

植物器官大小调控因子研究进展

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摘要: 植物器官的大小受遗传因子和环境信号的双重调节。植物器官的生长由细胞增殖和细胞扩张两个连续的过程组成, 许多遗传调控因子通过影响这两个过程来调控器官的大小。近年来, 植物器官大小遗传调控研究取得很大的进展, 这些遗传因子与其他因子相互作用形成决定器官生长和发育的调控网络。本文从植物激素、泛素途径、细胞色素P450蛋白和microRNA等几个方面综述植物器官大小调控因子的研究进展。

关键词: 器官大小; 细胞增殖; 细胞扩张; 调控因子

Research Progress of Regulators of Organ Size in Plants

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Abstract: Organ size in plants is controlled by both genetic factors and environmental signals. Organ growth occurs through the two successive processes of cell proliferation and cell expansion in plants, a number of genes influence these processes to regulate organ size. In recent years, there have been significant progress in identification genetic factors to control plant organ size, which constitute networks with other factors in regulating organ size. Here we summarized the progress of major regulators of organ size from plant hormones, ubiquitin pathway, Cytochrome P450 protein, microRNA and the other aspects in this field.

Key words: organ size; cell proliferation; cell expansion; regulators

植物不同物种之间器官的大小千差万别, 甚至相同物种不同品种器官的大小也存在着显著的差异; 然而, 特定植物品种器官的最终大小基本是一致的, 这表明植物器官的生长发育受到精确的调控(Granier和Tardieu 2009)。植物器官的形成是器官原基逐渐发育形成成熟器官的过程; 从细胞学水平上看, 植物器官的生长可以分为两个相互协调的过程: 细胞增殖和细胞扩张(Horiguchi等2006)。研究发现, 即使当植物细胞的增殖受到阻碍后, 植物仍可以通过增大细胞体积的补偿方式来达到器官的最终大小(Tsukaya 2002); 在许多植物组织中, 核内复制也可以使细胞获得更大的体积(Sugimoto-Shirasu和Roberts 2003)。近些年, 许多植物器官发育的生长促进因子和生长抑制因子陆续被鉴定, 为认识植物器官大小调控的机理奠定了基础。

植物的发育从受精卵的最初分裂开始, 经历

种子萌发、营养体形成、生殖体形成、开花、传粉与受精、结实和衰老死亡等阶段。在植物发育过程中, 分生组织细胞功能的分化形成了不同组织和器官原基, 随后的生长过程则导致植物细胞、组织和器官在数量上的不可逆的增加(Anastasiou和Lenhard 2007; Leever和McNeill 2005)。与动物不同是, 植物在特定的部位保留具有分生能力的细胞群, 可以在一生中不断地形成新的组织和器官; 譬如, 树木的根和茎可以长到很大, 但叶片和花只能长到其特定的大小(Steeves和Sussex 1989)。植物地上部分来自顶端分生组织产生的器

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官原基的生长和分化, 首先, 在顶端分生组织叶原基起始区域生长素浓度增加, 同时果胶酶含量降低细胞壁变松弛有利于叶原基的起始(Benková等2003; Cosgrove 2005; Peaucelle等2011; Reinhardt等2003; Schopfer 2006); 叶原基形成后, 其中的细胞进行增殖, 随着器官的生长, 位于原基顶端的细胞增殖停止, 细胞开始扩张; 而叶片基部区域所有细胞增殖仍在持续进行, 伴随着更多远端增殖区细胞进入细胞扩张期(Donnelly等1999); 之后, 分散的分生组织细胞(如气孔细胞、导管前体细胞等)继续增殖; 最后, 叶片基部细胞增殖区消失, 叶片以细胞扩张方式持续生长直到其达到的最终大小(White 2006; Timmermans 2010)。因此, 在植物器官的生长发育过程中, 细胞增殖和细胞扩张进程可以交替进行。

植物器官发育到特定的大小是植物体适应外界生存环境长期进化的结果; 大量的实验证实, 植

物器官大小是由多基因控制的复杂的性状, 其调控可能涉及到多组分、多途径的复杂基因网络(Huang等2010; Zhao等2011)。近年来, 在拟南芥和水稻等植物中分离到多个控制植物器官大小的基因, 使此领域的研究成为了植物发育研究一个重要组成部分。本文以拟南芥为例, 从植物激素、泛素途径、细胞色素P450蛋白、microRNA和其他作用因子五个方面介绍植物器官大小控制因子的最新研究进展(图1)。

1 植物激素参与调控植物器官大小

植物激素是植物自身代谢产生的一类微量有机物质, 在极低浓度下就有显著的生理效应, 包括生长素(auxin)、细胞分裂素(cytokinin, CTK)、油菜素甾醇(brassinosteroid, BR)和赤霉素(gibberellin, GA)等, 它们分别或相互协调共同调控植物的生长、分化以及发育等过程(Santner等2009; Wolters和Jürgens 2009)。

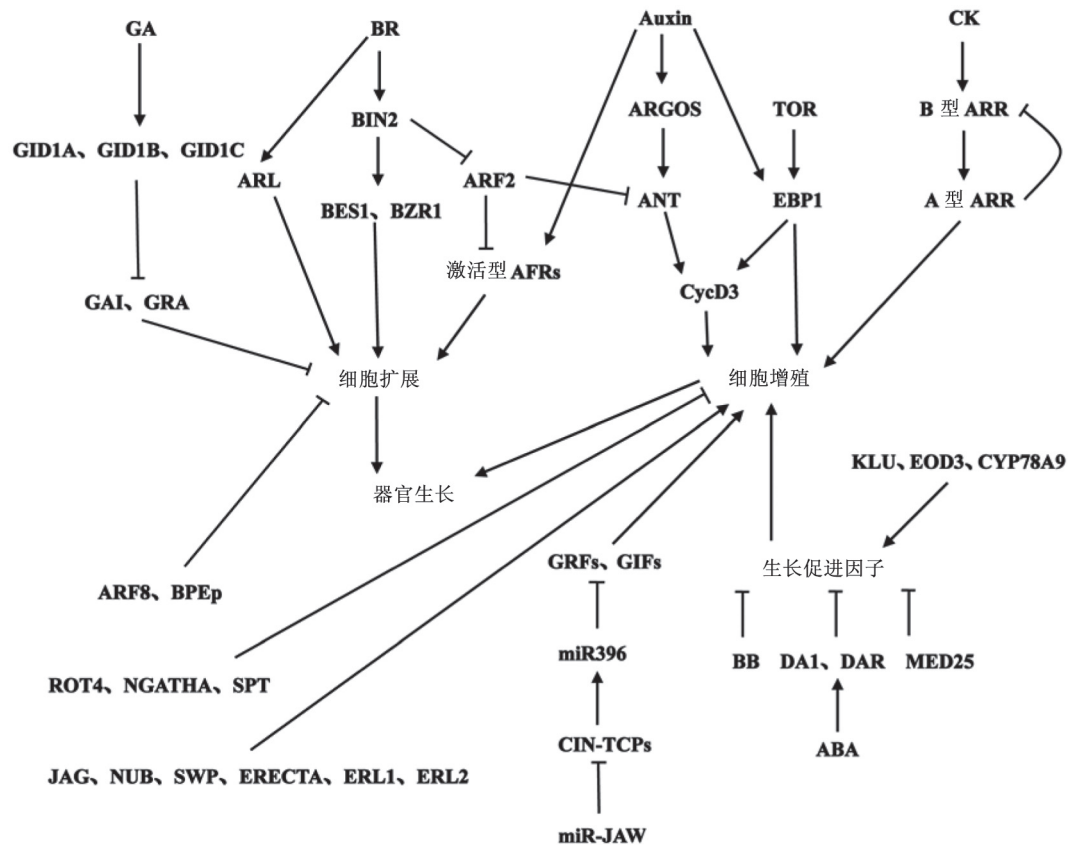


图1 拟南芥中参与调控器官大小的因子

Fig.1 Genetic factors involved in the regulation of organ size in *Arabidopsis thaliana*

在植物的发育过程中,生长素可以通过多个途径来调控植物器官的大小。生长素级联信号可以通过调控与细胞生长相关EBP1 (ERBB-3 BINDING PROTEIN 1)的稳定性来控制器官大小。拟南芥*EBP1*基因编码一个细胞生长调节蛋白,参与核糖体的组装并抑制转录起始因子eIF2的磷酸化,调控细胞增殖生长的速率和持续时间(Eguchi等2006; Gingras等2001; Squatrito等2006; Zhang等2005)。同时,*EBP1*的表达还受TOR (*TARGET OF RAPAMYCIN*)的调控,过量表达*EBP1*和TOR都会引起植物叶片等器官的变大(Horváth等2006; Deprost等2007; Menand等2002; Wullschlegler等2006)。*ARGOS* (*AUXIN-REGULATED GENE INVOLVED IN ORGAN SIZE*)基因受生长素诱导,参与器官大小调控,过量或降低表达*ARGOS*基因分别产生较大或较小的侧生器官(Hu等2003; Dewitte等2007)。*ANT* (*AINTEGUMENTA*)基因位于*ARGOS*下游,编码具有AP结构域的转录因子,调节侧生器官原基的起始和生长(Elliott等1996; Klucher等1996),过量表达*ANT*增加叶片、花序和花等器官的大小(Krizek 1999; Mizukami和Fischer 2000)。生长素可诱导*ARF2* (*AUXIN RESPONSE FACTOR 2*)基因的表达(Schruff等2005),*ARF2*编码一个生长素响应转录因子,通过抑制细胞增殖和细胞扩展,调控器官大小。*ARF2*在生殖器官中表达,*ARF2*功能缺失产生较大的花器官和种子等表型(Okushima等2005; Ellis等2005)。

CTK可调控茎顶端和根分生组织的活性,影响器官大小。植物中细胞分裂素的水平主要受*IPT* (*ISOPENTENYL TRANSFERASE*) (Medford等1989; Takei等2001; Haberer和Kieber 2002)和*CKX* (*CYTOKININ OXIDASE/DEHYDROGENASE*) (Galuszka等2007; Werner等2001; Ashikari等2005)基因的调控。在烟草中过量表达*AtIPT*,植物顶端优势降低,根生长受到抑制;过量表达*AtCKX*,抑制植物地上部分生长,促进根的生长(Werner等2001)。细胞分裂素信号可以由A型和B型ARRs (*ARABIDOPSIS RESPONSE REGULATORS*)蛋白传递并激活下游生长调节基因的表达,来促进细胞的增殖(Ashikari等2005; Dello iolo等2007)。

BR参与调控植物器官发育的许多过程。BR

级联信号促使BIN2去磷酸化使其失活,解除BIN2对转录因子BES1/BZR1的抑制,使其具有转录活性从而调控下游生长调节因子的表达。BR激活的BIN2可磷酸化ARF2使其丧失DNA结合能力,使其他激活型的ARFs有更多机会结合生长素应答基因调控植物器官大小(Vert等2008; Hardtke 2007; Halliday 2004)。BR可诱导*ARGOS*同源基因*ARL* (*ARGOS-LIKE*)的表达,*ARL*位于*BRI1* (*BR INSENSITIVE 1*)的下游,过量表达*ARL*基因促进细胞扩张从而产生较大的侧生器官,如叶片和子叶等(Hu等2006; Gendron和Wang 2007)。

GA在植物器官发育中起重要作用,可以打破种子休眠和促进长日植物开花等。GA可通过其受体GID1A、GID1B和GID1C促进生长抑制蛋白DELLA的降解,解除DELLA蛋白对下游GA响应基因的抑制,促进植物器官的发育(Jasinski等2008; Achard等2009)。在拟南芥中DELLA蛋白包括GAI (*GIBBERELLIN INSENSITIVE*)、RGA (*REPRESSOR OF GA1-3*)、RGL1 (*RGA-LIKE 1*)、RGL2和RGL3。遗传分析表明,GAI和RGA协同抑制植物体节间的伸长、远轴面毛状体的突起及叶片的扩展;RGL1和RGL2则抑制种子的萌发(Ubeda-Tomás等2009; Silverstone等2001; Wang和Deng 2011)。另外生长素可诱导GA的生物合成,共同调控器官的大小。

2 泛素途径参与调控植物器官大小

泛素途径是生物体重要的、有高度选择性的蛋白质降解途径,由泛素激活酶、泛素结合酶、泛素蛋白连接酶和26S蛋白酶体组成,参与并调控植物生长发育的多个方面,如植物激素信号、形态建成和器官发育等(Attaix等2002; Azevedo等2001)。

BIG BROTHER (*BB*)基因编码一个泛素蛋白连接酶,该基因缺失时产生较大的花器官和较粗的茎;过量表达*BB*基因产生较小的花器官和叶片(Disch等2006)。进一步研究发现,*BB*基因调控生长促进因子的降解,抑制细胞的增殖;伴随着*BB*基因的表达,生长促进因子在器官中的水平逐渐降低,当生长促进因子的水平降低到一定程度时器官的生长就会停止(Disch等2006)。

泛素受体也是细胞内泛素信号的重要组分,

受体的N端具有一个类泛素结构域以及一个至多个泛素结合结构域。泛素受体可以结合多泛素化的蛋白质并将其携带至蛋白酶体进行降解(Hoeller等2006; Di Fiore等2003)。

*DAI*基因编码一个泛素受体,通过抑制细胞持续增殖生长的时间,调控器官大小(Li等2008)。由于单碱基的替换*dal-1*突变体表达DAI^{R358K}蛋白,该蛋白能负调控*DAI*和*DAR* (*DAI-RELATED*)基因的表达,促进细胞增殖产生较大的叶片、角果和花等表型;在拟南芥野生型中过表DAI^{R358K} cDNA同样产生较大的种子和器官。此外,*DAI*基因的表达受ABA诱导,表明*DAI*基因可能联系环境信号来影响器官大小(Li等2008)。

3 细胞色素P450蛋白参与调控植物器官大小

细胞色素P450 (CYP450)蛋白是广泛存在于动植物及细菌等细胞内,与内质网、线粒体、高尔基体等细胞器膜结合的一类具有多种功能的血红素氧化酶家族,参与多种类型的氧化反应,在植物器官发育中具有重要功能(Chapple 1998; Luien等1999; Haudenschild等2000)。

*KLU*基因编码一个细胞色素P450单加氧酶CYP78A5 (Anastasiou等2007)。*CYP78A5*功能缺失突变体*klu*在发育过程中细胞的有丝分裂提前终止,产生较小的器官;而过量表达*KLU*则产生较大的种子和花器官(Adamski等2009)。研究发现,*KLU*基因的作用与已知的植物激素或其它调控植物生长的母体因子的作用方式不同,是一条新的控制种子大小的调控途径。进一步研究发现,*KLU*蛋白本身并不具有移动性,它的作用可能是通过调节其下游某些可移动生长因子(mobile growth factor, MGF)实现的(Adamski等2009; Kazama等2010; Anastasiou等2007)。

在最新研究中,李云海课题组筛选到*dal-1*的另一个增强子*eod3-1D*,*EOD3*基因编码细胞色素P450单加氧酶CYP78A6 (Fang等2012)。过量表达*EOD3*能显著增加野生型植株种子的大小;而*EOD3*基因功能缺失突变体则形成较小的种子。*EOD3*调控种子大小主要是通过影响珠被细胞的大小来实现,但是*EOD3*基因不在珠被和种子中表达,这提示*EOD3*可能产生某些可移动的生长物质,从其他组织移动到珠被中发挥功能。*EOD3*同源

基因*CYP78A9*功能的缺失能协同地增强*eod3*小种子的表型,表明*EOD3*基因和*CYP78A9*基因功能冗余地影响种子器官的大小(Fang等2012)。

4 microRNA参与调控植物器官大小

MicroRNA (miRNA)是一类20~24 nt的非编码小RNA,通过与靶基因mRNA特异序列互补配对,抑制其表达或者使其降解(Schwab等2005)。在植物组织形态建成、器官发育和信号转导等方面发挥着重要功能(Shukla等2008; Garcia 2008)。

拟南芥*miR319*靶向作用于TCP转录因子家族部分成员(*TCP2*、*TCP3*、*TCP4*、*TCP10*和*TCP24*)来调控植物的生长发育。研究发现在*jaw-D*突变体中可以增加*miR319*的表达,miR319的增加抑制这些TCP基因的表达,从而导致植物叶片边缘细胞分裂加快,叶片边缘呈现波浪状(Palatnik等2003; Nag等2009)。金鱼草中,*CIN*基因也编码一个TCP转录因子家族成员,*cinnata* (*cin*)突变体具有与*jaw-D*突变体相似的发育表型(Nath等2003)。

拟南芥*miR396*可调控*GROWTH-REGULATING FACTOR* (*GRF*)家族中的7个成员(*GRF1*、*GRF2*、*GRF3*、*GRF4*、*GRF7*、*GRF8*和*GRF9*)的表达(Rodriguez等2010)。过量表达*miR396*导致植株矮小、叶片变窄及花器官发育异常等表型,推断是由于*miR396*通过调控*GFR*基因的活性以及细胞周期基因的表达,控制器官中细胞的数目,最终决定器官的大小(Lee等2009; Kim等2003; Kim和Kende 2004)。最新研究发现,*miR396*还能调控bHLH (BACIS HELIX-LOOP-HELIX)转录因子家族成员,过量表达miR396结合位点同义突变的*rb-HLH74*导致植株叶片变窄,叶脉也发生显著的变化;而功能缺失突变体*bhlh74*叶片变大变圆(Debernardi等2012)。*TCP4*能抑制*miR396*的表达,从而上调*GRFs*基因的表达,*GRFs*基因通过与转录共激活基因*GIF* (*GRF-INTERACTING FACTOR*)互作共同调控器官大小(Horiguchi等2005)。同时还有研究表明,microRNA也可通过调控植物激素的生物合成和降解调节器官大小(Zhang等2011)。

5 其他调控器官大小的因子

植物组织除顶端分生组织外,还存在具有分生能力的单个细胞称为分散分生组织细胞(dispersed meristematic cells, DMCs),如气孔细胞、导

管前体细胞等, 这些细胞的增殖受到*PPD1* (*PEA-POD1*)和*PPD2*的调控; *ppd1ppd2*双突变体由于*PEAPOD*基因功能缺失导致DMCs持续增殖产生较大的钟形叶片(White 2006)。

BPEp (*BIGPETALp*)基因编码一个bHLH转录因子, 通过限制细胞的扩张调节器官大小, 因此*bpe-1*突变体产生较大的花瓣。*arf8*突变体产生比*bpe*更大的花瓣, *bpearf8*分析表明在花瓣发育早期*BPEp*和*ARF8*协同限制细胞的有丝分裂生长; 而在花瓣发育后期*BPEp*和*ARF8*相互作用限制细胞扩张, 从而调控花瓣的最终大小(Szécsi等2006; Vauraud等2011)。

MED25 (*MEDIATOR COMPLEX SUBUNIT 25*)基因编码中介复合体亚基25, 中介复合体是转录因子和RNA聚合酶II相互作用的桥梁, 调控基因的转录。*MED25*基因突变导致细胞增殖和细胞扩张的时间延长形成较大的器官; 而过量表达*MED25*则引起细胞数目和细胞体积的降低形成较小的器官(Xu和Li 2011)。

拟南芥受体样激酶(RECEPTOR-LIKE KINASE, RLK) *ERECTA*、*ERL1* (*ERECTA-LIKE 1*)和*ERL2*可通过调控细胞增殖来决定地上器官的大小(Shpak等2004); *NUBBIN*和*JAGGED*以冗余的方式调控雄蕊和心皮的大小(Dinneny等2006); *NGATHA* (*NGA1-NGA4*)和*STYLISH1*参与调控侧生器官和花柱的发育(Alvarez等2009); *SPL* (*SPATULA*)则控制分生组织大小及心皮和角果的发育(Groszmann等2008; Makkena和Lamb 2013); *SWP* (*STRUWWELPETER*)通过调控细胞持续增殖的时间影响叶片发育(Autran等2002); *ROT4*基因能沿体轴影响细胞的位置信息及细胞的增殖从而调控器官大小(Ikeuchi等2011; Narita等2004)。

6 展望

植物器官发育是一个极为复杂的生理生化过程, 其中涉及大量特定发育调控基因的相互作用。近年来, 通过对大量控制植物器官大小的控制因子的鉴定和分离, 使我们对于植物器官大小调控的分子机制有了进一步深入了解。但是其中仍有许多重要的问题需要阐明, 譬如不同遗传途径的调控因子是如何整合在一起共同调节植物器官的大小? 环境信号如何协同不同的遗传因子调

节植物器官的大小? 植物器官的生长发育与器官大小决定机制又是如何有机偶联的? 相信随着研究的深入, 一个更为清晰的调控植物器官大小基因网络将会被认知。

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