

## 综述 Review

## MAPK级联途径激酶结构特点及其信号转导途径在园艺作物逆境中的作用

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**摘要:** 促分裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK)是一类受胞外刺激、通过MAPK级联反应(MAPKKK-MAPKK-MAPK)而激活的丝氨酸/苏氨酸蛋白激酶。MAPK级联途径是真核生物中广泛存在且高度保守的信号转导途径, 通过蛋白质磷酸化作用将上游信号级联放大传递至下游应答分子。该途径在植物应对各种生物与非生物胁迫以及激素信号转导过程中起关键作用。本文着重介绍MAPK级联途径激酶结构特点及其信号转导途径在园艺作物逆境胁迫中的应答反应, 以期为该领域的相关研究提供参考。

**关键词:** MAPK级联途径; 信号转导; 生物胁迫; 非生物胁迫; 激素信号

植物在生长发育周期中, 经常遭受非生物胁迫(低温、干旱、盐渍等)及生物胁迫(病、虫、草害等)的影响, 这些逆境胁迫通常会造成一定程度上的细胞损伤, 进而影响植物的生长发育、产量及品质。因此, 研究植物在逆境胁迫下造成的伤害及应答机制对于提高植物的抗逆性具有重要意义(Chen等2012)。

MAPK级联途径包括促分裂原活化蛋白激酶激酶激酶(mitogen-activated protein kinase kinase kinase, MAPKKK或MAP3K或MEKK), 促分裂原活化蛋白激酶激酶(mitogen-activated protein kinase kinase, MAPKK或MAP2K或MKK或MEK)和促分裂原活化蛋白激酶(mitogen-activated protein kinase, MAPK或MPK)三组成员, 是真核生物中广泛存在且高度保守的信号转导途径, 参与植物细胞分化与发育(Takahashi等2010; Zhao等2013; Zhang等2018)、成熟、激素信号转导(Kieber等1993; Bari和Jones 2009; de Zelicourt等2016)及免疫等过程(Asai等2002; Genot等 2017; Devendrakumar等2018); 同时, 响应多种生物与非生物胁迫(Shitamichi等2013; Meng和Zhang 2013; Çakır和Kılıçkaya 2015; Zhu 2016)。其中, 促分裂原活化蛋白激酶(MAPK)是一类受胞外刺激, 通过MAPK级联反应(MAPKKK-MAPKK-MAPK)而激活的丝氨酸/苏氨酸蛋白激酶, 通过蛋白质磷酸化作用将上游信号级联放大传递至下游应答分子, 从而激活抗逆基因的表达, 使植物对逆境有一定的适应能力。

近年来, 随着园艺作物基因组测序的相继完

成, MAPK级联途径基因家族成员已被先后鉴定出来, 发现MAPK级联反应途径三组成员的基因数量为MAPKKK>MAPK>MAPKK (表1)。同时, 随着RNA干扰(RNA interference, RNAi)技术、病毒诱导基因沉默(virus induced gene silencing, VIGS)技术和其他技术的运用以及基因功能获得型与基因功能缺失型突变体的获得, MAPK级联途径在植物逆境胁迫应答和激素信号转导等几个方面功能得到了进一步确定。伴随着酵母双杂交(yeast two-hybrid)、双分子荧光互补(bimolecular fluorescence complementation, BiFC)、免疫共沉淀(Co-immunoprecipitation, Co-IP)和cDNA文库构建等技术的完善, 进一步揭示了MAPK级联途径激酶之间在蛋白水平上的互作关系(于太飞等2014)。本文着重介绍MAPK级联途径激酶结构特点及其信号转导途径在园艺作物逆境胁迫中的应答响应, 以期为该领域的相关研究提供参考。

## 1 MAPK信号转导途径激酶的蛋白结构特点

### 1.1 MAPKKKK基因家族的蛋白结构特点

典型的MAPK级联反应途径由MAPKKK、MAPKK和MAPK组成。然而, 通过生物信息学分析发现, 有些植物MAPKKK是被MAPKKKK磷酸化并激活, 并非都是由细胞膜上的受体蛋白激活。

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表1 主要模式作物及园艺作物中MAPK级联反应途径激酶基因家族成员数量

Table 1 Number of kinase genes in the main model crops and horticultural crops MAPK cascades

植物	MAPKs数量/个	MAPKKs数量/个	MAPKKKs数量/个			参考文献
			MEKK	Raf	ZIK	
拟南芥( <i>Arabidopsis thaliana</i> )	20	10	21	48	11	Jonak等2002 Colcombet和 Hirt 2008
烟草( <i>Nicotiana tabacum</i> )	17	—	—	—	—	张兴坦2015
棉花( <i>Gossypium</i> spp)	21	11	22	44	12	Yin等2013 Zhang等2016
苹果( <i>Malus domestica</i> )	26	9	33	72	11	Zhang等2013 Sun等2017
葡萄( <i>Vitis vinifera</i> )	12	5	9	48	9	Wang等2014; 王刚2014
番茄( <i>Lycopersicon esculentum</i> )	16	6	33	40	16	王洁2015
黄瓜( <i>Cucumis sativus</i> )	14	6	18	31	10	Wang等2015
西瓜( <i>Citrullus lanatus</i> )	15	6	—	—	—	Song等2015
油桃( <i>Prunus persica</i> var. <i>nectarina</i> )	15	8	—	—	—	杜培勇等2016
香蕉( <i>Musa nana</i> )	25	10	14	48	15	Wang等2017b
草莓( <i>Fragaria</i> × <i>ananassa</i> )	12	7	30	43	0	Zhou等2017

“—”表示尚无相关基因数量的报道。

MAPKKKK可分为Gck、Mst、Tao、Sok、PAK-related、Ste/PAK等8个亚族(Champion等2004)。此外,在系统关系树中观察到MAPKKK和MAPKKKK子家族包含了许多不在MAPK模块中心核心功能的成员(Qi和Elion 2005)。因此对于MAPKKKK的命名指的是MAPKKK和MAPKKKK系统基因上的相似性,而不一定是生物化学功能上的相似性。植物中绝大多数的MAPKKKK均具有N末端催化结构域;而且,通过对MAPKKKK的激酶结构域分析发现,有些植物MAPKKKK的激酶结构域位于序列中央(Dan等2001)。利用生物信息学分析推测MAPKKKK在第VII和第VIII结构域之间存在与MAPKK相同的磷酸化位点S/T-XXXXX-S/T(S: 丝氨酸; T: 苏氨酸; X: 任意氨基酸)(Qi和Elion 2005; Champion等2004),其保守结构域为TFVGT-PxWMAPEV(Jonak等2002)。现已从葡萄中鉴定出7个MAPKKKK基因(Wang等2014),草莓中鉴定出1个MAPKKKK基因(Zhou等2017),但其基因功能尚无相关报道。

### 1.2 MAPKKK基因家族的蛋白结构特点

MAPKKK是一类丝氨酸/苏氨酸激酶,能通过对下游MAPKK活化环S/T-XXXXX-S/T基序中丝氨酸/苏氨酸残基的磷酸化激活MAPKK。根据其

激酶催化功能域的分析,可将植物中的MAPKKK分成MEKK亚族、Raf亚族和ZIK亚族,其保守结构域分别为FG(T/S)Px(W/Y/F)MAPEV、GTxx(W/Y)MAPE和GTPEFMAPE(L/V)(Y/F)(Dan等2001; Singh等2014; Çakır和Kılıçkaya 2015; Jiang等2015; Wang等2015),其中MEKK亚族的蛋白质结构保守性与ZIK亚族和Raf亚族相比相对较低(Qi和Elion 2005)。在葡萄中,Raf亚族和ZIK亚族在C端具有激活域(kinase domain, KD),在N端具有调节域(regulatory domain, RD),研究表明RD可能在招募下游激酶的搭架过程中起到一定作用(Wang等2014)。在苹果中,几乎所有的Raf亚组成员均在C端具有激活域,在N端具有调节域;大部分ZIK亚族成员在N端具有激活域;MEKK亚族的激活域则有可能在N端、C端或中央(Sun等2017)。在黄瓜中,泛素结构域和ACT结构域仅分别存在于CsRAF4和CsRAF37中,可以广泛调节受氨基酸调控的相关酶活代谢反应(Wang等2015)。

### 1.3 MAPKK基因家族的蛋白结构特点

MAPKK是一类双特异性蛋白激酶,位于MAPK级联信号系统的中枢位置。能够被上游MAPKKK磷酸化激活,进而通过对MAPK活化环中T-X-Y(T: 苏氨酸; Y: 酪氨酸; X: 任意氨基酸)基序的苏氨酸/

酪氨酸残基的磷酸化激活MAPK。根据MAPKK高度保守的磷酸化位点S/T-XXXXX-S/T序列和CD位点, MAPKK被分成A、B、C、D 4个亚族, 其催化区域氨基酸序列为VGE<sub>xx</sub>YMSPER (Çakır和Kılıçkaya 2015)。

#### 1.4 MAPK基因家族的蛋白结构特点

MAPK是一类混杂的丝氨酸/苏氨酸激酶, 位于MAPK级联信号系统的下游, 可以磷酸化多种底物。研究发现, 其激酶结构具有11个亚结构域(I~XI), 是丝氨酸/苏氨酸蛋白激酶发挥催化作用所必需的(Garrington和Johnson 1999; Chang和Karin 2001; Nakagami等2006; Rodriguez等2010; Kumar等2016)。MAPK在第VII和第VIII亚结构域之间含有一个高度保守的T-X-Y活化环, TXY基序在结构上也被称为“T环结构”(T-loop), 是被MAPKK磷酸化的基序, 是决定MAPK活性的关键部位(Zhang等2014)。根据T-X-Y序列, 可将MAPK分为2个亚组TEY和TDY。其中TEY可进一步分成A类、B类和C类, 目前对于D类的TDY亚组的功能研究较少(Champion等2004; Liang等2013)。有些MAPK还含有CD (common docking domain)结构域, 其保守序列为(LH)DXXDE(P)X。通过生物信息学方法分析了40个植物中的589个MAPK基因, 发现存在一些新的活化环基序, 如*OsMPK2*、*BdMPK11*及*SIMP6*的保守位点则是MXY (Kumar等2016)。在烟草中*NtMPK4*的同源基因*NtMPK4-like* (*NtMPK4L*)基因的保守位点为MEY, 利用基因沉默技术获得的*NtMPK4L*转基因植株发现其叶片气孔张开的数量显著高于对照, 蒸腾速率加快, 且对臭氧高度敏感, 完全失去了在臭氧胁迫下的气孔关闭能力(Lyu等2015; Yanagawa等2016)。因此推测烟草*NtMPK4L*的保守位点为MEY在臭氧耐受性及气孔关闭调节中起作用。

## 2 MAPK信号转导途径在逆境胁迫中的功能

植物在生物或非生物胁迫下, 呼吸爆发同源氧化酶(respiratory burst oxidase homolog, Rboh), 也称为NADPH氧化酶, 可以诱导生成细胞外的超氧阴离子。超氧阴离子通过歧化酶形成过氧化氢(H<sub>2</sub>O<sub>2</sub>), 同时胞外过氧化氢也可以由过氧化物酶(peroxidase, PRX)或O<sub>3</sub>生成。过氧化氢作为信号物质可以通过水通道蛋白进入细胞。在细胞内,

H<sub>2</sub>O<sub>2</sub>触发活性氧(reactive oxygen species, ROS)信号和响应, 从而干扰ROS稳定。其中含有胁迫作用时间点依赖激活激酶、胁迫作用强度依赖激活激酶和胁迫作用持续时间依赖激活激酶, 3种不同激酶的不同组合可能决定了植物体内前馈或反馈的结果。MAPK信号通路作用于受体蛋白激酶(receptor-like protein kinases, RLKs)和ROS信号的下游, 以调节与ROS相关的基因表达和细胞程序性死亡(programmed cell death, PCD) (图1) (Liu和He 2017)。

### 2.1 MAPK级联途径参与调控植物生物胁迫下的信号转导

植物在整个生长发育过程中, 经常会被细菌、真菌和病毒侵害。在长期的进化过程中, 形成了多种先天免疫机制(Jones和Takemoto 2004), 诸如细胞程序性死亡、细胞壁的加厚、病程相关蛋白(pathogenesis-related protein, PR)的合成、活性氧的猝发以及防卫基因转录的激活等抵御侵害机制。一般植物的先天免疫系统主要有两个分支: 病原相关分子模式激发的免疫(PAMP-triggered immunity, PTI)和病原菌效应因子触发的免疫(effector-triggered immunity, ETI) (Jones和Dangl 2006)。病原体可以通过抑制宿主免疫系统从而入侵并侵染宿主, 其中细菌性病原体可以通过分泌效应因子抑制防御信号通路(Schechter等2006), 而真菌性病原体会在宿主细胞中分泌大量的效应物来控制植物免疫(Yu等2012)。在复杂的信号网络中, MAPK级联途径参与植物中PAMP识别诱导的细胞反应(Asai等2002), 是识别和放大外部信号到细胞内的主要模块(Meng和Zhang 2013; Rodriguez等2010)。

拟南芥中, 用细菌鞭毛蛋白(fl<sub>g</sub>22)处理拟南芥原生质体后检测MAPKs活性, 发现MEKK1-MKK4/5级联途径激活了下游激酶MPK3/6, 同时活化的MPK3/6激活了下游转录因子WRKY22/29/33, 进而提高了植物保护素(phytoalexin)的合成与抗病基因的转录, 因此MEKK1-MKK4/5-MPK3/6-WRKY22/29/33级联途径提高了拟南芥的抗病性(Asai等2002; Ren等2008; Mao等2011)。此外, 还发现fl<sub>g</sub>22处理拟南芥后MEKK1-MKK1/2-MPK4级联途径负调控拟南芥的抗病反应(Meszáros等2006; Ichimura等2006; Suarez-Rodriguez等2007; Pitzschke等2009)。最新研究表明, MAPKKK3/5-MKK4/5-

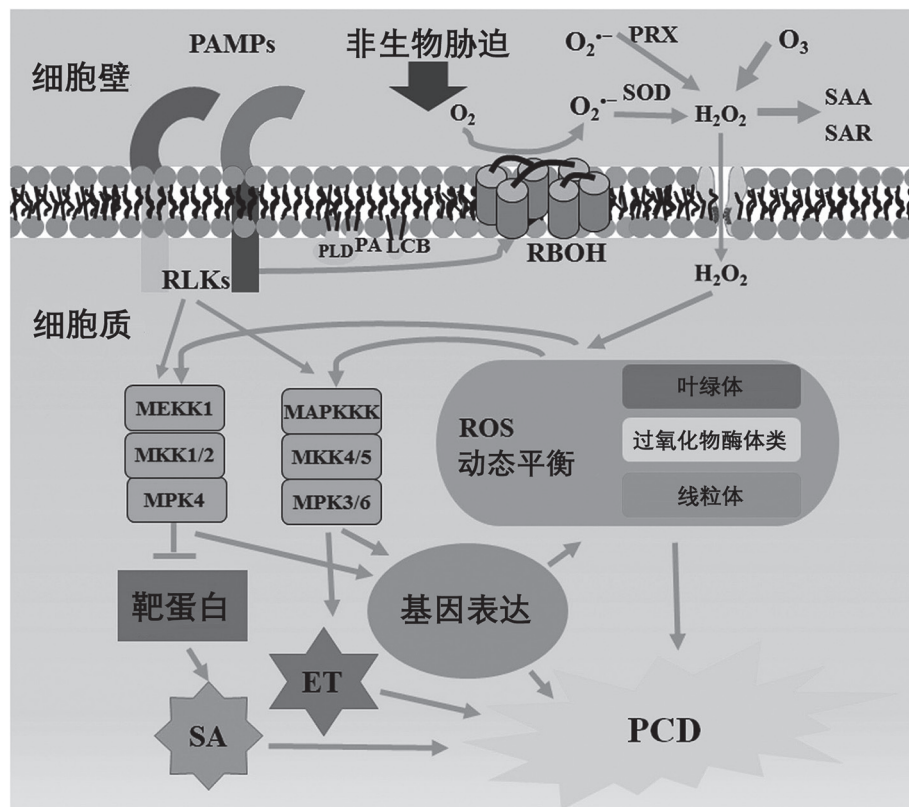


图1 典型MAPK级联途径参与ROS响应与调控模式图

Fig.1 Schematic representation of MAPK pathways in ROS signaling and responses

本图引自Liu和He (2017)一文, 略作修改。

MPK3/6级联途径在植物防御病原体过程中参与了多种途径, 包括乙烯与植物保护素的合成、吲哚硫代葡萄糖苷生物合成途径和气孔免疫(Xu等2016; Su等2017; Bi等2018; Sun等2018)。由此可见, 3条途径交互作用构建了拟南芥的防御系统。

在甘蓝型油菜中, 通过对*BnMAPK1*启动子序列分析, 发现其含有多个逆境胁迫响应和激素响应元件, 接种核盘菌(*Sclerotinia sclerotiorum*)后, *BnMAPK1*在转录水平上被激活, 同时茉莉酸(jasmonic acid, JA)信号途径中标志性基因*PDF1.2*的表达量上升, 但抑制了水杨酸(salicylic acid, SA)信号途径中标志性基因*PR1*的表达, 结果表明甘蓝型油菜可能通过JA信号途径响应病原菌的入侵(陆俊杏等2013)。在葡萄中, 白粉病侵染后, *VvMPK5*和*VvMPK6*基因下调表达, 而*VvMPK1*和*VvMPK10*基因分别在被侵染12和48 h后显著上调表达, *VvMPK9*基因的表达量随侵染时间而增加(王刚2014)。在西瓜中, 枯萎病菌侵染后第9天, *CIMP3*、*CIMP7*

和*CIMKK5*的表达量与对照相比高出6倍至13倍, 利用农杆菌介导的瞬时表达技术将*CIMP7*在本氏烟中瞬时表达, 之后对转基因烟草接种灰霉病菌, 发现其可以诱导活性氧的积累与相关防卫基因的表达, 进而减轻灰霉病对本氏烟的侵害(宋秋明2015)。用植物病原菌蛋白AvrPto/AvrPtoB侵染番茄, 发现能够激活LeMPK1、LeMPK2和LeMPK3, 该结果与在番茄中过表达LeMAPKKK $\alpha$ 和LeMKK2相同, 通过体内外激酶试验发现三者之间为上下游关系(del Pozo等2004)。同时, Stulemeijer等(2007)发现LeMKK2和LeMPK2沉默番茄植株中野油菜黄单胞菌的数量明显大于对照。上述结果表明, LeMAPKKK $\alpha$ -LeMKK2-LeMPK1/LeMPK2/LeMPK3途径参与了番茄的抗病反应。在棉花中, 通过病毒诱导基因沉默(VIGS)技术分别获得*GhM-KK4*、*GhMPK20*和*GhWRKY40*转基因植株, 发现其对枯萎病的抗性显著提高, 同时通过酵母双杂和免疫共沉淀技术验证了这三个基因的互作关系,

之后分别在烟草中过表达*GhMKK4*、*GhMPK20*和*GhWRKY40*,发现其对枯萎病高度敏感,以上结果表明MKK4-MPK20-WRKY40途径在对枯萎病的抗性中起到负调控的作用(Wang等2017a)。可见,MAPK级联途径在植物生物胁迫下的信号转导中起到调控作用。

## 2.2 MAPK级联途径参与调控植物非生物胁迫下的信号转导

植物的生长发育会受到极端环境温度、干旱、盐害以及渗透胁迫等非生物胁迫的影响。植物体本身具备一些特异性调控机制,通过信号转导,调控一系列相关抗性基因的表达,从而调节渗透平衡、离子平衡和氧化还原平衡,进而改变植物器官形态,最终提高植物在抵御逆境胁迫中的能力。

### 2.2.1 MAPK级联途径对低温的响应

环境温度变化是植物生长周期中必需适应的环境因素之一。相关研究表明,在拟南芥中,低温会迅速诱导*AtMPK3*的表达,同时*AtMPK4*和*AtMPK6*的激酶活性被激活(Duttilleul等2012; Ichimura等2000; Teige等2004)。MEKK1-MKK2位于MPK4和MPK6上游,对于低温激活MPK4和MPK6的活性起到关键的作用(Ichimura等2000; Teige等2004; Mizoguchi等1996)。通过表型分析发现,*mkk2*突变体表现出低温敏感的表型,而过表达*MKK2*表现出抗低温的表型(Teige等2004)。这些结果表明MEKK1-MKK2-MPK4/MPK6级联信号途径在植物抵御低温中发挥重要作用(Furuya等2014)。

Li等(2017a)通过酵母双杂技术筛选ICE1的互作蛋白,发现蛋白激酶MPK3和MPK6能够与ICE1发生相互作用。遗传证据表明,*MPK3/6*突变导致植物抗冻能力提高,*MPK3/6*位于ICE1的上游。进一步研究发现,低温激活MPK3/6的激酶活性,激活状态的MPK3/6通过磷酸化ICE1蛋白,抑制其在低温下的稳定性和转录活性,从而抑制CBF基因的表达(图2)。以上证据表明MAPK级联途径在植物适应低温的过程中起到重要的作用,MPK3/6通过磷酸化ICE1负调控拟南芥对低温的耐受能力。

### 2.2.2 MAPK级联途径对其他非生物胁迫的响应

在拟南芥中,干旱胁迫能够迅速诱导MPK3的表达(Mizoguchi等1996)。拟南芥中过表达*MdRaf5*可以提高植株对干旱的耐受性(Sun等2017)。通过

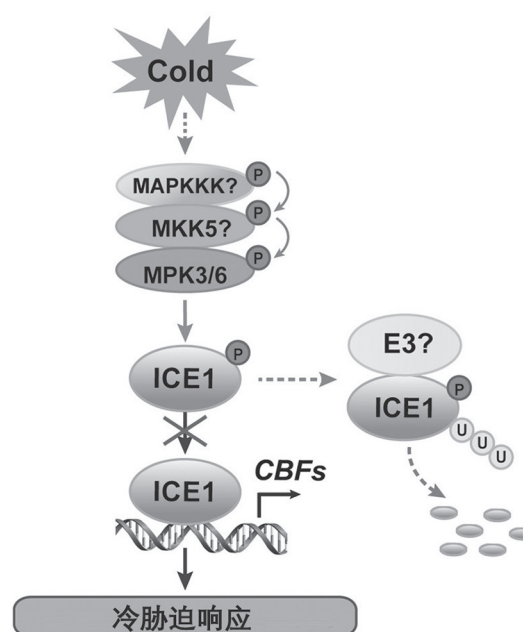


图2 MPK3/6在植物响应低温胁迫中作用模式图

Fig.2 Model of the role of MPK3/MPK6 in plant responses to cold stress

本图引自Li等(2017a)一文,略作修改。

病毒诱导基因沉默(VIGS)技术获得棉花*GhRaf19*转基因植株,发现其积极响应低温胁迫,负调控盐与干旱胁迫(Jia等2016)。在干旱胁迫下,葡萄中的MAPKKK基因均上调表达,有些MAPKKK基因表达量甚至比对照高出10倍到20倍,说明葡萄中MAPKKK基因家族积极响应干旱胁迫(Wang等2014)。以上研究表明,MAPK级联途径在植物抵御干旱胁迫中响应并起调控作用。

拟南芥*raf43-1*突变体增加了对甘露醇、NaCl和H<sub>2</sub>O<sub>2</sub>的敏感性(Virk等2015)。陈莎莎等(2013)在藜中分离出*CaMAPKK2*,并检测出该基因在NaCl和H<sub>2</sub>O<sub>2</sub>诱导下上调表达,通过外施H<sub>2</sub>O<sub>2</sub>和ABA抑制剂发现该基因在盐胁迫下的表达受到显著抑制,推测盐胁迫可能诱导H<sub>2</sub>O<sub>2</sub>和ABA的积累从而使*CaMAPKK2*表达量上升。

宋秋明(2015)通过实时荧光定量技术分析了西瓜15个MAPK基因在干旱、高温、低温和高盐等非生物胁迫下的表达模式,结果表明,*CIMPK4-2*、*CIMPK7*的表达量在干旱处理后明显高于其他基因;*CIMPK7*响应盐胁迫;低温处理后,*CIMPK7*、*CIMPK9-1*、*CIMPK9-2*和*CIMPK9-4*显著下调;高温处理后,*CIMPK7*、*CIMPK20-1*和*CIMPK9-4*显著

上调。说明MAPK家族成员不同基因可能参与调控不同的逆境响应途径。在黄瓜中,检测到58个MAPK级联途径激酶基因,发现多数MAPK级联途径的旁系和直系同源基因在干旱、寒冷和高温等胁迫下具有相似的表达模式,可以推测这些基因可能具有相似的功能;但一些旁系同源的MAPKK基因对同种胁迫表现出不同的表达模式,说明这些基因可能调控不同的信号转导途径;少数直系与旁系同源基因在表达模式上有显著差异,表明这些基因可能在进化中获得了新的功能(Liang等2013; Zhang等2014; Wang等2015)。Ding等(2018)通过蛋白纯化及MS/MS质谱分析,在番茄中获得高温响应的*SIMPK1*;并且,*SIMPK1*-RNAi植株能够应答高温信号,具有明显的耐高温表型,存活率高,而过表达植株耐高温能力下降;通过蛋白质组学及生理生化方法进一步发现*SIMPK1*应答高温的机制与*SIMPK1*介导的抗氧化系统防护及氧化还原代谢有关;最后,通过酵母双杂交鉴定了一个与*SIMPK1*互作蛋白*SISPRH1*。研究发现,*SISPRH1*是*SIMPK1*的靶蛋白,能够被*SIMPK1*磷酸化。过表达*SISPRH1*能够降低植物的耐高温性,且与*SISPRH1*的磷酸化相关。该研究表明*SIMPK1*-*SISPRH1*作用模块在高温应答过程中负调控高温信号且协同抗氧化胁迫系统。以上结果表明,MAPK级联途径激酶广泛参与植物所遭受的不同非生物胁迫。

### 2.3 MAPK级联途径参与调控植物激素信号转导

植物免疫系统受到许多激素和一系列复杂的信号转导过程严格调控。植物激素是指在特定环境条件下,植物细胞在代谢过程中产生的一类有机物质,在低浓度下就可发挥作用,能有序调节植物生理生化反应,在细胞分裂伸长、组织器官生长分化、植株成熟与衰老方面起重要作用。在植物细胞内,激素可通过多种信号转导通路,影响植物的生理生化反应。水杨酸(SA)和茉莉酸(JA)是植物免疫系统中重要的激素(Thaler等2012),将喷施SA的拟南芥用灰霉病菌侵染,发现拟南芥的发病率降低(王媛2007)。

对不同植物基因组的生物信息学研究发现,MAPK级联反应途径激酶基因启动子序列中存在大量的胁迫应答与激素应答元件。通过对辣椒中24个MAPK级联途径激酶基因的启动子分析,发现了多种应答元件,如ABA应答元件、SA响应元

件、茉莉酸甲酯(methyl jasmonate, MeJA)响应元件等,可以推测出逆境胁迫下具有相同应答元件的MAPK级联途径激酶基因可能被共同调控表达,并在植物抗逆中发挥作用(Liu等2015)。

植物体内ABA含量在低温、干旱及盐胁迫等逆境胁迫下均会导致不同程度的增加(Nayyar等2005; Munns等2006; 贾瑞丰等2013)。多数二穗短柄草的MAP3K基因在聚乙二醇(PEG6000)模拟干旱和H<sub>2</sub>O<sub>2</sub>胁迫下的表达模式与ABA处理后的表达模式相似,说明胁迫诱导的MAPK信号转导途径可能与植物激素变化有关联(Jiang等2015)。在拟南芥中超表达的*AtMCK3*功能与玉米*ZmMCK3*基因功能相似,对ABA诱导后产生过多活性氧而引起的气孔关闭起正调控作用(Hwa和Yang 2008)。拟南芥中*AtMCK2*和高盐及冷胁迫有关(Teige等2004),也可以通过调节SA和JA的含量来提高植株的抗逆性(Brader等2007)。

Mitula等(2015)研究表明,*MAP3K18*也受到ABA核心模块的直接调控,其直接与PP2C磷酸酶ABI1相互作用;在缺乏ABA的情况下,*ABI1*抑制了SNF1-相关蛋白激酶2(SnRK2)激酶的自磷酸化,并诱导MAP3K18蛋白酶体降解(图3-A)。除此之外,作为ABA信号途径核心模块的参与者之一,*ABI1*去磷酸化MAP3K18,然后被蛋白酶降解。当ABA被激活时,PYR/PYL受体会阻断*ABI1*激活,结果导致SnRK2s的自动激活,使其下游目标磷酸化,进而建立ABA快速响应机制;同时*ABI1*的抑制会通过一个未知的机制使MAP3K17/18蛋白稳定,进而能够激活信号模块的下游因子,进而调控后期ABA响应途径(图3-B)。最新研究表明,拟南芥MAPK-KK17/18-MKK3-MPK1/2/7/14途径响应ABA诱导的信号途径(Danquah等2015),并在ABA调控叶片衰老中起重要作用(Matsuoka等2015)。因此,MAPK级联反应途径能响应激素信号,同时可以与激素信号途径协同调控,从而对非生物胁迫产生应答。

拟南芥ANP3-MKK6-MPK4和YDA-MKK4/5-MPK3/6途径分别调控胞质分裂和气孔发育(Zeng等2011; Wang等2007); AIK1-MKK5-MPK6途径积极响应ABA并调控ABA诱导的根部发育及气孔开闭(Li等2017b); *HTI* (MAPKKK基因成员之一)调控CO<sub>2</sub>胁迫下拟南芥的气孔开闭(Hashimoto-Sugimoto等2016)。

在油桃花芽休眠解除过程中,发现有6个

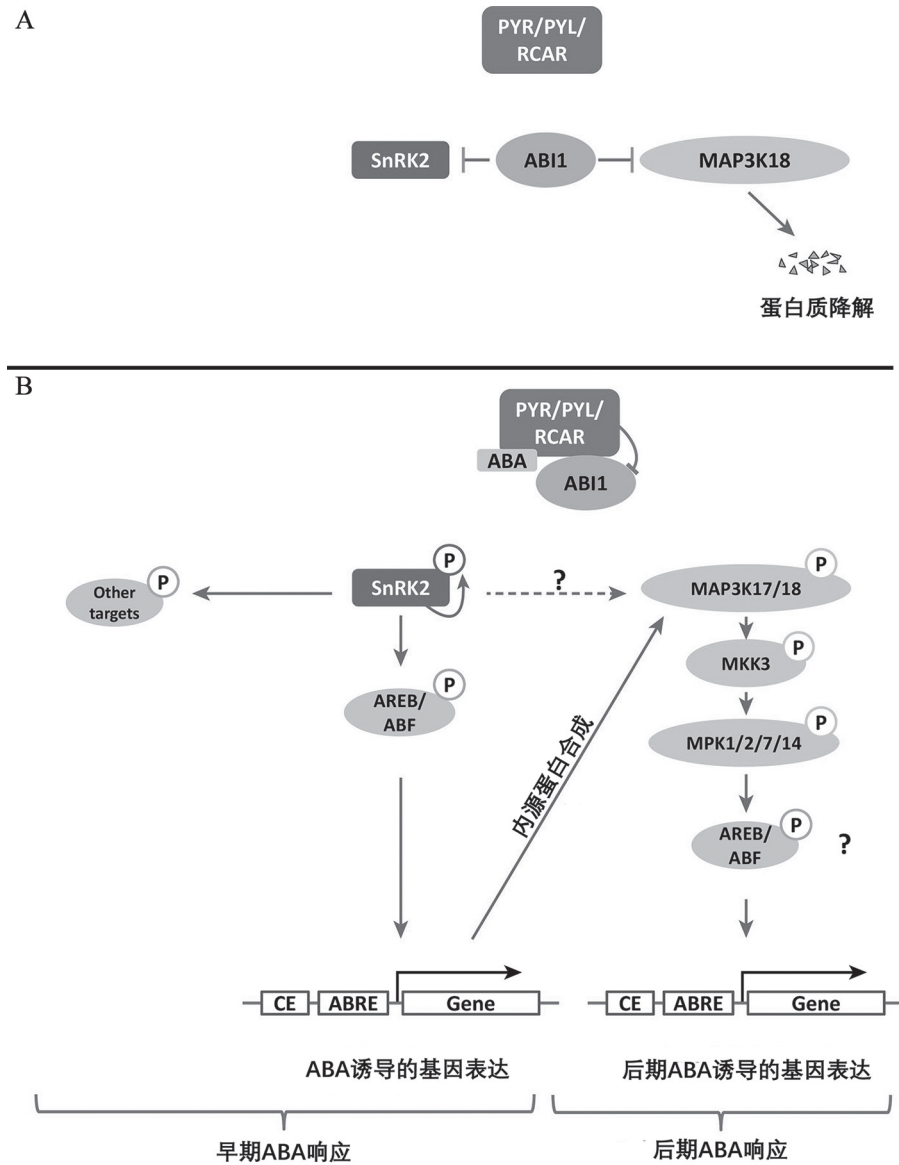


图3 MAPK级联途径参与ABA信号调控模式图

Fig.3 Model of MAPK cascaded pathway participates in the regulation pattern of ABA signal

本图引自de Zelicourt等(2016)一文, 略作修改。

MAPKs和4个MAPKKs呈现表达量下降的趋势, 这与该过程中ABA、 $H_2O_2$ 含量的下降趋势相似, 说明MAPK相关基因很可能在油桃花芽休眠解除过程中参与ABA和 $H_2O_2$ 的信号转导, 进而解除花芽休眠。在花芽休眠解除期进行 $H_2O_2$ 处理, 发现对芽内 $H_2O_2$ 含量与过氧化氢酶(catalase, CAT)活性无显著影响, 但提高了5个MAPK基因的转录水平; 在休眠中期对花芽进行MAPK抑制剂PD98059处理, 发现同样对芽内 $H_2O_2$ 含量与CAT活性无显著影响, 但降低了*PpMPK12*、*PpMPK13*和*PpMKK4*的转录

水平(杜培勇等2016), 进一步说明了MAPK级联途径可能参与油桃休眠解除的调控过程。

以上结果表明, MAPK级联途径与植物激素信号转导途径密切相关, 进而对植物遭受逆境胁迫时产生应答并参与调控, 提高植物的抗逆性。

### 3 展望

近几年, 随着越来越多植物的全基因组测序完成, 为我们利用生物信息学对海量的测序数据进行系统的整理、分析和研究奠定了基础。MAPK

级联途径广泛参与植物抵御逆境胁迫的调控,因此,对MAPK级联途径激酶基因成员及其调控机制的研究,对于今后利用基因工程技术提高作物抗逆性起到重要的作用。目前,对植物中MAPK级联途径的研究起步较晚,大多数研究集中在模式植物拟南芥上,对其他植物的研究正处于基因家族成员鉴定及表达模式构建阶段。由于MAPK级联途径激酶基因成员数量庞大,为科研工作带来了一些困难,因此,探求更高效的研究方法是解决问题的关键所在。本课题组已从甜瓜全基因组网站中成功鉴定出14个MAPKs、6个MAPKKs和64个MAPKKKs,并发现其广泛响应生物胁迫和非生物胁迫(数据未发表),但其基因家族在抗逆境中的作用机制尚不明确,是我们下一步研究的重点。

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## Structural characteristics of MAPK cascade kinase and the function of signal transduction pathway in adversity stress of horticultural crop

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**Abstract:** Mitogen-activated protein kinase (MAPK) is one kind of serine/threonine protein kinase, which activated by extracellular stimulation through the MAPK cascade (MAPKKK-MAPKK-MAPK). MAPK cascade pathway widely exist in eukaryotes organism and highly conserved. They participate in plant responses to various biological stress, abiotic stress and hormone signal conditions through the protein phosphorylation signal cascade amplifier to downstream response. This paper focuses on the structural characteristics of MAPK cascade kinase structure in plants and its response of signal transduction pathway under adversity stress in horticultural crop. The purpose is to provide some references for relevant researches in this field.

**Key words:** MAPK cascades; signal transduction; abiotic stresses; biotic stress; hormonal signal

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