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植物 *SWEET* 基因家族促进病害发生的研究进展

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摘要： 糖的运输和分配在调节植物的生长发育和应对生物和非生物胁迫中起着关键作用。在植物-病原菌相互作用过程中,存在着对糖的竞争,这种竞争由膜运输体控制且对植物和病原互作的结果具有决定性作用。SWEET 糖转运蛋白是细胞外病原菌的靶向目标,病原菌通过修改其表达水平以获得生长所需的糖分营养。本文阐述了植物中 SWEET 家族的分布和结构,归纳总结了 SWEET 在细菌、真菌和卵菌入侵寄主植物过程中所扮演的角色,最后展望了通过基因工程手段操纵 *SWEET* 基因的表达对于开发抗病栽培品种的前景。

关键字： SWEET; 糖转运蛋白; 植物-微生物互作; 基因工程; 生物胁迫
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Advances in the study of plant *SWEET* gene family for disease development

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Abstract: Sugar transport and distribution play a key role in regulating plant development and responding to biotic and abiotic stresses. In the process of plant-pathogen interactions, there is competition for sugars, which is controlled by membrane transporters and is decisive for the outcome of plant-pathogen interactions. SWEET sugar transporters are targeted by extracellular pathogens, which modify their expression levels to obtain sugar nutrients for growth. This paper firstly described the distribution and structure of the SWEET family in plants. Secondly, it summarized the role of SWEET in the invasion of host plants by bacteria, fungi and oomycetes. Finally, the paper also looked at the prospects of manipulating SWEET expression by means of genetic engineering for the development of disease-resistant cultivars.

Key words: SWEET; sugar transporter; plant-microbe interactions; genetic engineering; biotic stress

植物在整个生命周期中,会暴露在影响其发育和功能的环境胁迫中。它们还必须应对一系列的微生物,这些微生物极有可能具有致病性。全球每年由于细菌、真菌、卵菌和病毒病原菌引起的作物病害造成的损失高达数十亿美元[1]。在与病原菌的相互作用中,植物感知微生物信号或相关的分子(如碳水化合物、脂类、肽、蛋白质),并根据涉及的特定模式识别受体制定应对策略[2]。因此,植物在适应极端环境过程中已经进化出复杂而协调的分子和代谢网络,包括基因、代谢物和适应反应,它们调节生长、光合作用、渗透压和碳水化合物的平衡。在特定的压力条件下,糖类在压力感知、信号传递中起着关键作用,是压力介导的基因表达调节中心,确保渗透调节的反应,清除活性氧(ROS),并通过碳分配维持细胞的能量状态[3]。

SWEET(Sugar will eventually be exported transporter)是一类新型的糖类转运蛋白,其功能为促进

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糖类沿浓度梯度跨细胞膜扩散,在古细菌、植物、某些真菌和动物中存在同源转运蛋白[4]。SWEET广泛存在于植物中,并在许多生理生化过程中发挥核心作用,包括长距离运输糖的韧皮部装载、花粉营养、花蜜分泌、种子填充、果实发育、植物与病原菌的相互作用以及对非生物胁迫的反应[5]。有趣的是,SWEET转运体是细胞外病原菌的目标,病原菌改变其表达以获得生长所需的糖[6]。内源性糖在介导植物免疫应答和对抗病原菌攻击中的作用越来越受到关注,因此出现了“甜味免疫”或“糖增强防御”的概念[7-8]。针对这些层次的调控将对作物改良有重要意义。

1　植物中*SWEET*基因家族的分布和结构特征

*SWEET*基因家族在植物物种中分布广泛,从2010年拟南芥第一个*SWEET*基因家族被鉴定出来[6],截至目前已经超过50多种植物中*SWEET*基因家族被鉴定出来。比如,在拟南芥中有17个成员,在水稻中有21个成员,在葡萄中有17个成员,在模式豆科植物蒺藜苜蓿中有24个成员[6,9-11]。事实上,在大多数已测序的植物基因组中已经鉴定出*SWEET*基因,表1为一些植物*SWEET*基因家族的分布信息(表1)。

表1　*SWEET*基因家族在植物中的分布

Table 1　Distribution of the *SWEET* gene family in plants

物种	*SWEET*基因数目	进化分枝	参考文献
拟南芥(*Arabidopsis thaliana*)	17	4	[6]
水稻(*Oryza sativa*)	21	4	[9]
葡萄(*Vitis vinifera*)	17	4	[10]
蒺藜苜蓿(*Medicago truncatula*)	25	4	[11]
木薯(*Manihot esculenta*)	28	4	[12]
苹果(*Malus domestica*)	33	4	[13]
柑橘(*Citrus sinensis*)	27	4	[14]
无油樟(*Amborella trichopoda*)	9	4	[15]
大桉(*Eucalyptus grandis*)	52	4	[16]
番茄(*Solanum lycopersicum*)	29	4	[17]
大豆(*Glycine max*)	52	3	[18]
玉米(*Zea mays*)	24	4	[19]
马铃薯(*Solanum tuberosum*)	35	4	[20]
高粱(*Sorghum bicolor*)	23	4	[21]
陆地棉(*Gossypium hirsutum*)	55	4	[22]
黄瓜(*Cucumis sativus*)	17	4	[23]
白梨(*Pyrus bretschneideri*)	18	4	[24]
香蕉(*Musa acuminata*)	25	4	[25]
百脉根(*Lotus japonicus*)	13	3	[26]
橡胶树(*Hevea brasiliensis*)	36	4	[27]
小麦(*Triticum aestivum*)	105	5	[28]
菠萝(Ananas comosus)	39	5	[29]
甜根子草(*Saccharum spontaneum*)	22	4	[30]
白菜(*Brassica rapa*)	34	4	[31]
茶树(*Camellia sinensis*)	28	4	[32]
豌豆(*Pisum sativum*)	22	4	[33]
野草莓(*Fragaria vesca*)	20	4	[34]
荔枝(*Litchi chinensis*)	16	4	[35]
花椰菜(*Brassica oleracea*)	30	4	[36]
枣(*Ziziphus jujuba*)	19	4	[37]
核桃(*Juglans regia*)	25	4	[38]
毛果杨(*Populus trichocarpa*)	27	4	[39]
草地早熟(*Poa pratensis*)	13	4	[40]
油桐(*Vernicia fordii*)	18	4	[41]
蓖麻(*Ricinus communis*)	18	4	[41]
麻风树(Jatropha curcas)	21	4	[41]
日本杏(*Prunus mume*)	11	4	[42]
桃树(*Prunus persica*)	17	4	[42]
银杏(*Ginkgo biloba*)	17	4	[15]
石榴(*Punica granatum*)	20	4	[43]
菜豆(*Phaseolus vulgaris*)	24	4	[44]
杨桃(*Averrhoa carambola*)	10	3	[45]
铁皮石斛(*Dendrobium officinale*)	22	3	[46]
蝴蝶兰(*Phalaenopsis equestris*)	16	3	[46]
猪笼草(*Nepenthes sp.*)	20	4	[47]
黄花菜(*Hemerocallis fulva*)	19	4	[48]
油菜(*Brassica napus*)	68	4	[49]
南瓜(*Cucurbita moschata*)	21	4	[50]
毛竹(*Phyllostachys edulis*)	30	4	[51]
西瓜(*Citrullus lanatus*)	22	4	[52]

通过对 SWEET 蛋白的跨膜结构进行分析发现,真核生物 SWEET 具有多达 7 个跨膜螺旋(TM-Hs)结构域,这些结构域被组织为 2 个 3-TM 结构域(包含 2 个保守的 MtN3/Saliva 基序)的串联重复,由单个 TM 分隔[4]。而在原核生物中,该结构域被称为 SemiSWEET,且只有一个 3-TM,但仍然能够运输糖[4]。这一结构特征赋予其能够选择性地转运不同种类的糖底物,包括蔗糖、果糖和葡萄糖[9]。

对 5 种植物(拟南芥、水稻、玉米、葡萄、番茄)中 *SWEET* 基因家族的系统发育分析结果表明,植物 SWEET 可分为 4 个亚群(进化分枝Ⅰ-Ⅳ)(图 1)。进化分枝Ⅰ、Ⅱ和Ⅳ中的 SWEET 主要用作单糖外排转运蛋白,转运葡萄糖、半乳糖或果糖,而进化分枝Ⅲ成员优先转运二糖蔗糖[16]。此外,除进化分枝Ⅳ成员外,所有 SWEET 都定位于质膜。与其他进化分枝相比,进化分枝Ⅳ含有相对较少数量的 *SWEET* 基因,且进化分枝Ⅳ中的 *SWEET* 定位于液泡膜,并且已被证明主要由控制果糖通过液泡膜的转运蛋白组成[4-6]。

拟南芥 17 个 SWEET 家族成员的 4 个系统发育进化分枝已经被广泛研究,其中 AtSWEET1~AtSWEET3 在进化枝Ⅰ中,AtSWEET4~AtSWEET8 在进化枝Ⅱ中,AtSWEET9~AtSWEET15 在进化枝Ⅲ中,AtSWEET16~AtSWEET17 在进化枝Ⅳ中[16]。大多数其他植物的 SWEET 都是按照拟南芥采用的命名法命名[6]。*SWEET* 基因在植物中的功能广泛。例如,AtSWEET1 充当葡萄糖转运蛋白[3],而 AtSWEET9 是蜜腺特异性糖转运蛋白,对花蜜生产至关重要[53]。AtSWEET11 和 AtSWEET12 催化蔗糖从源叶中韧皮部薄壁细胞流出,并在韧皮部负载中发挥关键作用[54]。AtSWEET16 和 AtSWEET17 作为液泡 SWEET 蛋白,起到果糖特异性输出蛋白的作用,将液泡腔连接到胞质溶胶[55]。在水稻中,位于质膜上并在叶片韧皮部表达的 OsSWEET11 与韧皮部负载有关,功能与其拟南芥同源物 AtSWEET11 和 AtSWEET12 一样[56]。*OsSWEET14* 敲除突变体导致种子不饱满,生长迟缓,表明 OsSWEET14 在籽粒灌浆中起作用[57]。同时,OsSWEET1a、OsSWEET2a、OsSWEET3a、OsSWEET4、OsSWEET5 和 OsSWEET15 在植株花和穗中均有高表达,表明这些转运蛋白在水稻生殖发育中也发挥了一定的作用[58]。此外,SWEETs 还参与离子转运、叶片衰老、植物-病原菌互作和非生物胁迫等过程,比如细菌效应子与 OsSWEET11 和 OsSWEET14 的启动子直接结合[59]。

2　SWEET 参与细菌的致病过程

病原菌主要通过感染植物细胞来获取营养物质,特别是糖类,以促进自身的生长和繁殖,而这往往要以牺牲植物正常生长为代价。比如,引起水稻细菌性白叶枯病的黄单胞菌属利用植物 SWEET 运输器获取寄主的糖分储备[6,60]。这些细菌利用它们的Ⅲ型分泌系统分泌一系列效应蛋白,包括转录激活样效应子(TALEs)进入寄主细胞,直接针对特定 *SWEET* 基因的表达进行调控(图 2)[10]。

目前,此类研究主要集中于水稻上,作为引起细菌性叶枯病的一个关键侵染策略,黄单胞菌(Xoo)向植物细胞注入 TALEs 的 DNA 结合蛋白,这些蛋白质以序列特异性方式与效应物结合元件(EBEs)结合,诱导寄主基因的表达(表 2)。比如,来自第 3 进化分枝的 5 个 *SWEET* 基因是黄单胞菌转录激活效应子的靶标[61]。在这 5 个基因中,*OsSWEET11* 和 *OsSWEET13* 分别被 TAL 效应子 PthXo1 和 PthXo2 诱导,而 *OsSWEET14* 基因被 AvrXa7、PthXo3、TalC 和 Tal5 当作侵染的关键目标,在水稻-Xoo 相互作用过程中作为主要的易感因子,这 3 个基因编码蔗糖从细胞膜到质外体空间的外流[62-63]。利用设计的异位诱导 *OsSWEET11b* 使无 TAL 的 Xoo 致病,发现 *OsSWEET11b* 是潜在的易感基因,并证明诱导寄主蔗糖活性是 Xoo 致病的关键[64]。此外,这些细菌病原菌还针对其他植物物种中的 SWEET 转运蛋白,比如在木薯中,易感基因 *MeSWEET10a* 被来自细菌性枯萎病菌的 TAL 效应器($TAL20_{Xam668}$)特异性诱导[60]。在柑橘中,病原菌黄单胞菌导致柑橘细菌性溃疡病,此病原菌也是以 TAL 效应子依赖性的方式诱导 *CsSWEET1* 的表达[65]。在棉花中,*SWEET* 同源的隐性基因 *b6* 参与了棉花品系 Acala-44 对棉花角斑病菌的抗性反应[66]。

被黄单胞菌劫持的 SWEET 转运蛋白的活性对病原菌的生长和增殖至关重要,携带截断版 TAL 效应子的细菌突变株,甚至在 TAL 效应子结

合的启动子区域发生突变,均会导致细菌含量降低,植物产生抗性[6,67]。TAL效应子一般与效应子TATAA元件结合,因此可以利用基因组编辑对这些区域进行修饰,改变植物-病原菌互作反应,使寄主植物产生从感病性到抗性的转变[68]。隐性抗性基因 *xa13* 和 *xa25* 分别是 *SWEET11* 和 *SWEET14* 的突变形式,在抵抗Xoo侵染中发挥积极作用[69]。同一个 *SWEET* 成员可以被不同的病原菌菌株特异性效应子作为目标,因为它们可以与同一个启动子的不同区域结合。因此,*SWEET* 基因启动子区域的隐性突变可以增加植物的抗性而不失去糖的运输功能使用[57]。OLIVA等[70]、XU等[71]使用CRISPR/Cas9基因编辑手段对水稻品种IR64和Ciherang-Sub1的 *SWEET11*、*SWEET13* 和 *SWEET14* 基因启动子的EBEs进行了多重编辑。同样,利用CRISPR/Cas9敲除水稻 *OsSWEET11* 基因后,纯合突变体对Xoo的抗性显著增强[72]。对编辑过的品系产量性状分析发现,启动子编辑过的植株与其野生型亲本之间没有明显的差异,但 *SWEET* 编辑过的水稻品系对Xoo的抗性有所增强[70-72]。

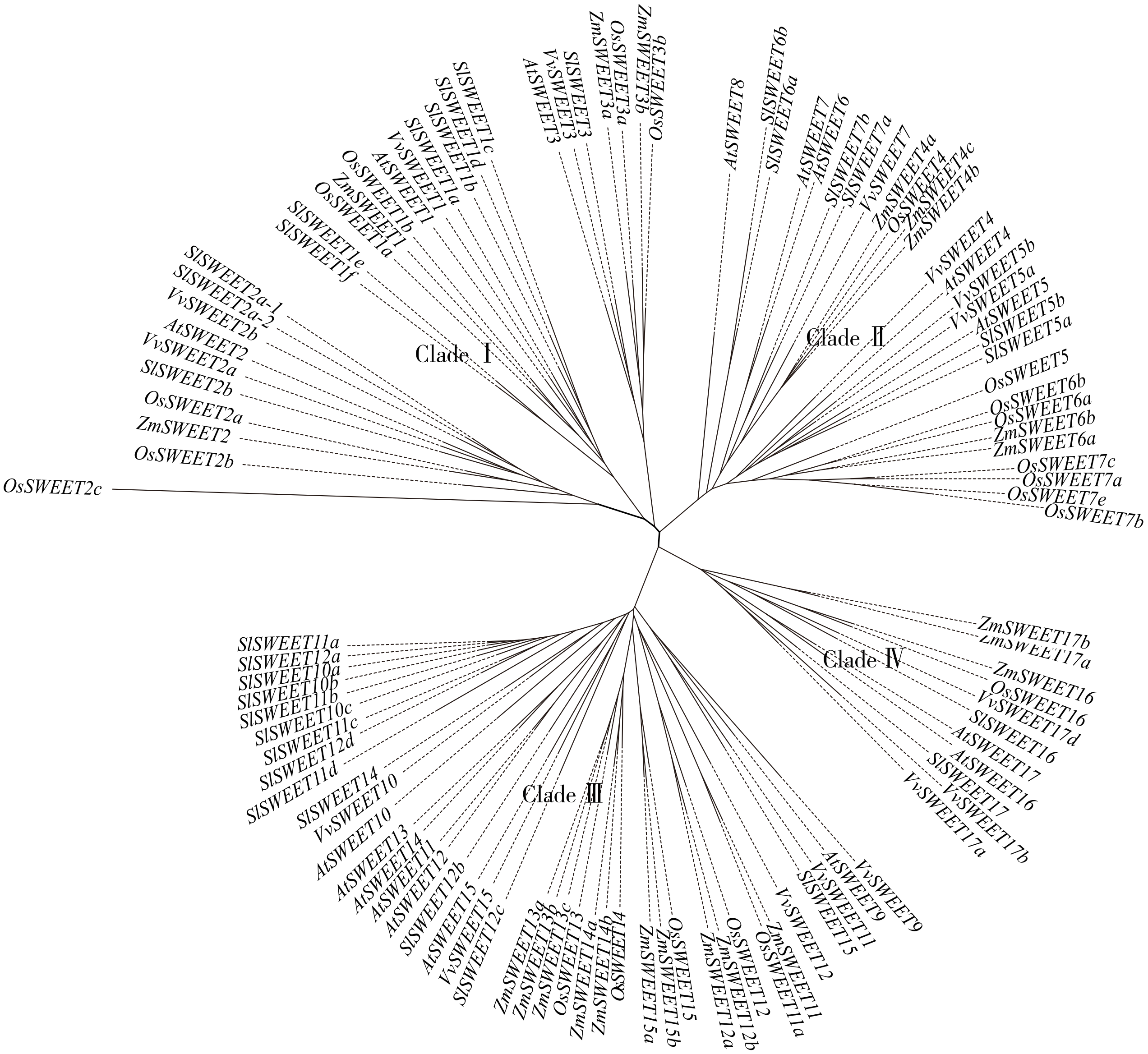

图1　5个植物物种 *SWEET* 基因家族系统发育树分析

Fig.1　Phylogenetic tree analysis of *SWEET* gene family in five plant species

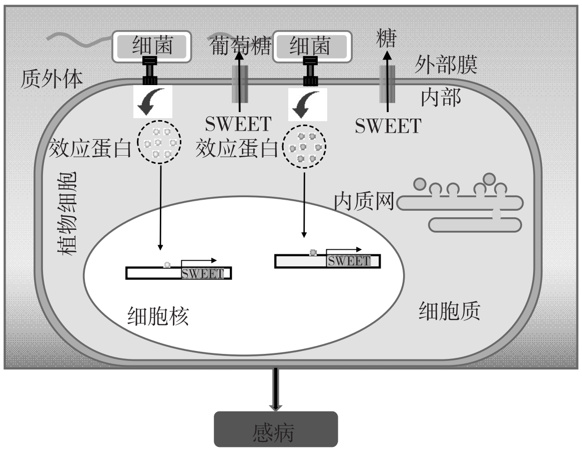

图 2　植物 SWEET 糖转运蛋白在微生物营养中作用的简化模型

Fig.2　A simplified model for the role of plant SWEET sugar transporters in microbial nutrition

3　SWEET 参与真菌和卵菌的致病过程

一些研究结果表明,在感染真菌和卵菌后,寄主体内糖的运输和分配受到影响,寄主细胞成为满足病原菌生长和感染营养需求的一个养料储存库(表 3)。除 *SWEET* 进化分枝Ⅲ外,来自其他支系的 *AtSWEETs* 的表达可以被 *Pseudomonas syringae* pv. tomato strain DC3000、*Golovinomyces cichoracearum* 或 *Botrytis cinerea* 诱导。在植物与真菌的相互作用过程中,寄主细胞的糖外流和转化酶活性的增强也会导致蔗糖和己糖积聚到叶绿体中,被真菌的糖运输器吸收。立枯丝核菌感染显著增强了 *OsSWEET11* 的表达,突变体对水稻纹枯病的敏感性降低,而过表达 *OsSWEET11* 对病菌的敏感性升高,表明可能通过激活 *OsSWEET11* 的表达从水稻叶片中获取糖分[59]。成功的营养性病原菌可以将寄主的营养转移到感染部位,比如,十字花科根肿病菌感染拟南芥导致糖在韧皮部的特异性积累,糖转运蛋白 SWEET11 和 SWEET12 促使糖向病原菌感染的部位分布[73]。GhSWEET42 通过葡萄糖转运在大丽轮枝菌感染中起着关键作用,通过操纵 *GhSWEET42* 的表达以控制感染部位的葡萄糖含量是抑制大丽轮枝菌感染的有效方法[74]。

表 2　被细菌白叶枯病菌靶向的来自进化分枝Ⅲ的 SWEET 转运蛋白

Table 2　Clade Ⅲ SWEET transporters targeted by the bacterial blight pathogen

基因	物种	病原菌	病害	作用机制	参考文献
MeSWEET10	木薯(*Manihot esculenta*)	黄单胞菌(*Xanthomonas axonopodis* pv. manihotis)	细菌性枯萎病	受病菌诱导上调表达	[60]
OsSWEET11	水稻(*Oryza sativa*)	水稻黄单胞菌[*Xanthomonas oryzae* pv. *Oryzae* (Xoo) strain PXO99]	水稻白叶枯病	受病菌诱导上调表达,启动子突变/ RNA 干扰后产生抗性	[75]、[76]
OsSWEET11b	水稻(*Oryza sativa*)	黄单胞病菌[*Xanthomonas oryzae* pv. oryzae (Xoo)]	水稻白叶枯病	干扰后抗性增强	[63]
OsSWEET12	水稻(*Oryza sativa*)	水稻黄单胞菌(*Xanthomonas oryzae* pv. oryzae)	水稻白叶枯病	受病菌诱导上调表达	[77]
OsSWEET13	水稻(*Oryza sativa*)	水稻黄单胞菌(*Xanthomonas oryzae* pv. oryzae)	水稻白叶枯病	受病菌诱导上调表达,天然变异/突变产生抗性	[10]、[67]
OsSWEET14	水稻(*Oryza sativa*)	水稻黄单胞菌(*Xanthomonas oryzae* pv. oryzae)	水稻白叶枯病	受病菌诱导上调表达,启动子突变产生抗性	[57]、[62]
OsSWEET15	水稻(*Oryza sativa*)	水稻黄单胞菌(*Xanthomonas oryzae* pv. *oryzae*)	水稻白叶枯病	受病菌诱导上调表达	[61]
CsSWEET1	柑橘(*Citrus sinensis*)	黄单胞菌(*Xanthomonas citri* subspecies citri strain Xcc306)	柑橘细菌性溃疡病	受病菌诱导上调表达,启动子突变产生抗性	[65]
GhSWEET10	棉花(*Gossypium spp.*)	棉花角斑病菌[*Xanthomonas citri* subsp. malvacearum (Xcm)]	棉花白叶枯病	受病菌诱导上调表达,沉默后感病性下降	[66]
MeSWEET10	木薯(*Manihot esculenta*)	黄单胞菌(*Xanthomonas axonopodis* pv. manihotis)	细菌性枯萎病	受病菌诱导上调表达	[60]

沉默 *IbSWEET10* 基因,导致甘薯对尖孢镰刀菌的感病性增加,而过表达增强了抗性,这与水稻和棉花中的发现相反。进一步研究发现,甘薯中 *IbSWEET10* 的表达下调可能通过减少果胶和纤维素的沉积而损害维管组织的细胞壁完整性,导致对尖孢镰刀菌的抵抗力下降,RNAi 植株在感染后表现出

被破坏的髓部结构[78]。在拟南芥的根部，尽管土传卵菌腐霉病菌的感染导致 *AtSWEET2* 基因表达量增加了 10 倍以上，但功能缺失的 *SWEET2* 突变体更容易受到感染，当遭遇卵菌侵染时显示生长受损，这表明 *AtSWEET2* 转运体将糖从细胞膜转运到液泡，以限制它们渗漏到细胞外空间，可能为病原菌提供食物[79]。因此，可以认为在病原菌攻击时，各种糖信号级联被破坏以减少植物的防御反应，从而为病原菌的生长提供更有利的环境。

表 3 植物中被真菌/病毒靶向的 SWEET 转运蛋白

Table 3 SWEET transporters targeted by the fungi/viruses in plants

SWEET 转运蛋白	物种	病原菌	病害	类型	作用机制	参考文献
AtSWEET12	拟南芥（*Arabidopsis thaliana*）	白粉病菌（*Golovinomyces cichoracearum*）	白粉病	真菌	受病菌诱导上调表达	[6]
VvSWEET4	葡萄（*Vitis vinifera L.*）	灰葡萄孢菌（*Botrytis cinerea*）	葡萄灰霉病	真菌	受病菌诱导上调表达，突变后丢失感病性	[10]
MaSWEET4c、MaSWEET4d、MaSWEET14h	香蕉（*Musa nana Lour.*）	香蕉枯萎病菌（*Fusarium odoratissimum*）	枯萎病	真菌	受病菌诱导上调表达	[25]
AtSWEET11、AtSWEET12	拟南芥（*Arabidopsis thaliana*）	稻曲病菌（*Ustilaginoidea virens*）	稻曲病	真菌	受病菌诱导上调表达	[80]
AtSWEET11、AtSWEET12	拟南芥（*Arabidopsis thaliana*）	十字花科根肿病菌（*Plasmodiophora brassicae*）	根肿病	真菌	受病菌诱导上调表达，sweet11/sweet12 双突变体干扰了病原菌的糖运输，延缓病害进程	[73]
BrSWEET1a、BrSWEET2a、BrSWEET2b、BrSWEET9、BrSWEET11a、BrSWEET14c、BrSWEET15b、BrSWEET15c、BrSWEET16a、BrSWEET17	芜菁（*Brassica rapa*）	十字花科根肿病菌（*Plasmodiophora brassicae*）	根肿病	真菌	受病菌诱导上调表达	[81]
CsSWEET3	茶树（*Camellia sinensis*）	茶树炭疽病菌（*Colletotrichum camelliae*）	茶炭疽病	真菌	受病菌诱导上调表达	[82]
GhSWEET42	棉花（*Gossypium spp.*）	大丽轮枝菌（*Verticillium dahliae*）	棉花黄萎病	真菌	过表达导致感病性增强，缺失导致抗性增强	[74]
IbSWEET10	甘薯（*Ipomoea batatas*）	尖孢镰刀菌（*Fusarium oxysporum* Schlecht. f. sp. batatas）	甘薯蔓割病	真菌	受病菌诱导上调表达，过表达产生抗性，RNAi 得到相反结果	[78]
MaSWEET4c、MaSWEET4d、MaSWEET14h	香蕉（*Musa nana Lour.*）	香蕉枯萎病菌（*Fusarium odoratissimum*）	枯萎病	真菌	受病菌诱导上调表达	[25]
OsSWEET11	水稻（*Oryza sativa*）	立枯丝核菌（*Rhizoctonia solani*）	水稻纹枯病	真菌	受病菌诱导上调表达，过表达更感病，突变产生抗性	[59]
SlSWEET15	番茄（*Solanum lycopersicum*）	灰葡萄孢菌（*Botrytis cinerea*）	灰霉病	真菌	受病菌诱导上调表达	[83]
TaSWEET2b、TaSWEET5a、TaSWEET14g、TaSWEET14i	小麦（*Triticum aestivum*）	禾柄锈菌（*Puccinia graminis*）	秆锈病	真菌	受病菌诱导上调表达	[84]
VvSWEET7	葡萄（*Vitis vinifera L.*）	灰葡萄孢菌（*Botrytis cinerea*）	葡萄灰霉病	真菌	受病菌诱导上调表达，通过从质外体去除病原菌合成的甘露醇而参与植物防御	[85]
VvSWEET4	葡萄（*Vitis vinifera L.*）	灰葡萄孢菌（*Botrytis cinerea*）	葡萄灰霉病	真菌	受病菌诱导上调表达，突变后丢失感病性	[10]
ZmSWEET4a、ZmSWEET4b	玉米（*Zea mays*）	玉米黑粉菌（*Ustilago maydis*）	黑粉病	真菌	受病菌诱导上调表达	[86]
AtSWEET2	拟南芥（*Arabidopsis thaliana*）	腐霉病菌（*Pythium irregulare*）	根腐病	卵菌	受病菌诱导上调表达，功能缺失导致感病性增强	[79]
VvSWEET4	葡萄（*Vitis vinifera L.*）	腐霉病菌（*Pythium irregulare*）	根腐病	卵菌	受病菌诱导上调表达，VvSWEET4 在葡萄毛状根中的过表达提高了对假单胞菌的抗性	[87]

SWEET 是病原菌操纵的理想目标，它们的表达在感染期间可能会被转录重编。玉米黑粉菌对玉米

的糖分生理和产量产生强烈的负面影响，将糖分从发育中的果穗转移到与真菌有关的富含糖分的器官，研究结果表明黑粉菌诱导了 SWEET 的局部上调表达，然后 SWEET 转运蛋白被招募，在生物营养层面将糖分渗入细胞质[85]。来自葡萄的葡萄糖转运体 VvSWEET4 参与了与灰霉病菌的相互作用，其在受到 ROS 和大面积细胞死亡的刺激后会过度表达，同源的 *AtSWEET4* 突变体对灰霉病菌的敏感性较低，表明其能够促进葡萄糖流出到细胞壁空间以增强病菌生长[87]。

4　展　望

糖的运输和分布在调节植物生长和发育以及应对生物和非生物胁迫方面起着重要作用[88-89]。因此，研究糖类运输体在植物生长的各个阶段如何运输和重新分配糖类是特别必要的。在过去的 10 年中，SWEET 蛋白的研究取得了许多重要进展，但仍有许多问题没有得到解决。比如大多数植物含有 *SWEET* 基因家族的多个成员，这些基因如何协同工作，如何被调控，是否在转录或翻译水平上被调控，以及如何实现功能的多样化，仍然不清楚[90]。

病原菌对植物 SWEET 转运蛋白的诱导与病原体获得寄主来源糖用于营养的能力增加有关。虽然人们普遍认为糖的代谢和调配是决定植物和病原菌在感染过程中持续战斗的重要角色，但植物易感性或抗性反应的代谢特征及其调控模式仍然知之甚少[71]。随着基因工程技术的发展，TALEN 和 CRISPR/Cas9 技术可以被广泛用于编辑植物的易感基因来实现广谱抗性工程[91]。鉴于糖是植物生长、发育和作物产量各个方面的核心营养，随着这一领域研究的进展，可以预期会有更多令人兴奋的发现。

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