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·专题论坛·

植物微管骨架参与下胚轴伸长调节机制研究进展

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摘要 微管作为细胞骨架的重要成员, 在植物生长发育过程中起重要作用。下胚轴作为研究细胞伸长的模式系统之一, 其伸长受到多种信号的调节。该文综述了微管骨架在响应环境和生长发育信号调节下胚轴伸长过程中的作用及机制, 旨在帮助读者深入理解微管骨架响应上游信号在植物下胚轴伸长中的作用机理。

关键词 微管, 下胚轴, 伸长, 环境信号, 生长发育信号

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植物细胞骨架由微管和微丝组成。微管作为植物细胞骨架成员之一, 在植物生长发育过程中起重要作用(Hashimoto, 2003; Lloyd and Chan, 2004; Hashimoto and Kato, 2006)。下胚轴作为研究细胞伸长的模式器官, 其伸长既受到许多上游信号的调控也受到微管骨架的调节。早期关于下胚轴伸长的研究中, 细胞骨架和上游信号的调节处于相对独立状态。随着研究的不断深入, 发现微管受到上游信号的调控, 进而参与下胚轴伸长的调节。因此本文对近年来关于微管骨架响应环境和生长发育信号参与下胚轴伸长调节机制的研究进展进行了总结。

1 微管及其功能

微管的基本组成单位是由α-微管蛋白和β-微管蛋白构成的微管蛋白异二聚体, 微管蛋白异二聚体首尾相连并线性排列为1根原纤丝, 13根原纤丝平行排列构成中空的管状结构即为微管。植物细胞中的微管始终处于高度动态状态, 描述微管动态特性的模型有2个: (1) 动态不稳定模型。该模型认为单根微管始终处于动态不稳定状态, 单根微管的两端以一定的“收缩速率”解聚或者以一定的“生长速率”聚合, 整体的微管解聚量和聚合量相对平衡, 因此群体微管处于稳定状态(Mitchison and Kirschner, 1984); (2) 踏车模型。该模型认为单根微管一端不断解聚失去微管蛋白亚基, 另一端则有微管蛋白亚基持续聚合加在其上, 整体表现出单根微管一端不断收缩, 另一端持续生长的踏车现象, 使整根微管保持平衡状态(Margolis and Wilson, 1981)。植物细胞中动态的微管系统在细胞周期中形成4种微管列阵, 分别为间期周质微管列阵、早前期微管带、纺锤体微管列阵和成膜体微管列阵(何群和尤瑞麟, 2004; 李志刚等, 2008)。植物细胞中微管的组织动态均由微管相关蛋白(microtubule-associated proteins, MAPs)调控。

微管在植物多种生理活动中起重要作用, 如维持细胞形态、控制细胞极性生长、调控细胞有丝分裂与细胞分化以及参与囊泡运输和信号转导(Kost and Chua, 2002; Hashimoto, 2003; Lloyd and Chan, 2004; Hashimoto and Kato, 2006)。4种微管列阵随着细胞周期依次转化, 执行相应的生理功能。其中,

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周质微管列阵与植物细胞形态和生长方向等密切相关(Ehrhardt and Shaw, 2006)。在快速伸长的根或黄化下胚轴细胞中，周质微管表现为密集的横向平行排列(垂直于细胞的伸长方向) (Baskin et al., 2004)。当植物根细胞中的周质微管排列方向由横向变为左手螺旋时，植物根细胞则转变为右手螺旋方向生长，即根由向下变为向右生长；相反，植物根细胞中的周质微管排列方向由横向变为右手螺旋时，根细胞则转变为左手螺旋方向生长，即根由向下变为向左生长(Furutani et al., 2000; Thitamadee et al., 2002; Nakajima et al., 2004)。

2 下胚轴的生长特点

下胚轴是高等植物的胚性器官，指从子叶着生处以下生出的最初茎的部分。种子在土壤中萌发后，下胚轴在黑暗条件下快速伸长以破土而出，使子叶见光生长，因此下胚轴伸长过程对于植物能否见光生长至关重要。拟南芥(*Arabidopsis thaliana*)作为模式植物，其黑暗条件下生长的下胚轴(黄化下胚轴)为研究细胞伸长提供了良好的系统。拟南芥下胚轴由根(下)至子叶(上)一列表皮细胞的数目约为20个。黑暗条件下，拟南芥下胚轴不同位置的细胞生长速率会随时间发生变化，即下胚轴细胞的伸长表现出时空梯度特点。种子萌发后，主要是靠近下胚轴基部的细胞伸长，在黑暗条件下培养3天后，靠近基部1–5个细胞的长度占整个下胚轴长度的一半；继续黑暗培养至4–5天，下胚轴基部的5个细胞伸长变慢，中部的6–11个细胞以及上部的9个细胞快速伸长；黑暗生长6天后，中部及上部细胞生长速度减慢，顶端弯钩处细胞伸长；延长培养时间至7天后，下胚轴细胞的伸长基本停滞(Gendreau et al., 1997)，表明黄化下胚轴细胞的伸长受时间和空间的精确调控。

3 微管响应环境信号调节下胚轴伸长

植物因固着生长，其生长发育受到环境因素的影响。下胚轴作为植物体重要的组织器官之一，其伸长生长受光信号调节。

光是下胚轴伸长的主要调控因子之一。黑暗条件下，植株下胚轴表现为黄化生长且快速伸长，见光后下胚轴的伸长速率下降，说明光对下胚轴伸长有强烈的抑制作用。Le等(2015)研究表明，在快速伸长的下胚轴细胞内，周质微管垂直于伸长轴，表现为横向排列方式，而在伸长缓慢或停止伸长的下胚轴细胞内，周质微管表现为斜向或纵向排列；快速伸长生长的黄化下胚轴见光后，周质微管由横向平行排列变为斜向或纵向排列，进而有利于抑制下胚轴的伸长。对光信号调节微管重排的研究发现，光信号通过改变下胚轴细胞中周质微管的动态及转换能力调控其排列方式，进而调节下胚轴的伸长。下胚轴细胞在快速伸长之前，细胞内的微管会形成一种具有双极性的纵向列阵，并转换为放射状的星状微管列阵，之后开始进入快速伸长生长。在快速伸长的植株细胞内，微管的聚合和重排速率都更快(Sambade et al., 2012)。此外，蓝光可在15分钟内诱导拟南芥下胚轴细胞中横向排列的周质微管完成90度重排。具体机理是：蓝光照射后微管切割蛋白katanin切割交叉部位的微管产生新末端，微管正端结合蛋白CLASP (cytoplasmic linker protein-associated protein)稳定新形成的微管末端，使新末端在伸长过程中改变微管的排列方式为纵向排列(Lindeboom et al., 2013; Wang et al., 2017; Lindeboom et al., 2019) (表1)。该研究结果为揭示光诱导微管重排的分子机理提供了重要线索。

此外，还发现一些参与光信号调节微管重排的微管相关蛋白在下胚轴伸长中起重要作用，但目前仍不清楚光信号如何调控这些微管相关蛋白。微管去稳定蛋白25 (microtubule destabilizing protein25, MDP25)在光抑制下胚轴伸长中起重要作用。光信号引起下胚轴细胞中钙离子浓度增加，使MDP25蛋白从质膜上脱离并进入细胞质，通过调节周质微管从横向变为斜向或纵向排列，在下胚轴由黑暗转移至光下后抑制光下下胚轴伸长过程中起重要作用(Li et al., 2011)。Liu等(2013)发现了1个新的在光抑制下胚轴伸长过程中起正调控作用的微管相关蛋白WDL3 (wave-dampened2-like3)。黑暗条件下，WDL3被26S蛋白酶体降解，无法抑制下胚轴伸长，而当黄化苗被转移至光下后，WDL3蛋白能稳定表达，并通过调节下胚轴细胞内周质微管的组织动态抑制下胚轴伸长。Lian等(2017)研究发现，黑暗条件下，植物光形态建成的核心调控因子E3泛素连接酶COP1 (constitutive

表1 参与调节下胚轴伸长的微管相关蛋白

Table 1 Representative microtubule-associated proteins that are involved in the hypocotyl elongation

蛋白名称	对微管的调节	在下胚轴伸长中的作用	参考文献
Katanin	依赖ATP切割微管	通过蓝光刺激诱导，在微管交叉部位切断微管，产生新末端并迅速由横向变为纵向生长，从而导致下胚轴细胞的生长方向改变	Lindeboom et al., 2013; Wang et al., 2017
CLASP	稳定微管正端	维持下胚轴正常生长，CLASP缺失突变体*clasp-1*下胚轴明显短于野生型	Ambrose et al., 2007
MDP25	解聚微管	作为下胚轴伸长的负调节因子，MDP25可直接与微管结合，促进微管解聚，*mdp25*突变体的黄化下胚轴更长，而*MDP25*过表达植株下胚轴较短	Li et al., 2011
WDL3	稳定并重排微管	黑暗下，WDL3被26S蛋白酶体降解，促进下胚轴伸长；光调节微管重排过程中, WDL3通过调节下胚轴细胞中微管成束抑制下胚轴伸长	Liu et al., 2013
MDP60	去稳定并重排微管	通过PIF3介导光和乙烯信号，协同调控微管去稳定蛋白，促进下胚轴伸长	Ma et al., 2018
SPR1	稳定微管	下胚轴伸长的正向调节因子SPR1在快速生长的下胚轴中高表达，通过调节微管动态促进黑暗下下胚轴伸长	Nakajima et al., 2004, 2006
WDL5	稳定并重排微管	乙烯激活EIN3，EIN3直接调控*WDL5*上调表达，WDL5通过维持微管纵向排列抑制黄化下胚轴伸长	Sun et al., 2015
MDP40	去稳定并重排微管	油菜素甾醇激活BZR1，BZR1直接结合到*MDP40*的启动子上并上调其表达，MDP40解聚微管使其变为横向排列，从而促进黄化下胚轴伸长	Wang et al., 2012

CLASP: 内膜和骨架连接蛋白互作蛋白; MDP25: 微管去稳定蛋白25; WDL3: 抑制波动生长2类似3; MDP60: 微管去稳定蛋白60; SPR1: 螺旋生长1; WDL5: 抑制波动生长2类似5; MDP40: 微管去稳定蛋白40; PIF3: 光敏色素互作因子3; EIN3: 乙烯不敏感3; BZR1: 油菜素甾醇抗性1

CLASP: Cytoplasmic linker protein-associated protein; MDP25: Microtubule destabilizing protein 25; WDL3: Wave-dampened 2 like 3; MDP60: Microtubule destabilizing protein 60; SPR1: Spiral 1; WDL5: Wave-dampened 2 like 5; MDP40: Microtubule destabilizing protein 40; PIF3: Phytochrome-interacting factor 3; EIN3: Ethylene-insensitive 3; BZR1: Brassinazole-resistant 1

photomorphogenic1)可直接与WDL3结合并使其降解，该研究揭示了光信号通过直接调控微管相关蛋白水平来调控周质微管重排的新机制。此外，还有一些微管相关蛋白只特异性地在光下或黑暗下调节下胚轴的伸长。例如，微管去稳定蛋白MDP60 (microtubule destabilizing protein60)和微管稳定蛋白SPR1 (SPIRAL1)。*MDP60*主要在下胚轴表达，通过改变微管组织和动态来调节下胚轴伸长，光通过其信号通路的核心转录因子PIF3 (phytochrome-interacting factor 3)负调控*MDP60*的表达。PIF3作为乙烯促进光下下胚轴伸长的下游关键调节因子，其蛋白水平受26S蛋白酶体对光信号响应的调节。在光介导的下胚轴伸长过程中, PIF3与*MDP60*启动子特异性结合，从而提高*MDP60*的表达水平，MDP60通过改变微管排列促进下胚轴伸长(Ma et al., 2018)。微管正端结合蛋白SPR1促进黑暗下生长的下胚轴细胞伸长，在黑暗下生长的下胚轴中可检测到*SPR1*的表达，而在光下生长的下胚轴中未检测到*SPR1*的表达，表明光影响*SPR1*表达(Nakajima et al., 2004, 2006; Wang and Mao, 2019)。但尚不清楚响应光调节*SPR1*表达的上游转录因子，具体机理有待后续深入研究。

4 微管响应生长发育信号调节下胚轴伸长

植物激素参与调控植物生长发育的各个方面，下胚轴伸长也受多种激素调控，如生长素、赤霉素、乙烯和油菜素甾醇，这些激素处理均可改变下胚轴细胞内微管的排列方式。

4.1 生长素

生长素(auxin)在控制细胞伸长过程中起重要作用。生长素的合成或运输受到影响均会改变拟南芥下胚轴的长度。生长素转运抑制剂NPA (1-naphthylphthalamic acid)处理和生长素输出载体PIN1 (pin formed1)

突变均可抑制光下下胚轴的伸长(Jensen et al., 1998; Friml et al., 2002), 而PIN1过表达可促进光下下胚轴的伸长(De Grauwe et al., 2005)。外源施加生长素或上调生长素合成酶基因的表达都能促进光下生长的拟南芥下胚轴伸长, 黑暗下并无类似作用(Romano et al., 1995; Gray et al., 1998; van der Graaff et al., 2003)。但也有研究表明, 提高生长素的水平会抑制黑暗下下胚轴的伸长。例如, 生长素合成酶基因*YUCCA*过表达植株, 光下下胚轴比野生型长而黑暗下下胚轴比野生型短, 说明在光暗两种条件下生长素可能发挥不同的作用或通过不同的信号途径发挥作用(Zhao et al., 2001)。

生长素促进下胚轴伸长可通过调节周质微管为横向排列实现。植株体内缺少生长素会抑制其生长, 细胞内的微管以纵向排列为主, 纵向排列的微管可通过外源添加生长素改变为横向排列, 且这种转变具有剂量依赖效应(Fischer and Schopfer, 1997)。关于生长素信号调控微管骨架排列方式分子机制的研究, 从发现生长素能够调节下胚轴细胞内微管的重新排列就已开始。Chen等(2014)研究表明, 生长素通过生长素结合蛋白1 (auxin binding protein 1, ABP1)调节ROP (Rho of plants) GTPase、ROP的互作蛋白RIC1 (ROP-interactive CRIB motif-containing protein 1)和微管切割蛋白katanin来调控下胚轴细胞内的微管骨架重排。True和Shaw (2020)发现, 外源生长素诱导下胚轴细胞周质微管重排需要转运抑制因子/生长素F-box (transport inhibitor 1/auxin F-box, TIR1/AFB)转录途径。但是关于生长素促进下胚轴伸长与调控微管重排之间的关系尚存在不同观点, 有研究者认为, 下胚轴细胞内周质微管重排由生长本身引起, 而不依赖于生长素(Adamowski et al., 2019)。目前, 在生长素调控下胚轴伸长过程中, 并未发现受生长素信号直接调控的微管蛋白或微管相关蛋白, 对于微管骨架响应生长素信号调节下胚轴伸长的机理也需深入研究。

4.2 赤霉素

赤霉素(gibberellin, GA)也参与调控植物下胚轴的伸长(Cowling and Harberd, 1999)。GA可以促进黄瓜(*Cucumis sativus*)、生菜(*Lactuca sativa* var. *ramosa*)和拟南芥等植物下胚轴的伸长。外源添加赤霉素能促进光下生长的拟南芥下胚轴伸长, 但对黑暗下生长的下胚轴无促进效果, 这说明黑暗条件下下胚轴伸长对赤霉素的响应存在饱和效应(Sauret-Güeto et al., 2012)。下胚轴伸长受光和赤霉素的拮抗作用(光抑制细胞伸长, 而赤霉素促进细胞伸长)。具体调节机制为: 在光下, 光受体phyB介导光敏色素互作因子4 (PIF4)降解, PIF4调控的促进下胚轴细胞伸长的下游基因表达受到抑制, 进而抑制下胚轴伸长(Duek and Fankhauser, 2005; de Lucas et al., 2008)。此外, 光使幼苗中赤霉素生物合成基因的表达瞬时下调, 编码赤霉素失活酶基因的表达上调, 因此可能导致活性赤霉素减少及DELLAs (赤霉素信号的负调控因子)蛋白在下胚轴细胞中积累(Peng et al., 1997; Silverstone et al., 1998; Reid et al., 2002; Achard et al., 2007; Alabadíet et al., 2008; Harberd et al., 2009)。DELLA蛋白与促进细胞伸长的转录因子PIF3和PIF4互作抑制其活性, 进而使下胚轴伸长受到抑制。当赤霉素存在时, 赤霉素与受体结合, 促进受体与DELLA蛋白互作, 使DELLAs降解, PIF3和PIF4能发挥其转录活性, 进而促进下胚轴伸长(Feng et al., 2008; de Lucas et al., 2008)。

有研究者对赤霉素促进光下下胚轴伸长过程中微管骨架的功能进行分析, 发现赤霉素通过使下胚轴细胞内周质微管重排为横向进而促进下胚轴伸长(Shibaoka, 1974, 1993)。Vineyard等(2013)使用生长素和赤霉素双激素处理的方法研究了光下生长的下胚轴细胞内横向排列周质微管形成的机制, 发现双激素处理能在2小时内同步诱导光下下胚轴细胞内大部分周质微管变为横向排列。激素处理初期, 正在聚合的微管正端减少约1/3; 继续用激素诱导45分钟后, 横向排列的微管最初在细胞中间部位形成, 然后以双向的方式逐步向细胞顶端和底端扩展(Vineyard et al., 2013)。但也有研究发现, 对光下生长的拟南芥下胚轴外源瞬时施加赤霉素会导致下胚轴细胞的伸长速率瞬时增加, 然后恢复至正常状态, 这一过程伴随DELLAs蛋白中赤霉素合成缺陷突变体抑制子RGA (repressor of *ga1-3*)蛋白降解及恢复, 但下胚轴表皮细胞外切壁中的周质微管并未变为横向排列, 推测可能光下下胚轴细胞伸长速率的增加并不需要外切壁细胞中周质微管变为横向排列(Sauret-Güeto et al., 2012)。关于微管骨架在赤霉素促进光下下胚轴伸长过程中的作用机制目前仍不十分清楚, 因此, 对微管

骨架响应赤霉素信号调节下胚轴伸长的机理也需进一步探索。

4.3 乙烯

乙烯是一种气体激素，在调控植物下胚轴伸长中起重要作用(Smalle et al., 1997; Zhong et al., 2012)。乙烯可根据光照条件促进或抑制拟南芥下胚轴伸长(Ecker et al.,1995; Smalle et al., 1997)。光照条件下，乙烯或者其前体ACC (1-aminocyclopropane-1-carboxylic acid)处理可促进下胚轴伸长；黑暗条件下，乙烯则抑制下胚轴伸长(Zhong et al., 2012; Yu et al., 2013)。乙烯通过转录因子EIN3激活PIF3依赖的生长促进途径及乙烯响应因子1 (ethylene response factor 1, ERF1)介导的生长抑制途径来调控下胚轴生长。在光下，乙烯通过其信号途径关键转录因子EIN3直接结合*PIF3*的启动子区激活其表达，从而促进光下下胚轴伸长；黑暗条件下，乙烯可诱导抑制伸长的ERF1蛋白积累，进而抑制黄化下胚轴伸长(Zhong et al., 2012)。此外，乙烯还可通过COP1介导的HY5 (hypocotyl 5)蛋白降解来促进光下下胚轴的伸长(Yu et al., 2013)。

用外源乙烯或ACC处理时，黄化下胚轴细胞内周质微管由横向变为纵向排列，说明乙烯通过调节微管的排列方式参与调节下胚轴的伸长(Soga et al., 2010)。在乙烯调节下胚轴细胞周质微管排列过程中有微管相关蛋白参与。研究表明，微管相关蛋白WDL5参与乙烯抑制黄化下胚轴伸长的调节(Sun et al., 2015)。黑暗条件下，乙烯信号通路下游的关键转录因子EIN3直接结合到*WDL5*的启动子上并上调其表达，WDL5通过稳定并重排微管进而抑制黄化下胚轴的伸长(Sun et al., 2015)。

4.4 油菜素甾醇

油菜素甾醇(brassinosteroids, BRs)是一种重要的调节植物生长发育的植物激素(Clouse, 2011; Ye et al., 2011)。BRs通过受体激酶BRI1 (brinsensitive1)以及特定的信号转导途径激活2个关键转录因子BZR1 (brassinazole-resistant 1)和BES1/BZR2 (brinsensi-

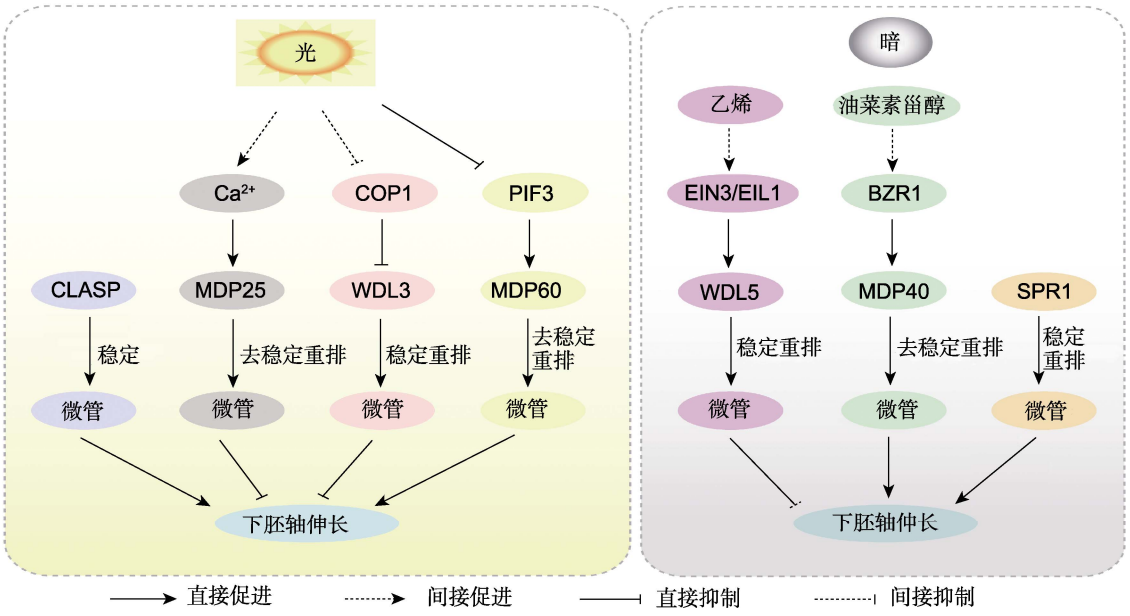

图 1 响应光和激素信号调控下胚轴伸长的微管相关蛋白

COP1: 持续光形态建成1; EIN3/EIL1: 乙烯不敏感3/乙烯不敏感3类似1. CLASP、MDP25、WDL3、MDP60、SPR1、WDL5、MDP40、PIF3、EIN3和BZR1同表1。

Figure 1 Microtubule-associated proteins that are involved in hypocotyl elongation and regulated by light and phytohormones

COP1: Constitutive photomorphogenic1; EIN3/EIL1: Ethylene-insensitive 3/EIN3 like 1. CLASP, MDP25, WDL3, MDP60, SPR1, WDL5, MDP40, PIF3, EIN3 and BZR1 see Table 1.

tive1-EMS-suppressor1/brinsensitive2)来起作用(Li et al., 2010; Kim and Wang, 2010; Clouse, 2011; Gudesblat and Russinova, 2011)。许多油菜素甾醇缺陷及不敏感突变体的黄化下胚轴变短且光下生长的植株矮小。例如, 油菜素甾醇合成缺失突变体*det2* (*de-etiolated-2*)在黑暗下生长时子叶张开且下胚轴伸长受到抑制(Chory et al., 1991; Wang et al., 2001); 油菜素甾醇受体BRI1的无效突变体*bri1-116*植株也表现出黄化下胚轴短的表型; 油菜素甾醇信号途径转录因子BZR1的激活标签突变体*bzr1-1D*则表现出黄化下胚轴长且弯曲的表型; 油菜素甾醇信号途径的负调控因子BIN2的显性突变体*bin2-1*植株黄化下胚轴伸长也受到抑制; 油菜素甾醇信号通路中的上游组分BSKs和BSU1通过改变转录因子BZR1的磷酸化状态调控下胚轴的伸长(Tang et al., 2008; Kim et al., 2010; Gudesblat and Russinova, 2011)。上述结果表明, BRs在调控下胚轴伸长方面起重要作用。

BRs可通过去稳定周质微管改变黄化下胚轴细胞内周质微管由纵向变为横向排列, 进而促进黄化下胚轴的伸长。微管去稳定蛋白参与BRs调控黄化下胚轴细胞中周质微管的重排(Wang et al., 2012)。BRs通过其信号转导途径关键转录因子BZR1结合至编码微管去稳定蛋白MDP40 (microtubule destabilizing protein40)的基因启动子区诱导*MDP40*表达, MDP-40通过去稳定周质微管并使其发生重排, 进而促进黄化下胚轴的伸长(Wang et al., 2012)。但在BRs调控植株下胚轴伸长过程中, 微管相关蛋白是瞬时还是持续调节周质微管以及是否有其它微管相关蛋白参与维持动态的周质微管列阵尚不清楚。为更好地理解BRs介导的下胚轴伸长过程中微管及微管相关蛋白的作用, 未来需要通过多种遗传学及生理学实验进行验证。

5 总结与展望

微管骨架是细胞骨架的重要成员之一, 参与多种细胞学过程。下胚轴作为研究植物细胞伸长的模式系统, 微管的组织动态变化会影响下胚轴的伸长。同时, 下胚轴伸长受到多种内部和外部信号调控, 这些信号在调控下胚轴伸长过程中均伴随着周质微管组织排列方式的变化, 但微管骨架响应各种内部及外部信号参与调节下胚轴伸长的机理, 以及微管在信号间互相促进或拮抗调控下胚轴伸长中的作用等问题目前仅进行了初步研究, 还有很多科学问题尚待进一步探索。我们对参与下胚轴伸长调节的微管相关蛋白进行了总结(表1), 并对这些微管蛋白如何响应上游信号参与调节下胚轴伸长进行了归纳(图1)。农业生产上, 种子在土壤中萌发后, 胚轴快速伸长以破土而出, 使子叶见光, 进行光合作用。因此, 阐明微管响应各种内部及外部信号转导途径, 调节下胚轴伸长的机理对于解析下胚轴伸长调节的分子机制和农业生产上提高种子萌发率均具有重要意义。

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Research Advances in the Molecular Mechanisms of Plant Microtubules in Regulating Hypocotyl Elongation

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Abstract As one of the major members of cytoskeleton, microtubules play important roles in plant growth and development. Hypocotyl has become a model system to study cell elongation, which is regulated by multiple internal and external signalings. Here, we reviewed the recent research progress for the roles of microtubules in regulating the hypocotyl elongation in response to diversed environmental and developmental cues, which will extend our understanding on how microtubules response to the upstream signal and play roles in the elongation of plant hypocotyls.

Key words microtubule, hypocotyl, elongation, environmental signals, growth and developmental cues

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