKK 激活多个 MAPKs，或者多个 MAPKKs 激活同一个 MAPK[1,2]，说明参与 MAPK 信号级联途径的组分可能有多重组合方式，这些复杂的组合方式增加了研究 MAPK 信号转导机制的难度，而且信号的交联激活作用使部分 MAPK 信号转导失去了特异性[3]。信号传导的特异性取决于参与信号传导组分的组织表达定位，即在细胞中定位的器官是否相同，上下游蛋白之间能否相互作用[1]。同时，信号转导的特异性也与上游传递信号组分的特异性、空间分布及形成的多酶复合体等有关[4]。

MAPK 级联途径信号转导的一般模式为：在应答外在环境刺激时，质膜上的 MAPKKKs 或 MAPKKKKs 被激活，活化的 MAPKKKs 通过磷酸化激活 MAPKKs，而 MAPKK 通过磷酸化 MAPKs 传递信号，然后 MAPK 再磷酸化下游靶蛋白或转录因子，从而调控植物生长发育[5]（图 1）。MAPKKKKs 是将外界刺激信号传递给 MAPK 级联途径



MAPKKKK：Mitogen-activated protein kinase kinase kinase kinase；MAPKKK：Mitogen-activated protein kinase kinase kinase；MAPKK：Mitogen-activated protein kinase kinase；MAPK：Mitogen-activated protein kinase；TF：Transcription factor.

图 1 磷酸化介导的 MAPK 级联途径信号传递模式图

Fig. 1 Model of phosphorylation-dependent MAPK cascade

的转接器，MAPKKKs 是苏氨酸/丝氨酸蛋白激酶，能够磷酸化 MAPKK 激活区域的 S/T-X_{3-5}-S/T（S 为丝氨酸，T 为苏氨酸，X 为其它氨基酸）元件上的丝氨酸与苏氨酸，而 MAPKs 响应不同刺激对底物的不同选择是 MAPK 信号转导特异性的又一因素。MAPKs 激活区域中，保守 T-X-Y（Y 为酪氨酸）基序上的苏氨酸和酪氨酸能被 MAPKKs 磷酸化激活[6]，依据 T-X-Y 基序序列的不同，MAPK 被分为四类，其中三类含有 T-E-Y（E 为谷氨酸）基序，另一类含 T-D-Y（D 为天冬氨酸）基序。MAPKs 能磷酸化下游激酶或转录因子，完成外界刺激信号向核内的传递过程，从而响应外界刺激。

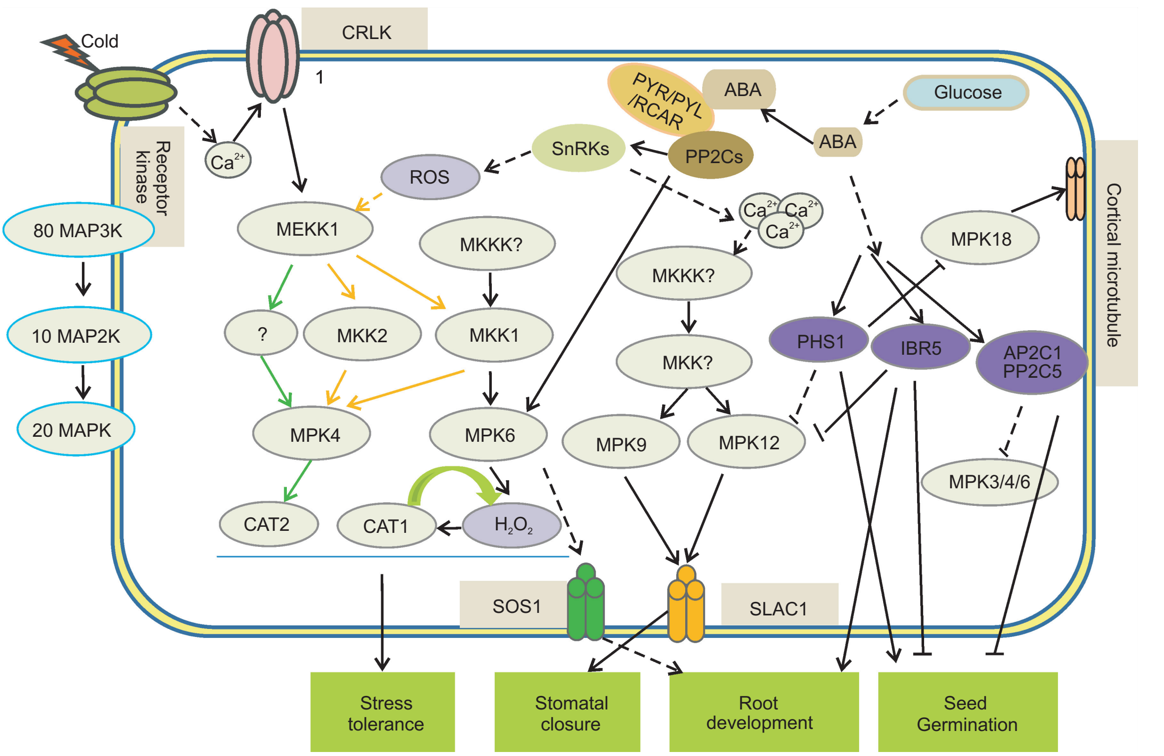
在植物中，MAPK 信号级联途径能被多种生物胁迫和非生物胁迫因素激活，非生物胁迫包括：冷、盐、触摸、创伤、紫外光、高温、渗透胁迫和重金属等。本文主要介绍植物 MAPK 级联途径参与 ABA 信号转导，它们协同作用调控植物的生长发育过程。

1 植物 MAPK 级联途径的组分在转录水平受 ABA 调控

目前发现的 ABA 受体（ABA Receptor，ABAR）有 PYR/PYL/RCARs（Pyrabactin Resistance，PYR；PYR1-like，PYL；Regulatory Component of ABA Receptor，RCAR），它们是植物中 ABA 信号网络的核心调节组分，参与信号转导早期对 ABA 的感知过程。即 ABA 与 ABAR 结合并改变 ABAR 的构象，然后与 PP2C（type 2 C Protein Phosphatases）结合形成三元复合体，抑制 PP2C 蛋白磷酸酶的活性，从而使 PP2C 抑制的 SnRK2s（SNF1-Related Protein Kinases）能够自磷酸化。自磷酸化的 SnRK2s 可通过调控 NADPH（β-Nicotinamide Adenine Dinucleotide 2’-Phosphate Reduced Tetrasodium Salt）氧化酶和离子通道的活性来调控植物许多基因的表达和蛋白激酶的活性；还可通过调节含有亮氨酸拉链（basic leucine Zipper，bZIP）结构的 ABA 应答转录因子（Transcription Factors，TFs）的表达水平[7,8]。

ABA 信号转导所调控的蛋白激酶中，有很多参与了 MAPK 级联途径，表明 MAPK 级联途径在

ABA 信号转导中起重要的调控作用(图 2)。很多研究发现，MAPK 级联途径参与植物多种 ABA 应答的调控，如种子萌发、气孔运动和抗氧化胁迫等[9-12]。拟南芥中约有 10%基因的转录水平受 ABA 调控[13]，其中参与 MAPK 级联途径的基因有 *MPK3*、*MPK5*、*MPK6*、*MPK7*、*MPK18*、*MPK20*、*MAPKKK10*、*MAPKKK14*、*MAPKKK15*、*MAPKKK16*、*MAPKKK17*、*MAPKKK18*、*MAPKKK19*、*Raf6*、*Raf12*、*Raf35*[14,15]。水稻中也发现了转录水平受 ABA 调控的类似基因，如 *OsMPK2*(*Oryza sativa*)、*OsMPK5*、*OsMSRMK2*(Multiple Stress Responsive MAP Kinase)、*OsMSRMK3*、*OsBIMK1*(Benzothiadiazole-induced MAP Kinase 1)、*DMS1*(Deffective in Meristem Silencing 1)、*OsEDR1*(Enhanced Disease Resistance 1)、*OsMPK44*、*OsSIPK*(Salicylic acid-induced Protein Kinase)、*OsWJUMK1*(Wound and JA-uninducible MAP Kinase)、*OmMKK1*(*Oryza minuta*)[16-29]，其中 ABA 诱导的 *OsMPK5* 在非生物胁迫中起正调控作用，而在广谱抗病性和抗病基因的表达上起负调控作用[23]。玉米 *ZmMPK3*(*Zea mays*)、*ZmMPK7*、*ZmMPK17*、*ZmSIMK1*、*ZmMKK3* 的表达受 ABA 诱导[11,30-32]，同时在其它植物中也发现有 MAPK 级联途径的组分被 ABA 诱导，如 *CbMPK3*(*Chorispora bungeana*)、*CsNMPK*(*Cucumis sativus* L. ‘Xintaimici’)、*AhMPK3*(*Arachis hypogaea*)、*BnOIPK*(*Brassica napus*)、*BnMPK3*、*MdMPK1*(*Malus domestica* Borkh. ‘Golden Delicious’)、*RaMPK1*(*Rheum australe*)、*RaMPK2*、*RsMPK2*(*Reaumuria soongorica*)、*StMPK1*(*Solanum tuberosum*)及桑树的 9 个 *MnMPKs*(*Morus* sp.)[33-41]。另外，在烟草中超表达棉花 GhMKK4(*Gossypium hirsutum*)增强了烟草植株对 ABA 的敏感性[42]。在不同植物中发现的类似于MAPK级联途径成员也受ABA诱导，



CRLK：Calmodulin-regulated receptor-like kinase；MAP3K/MKKK/MEKK：Mitogen-activated protein kinase kinase kinase；MKK：Mitogen-activated protein kinase kinase；MPK/MAPK：Mitogen-activated protein kinase；CAT：Catalase；ROS：Reactive oxygen species；PP2C：Type 2 C protein phosphatases；PYR：Pyrabactin resistance；PYL：PYR1-like；RCAR：Regulatory component of ABA receptor；SnRK2s：SNF1-related protein kinase；SLAC1：Slow anion channel-associated 1；SOS1：Salt overly sensitive 1；PHS1：Propyzamide-hypersensitive 1；IBR5：Indole-3-butyric acid response 5；AP2C1：Clade B of the PP2C-superfamily member.

图 2　拟南芥 MAPK 级联途径参与 ABA 信号转导调控模式图

Fig. 2　General schematic presentation of MAPK cascade involved in regulating ABA signaling transduction

表明 MAPK 级联途径可能广泛参与 ABA 应答的各种生理反应的调控。目前，对这些在转录水平受 ABA 调控的 MAPK 级联途径中的基因及功能已有部分报道，但许多激酶的功能和它们受 ABA 信号转导调控的机制还知之甚少。

2 ABA 能激活植物 MAPK 级联途径中的蛋白激酶

植物 MAPK 级联途径的很多组分受 ABA 诱导，目前已经发现了一些活性受 ABA 激活的蛋白激酶，参与调控 ABA 应答的不同生理过程[9,10,43,44]。如 ABA 激活大麦糊粉层原生质体中一些分子量为 40 ~ 43 kD 的 MAPK 激酶[45]，苔藓 PK38 和 PK46[46]，还有玉米的 ZmMPK5[44,47,48] 被 ZmCPK11(Calcium Dependent Protein Kinase 11)激活，参与 ABA 诱导的抗氧化防御反应[49]；在豌豆中发现 PsMAPK(*Pisum sativum*)受 ABA 激活并参与保卫细胞信号转导的调控[50,51]；水稻 OsMPK5 受 ABA 激活并参与植物对病害和非生物胁迫抗性的调控[23]。

在拟南芥中已经发现多种 MAPK 受 ABA 激活，如 MPK4 和 MPK6 受不同的外界信号刺激激活，参与调控不同的信号转导途径，其中包括 ABA 信号转导途径[52]；MPK3 同时受 ABA 和过氧化氢(H_2O_2)激活，参与种子的萌发和生长发育的调控[43]；MPK6 受 ABA 激活依赖于 MKK1，它通过调节 *CAT1*(Catalase 1, CAT1)基因的表达调控植物活性氧的稳态；两种在保卫细胞中表达的 MAPK(MPK9 和 MPK12)受 ABA 激活，参与 ABA 对气孔运动的调控过程[9]；与 MAPK 互作的负调控因子 PP2C5 和 AP2C1(clade B of the PP2C-superfamily)，参与 ABA 激活 MPK3 和 MPK6 活性的调控[53]；MPK1 和 MPK2 受 ABA 激活参与植物对免疫反应的调控[54,55]。

3 MAPK 级联途径参与 ABA 信号转导的调控

植物激素 ABA 参与许多生理过程，包括胚的发育、种子休眠与萌发、植物适应水分胁迫和根系的形态建成等。对豌豆表皮细胞上气孔的研究中发现，MAPK 的抑制剂 PD98059 能降低 ABA 诱导的气孔关闭效应，表明 ABA 参与了 MAPK 级联信号途径[50]。

拟南芥中 MPK3 能被 ABA 和过氧化氢激活，从而调控气孔运动。*MPK3* 的 RNAi 转基因沉默植株中 ABA 刺激产生过氧化氢，但气孔张开受过氧化氢和 ABA 抑制相对于野生型拟南芥不敏感，而 ABA 处理下表现正常的气孔关闭表型，表明 MPK3 参与了保卫细胞中的 ABA 信号转导，位于过氧化氢下游[56]。拟南芥中编码过氧化氢酶的基因有 3 个：*CAT1*、*CAT2* 和 *CAT3*[57]，ABA 能诱导 *CAT* 基因的表达；*mkk1* 突变体丧失了 ABA 诱导叶片 *CAT1* 和 *CAT3* 基因表达的功能，同时 *CAT2* 基因也不能响应 ABA 的诱导表达，致使 *mkk1* 突变体的种子萌发和气孔运动受 ABA 抑制的敏感性减弱；超表达 *MKK1* 能显著增强植物体内 *CAT1* 的表达水平和过氧化氢的产生。MPK6 受 ABA 激活，但 MPK6 受 ABA 激活的活性在 *mkk1* 中受到抑制，表明 MKK1-MPK6 的级联途径参与了 ABA 诱导的过氧化氢积累过程，从而调节种子萌发和植物抗逆性[9, 58]。有趣的是，*CAT1* 在 *mpk4* 突变体中受 ABA 诱导表达，而 MEKK1-MKK1/2-MPK4 级联途径在植物抗病原菌侵害中与维持活性氧稳态有关[59–62]，因此 ABA 激活的 MKK1-MPK6 级联途径与 H_2O_2 激活的 MKK1-MPK4 级联途径受不同的 MAPKKK 激活，处于不同的信号通路中。在 *mpk4* 突变体中 *CAT2* 的表达量下调，*CAT1* 和 *CAT3* 的表达量无明显变化，而在 *mkk1/mkk2* 双突变体中 *CAT2* 的表达量没有变化[61]，表明三种过氧化氢酶受两种不同的 MAPK 级联途径调控。

拟南芥中 *mpk9/mpk12* 双突变体表现出失水快，气孔运动对 ABA 和 H_2O_2 不敏感，其调控机制与保卫细胞中几丁聚糖调节的气孔关闭有关[10,63]，表明 MPK9/12 是保卫细胞中 ABA 信号传导的正调控因子。MPK9/12 的活性受钙离子螯合剂的抑制，表明 MPK9/12 处于钙离子的下游；MPK9/12 激活 ABA 信号转导中的关键成分 SLAC1(Slow Anion Channel-Associated 1)[10]，但两者(MPK9/12 与 SLAC1)之间的具体调控机制尚不清楚。ABA 在气

孔对细菌入侵的先天免疫反应中起调节作用，研究发现 MPK3/6 和 SA(Salicylic Acid)参与 flag22 引起的气孔关闭调节，而 MPK9/12 与 OST1(Open Stomata 1)在此过程中的 ABA 信号转导中起调节作用[64]。此外，MPK6 能激活 Na^+/H^+ 反向运输体 SOS1(Salt Overly Sensitive 1)[65]，钙离子依赖蛋白激酶 CPK3/6 可能与 MAPK 途径共同调节气孔运动[66-69]，MPK6 可能通过影响钙离子依赖的 SOS1 活性调控拟南芥根系的形态建成[70]。

MKPs(MAPK phosphatases)是一类对 MAPK 级联途径起负调控作用的蛋白磷酸酶。拟南芥中已经发现了 5 种 MKPs，其中 PHS1(Propyzamide-Hypersensitive 1)能与 MPK18 相互作用，调控皮层微管的稳定性[71]；突变体 *ph1-3* 的种子萌发对 ABA 不敏感[72]，表明 *PH1-3* 可能参与了 ABA 信号转导和 MAPK 级联途径的调控；蛋白磷酸酶 IBR5(Indole-3-Butyric Acid Response 5)对 ABA 抑制的种子萌发和根生长不敏感[73]，它能与 MPK12 相互作用并使其去磷酸化[74]，表明 IBR5 负调控 MAPK 级联途径，参与 ABA 信号转导的调节。除了 MKPs 类的蛋白磷酸酶，PP2Cs 类的蛋白磷酸酶也参与 MAPK 级联途径的调控，其中 ABI1(ABA Insensitive 1)能与 MPK6 相互作用[75]，但其调控机制还不清楚；PP2C5 能与 MPK3/4/6 相互作用，*pp2c5* 突变体中 MPK3/6 活性因受 ABA 激活而增强[53]；AP2C1 与 PP2C5 的同源性很高，它们的单突变体都表现出气孔开度大和种子萌发对 ABA 不敏感的特性[53]。

4　展望

ABA 除了应答植物对生物和非生物胁迫外，还参与植物生长发育的很多过程，包括种子的发育，调节种子的干燥、休眠和萌发，幼苗的发育，营养生长和增殖。促分裂原活化蛋白激酶级联途径是植物长期进化中保守的信号传导方式，它通过 MAPKKK-MAPKK-MAPK 的级联效应广泛参与植物对各种生物胁迫和非生物胁迫的应答，从而将外界的刺激传递到细胞内，激活下游激酶或调控转录因子，调控植物的生长发育。基因表达分析和酶活性检测表明，MAPK 级联途径参与 ABA 信号转导并与其协同作用，应答各种非生物胁迫和调节植物的生长发育。然而，由于 MAPK 级联途径的基因家族成员较多，基因功能的冗余性和其信号转导的收敛和发散形式，限制了研究 MAPKs 信号级联途径的进程；同时，ABA 信号转导的组分多为多基因家族成员，基因功能的冗余性限制了 ABA 信号转导的研究进展；磷酸化作用是 MAPK 级联途径与 ABA 信号转导共同的信号传递方式，然而，参与 ABA 信号转导的蛋白磷酸酶、蛋白激酶与 MAPK 级联途径的蛋白激酶间的关系如何，目前还知之甚少。

MAPK 下游的激活底物差别很大，一个 MAPK 可能有多个底物，不同的底物受不同的刺激激活，因此，对 MAPK 下游底物的筛选是完善 MAPK 级联途径的任务之一。目前研究已经表明，MAPK 级联途径与 ABA 信号转导协同调控植物种子萌发、气孔运动和根的生长发育，MAPK 级联途径以 ABA 依赖与非依赖的方式调控气孔运动，一些信号分子如一氧化氮和过氧化氢参与 MAPK 级联途径调控的气孔运动，但其具体的调控机制还不清楚。MAPK 级联途径的抑制因子 PHS1、IBR5 等受 ABA 信号转导调控，使 MAPKs 去磷酸化，但它们在 ABA 信号转导中的功能还是未知的，各种刺激因素是否调节 MAPK 上游参与磷酸化传递的 MAPKKK 和 MAPKK，下游底物有哪些等，这些问题都需要更多的研究来解答。

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