寒旱农业科学 2023,2(1):5-12
Journal of Cold-Arid Agricultural Sciences

植物 SWEET 蛋白的结构与分类及功能研究进展

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摘要： 植物 SWEET 蛋白是一类重要的转运蛋白，研究其生理生化功能，有助于分子辅助育种，缩短育种年限。本文基于文献资料，梳理归纳了近年来国内外的植物 SWEET 蛋白的结构、分类、转运底物和功能方面的相关研究进展，阐述表明 SWEET 蛋白是植物中广泛存在的一类糖转运体，既能转运单糖又能转运蔗糖，属于 Mt N3 家族。不同植物间的 SWEET 蛋白具有一定的保守性，根据亲缘关系 SWEET 家族可以分为四类。植物 SWEET 蛋白是位于膜系统上，参与糖分的跨膜转运，在植物生长发育及逆境胁迫中均有不同程度的调控作用，如调控花蜜的分泌、花粉的营养、灌浆期种子的发育、果实发育、植物抗逆性和抗病性等。然而不同植物的 SWEET 蛋白转运底物和调控功能不同，目前仅在拟南芥等少数植物中研究较为深入。

关键词： SWEET；糖转运蛋白；糖；结构；分类；功能
中图分类号： S184；Q51　　**文献标志码：** A　　**文章编号：** 2097-2172(2023)01-0005-08
doi:10.3969/j.issn.2097-2172.2023.01.002

Advances in Structure, Classification and Functions of SWEET Protein in Plants

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Abstract: The yield and quality of crops depend on sugar transport and regulation. In this paper, we reviewed the structure, classification, transport substrates and functions of SWEET protein, in order to lay a foundation for the study of SWEET protein in other plants. SWEET transporter is a newly discovered sugar transporter located in membrane system, which can transport both hexose and sucrose and belongs to Mt N3 family. SWEET proteins are conserved in different plants, and the SWEET family can be divided into four groups according to their relatives. plant SWEET protein plays an important role in plant growth and development, biological and abiotic stress response, such as regulating nectar secretion, pollen nutrition, seed development during grain filling, fruit development, plant stress resistance and disease resistance. However, the transport substrates and regulatory functions of SWEET proteins are different in different plants, and only in a few plants such as *Arabidopsis thaliana* had this protein been studied in depth.

Key words: SWEET; Sugar transporter; Sugar; Structure; Classification; Function

糖是植物的重要能源。植物叶片通过光合作用进行碳固定，形成糖类物质，除自身消耗外，其余大部分运输到库器官，供库器官生长发育，而糖类物质从源到库的运输离不开糖转运蛋白的参与。植物的糖转运蛋白分为 3 类，即蔗糖转运蛋白（Sucrose transporters，SUTs）、单糖转运蛋白（Monosaccharide transporters，MSTs）和 SWEET 糖转运蛋白（Sugars Will Eventually be Exported Transporters）[1]。单糖转运蛋白和蔗糖转运蛋白分别主要负责单糖和蔗糖的转运，而 SWEET 蛋白既能转运单糖又能转运蔗糖[2]，是植物中最新发现的一类转运蛋白，除了糖转运外 SWEET 蛋白在植物生长发育和抗逆性等方面均发挥着重要的作用[3-5]。

SWEET 蛋白最先在拟南芥(*Arabidopsis thaliana*)中发现并鉴定[6]，随后逐渐在水稻(*Oryza sativa*)、葡萄(*Vitis vinifera*)、木薯(*Manihot esculenta*)、苹

收稿日期： 2022-07-11；**修订日期：** 2022-12-09
基金项目： 甘肃省农业科学院生物育种专项(2022GAAS05)；国家自然科学基金(31960523)。
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果(*Malus domestica*)、甜橙(*Citrus sinensis*)等作物中陆续被鉴定[7-11]。目前，SWEET蛋白在模式植物拟南芥中的研究较为深入，很多其他植物的报道少且深度不够。我们综述了近年来已经鉴定的SWEET蛋白相关研究，以期为其他植物的SWEET转运蛋白研究提供参考。

1 植物SWEET蛋白结构与分类

SWEET蛋白是植物、动物和微生物中广泛存在的、定位于膜结构的糖转运蛋白[6,12-14]，属于Mt N3家族。真核生物SWEET蛋白具有7个TM螺旋（transmembrane domains），N端THB由TMs 1–3组成，C端THB由TMs 5–7制成，且N端与C端THB结构相似，均以平行方向排列，各自为1个单元(图1)。TM4作为连接螺旋，连接N端和C端的THB，不同SWEET蛋白中连接螺旋的蛋白序列是不保守的（图1）[14-16]。原核生物的semiSWEET蛋白仅含有单个THB结构，也具有糖转运功能[13,17-18]。Yuan等[7]认为真核生物SWEET基因可能是原核生物*semiSWEET*基因复制的结果，TM4是转运体的一部分；而Hu等[19]提出一个基因融合假设理论，认为在进化过程中当产甲烷古菌吞噬细菌时，会导致*semiSWEET*基因转移到宿主基因组中，因此细菌的*semiSWEET*和寄主基因结合形成了1个双THB的*SWEET*，但保守的TM4是如何在2个THB之间插入或产生的仍不清楚。基因复制和基因融合是SWEET转运体进化的主流理论，然而不论哪种进化理论，SWEET中涉及糖运输的关键残基在进化过程中是保守的[20]。

随着SWEET家族研究的深入，不少植物的SWEET蛋白被鉴定，表1为已经发表的几种植物

表1 不同植物*SWEET*基因家族成员数量

物种	*SWEET*基因数量/个	参考文献
拟南芥 *Arabidopsis thaliana*	17	[6]
水稻 *Oryza sativa*	21	[7]
葡萄 *Vitis vinifera*	17	[8]
木薯 *Manihot esculenta*	23	[9]
苹果 *Malus domestica*	33	[10]
甜橙 *Citrus sinensis*	16	[11]
无油樟 *Amborella trichopoda*	8	[22]
巨桉 *Eucalyptus grandis*	47	[22]
小立碗藓 *Physcomitrella patens*	6	[22]
番茄 *Solanum lycopersicum*	29	[23]
大豆 *Glycine max*	52	[24]
玉米 *Zea mays*	24	[25]
苜蓿 *Medicago truncatula*	26/25	[26–27]
马铃薯 *Solanum tuberosum*	35	[28]
高粱 *Sorghum bicolor*	23	[29]
棉花 *Gossypium hirsutum*	55	[30]
黄瓜 *Cucumis sativus*	17	[31–32]
梨 *Pyrus bretschneideri*	18	[33]
香蕉 *Musa acuminata*	25	[34]
百脉根 *Lotus japonicus*	13	[35]
橡胶树 *Hevea brasiliensis*	36	[36]
琵琶 *Eriobotrya japonica*	7	[37]
小麦 *Triticum aestivum*	59/108	[38–39]
菠萝 *Ananas comosus*	39	[40]
甜根子草 *Saccharum spontaneum*	22	[41]
芜菁 *Brassica rapa*	32	[42]
茶树 *Camellia sinensis*	13	[43]
豌豆 *Pisum sativum*	26	[44]
草莓 *Fragaria vesca*	20	[45]
荔枝 *Litchi chinensis*	16	[46]
甘蓝 *Brassica oleracea*	30	[47]
枣 *Ziziphus jujuba*	19	[48]
核桃 *Juglans regia*	25	[49]
毛果杨 *Populus trichocarpa*	27	[50]
草地早熟禾 *Poa pratensis*	13	[51]
杨桃 *Averrhoa carambola*	10	[52]
石榴 *Punica granatum*	20	[53]
菜豆 *Phaseolus vulgaris*	24	[54]

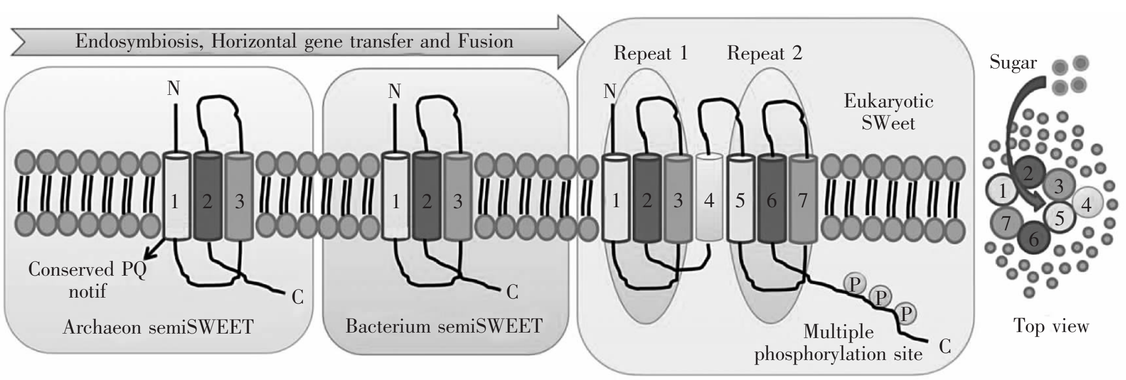

图1 SWEET转运蛋白结构模型

SWEET 蛋白家族成员数量。对拟南芥的 17 个、水稻的 21 个、黄瓜的 17 个 SWEET 家族蛋白成员利用 MAGA11 软件采用邻接发构建系统进化树，结果见图 2。植物的 SWEET 家族蛋白分为 4 个分支。以拟南芥为例，分支Ⅰ有 AtSWEET1-3，分支Ⅱ有 AtSWEET4-8，分支Ⅲ有 AtSWEET9-15，分支Ⅳ有 AtSWEET16 和 AtSWEET17[2,6,21]。

2　植物 SWEET 蛋白转运底物

植物 SWEET 蛋白大多位于质膜，少数位于液泡膜，具有不依赖能量的跨膜转运糖分的功能。拟南芥 SWEET1 蛋白具有跨膜转模葡萄糖的功能[6]，SWEET2 蛋白跨膜转运 2-脱氢葡萄糖[55]，SWEET4 蛋白跨膜转运葡萄糖和果糖[56]，SWEET5 蛋白跨膜转运葡萄糖和半乳糖[57]，SWEET8 蛋白跨膜转运葡萄糖[58]，SWEET9、SWEET11、SWEET12、SWEET13、SWEET14 和 SWEET15 蛋白跨膜转运蔗糖[59-62]，SWEET16 蛋白跨膜转运葡萄糖、果糖和蔗糖[2]，SWEET17 蛋白跨膜转运果糖（表 2）[21]。

此外，不同植物间 SWEET 蛋白的转运底物也略有不同。茶树的 SWEET1a 蛋白可跨膜转运葡萄糖、半乳糖和蔗糖[43]，SWEET16 蛋白可跨膜转运葡萄糖、果糖和蔗糖[43]，SWEET17 蛋白可跨膜转运葡萄糖、果糖、半乳糖、甘露糖和蔗糖等多种糖分[43]；葡萄 SWEET4、SWEET10 蛋白可跨膜转运葡萄糖和果糖的功能[5,63]；百脉根 SWEET3 蛋白可跨膜转运蔗糖的功能[35]；番茄 SWEET7a、SWEET14 蛋白可跨膜转运葡萄糖、果糖和蔗糖

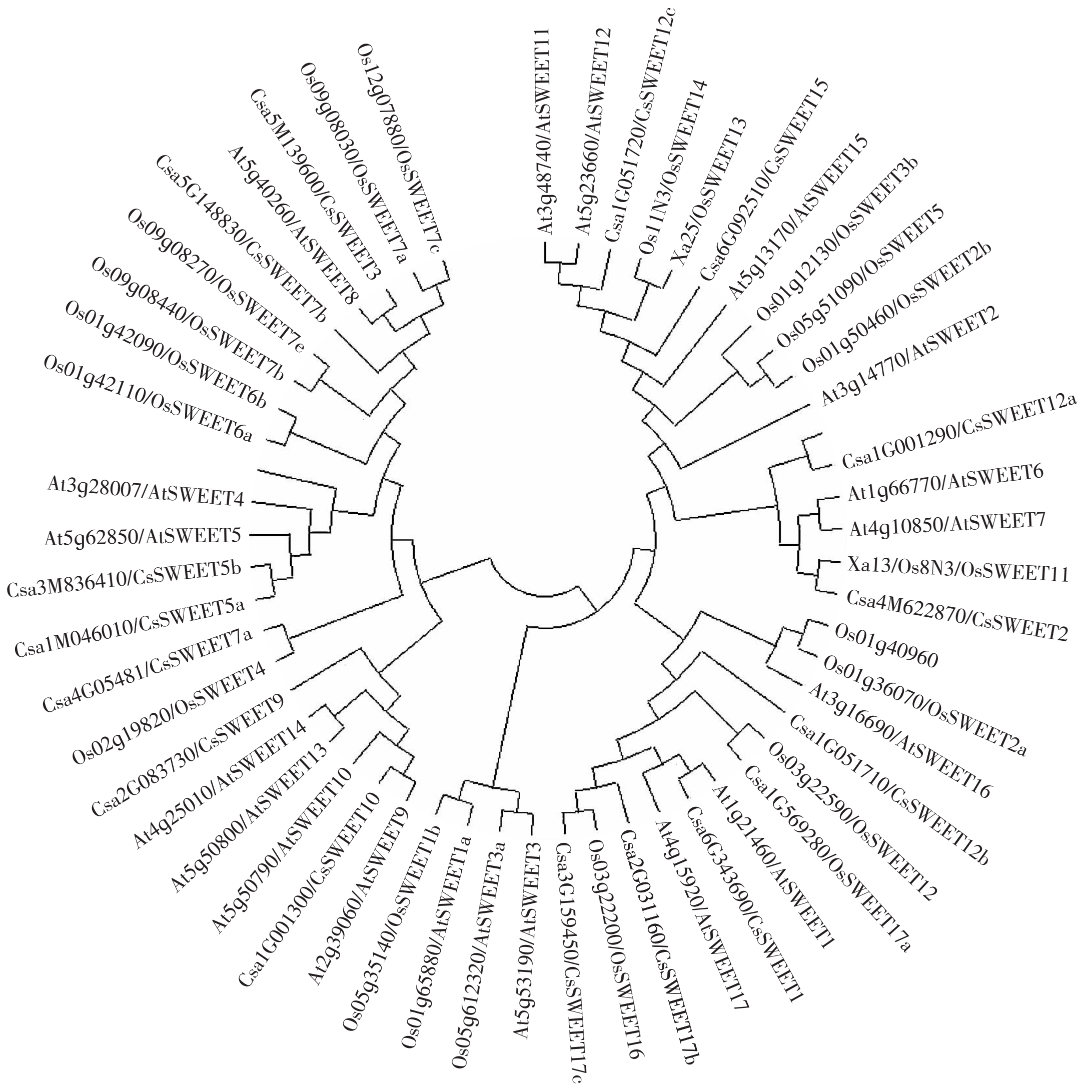

图 2　拟南芥、水稻和黄瓜 SWEET 家族蛋白系统发育进化树

(表2)[3]。

3 植物SWEET蛋白功能

植物SWEET蛋白参与糖分的转运，而糖不仅可以作为养分物质供植株生长，也可作为信号因子，因此SWEET蛋白在植物生长发育、响应生物与非生物逆境胁迫过程中均有不同程度的调控作用(表2)。

3.1 植物SWEET蛋白的生理功能

SWEET蛋白可以调控花蜜的分泌。拟南芥SWEET1蛋白具有给配子体或花蜜提供营养的作用[6]，拟南芥和芜菁的SWEET9蛋白也具有调控花蜜分泌的功能[59]。SWEET蛋白可以调控花粉的发育，拟南芥的SWEET5、SWEET8、SWEET13、SWEET14蛋白均具有调控花粉营养与萌发的功能[57-58, 61]。SWEET蛋白可以调控灌浆期种子的发育，例如Chen等[62]的研究表明，拟南芥SWEET11、SWEET12和SWEET15蛋白可以调控种子发育。此外，SWEET蛋白可以调控果实发育，如葡萄SWEET10蛋白介导了果实中糖分的积累[63]。

表2 植物SWEET蛋白转运底物及功能

基因	物种	亚细胞定位	转运底物	功能	参考文献
SWEET1	拟南芥 *Arabidopsis thaliana*	质膜	葡萄糖	配子体或蜜腺提供营养	[6]
SWEET1a	茶树 *Camellia sinensis*	质膜	葡萄糖、蔗糖、半乳糖	冷胁迫耐受性	[43, 64]
SWEET2	拟南芥 *Arabidopsis thaliana*	液泡膜	2-脱氢葡萄糖	液泡糖运输；增强腐霉抗性	[55]
SWEET3	百脉根 *Lotus japonicus*	质膜	蔗糖	结节中的糖转运	[35]
SWEET4	拟南芥 *Arabidopsis thaliana*；葡萄 *Vitis vinifera*	质膜	已糖(葡萄糖、果糖)	植株生长；抗冻性；抗病性	[5, 56]
SWEET5	拟南芥 *Arabidopsis thaliana*	质膜、内室膜	葡萄糖、半乳糖	花粉萌发	[57]
SWEET7a	番茄 *Solanum lycopersicum*	质膜	葡萄糖、果糖、蔗糖	植株生长和生殖发育	[3]
SWEET8	拟南芥 *Arabidopsis thaliana*	质膜	葡萄糖	花粉发育	[58]
SWEET9	拟南芥 *Arabidopsis thaliana*；芜菁 *Brassica rapa*	质膜	蔗糖	花蜜分泌	[59]
SWEET10	甘薯 *Ipomoea batatas*	质膜	蔗糖	病原抗性	[4]
SWEET10	葡萄 *Vitis vinifera*	质膜	已糖（葡萄糖、果糖）	提高果实糖含量	[63]
SWEET11	拟南芥 *Arabidopsis thaliana*	质膜	蔗糖	韧皮部装载；种子灌浆；木质部发育；干旱；冷害；病原菌互作	[59, 61-62]
SWEET12	拟南芥 *Arabidopsis thaliana*	质膜	蔗糖	韧皮部装载；种子灌浆；木质部发育；干旱；冷害；病原菌互作	[60, 62, 65]
SWEET13	拟南芥 *Arabidopsis thaliana*	质膜	蔗糖	花粉发育；调控GA反应	[61]
SWEET14	拟南芥 *Arabidopsis thaliana*	质膜	蔗糖	花粉发育；调控GA反应	[61]
SWEET14	番茄 *Solanum lycopersicum*	质膜	葡萄糖、果糖、蔗糖	植株生长和生殖发育	[3]
SWEET15	拟南芥 *Arabidopsis thaliana*	质膜	蔗糖	种子填充灌浆	[62]
SWEET16	拟南芥 *Arabidopsis thaliana* 茶树 *Camellia sinensis*	液泡膜	葡萄糖、果糖、蔗糖	种子发芽；冷胁迫耐受性	[2, 43]
SWEET17	拟南芥 *Arabidopsis thaliana*	液泡膜	果糖	液泡果糖转运；根系发育和抗旱性	[21, 66]
SWEET17	茶树 *Camellia sinensis*	质膜	葡萄糖、果糖、半乳糖、甘露糖、蔗糖	冷胁迫耐受性	[43, 64]

3.2 植物 SWEET 蛋白对逆境胁迫的调控

SWEET 蛋白可以调控植物对非生物胁迫的抗性。过表达茶树 *SWEET1a*、*SWEET16*与*SWEET17*基因和过表达拟南芥 *SWEET4* 与 *SWEET16* 基因，可以提高茶树和拟南芥对冷胁迫的耐受性[2, 43, 56, 64]；拟南芥水分胁迫下通过调控 *SWEET11* 和*SWEET12*基因的表达将更多的糖分从叶片运输到根部，以维持根的生长发育，从而增强对水分胁迫的适应性[60]；拟南芥 *SWEET11* 和 *SWEET12* 可协同作用调控植株抗冻性，冷胁迫处理下拟南芥 *SWEET11* 和 *SWEET12* 表达下调，且 *sweet11* 和 *sweet12* 双突变体表现出抗冻性[60]；拟南芥 *sweet17* 敲除突变体表现出侧根减少和侧根发育相关转录因子表达减少，导致耐旱性降低[66]。

SWEET 蛋白可以调控植物对生物胁迫的抗性。过表达 *SWEET2* 可以增强拟南芥对腐霉的抗性；过表达葡萄 *SWEET4* 可促进具有真菌抗性的黄酮类化合物的生物合成，增强对真菌的抗性[5]；过表达甘薯 *SWEET10* 可通过降低甘薯的糖含量来增强了对尖孢菌的抗性[4]；拟南芥 SWEET11 和 SWEET12 蛋白参与病原体驱动下胚轴内蔗糖分布的调控，进而对甘蓝根肿菌的侵染产生负面影响[65]。

4 小结与展望

SWEET 蛋白是植物中广泛存在的一类糖转运体，其既能转运单糖又能转运蔗糖，属于 Mt N3 家族。不同植物间的 SWEET 蛋白具有一定的保守性，根据亲缘关系 SWEET 家族可以分为四类。植物 SWEET 蛋白是位于膜系统上，参与糖分的跨膜转运，在植物生长发育及逆境胁迫中均有不同程度的调控作用，例如调控花蜜的分泌、花粉的营养、灌浆期种子的发育、果实发育、植物抗逆性和抗病性等。因此，植物 SWEET 蛋白是一类重要的转运蛋白，研究其生理生化功能，有助于分子辅助育种，缩短育种年限。

目前，SWEET 蛋白在模式植物拟南芥中的研究较为深入，在其他植物的研究还相对较少且深度不够。今后的研究重点应从以下几点入手，一是作物生长调控，如水稻、玉米等作物，研究营养器官与生殖器官的关系，保证充足营养面积的基础上更多的糖分转运到种子 / 果实中，以提高产量和品质；二是园艺瓜果植物的高品质育种，深入研究葡萄、苹果、甜瓜、西瓜等园艺植物 SWEET 蛋白的功能，利用生物技术手段进行高品质育种；三是植物抗性育种，挖掘植物 SWEET 蛋白的功能，通过 SWEET 蛋白对糖的调控增强植物对生物与非生物胁迫的耐受性，结合分子生物学手段，达到抗性育种的目的。

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