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综 述 Reviews

质膜H^+-ATPase影响植物生长发育及逆境响应研究进展

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摘要: H^+-ATPase作为植物生命活动的“主宰酶”, 在植物许多生命活动中发挥重要作用。一般情况下, 质膜H^+-ATPase通过排出质子产生电化学势梯度, 水解ATP释放能量应用于植物的生长发育及抗逆响应。鉴于质膜H^+-ATPase在植物生长发育和逆境胁迫响应过程中的作用, 本文综述了质膜H^+-ATPase结构、生理功能及其对植物生长发育的影响, 讨论逆境胁迫下质膜H^+-ATPase的变化特征及其调节途径, 为充分利用质膜H^+-ATPase提高水稻等作物产量品质提供重要参考。

关键词: 质膜H^+-ATPase; 植物生长发育; 逆境响应; 能量代谢

Research progress of plasma membrane H^+-ATPase functioned in plant growth and development and its response to abiotic stress

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Abstract: As the “master enzyme” of plant life activities, H^+-ATPase plays an important regulatory role in many plant life activities. In general, plasma membrane H^+-ATPase generates an electrochemical potential gradient by excreting protons, and hydrolyzes ATP to release energy for plant growth and development and stress response. In view of the role of plasma membrane H^+-ATPase in plant growth and development and stress response, the structure and physiological function of plasma membrane H^+-ATPase and its effect on plant growth and development were reviewed in this paper. The variation characteristics and regulation pathways of plasma membrane H^+-ATPase under stress were discussed, which provided an important reference

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for making full use of plasma membrane H^+-ATPase to improve the yield and quality of rice and other crops.
Key words: plasma membrane H^+-ATPase; plant growth and development; stress response; energy metabolism

质膜H^+-ATPase是一类利用电化学势梯度进行跨膜运输的膜蛋白, 通过催化ATP水解释放能量驱动质子转运和物质跨膜运输(张雅芬等2021; 周思婕2023)。植物质膜H^+-ATPase还参与调控气孔开闭、调节胞内酸碱度和离子平衡、促进细胞伸长生长等生理过程, 在非生物胁迫响应中发挥着重要作用(Li等2022a; Havshøi和Fuglsang 2022)。因此, 本文就质膜H^+-ATPase影响植物生长发育及逆境响应研究进展进行概述, 以期为深入研究质膜H^+-ATPase在影响水稻(*Oryza sativa*)等作物产量品质形成中的作用提供参考。

1 质膜H^+-ATPase结构

H^+-ATPase水解ATP产生的能量可用于驱动离子逆电化学势梯度进行跨膜运输(Palmgren 2001)。植物细胞中的H^+-ATPase根据结构、功能和定位可分为质膜H^+-ATPase (P型)、液泡膜H^+- ATPase (V型)和线粒体膜与叶绿体膜H^+-ATPase (F型) 。此外, 还有一类主要分布于细胞膜和细胞器膜上的ABC转运蛋白, 也称腺苷三磷酸结合盒转运体(ATP-binding cassette transporter) (Morth 等 2011)。P型H^+-ATPase由单条多肽链组成, 水解ATP的活性位点位于细胞质膜, 水解ATP产生的能量用于逆向转运质子, 驱动转运溶质进入细胞; V型H^+-ATPase是多亚基构成的复合体, 水解ATP的活性位点位于细胞内的液泡膜、内质网膜等膜上, 水解ATP产生能量, 逆浓度梯度从细胞质转运H^+至细胞器内, 维持细胞质基质中性; F型H^+-ATPase是多亚基构成的复合体, 是氧化磷酸化和光合磷酸化的偶联因子, 位于线粒体膜和叶绿体膜, 顺浓度梯度转运H^+驱动ATP合成; ABC转运蛋白可利用ATP水解产生的能量将糖、氨基酸、肽、蛋白质、脂质、金属离子等物质逆浓度梯度跨膜运输。

质膜H^+-ATPase定位于植物根系等细胞质膜, 属于P型质子泵家族之P3亚家族, 是由一条多肽链折叠成的功能性蛋白(Morth等2011; Falhof等2016)。作为六聚体和二聚体复合物, 质膜H^+-ATPase含有10个跨膜螺旋构成的结构域(M), 包括位于细胞质内侧亲水性氨基末端片段(N-末端)和羧基末端片段(C-末端), 以及核苷酸结合域(N)、磷酸化结构域(P)、C-末端调节结构域(R)和自激动结构域(A)等四个细胞质结构域(Falhof等2016; Ruiz-Granados等2019)。N-末端是H^+的入口, C-末端是H^+的出口, 同时也是调控酶活力的自抑制区域(Ekberg等2010; Wielandt等2015); 核苷酸结合结构域(N)是ATP结合的位点(Palmgren 2001); 在磷酸化结构域(P)中, 天冬氨酰残基在催化循环中被磷酸化, 形成磷酸化中间体(Falhof等2016); 在质膜H^+-ATPase C-末端发现的调节结构域(R)具有两个自动抑制区和一个14-3-3蛋白结合位点(Duby和Boutry 2009; Haruta等2015); 自激动结构域(A)则由氨基末端片段和小环组成(Michalak等2022)。

质膜H^+-ATPase存在E1和E2两种构象(Morsomme和Boutry 2000; Yatime等2009)。在催化循环期间, 构象互变是ATP水解和离子运送偶联的基础(杨阔2017)。当处于E1状态时, 质膜H^+-ATPase对ATP高度亲和, 其水解ATP同时将H^+转运到细胞质外侧形成跨膜质子梯度, 故其跨膜结合位点位于胞质一侧。E1构象通过天冬氨酸的磷酸化作用变为E2构象; 当处于E2状态时, 质膜H^+-ATPase对ATP具有较低的亲和力, 跨膜结合位点位于膜外侧。酶蛋白的去磷酸化作用使处于E2构象又变为E1构象(Palmgren 2001)。

2 质膜H^+-ATPase对植物生长发育的影响

作为植物生命活动的“主宰酶”, 质膜H^+-ATPase是广泛存在于植物细胞膜上的一类跨膜蛋白, 能通过水解ATP释放能量, 将H^+逆浓度梯度从细胞质泵出至质外体, 酸化质外体空间, 建立和维持跨膜H^+电化学梯度。另外, 质膜H^+-ATPase还参与调节植物物质跨膜运输、气孔运动、胞内pH稳态、细胞伸长、组织着色和果实酸度等多种生理过程,

在次级主动运输中发挥重要作用。

2.1 调节物质跨膜运输

物质跨膜运输是指物质通过细胞膜的运输过程, 对维持细胞内外物质平衡和生理功能正常运转至关重要(许飞云等2016)。根据是否需要能量和载体蛋白, 物质跨膜运输可以分为三大类: 被动运输、主动运输和膜泡运输。细胞膜上存在具有跨膜运输功能的通道蛋白或转运蛋白, 可选择性运输离子、小分子和大分子等特定物质。通过驱动质子转运, 质膜H^+-ATPase建立质子电化学梯度, 逆浓度梯度运输Na、K、N、S等细胞必需元素和糖、氨基酸、脂类等有机成分(Sondergaard等2004)。根据蔗糖-质子同向运输模型(Laust等2023), H^+-ATPase将H^+泵到质外体, 形成跨膜电化学势差; H^+趋于平衡回流到共质体时, 通过质膜上的蔗糖/H^+同向运输器, 利用质子的顺电化学势梯度进行扩散, 将质外体中的H^+和蔗糖共同转运至筛分子-伴胞复合体的共质体。研究发现, 光合作用产生的糖不断积累可激活质膜H^+-ATPase活性(Okumura等2016)。质膜H^+-ATPase还与其他转运蛋白互作, 催化ATP水解产生的能量将钾离子(K^+)、钠离子(Na^+)、铵根离子(NH_4^+)和硝酸根离子(NO_3^-)等特定矿物质离子通过载体蛋白和通道蛋白输入细胞(Morales-Cedillo等2015; Alvarez-Pizarro等2011; Yang等2021; Wang等2022; Kinoshita等2023)。为防止植物Na^+中毒, Na^+/H^+反转运体可将Na^+从细胞质转运至质外体或液泡, 而这一过程由质膜H^+-ATPase水解ATP完成(Yang等2007)。研究表明, 甲哌鎓(mepiquat chloride)能激活质膜H^+-ATPase调节棉花(*Gossypium* spp.)根系K^+通道活性, 促进K^+吸收(Zhang等2021a)。此外, 质膜H^+-ATPase激活剂壳梭孢菌素(fusicoccin, FC)可促进水稻根系对NH_4^+的吸收, 而质膜H^+-ATPase抑制剂钒酸盐则降低水稻根系吸收NH_4^+ (Ding等2021)。总之, 质膜H^+-ATPase在植物细胞中通过建立质子电化学梯度, 跨细胞膜转运特定矿物质离子, 是植物细胞对矿质元素吸收及转运的重要调节机制之一。

2.2 调控气孔运动

气孔是由一对保卫细胞围成的孔状结构, 能调节植物与大气之间的气体交换。作为植物气体交换的门户, 气孔开度大小与植物生长发育、光合作用、能量代谢等过程密切相关(胡健2019)。研究表明, 保卫细胞中的质膜H^+-ATPase可通过倒数第二个残基苏氨酸(Thr)磷酸化激活, 诱导细胞内气孔开闭(Kinoshita和Shimazaki 1999; Kollist等2014)。气孔开放过程中, 质膜H^+-ATPase泵出质子, 降低气孔两侧细胞内pH值, 酸化细胞外间隙环境, 提高细胞内沉积的离子和有机酸浓度(Shimazaki等2007; 周露艳2023)。这种酸性环境以及高浓度离子和有机酸促进气孔周围细胞不断摄取水分并膨胀, 进而推动气孔开放; 气孔闭合过程中, 质膜H^+-ATPase活性降低, 细胞内质子泵出减少, 细胞外间隙pH值升高, 细胞外离子浓度降低, 导致气孔周围细胞的水分排出和膨胀减少, 从而推动气孔闭合(Kinoshita和Hayashi 2011)。据报道, 质膜H^+-ATPase能通过调节钾离子(K^+)转运影响气孔运动; 气孔开放过程中, 质膜H^+-ATPase水解ATP促进H^+向细胞外转运, K^+_{in}通道感受器感知到电位变化后打开K^+_{in}通道, K^+积累促进细胞体积膨大、诱导气孔开放(Sharma等2013; Wong等2021; 吴雨衡2022)。另外, 保卫细胞中质膜H^+-ATPase磷酸化水平及其与14-3-3蛋白互作能调控蚕豆(*Vicia faba*)气孔运动(孙慧群2017); 拟南芥(*Arabidopsis thaliana*)蛋白RIN4与质膜H^+-ATPase互作可调节气孔运动, 并抑制细菌病原体在感染期间进入植物叶片(Elmore和Coaker 2011)。综上所述, 质膜H^+-ATPase通过调节细胞外间隙pH、K^+转运以及与其他蛋白质互作, 调控植物气孔运动。

2.3 维持细胞内pH稳态

细胞内pH稳态是指在细胞内维持一定的酸碱平衡状态。维持相对恒定的细胞pH值能够保证植物正常生长所需的基本生理活动, 也是调节植物生长发育和环境胁迫响应的基础(赵振杰等2020; 张海龙2023)。研究表明, H^+-ATPase可在细胞内把ATP形式转化为跨膜H^+电位差, 有助于细胞维持细胞内pH稳态(赵敏华等2022)。另外, 初级H^+-ATPase和次级离子/H^+交换器之间的协调能维持内膜pH稳态, 进而在液泡和分泌/内吞途径的隔室中维持合适腔内pH (Pittman 2012; Zhou等2021)。据报道, γ-氨基丁酸(γ-aminobutyric acid, GABA)可通

过激活质膜H^+-ATPase维持细胞内pH稳态(Guo等2023)。鉴此, 质膜H^+-ATPase主要将质子主动运输到质外体促使细胞质环境相对碱化, 维持胞质pH稳态, 为细胞正常生命活动提供重要保障。

2.4 促进细胞伸长

植物细胞壁主要由纤维素、半纤维素和可溶性多糖组成, 其中纤维素是主要结构支持物质(Rayle和Cleland 1992; Hager 2003)。根据细胞酸生长理论, 细胞壁伸长通过酸性松弛和渗透膨胀实现(周影等2019)。酸性松弛过程中, 质膜H^+-ATPase将质子从细胞内泵出, 降低细胞壁基质溶液pH值, 形成酸性环境(Dayod等2010)。pH值降低致使细胞壁对酸不稳定的氢键断裂, 提高细胞壁纤维素酶活性, 导致木葡聚糖与纤维素微纤丝之间的键断裂, 造成细胞壁松弛; 渗透膨胀过程中, 细胞内离子、葡萄糖和其他溶质进入细胞外间隙, 增加细胞外间隙渗透浓度, 促使水分子进入细胞外间隙, 提高细胞壁对内部压力的抵抗, 引发细胞壁伸长(Wang等2013; 张保才和周奕华2015; 王延泽2023)。研究表明, 喷施质膜H^+-ATPase激活剂, 可促进植物细胞质外体酸化、细胞壁疏松而使细胞生长(韩秀丽2020)。由此表明, 质膜H^+-ATPase主要通过提高细胞壁酸性化促进细胞伸长。

2.4.1 下胚轴伸长

下胚轴是种子萌发过程中连接胚根和胚芽的部位(杨东旭等2023), 在水分、无机成分、有机营养和植物激素等物质运输过程中发挥重要作用(吴羚阁等2024)。种子萌发过程中, 下胚轴伸长将胚根推出种皮, 吸收水分及营养物质, 随后子叶破土而出并进行光合作用(宋雨函和张锐2021; 尹守鹏2022)。该过程与质膜上H^+外排和离子平衡调节有关, 即质膜H^+-ATPase促进H^+主动外排, 使下胚轴细胞外形成负电位, 构成电位梯度驱动离子进入下胚轴细胞, 调节细胞内离子平衡(Yuan等2017)。质膜H^+-ATPase参与的调节植物细胞酸碱平衡促进了下胚轴伸长; 质膜H^+-ATPase运输质子至细胞壁, 与阴离子形成酸性环境, 有利于松弛细胞壁, 促使下胚轴细胞伸长(Majumdar和Kar 2018)。据报道, 油菜素甾醇(brassinosteroids, BRs)能激活质膜H^+-ATPase磷酸化, 促进14-3-3蛋白与质膜H^+-ATPase结合, 诱导幼苗下胚轴伸长(Minami等2019)。另外, 跨膜激酶I TMK1 (transmembrane kinase 1)和TMK4 (transmembrane kinase 4)可激活质膜H^+-ATPase, 促进质外体酸化和下胚轴细胞扩增(Lee等2015)。与之相反, 脱落酸(abscisic acid, ABA)能通过诱导质膜H^+-ATPase去磷酸化抑制下胚轴伸长(Hayashi等2014)。研究发现, 将质膜H^+-ATPase基因*AHA2*敲除后, 拟南芥下胚轴的伸长速率明显减慢(Hayashi等2014; Haruta等2015); 而水稻‘日本晴’过表达质膜H^+-ATPase基因*OsA8*株系的根伸长速率高于野生型(Chen等2017)。

2.4.2 花粉管生长

花粉管是植物花粉粒在柱头萌发后产生的细胞结构; 花粉管在雌蕊组织的迅速生长是指花粉管高度极化的顶端生长将精细胞送达子房胚珠完成受精的过程(Hoffmann等2020; Li等2023a)。花粉管生长与细胞内膨胀压力、囊泡转运、内吞作用、胞吐作用以及细胞壁的构建有关, 这些细胞生命活动所需能量依赖于质膜H^+-ATPase水解ATP (Rottmann等2016; Goetz等2017; Ge等2019)。质膜H^+-ATPase在花粉管的顶端产生质子梯度, 驱动K^+和Ca^{2+}从细胞外转运到细胞内, 调节细胞内外电位差和渗透势, 促进细胞水分摄取和膨胀, 推动花粉管生长(Pertl-Obermeyer等2014; Safiarian等2015)。据报道, 壳梭孢菌素通过与14-3-3蛋白相互作用激活质膜H^+-ATPase活性, 调控百合(*Lilium brownii* var. *viridulum*)花粉萌发和花粉管生长速率(Pertl等2001)。进一步研究表明, 14-3-3蛋白与质膜H^+-ATPase的R结构域磷酸化相互作用是花粉管生长开始的重要步骤(Pertl-Obermeyer等2022)。综上所述, 质膜H^+-ATPase通过影响细胞外间隙离子浓度以及与细胞内调控蛋白相互作用, 调节花粉管生长。

2.5 促进组织着色

2.5.1 花瓣着色

植物花瓣颜色是多种化合物相互作用的结果, 其中类胡萝卜素和花青素是其中的重要组成物质(李芋蓉2021)。据报道, H^+-ATPase参与类胡萝卜素和花青素合成, 并维持或增强花瓣中色素的稳定性(Verweij等2008; 周伟权2021)。研究表明, 类胡萝卜素合成途径中的八氢番茄红素合成酶(phy-

toene synthase, PSY)和八氢番茄红素去饱和酶(phytoene desaturase, PDS)可利用质子梯度产生的能量, 将底物转化为最终产物(周伟权2021)。花瓣色素含量容易受到环境条件(如光照、温度等)和氧化损伤的影响, 而质膜H^+-ATPase可维持色素稳定性, 延长色素寿命, 减轻外界环境因素损害色素(王晰锐2012)。有研究表明, 质膜H^+-ATPase两种同系物PH5 (pleckstrin homologue 5)和PH1 (pleckstrin homologue 1)相互作用形成的复合物, 能促进矮牵牛花(*Petunia* × *hybrida*)液泡酸化, 改变花瓣颜色(Verweij等2008; Faraco等2014)。由此可知, 花瓣着色是一个复杂的过程, 质膜H^+-ATPase可调节细胞外间隙pH值, 调控着色物质的合成和聚集。

2.5.2 果实着色

果实着色是水果成熟过程中最明显的变化, 参与的色素包括叶绿素、类胡萝卜素和花青素(周玉平2022)。水果成熟过程中, 细胞内质子泵活性增加, 在膜上形成质子梯度, 驱动色素从细胞质被转运到色素体或其他细胞器。对于大多数葡萄(*Vitis vinifera*)品种, 浆果皮花青素积累是颜色出现的主要原因(Li等2023b)。在葡萄果实发育和成熟过程中, H^+-ATPase参与原花色素运输, 通过主动转运质子从葡萄果实细胞内部向胞外泵出, 维持果实细胞外液较低的pH值, 促进细胞内原花色素溶解和解聚, 有利于色素释放(龙勇益等2024)。溶解和解聚的原花色素通过细胞膜上的离子通道和转运载体进行跨膜运输, 进入细胞外液使果实呈现紫色(郭建勇2022)。

2.6 调控果实酸度

酸度是影响果实风味和品质的关键因素之一, 植物细胞中有机酸积累主要取决于有机酸代谢、转运及液泡储存(Zheng等2023)。定位于液泡膜的V-ATPase和V-PPase为有机酸的输送提供合适的条件(Sze等1999; Martinoia等2007)。有关质膜H^+-ATPase参与调控植物果实的报告陆续见于柑橘(*Citrus reticulata*)和苹果(*Malus pumila*) (石彩云2022; 黄晓玉2023)。质膜H^+-ATPase在果实发育和成熟过程中通过泵出质子, 降低细胞内pH值, 导致果肉细胞外间隙呈现酸性环境, 促进有机酸合成和积累。苹果酸作为主要的有机酸, 约占总有机酸含量的90% (Ma等2015), 编码质膜H^+-ATPase的*MI0*基因(MDP0000810883)能促进苹果酸盐进入液泡, 调节果实酸度(Ma等2019)。鉴于质膜H^+-ATPase受多种环境因素影响, 植物能根据外界环境和内部信号调节质膜H^+-ATPase活性, 改变果实酸度。总之, 质膜H^+-ATPase可通过影响细胞外间隙的酸性环境调节果实酸度。

3 质膜H^+-ATPase对逆境胁迫的响应

植物质膜作为植物细胞与外界进行能量交换的屏障, 首先与环境因子接触, 是应对逆境胁迫的第一道防线。H^+-ATPase作为质膜上最丰富的蛋白质, 在响应干旱胁迫、盐碱胁迫、高温胁迫、重金属胁迫、酸雨胁迫等逆境胁迫的应答中均具有重要作用(Vitart等2001; Chang等2009; Zhu等2009; Cao等2020)。

3.1 干旱胁迫

干旱胁迫下, 植物体内可利用水分下降, 植株正常生长和发育受阻、机体受到损伤(杜琳颖2023)。研究表明, 碳水化合物、可溶性蛋白、脯氨酸、甜菜碱等渗透物质以及超氧化物歧化酶(SOD)、过氧化物酶(POD)、过氧化氢酶(CAT)、还原性抗坏血酸(AsA)、还原性谷胱甘肽(GSH)、抗坏血酸过氧化物酶(APX)、谷胱甘肽还原酶(GR)等抗氧化酶活性的变化是植物干旱胁迫响应的重要特征, 可反映出植物对干旱的抵抗能力(Hassanpouraghdam等2020; Ran等2019; 刘金英2023; 宋松波2023)。干旱胁迫下, 植物水分供应减少, 细胞内水分压力降低, 细胞内外pH值发生变化; H^+-ATPase通过调节细胞膜上的质子泵活性, 维持细胞内pH和电化学梯度稳定及细胞基本功能, 提高干旱适应性(薛媛2019; Siddiqui等2021)。研究表明, 干旱胁迫会增加蚕豆根系中过氧化氢(H_2O_2)积累, 抑制质膜H^+-ATPase磷酸化水平进而降低质膜H^+-ATPase活性(吴怀胜2016)。许飞云等(2021)研究发现, 干旱胁迫下, 印度梨形孢(*Piriformospora indica*)通过提高旱稻根系生长素含量, 调控根系细胞膜H^+-ATPase活性, 促进根毛发育。H^+-ATPase还可作为信号分子与其他蛋白质相互作用, 激活或抑制干旱响应相关基因的表达, 调节植物对干旱的应答

(Li等2022b)。据报道, 聚乙二醇(PEG)模拟干旱处理条件下, 质膜H^+-ATPase活性显著增强, 有效调节离子转运, 提高水稻对干旱的适应能力(Agrawal等2002; Wang等2019)。总之, 干旱胁迫下, 质膜H^+-ATPase通过调节细胞内外的酸碱平衡和离子通量, 参与信号传导等方式维持细胞正常功能、提高植物干旱适应性。

3.2 盐碱胁迫

盐胁迫指盐土中过量存在的Na^+、Cl^-等干扰植物生理代谢活动, 抑制植物正常生长, 导致植物早衰甚至死亡(余贝等2023); 碱胁迫指土壤中碱性盐$NaHCO_3$、Na_2CO_3含量过高, 造成植物根际土壤环境pH值明显上升, 土壤呈碱性(贾美美2023; 靳亚楠等2023)。高盐碱环境下, 细胞内活性氧积累大量, 细胞膜脂质过氧化反应及透性增加(邱雨后等2024)。研究表明, 质膜H^+-ATPase是盐胁迫下维持离子稳态的中枢调节因子之一(Yang等2021); 在烟草(*Nicotiana tabacum*)中过表达胡杨(*Populus euphratica*)转录因子基因*PeWRKY1*能够激活质膜H^+-ATPase基因*NtHA4*的表达, 增强Na^+外排, 提高烟草耐盐性(Yao等2020)。质膜H^+-ATPase还与其他抗逆蛋白质相互作用, 激活胁迫响应相关基达的调控, 增强植物对盐碱胁迫抵抗能力。据报道, 碱胁迫下, 细胞膜Ca^{2+}水平升高, 触发钙信号系统, 诱导TaCCD1和TaSAUR215相互作用, 提高TaHA2磷酸化水平, 增强小麦质膜H^+-ATPase活性及碱胁迫耐受性(Cui等2023)。来自淀粉芽孢杆菌PDR1的挥发性有机化合物(VOCs)通过调节质膜H^+-ATPase活性增强拟南芥对碱胁迫的抗性(Li等2020)。综上所述, 质膜H^+-ATPase可通过调节细胞膜稳定、维持离子及pH值平衡的途径, 提高植物对盐碱胁迫的耐受性。

3.3 重金属胁迫

细胞膜系统受损是重金属毒害植物的重要特征(Janicka-Russak等2008)。研究表明, Cu^{2+}可降低小麦根质膜微囊H^+-ATPase活性, 致使根质膜微囊膜脂过氧化, 抑制根系营养元素的吸收及转运, 干扰植物生长发育(杨颖丽等2005)。然而, 植物在受到重金属胁迫时, 质膜H^+-ATPase产生的质子电化学梯度可提供大量的能量, 将重金属离子排出细胞质, 缓解重金属伤害(赵敏华等2022)。和敏感黑大豆(*Glycine max*)相比, 铝胁迫可增强耐铝黑大豆根中质膜H^+-ATPase磷酸化及其与14-3-3蛋白的相互作用, 提高质膜H^+-ATPase活性(Guo等2013)。由此可知, 质膜H^+-ATPase在植物抗重金属胁迫中起着积极防御作用, 而外施BR激活质膜H^+-ATPase活性可增强黄瓜(*Cucumis sativus*)对镉胁迫的耐受性(Jakubowska和Janicka 2017)。

3.4 温度胁迫

3.4.1 高温胁迫

高温胁迫通常会导致植物生长和发育受到不可逆的损害。据Horváth等(2012)提出的膜感应假说, 认为质膜是细胞热传感器。高温下, 细胞内活性氧物质积累, 导致细胞膜脂质过氧化反应增强, 细胞膜透性增加; 质膜H^+-ATPase通过调节细胞膜离子泵活性, 维持细胞内外离子浓度平衡, 减轻细胞膜损伤, 保持细胞膜稳定性。高温下水稻品种‘SDWG005’通过苯丙烷代谢, 调节抗氧化酶活性, 提高颖花淀粉含量、蔗糖合酶及ATPase基因的表达量(汪胜勇2023)。石庆华等(2006)研究发现, 高温胁迫下, 质膜H^+-ATPase活性在早稻耐高温品种‘农大228’和‘082’中提高, 而在热敏感品种‘茉莉占’和‘协青早B’中降低。另外, 田婧等(2011)发现叶面喷施亚精胺(Spd)可显著降低高温胁迫下黄瓜幼苗叶片脂质过氧化, 增加质子泵活性, 稳定叶片膜结构和功能, 减轻高温胁迫引起的损伤。

3.4.2 冷冻胁迫

低温冷害导致的质膜过氧化氢累积是抑制H^+-ATPase活性的重要因素之一。低温下, 质膜H^+-ATPase受抑, 细胞间液流传导速度降低, 细胞内离子平衡被打破, 造成植物体生理代谢紊乱(张向荣2009; Nagler等2015)。在玉米(*Zea mays*)根系中, 14-3-3蛋白通过与H^+-ATPase结合, 激活H^+-ATPase活性, 引起K^+内流和水分吸收参与低温响应(Cao等2016)。对此, Lee等(2004)认为低温胁迫导致的水分吸收能力降低和H^+-ATPase活性有关。另外, Kim等(2013)发现低温胁迫对亚麻荠(*Camelina sativa*)和油菜(*Brassica napus*) H^+-ATPase活性的影响

与14-3-3蛋白的表达差异有关。

3.5 酸雨胁迫

酸雨通常会破坏植物叶片细胞结构, 造成细胞外H^+浓度增加; 质膜H^+-ATPase能调节胞内pH稳态、维持渗透压平衡、保障细胞生命活动有序进行, 是植物响应酸雨胁迫的重要指标之一(柳参奎等2004; 葛玉晴2013; Liang和Zhang 2018)。据报道, pH 4.5酸雨能促进水稻和大豆质膜H^+-ATPase基因的表达和H^+-ATPase的磷酸化, 提高作物抗酸能力(Liang和Zhang 2018)。研究表明, 酸雨胁迫下水稻质膜H^+-ATPase活性的改变是质膜H^+-ATPase同工酶和基因表达共同调节的结果(葛玉晴2013)。pH 4.5酸雨胁迫下, 外施Ca^{2+}能提高大豆根部质膜质子泵活性, 表明Ca^{2+}可有效缓解酸雨伤害植物生长发育(张冰洁2017; Liang和Zhang 2018)。

4 质膜H^+-ATPase的调控途径

植物质膜H^+-ATPase存在两种活性状态: 一种是ATP水解与H^+运输松散耦合的自抑制状态, 另一种是ATP水解与H^+泵送紧密耦合的上调状态(Pedersen等2015; Falhof等2016)。质膜H^+-ATPase的调控有三个方面: 一是增加单位面积质膜上的H^+-ATPase数量(张冰洁2017); 二是H^+-ATPase基因转录翻译水平(贾毅等2002; Fuglsang等2014); 三是磷酸化水平的变化(Haruta等2015)。

4.1 外源调控

外源化学物质是调控质膜H^+-ATPase活性的重要因素。张雅芬等(2021)利用酵母双杂交技术在水稻中筛选到了一种可能与bip130 (BR11-interacting protein 130)相互作用的质膜H^+-ATPase *OSA7*, 外施ABA处理后bip130过表达株系质膜H^+-ATPase活性显著增加。据报道, 溶血磷脂酰胆碱(lysophosphatidylcholine)可激活燕麦(*Avena sativa*)和玉米根系质膜囊泡中H^+-ATPase活性, 促进ATP水解(Palmgren和Sommarin 1989; Pedchenko等1990)。另外, H_2S介导的*S*-巯基修饰可提高拟南芥和玉米幼苗质膜H^+-ATPase活性, 加速Na^+/H^+反向运转蛋白运转, 促进Na^+外排, 缓解盐胁迫对植物造成的伤害(刘珂娜2020)。

4.2 分子水平层面调控

4.2.1 基因转录翻译水平

一般情况下, 基因转录被认为是DNA分子转录成RNA, 而翻译是指mRNA在核糖体作用下翻译成肽链; 基因表达是转录翻译的统一, DNA转录成RNA后被翻译成肽链, 最终折叠成有意义蛋白质的过程。正常条件下, 大豆野生型和过表达*HA12*株系的发芽和生长差异不明显; 但在含有$NaHCO_3$培养基中, *HA12*株系的存活率高于野生型, 表明HA12有助于提高植物的$NaHCO_3$胁迫耐受性(Jia等2023)。据报道, 类受体蛋白激酶基因*LRRK1* (*leaf rolling receptor-like cytoplasmic kinase 1*)在水稻中过表达后, LRRK1与卷叶性状调控相关的蛋白OsGF14e互作, 降低质膜H^+-ATPase活性, 导致水稻叶片卷曲(罗琼2021)。干旱胁迫下, 拟南芥中ABA的积累可促进蛋白VAMP711 (vesicle-associated membrane protein711)与质膜H^+-ATPase持续激活的突变体*ost2-2D* (质膜H^+-ATPase家族成员*AHA1*基因突变)互作, 抑制质膜H^+-ATPase活性, 诱导气孔关闭, 减少植物体内水分损耗, 提高植物耐旱性(薛媛2019)。另外, ABA还可激活BRI1相关受体激酶BAK1 (BRI1-ASSOCIATED RECEPTOR KINASE 1), 提高质膜H^+-ATPase活性, 引发保卫细胞发生瞬时质子外排, 致使胞质碱化, 积累活性氧诱导气孔关闭(Pei等2022)。Zhang等(2021b)的研究表明, 过表达*OSA1* (编码质膜H^+-ATPase)能促进水稻根系对铵的吸收同化, 增强光诱导的叶片气孔开放及光合能力, 提高氮肥利用率及产量。

4.2.2 蛋白质磷酸化水平

蛋白质磷酸化是调节、控制蛋白质活力和功能最重要的机制, 是指在蛋白质激酶的催化下, 把ATP或GTP的γ位磷酸基转移到底物蛋白质氨基酸残基上的过程。研究表明, H^+-ATPase活性受C端多个位点磷酸化影响, 其中以倒数第二个苏氨酸(Thr)的磷酸化位点最多(Palmgren 2001; Inoue和Kinoshita 2017)。在磷酸激酶作用下, 磷酸化的质膜H^+ATPase与14-3-3蛋白结合形成蛋白复合体, 调节植物细胞离子通道参与非生物胁迫响应过程 (Du等2010)。研究发现, PP2C家族中进化枝D的两个亚型PP2C.

D6和PP2C.D9, 可去磷酸化保卫细胞质膜H^+-ATPase调控气孔运动(Akiyama等2022)。

4.3 栽培技术调控

水肥管理是影响水稻生长发育、产量品质及抗逆性的重要途径。研究表明, 氮磷钾均能影响水稻叶片ATPase活性, 其中以氮素的影响最大, 其次分别为磷和钾(Ma等2022)。维持较高的质膜H^+-ATPase活性对植株充分吸收利用氮磷钾及其正常生长发育有重要作用(常春荣2008)。据报道, 强光条件下, 铵态氮植株的根系质膜H^+-ATPase活性显著高于硝态氮处理的植株(刘永华等2005)。另外, 低氮条件下, 硝酸盐受体NRT1.1可促进受体激酶QSK1磷酸化, 形成NRT1.1-QSK1复合物, 将低氮信号传递至质膜H^+-ATPase AHA2调节侧根生长(Zhu等2024)。在水分管理方面, 研究表明与常规灌溉处理相比, 中度干旱处理显著提高弱势粒ATP含量及质膜H^+-ATPase活性, 氮对强势粒无显著影响, 而在重度干旱下则强势粒和弱势粒ATP含量及质膜H^+-ATPase活性均显著下降(张伟杨等2018)。由此可知, 灌溉及施肥方式均可能通过影响植株质膜H^+-ATPase促进水稻产量品质的形成。

5 展望

质膜H^+-ATPase通过维持细胞质膜质子梯度和细胞内pH平衡, 参与细胞逆境应答, 在植物抵抗逆境胁迫中发挥重要作用(图1)。虽然对质膜H^+-ATPase的研究较多, 但对其作用机制及调控途径的了解还存在明显不足, 尤其在靶向外源化学调控和栽培技术方面。对此, 可利用转录组学、蛋白质组学和代谢组学等方法, 系统研究与质膜H^+-ATPase相关的基因、蛋白质和代谢物在作物生长发育、产量、品质及逆境响应中的变化特征, 以此为基础研发出能调控质膜H^+-ATPase活性的高效靶向植物生长调节剂以及水肥调控栽培技术, 提高作物应对极端灾害气候的能力。此外, 还可通过基因编辑调控H^+-ATPase的基因, 创建H^+-ATPase活性高的作物种质资源, 培育丰产、优质及抗逆性强的品种, 促进农业的可持续发展。总之, 随着对质膜H^+-ATPase生理功能和逆境胁迫响应的深入研究, 与其相关的基因和蛋白将陆续被挖掘与鉴定, 高效靶向调控产品及技术逐渐完善, 质膜H^+-ATPase将在农业生产发挥重要的作用。

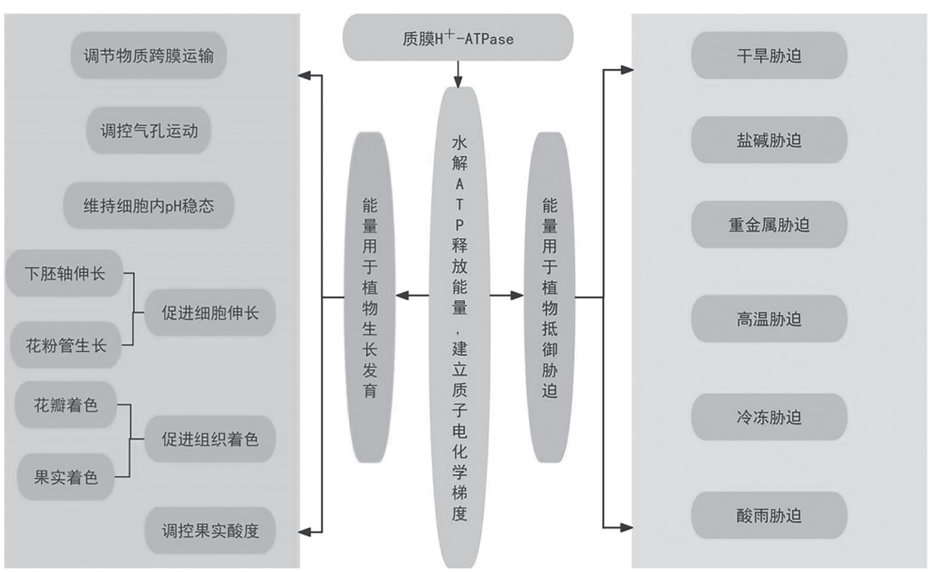

图1 质膜H^+-ATPase影响植物生长发育及逆境响应

Fig. 1 Plasma membrane H^+-ATPase affects plant growth and development and stress response

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