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·专题论坛·

植物胞吞和胞吐的耦合调控

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摘要 真核细胞通过胞吞和胞吐作用将大分子和颗粒性物质运出或运送至质膜, 其中包括一些具有重要生物学功能的蛋白质。胞吞和胞吐途径之间的耦合对维持质膜的完整性以及调控质膜蛋白的丰度和活性至关重要。动物中, 突触小泡的胞吞和胞吐在时空上紧密耦合已被证明是持续神经传递的必要条件。近年来, 随着对植物囊泡运输的深入研究, 越来越多的证据表明, 植物细胞的胞吞和胞吐间同样存在耦合调控, 且在植物生长发育和对外界环境的响应中扮演重要角色。该文综述了植物协同调控胞吞和胞吐的生理学意义, 并结合网格蛋白介导囊泡运输的最新研究进展探讨了其可能的耦合机制。

关键词 网格蛋白, 耦合, 胞吞, 胞吐

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真核生物通过质膜将细胞内部与外部环境分隔, 通过控制物质进出和信号传递维持胞内环境稳定。许多重要的质膜蛋白(包括激酶受体和转运蛋白等)在核糖体合成后, 经内质网和高尔基体加工, 被反式高尔基网状结构(*trans*-Golgi network, TGN)分选, 最后通过胞吐作用(exocytosis)运输至细胞表面。大部分质膜蛋白利用胞吞作用(endocytosis)从细胞表面进入胞内, 经过TGN分选后, 通过再循环(recycling)途径重新回到质膜或被液泡前体/多囊泡体(PVC (pre-vacuolar compartment)/MVB (multivesicular body))分选而进入降解途径, 以此调控其质膜丰度。真核细胞中, 货物蛋白被包裹在特定囊泡进行胞吞和胞吐的定向转运, 这种机制被称为囊泡运输(vesicle trafficking)。胞吞和胞吐这2种囊泡运输过程既相对独立又紧密联系, 它们决定着质膜蛋白的定位和丰度, 以及整个质膜表面积大小和构成组分。神经元突触小泡(synaptic vesicle)通过胞吐作用被运输至突触前膜, 囊泡与前膜融合后释放出神经递质(neurotransmitter), 之后通过胞吞作用及时回收突触小泡的膜结构和蛋白来维持突触结构的稳定和持续的神经传递(Lou, 2018; Maritzen and Haucke, 2018)。由此可见, 动物中胞吞和胞吐的协同调控是维持细胞正常生命活动所必需, 它保证了细胞质膜的稳定以及胞内物质的高效利用。与动物细胞不同, 植物细胞具有细胞壁和液泡, 使胞内形成巨大的膨压, 不利于质膜内陷进行胞吞。20世纪80年代, 人们对植物中是否存在胞吞途径仍持怀疑态度。然而, 随着电镜技术的发展, 在不同种类植物中都清晰地观察到胞吞囊泡在质膜形成(Derksen et al., 1995; Robinson, 1996; Fowke et al., 1999; Dhonukshe et al., 2007), 无可辩驳地证明了膨压无法阻止植物细胞胞吞的发生(Gradmann and Robinson, 1989)。相较于动物, 缺乏活动能力的植物除依赖胞吞和胞吐间的配合来调控生长发育外, 还需以此感知并适应周围环境的变化, 这直接关系到它们的生存和繁衍。近年来, 植物中依赖网格蛋白的囊泡运输途径由于其介导多种重要蛋白的膜泡转运而备受关注(Reynolds et al., 2018)。最新研究发现, 拟南芥(*Arabidopsis thaliana*)通过联动网格蛋白及其辅助因子在质膜和反式高尔基网状结构/早期内吞体(*trans*-Golgi network/early endosome, TGN/EE)的招募实现了胞吞和胞吐耦合(Yan et al., 2021)。本文综述了植物中胞吞协同胞吐对多种生命活动的调控,

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并结合最新研究进展对其潜在的耦合机制进行探讨，以期为探究植物囊泡运输的分子机制提供新思路。

1 植物耦合调控胞吞和胞吐的生理学意义

1.1 调控生长发育

花粉管和根毛是植物中典型的极性生长细胞，其顶端生长所需物质的时空分布受囊泡运输调节。其中，花粉管作为研究胞吞胞吐囊泡运输的模式细胞受到广泛关注。当花粉接触到雌蕊柱头后，花粉管开始萌发，通过快速地极性生长到达珠孔，从而将精细胞运送至胚囊完成受精作用(Higashiyama and Takeuchi, 2015; Higashiyama, 2018; Johnson et al., 2019)。为满足花粉管的快速伸长，需要将大量携带细胞壁组分、蛋白质以及脂质等生长所需物质的胞吐囊泡运送到顶端生长区域。这些囊泡与花粉管顶端质膜融合，将内容物释放出来(McKenna et al., 2009; Bloch et al., 2016; Cameron and Geitmann, 2018; Meng et al., 2020)。定量分析发现，胞吐囊泡与质膜融合的速率远高于花粉管顶端扩展所需，多余物质就要依靠胞吞途径将其再次回收利用，以维持花粉管的正常生长(Derksen et al., 1995; Campanoni and Blatt, 2007; Ketelaar et al., 2008)。因此，胞吞和胞吐之间的精确配合对于维持花粉管的顶端极性生长不可或缺(Zhao et al., 2020)。同样，根毛的正常伸长也离不开胞吞胞吐间的协同合作，一旦胞吞胞吐途径被破坏，根毛会出现形态异常且/或变短(Preuss et al., 2004; Stenzel et al., 2008; Ichikawa et al., 2014; Larson et al., 2014; Gutkowska et al., 2015)。

除调控极性生长外，胞吞胞吐还在植物细胞分裂过程中发挥重要作用。植物在细胞中央形成细胞板，从而将2个子代细胞分隔，实现胞质分裂(Staehelin and Hepler, 1996; Livanos and Müller, 2019)。有证据表明，细胞板上的质膜蛋白和细胞壁组分除来源于高尔基体新生成的胞吐囊泡外，还有一部分来自亲代细胞的表面(Richter et al., 2014)。进行胞质分裂的植物细胞通过提高胞吞速率，将亲代细胞表面现存的物质原料迅速运送到中央区域，在数分钟内形成1/3细胞板(Dhonukshe et al., 2006)。此外，胞质分裂时介导囊泡融合的KNOLLE突触融合蛋白需要依赖网格蛋白介导的胞吞(clathrin-mediated endocytosis, CME)作用才能正确定位到细胞板，胞吞受阻会引发KNOLLE定位异常，导致细胞板形成受阻(Boutté et al., 2010; Gadeyne et al., 2014)。另有研究表明，拟南芥CME参与调控细胞板上生长素输出载体PIN (PIN-formed)的定位，这对细胞的极性建立极其重要(Mravec et al., 2011)。

1.2 响应外界环境

低温是一种常见的逆境胁迫，会造成植物细胞脱水和机械损伤，破坏细胞膜的完整性使内容物泄漏，抑制植物生长并减少作物产量(Webb and Steponkus, 1993; Yamazaki et al., 2008)。高等植物中，细胞会重新密封因低温而破裂的细胞膜，以此减少对细胞活性的伤害(Yamazaki et al., 2008)。该密封修复过程需要胞吞以及胞吐囊泡运输的共同参与(Togo et al., 1999; McNeil et al., 2003; Schapire et al., 2009; Tam et al., 2010)。胞吐囊泡可为细胞受损部位提供膜结构，以减小质膜张力(Togo et al., 2000)，而胞吞囊泡可回收受损部位的膜结构(Idone et al., 2008)。在拟南芥中过表达胡杨(*Populus euphratica*)三磷酸腺苷双磷酸酶，可有效减弱低温诱导的eATP对胞吞胞吐囊泡运输的抑制作用，从而增强细胞的自我修复能力，增强植株的耐寒性(Deng et al., 2015)。

植物需要对外界渗透压作出实时反应，才能保证细胞质膜的完整性(Cutler et al., 1977)。当植物处于高渗透压环境时，细胞失水导致膨压降低，细胞缩小，造成质膜损伤，情况严重时则会导致细胞死亡(Zonia and Munnik, 2007)。相反，低渗透压下细胞吸水，导致细胞体积变大，质膜表面积增加。为应对渗透压引起的细胞体积与表面积比率变化，植物需要对胞吞和胞吐途径进行相应调整，以维持质膜蛋白合适的丰度(Hachez et al., 2013)。研究发现，高渗透压处理时，植物在增强根部细胞胞吞作用的同时会减弱胞吐作用；相反，低渗透压处理时植物在减弱根部细胞胞吞作用的同时会增强胞吐作用(Zwiewka et al., 2015)。胞吞途径被破坏的拟南芥网格蛋白*chc2*突变体植株无法通过对囊泡运输的正确调控来应对渗透压变化，导致对高渗透压的敏感性显著高于野生型(Zwiewka et al., 2015)，这进一步证明了胞吞和胞吐途径的协同调控对植物适应外界渗透压的重要作用。

叶表皮气孔由保卫细胞组成, 它是植物与外界环境进行气体交换的重要通道。保卫细胞通过调节气孔孔径大小控制光合和蒸腾作用速率。保卫细胞体积变大时, 表面积增加, 气孔打开; 体积缩小时则气孔闭合(Blatt, 2000; Shope et al., 2003; Meckel et al., 2007)。保卫细胞体积的大小取决于溶质的吸收和流失, 而囊泡运输在其中发挥重要调节作用, 胞吞或胞吐途径被破坏均会阻碍气孔开闭(Leyman et al., 1999; Blatt, 2000; Eisenach et al., 2012)。研究发现, 拟南芥*chc2*突变体中胞吞和胞吐途径均被抑制, 使气孔闭合的速度减慢, 并且一旦闭合很难再次开启(Larson et al., 2017)。由于气孔对环境响应迟缓, *chc2*突变体在强光照低湿度的环境下无法快速切换气孔的开闭状态, 以致光合作用减弱, 其莲座叶明显小于同等环境下生长的野生型(Larson et al., 2017)。由此可见, 植物通过对保卫细胞胞吞和胞吐的调控来及时响应光照和湿度的变化, 从而合理安排光合和蒸腾作用。

向地性可引导植物扎根, 在固定植株的同时有利于根部从土壤中吸收水分和矿质营养。生长素输出载体PIN2介导的生长素极性运输调控在植物根尖的向地性过程中发挥重要作用(Abas et al., 2006)。PIN2作为质膜蛋白, 其极性定位和丰度受囊泡运输调控, 胞吞和胞吐共同调控植物根部的向地性响应(林雨晴和齐艳华, 2021)。此外, 拟南芥、番茄(*Lycopersicum esculentum*)和高粱(*Sorghum bicolor*)主根在向地性生长过程中会避开盐离子浓度较高的区域, 这种避盐性(halotropism)提高了植株的耐盐能力。研究发现, 避盐性发生的原因是根尖两侧生长素的不对称分布, 而PIN2的囊泡运输在其中发挥关键作用。植物通过增强靠近盐离子浓度较高一侧根尖表皮细胞PIN2的胞吞作用, 减少其质膜丰度, 进而使另一侧根尖的生长素含量升高, 根部得以向盐离子浓度较低的一侧弯曲生长(Galvan-Ampudia et al., 2013)。

在植物免疫反应中, 胞吞和胞吐同样行使重要功能(崔亚宁等, 2020)。FLS2 (flagellin sensing 2)是一种定位于质膜的受体激酶, 可识别细菌鞭毛蛋白(flg22)并通过胞吞作用使其进入胞内小体, 激活免疫反应(Boller and Felix, 2009; Beck et al., 2012)。同时, 胞吐途径也被证明参与植物的免疫响应, 胞吐相关的SNARE (soluble N-ethylmaleimide-sensitive factor attachment protein receptor)蛋白SYP121/PEN1会在植物的感染部位大量积累(Kalde et al., 2007; Cao et al., 2019); 敲除水稻(*Oryza sativa*)胞吐复合体(exocyst)亚基OsSEC3A, 会引发植株的防御反应(Ma et al., 2018), 暗示由病原体诱发的胞吞和胞吐之间的平衡状态为植物细胞正确产生免疫反应所必需(Robatzek, 2007)。

2 植物耦合胞吞和胞吐的调控机制

2.1 植物激素对囊泡运输的调控

激素是代谢产生的小分子有机化合物, 目前已知的植物激素包括生长素、细胞分裂素、赤霉素、乙烯、脱落酸、茉莉酸、水杨酸、油菜素甾醇和独脚金内酯等。这些激素作为信号分子调控各项生命活动, 在植物生长发育和外界环境的感知及响应中发挥重要作用。植物激素通过不同的信号通路调控囊泡运输, 介导功能蛋白的定位和丰度。拟南芥中, 生长素通过抑制CME来增加PIN的质膜丰度, 从而调控自身的浓度和定位(Robert et al., 2010; Wang et al., 2013)。水杨酸同样能够抑制CME途径, 但网格蛋白对水杨酸的响应速度明显慢于生长素, 暗示两者间的作用机理可能存在差异(Du et al., 2013; Wang et al., 2016; Ke et al., 2021)。此外, 低浓度的茉莉酸可通过抑制胞吞来提高PIN2的质膜丰度(Sun et al., 2011)。植物激素不仅能负调控囊泡运输, 有些激素还被证明具有正向调节作用。例如, 脱落酸可诱导拟南芥叶表皮细胞和保卫细胞中K^+通道蛋白的胞吞(Sutter et al., 2007); 细胞分裂素可将胞内的PIN1输送至液泡降解以降低其质膜丰度(Marhavý et al., 2011); 低浓度的赤霉素促进PIN2输送到液泡降解, 而高浓度的赤霉素促进PIN2回到质膜的再循环(Salanenka et al., 2018); 具有独脚金内酯活性的化合物GR24能够促进PIN2的胞吞并且增强其质膜的极性定位(Pandya-Kumar et al., 2014)。

随着研究的不断深入, 人们发现植物对某个生命活动的调控往往不是由单个植物激素独立完成, 而是需要多种植物激素在时空上相互配合才能实现。不同激素间的协同互作, 在植物中构成复杂而精密的调控网络。植物顶端分生组织的形成, 主根、侧根和生殖细胞的发育, 以及枝条和叶序的形成等生理过程均需

要生长素和细胞分裂素的协同调控(Müller and Leyser, 2011; Chandler and Werr, 2015; Schaller et al., 2015; Jing and Strader, 2019)。根部分生区的大小不仅由生长素和细胞分裂素决定，赤霉素、油菜素甾醇、脱落酸和独脚金内酯也在其中发挥重要作用(Pacifici et al., 2015)。除对生长发育进行调控，激素互作网络还在植物应对生物和非生物胁迫中发挥重要作用，尤其是乙烯、脱落酸、茉莉酸和水杨酸等与植物抗性相关的激素分子通路之间协同和拮抗作用的整合，可在基因转录和蛋白稳定性等方面调节植物的生理活动，以帮助其应对逆境(Bielach et al., 2017; Jiroutova et al., 2018; Li et al., 2019; Aerts et al., 2021)。

综上，多种植物激素在上游综合调控不同途径囊泡运输的数量和速度，使胞吞和胞吐间维持适当的动态平衡，从而精准应答内在的植物发育信号和外在的环境刺激信号。

2.2 网格蛋白介导的胞吞和胞吐的耦合调控

目前，植物激素对囊泡运输的调控中，研究得较为清楚的是生长素和水杨酸对CME的抑制作用，它们通过减少网格蛋白的质膜招募来阻断货物蛋白的胞吞，这一机制与植物根的向地性生长、下胚轴的向光性弯曲以及顶端弯钩(apical hook)的形成密切相关(Du et al., 2013; Wang et al., 2013, 2016; Yu et al., 2016; Zhang et al., 2017; Ke et al., 2021)。

CME是进化上高度保守的胞吞途径，也是植物细胞进行胞吞的主要方式。网格蛋白复合体是由3条轻链(clathrin light chain, CLC)和3条重链(clathrin heavy chain, CHC)组成的三脚架结构(Ekanayake et al., 2019)，多个三脚架结构组装成网格状包被，将货物包裹在内(Ekanayake et al., 2019)。植物中，接头蛋白复合体AP-2 (adaptor protein 2)和TPC (TPLATE complex)识别货物蛋白并招募网格蛋白到质膜，接着质膜逐渐向胞内凹陷形成CCP (clathrin coated pit)，然后动力蛋白(dynamin)催化GTP水解使CCP与质膜连接处断裂，CCP进入胞内成为CCV (clathrin coated vesicle)，最后在auxilin (Adamowski et al., 2018)等脱包被因子的作用下CCV包被脱落，释放出包被内的小泡，网格蛋白和其它CME元件则重新返回质膜进行下一轮胞吞或进入降解途径(Ekanayake et al., 2019)。这些元件环环相扣，通过不同的机制紧密联系，最终使植物细胞顺利完成CME过程(McMahon and Boucrot, 2011; Paez Valencia et al., 2016)。尽管人们对植物网格蛋白的关注点主要在胞吞途径，但网格蛋白不仅定位于质膜，而且聚集在胞内的TGN/EE，TGN/EE负责介导可溶性蛋白和膜蛋白的降解或回到质膜的后高尔基运输(post-Golgi trafficking)，暗示植物网格蛋白除介导质膜胞吞外，还可能在胞吐途径中发挥重要作用。Shimizu等(2021)利用超高分辨率激光共聚焦显微镜观察植物细胞TGN/EE上各类蛋白的3D定位和4D动态，发现网格蛋白和接头蛋白复合体AP-1 (adaptor protein 1)处于同一区域，表明它们之间可能存在功能相互作用。最新研究发现，拟南芥*ap-1*突变体中网格蛋白在TGN/EE的定位显著减少，并且网格蛋白或AP-1功能破坏会导致细胞分泌和再循环途径受阻(Yan et al., 2021)。上述结果表明，AP-1招募网格蛋白到TGN/EE，用以形成CCV，进行网格蛋白介导的胞吐(clathrin-mediated exocytosis, CMX)。

Wang等(2013, 2016)研究发现，生长素对网格蛋白质膜和TGN/EE丰度的调控一直处于同步状态，表明CME和CMX始终保持耦合。最新研究表明，在拟南芥AP-1功能缺陷的CMX破坏突变体中，网格蛋白、AP-2、TPC和DRP1 (dynamin-related protein1)的质膜招募显著减少，CME被抑制(Yan et al., 2021)。此外，胞吐抑制剂ConcA (Gendre et al., 2011)、ES2 (Zhang et al., 2016)和ES16 (Li et al., 2017)处理同样会减少CME元件在质膜的招募，减慢胞吞速率(Yan et al., 2021)。反之，在拟南芥CME破坏突变体*ap-2*和*tpc*中，网格蛋白和AP-1在TGN/EE上的招募显著减少，CMX被抑制(Yan et al., 2021)。这些发现证明，植物通过调控网格蛋白及其辅助因子在质膜和TGN/EE的招募来分别影响胞吞CCV和胞吐CCV的形成，从而耦合CME与CMX (图1)。

目前，CME-CMX耦合的分子机制尚不清楚，AP1/2β亚基可能是其中的关键因子。拟南芥AP1/2β亚基AP1/2β1和AP1/2β2与网格蛋白在质膜和TGN/EE共定位，被AP-1和AP-2共享(Bassham et al., 2008; Wang et al., 2016)，它可作为协同调控的枢纽将质膜以及TGN/EE上CCV的形成紧密相连。TGN/EE的胞吐CCV在到达质膜前脱包被，脱落的AP1/2β亚基被招募到质膜并参与形成胞吞CCV；胞

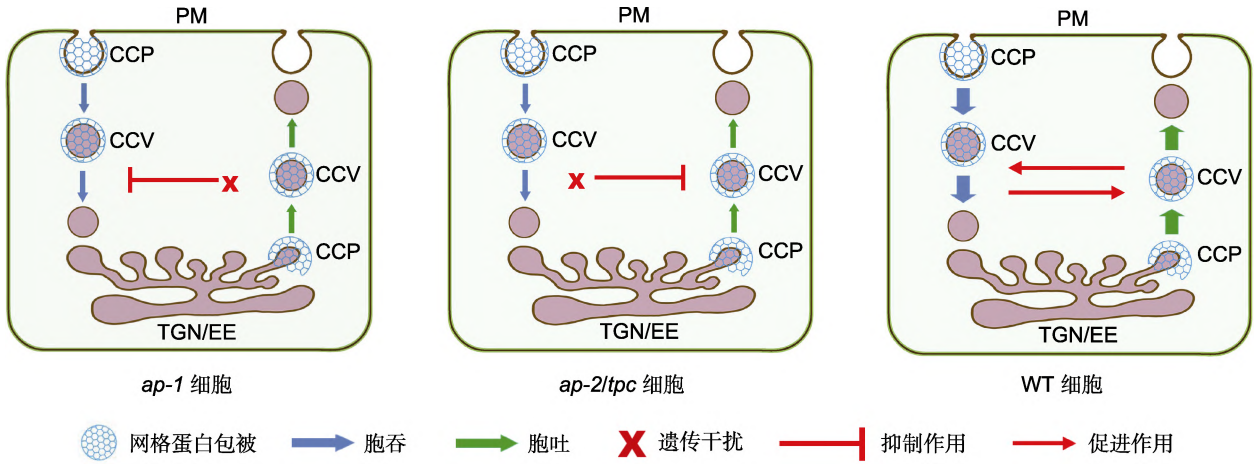

图1 网格蛋白介导的胞吞和胞吐的耦合调控

PM: 质膜; TGN/EE: 反式高尔基网状结构/早期内吞体; CCP: 网格蛋白包被小窝; CCV: 网格蛋白包被囊泡; *ap-1*: AP-1功能缺陷; *ap-2/tpc*: AP-2或TPC功能缺陷; WT: 野生型

Figure 1 Coupling regulation of clathrin-mediated endocytosis and exocytosis

PM: Plasma membrane; TGN/EE: *Trans*-Golgi network/early endosome; CCP: Clathrin coated pit; CCV: Clathrin coated vesicle; *ap-1*: AP-1 deficient; *ap-2/tpc*: AP-2 or TPC deficient; WT: Wildtype

吞CCV在到达TGN/EE前脱包被，脱落的AP1/2β亚基被招募到TGN/EE参与形成胞吐CCV; 当CMX或CME破坏导致AP1/2β亚基在质膜或TGN/EE附近缺乏时，网格蛋白及其辅助因子的招募将受到干扰，从而抑制胞吞或胞吐CCV的形成。Wang等(2016)研究发现，拟南芥*ap-2*突变体中AP1/2β1亚基在质膜以及TGN/EE的定位显著减少。此外，Narasimhan等(2020)研究表明，植物胞吞CCV在非常接近TGN/EE时才逐步脱包被，该结论支持了胞吐CCV的AP1/2β亚基来自胞吞CCV的猜测。虽然依赖AP1/2β耦合的假设可解释AP-1与AP-2之间表现出的高度依存现象，但尚缺乏明确的证据。

2.3 细胞骨架对胞吞和胞吐的调控

细胞骨架具有定向指引囊泡运输的功能，是联系胞吞和胞吐的桥梁(Alabi and Tsien, 2013)。植物中，微丝和微管控制囊泡的运输方向，介导多种物质原料前往指定区域，以供植物生命活动所需。例如，微丝和微管通过调控纤维素合成酶复合体(cellulose synthase complex)分泌囊泡以及多糖的转运，帮助形成细胞壁(Crowell et al., 2009; Bashline et al., 2014; Rounds et al., 2014; Zhang et al., 2019a)。此外，细胞骨架还参与调控甾醇和细胞外液的胞吞过程(Grebe et al., 2003; Baluska et al., 2004)。凭借其囊泡指向标的功能，细胞骨架在植物的极性生长中发挥重要作用。Cheung和Wu (2008)研究表明，花粉管中的胞吐囊泡沿着微丝到达顶端生长点; 微管的聚合促进花粉管顶端质膜的胞吞，解聚则会引发胞吞囊泡错误定位，导致多余胞吐物质无法被正确回收，降低后续胞吐速率(Idilli et al., 2013)。同样，根毛的极性生长也离不开细胞骨架对胞吞和胞吐囊泡运输的精确调控(Sieberer et al., 2005)。

目前的研究表明，植物细胞骨架与CME之间关系密切。拟南芥CLASP (CLIP-associated protein)和水稻RMD (rice morphology determinant)分别通过调控微管和微丝的组装来调节CME速率，引导PIN蛋白的极性定位(Kakar et al., 2013; Li et al., 2014)。微丝骨架除与AtEH等CME元件共同诱导自噬体在内质网与质膜连接部位形成外(Wang et al., 2019)，还在ROP2信号通路中发挥抑制CME及促进PIN1极性定位的作用(Nagawa et al., 2012)。然而，细胞骨架是否参与CMX的调控仍有待进一步探究。

2.4 SNARE蛋白对胞吞和胞吐的调控

囊泡经历起始的出芽、货物选择和定向运输后，在胞泌复合体(exocyst complex)的帮助下栓系(tether)到

靶膜(李彤辉等, 2019), 然后依靠SNARE蛋白介导膜融合并释放内容物(鲍永美等, 2005)。拟南芥中已发现60多种SNARE蛋白, 它们广泛分布在细胞内膜系统, 如内质网、高尔基体、TGN/EE、质膜、PVC和液泡(Uemura et al., 2004)。这些SNARE蛋白介导不同细胞器之间的囊泡运输, 使物质和信号高效地在整个内膜系统中传递, 调控植物众多生理活动的正常运行(Lipka et al., 2007)。

多数植物SNARE蛋白在胞吐过程中发挥作用。但最近有研究表明, 拟南芥SNARE蛋白SYP121和VAMP721/22与胞吞途径也存在密切联系。*syp121*突变体中, 除分泌途径被破坏外, 胞吞也受到干扰, 并且植株表现出的生长缺陷与网格蛋白突变体*chc2*极其相似(Larson et al., 2017)。拟南芥VAMP721/22分布于质膜和TGN/EE, *vamp721*/*vamp722*突变体的胞吞和再循环途径均被抑制, 原本定位于质膜的生长素运输载体PIN1、PIN2以及AUX1在胞内积累, 导致生长素分布异常(Zhang et al., 2021)。Fujimoto等(2020)发现, 拟南芥PICALM1a/b可作为接头蛋白与质膜定位的VAMP721/22和网格蛋白相互作用, 从而介导VAMP721/22的胞吞。*picalm1a*/*picalm1b*突变体中, VAMP721的质膜定位显著增加, 而TGN/EE定位显著减少, 说明VAMP721从质膜进入胞内依赖于PICALM1a/b介导的CME (Fujimoto et al., 2020)。此外, 超高分辨率共聚焦显微镜观察结果显示, VAMP-721与网格蛋白/AP-1共定位于TGN/EE, 暗示VAMP-721/22在TGN/EE上介导的囊泡运输与CMX相关(Shimizu et al., 2021)。综上所述, SNARE作为囊泡运输最后环节的调控蛋白, 很可能在植物CME以及CMX的耦合中发挥重要作用。

3 研究展望

胞吞和胞吐是控制质膜组分的关键途径, 二者之间的耦合对植物信号转导以及营养吸收、细胞壁生物发生和病原体防御等生理活动至关重要。植物CME-CMX耦合机制的发现, 揭示了细胞维持胞吞和胞吐平衡的新方式, 为增强农作物的抗胁迫能力以及提高产量提供了新思路。同时, 鉴于网格蛋白进化上的高度保守性, 该耦合机制对解析动物及其它物种中囊泡运输的分子机理同样具有重要参考价值。此外, SYT (synaptotagmin)、PI(4,5)P2 (phosphatidylinositol (4,5) bisphosphate)以及Rab GTPase家族成员Rab-H1b、ECH (echidna)和SCD (stomatal cytokinesis defective)被陆续证明在植物胞吞胞吐的联动中起重要作用(Gendre et al., 2013; Ischebeck et al., 2013; McMichael et al., 2013; Kim et al., 2016; Mayers et al., 2017; He et al., 2018; Ravikumar et al., 2018), 但它们是否参与调控CME和CMX的耦合, 目前尚不清楚。

除CME和CMX外, 植物还存在其它胞吞胞吐途径。近年来, 植物中非网格蛋白依赖的胞吞(clathrin-independent endocytosis)逐渐受到人们的关注(Paez Valencia et al., 2016)。其中包括膜微区(membrane microdomain)脂筏(lipid raft)介导的胞吞, 该胞

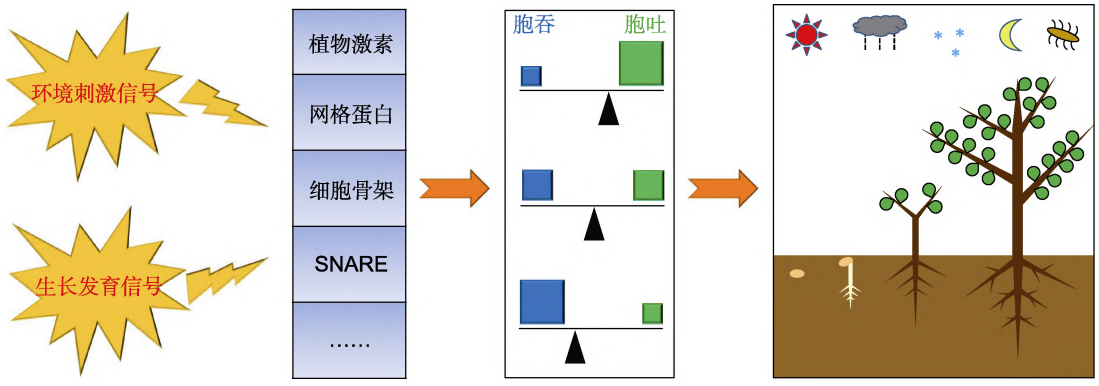

图2 植物耦合调控胞吞胞吐以适应环境并生长繁衍
SNARE: 可溶性N-乙基马来酰亚胺敏感因子附着蛋白受体

Figure 2 Plants adapt to the environment for growth and reproduction by coupling regulation of endocytosis and exocytosis
SNARE: Soluble-N-ethyl-maleimide-sensitive fusion protein attachment protein receptor

吞途径与CME协同调控质膜上RbohD (respiratory burst oxidase homolog D)的活性(Li et al., 2012; Hao et al., 2014)。经典分泌途径中, 蛋白质首先在内质网合成, 接着依次经过高尔基体和TGN, 最终到达质膜或胞外(Cai et al., 2011)。非经典分泌途径主要包括MVB (An et al., 2006; Meyer et al., 2009; Nielsen and Thordal-Christensen, 2013)、液泡(Hatsugai et al., 2009; Hara-Nishimura and Hatsugai, 2011)以及拟南芥和烟草(*Nicotiana tabacum*)中新发现的球形双膜细胞器EXPO (exocyst-positive organelle)介导的分泌途径(Wang et al., 2010)。这些非经典胞吞胞吐途径的耦合调控机制仍有待进一步解析。总之, 植物在收到外界刺激和自身的生长发育信号后, 通过激素和网格蛋白等囊泡运输调控因子实现特定组织细胞中胞吞和胞吐的动态平衡, 从而适应复杂多变的环境并完成其生命周期(图2)。

随着电子显微镜的升级换代和制样方法的不断更新, 人们可更为直观和精确地观察植物囊泡的构造(Mosesso et al., 2019; Narasimhan et al., 2020)。3D重组断层扫描电子显微镜技术的发展使得对囊泡的分析更为立体(Cui et al., 2019), 而超高分辨率共聚焦显微镜和全内反射荧光显微镜在植物研究中的应用, 使动态分析植物囊泡运输成为可能(Zhang et al., 2019b; Shimizu et al., 2021)。相信在不久的将来, 对植物胞吞和胞吐耦合调控的研究将会取得更大的突破, 为揭示植物的生长发育机制以及培育抗逆作物提供新思路。

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Coupling Regulation of Endocytosis and Exocytosis in Plants

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Abstract Eukaryotic cells transport macromolecules and particulate matter away or to the plasma membrane through endocytosis and exocytosis, including certain proteins with important biological functions. The coupling between these two vesicle transport pathways is essential for maintaining the integrity of the plasma membrane as well as regulating the abundance and activity of plasma membrane proteins. In animals, the spatiotemporal coupling of synaptic vesicle endocytosis and exocytosis has been shown to be necessary for the continuation of neurotransmission. In recent years, increasing evidences on the plant vesicle trafficking show the existence of a coupling regulation between endocytosis and exocytosis, which plays an important role in plant growth and development as well as responses to the environment. Here we summarize the physiological significance of plant cooperative regulation of endocytosis and exocytosis, and discuss the potential coupling mechanisms based on the recent progress in the study of clathrin-mediated vesicle trafficking.

Key words sclathrin, coupling, endocytosis, exocytosis

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