

· 热点评 ·

中国科学家在解析独脚金内酯调控水稻株型的分子机制研究中取得突破性进展

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摘要 阐明植物激素作用的分子机理一直是植物学研究的前沿和热点。如何调控作物的株型等重要农艺性状是绿色革命的核心内容。最近, 中国科学家在解析新型植物激素独脚金内酯的信号途径和阐明独脚金内酯调控水稻(*Oryza sativa*)株型的分子机制等方面所取得的重大原创成果入选“2014年度中国科学十大进展”。

关键词 独脚金内酯, 信号途径, 水稻, 分蘖, 株型

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2015年2月10日, 李家洋研究组和万建民研究组在解析新型植物激素独脚金内酯的信号途径和阐明独脚金内酯调控水稻(*Oryza sativa*)株型的分子机制等方面取得的重大原创成果入选“2014年度中国科学十大进展”。

众所周知, 植物激素是植物自身合成且在低浓度下调控植物生长发育和逆境响应的微量有机物, 对其作用分子机理的阐释一直是植物学领域的前沿和热点。在已知的几大类植物激素中, 独脚金内酯(strigolactone, SL)的发现较晚。目前已鉴定的天然SL类物质有近20种(Zwanenburg and Pospisil, 2013)。SL通常由植物根部释放到土壤中, 能够刺激独脚金(*Striga* spp.)等寄生植物的种子萌发, 使其根系感知并朝向寄主方向生长(Bouwmeester et al., 2007)。尽管前人早已从植物根系中分离纯化了SL(Cook et al., 1966), 并鉴定出其化学结构(Cook et al., 1972), 但直到发现其具有促进菌丝分枝(Akiyama et al., 2005)和抑制植物分枝(Gomez-Roldan et al., 2008; Umehara et al., 2008)等生理功能, SL才被公认为新的植物激素。近年来, 植物学界高度重视对独脚金内酯的研究, 其信号途径的解析取得了显著进展。一些多年前获得的突变体如豌豆(*Pisum sativum*)多分枝(ramosus)突变体*rms4* (Beveridge et al., 1996)于近年被证明与SL信号途径相关(Beveridge et al., 2009)。同时, 通过对拟南芥(*Arabidopsis*

thaliana)中多侧生分生组织(more axillary meristem)突变体*max2* (Stirnberg et al., 2002)、水稻中丛矮(tillering dwarf)突变体*d3* (Ishikawa et al., 2005)和*d14* (Arite et al., 2009)以及矮牵牛(*Petunia hybrida*)弱顶端优势(decreased apical dominance)突变体*dad2* (Hamiaux et al., 2012)等一系列相关突变体的深入研究, 发现*RMS4/D3/MAX2*编码形成SL信号转导所需的F-box蛋白, 而*DAD2/D14*编码能与GR24(germination releaser 24, 人工合成的SL类似物)特异结合的候选受体(α/β 水解酶), 且能与*RMS4/D3/MAX2*类F-box蛋白相互作用。随后D14的晶体结构和信号感受机制也得到解析(Zhao et al., 2013; Nakamura et al., 2013)。这些研究进展促使植物学家推测在SL信号途径中也存在类似于生长素(IAA)、茉莉酸(JA)和赤霉素(GA)信号途径中对抑制蛋白进行泛素化降解的去抑制激活过程(Nelson et al., 2011; Hamiaux et al., 2012)。因此, 许多植物学家都致力于寻找遗传学与分子生物学证据来证实上述设想。至此, 揭示SL信号转导途径分子机制的难点和关键已经聚焦到如何尽快证实SL转录抑制蛋白的存在并解析其泛素化降解过程, 对该科学问题的突破为植物激素领域同行所期盼。

在作物领域, 分枝(在水稻中称为分蘖)是决定植物株型发育的主要因素, 也是影响产量的重要农艺性状。调控作物株型是绿色革命的重要内容之一。因此,

水稻分蘖对于培育具高产潜力的理想株型(ideal plant architecture, IPA)十分重要(Jiao et al., 2010)。研究表明,植物分枝发育大致可分为侧生分生组织(AMS)形成和腋芽生长两个阶段,而IAA和CTK是调控株型建成的主要激素。其中,AMS的形成需要IAA介导,IAA从茎顶端向下运输,抑制腋芽的生长,形成顶端优势,通过下调IAA外流蛋白OsPIN1表达来弱化顶端优势会引起水稻分蘖增加(Xu et al., 2005)。而CTK从根系向上运输则促进腋芽的生长(Müller and Leyser, 2011)。对于水稻而言,作为能结实的特化分枝,形成于未伸长母茎基节上的分蘖具有自身的不定根,其生长发育相对独立于母茎,主要受遗传因素控制(Wang and Li, 2011)。研究发现,一系列植物激素相关基因参与水稻分蘖形成与发育的调控。采用图位克隆方法从水稻独秆无分蘖(mono culm)突变体中克隆的MOC1编码GRAS家族转录因子,主要调控蘖芽的形成和萌发(Li et al., 2003)。从细秆(fine culm)水稻突变体克隆的FC1/OsTB1编码TCP结构域的转录因子,作为腋芽生长的负调控因子,抑制从腋芽原基到分蘖形成的生长过程(Takeda et al., 2003)。从T-DNA插入突变体中克隆的OsPUP7编码嘌呤转移酶,通过CTK调控分蘖和株高等性状(Qi and Xiong, 2013)。近年来,随着d3、d10 (Arite et al., 2007)、d14、d27 (Lin et al., 2009)和htd1 (Zou et al., 2006)等大量突变体的发现,越来越多的证据表明,SL参与对水稻分蘖的调控,主要方式是调控SL的生物合成(d10、d2和htd1)或信号转导(d3和d14)。因此,在水稻株型及其相关领域,迫切需要通过揭示SL信号转导途径来阐明SL参与调控分蘖的分子机制,这一难题的突破将同时具有重要的理论意义和实用价值。

针对解析SL的信号途径并阐明其对水稻分蘖的调控机制等科学问题,李家洋研究组基于对GR24不敏感的水稻丛矮突变体e9开展相关研究,取得了原创性的重大进展。他们通过对外源GR24的敏感性实验证明e9为SL信号途径突变体;进而采用图位克隆方法成功克隆了水稻SL转录抑制蛋白D53基因;通过D53-GFP系统结合外源GR24以及蛋白酶抑制剂MG132处理解析了D53的泛素化降解过程;用蛋白体外结合实验确证了D14、D53和D3之间的互作;分别用双杂交和蛋白体外结合实验确证了D53和另一类转录抑制因子TPL (Yoshida et al., 2012)类似蛋白

TPR之间的互作。以上研究结果清晰地揭示了SL信号途径的核心环节——SL诱导了转录抑制蛋白D53的泛素化降解过程。D53基因编码转录抑制蛋白, D53作用于TPR并与之形成复合物,协同抑制信号途径下游SL效应基因的表达,从而负调控SL信号转导。SL通过与候选受体D14结合并借助于泛素连接酶D3,诱导D53泛素化并通过蛋白酶降解。转录抑制蛋白D53的降解导致去抑制化,激活下游SL效应基因的表达,因而促进分蘖的伸长生长。在d53显性突变体中, D53基因的突变使其蛋白不能被降解,组成型抑制SL信号通路,从而导致d53突变体产生丛矮的表型(Jiang et al., 2013)。与此同时,万建民研究组基于对SL不敏感的水稻丛矮突变体d53独立开展D53基因功能的研究,通过图位克隆和功能分析,获得与李家洋研究组类似的研究结果并在同一刊物同期发表(Zhou et al., 2013)。在协助上述两个研究组开展研究的过程中,钱前和徐华强等多个研究组分别在突变体材料和有关蛋白质晶体结构解析等方面亦作出了重要贡献(Jiang et al., 2013; Zhou et al., 2013)。

中国科学家的一系列重要成果首次证实了D53蛋白是SL信号途径的抑制因子,并解析了其在SL诱导下的泛素化降解过程,是SL信号转导分子机制研究领域的奠基性发现,具有重要的科学意义和应用价值。研究结果不仅回答了SL作用分子机理中的关键科学问题,而且也作为农作物的株型改良和杂种优势的利用奠定了重要的理论基础。此外,有关结果也显示多种激素信号途径中存在的去抑制激活机制在植物进化中具有重要意义,这对于今后解析其它信号物质的分子机制具有重要的参考价值。这些开创性工作得到了国际同行的高度评价(Smith, 2013; Zheng et al., 2014)。

上述研究重点回答了SL作用分子机理中抑制因子及其泛素化降解的关键科学问题。同时,这些发现也因此引出更多亟待探索的新问题。首先, D53的泛素化降解只是SL信号途径的一部分,该信号途径的许多环节仍然未知。最近发现SL同时诱导D14的降解(Chevalier et al., 2014),其在SL信号途径中的意义以及与D53降解的关系等许多新问题亟待阐明。其次,除已知的IAA、CTK和SL三种激素外,发现GA和芸薹素(BR)信号途径分别通过SLR1和BES1与SL信号途径互作(Nakamura et al., 2013; Zheng et al., 2014),

另外, microRNA (Xie et al., 2006; Chen et al., 2015) 以及与之互作的 *Osmt1* (Liu et al., 2015) 等多种因素也能调控植物分枝。植物分枝的协同调控网络一直备受关注(许智宏和薛红卫, 2012; Jong et al., 2014; Sang et al., 2014), 那么SL与其它因素之间如何协同作用尚需深入探讨。第三, 除了抑制分枝外, SL具有多种生理功能, 如作为植物与菌根以及寄生植物间的信号物质等(Zwanenburg and Pospisil, 2013; Ha et al., 2014; Sun et al., 2014), 因此, 在应用方面, 如何将 *D53* 以及其它SL信号途径相关理论成果应用于塑造农作物理想株型、提高抗逆性和作物营养利用效率以及降低寄生杂草的危害值得进一步研究。总之, 对这些新问题的探索将有助于更深入地解析SL信号途径和植物分枝调控的分子机制, 并将SL相关研究的成果应用于生产实践。

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Chinese Scientists Made Breakthrough Progresses in Elucidating the Molecular Mechanism of Regulating Plant Architecture by Strigolactones

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Abstract To elucidate the molecular mechanism of phytohormones has always been the research frontier and the hot spot in biology, while how to regulate the plant architecture of crops remains a key task of the green revolution. Recently, Chinese scientists have made breakthrough progresses in the signaling pathway of the new phytohormones strigolactones, as well as in their molecular mechanisms for plant architecture regulation in rice. The findings have been awarded “2014 Top 10 Science Breakthrough Progresses in China”.

Key words strigolactones, signal transduction, rice, tillering, plant architecture

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