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·专题论坛·

被子植物下胚轴细胞伸长的分子机理

王红飞，尚庆茂*

中国农业科学院蔬菜花卉研究所，农业部园艺作物生物学与种质创制重点实验室，北京 100081

摘要 作为一种正常的生命现象，植物下胚轴伸长是长期自然选择的结果，也是植物进行光合作用、实现自养的必要前提。但下胚轴过度伸长容易造成幼苗徒长，使植株长势弱，抗逆能力差，不利于产量提高和品质改良。该文综述了被子植物下胚轴的发育过程、下胚轴伸长的细胞学机制、植物激素及环境信号调控下胚轴细胞伸长分子机制的最新研究进展，并展望了未来的研究方向。

关键词 下胚轴，伸长，形态建成，决定因子，分子机制

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植物下胚轴是连接子叶和根的胚性部分，由成熟胚中位于顶端和基部分生组织之间的细胞发育而成，为植物茎和根的分界区域(郑相如和范雅兰, 1998)。下胚轴承担着植物体内水分、无机盐、有机营养和植物激素等物质的运输任务，是植物进行正常生命活动的保障(姜楠等, 2014)。在种子萌发过程中，下胚轴伸长有利于将胚根推出种皮，吸收环境中的水分及营养物质，加快种子萌发(Sliwinska et al., 2009)。种子萌发后，下胚轴继续伸长，将子叶推出土层，进行光合作用。了解下胚轴的生长发育规律、下胚轴伸长的细胞学基础、环境及植物激素调控下胚轴细胞伸长的分子机制，可为深入挖掘调控下胚轴伸长的关键位点奠定基础。

1 下胚轴的发育过程

植物下胚轴发育经历了分化、初始伸长和快速伸长3个阶段。下胚轴分化在母体植株上进行，主要由细胞分裂和分化引起。下胚轴的初始伸长和快速伸长主要发生在个体植株上，此时细胞分裂和伸长对下胚轴伸长的贡献率因植物种类和生长环境而异。

1.1 分化期

下胚轴源于八分体胚时期的下层细胞。在植物胚胎发生过程中，受精卵(合子)首先经过1次横向分裂(部分植物为纵、斜向分裂)，形成2个具有极性的子细胞，其中靠近珠孔的为基细胞，远离珠孔的为顶细胞。顶细胞经过1次横向分裂和1次纵向分裂，形成四分体胚。四分体胚进一步横向分裂形成八分体胚，分为上层细胞和下层细胞。上层两侧细胞生长较快，发育为子叶，2片子叶间细胞发育为胚芽；下层细胞发育为下胚轴和胚根(Scheres et al., 1994; Laux and Jürgens, 1997; 宋丽珍等, 2013)。此后八分体胚细胞进行平周分裂，表层细胞分化形成原表皮，形成16个细胞的原胚。原胚细胞进一步分裂形成具有原表皮的幼胚(32个细胞)，此时中央细胞保持分裂活性，经过1次横向分裂和1次纵向裂，形成64个细胞的球形胚。球形胚两侧细胞迅速分裂，发育成子叶原基；2片子叶间的细胞发育成茎端分生组织，此时球形胚进入心形胚发育阶段。在子叶发育的同时，胚细胞进一步分裂分化，下胚轴不断伸长，心形胚发育成鱼雷形胚，此时胚胎发育成熟，下胚轴原始形态建成。

1.2 初始伸长期

种子发育成熟后进入休眠期，在适宜的环境条件下开始萌发。拟南芥(*Arabidopsis thaliana*)、生菜(*Lactuca sativa*)、菜豆(*Phaseolus vulgaris*)和蚕豆(*Vicia faba*)种子萌发时，下胚轴迅速伸长，促使胚根突破种皮，萌发结束(Srivastava and Paulson, 1968; Obroucheva

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* 通讯作者。E-mail: shangqingmao@caas.cn

et al., 1995; Yamaguchi et al., 2001; Antipova et al., 2003)。细胞分裂和伸长均可导致下胚轴伸长，但细胞分裂多存在于拟南芥和油菜(*Brassica napus*)胚胎发生过程中。在种子萌发时，胚细胞分裂活性逐渐降低，萌发结束后，细胞分裂仅局限于茎端和根端分生组织(Raz and Koornneef, 2001; Barrôco et al., 2005)。下胚轴基部细胞是拟南芥种子萌发过程中最先伸长的细胞，随后伸长区沿下胚轴和下胚轴-胚根转换区上下移动，直至将胚根推出种皮，此时下胚轴和胚轴-胚根转换区细胞分别伸长至原来的152%和208%，而胚根细胞长度仅为原来的115% (Sliwinska et al., 2009)。

1.3 快速伸长期

种子萌发结束后，幼苗快速生长。子叶留土植物下胚轴停止伸长，通过上胚轴伸长将植物叶片推出土层，进行光合作用；而子叶出土植物下胚轴快速伸长，将子叶和胚芽送出土面，进行光合作用。此时细胞分裂和伸长对下胚轴伸长的贡献率因植物种类和生长环境而异。拟南芥下胚轴较短，形态结构简单，纵向结构包含20多层细胞，多数细胞在胚胎时期分裂形成，仅少数细胞在种子萌发后由细胞分裂形成，因此细胞伸长是引起拟南芥下胚轴伸长的主要原因(Scheres et al., 1994; 姜楠等, 2014; Boron and Vissenberg, 2014)。拟南芥*LKP2* (*LOV KELCH PROTEIN 2*)过表达植株的下胚轴、表皮细胞和皮层细胞长度分别为对照(Columbia)的2.9、2.9和1.8倍。与野生型相比，其表皮细胞数量未发生变化，而皮层细胞数量增至1.4倍(Miyazaki et al., 2011)。Kutschera和Niklas (2013)认为，在黑暗条件下向日葵(*Helianthus annuus*)下胚轴顶端分生组织细胞不断分裂，纵向细胞数量增多，下胚轴基部细胞显著伸长，细胞分裂与细胞伸长共同导致向日葵下胚轴伸长。弱光(40 μmol·m^{-2}·s^{-1})条件下，黄瓜(*Cucumis sativus*)下胚轴伸长主要由细胞伸长引起，而在强光(120 μmol·m^{-2}·s^{-1})条件下，细胞分裂与细胞伸长共同导致其下胚轴伸长(López-Juez et al., 1995)。

种子萌发结束后，拟南芥下胚轴的20余层细胞间生长速率不一致，引起下胚轴伸长的动态学变化。下胚轴伸长经历2个阶段，第1阶段(种子萌发至生长48小时)，下胚轴全部细胞均以<0.1 mm·h^{-1}的速率同步生长；第2阶段(生长48小时以后)，生长速率加快且伸长区由基部向上部转移(Refrégier et al., 2004)。拟南芥种子光照4小时诱导萌发后转至黑暗条件下生长48小时，测定下胚轴细胞长度，发现下胚轴基部5、6层细胞显著伸长；生长72小时，伸长区上移至12、13层细胞处；而生长96小时，细胞伸长区延伸至第16及17层细胞(Paque et al., 2014)。拟南芥下胚轴表皮细胞在生长期内持续生长，先是基部第1层细胞快速伸长，后伸长速率降低，接着第2层细胞快速伸长，依次类推，在萌发后3–5天内生长速率达到最大，为0.3–0.4 mm·d^{-1} (Gendreau et al., 1997)。生长120小时的黄瓜幼苗，其下胚轴顶部与基部细胞壁的延展性不同，顶部细胞壁延展性显著高于基部细胞，而基部细胞壁的延展性不受酸性条件诱导，表明基部细胞已经停止生长，此时下胚轴伸长主要由上部细胞伸长引起(Pereyra et al., 2010)。

2 下胚轴伸长的细胞学机制

2.1 膨压

膨压是胞质内水分流动对细胞壁产生的压力，在菌类和高等植物细胞生长过程中，膨压能促使细胞壁松弛及新细胞壁组分渗入，从而促进细胞膨大(Proseus and Boyer, 2005, 2006a, 2006b; Schopfer, 2006; Lew, 2011; Chen et al., 2015)。轮藻(*Chara corallina*)节间细胞及向日葵叶细胞膨压增加0.05–0.1 MPa，细胞生长速率提高2倍(Boyer, 2009)。萝卜(*Raphanus sativus*)子叶细胞膨压在0.3–0.6 MPa范围内增大，细胞纵径显著加大，而细胞膨压大于0.5 MPa时，能够显著提高细胞数量(Kirkham et al., 1972)。花粉管伸长是典型的顶端生长，其顶端细胞伸长受膨压影响，在生长停滞之前，其伸长速率与细胞膨压大小成正比，当膨压低于临界值时，伸长停止(Zerzour et al., 2009; Kroeger et al., 2011)。

膨压的变化与液泡内渗透调节物质含量相关，蔗糖、葡萄糖和果糖是细胞内主要的渗透调节物质。在下胚轴细胞伸长过程中，液泡内贮藏的蔗糖在酸性转化酶的作用下，分解成葡萄糖和果糖，导致渗透调节物质含量增加，渗透势增大，细胞吸水膨胀，推动纤维多糖蠕动，从而促进细胞生长(Kutschera, 2000)。

2.2 细胞壁延展性

细胞壁是植物细胞的屏障，对维持细胞形状有重要作

用(Szymanski and Cosgrove, 2009; Kutschera and Niklas, 2013)。植物初生细胞壁主要由纤维素、半纤维素和果胶等构成，其对环境的适应、胁迫的应答以及激素的响应最终会在细胞壁的成分和结构上体现出来(张保才和周奕华, 2015)。细胞的生长方向由内切向壁纤维素微纤丝排列方向决定(Baskin, 2005; Crowell et al., 2011; Xiao et al., 2016)，半纤维素糖基组成及含量对纤维素排列方向有重要影响(Park and Cosgrove, 2015; Xiao et al., 2016)。果胶的糖基组成对细胞壁孔隙度和延展性有重要影响(Dick-Pérez et al., 2011; Xiao et al., 2014)，其甲酯化程度与细胞的可塑性相关，低于60%时，细胞不能进行正常的伸长生长(Derbyshire et al., 2007)。

细胞壁的延展性受两大蛋白家族——膨胀素(expansin)和木葡聚糖内转糖苷酶(xyloglucan endotransglucosylase/hydrolase, XET/XTH)的调控(Van Sndt et al., 2007)。膨胀素在酸性条件下能弱化细胞壁多糖之间的非共价键，导致纤维素聚合体在膨压驱动下蠕动，促使细胞膨大(Cosgrove, 2000, 2005)。依据蛋白质结构特征XET/XTH可分为3类：I和II类具有转糖基酶活性，催化木葡聚糖分子自身连接；III类具有水解酶活性，专一性水解木葡聚糖β-1,4糖苷键(杜丽萍等, 2010)。*XTH*在根细胞中表达，能够促使细胞壁疏松，引发根毛的起始(Vissenberg et al., 2005)。*XET*/*XTH*过表达植株的下胚轴和茎尖细胞生长速率显著加快(Ookawara et al., 2005; Liu et al., 2007; Genovesi et al., 2008)。

3 植物激素调控下胚轴细胞伸长的分子机制

3.1 生长素

生长素(IAA)是最早发现的一类植物激素，对植物胚胎发育、器官发生和配子体形成等生长发育过程具有重要调控作用(宋丽珍等, 2013; 翟开恩等, 2015)。IAA合成途径分为2种：从头合成途径和依赖色氨酸的合成途径。依赖色氨酸的合成途径又可以根据中间代谢产物的丰度分为：色胺(tryptamine)途径、吲哚乙醛(indole-3-acetaldoxime, IAOx)途径、吲哚乙酰胺(indole-3-acetamide, IAM)途径和吲哚丙酮酸(indole-3-pyruvic acid, IPA)途径(Woodward and Bartel, 2005; Lehmann et al., 2010; Zhao, 2010; 王家利等, 2012; Kasahara, 2015)。其中吲哚丙酮酸途径中色氨酸转氨酶基因*TAA1* (*TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1*)及类黄素单加氧酶基因*YUC8*/*9* (*YUCCA8*/*9*)是生长素合成的限速酶基因(Mashiguchi et al., 2011)。

TIR1 (transport inhibitor response 1)是IAA的核受体，在IAA信号传递过程中发挥关键作用(Dharmasiri et al., 2005)。TIR1与ASK1 (Arabidopsis Skp1-like 1)、ASK2 (Arabidopsis Skp1-like 2)及Cullin形成SCF^{TIR1}复合体，参与生长素应答反应。植物体内IAA含量较高时，其侧链羧基端与TIR1结合，进而促进AUX/IAAs (Auxin Response Factor)蛋白结合到SCF^{TIR1}-Auxin复合体中的IAA上，形成SCF^{TIR1}-Auxin-AUX/IAAs复合体，导致AUX/IAAs蛋白的泛素化降解，解除其对*ARF* (*Auxin Response Factor*)的转录抑制作用(Tan et al., 2007)。ARF是一类转录因子，通过激活或抑制靶基因的表达影响下胚轴细胞伸长(Oh et al., 2014; Challa et al., 2016)。*GH3* (*Gretchen Hagen 3*)是另一类生长素早期响应基因，其编码蛋白具有生长素氨基酸化合成酶活性。当植物体内IAA浓度增加时，GH3蛋白能够促进游离态IAA与氨基酸结合，然后经降解途径降解，以维持IAA的动态平衡，实现其对下胚轴细胞生长的调控(Zheng et al., 2016)。此外，生长素可以影响细胞壁延展性和膨压。生长素促使H^+-ATPase C-末端倒数第2个苏氨酸磷酸化，活化H^+-ATPase，向外泵出质子，酸化细胞壁，增强细胞壁的可塑性。此外，细胞壁中的膨胀素蛋白在酸性条件下作用性增强。IAA对H^+-ATPase活性的调控不受TIR1介导的信号转导影响(Takahashi et al., 2012)，也不引起H^+-ATPase编码基因*AHA1*与*AHA2*表达量的变化(Hayashi et al., 2010)。液泡膜上H^+-ATPase活化，将胞质内H^+泵入液泡内，激活酸性转化酶，将蔗糖分解成葡萄糖和果糖，胞内渗透势大于外界渗透势，水分内流，膨压增大。同时，TIR1介导的生长素信号转导能促使质膜上的K^+通道蛋白基因*KAT1* (*K^+ transporter of Arabidopsis thaliana 1*)表达量升高，导致细胞对K^+的吸收量增加，渗透势增加，细胞吸水，膨压增大，进而推动细胞膨大(Philippar et al., 2004)。

3.2 赤霉素

赤霉素(GA)主要通过调控DELLA蛋白含量影响下胚

轴细胞伸长。DELLA蛋白是GA信号传递的关键作用元件, 能与PIFs (PHYTOCHROME INTERACTING FACTORs)结合, 导致PIFs的转录激活作用受到阻遏(De Lucas et al., 2008; De Lucas and Prat, 2014)。PIFs是一类bHLH类转录因子, 通过促使生长素合成关键酶基因*YUC8*/*9*的表达上调影响下胚轴伸长, 从而抑制光形态建成(Franklin et al., 2011; Mashiguchi et al., 2011; Sun et al., 2012)。植物体内GA含量增加后, 与受体GID1 (GA INSENSITIVE DWARF1)结合并识别与PIFs结合的DELLA蛋白, 诱导DELLA蛋白泛素化降解, 解除其对PIF3/4/5的抑制作用(Feng et al., 2008; Sun, 2010)。

3.3 油菜素内酯

油菜素内酯(BR)与膜受体激酶BRI1 (BRASSINOSTEROID INSENSITIVE1)结合, 通过一系列磷酸化与去磷酸化反应, 激活细胞核内的转录因子BZR1/BZR2, 活化的转录因子能调控靶基因的表达, 影响植物生长发育(Kim and Wang, 2010; Clouse, 2011; Oh et al., 2012)。BZR1 (Brassinozale-Resistant 1)与PIF4直接互作形成异源二聚体, 调控基因表达, 其中包括编码HLH蛋白的*PREs* (*paclobutrazol resistance factors*)基因家族。当*PRE1*、*2*、*5*和*6*表达量降低时, 植株表现出矮小、叶片深绿及育性降低等性状; 过表达*PRE1*能抑制*pifq*突变体矮化表型的出现, 促进植株下胚轴伸长(Bai et al., 2012; Oh et al., 2012)。

此外, BR能强化碳水化合物对黑暗条件下拟南芥(包括野生型Col-0、BR合成突变体*det2-1*和BR不敏感突变体*bri1-5*)下胚轴伸长的促进作用, 但对BR超敏突变体(*bzr1-1D*和*bes1-D*)不起作用, 表明这种强化作用并不是通过改变内源BR含量引起的。进一步的实验结果表明, BR与可溶性碳水化合物协同上调BZR1与BES1 (bri1-EMSSUPPRESSOR 1) 2个转录因子的表达, 进而促进下胚轴伸长(Zhang et al., 2015)。

3.4 脱落酸

脱落酸(ABA)对细胞伸长的调控作用与生长素相拮抗。一方面脱落酸能促使H^+-ATPase C-末端倒数第2个苏氨酸去磷酸化, 抑制H^+-ATPase活性, 细胞酸性生长受到抑制, 膨胀素和酸性转化酶活性降低, 细胞壁延展性和渗透势降低, 不利于细胞生长。ABA对H^+-ATPase活性的抑制作用主要依赖于生长素早期响应基因*SAUR* (*SMALL AUXIN UP-RNA*) (Ren and Gray, 2015)。SAUR能够与PP2C-D磷酸酶直接互作并抑制其活性, 从而促使H^+-ATPase活性提高(Spartz et al., 2014)。另一方面, 脱落酸信号转导蛋白ABI1 (ABA-insensitive 1)能抑制K^+内流通道蛋白基因*KAT1*的表达。作为植物细胞内的主要渗透调节物质之一, K^+的内流量降低, 细胞渗透势和吸水能力随之降低, 不利于细胞膨大(Hayashi et al., 2014)。

3.5 独脚金内酯

独脚金内酯(strigolactones, SLs)是一类萜酯化合物, 作为一种新型植物激素, SLs对植物分枝生长、侧根的形成及下胚轴伸长等生长发育过程均具有重要调控作用(Umehara et al., 2008; Kapulnik et al., 2011; Brewer et al., 2013)。SLs对下胚轴伸长的抑制作用主要依赖于蓝光及红光/远红光受体介导的信号转导过程。SLs通过信号转导蛋白MAX2 (MORE AXILLARY GROWTH 2)促使光信号转导关键因子HY5 (LONG HYPOCOTYL5)表达上调, HY5蛋白积累能促使植物光形态建成, 抑制下胚轴伸长(Waters et al., 2012; Jia et al., 2014)。

4 环境信号调控下胚轴细胞伸长的分子机制

温度、光及水分作为植物赖以生存的环境条件, 既能单独发挥作用, 又能协同作用, 调控下胚轴伸长, 但不同环境因子的作用机制却不尽相同(Toledo-Ortiz et al., 2014)。国内外众多学者针对温光信号对下胚轴生长的影响进行了深入研究, 揭示了环境信号调控下胚轴伸长的分子机制(Josse et al., 2008; Franklin and Quail, 2010; Sun et al., 2012; Ma et al., 2016)。

4.1 光信号

光信号的感知与传递主要依赖光受体, 包括红光/远红光受体PHYs (Phytochromes)以及蓝光受体CRYs (Cryptochromes)等(Josse et al., 2008; Franklin and Quail, 2010; Möller et al., 2010; Casal, 2013)。目前已发现5种红光/远红光受体PHYA–E。PHYs受光激

发后，由生理失活型Pr转化为生理活跃型Pfr，同时由细胞质向细胞核迁移并在细胞核中发挥作用，促进光形态建成(Kircher et al., 1999)。PHYA的Pfr态不稳定，转化后迅速降解，PHYB–E的Pfr态能在光下稳定存在(Clack et al., 1994; Franklin et al., 2003)。拟南芥体内存在2种蓝光受体，即CRY1和CRY2，CRY1在蓝光下稳定存在，CRY2遇光(蓝光、绿光和紫外光)迅速降解，但二者在光信号转导过程中功能相似(闫海芳等, 2004)。

4.1.1 光质

受远红光/红光激发，PHYA/B转化为生理活跃型Pfr，在细胞核中与光敏色素互作蛋白PIFs结合，诱导PIFs磷酸化降解(Nozue et al., 2007; Shen et al., 2007; Leivar et al., 2008; Jeong and Choi, 2013)。PIFs是一类bHLH转录因子，PIFs磷酸化降解导致生长素合成限速酶基因*TAA1*和*YUC8*/*9*的表达下降，IAA的合成量减少，对下胚轴伸长的促进作用减弱(Möller et al., 2010; Wu et al., 2012; Leivar and Monte, 2014)。此外，PHYA和PHYB生理激活型向细胞核中迁移后，与SPA1 (SUPPRESSOR OF PHYTOCHROME A 1)结合，抑制COP1 (CONSTITUTIVE PHOTOMORPHOGENIC 1)/SPA1复合体的泛素(E3)连接酶活性，从而导致COP1/SPA1的靶蛋白HY5在细胞核中积累，而HY5是光形态建成的正调控因子，能抑制下胚轴细胞的伸长(Lu et al., 2015; Srivastava et al., 2015)。蓝光对下胚轴伸长的调控机制与红光相同，一方面CRY1和CRY2与PIF4和PIF5直接作用，阻遏PIFs对下游基因的转录激活作用，抑制下胚轴细胞伸长(Pedmale et al., 2016)；另一方面CRY1与COP1/SPA1复合体中的SPA1直接结合，导致复合体中的E3连接酶活性降低，HY5转录因子积累，从而促进光形态建成(Weller et al., 2001; Lian et al., 2011; Liu et al., 2011; Lau and Deng, 2012)。

4.1.2 光照强度

光强与光质调控下胚轴细胞伸长的机制相同，主要是通过光受体PHYA、PHYB、CRY1和CRY2调控PIFs，进而影响下游基因的表达，从而实现对下胚轴伸长的调控。此外，光受体通过抑制COP1的泛素连接酶活性，导致HY5转录因子及相应的靶基因表达上调，促使光形态建成(Reed et al., 1993; Park et al., 2007; Chia and Kubota, 2010; Procko et al., 2014)。

4.1.3 光周期

光周期对下胚轴细胞生长的调控，主要依赖于ELF4 (EARLY FLOWERING 4)-ELF3-LUX (LUX ARRHYTHMO)复合体(evening complex, EC) (Nusinow et al., 2011)，EC复合体能与*PIF4*/*5*的启动子直接结合，导致其转录表达受到抑制。植物对光周期的感知主要依赖于光受体PHYA/B和CRY1/2 (Yu et al., 2008)，并通过光受体活性影响细胞中COP1的活性。COP1能抑制EC复合体的形成，解除其对下游转录因子PIF3/4/5的抑制作用，促使PIFs表达量升高，从而促进下胚轴细胞伸长(Seaton et al., 2015)。植物表皮细胞率先感知外界的光周期信号，并通过CBF (C-REPEAT BINDING FACTOR)等受体传递给叶肉和脉管组织细胞，实现不同组织细胞的协同生长(Dong et al., 2011; Shimizu et al., 2016)。

4.2 温度信号

高温调控下胚轴伸长的机制与光信号相同，主要依赖于光受体PHYB (Koini et al., 2009; Kumar and Wigge, 2010; Delker et al., 2014)。高温促使细胞核中PHYB由生理活跃型Pfr向生理失活型Pr转变，并向细胞质中迁移(Legris et al., 2016; Halliday and Davis, 2016; Jung et al., 2016)，从而解除其对PIFs及COP1-SPA的抑制作用。一方面PIFs促使生长素合成酶基因表达上调，诱导下胚轴细胞伸长；另一方面COP1-SPA复合物的E3泛素连接酶活性升高，导致bZIP转录因子HY5降解，从而抑制光形态建成基因的表达，同时解除其对PIFs转录抑制作用(Nixdorf and Hoecker, 2010; Lau and Deng, 2012; Delker et al., 2014)。PIF4/5是生长素合成关键酶基因*YUC8*/*9*及*TAA1*的转录激活因子，*YUC8*/*9*及*TAA1*的表达上调促使IAA合成量增加，下胚轴伸长速率显著加快(Stavang et al., 2009; Franklin et al., 2011; Mashiguchi et al., 2011; Sun et al., 2012)。

4.3 复合环境因子

4.3.1 光照强度与温度

光照强度与温度作为最重要的环境因子，能协同调控

植物生长发育(Toledo-Ortiz et al., 2014)。红光受体PHYB对光强信号感知有重要作用，红光辐照度越大，对下胚轴细胞伸长的抑制作用越明显(Rausenberger et al., 2010; Oh et al., 2012)。高温能解除PHYB对下胚轴伸长的抑制作用，促进下胚轴伸长，但这种促进作用仅在光信号存在的条件下才能表现出来(Gray et al., 1998)。在17°C低温条件下，光照强度在0–100 μmol·m^{-2}·s^{-1}范围内增加时，能显著抑制拟南芥下胚轴伸长；当温度升高至27°C时，光照强度在0–1 μmol·m^{-2}·s^{-1}范围内增加时能显著抑制下胚轴伸长，而在1–100 μmol·m^{-2}·s^{-1}范围内增加时反而能促进下胚轴伸长(Johansson et al., 2014)。

4.3.2 光照强度与碳水化合物

植物光合作用合成的碳水化合物既能作为植物生长的能源物质，又能作为信号分子调控种子萌发、营养生长、生殖生长、果实成熟及衰老死亡等生长发育过程(Rolland et al., 2002, 2006; León and Sheen, 2003; Jiao et al., 2007; Wind et al., 2010)。可溶性糖不能单独调控植物的生长发育，需要与光信号协同发挥作用(Sairanen et al., 2012)。黑暗条件下，低浓度的碳水化合物促进拟南芥的生长(Roycewicz and Malamy, 2012)，主要通过促使GA合成关键酶基因*GA3ox1*、*GA3ox2*和*GA20ox1*的表达量上调，促进GA合成(Zhang et al., 2010)。GA通过其受体GID1促使DELLA蛋白泛素化降解，解除对PIFs和BZR1的抑制作用，从而促进下胚轴细胞伸长(Feng et al., 2008; Sun, 2010)。

5 问题与展望

下胚轴是植物的重要组成器官，下胚轴伸长是一个精细而复杂的过程。国内外众多学者利用拟南芥突变体研究了单一环境因子调控下胚轴伸长机制，但因突变体种类有限，制约了下胚轴伸长机制全面而深入的研究。此外，植物生活在复杂多变的环境中，下胚轴伸长同时受多种环境因子影响，单一环境因子的调控机制不足以揭示植物响应外界信号因子，从而调整自身代谢实现下胚轴定向生长的机理。依据目前的研究进展，未来应着重研究细胞分裂及伸长的调控机制，并掌握其在胚胎发生期、种子萌发期和幼苗生长期的下胚轴形态建成过程中的作用机理，从而全面掌握植物下胚轴的生长发育规律。其次，还需进行下胚轴伸长的多组学研究，完善环境因子调控下胚轴伸长的信号通路，分析不同环境因子的交叉调控位点，挖掘交叉位点的生物学功能，利用遗传学、分子生物学及生物化学相结合的方法实现对交叉位点的定向调控。此外，目前对下胚轴伸长机制的研究主要集中在模式植物拟南芥上，对葫芦科、茄科和十字花科等苗期易徒长蔬菜作物下胚轴伸长机制的研究相对较少，今后的研究可以围绕上述蔬菜作物展开。

随着下胚轴伸长机制研究的不断深入及基因组、蛋白质组和代谢组学的广泛应用，调控下胚轴伸长的信号转导网络将不断丰富，关键位点也将得到进一步解析，这将为人们深入了解下胚轴伸长机制奠定基础，并为解决蔬菜幼苗徒长问题提供参考。

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Molecular Mechanisms of Cell Elongation in Angiosperm Hypocotyl

Hongfei Wang, Qingmao Shang*

Key Laboratory of Horticultural Crop Biology and Germplasm Innovation, Ministry of Agriculture, Institute of Vegetables and Flowers, Chinese Academy of Agricultural Sciences, Beijing 100081

Abstract As a normal life phenomenon, hypocotyl elongation is the result of long-term natural selection as well as a necessary prerequisite for photosynthesis and autotrophy. However, leggy seedlings are weak and have poor adaptability for overelongated hypocotyls, which negatively affects yield and quality improvement. This review summarizes research and development progress, the cytological mechanism of hypocotyl elongation and the molecular regulatory mechanisms of hypocotyl elongation by hormones and environmental factors and overviews the direction of future related research.

Key words hypocotyl, elongation, morphogenesis, determinative factor, molecular mechanism

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* Author for correspondence. E-mail: shangqingmao@caas.cn

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