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·热点评述·

生长素通过MAPK介导的超长链脂肪酸合成调控侧根发育

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摘要 促分裂原活化蛋白激酶(MAPK)信号级联通路是真核生物中高度保守的重要信号系统，通过激酶逐级磷酸化传递并放大上游信号，进而调控细胞反应。MAPK信号通路不仅介导植物响应环境变化，而且在调节植物生长发育过程中发挥重要作用。近期，山东大学丁兆军课题组研究发现，植物重要激素生长素能够通过激活MPK14调控下游ERF13的磷酸化，进而影响超长链脂肪酸的合成并调控侧根发育。该研究从全新的角度解析了侧根起始的新机制，并进一步证实生长素和古老的信号转导模块MAPKs相偶联的分子机制。侧根作为植物响应环境最重要的器官之一，MAPK信号通路在侧根发育过程中的功能解析可为阐明植物如何整合发育和环境信号提供新思路。

关键词 MAPK级联反应，生长素，超长链脂肪酸，侧根发育

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促分裂原活化蛋白激酶(MAPK)级联反应是一类真核细胞中高度保守的、介导细胞信号转导的激酶调控模块。MAPK级联反应通常由MAPKKK (MAP3K或MEKK)、MAPKK (MKK或MEK)和MAPK (MPK)三部分组成。由于植物中MAPK家族成员众多，不同的激酶三联组合造就了MAPK信号调控网络的功能多样性和复杂性，赋予了MAPK通路在调控植物生长发育和介导逆境胁迫响应中的多面性。

MAPK级联反应不仅参与调控植物细胞应对复杂多样的生物/非生物胁迫以及响应各种生理应激(Nakagami et al., 2005; Pitzschke et al., 2009)，而且几乎调节植物生长发育的各个方面：从配子形成、胚胎发生、器官形态建成到器官脱落、植物衰老以及种子形成等(Xu and Zhang, 2015)，展现出MAPK信号通路在调控植物生长发育及响应整合外界环境信号中的强大功能。

根系是植物固着生长的重要器官，具有很强的可塑性，以适应周边复杂且变化的环境。根系主要由主根和侧根组成。与主根不同，侧根的形成属于胚后发育过程，由中柱鞘细胞经命运转变而来。侧根的发育过程包括建成细胞的命运确定、侧根原基的形态建成以及侧根的成形(Malamy and Benfey, 1997; Péret et al., 2009; He and Meng, 2020)。前期研究发现，侧根发育的一系列过程都与生长素的时空分布有关，其中侧根起始位置与生长素沿主根的节律性振荡有关，而侧根发育又与局部生长素的有序累积有关(黎家和李传友，2019)。生长素通过TIR1/AFB-Aux/IAA介导的转录调控模式精准调控侧根发育的各个过程，包括通过TRI1-IAA28-ARF5/6/7/8/19调控*GATA23* (*GATA-type transcription factor 23*)基因的表达，诱发侧根建成细胞的命运转变(De Rybel et al., 2010)；通过激活IAA14-ARF7/19和IAA12-ARF5协同影响中柱鞘细胞核的位移，驱动早期侧根原基的不对称分裂(Hamann et al., 2002; Lee et al., 2009)；通过IAA3-ARF7和IAA14-ARF7/19促进*CWR* (*cell wall remodeling*)基因的表达，消融细胞壁，从而使侧根原基突破内皮层并外露成形(Goh et al., 2012; Lavenus et al., 2013; Zhu et al., 2019)。

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侧根形成过程不仅需要转录水平重编程来促进侧根细胞的分化成形，也需要在时间和空间上对细胞形态和分裂进行有序调控，必然存在细胞水平的非转录调控机制。山东大学丁兆军课题组最近发现，生长素以不依赖于TIR1-AUX/IAA转录机制的方式调控侧根发育(Lv et al., 2021) (图1)。

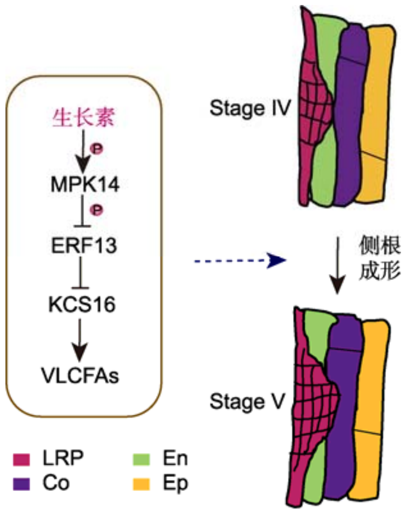

图1 MPK14介导的生长素信号通路调控侧根发育工作模型
LRP: 侧根原基; En: 内皮层; Co: 皮层; Ep: 表皮

Figure 1 A working model of MPK14-mediated auxin signaling to control lateral root development
LRP: Lateral root primordium; En: Endodermis; Co: Cortex; Ep: Epidermis

研究发现，外源施加生长素类似物NAA可以激活MPK家族C亚家族成员MPK1、MPK12和MPK14，且该过程不受生长素核内受体TIR1抑制剂PEO-IAA的影响，表明生长素以独立于TIR1信号通路的方式调控MPK1/2/14的激酶活性。遗传分析表明，*mpk1/2/14*三突变体具有严重的侧根发育缺陷，其侧根原基发育停滞在stage IV期，表明MPK1/2/14是侧根发育调控的关键元件。用MAPK激酶抑制剂U0126处理导致生长素诱导的侧根减少；而MAPK激酶激活剂表皮生长因子(epidermal growth factor, EGF)处理会诱导产生大量侧根，进一步证明MAPK信号通路对于侧根发育的重要性。徐通达课题组前期研究发现，生长素通过TMK1/4激活MKK4/5-MPK3/6级联模块来调控侧根原基细胞的分裂模式，最终影响侧根的发育(Huang et al., 2019)；徐娟课题组发现MKK4/5-MPK3/6级联模块在IDA-HAE/HSL2介导的信号通路中响应生长素调控侧根外露的成形过程(Zhu et al., 2019)。上述研究结果表明，MAPK信号通路在介导生长素对侧根发育调控中发挥关键作用。

生长素激活MPK信号通路后如何进一步调控侧根发育？Lv等(2021)进一步的生化和遗传实验表明，MPK14直接与乙烯响应因子ERF13互作并磷酸化ERF13，进而调控ERF13蛋白的稳定性。有意思的是，ERF13对侧根发育的调控部分依赖于超长链脂肪酸(very-long-chain fatty acids, VLCFAs)合成途径，通过抑制VLCFA途径中β-酮脂酰辅酶A合成酶(KCS16)的转录水平来实现。VLCFA是一类由22及更多碳原子组成的脂肪酸，是植物种子甘油三脂、表皮和表皮蜡质以及鞘脂的组成部分。前期研究表明，VLCFA在植物的抗逆性(Seo and Park, 2011)、花粉发育(Smirnova et al., 2013)、棉纤维细胞伸长(Qin et al., 2007)、生长素极性运输(Roudier et al., 2010)以及有丝分裂赤道板形成(Bach et al., 2011)等过程中发挥重要作用。

VLCFA是细胞壁的重要组分(Bach and Faure, 2010)。Lv等(2020)研究表明，VLCFA通过影响细胞壁成分果胶质的降解来限制侧根突破内皮层，从而导致成形侧根数量减少，而过量表达*KCS16*或外源施加VLCFA均可恢复*ERF13*过量表达植株中侧根突破障碍的缺陷表型，最终证明VLCFA在植物侧根发育过程中具有重要作用。有意思的是，胡玉欣课题组发现VLCFA及其衍生物作为细胞层特异的信号分子，抑制植物中柱鞘类细胞命运转变，从而调控愈伤组织的形成(Shang et al., 2016)。在拟南芥中，侧根的起始和愈伤组织的形成均源于中柱鞘细胞的转分化(Che et al., 2007; Atta et al., 2009; Sugimoto et al., 2010)，而VLCFA在这2个过程中都发挥至关重要的作用，表明VLCFA可能参与植物细胞分化的重要过程。

综上所述，该研究揭示了一条从上游信号生长素到MPK1/2/14的激活，进而通过磷酸化调控ERF13蛋白的稳定性来影响下游超长链脂肪酸的合成及细胞壁组成，最终决定侧根发育的完整信号通路。此外，进一步证实生长素存在不依赖于TIR1模块的信号转导机制。该研究深化了我们对植物侧根形态建成多层次、多维度调控机制的理解，也拓宽了对生长素调控侧根发育模式的认知。

同时，该研究也提出了许多新的问题有待进一步

解析。例如，生长素如何调控MPK1/2/14的磷酸化水平？是否通过TMK信号通路，或者存在其它的激酶？MAPK信号通路被生长素激活之后是否参与侧根的抗逆反应？MAPK信号通路有哪些下游靶标底物，并如何行使其特异性功能？以及生长素-VLCFA是否参与调控其它生物学过程？对上述问题的回答，将有助于我们深入理解生长素如何精准实现其复杂功能，对于该领域的研究具有重要意义。

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Auxin Regulates the Lateral Root Development Through MAPK-mediated VLCFAs Biosynthesis

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Abstract Mitogen-activated protein kinase (MAPK) cascade is an important and highly conserved cellular signal transduction pathway by delivery and amplification of upstream signals through protein kinase cascade phosphorylation in eukaryotes. In plants, MAPK signaling pathways not only mediate plant responses to environment, but also play crucial roles in regulating plant growth and development. A recent study from the Zhaojun Ding's group of Shandong University uncovered a novel molecular mechanism of MPK14-mediated auxin signaling in lateral root development via ERF13-regulated very-long-chain fatty acids (VLCFAs) biosynthesis. This study reveals the molecular mechanism of the lateral root development from a new perspective, and further confirms the coupling between the vital phytohormone auxin and the ancient MAPKs module. Since lateral roots act as essential organs for plants in response to environment, deciphering the MAPK signaling pathway in regulation of lateral root development will provide a new strategy for how plants integrate development signals and environmental cues.

Key words MAPK cascade, auxin, VLCFA, lateral root development

Huang RF, Xu TD (2021). Auxin regulates the lateral root development through MAPK-mediated VLCFAs biosynthesis. *Chin Bull Bot* **56**, 6–9.

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