综 述 Review

植物中糖信号及其对逆境调控的研究进展

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摘要: 糖不仅作为淀粉合成的底物, 而且还具有信号转导的功能。近年的研究表明, 糖在植物生长发育、应激反应和产量形成等生命活动中作为渗透保护剂和(或)抗氧化剂起重要的防护作用。本文总结了植物中糖信号产生的途径、系统的组成、作用机制、对外界环境的响应以及其对逆境调控的最新研究进展, 并对未来的研究方向作出展望。

关键词: 糖; 糖信号; 生长发育; 抗逆反应

植物的糖不仅是能量来源和结构物质的重要组成元件, 能够与蛋白质等结合成复杂的化合物, 参与细胞识别和细胞间物质运输等生命活动(如糖蛋白), 而且还具有信号功能, 调节相关基因的表达和酶活性(Proels和Hückelhoven 2014; Kunz等2014; Sleiman等2014), 同时, 还可以直接作为抗氧化剂淬灭氧化物质(Keunen等2013; Kunz等2014), 调节植物生长发育和应对不良环境(Granot等2014; Chincinska等2013; Yonekura等2013; Lastdrager等2014; Lu等2015)。此外, 在植物生长发育过程中, 糖还可以与其他信号如植物激素、氮信号及光信号等形成复杂的信号网络体系。近年来, 糖信号一直是植物科学研究的热点。本文旨在通过综述植物糖信号及其在抗氧化防护中作用的研究进展, 拓展对植物糖在生长发育中功能的新认识, 为植物抗逆机理的研究提供新思路。

1 植物的糖信号

糖信号是单独出现, 或是通过特定糖分子的积累, 还是通过代谢的流通作为动力传递给信号? 这方面仍存在争议, 但就目前的研究进展可以作出定论, 几乎所有的糖及它们的衍生物均可以作为糖信号。迄今已经证明, 具有重要作用的糖信号主要是二糖和单糖。二糖主要有蔗糖(Koch 1996; Horacio等2013)和海藻糖-6-磷酸(trehalose-6-phosphate, T6P) (Halford等2009; Zhang等2009); 单糖主要包括己糖葡萄糖(Moore等2003)和果糖(Cho等2011; Li等2011), 还有部分葡萄糖的衍生物, 如葡萄糖-1-磷酸(glucose-1-phosphate, G1P)和葡萄糖-6-磷酸(glucose-1-phosphate, G6P) (Nunes等2013)等, 均可作为信号分子在植物生长发育和响应逆境中发挥重要作用。

1.1 糖信号产生的途径

现有的研究表明, 植物体中己糖激酶、蔗糖转运体、葡萄糖转运体、膜感受器以及细胞壁上的转化酶、液泡转化酶、细胞质转化酶、乙酸盐或呼吸代谢物丙酮酸等都与糖信号的感知和产生存在偶联(Koch 1996; Barratt等2009; Wang等2015; Deng等2015), 糖信号作为其中一种组分参与到植物信号传导途径中。已报道的转导这些信号的元件有WD蛋白(tryptophan-aspartic acid residues)、钙依赖蛋白激酶(Ca^{2+}-dependent protein kinases, CDPK)、蛋白磷酸化酶(protein phosphatase, PP)、促分裂原活化蛋白激酶(mitogen-activated protein linase, MAPK)、蔗糖非酵解型蛋白激酶(sucrose non-fermenting-related kinase, SnRK)、SCF (Skplp-cullin-F-box protein)类似物、MsK4 (glycogen synthase kinase 3-like kinase, minimum-shift keying)、转录因子以及多酶复合体等(Bhalerao等1999; Rolland等2002; Kempa等2007), 这些元件将糖信号转导到细胞核或细胞器目标基因的转录起始位点上, 控制相关基因的转录, 从而引起生理生化的变化, 进而调控植物的生长发育。植物体响应这些糖信号后还会伴随能量、酶和植物激素等的变化, 这些都是植物的关键生命元件(Sleiman等2014)。

1.2 糖信号系统的组成

糖信号系统在植物体中主要以依赖己糖激酶

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(hexokinase, HXK)、依赖糖酵解和不依赖HXK这3种信号通路存在(Smeekens等2000)。其中, HXK是一种多功能蛋白, 既能催化糖酵解的第一步, 又参与植物糖感知和糖信号转导过程(Granot等2014)。HXK能磷酸化的底物有葡萄糖、果糖、甘露糖和半乳糖等, 它还是联系植物糖和植物激素的关键元件(Cho等2009)。这些糖首先经载体运输进入细胞, 然后己糖激酶感知糖, 并通过与其它蛋白作用形成复合体(Hsp70 interacting protein, HIP)或者糖酵解途径引发信号流, 通过级联放大, 最终调节基因转录表达。另外, HXK也可能迁移到核内直接影响转录(Rolland等2002)。在果糖信号的研究中, 已经报道FINS1作为一个信号组件, 作用独立于其催化活性, 也独立于HXK功能(Cho和Yoo 2011)。

2 植物中糖信号的作用机制

植物中糖传感和介导信号转导途径的分子细节到目前为止尚不清楚, 一般认为, 激活的糖感受器产生的信号通过级联反应, 从而导致生理生化的变化。

2.1 与蔗糖非酵解型蛋白激酶(SnRK)相关的作用机制

蔗糖非酵解型蛋白激酶(SnRK)是一类广泛存在于植物体的蛋白激酶, 它与酵母蔗糖非发酵1 (sucrose-non-fermenting 1, SNF1)和哺乳动物AMP活化蛋白激酶(adenosine monophosphate dependent kinase, AMPK)密切相关(Baena-González等2007; Hardie等2007), 其参与植物体多种信号转导途径。植物中糖水平的感知以及糖信号的转导都需要SnRK1。低浓度的葡萄糖、高浓度的蔗糖和改变暗期长短都会激活SnRK1 (Polge等2006)。SnRK1一旦激活, 其磷酸化并激活或使一些关键代谢酶失活, 已发现硝酸还原酶(nitrate reductase, NR)、3-羟基-3-甲基戊二酰-辅酶A还原酶(3-hydroxy-3-methylglutaryl-CoA reductase, HMG-CoA还原酶)、蔗糖磷酸合酶(sucrose phosphate synthase, SPS)和海藻糖磷酸合酶(trehalose phosphate synthase, TPS)均是SnRK1家族的胞内底物(Polge等2006; Schwachtje等2006; Lu等2007)。SnRK1还激活蔗糖合酶和α-淀粉酶的转录, 间接刺激AGP酶(淀粉合成关键酶)的活性, 抑制激酶复合物成员的表达, 导致花粉败育、器官萎缩、发育或衰老的延迟。这种激酶还参与应激反应, 如盐胁迫、与病原体的相互作用等(Polge等2006; Cho等2009)。同时, 已经确定拟南芥中2个SnRK1 (AKIN10/AKIN11)是响应黑暗和多种类型胁迫信号转录组调控的中心(Baena-González等2007)。在拟南芥中还鉴定出SnRK1活性的直接识别靶蛋白, 如细胞周期抑制剂KRP6 (Kip-related protein 6)和KRP7 (Kip-related protein 7) (Guérinier等2013)以及B3结构域转录因子FUS3 (FUSCA3)蛋白(Tsai和Gazzarrini 2012), 进一步提供了SnRK1作为信号组分参与细胞周期和发育调控直接蛋白的证据。此外, 研究还表明, G1P、G6P和T6P单独作用会抑制植物SnRK1的活性, 而G1P与T6P的结合则对SnRK1活性有协同效应(Baena-González等2007)。有趣的是, 通过数学模型揭示, HXK的代谢功能促进T6P从蔗糖中产生。通过对HXK过表达谱系与正常幼苗的比较发现, HXK与SnRK1信号之间有很强的相互作用, SnRK1与HXK的代谢反馈调节足以控制糖从能源消耗到全面复苏的平衡(Nägele和Weckwerth 2014)。

2.2 与海藻糖-6-磷酸(trehalose-6-phosphate, T6P)相关的作用机制

海藻糖-6-磷酸(T6P), 海藻糖生物合成途径的前体, 是植物生长发育中调节碳可用性的一个重要的信号代谢物。各种糖处理和糖饥饿对植物生理反应影响的研究证明: T6P是作为信号分子而不是作为代谢物, 并与Suc有很高的相关性(Paul等2008; Zhang等2009; Nunes等2013; Nägele和Weckwerth 2014)。与Suc相比, T6P在植物体中以微量形式存在, 且不能够运输, 在各个细胞内均需要从头合成(Paul等2008; Tsai和Gazzarrini 2014)。植物体除了自身的海藻糖合成途径外, 由病原菌产生的海藻糖或T6P也能够导致植物代谢和发育的重新编程。植物从胚胎发育到叶片的衰老均受T6P调节, 这些过程中的一些调节还与生长素等植物激素相互作用(O'Hara等2013)。对不同拟南芥突变体中海藻糖形成关键酶海藻糖-6-磷酸合酶(T6P synthase, TPS)和海藻糖-6-磷酸磷酸酶(T6P phosphatase, TPP)的研究证明: T6P的生物合成对于生长和发育是必不可少的(Tsai和Gazzarrini 2014)。有研究表明, 海藻糖-6-磷酸磷酸酶基因(*OsTPP1*)

在水稻中过表达, 能够活化逆境应答基因, 从而提高对逆境条件的耐受性(Cho等2009), 此外, 还观察到各类T6P对碳分配、胚胎发生、叶生长和繁殖的专一性作用(Paul等2008; Lunn等2014)。T6P还参与AGP酶的氧化还原, Schluepmann等(2012)提出, T6P在植物中也影响NADPH (triphosphopyridine nucleotide)依赖性氧化还原信号, 这可能是一个通过T6P激活AGP酶氧化还原的方法。

糖信号的调节机制十分复杂, 糖能够调节蛋白质的翻译和蔗糖控制C/S1-bZIP (Group C and S1 basic leucin zipper transcription factor)监管网络等(Ge等2008)。有研究指出SnRK1基因的表达与T6P含量有关, T6P处理导致拟南芥粗提液中SnRK1活性受抑制(Baena-González和Sheen 2008; Zhang等2009)。此外, 最近在T6P/SnRK1监管途径中鉴定出转录因子bZIP11, 研究表明, 其可以通过抑制SnRK1和T6P促进生物合成反应, 从而提高作物的产量等(O'Hara等2013)。对于胞内T6P可用性的响应, 推测SnRK1诱导C/S1-bZIP转录因子和miR156的转录、翻译, 导致从幼年至成年和营养生长到生殖生长转变受抑制(Wahl等2013; Tsai和Gazzarrini 2014), 但是, T6P参与SnRK糖传感具体的分子机理尚未知。

2.3 植物糖信号与植物激素的互作

激素对植物生长发育的调节具有重要作用, 因此, 植物糖对激素的调节一直是植物学科研究的热点。研究表明, 植物糖在调控植物基因表达和生长发育过程中具有与激素类似的作用, 而且通过对拟南芥糖信号转导突变体与激素信号转导突变体在表型、遗传、生理和分子生物学等中关系的研究证实, 糖与ABA、乙烯、IAA、CTK以及GA等主要激素之间均有联系(Smeekens 2000; Gazzarrini和McCourt 2001; Finkelstein和Gibson 2002; Chincinska等2013)。如水稻SnRK2基因家族均可被高渗应激诱导, 其中有三个还可以被ABA诱导(Umezawa等2004); SnRK2和SnRK3参与ABA和/或胁迫信号传导途径(Hrabak等2003; Halford等2003)。拟南芥SnRK2的过表达能够调控胁迫应答基因的表达, 进而提高对干旱条件的耐受性(Umezawa等2004)。葡萄糖与油菜素内酯相互作用能够调控拟南芥侧根的发育(Gupta等2015)。蔗糖与ABA协同调控水稻悬浮细胞中ADP-葡萄糖焦磷酸化酶和淀粉含量基因的表达(Akihiro等2005)。此外, 使用分子手段鉴定多个蔗糖不敏感突变株发现, 许多突变株都存在ABA生物合成或信号缺陷, 包括*gin1*/*ABA2*、*gin5*/*ABA3*和*sun6*/*ABI4*, 表明蔗糖与ABA信号间存在紧密的正向互作(Lu等2015)。

糖基化修饰被认为是调控激素活性水平的最重要方式之一, 多种植物激素的糖基化修饰机制和功能逐渐被揭示(Ostrowski等2014; Liu等2015), 糖基化修饰改变了修饰产物(糖蛋白、糖脂以及一些小分子糖苷或糖酯化合物等)的生物活性、稳定性, 改变了在细胞和植株中的亚细胞定位、运输特性以及受体信号的识别和结合特性等, 从而有利于激素发挥生物学功能。

3 糖信号对外界因子的响应

3.1 氮素

在生长过程中糖信号与氮信号之间存在互作。糖信号能够反映植物所处的环境条件及其生理状态, 而且与氮素的吸收、运转和代谢相协调。此外, 有研究显示, 烟草成熟期叶片的淀粉含量、蔗糖磷酸合成酶(sucrose phosphate synthase, SPS)活性与施氮量呈负相关, 淀粉酶活性随施氮量增加呈下降趋势, 氮素可通过诱导有机酸而抑制淀粉代谢(Scheible等1997)。糖与氮之间的相互作用还受到酶活性的调节, 如编码硝酸盐载体、NR、天冬酰胺合成酶(asparagine synthetase, ASN)和谷氨酰胺合成酶(glutamine synthetase, GS), 其基因均能够被糖激活, 而*ASN1*基因的表达则受糖的抑制(Lam等1998), 而且, 糖对*ASN1*和*GS2*的调节属于不依赖于HXK的信号途径。

3.2 光

同样, 糖信号与光也存在互作。例如, 几乎所有的糖(>100 mmol·L^{-1})均会显著增加叶片中花青素的含量, 这关系到花青苷生物合成的酶对Suc依赖性转录调控(Stevenson和Harrington 2009)。此外, 对光合作用有关葡萄糖依赖性基因表达进一步分析表明, 可溶性糖在叶中积累会抑制光合作用(Koch 1996)。而植物长期暴露在高光条件下会触发氧化还原失衡以及代谢变化, 如花青素和可溶性糖的积累(Schmitz等2014)。使用代谢组学和转

录组学研究高光敏感基因型突变体*adg1-1/tpt2*, 可以区分CH (carbohydrates)和氧化还原/活性氧(reactive oxygen species, ROS)信号对核基因表达的重要性, 其也伴随高光驯化反应(Schmitz等2014)。光周期调控蔗糖转运体StSUT4, 会影响昼夜调节基因的表达和乙烯的产生(Chincinska等2013), 而且, 水稻中蔗糖磷酸合成酶基因的启动子*OsSPS1*和*OsSPS11*的活性并不受蔗糖控制, 而是通过光和生物钟控制(Yonekura等2013)。

此外, 糖响应的外界因子不仅仅只有氮素和光, 还与碳水化合物及其相关的代谢酶、营养、环境以及病原体的侵染等都有着密切的联系。

4 植物糖对逆境的调控

植物生长在一个不断变化的环境中, 会不可避免地遭受一系列不同程度的生物或非生物胁迫, 像病原体的攻击、土壤的盐渍, 水分和气温的胁迫, 紫外线辐射、金属和百草枯的毒害等, 都会对作物产量和品质产生负面影响。产生这种不利影响的一个主要原因是ROS积累造成的氧化损伤。在植物体中, 胁迫诱导积累的ROS可以通过避免产生和清除2个不同的过程抵消(Gill和Tuteja 2010)。而可溶性糖对ROS有双重作用, 即同时作为促氧化剂和抗氧化剂, 它们既可以参与ROS的产生途径, 也可以参与NADPH的产生途径如氧化戊糖磷酸途径(pentose phosphate pathway, OPP), 从而促进ROS的清除(Couée等2006; Bolouri-Moghaddam等2010)。

己糖、Suc、果聚糖(果糖基寡糖和多糖)、棉子糖寡糖家族和糖类化合物(如甘露醇、山梨醇等)均可协助调整渗透压以及在膜和蛋白质中的稳定。在拟南芥中使用转录组分析表明, 蔗糖对抗氧化胁迫基因如过氧化氢酶的激活具有重要作用(Contento等2004)。在新兴“糖作为抗氧化剂”的概念中, 果聚糖可作为液泡中ROS的清除剂, 棉子糖寡糖家族对叶绿体中ROS的解毒起重要作用(Nishizawa等2008)。此外, 在胁迫条件中, 细胞质和细胞器中转化酶介导Suc的裂解有助于维持胞内稳态。糖在真核生物细胞活性氧动态平衡中的作用也受到广泛的认可(Van和Valluru 2009; Keunen等2013; Matros等2015)。此外, 在拟南芥中使用三氯蔗糖(sucralose, 蔗糖的人工类似物)的研究进一步证明, 糖类可以直接作为羟自由基的清除剂, 通过与羟自由基的非酶反应清除ROS, 促进细胞活性氧动态平衡(Matros等2015)。而且, 通过糖基化修饰也会降低或去除内源、外源毒性物质, 从而减少对植物细胞的伤害(Lim和Bowles 2004; Strasser等2014)。

4.1 对生物胁迫的调控

病害是威胁作物产量的一个主要因子。越来越多的证据表明, 病原体通过SnRK1介导(Shen和Hanley-Bowdoin 2006), 改变植物主要碳水化合物的代谢(Bonfig等2010; Proels和Hückelhoven 2014), 如, *Sus*在棉花中过表达会缓解种子败育(Xu等2012)。而且, 病原菌侵入到植物时, 一系列糖基水解酶的活性被诱导, 如转化酶(invertase, INV) (Proels和Hückelhoven 2014)。此外, 马铃薯在存储期间抑制液泡转化酶(vacuolar invertase, VIN)的表达, 可以减少马铃薯发芽和疾病感染(Bhaskar等2010)。还有研究表明, 通过将病原菌和植物细胞壁上的多糖降解为寡糖片段, 可以激发植物产生强烈的抗病反应, 因为极微量的寡糖可诱导糖信号途径(Cabrera等2013)。此外, 有研究发现, 叶枯病细菌可通过分泌效应与*SWEET*启动子结合, 并直接诱导水稻*SWEET*基因表达。此结果提示, 阻止其结合会饿死细菌, 从而避免感染, 提高作物产量和抗病性(Antony等2010; Chen等2012)。该研究提供了通过鉴定SWEET糖转运病原体抗性基因位点从而获得植物抗病性的新途径。

4.2 对非生物胁迫的调控

在轻度胁迫条件下, 植物的生长会受抑制, 但仍能进行较弱的光合作用, 可以观察到ROFs和果聚糖的积累(Van和Peshev 2013)。在非生物胁迫中, 携带额外有关糖代谢的转基因植物支持糖的保护性。在干旱胁迫下, 拟南芥通过脯氨酸、花青素和可溶性糖的积累以及它们之间的相互作用来维持抗氧化保护(Sperdouli和Moustakas 2012)。此外, 非生物胁迫条件例如盐胁迫会使胞外INV上调, 从而使碳水化合物在库中累积(Roitsch等2003)。在胁迫条件下, 细胞壁多糖也会分解, 例如, 寡聚半乳糖醛酸苷可能会产生糖信号(Camejo等2012)。此外, 研究表明在苜蓿根中的寡聚半乳糖醛酸苷能够刺激酶和代谢抗氧化防御系统(Camejo等2012)。另外, 使用海藻糖在拟南芥上的研究发现, 海藻糖

表1 不同糖在植物中对非生物胁迫耐受性的改善

Table 1 Different sugar improved abiotic stress tolerance in plants

糖化合物		基因	植物种类	增强的耐受逆境	参考文献
二糖	蔗糖	蔗糖磷酸合成酶	拟南芥	寒冷	Nägele等2012
		蔗糖磷酸合成酶	水稻	干旱	Yang等2001
	海藻糖	海藻糖合成酶	烟草	干旱、盐	Zhang等2005
		海藻糖磷酸酶	烟草	干旱	Han等2005
		海藻糖-6-磷酸合酶	番茄	干旱、盐胁迫、氧化应激(百草枯或H_2O_2)	Cortina和Culiáñez-Macià 2005
		海藻糖-6-磷酸合酶和磷酸酶	拟南芥	干旱、盐、温度变化	Miranda等2007
棉子糖	半乳糖苷	半乳糖苷合酶	拟南芥	氧化应激(百草枯)、寒冷、干旱、盐胁迫	Nishizawa等2008
	棉子糖	α-半乳糖苷酶	矮牵牛	冻害	Pennycooke等2003
		UDP-葡萄糖4-差向异构酶	拟南芥	干旱、冻害、盐胁迫	Liu等2007
果聚糖	果聚糖	果聚糖蔗糖酶	烟草	冻害	Parvanova等2004
		蔗糖: 蔗糖1-果糖转移酶	烟草	冻害	Li等2007
		蔗糖: 蔗糖1-果糖转移酶和蔗糖: 果聚糖6-果糖转移酶	水稻	冷害	Kawakami等2008
糖醇	甘露醇	甘露醇-1-磷酸脱氢酶	烟草	氧化应激(百草枯)	Shen等1997
		甘露醇-1-磷酸脱氢酶	水稻	干旱、盐胁迫	Pujni等2007
		甘露醇-1-磷酸脱氢酶	矮牵牛	寒冷	Chiang等2005
		甘露醇-1-磷酸脱氢酶	火炬松	盐胁迫	Tang等2005
		甘露糖-6-磷酸还原酶	拟南芥	盐胁迫	Zhifang和Loescher 2003
	山梨(糖)醇	葡萄糖-6-磷酸脱氢酶	火炬松	盐胁迫	Tang等2005
		山梨糖醇-6-磷酸脱氢酶	柿树	盐胁迫	Deguchi等2004

代谢与植株根肿病的关系密切(Gravot等2011)。在生物和非生物胁迫中, 信号之间会相互重叠也会互作来提高植物的抗逆性(Bolouri-Moghaddam等2010; Van和 Peshev 2011)。

5 结论与展望

糖在调控植物生长发育、逆境响应和生物防御反应等生理过程中发挥重要作用。尽管目前对糖信号的研究已经取得了重要的进展, 但是, 对于植物体内糖的多样性及其生理功能和复杂而精细的调节机制来说, 目前的研究还是远远不够, 很多具体的信息仍不明确, 需要进一步完善。现有的信息为未来相关研究提供了很重要的线索, 根据目前的进展来看, 今后的研究还需从以下4个方面入手: (1)不同糖信号在组织和细胞中受体的发现和鉴定, 从而可以了解其是怎样感知外界环境以及植物细胞是如何区分不同糖分子, 如蔗糖, 葡萄糖和果糖等; (2)糖感知信号以及传递组分和机制的确定, 植物在接收糖信号之后在组织和细胞中传递糖信号的基因在传输和识别不同糖分子中的机制; (3)糖信号与激素信号互作机制的揭示, 如确定水稻等作物激素糖基转移酶基因上游的调控基因, 以及激活相关基因表达的分子机制, 这将是揭示糖信号和激素信号作用机制的关键, 也是提高作物耐性改良的有效策略之一; (4)糖信号与其他信号传导机制之间的cross-talk, 进一步探索植物糖信号途径与其他信号之间的交叉, 这是全面了解植物应对外界环境的重要方面。

目前, 随着对糖信号相关理论研究的不断深入, 以及不同组学技术的应用, 将逐渐丰富糖在植物体中信号转导的网络, 从而加深对植物生命活动的全面解析, 也丰富植物信号传导途径信息, 并最终为从糖信号角度改良植物的抗性提供新的有效途径。

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Research progress in sugar signal and its regulation of stress in plants

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Abstract: Sugar, as the substrate of starch synthesis, is also involved in signal transduction. In recent years, studies have shown that, as osmoprotectant and (or) antioxidant, sugar plays a protective role in plant life cycles, including its growth and development, stress response, yield formation and so on. This paper summarizes the lastest research concerning the pathway plant sugar signal is produced, systematic composition, mechanism, the response to external environment and its regulation to adversity, and overviews the direction of relative research in the future.

Key words: sugar; sugar signal; growth and development; stress tolerance response

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