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TOR 激酶: 一个调控植物生长发育和应激反应的核心蛋白

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摘要 为深入了解雷帕霉素靶蛋白(Target of rapamycin, TOR)信号调控网络以及在植物生长发育和胁迫响应中的生物学功能,以“TOR”“葡萄糖”“生长发育”“SnRK1”“信号网络”为关键词,在 Web of Science 和 National Center for Biotechnology Information 等数据库检索,共获取 78 篇相关文献,并归纳总结了植物 TOR 激酶的基本结构信息、TOR 信号网络、Glc-TOR 信号通路以及 TOR 和 SnRK1 的调控机制,分析了 TOR 信号通路在调控植物生长发育及应对逆境胁迫等多个方面的功能。结果表明:绝大多数植物中只含有 1 个 TOR 激酶,且 TOR、RAPTOR 亚基以及 LST 8 亚基组成 TORC1 发挥作用;TOR 激酶包含 HEAT、FAT、FRB、Kinase 和 FATC 5 个结构域;TOR 激酶通过响应光、氨基酸、激素等信号,调控细胞生长发育过程中的蛋白质合成;TOR 激酶在调控植物根的分枝、逆境胁迫响应、ABA 信号和矿质元素吸收方面发挥作用;TOR 与 Glc、SnRK1 等其他营养信号网络协同作用,实现基因表达、代谢、生长和生存的整合与协调。

关键词 TOR; 葡萄糖; 生长发育; SnRK1; 信号网络

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TOR kinase: A core protein regulating plant growth, development and stress response

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Abstract To better understand the regulatory network of the target of rapamycin (TOR) signaling and its biological functions in plant growth and development and stress response, a literature search was conducted in databases such as Web of Science and the National Center for Biotechnology Information by taking “TOR”, “glucose”, “growth and development”, “SnRK1” and “signaling network” as keywords. A total of 78 relevant articles were obtained. By summarizing and analyzing these studies, the basic structural information of plant TOR kinase, the TOR signaling network, the Glc-TOR signaling pathway and the regulatory mechanisms between TOR and SnRK1 were elucidated. Furthermore, the key roles of the TOR signaling pathway in regulating plant growth, development and responses to abiotic stresses were reviewed. The results indicate that: Most plants contain only one TOR kinase. TORC1 is composed of TOR, RAPTOR and LST8 subunits. TOR kinase contains HEAT, FAT, FRB, Kinase and FATC domains. TOR kinase regulates protein sythesis during cell growth and development by responding to light, amino acids, hormones, etc. TOR kinase plays a role in the regulation of root branching, stress, ABA signaling and mineral uptake. TOR functions collectively with other nutrient signaling networks such as Glc and SnRK1 to achieve integration and coordination of gene expression, metabolism, growth and survival.

Keywords TOR; glucose; growth and development; SnRK 1; signaling networks

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生命体的生长与发育需要持续从外界获取能量,并将其吸收转化为自身所需营养成分^[1]。植物作为固着生物,除了依赖从土壤中吸收营养物质外,还通过光合作用合成部分自身所需的营养成分^[1]。营养信号通过与其他内在调节因子相互作用,调控细胞各项生命活动^[1]。因此,植物在进化过程中形成了一系列关键调控蛋白,这些蛋白与营养信号网络协同作用,实现了基因表达、代谢、生长和生存的整合与协调^[1-2]。这种复杂的信号网络能够响应环境变化,优化植物的生长发育过程^[1]。雷帕霉素靶蛋白(Target of rapamycin, TOR)即是此类关键调控蛋白的典型代表,其通过与营养和环境因子的协同作用,调控植物的生长、发育及逆境胁迫应答机制,体现了其在维持植物生长发育稳态中的核心作用^[1-3]。系统总结TOR激酶在植物生长发育和应激反应中的作用机制,可以为进一步探究TOR信号网络,揭示TOR上下游信号分子提供一定的参考,为将来从分子生物学手段提高植物抗逆性提供理论基础和依据。

20世纪70年代,在南太平洋东部复活节岛的土壤样本中发现了1种强效的抗真菌代谢物,这种代谢物由细菌 *Streptomyces hygroscopicus* 产生,经过纯化,该代谢物被确认属于大环内酯类,并以其发现地命名为雷帕霉素(Rapamycin)^[4-6]。而TOR就是雷帕霉素的靶蛋白,是大型的丝氨酸/苏氨酸蛋白激酶(Protein kinase, PK),分子量约280 kU,属于磷脂酰肌醇3激酶相关蛋白激酶(PIKK)家族。TOR存在于酵母、植物和人体中,且序列相似性为40%~60%,是1种高度保守的蛋白激酶^[4, 7-10]。TOR基因的分离鉴定使得科学家可以对其信号功能进行深入研究;并且TOR作为所有真核生物中的核心蛋白,可以协调细胞生长与发育,响应光、生长素、葡萄糖和氨基酸等多种信号^[1, 11-16]。

TOR基因在不同生物体中的结构也有所不同^[17]。但是,所有的真核生物基因组都含有TOR基因,包括酵母、植物、动物、藻类和黏菌。与酵母的2个TOR基因相比,大多数植物、动物和人类基因组只有1个TOR基因,目前发现在大豆(*Glycine max* L.)、杨树(*Populus trichocarpa* Torr. & A. Gray ex. Hook.)和青菜(*Brassica rapa* L.)基因组中存在2个TOR基因^[1, 4, 18-19]。哺乳动物虽然仅有1个TOR基因,可形成2个TOR复合体,分别称为mTORC1(Mammalian

TOR Complex1)和mTORC2。这2个复合体由不同的蛋白组成^[9, 20-21]。mTORC1由mTOR、RAPTOR(Regulatory-associated Protein of mTOR)和mLST8(Lethal with SEC13 Protein 8)蛋白组成^[22-23]。mTORC2也包含mTOR和mLST8,但RAPTOR被RICTOR(Rapamycin-insensitive companion of mTOR)所替代^[4, 24]。大部分植物中仅存在TORC1, TORC2缺失,这是植物与哺乳动物之间的1个关键进化差异^[25]。尽管如此,植物中可能存在其他未被发现的特殊TOR复合体,或者植物TORC1可能具备部分哺乳动物TORC2的功能^[18]。随着对TOR的研究不断深入, TOR信号网络被逐步挖掘,关于TOR的信息也越来越多,但是目前,全面探讨植物TOR生物学功能的研究鲜见报道。本研究在Web of Science和National Center for Biotechnology Information等数据库检索,获取相关文献,归纳总结了植物TOR激酶的基本结构信息、TOR信号网络、Glc-TOR信号通路、TOR和SnRK1的调控机制,以及TOR信号通路在调控植物生长发育和应答逆境胁迫等多方面的功能,旨在深入阐述TOR激酶调控网络以及在植物生长发育和胁迫响应中的生物学功能,以期植物抗逆基因功能研究提供参考。

1 文献来源

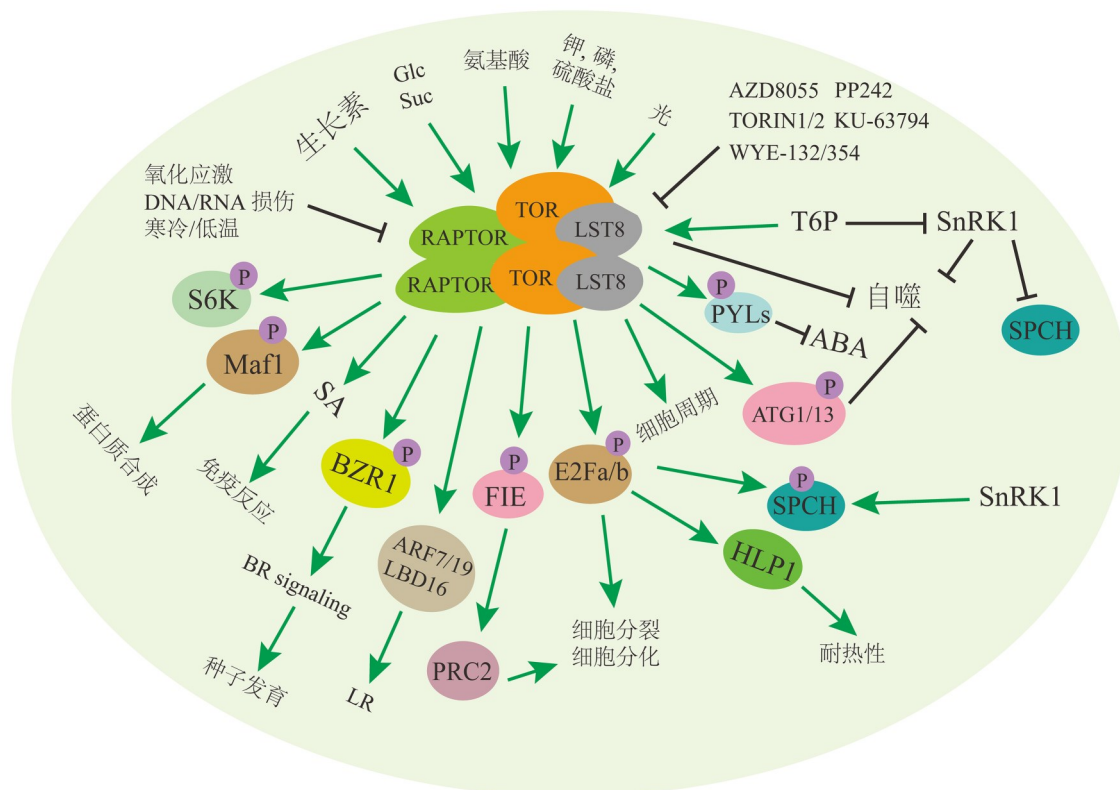
在Web of Science和National Center for Biotechnology Information等数据库,以“TOR”“葡萄糖”“生长发育”“SnRK1”“信号网络”为关键词检索,共获取TOR激酶相关文献78篇。

2 植物中的TOR蛋白复合物

植物TORC1由TOR蛋白、RAPTOR亚基和LST8亚基组成(图1)。TOR蛋白的N端区域包含约1200个氨基酸,由20个HEAT(Huntington、EF3A、ATM、TOR)重复构成,并形成2个反向平行的 α 螺旋,这些结构已被证明能够介导蛋白之间的相互作用^[1, 9]。FAT(Focal adhesion target)区域位于HEAT重复的C端,包含约800个氨基酸,也与蛋白之间的相互作用有关^[1, 9]。TOR蛋白中的HEAT重复和FAT结构域在信号传导中发挥作用^[4]。与FAT结构域的C端相邻的是FRB(FKBP12和Rapamycin结合位点)结构域。植物中由于FKBP12蛋白的突变,导致其与TOR和雷帕霉素不能形成稳定的抑制

复合体,从而使得植物对雷帕霉素不敏感,妨碍了雷帕霉素对 TOR 激酶的抑制作用^[20, 26]。为此,科研工作者开发了新一代的植物 TOR 蛋白抑制剂,如 AZD8055、TORIN1/2、WYE132/354、PP242 和 KU63794 等,这些抑制剂通过与 ATP 竞争,可以直

接结合到 TOR 的激酶结构域,从而抑制 TOR 激酶活性^[7-8, 27-28](图 1)。TOR 的激酶结构域(Kinase)包含 1 个保守 Ser/Thr 激酶基序, Kinase 结构域和其后的 FATC(C 端 FAT)结构域均对蛋白质相互作用和激酶活化有重要贡献^[5, 29-31]。



TOR, 雷帕霉素靶蛋白; RAPTOR, TOR 相关调节蛋白; LST8, TOR 相关调节蛋白; Glc, 葡萄糖; Suc, 蔗糖; ABA, 脱落酸; T6P, 6-磷酸海藻糖; SnRK1, 蔗糖非发酵相关代谢酶 1; S6K, 40S ribosomal S6 protein kinase; Maf1, RNA 聚合酶 III (Pol III) 的抑制因子; SA, 水杨酸; BZR1, 油菜素内酯信号转导转录因子; BR, 油菜素内酯; FIE, 不依赖于受精的胚乳自主发生基因; PRC2, 多梳蛋白抑制复合物 2; E2Fa, 调节细胞周期的转录因子; HLP1, 拟核蛋白 1; ATG1/13, 自噬调节蛋白; AZD8055, TORIN1/2, WYE-132/354, PP242, KU-63794 是 5 个 TOR 蛋白化学抑制剂; LR, 侧根; P, 磷酸化作用; ARF7/ARF19/LBD16, 生长素相关因子; SPCH, bHLH 转录因子; PYLs, ABA 相关受体蛋白。数据来源于文献 [1-2]、[7-9]、[13-14]、[20]、[27-28]、[32-78]。

TOR, target of rapamycin; RAPTOR, regulatory-associated protein of mTOR; LST8, lethal with SEC13 protein 8; Glc, glucose; Suc, sucrose; ABA, abscisic acid; T6P, trehalose 6-phosphate; SnRK1, sucrose non-fermenting-related protein kinase 1; S6K, 40S ribosomal S6 protein kinase; Maf1, a global repressor of RNA polymerase III (Pol III); SA, salicylic acid; BZR1, brassinazole-resistant 1; BR, brassinosteroid; FIE, fertilization-independent endosperm; PRC2, polycomb repressive complex 2; E2Fa, transcription factors; HLP1, hikiishi-like protein 1; ATG1/13, autophagy-related protein 1/13; AZD8055, TORIN1/2, WYE-132/354, PP242, KU-63794 are TOR inhibitors; LR, lateral root; P, phosphorylation; ARF7/19, auxin response factor 7/19; LBD16, lateral organ boundaries-domain 16; SPCH, Speechless; PYLs, pyrabactin resistance1-like. The data shown in this figure are adapted from references [1-2], [7-9], [13-14], [20], [27-28] and [32-78].

图 1 植物中 TOR 信号网络

Fig. 1 TOR signaling network in plants

RAPTOR 与 TOR 蛋白结合形成 TORC1, 在目前所有测序物种中均有发现, 也具有高度保守的结构域, 包括 RAPTOR 的 N 端保守结构域(RNC)、3 个 HEAT 重复和 WD40 重复^[32]。RAPTOR 与 TOR 的 HEAT 结构域相互作用, 调节底物的活性^[32]。RAPTOR 是植物和酵母之间 TOR 复合体

中功能上最保守的成分^[32]。不同植物的 RAPTOR 基因拷贝数量各不相同, 例如, 目前已有研究发现, 在拟南芥中存在 2 个 RAPTOR 蛋白的编码基因, 因其分别定位到 3 号和 5 号染色体上, 分别称为 Raptor3g 和 Raptor5g^[7-8, 26]。所有已测序植物物种中也发现了由 LST8 基因编码的 LST8 蛋白, 该蛋白

含有7个WD40重复,能够形成类似螺旋桨的结构^[7, 33]。然而,LST8在TORC1中的具体功能尚不完全清楚^[30]。

3 TOR信号调控网络

TOR感知多种上游信号,并通过直接或间接的方式激活下游信号,调控细胞生长和增殖(图1)。S6K(40S ribosomal S6 protein kinase 1/2)是TOR蛋白的关键下游信号分子之一,可以被TOR直接磷酸化,从而调控下游的转录翻译等进程,可通过检测S6K的磷酸化水平来检测TOR激酶的活性^[20]。

TOR作为关键调控因子,在控制植物根的分枝方面发挥核心功能^[2, 34]。在拟南芥侧根形成过程中,部分生长素相关基因(如*ARF7*、*ARF9*和*LBD16*)也会参与其中^[2]。Stitz等^[2]研究表明,抑制TOR活性会减少ARF19、ARF7和LBD16的翻译,从而影响这些关键调控因子的表达,进而影响侧根形成。TOR在植物应对各种生物和非生物压力中也扮演着多重角色(图1)。如,TOR在植物应对氧化应激和DNA/RNA损伤的响应中起负调节作用^[35]。在番茄中,TOR活性被抑制后通过水杨酸(Salicylic acid, SA)依赖性机制激活免疫反应,并降低番茄对多种病原的易感性^[35]。Maf1是1种高度保守的RNA聚合酶III抑制因子,且Maf1的去磷酸化可以促进其自身的抑制活性^[36]。在柑橘中,Maf1可与柑橘疫病诱导因子结合,抑制柑橘中与病害发展相关的细胞生长^[36]。Ahn等^[36]研究表明,TOR被抑制后,导致Maf1去磷酸化,从而抑制柑橘疫病的发生。通过这种机制,植物可以减缓蛋白质合成和细胞生长或分裂,以应对胁迫反应(图1)。

TOR可在植物对干旱和渗透胁迫的响应中发挥正调节作用^[37-38]。高浓度KCl溶液中,拟南芥TOR基因过表达植株的主根长度显著大于野生型^[38]。拟南芥中的TOR基因在水稻中异源表达,可以提高水稻的水分利用效率、促进植株生长,从而提高产量^[39]。温度对TOR活性亦有显著影响,在4℃低温胁迫下24 h,拟南芥的TOR活性短时间内会受到抑制,表明TOR抑制是植物抵御寒冷胁迫的重要机制^[40]。而且,TOR-RNAi(RNA interference)拟南芥株系对寒冷表现出超敏感性^[41]。除了冷胁迫,TOR还参与高温耐受性。外源性添加葡萄糖、TOR过表达及E2Fa过表达均能促进拟南芥HLP1(*Hikeshi-like protein 1*)基因

的表达,从而提高幼苗在热应激恢复后的存活率;TOR活性下调以及使用TOR抑制剂AZD8055处理均可导致幼苗存活率降低^[42]。Glc-TOR激活的E2Fa转录因子直接结合HLP1的启动子以激活其表达;AtHLP1又直接结合多个热休克基因的启动子,从而激活并维持热记忆,增强了植物的耐热性^[42](图1)。

TOR和脱落酸(ABA)信号通路之间的相互作用对于维持植物生长与应答/抵御胁迫反应之间的平衡至关重要^[43](图1)。RAPTOR是TOR复合体的重要组成部分。在胁迫条件下,ABA激活SnRK2s(SNF1-related protein kinase 2),这些蛋白随后通过磷酸化抑制TOR活性,从而抑制植物生长。此外,ABA的受体PYLs(Pyrabactin Resistance1-like)也参与了这一调控机制^[43-44]。在高养分条件下,TOR通过磷酸化PYLs抑制ABA信号,从而促进植物生长^[43-44]。

TOR信号通路在植物矿质元素的调控中发挥着至关重要的作用(图1)。Couso等^[45]研究发现,TOR是磷信号转导的重要组分,磷的缺乏会导致LST8的表达量降低,从而影响TOR的活性。缺磷也会引发早期根系生长抑制,而拟南芥根系特异性激酶1(ARSK1)在磷缺乏时可以减轻根系生长抑制^[46];ARSK1能够磷酸化并稳定TORC1的调节相关蛋白RAPTOR1B,以调整根系生长与磷的可用性之间的平衡^[46]。硫酸盐限制会导致TOR活性下降,激活细胞自噬,从而帮助植物调节碳平衡^[47]。硫酸盐也能高效地激活TOR和细胞增殖,从而促进叶片发育^[48]。TOR与钙调节蛋白(CBL)和CBL相互作用激酶(CIPK)组成的低钾反应信号网络也具有一定的联系^[49]。钾营养充足时,植物TORC1迅速被激活,进而关闭CBL2/3-CIPKs低钾胁迫响应通路^[49]。而在低钾胁迫条件下,Ca²⁺-CBL2/3-CIPKs信号通路被激活,通过磷酸化RAPTOR1B抑制TORC1的活性,从而抑制植物生长,确保植物能够在逆境中生存^[49]。

4 Glc-TOR信号调控植物生长发育

光合作用产生的葡萄糖(Glucose, Glc)是调控TOR激酶的关键信号分子,Glc及其在三羧酸循环(TCA)中产生的代谢产物是激活植物TOR活性的重要因子^[1, 13-14, 50](图1)。在拟南芥(*Arabidopsis*)幼苗中,Glc能够显著激活TOR激酶,并在根毛发育中发挥核心作用^[21]。茎部光合作用产生的Glc通过糖酵解和线粒体能量代谢驱动TOR信号的传

递,从而调节根尖分生组织的活性^[14, 21, 51]。Glc-TOR信号通路调控涉及中心和次级代谢、细胞周期、转录、信号传导和蛋白质折叠等关键基因的转录重编程^[14, 21, 51]。Li等^[52]研究显示,即使在缺乏光照的条件下,葡萄糖也能有效促进初生根的快速生长(图1)。

油菜素内酯(Brassinosteroid, BR)信号转导转录因子BZR1(Brassinazole-resistant 1)对植物生长至关重要^[53]。Zhang等^[54]研究发现,糖信号通过TOR途径控制BZR1的积累(图1)。外源糖的施加能够促进BZR1的积累和种子生长,但这种效应在TOR失活的情况下几乎完全消失,而TOR失活对BZR1降解的影响可通过抑制自噬得以阻止。这些发现表明,Glc-TOR信号对BZR1的调控能够有效的促进植物生长,确保植物生长中的供需平衡^[54]。E2F转录因子在植物和哺乳动物细胞周期进程及DNA复制中的调控作用已得到广泛研究^[51]。层次聚类分析揭示,多个由Glc-TOR通路激活的基因与典型的S期基因具有显著的匹配性^[51]。后续研究进一步证明,Glc和蔗糖能够特异地激活E2Fa靶基因,而其他糖则没有类似的激活效应^[51]。这些结果表明,Glc-TOR信号通路可能通过E2Fa调控细胞周期的进程和基因表达。此外,TOR-E2Fa模块在拟南芥中对糖依赖性的愈伤组织形成也具有调控作用^[55]。这进一步证实,TOR-E2Fa信号通路在植物细胞增殖和分化过程中发挥着关键作用。Glc-TOR信号通过协调转录激活,提供必需的能量、代谢物、生物物质等,支持细胞的各项功能^[51](图1)。

海藻糖-6-磷酸(T6P)不仅是一种糖分子,更是一种重要的信号调节因子^[56]。T6P可以通过抑制SnRK1激酶来抑制细胞自噬;同时,糖信号能够激活TOR蛋白,进一步抑制细胞自噬^[7, 57](图1)。细胞壁转化酶将蔗糖转化为葡萄糖和果糖,产生的葡萄糖通过与G蛋白调节因子(RGS1)相互作用,诱导自噬,从而去除细胞质中过量的糖,调节可用糖的水平^[18, 58]。因此,TOR与自噬机制协同调控细胞中的糖稳态^[4, 7, 56-57, 59]。FIE(Fertilization-independent endosperm)作为PRC2(Polycomb repressive complex 2)的核心组分,是TOR蛋白的一个重要靶标^[14]。Glc-TOR-FIE-PRC2信号通路在植物细胞分化中发挥着重要的调控作用^[14](图1)。最新研究发现,Glc-TOR信号通路在调整昼夜节律

周期中也发挥着关键作用^[60]。外源施加Glc激活TOR并缩短昼夜节律周期;相反,通过雌二醇诱导的TOR沉默则导致昼夜节律周期显著延长,并完全阻碍了外源Glc恢复昼夜节律周期的作用^[1, 60]。除此之外,还有许多其他因子可以调控TOR信号。光合作用吸收固定二氧化碳可以刺激增强TOR信号,氨基酸水平和TOR活性之间也具有紧密的联系^[61-62]。生长素(Auxin)也可以激活TOR-S6K信号^[8, 28, 63]。

在漫长的进化过程中,植物演化出相对成熟的TOR信号网络,这一网络对植物的生长繁殖以及抵御环境压力和生物胁迫起着重要作用^[1, 28, 55]。TOR在哺乳动物抵御癌症及其他疾病方面也发挥着至关重要的作用^[64]。因此,揭示植物Glc-TOR信号网络在代谢和细胞周期控制中的作用,可能为动物或人类癌症中的mTORC1转录网络提供新的见解^[14, 16, 64]。

5 TOR与SnRK1信号

在植物的生长发育过程中,TOR和SnRK1经常作为对立调节因子发挥作用^[14, 16, 64]。在营养充分的条件下,TOR通过感知高能量供应和充足的营养来发挥作用,而SnRK1则在低能量状态下被激活,通过维持能量积累和提高抗逆性来保障生存^[65-66]。TOR和SnRK1之间的这种动态协调作用使植物能够高效地管理能量资源,确保适当的发育、增长以及对生物和非生物逆境胁迫的适应^[65-66]。

气孔在植物与大气之间的气体交换中起着关键作用^[67]。SPCH(Speechless)作为bHLH转录因子,可以整合多种环境和激素信号,调控气孔发育^[67-69]。Han等^[67]研究发现,TOR和SnRK1通过调节SPCH而调节气孔发育。在低蔗糖水平下,蔗糖激活TOR,导致E2Fa和E2Fb的磷酸化,从而进一步激活SPCH表达以促进气孔发育。同时,SnRK1磷酸化SPCH,不仅提高了SPCH蛋白的稳定性,还增强其促进气孔发育的能力^[67, 70]。在高蔗糖水平下,蔗糖供应增强了T6P的丰度,进而减少SnRK1.1与SnAK1/2(SnRK1激酶1/2)之间的相互作用,抑制了SnRK1.1的活性,从而促进SPCH降解并抑制气孔发育^[67, 71-72]。此外,T6P还通过控制SnRK1、TOR和生长素调节植物根的分枝。生长素通过IAA14-ARF7/19(吲哚-3-乙酸14-生长

素响应因子7/19)信号通路下调海藻糖磷酸酶的表达,促进T6P的积累,T6P再通过抑制SnRK1和激活TOR调节根分枝的形成^[34,73]。

TOR和SnRK1激酶都参与调节细胞自噬^[65-66]。正常情况下,TOR通过磷酸化ATG1/13(Autophagy-related protein 1/13)负调控自噬^[74-75](图1)。但在营养不足条件下,SnRK1.1可以直接磷酸化ATG1和ATG6来激活自噬通路,或者SnRK1.1通过磷酸化RAPTOR激活自噬,从而使TOR激酶失活^[76-77]。Zhao等^[50]在葡萄中发现TOR与SnRK1.1相互作用可以调节糖代谢相关的基因表达。TOR和SnRK1信号也可以平衡植物生长和应激反应,FLZ8蛋白在此过程中发挥着反馈调节作用^[78]。在糖充足的条件下,TOR诱导FLZ8的表达上调。然后,FLZ8通过增强SnRK1.1与RAPTOR1B蛋白的结合,抑制TOR的活性,负向调节TOR信号通路,防止TOR被过度激活^[78]。相反,在FLZ8缺失的情况下,TOR被过度激活,增加了植物对胁迫的敏感性^[78]。

6 结 语

TOR作为1个重要的蛋白激酶,能够有效感知和转导营养、能量、激素、代谢以及环境胁迫等信号,从而引发植物在生长和应答逆境胁迫时的生理反应。尽管目前对TOR信号网络构成和调控的了解逐渐清晰,却仍有诸多未解之谜亟待探讨。TOR底物S6K激酶被视为内源性TOR活性的保守指标。因此,开发组织特异性和荧光可视化的TOR激酶活性标记物,将有助于定量测量TOR在不同组织器官中的活性及其特定的信号输出路径。这一方法可以帮助理解在不同环境条件下,TOR信号受到干扰时所导致的不同表型。尽管TOR和SnRK1在植物信号转导和基因调控中发挥了重要作用,但目前对于具体调控机制的认知仍然十分有限。未来需要进一步研究TOR和SnRK1之间具体的相互作用机制,并揭示它们之间特定的调节网络,鉴定出更多的TOR-SnRK1信号网络下游因子。

尽管TOR蛋白功能强大,但由于其分子量高达280 kU,这给研究TOR信号功能带来了很大的困难,所以目前关于TOR的解析主要集中于模式植物拟南芥,未来应开发更多研究TOR功能的物种材料,推动TOR在其他物种中的研究进展。

TOR激酶在植物信号转导和基因调控方面的

多种功能,使得它具有改善作物品质、提高产量以及增强植物对各种逆境抵抗力的潜力。深入探索TOR调控网络,将有助于未来在分子水平上调控果实的大小和品质,进而改善园艺作物的质量特征和农艺性状,如果实的质地、颜色和风味,可能为园艺作物的调控提供新的途径。

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