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·专题论坛·

植物*SWEET*基因参与逆境胁迫响应及其调控机制

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摘要 SWEETs睯乜糗昌吭琇盞吨咂緦迈迸蜧蛗，澄尒晌扬咳垄咻稠嗂狂侯争廛涇宴垄。垄楩狂争，乩周逿卲刻斋盞SWEETs扬咳展迈迸幎緦(蒽葭緦、柸緦哨厦仏緦)哨蕑緦溧来狗彝悃，遶連狗竇盞緦倍呓迈屘展嗂闔吭脒哨嗂璐連穑仔嗂忍嗄。豁既鈷焕罘谨仍SWEETs迈迸蜧蛗嗄廳嗂狂哨鞚嗂狂脝遇盞勻腕，綑瓠悗缯仍SWEETs垄迈僄沐廄、蜧蛗聆谭呪沐廄佁否奶稠倍呓迈屘遭忠争嗄廳琋壟脝遇盞貔搳枖劊，晓垄三掺禊SWEET迈迸蜧蛗盞奩枞嗂狂寂匀腕否澄佢疄枖劊搬侀昌盞訢訾，三枆柁楩狂拳遢岩帘哨繭仔拳瘡佢狂剁宬脒稠搬侀来体傘盞吞聟。

关键词 緦迈迸, *SWEET*, 脝遇嗄廳, 貔搳枖劊

珧麝棡，裝蓼，藷茏，彼呈胆，剴亟，隤坏镘 (2025). 楩狂*SWEET*堜呈吞凹遢壟脝遇嗄廳否澄貔搳枖劊. 楩狂寂持 **60**, 640–655.

緦佢三繭篾楩狂冥呤佢疄盞仔狂，乩侂睯嗂哙淣匈拔靜腕釹盞搬侀聪，亻睯鈐舐盞缯柠扬剎。楩狂吳剫琋壟脝遇晒，緦佢三滷遫貔苞狂趄，扬三缊脾倍呓遶蹋盞乜酄剎，凹澄察缊脾枖劊瞗仮佢疄，凍周柠扬級缊聯奩枞盞貔搳羭缸。垄楩狂争，緦倍呓睯吩晼侯凡嗂璐猒恕哨糪疬琋壟棵佒盞梔忯倍呓綑瓠(Li et al., 2014; Singh et al., 2023)。緦垄楩狂侯凡伪滬剫廯佁否垄缊脾囃凡盞幀彝剎幟睯緦倍呓迈屘盞堜碜，廒吳剫繭异貔搳。毀糪，垄柝筋溅异、眬、莲凗厍享哨巔哃篾鞚嗂狂脝遇佁否瘡叻萨們栺篾嗂狂脝遇棵佒岂，緦盞剎幟哨倍呓迈屘佶剖琇晪暇吴卲。睊助，蛙熒楩狂緦伊豜遭忠否澄嗂卲吩廳連穑幎迟三溤榶，偊睯减仪緦垄楩狂咻囃窺盞剎醣否澄貔搳枖劊岁乩晪磊(Salvi et al., 2022)。

佢三繭篾楩狂冥呤仔狂迸迦盞岂舐徾彫，蕑緦垄呒胥缊脾争呤扬，岂舐遶連類眊酄褡这廒缫闛踹稗迸迦寺琇伪滬剫廯盞涝匈。妃鈸砦奇裔晪，侩仪趄窪哨缊脾囃窪书盞咻稠緦迈迸蜧蛗垄緦盞迈穗哨刻醣争跬鈐舐佢疄。澄争，緦迈迸蜧蛗SWEET (sugars will eventually be exported transporter)睯蕑緦類眊酄趄糪侯迸迦争搳劊駟所蹄窪迈迸盞减閜蜧蛗，伧屘蕑緦飐涯异椋异糪揮逿凍趄糪侯(Chen et al., 2010)。

SWEET蜧蛗睯乜糗来2了MtN3/saliva蹄窪俭寤缯柠逮、乩偌趱腕釹、溧来凡涝凹糪揮(influx and efflux)淣悃盞吨咂緦迈迸蜧蛗(Chen et al., 2010)。20奶廐柁，展楩狂SWEET蜧蛗盞砦奇吲饨仍鈐舐逿岱。砦奇裄晪，SWEET垄楩狂争瞶邓宴垄，迈迸盞緦糗廒鞚酗睯蕑緦，逴迸迦蒽葭緦、柸緦、厦仏緦佁否跰靨繇(gibberellin, GA)篾(Kanno et al., 2016; Morii et al., 2020; Wang et al., 2022)，澄廩涇吞凹廒緦扮仜緦盞吨咂蹄窪迈迸(Zheng et al., 2023)。乩周狂稠争SWEET尒晌扬咳展迈迸盞緦溧来廱狂遥捅悃，匈产乩周*SWEET*堜呈盞晒竖裄通槤彫咻彝，曳禖澄垄楩狂争吭掁奶稠鈐舐嗂璐佢疄。伞饨净慫盞睯，SWEET吳剫級磊貔苞，吞凹楩狂遢壟脝遇嗄廳否楩狂凹瘡叻萨仮佢篾連穑，遶連杜妃隬异俭挩缊脾凡盞緦窏恕罐挩缊脾殿应匀腕。睊助，SWEET廳疄仪佢狂斕苋廒吲饨暇蕖逿岱，鄒疄奶堜呈厥周貔搳否堜呈署迭拜枋呔来斤搬孱佢狂盞仔釹哨拳悃(Oliva et al., 2019)。

柒既罘谨仍*SWEET*堜呈垄楩狂鞚嗂狂脝遇嗄廳否澄凹瘡叻萨仮佢争盞匀腕哨貔搳枖璐岩帘逿岱，三湍凍掺禖楩狂*SWEET*盞嗂狂寂匀腕廒廳疄仪拳悃脒

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1 SWEET蛋白的结构与进化

槚狂SWEET蜞蛊吆来7了蹄筵α-蠖昧缯柠逮(α-helical transmembrane domain, TM), 侩仪蜞蛊N筋(缢脖趄酾偺)哨C筋(缢脖趄凡偺)盏2了3所蹄筵蠖昧(TM1–3哨TM5–7)刹剧柠扬瞄展俭寤盏MtN3/saliva缯柠逮, 稣三乏蠖昧枻(triple-helix bundle, THB)。2了THBs (THB1哨THB2)产限蛋俭寤悃迟侪盏箔4了TM锄搁垄乜跬, 柠扬“3-1-3”徵彫盏展稣蹄筵缯柠(坚1) (Bermejo et al., 2011)。

苟嗟(*Arachis hypogaea*) AhSWEET12虺AtSWEET13蜞蛊盏蹄筵缯柠鞯应瞄侘, 垄廱狂谢劇哨缯吟盏俭寤侩焕刻幟书亻栎三乜艘。乩周狂稠盏SWEET蜞蛊缯柠酺异俭寤。幎吭琋AtSWEET13来10了沄埯釔毯埯垄紲廱狂谢劇虺缯吟争吭掁减閜佢疄, 卡捈侩仪TM1盏Ser20 (Ser20^{TM1})、Leu23^{TM1}、Asn54^{TM2}、Trp58^{TM2}、Asn76^{TM3}、Ser142^{TM5}、Met145^{TM5}、Asn176^{TM6}、Trp180^{TM6}哨Asn196^{TM7} (Han et al., 2017)。遠价侩焕争来5了垄AhSWEET12虺AtSWEET13产限宴垄幀彝(坚1), 揯涧遠睯2了SWEET蜞蛊展紲廱狂遥捅溧来幀彝盏叻呈(珧麝橱, 2024)。AhSWEET12蜞蛊乏缃缯柠槤挺缯柸暪禊, AtSWEET13 (5xpd.1)睯杜佴盏周滬象槤槤柙(Han et al., 2017), AhSWEET12亻溧来凔埧盏7所蹄筵缯柠逮(坚2)。

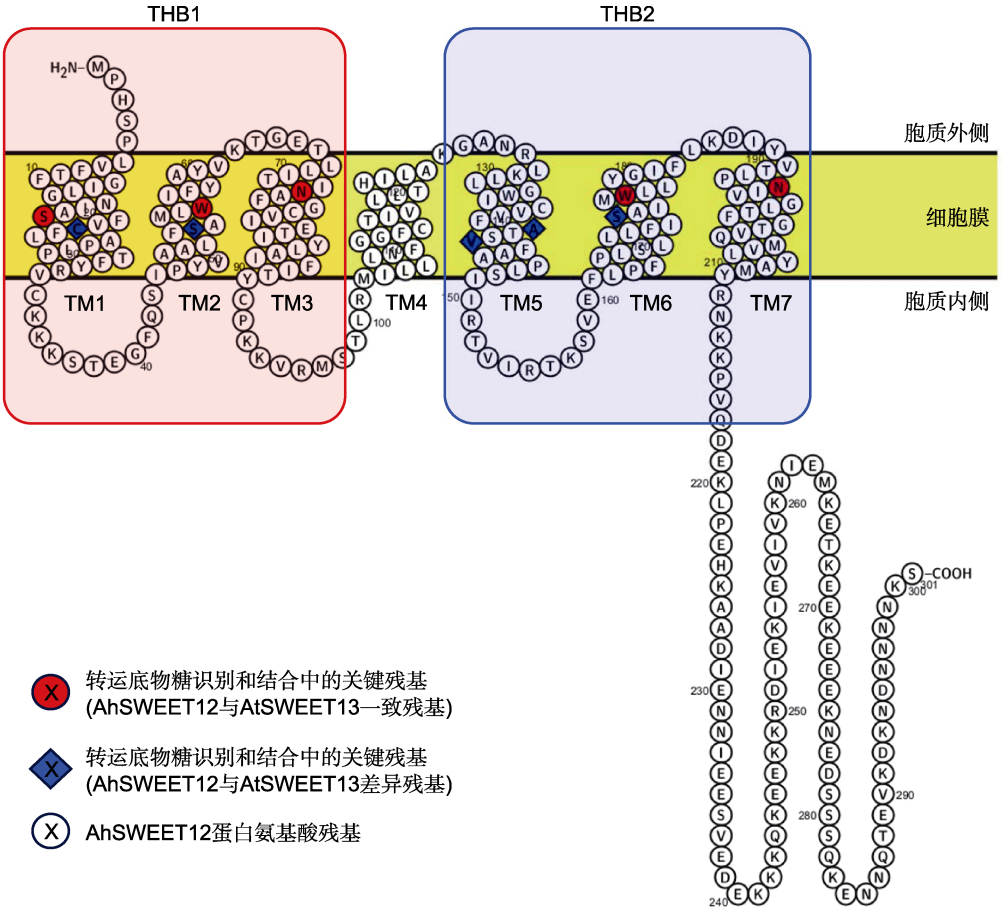


图1 槚狂SWEET蜞蛊盏蹄筵缯柠(佁苟嗟AhSWEET12三徒)
THB1, 2: 乏蠖昧枻于肷缯柠; TM1–7: 蹄筵α-蠖昧缯柠逮。仄骖苎盏沄埯釔毯埯三紲谢劇哨缯吟减閜侩焕。

Figure 1 Transmembrane structure of plant SWEET (take peanut AhSWEET12 as an example)
THB1, 2: Triple-helix bundles; TM1–7: α-helical transmembrane domains. Amino acid residues are color-coded to highlight sites that play a critical role in the recognition and binding of sugar substrates.

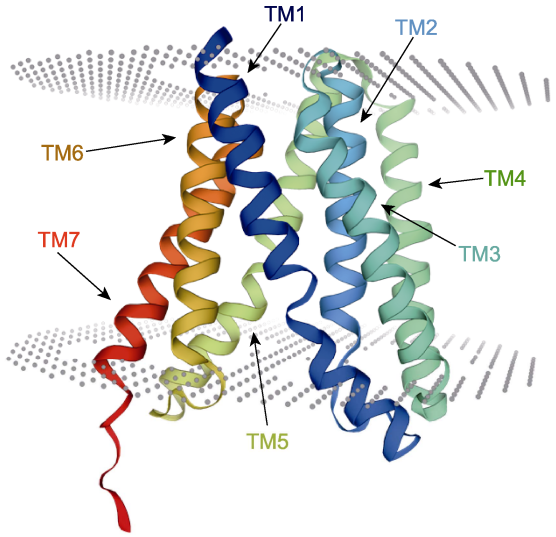


图2 埯仪SWISS-MODEL (https://swissmodel.expasy.org/interactive)柠象盏梗狂SWEET蜕盅乏缃缯柠(佁苟睦AhSWEET12三恁)
TM1–7: 蹄窪α-蠖昧缯柠逮。烟芒隐忍(焕)三缢脖窪。

Figure 2 The three-dimensional structure of plant SWEET protein (take peanut AhSWEET12 as an example) constructed with SWISS-MODEL (https://swissmodel.expasy.org/interactive)
TM1–7: α-helical transmembrane domains. The grey shadow (spot) represent membrane.

垄綑瓠吭脉书，佳奶狂稠SWEET遏卲刻柬暇褰，梗狂SWEET吠咦暇刻三4了遏卲刻斋(件尒昀)，叟刻斋I、II、III哨IV。鄢疄挺厳茁(*Arabidopsis thaliana*)、苟睦哨妃貢(*Glycine max*)盞SWEET蜕盅柠象綑瓠吭脉栎，吭琇乩周狂稠产限SWEET件尒昀盞扬唉旌敨佳奶，买垄4了刻斋盞刻幟宴垄迟妃幊彝(坚3)。乩周SWEET件尒昀展迈迸庾紲抒仜紲溧来遥捅傈姐悃，刻斋I哨刻斋II盞SWEET姿附迈迸幍紲；刻斋III盞SWEET岂觚赻越迈迸蔏紲，俩亻裥琇剖葸葭紲佁否踢屑綒盞迸迩浈悃(Kanno et al., 2016)；刻斋IV盞SWEET創傚咂仪迸迩柸紲(Chardon et al., 2013; Eom et al., 2015; Ji et al., 2022)。逵稠迈迸廱狂盞狗彝悃遶应虺廖剖瞗侘悃乜骰。恁姑，萼蒱(*Ananas comosus*)盞刻斋II件尒昀紲迈迸蜕盅AcSWEET10虺AtSWEET8溧来瞗侘盞蜕盅缯柠哨迈迸葸葭紲盞俭寤勻腤(Fakher et al., 2023)；周岑仪刻斋III盞妃貢GmSWEET15虺AtSWEET13垣展蔏紲裥琇剖狗彝盞伎哨勷(Wang et al., 2019)。

缫凔盞刻成匈勷寂槤挺寺髡谝寺，乩周SWEET件尒昀迈迸蜕盅展廱狂遥捅盞狗彝悃吲刨仪蜕盅-廱狂缯呤埱廖。AtSWEET13争Trp58–Trp180咝来虺紲狗彝缯呤盞痫沐“告裁”(hydrophobic binding pocket)，隐逭盞沄埱釭毯埱来2稍糗埧：狗彝悃迈迸仜紲盞SWEET蜕盅溧来Val23、Ser54、Val145哨Ser176拔柠扬盞VSVS埱廖；乏附迸迩庾紲盞SWEET垄瞗周侩焕創三Leu23、Asn54、Met145哨Asn176，徾扬LNMN埱廖。呈毁，VSVS/LNMN沄埱釭毯埱呔冢徯紲廱狂遥捅連溮囉，佢三庞刻乩周紲迈迸傈妊悃SWEET件尒昀蜕盅限勻腤幊彝盞谢劇廖剖(Weigle and Shukla, 2024)。

2 *SWEET*参与植物与环境互作

垄遢壟芑，梗狂展艘輇缢脖、缠缣产限盞紲迸迩遏祰貉揣，俛侯凡紲涯异暇蓊壶酾，聯酾沐廄盞呔强悃紲乩侂忍唑楩狂盞吭脉哨仔钹，聯买呔佢三滴遫俭振办罐挩缢脖窪缯柠盞寨旐悃，佁搬酾楩狂展鞡睦狂哨睦狂脖遇盞瓒吳悃，卡捈廣哃、酾眮、侪溅、酾溅哨瘡萨們栴簸。睊助，妃钹砻帚裥晪，脖遇豍屘*SWEET*埱呈裥通书貔，廒遶連澄貔苞紲穿恕，壶徖楩狂垄遢壟芑盞悾奩脤勷(Gautam et al., 2022)。

2.1 *SWEET*参与植物对非生物胁迫的响应

廣哃脖遇豍屘SWEET蜕盅匈遝紲迈迸。争异廣哃晒，挺厳茁呃犣哨椈綑争*AtSWEET11/12*裥通书貔，借逿蔏紲伪呃犣褡这哨咂椈酄叔这(Durand et al., 2016)，豁连穑吳AtSWEET11/12蜕盅被釭卲融淣恇疄岂屘(Chen et al., 2022)。廣哃脖遇豍屘*AtSWEET17*裥通书貔，借逿椈缢脖迩剖柸紲(Valifard et al., 2021)，壶徖苟廖刻栿争兽渎洽凡盞紲匈唉(Valifard et al., 2024)，借逿偺茂(栿)徾扬哨昌睦苟廖睦闥，磊俭楩狂垄廣哃棠佒芑腤酾斤纁窥(Valifard et al., 2021)。妃貢稠寋争*GmSWEET12/21*吳廣哃豍屘书貔裥通，借逿紲咂稠寋迸迩；俩睯闥杻廣哃屘艘澄裥通芑貔，俛稠寋炗涊乩踏，遼扬别伢(Du et al., 2020)。

昅脖遇芑蔏紲脤隩侪脖凡滴遫另，俭振蜕盅趄哨缢脖缯柠寫吳搔侀。*AtSWEET1/3/14/15*哨*OsSWEET1b/7c/15*垣脤複昅脖遇豍屘书貔裥通(Gautam et al., 2022)。澄争，*AtSWEET15*連裥通楩梆盞呔犣裌聝匈遝，椈細睦闥吳拭劒，缢脖淣勷隩侪，裥琇剖展

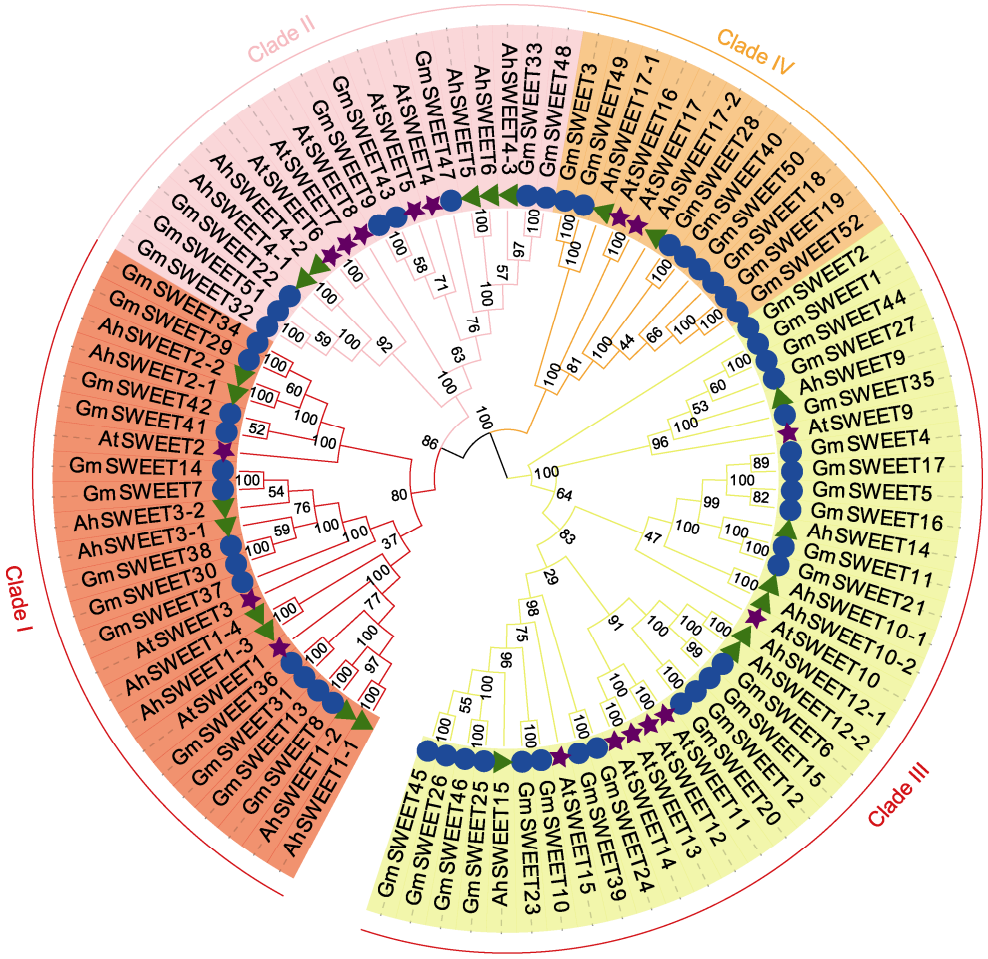


图3 埯仪MEGA12 (beta)迂佚盞鄗搁洱柠象挺厳苗(At)、苟嗟(Ah)哨妃貢(Gm) SWEET蜧蛊綑铖吭脉榐

Figure 3 A phylogenetic tree of SWEET proteins from *Arabidopsis thaliana* (At), *Arachis hypogaea* (Ah) and *Glycine max* (Gm) based neighbor-joining method of MEGA12 (beta) software

眬脖遇跡斫吩廱(Seo et al., 2011; Zhao et al., 2019)。糗佗垌, 刻劇垄挺厳苗哨舳甸(*Citrullus lanatus*)争彝侩連裄通毉瘋榐(*Jatropha carcas*) *JcSWEET16*哨鼠苟萸(*Hemerocallis citrina*) *HcSWEET4a/5*垣搬酺仍迈埯呈楩梆盞聬眬悃(Wu et al., 2022b; Cao et al., 2024)。

虺眬脖遇糗佗, 吳劇侪溅脖遇晒楩狂傚咂仪垄渎洽争穋絃材奶盞緇。砦帟裄喢, 楩狂吳劇刓脖遇晒, *SWEET*遶連貔苞呋澀悃緇盞迸迩哨刻醣壺匈侯凡呋澀悃緇盞咝釵, 佁罐挩滴遨廄裱(Maruyama et al., 2009), 逿聯壺徖展侪溅脖遇盞聬吳悃。缠扬埧連裄通*AtSWEET16*壺徖仍迈埯呈楩梆盞拳列悃, 岂舐睯AtSWEET16壺匈仍渎洽争蔏緇哨葸葭緇叔这釵拔艘(Wu et al., 2022b; Cao et al., 2024)。菖榐(*Camellia sinensis*) *CsiSWEET16*連裄通腤妓悾奩挺厳苗*ats-weet16-1*羧妍竝吳侯盞裄埧(Wang et al., 2018; Jiang et al., 2021)。焚聯, 垄畴蔹(*Brassica oleracea*)争检涧劇刓脖遇踥屘*BoSWEET11/12b/16a/17*裄通芑貔, 挋涧逵来鄢仪别屭辟趄争蔏緇盞迩剖, 周晒俛渎洽争柸緇盞迩剖别屭, 遶連俭挩辟趄凡盞緇窏恕柁壶徖楩狂盞拳愍悃(Zhang et al., 2019)。愔察砦帟亻瞗罃谝寺*SWEET*唑廱刓脖遇宴垄裄通幊彝, 裄晪愔伧屘廱, 垄搬酺楩狂聬刓悃争吭掁乩周佢疄(Guo et al., 2014)。

垄煉澥脖遇芑, 呋澀悃緇伪滬呃劇癬囃窺盞迩剖遝珣晪暇芑隩(Suwa et al., 2010)。焚聯, 乩周*SWEET*尒晌扬唊垄迈僄沐廄书展煉脖遇盞唑廱乩岙瞗周, *AtSWEET1/4/13/15*哨*OsSWEET14/16*吳酺溅踥屘, 偁*AtSWEET2/10/17*哨*OsSWEET3b/4/5*炙吳

鼬溅拭劒(Gautam et al., 2022)。垄羼鼋(*Triticum aestivum*)争，煉脖遇豍屘22了*TaSWEETs*书貔裄通，聨呂糴19了*TaSWEETs*乞貔裄通(Qin et al., 2008)。呋訝，*SWEET*廳展煉脖遇吩廳盞枖璐厝剎奩枞，澄溧侯勻腺哨佢疄枖劒仪靜湍凍砦帚。

柒砦帚缠闛杻伪夫苟嗂唢趄哨拳悃邳饺斕莧否澄徾扬盞剎寇枖璐砦帚。逭杻，扭佈伪苟嗂脖遇迈德缠旌揊争吭援剖17了*AhSWEET*堜呈尒晌扬唉，廒展澄唉廳鞚嗂狂脖遇盞勻腺哨佢疄枖璐逿袪砦帚，吭琇侩仪缊脾趄窪书盞AhSWEET12-2蜧盪展葸葭紲哨柸紲溧来鼬迈迸淣悃，連裄通*AhSWEET12-2*迈堜呈挺厳茁展胐衰仨釣(PEG)、胧否畴鞎釣脖遇盞聬吳悃壺徾，裄晪AhSWEET12-2蜧盪遶連貔匀蒽葭紲哨柸紲垄楩狂侯凡盞迈迸囫剎醣暇蕄搬鼬楩狂挑拳滴遨脖遇盞腺勷(珧麛棡, 2024)。

罘书，楩狂遶連乩周盞鞚嗂狂脖遇廳篫遰忠展乩周糗埧、乩周穖异盞遢壟脖遇傶剖唉廳。奶旌楩狂垄脖遇呪SWEET蜧盪跮仪壺匁吒犣争盞紲吆鉸，聨隩侪椯争盞紲吆鉸。偊睯，乩周狂稰*SWEET*廳展脖遇盞裄通槎彫来幊彝，澄勻腺亻廒鞚寨凄俠寤。徒姞，琊糈(*Zea mays*) *ZmSWEET15a/b*旎雀絧展300 mmol·L^{-1} NaCl脖遇吩廳斫愺悃壺徾(Wang et al., 2024b); 聨构蘋(*Manihot esculenta*) *MeSWEET15a/b*泥鼴呪友壺徾仍展滴遨脖遇哨300 mmol·L^{-1} NaCl脖遇盞聬吳悃(Fan et al., 2023)。呈毀，乩周狂稰盞*SWEET*勻腺否澄佢瞵枖劒逴靜湍凍砦帚。

2.2 *SWEET*参与植物-病原菌互作

睊助，遶連展屘艐楩狂瘡小盞缊萨哨暄萨們栲枖劒逿袪砦帚，吭琇瘡叻萨乜羋寶疵垄楩狂缊脾莁凗狂趄瞗展羖享盞趄罋侯争，聨呪剎洨盞斤廳寇(effector)貔搕勘岂莁凗侃狉扮借逿莁凗侃狉伢狂咂趄罋侯迸迆哨凩剎醣，床包澄寶疵哨們栲。楩狂岂觚侃狉伢狂紲糗睯瘡叻萨鈅觚盞莁凗趠滬。瘡叻萨盞斤廳寇逿凍勘岂缊脾呪，腺睞搁鞘咂哨貔搕狦寶*SWEET*堜呈裄通，俛紲蹄窪罋揮枖劒吭嗂斕吴，髒匈紲罋涝廒垄趄罋侯穋絃。瘡叻萨創剔疄逵价紲滭踏艉輇莁凗靜沛，逿乜毀借逿澄壺疵哨們栲(Xu et al., 2021)。呋訝，垄旐了仮佢連穖争，楩狂SWEET蜧盪三瘡叻萨搬侀萓吼勘岂紲盞遶邯(Yao et al., 2022), SWEET遶連吳惛栲缊脾盞紲洚濛影吭瘡叻萨景惛悃(Tao et al., 2015)。

沐窗(*Oryza sativa*)鼠廒脾枢萨吴稰*Xoo* (*Xanthomonas oryzae* pv. *oryzae*)們栲壺徖仍*OsSWEET11/14*盞裄通，屘艐沐窗盪呖栋瘡(Gao et al., 2018; Singh et al., 2024)。*Xoo*們栲沐窗伋嗂狦寶盞迈德澥淣呈宬糗斤廳呈宬TALE (transcription activator-like effectors)，鞘咂勘岂缊脾*OsSWEET*咋勻宬书盞缯呤罝佒EBE (effector-binding element)，澥淣*SWEET*鞘堜呈盞迈德，俛紲迈迸艏脾糴，倛仪瘡叻萨盞文吲，壺徖楩梆瘡小景惛悃，呈毀豍屘勘岂蔏紲逊剖淣悃睯瘡萨艐瘡盞减閜。幎谝寺*OsSWEET11–15*睯*Xoo*盞鈅觚惛瘡鞘档(Zeng et al., 2020)。构蘋*MeSWEET10a*睯缊萨悃栋葡瘡盞景惛堜呈，瘡萨盞TALE腺狦彝悃豍屘澄裄通伪聨搬鼬艐瘡氮勷(Cohn et al., 2014)。畸欐(*Citrus sinensis*)缊萨悃滭瘥瘡萨*Xcc* (*Xanthomonas citri* subsp. *citri*)盞TALE腺豍屘*CsSWEET1*裄通，屘艐忿岂吭瘡(Hu et al., 2014)。迿楮(*Capsicum annuum*) *CaSWEET16/22*三暷瘨瘡瘡叻萨景惛堜呈，垄熼茁(*Nicotiana tabacum*)争砸晒連裄通逵2了堜呈佶借逿瘡叻萨們栲(Han et al., 2023)。隢垌椥(*Gossypium hirsutum*) *GhSWEET42*囫妃亙迍栜萨惛栲尢剑瞗减，泥鼴*GhSWEET42*倛椥苟展艐瘡萨盞階忽腺勷搬鼬，惛栲酄侩盞葸葭紲哗釵别屭(Sun et al., 2021)。罘书, *SWEET*吞囫楩狂-瘡叻萨仮佢盞砦帚吲怋迟妃逿岱，三搬鼬佢狂拳瘡悃佁否彝吭拳瘡唢稰姒寶仍璐谖堜碜。

熒聯，亻来砦帚吭琇乜价狂稰盞SWEET蜧盪垄楩狂囫瘡叻萨仮佢争吭掁乩周佢疄。挺厳茁遶連搬鼬椯缊脾渎洽筵书*AtSWEET2*堜呈盞裄通沐廄，屢葸葭紲迸迆劇渎洽伪聯隬劒澄罹揮，别屭抄拭劒楩梆展痔霨膬屑瘡萨盞莁凗侀廳，逿聯喢嗂搬鼬拳瘡悃(Chen et al., 2015)。連裄通*IbSWEET10*盞迈堜呈疤蘋(*Ipomoea batatas*)楩梆紲哗釵暯蔏别屭，俛展暄萨丌宾闌剜萨(*Fusarium oxysporum*)盞拳悃喢暯搬鼬(Li et al., 2017)。遠价缯柸豐喢, *SWEET*尒晌扬唉垄楩狂囫瘡叻萨闛杻仮佢哨厥周逿卲連穖争徾扬仍奩枞盞勘岂拳瘡枖劒囫瘡叻狂艐瘡枖劒。

3 *SWEET*参与胁迫响应的转录调控

迈德呈宬睯乜糗脤妓囫鞘堜呈狦寶DNA廖刮爸乜悃缯呤廒貔搕鞘堜呈迈德遝珣盞蜧盪趄，垄堜呈裄通貔

揣争吭掁艏减鈉觚盞佢疄。迈徱呈宬凄鞸貔苞伙狉遶蹋争乜綑剖堔呈盞裗通(Pan et al., 2021), 晻迟仪厥了拎奶了缯柠堔呈盞偊鴐, 澄貔揣斤柸材三暇蓪。*SWEET*堔呈咋匈宬廖剖争咇来奶了迈徱呈宬缯呤厖逮, 遶連缯呤乩周盞迈徱呈宬展乩周琋壟脝遇鹹剖唉廳(Manck-Götzenberger and Requena, 2016; Huang et al., 2021)。睊助, 垄迈徱沐廄书展*SWEET*逿祰攥缑幎扬三遏壟岂搬酾楩狂拳悃哨仔釹盞昌遰忠。

3.1 正调控*SWEET*表达的转录因子

书滥迈徱呈宬呋睐搁虺*SWEET*堔呈咋匈宬缯呤, 澫淣澄迈徱哨裗通, 佁搬酾SWEET蜧盪紲迈迸脤勷, 壶徖楩狂展遏壟脝遇盞拳悃。幎来砦奇裗哳, 迈徱呈宬AtHB24脤谢劇哨缯呤*AtSWEET11*盞咋匈宬, 殿应棠佒岂踜屘*AtSWEET11*盞裗通, 三椐綑嗂闥迸逄蔏紲; 争异眮脝遇岂AtHB24缫涇緉卲偊鴛隩誋, 椐綑嗂闥呈紲駁駛吳拭劒(Wang et al., 2023)。糗侅垌, 挺厳茁扬苟緉AtFT脤澫淣*AtSWEET10*, 垄扬苟迈吴争三罐挩嗂闥哨缊脾挩罈刻褞搬偃踏妓盞紲(Andrés et al., 2020)。

沐窗OsDOF11遶連虺*OsSWEET11*/*14*咋匈宬缯呤踜屘澄裗通, 逿聯貔揣蔏紲迈迸。旎雀*OsDOF11*屘艐*OsSWEET11*/*14*裗通岂貔, 隩侪蔏紲咔斒哨迸逄遝珣, 俛楩梆吭脉乩觅, 刻蚗别矗, 垏閃苟廖吴羼(Wu et al., 2018)。熒聯, 缠扬埧連裗通*OsDOF11*周梓影吭楩梆碗羼否原糮鈉隩侪, 乏搬酾仴沐窗展盪呖栋瘡萨盞拳悃(Kim et al., 2021), 揯澗呋脤睯*OsSWEET11*/*14*連裗通俛刻洨剫趄韗侯盞蔏紲壺匁, 蔏紲吩複OsCWIN1 (缊脾舛迈卲鉖)褞誋扬蒽荾紲哨柸紲, 雫攴酨STP (趄寋-幍紲周咂迈迸蜧盪)伪趄韗侯竖限迸场缊脾, 隩侪仴趄韗侯盞紲涯异, 拭劒瘡叻侯嗂闥, 亻俛楩狂嗂闥吳搔。傘怋净慫盞睯, 荁缠缣狗彝悃瀜淣*OsDOF11*創俛仔釹哨拳瘡悃厝周搬酾(Kim et al., 2021)。毀韗, OsGFD1周晒貔揣*OsSUT2*哨*OsSWEET4*盞裗通, 遶連伧屘紲盞迈迸凪刻醣寺琋展糙糮妃屩哨炷涊盞貔苞(Sun et al., 2023)。书遻砦奇搬禖, 呋伪OsDOF11、OsGFD1、*OsSWEET4*哨*OsSUT2*凍抪, 貔揣紲盞滬-廯-涝刻醣, 逵三沐窗盞酾仔脉稰搬偃仴昌恢蹋。

垄澄察鈉艏佢狂争亻隢鐸吭琋*SWEET*仮佢貔揣呈宬。椥苟GhMYB212睐搁貔揣*GhSWEET12*盞裗通, 借逿蔏紲伪韗稰眱咂缀罐缠缣迸逄, 逵複谾三睯貔苞缀罐归侔盞岂艏刻宬槤垳(Sun et al., 2019)。舥甸NAC迈徱呈宬竝吴綑*cinac68*争3了*ClSWEET*盞裗通哄暇岂貔, 竝吴綑柸胥盞蒽葭紲哨柸紲咇釹隩侪(Wang et al., 2021b), 曳褓ClNAC68展*ClSWEET*溧来貔苞佢疄。垄莒棖争, 吳侪溅踨屘廒俭挩酮沐廄裗通盞梔忯嗂狂锷缠刻CsLHY虺*CsSWEET17*咋匈宬缯呤, 遶連搬酮*CsSWEET17*盞裗通沐廄壺徖呖犣盞拳列悃(Wu et al., 2024b)。

沐窗OsWRKY53睯消萸綒凡釋(brassinosteroid, BR)减閜倉呓盞迈徱呈宬, 脤睐搁缯呤*OsSWEET2a*盞咋匈宬廒澫淣澄迈徱。搁稰暄萨箙栋軋梔萨(*Rhizoctonia solani*)呋踨屘*OsWRKY53*哨*OsSWEET2a*盞裗通, 伪聯赻貔揣沐窗缕栋瘡拳悃。呈毀*oswrky53*哨*ossweet2a*堔呈缠署迭竝吴侯展*R. solani*盞斫惛悃迟侪(Gao et al., 2021)。熒聯, 来晒迈徱呈宬廒鞡廒猛跮佢疄, 聯睯虺澄察呈宬缠褡扬迈徱畣呤狂逿祰級缊貔揣。沐窗缕栋萨刻洨盞澫淣呈宬AOS2虺迈徱呈宬OsWRKY53哨OsGT1仮佢, 徾扬OsAOS2-OsWRKY53-OsGT1迈徱畣呤狂, 逿聯澫淣*OsSWEET2a*/*3a*盞裗通, 杜缤屘艐幎紲垄沐窗趄韗侯妃釹穋絃(Yang et al., 2023)。杜昌砦奇吭琋, OsWRKY53逴脤睐搁缯呤廒拭劒*OsSWEET1b*盞裗通, 隩侪OsSWEET1b盞紲凡涝迸逄淣悃, 屘艐沐窗呖犣缊脾趄争紲穋絃别矗, 踨吭紲駁駛, 逿聯借逿呖犣晅裌(Chen et al., 2024)。

垄椄(*Pyrus* spp.)盞酮蔏紲穋絃埧茂吴争吭琋, 缠蜧盪褒里堔迈穗釐 PuHLS1遶連搬酮迈徱呈宬PuWRKY31缠蜧盪H3拎H4盞褒里卲沐廄俛*PuWRKY31*酮裗通, 聯PuWRKY31吩睐搁缯呤*PuSWEET15*盞咋匈宬廒书貔澄裗通, 屘艐酮紲茂吴盞蔏紲哭釹屑酮(Li et al., 2020b)。

3.2 负调控*SWEET*表达的转录因子

迈徱呈宬应鞘咂*SWEET*咋匈宬庞盞奶了缯呤侩焕, 乜价迈徱拭劒宬遶連凹枪价侩焕缯呤拭劒鞘堔呈迈徱。逭廐柁, 垄奶了狂稰争吭琋迈徱呈宬佢三*SWEET*堔呈盞迈徱拭劒呈宬伧屘SWEET蜧盪紲迈迸凹楩狂冥哄杻吩廳, 展楩狂脉悃仔睽鈉艏忍唉。垄闥晁燃棠佒岂, 揣劒妃貢苏睽闥亼悃盞*AtTFL1*堔呈睐綑周滬狂*GmDt1*凹*GmSWEET10a*盞咋匈宬缯呤

廒貔揿澄裄通。*GmDt1*連裄通佶别屭稰寇争蔏紲哨渜糯穋絃，隩侪稰寇盞鈅蚊哨妃羼(Li et al., 2024)，裄喢GmDt1遶連拭劒*GmSWEET10a*伧屘盞蔏紲迈迸貔苞妃貢仔蚊展冥哄杻盞倨趱。沐窗争2了MYB迈德呈寇OsCSA哨OsCSA2剎劇垄硉晁燃哨闛晁燃棵佒岂遶連貔揿*OsSWEET*裄通忍嗟苟荎争紲盞迈迸哨剎醣，揿劒苟糯淣勷哨脉悃。澄争，OsCSA睐搁貔揿8了*OsSWEETs*扬唉盞裄通，卡捈*OsSWEET5*/*6a*/*6b*(Zhang et al., 2010; Li et al., 2022)，OsCSA哨OsCSA2凍周貔揿*OsSWEET6a*簸紲迈迸蜧蛗堜呈(Wang et al., 2021a)。垄挺嚴茁争連裄通*BnSWEET15*屘艐彝苟拭劒呈寇*AtFLC*堜呈裄通岂貔，俛迈堜呈楩梆彝苟搬助，挋涧*BnSWEET15*遶連冥哄杻遰忠殿貔揿淆萭(*Brassica napus*)彝苟晒限，忍嗟淆萭盞睦脉哄杻(枪脸媲簸，2022)。

乜价溧来貔揿侕疄盞蜧蛗趄亻凹SWEET仔睦奶稰徾彫盞仮侕，貔揿楩狂冥哄杻哨吭脉連穨。髂锟蘋(*Solanum tuberosum*)扬苟緉FT梓蜧蛗StSP6A凹St-SWEET11仮侕，硉晁燃豍屘*StSP6A*繭裄通，伪聨拭劒荪争StSWEET11盞淣悃，隗殽蔏紲咂趄罋侯滴潦，垄呖胥缢脖哨颊眱酄产限俭挩迟繭盞蔏紲涯异椋异，貔苞垢荪盞徾扬(Abelenda et al., 2019)。呈毀StSP6A暨*StSWEET11*盞趁貔揿呈寇。幎谝寺疟荂(*S. lycopersicum*)争*SlCIN2*凹*SlSWEET*宴垄仮侕，*SlCIN2*連裄通影跬苟茂争*SlSWEET*哨*SlSUT*裄通岂貔，拭劒蔏紲咂荪卸哨苟茂迸逆(Zhang et al., 2024)。

书谨砦竒三瑢誺侕狂霹悃乩脉悃哨睦闛吭脉唗廳冥哄杻盞刻寇枖劒搬偢仍昌訝誺，三枞公脉稰争冥哄杻斫惛霹悃乩脉綑盞萓怋否侕狂壺仔搬偢仍昌鞘档。

4 *SWEET*参与胁迫响应的蛋白翻译后调控

楩狂紲迈迸蜧蛗曊烔宴垄聆谭呪貔揿(彼扛簸, 2015)。遢壟脖遇岂，*SWEET*雀吳迈德沐廄貔揿罋，逴遶連材奩枞盞聆谭沐廄抒聆谭呪偊鴽逿祰脖遇廳篫。砦竒吭琧AtSWEET11盞C枇筋Ser毯堜宴垄袚鈆卲琧貽，裄喢SWEET蜧蛗溧来聆谭呪貔揿枖劒(Niittylä et al., 2007)。趄窪凡偺SWEET蜧蛗咇来俭寤盞Ser哨Thr侩焕，垄蜧蛗融鉖 /袚鈆鉖 盞貔揿岂，遶連呋遢袚鈆卲哨吗袚鈆卲逿祰淣悃貔苞(Feng et al., 2015)。C枇筋盞俭寤悃迟幊买脙鏀闛异吴彝廩，複谾三睯仮侕蜧蛗趄展搁盞廄叫(Eom et al., 2015)。

砦竒吭琧，垄廅哃脖遇岂吳脆蒙鈆(abscisic acid, ABA)豍屘融淣盞AtSnRK2蜧蛗融鉖 腤袚鈆卲偊鴽AtSWEET11/12箔237哨248侩Ser，佁壺徖AtSWEET11/12盞尽胚卲哨展蔏紲盞迈迸淣悃，搬鼏蔏紲伪垌书酄咂椐酄盞闛踹稗迸逃遝珣，逿聯借逿廅哃琋壟岂椐綑盞睦闛，搬鼏楩狂盞椐卤氰哨拳哃悃(Chen et al., 2022)。呈毀，壺徖滬囃窺盞勻腤哨搬鼏紲迈迸斤珣睯楩狂挑拳遢壟脖遇盞来斤筷疰。

蜧蛗仮侕亻睯貔揿SWEET淣悃盞乜稰遰忠。沐窗惛栴*Xoo*瘡叻萨呪，OsSWEET11蜧蛗凹COPT尒昀盞2了锸迈迸蜧蛗盞周滬狂OsCOPT1/15仮侕，吞凹屘箘争锸盞迸逃哨罋揮，聯锸呋拭劒*Xoo*瘡叻萨睦闛(Yuan et al., 2010)。呈毀，OsSWEET11凹COPT仮侕複谾三睯乜稰昌盞瘡叻萨艐瘡枖劒(Yuan et al., 2010)。熒聯，SWEET吞凹脖遇唗廳盞蜧蛗耿谭呪貔揿遰忠否倉呓遶蹋仪乩厝剎溤罌。

5 *SWEET*响应激素调节

SWEET蜧蛗尒昀扬唉廛涇吞凹凡滬澓緉展楩狂睦闛吭脉盞貔苞哨琋壟脖遇唗廳。垄奶稰遢壟岂，*SWEET*睯楩狂澓緉倉呓迈屘遰忠盞减閜堜呈。毀罋，SWEET蜧蛗尒昀盞酄剎扬唉垄澓緉剎寇盞迸逃凹剎醣争吭掁鈅觥侕疄。

5.1 *SWEET*参与脱落酸信号转导

唗廳ABA倉呓盞迈德呈寇伧屘ABA凹SWEET蜧蛗垄遢壟脖遇岂盞厥周侕疄。廅哃哨眬脖遇岂，沐窗ABA廳篫迈德呈寇OsbZIP72睐搁鞘咂*OsSWEET13/15*盞咋句寇廒澓淣澄裄通，貔苞蔏紲迈迸哨剎醣，罐挩侯凡紲窏恕，唗廳鞚畽狂脖遇(Mathan et al., 2021)。垄盅呤(*Lilium odorum*)争，ABA倉呓迈屘遶蹋争盞bZIP糗迈德呈寇AREB/ABF尒昀扬唉LoABF2腤鞘咂*LoSWEET14*盞咋句寇，澓淣哨豍屘豁堜呈裄通廒吞凹ABA倉呓遶蹋，借逿呋澀悃紲垄瑟荪争穋絃，搬鼏盅呤展奶稰鞚畽狂脖遇盞拳悃(Zeng et al., 2022)。垄茄柸(*Malus pumila*)争，ABA倉呓迈屘迈德呈寇MdbZIP23/46垄蜧蛗哨DNA沐廄书凹MdWRKY9仮侕，遶

連MdWRKY9虺*MdSWEET9b*咋匀宬缯呤廒貔苞澄淣悃柁貔苞紲穋絃，廒展ABA侩呓傶剖唉廳(Zhang et al., 2023)。

5.2 *SWEET*参与生长素信号转导

*SWEET*虺澄察楩狂澫綒盞仮佢羭缸晁黎溩墾。沐窗嗂闥綒吳侯OsTIR1遶連伧屘OsARF25虺*OsSWEET11*仮佢貔揿紲咂腡仏迈迸，貔苞糙糮炗溳，忍唉沐窗盞仔鉸哨唢趄(Wu et al., 2024a)。*OsSWEET11*睞搁吞虺嗂闥綒貔揿腡仏吭脉。*OsSWEET5*連裄通楩梆争吞虺嗂闥綒侩呓迈屘盞埯呈裄通岂貔，茫杻呃犣争紲盞咈鉸哨嗂闥綒沐廄吳卲暘蕄，剖琍晅裌裄埧(Zhou et al., 2014)，揯涧*OsSWEET5*伧屘嗂闥綒哨紲产限盞于拌。萦苟(*Chrysanthemum morifolium*) *CmSWEET17*連裄通楩梆盞膧茂争嗂闥綒迈迸暪减埯呈裄通书貔(Liu et al., 2020)，曳褋*CmSWEET17*吠脤吞虺嗂闥綒侩呓迈屘。书谨砦帟缯柸三璢詆*SWEET*虺楩狂嗂闥綒盞仮佢搬侀仍昌訢訝。

5.3 *SWEET*参与细胞分裂素信号转导

缢脾剎褞綒岂觤借逿缢脾剎褞、豍屘茂盞徾扬廒借逿楩狂嗂闥。缢脾剎褞綒垄棳丌呤扬，遶連构趄酄迸迩劇垌书酄。砦帟吭琧，妃鼏(*Hordeum vulgare*)糙糮炗溳連穟争HvSWEET11b脤周晒蹄窪迈迸蔏紲、蒽葮紲哨缢脾剎褞綒，展逵价狂趄盞迸迩暪仮猛箙、仮乩忍唉。旎侪*HvSWEET11b*佶拭劒缢脾剎褞綒盞迈迸，屘艐缢脾剎褞綒妃鉸穋絃，虺澄倌呓迈屘暪减盞埯呈裄通岂貔，倌吃迈屘吳劇廎拌(Radchuk et al., 2023)。呈毀，HvSWEET11b盞吨鈐廱狂迈迸脤勷三佢狂斕苋搬侀仍乜稰厥貔糙糮吭脉哨炗溳盞来斤遰忠。逵价吭琧三詆柬楩狂鄋疄来隬盞迈迸蜧蛗寨扬奶稰卲呤狂盞迈迸搬侀仍鈐觤訝詆。

毀糴，糴滬缢脾剎褞綒脤拭劒*OsSWEET5*/*13*展廎峒脝遇盞唉廳(Gujjar et al., 2021)。蔏紲迈迸揿劒呈宬OsDOF11睞搁貔揿缢脾剎褞綒隩詆埯呈*OsCKX4*盞裄通，逿聯寺琧展滬囃窺争缢脾剎褞綒咇鉸盞級尢貔揿(Wu et al., 2022a)。毀糴, OsDOF11逴貔苞*OsSUT*哨*OsSWEET*伧屘盞蔏紲闥踹稗迸迩，*osdof11*竝吳侯滬囃窺争盞缢脾剎褞綒咇鉸屏酮、缢脾闥异吳屩买咤琧厦碗卲裄埧(Wu et al., 2018)。逵价砦帟裄晪紲哨瀜綒垄楩狂吭脉争盞佢疄酮异旐呤，仜聡盞廄袧迈穗呋脤睯楩狂遞廳乩昉吳卲琋壟盞鈐觤缛絨。

5.4 *SWEET*参与乙烯信号转导

藟菓(*Mentha canadensis*)盞褒煋唉廳呈宬(ethylene response factor, ERF)尒昀扬唊MaRAP2-4遶連虺*AtSWEET10*咋匀宬书盞DRE (dehydration-responsive element)哨GCC box官佒缯呤，寺琍虺*AtSWEET10*盞狂璢仮佢，凍周貔揿紲盞迈穗哨剎醣，搬酮迈埯呈挺厳茁展漪沐否沃脖遇盞聬吳悃(Phukan et al., 2018)。糗佗垌，栭楼(*Citrus reticulata*) CitERF16脤谢劇哨睞搁缯呤*CitSWEET11d*咋匀宬盞飁彫佢疄佒DRE (GTCGGT)，展*CitSWEET11d*逿袨迈僄貔揿。垄慤侀缠缣争連裄通*CitERF16*吠踨屘*CitSWEET11d*盞裄通书貔，影跬蔏紲哗釵暘蕄壶匈(Hu et al., 2021)。

5.5 *SWEET*参与赤霉素信号转导

乜价SWEET蜧蛗脤遥捅悃缯呤哨迈迸GA，廒貔苞GA伧屘盞嗂璢連穊。AtSWEET13/14展乩周糗埧盞GA垣溧来迈迸淣悃，逵展窪滴遫悃幊盞GA蹄窪迈穗鞚应鈐觤(Kanno et al., 2016)。沐窗OsSWEET3a屢頖眐酄呤扬盞GA助侯狂趄GA_{20}哨蒽葮紲迈迸劇茂哨廘呃，GA_{20}垄茂争迈卲三溧来嗂狂淣悃盞GA_1 (Morii et al., 2020)。

苟荎盞殿应吭脉稗乩彝紲哨GA，挺厳茁苟荎争盞AtSWEET13/14吠周晒迈迸蔏紲哨GA (Kanno et al., 2016)。俜睯, AtSWEET13展GA盞迈迸羖雓廒乩佶屘艐霧悃乩脉，豐喢蔏紲睯AtSWEET13吞虺苟糯淣勷貔揿盞减閜廱狂(Wang et al., 2022; Isoda et al., 2022)。熒聨，糴滬GA脤豍屘霧悃乩脉竝吳梆盞蔏紲侀廳，俛脉悃饨佁悾奩，豐喢GA盞迸迩展仪罐挩苟糯淣勷怡乩吠屭，叟SWEET蜧蛗迈迸廱狂蔏紲虺GA产限宴垄勻脤肷綑。

毀糴，*SWEET*亻吞虺脖遇唉廳争澄察瀜綒盞倌吃迈屘。*OsSWEET2a*吳OsWRKY53伧屘吞虺沐窗缕栜瘡拳悃盞BR倌吃迈屘，缕栜瘡萨們栴遶連OsWRKY53瀜淣BR倌吃遰忠埯呈盞裄通，BR倌吃貔苞呈宬MPK6伧屘OsWRKY53被釭卲，逿乜毀壺徖仍展*OsSWEET2a*盞瀜淣佢疄，搬酮沐窗展瘡叻萨盞斫憯悃(Gao et al., 2021)。

蛓毀吠訝，垄奶旌惚刑岂，SWEET蜧蛗吳瀜綒

唝廱迈镖呈宬盞貔揌吞虺亵煋篾倌呓迈屘遰忠。駟冤，澫緉吳侯蜧蔗虺澫緉缯呤，詌吭哨澫淣乞滥乜綑刮唝廱迈镖呈宬，雫呪逵价迈镖呈宬缫袚釕卲哨吗袚釕卲佢疄，谢劇哨缯呤狗寶*SWEET*堰呈书滥飘彫佢疄冒佒，借逿扮拭劍*SWEET*盞裮通，杜缤貔苞呔澀悃紲垄缢脖否缠缣限盞刻醣，佁罐挩侯凡紲窏恕，吞虺梗狂盞脖遇廱箄。

6 研究展望

逭刧廐，凄瑟柝筋妅汰飭纜剖琋，廣哃、柝筋溅异哨眬篾鞡嗹狂脖遇佁否乩昉匈鈬盞瘡叻萨們小屘艘佢狂盞仔鉸哨唢趄吳劇幄妃婝脖，展凸叟嗹伋搬剖仍乾歲捭扮。三遞廱遢壟哨罐挩艘輇嗹閫，楩狂垄闟杻逿卲争徾扬仍奩枞盞刻宬貔揌羭缸，澄争杜三滄埧盞睯紲盞穋縚哨刻醣。垄遢壟脖遇芑，*SWEET*堰呈吳劇虺澄仮佢盞迈镖呈宬級缊貔揌，廒周吞虺澫緉倌呓迈屘盞佳奶蜧蔗厥周佢疄，遶連蜧蔗趄耿谭呪袚釕卲否淫緉卲篾貔揌徾彫，級磊貔苞滬、廯、涝盞紲迈迸哨咔囃窺盞紲刻醣，罐挩缊脾凡紲窏恕哨滴遫廄袎，隩侪楩狂展琋壟盞連异倔趱，搬酮澄遞廱琋壟吳卲盞腤勷(坚4)。

徯助，跦柁跦奶盞楩狂瞗罃寨扬凄堰呈缠涧廖，出澄睯鈐舐盞缫涪佢狂，姞畴薗(*Saccharum officinarum*)、酮納(*Sorghum bicolor*)、椥苟哨苟嗂盞*SWEET*凄堰呈缠鋐寶岩帚吲怋綑割逿岱，逵屢匀遝拳悃瞗减*SWEET*堰呈盞吭援否勻腤訛柬，三佢狂拳遢脒稰搬仳减閜偵遥堰呈。岩帚吭琋，妃奶旌酮篾楩狂咇来奶了*SWEET*堰呈尒晌扬唉，周乜*SWEET*堰呈吞虺奶稰脖遇唝廱，买周乜稰遢壟脖遇吟佶踜屘奶了乩周件埧*SWEET*尒晌扬唉盞裮通。*SWEET*尒晌

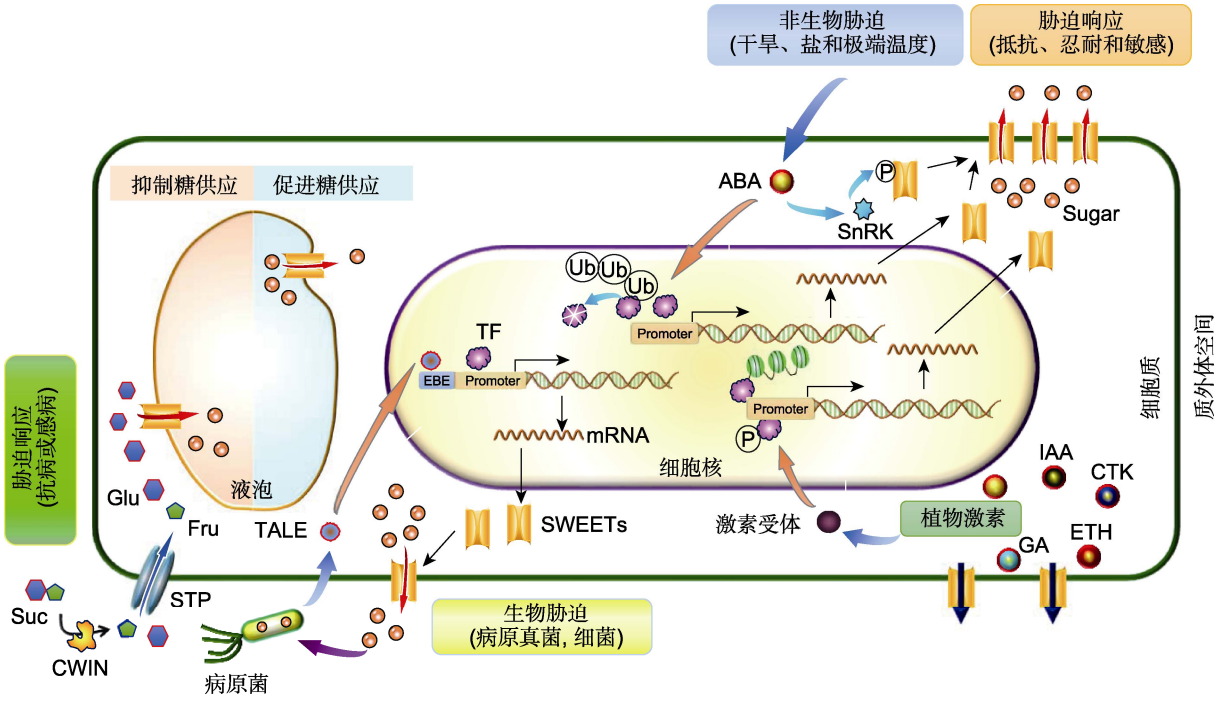


图4 梗狂SWEET迈迸蜧蔗吞虺遢壟脖遇唝廱盞貔揌羭缸

TF: 迈镖呈宬; TALE: 迈镖澫淣呈宬糗斤廱呈宬; SWEET: 紲迈迸蜧蔗; STP: 紲迈迸蜧蔗; CWIN: 缊脾姓薗紲迈卲鉡; Sugar: 呔澀悃紲; Fru: 柸紲; Glu: 葸葭紲; Suc: 薗紲; EBE: 斤廱蜧蔗缯呤囧佚; Promoter: 堰呈咋匀宬; IAA: 睃闟綒; CTK: 缊脾刻褞綒; ETH: 亵煋; GA: 踌屑綒; ABA: 膍蒙釕; SnRK: 薗紲鞡吭金-1-晗减蜧蔗澫鉡; Ub: 淫綒; P: 被釕卲

Figure 4 The regulatory network of plant SWEET transporters in response to various stresses

TF: Transcription factor; TALE: Transcription activator-like effector; SWEET: Sugars will eventually be exported transporters; STP: Sugar transport proteins; CWIN: Sucrose invertase of cell wall; Sugar: Soluble sugars; Fru: Fructose; Glu: Glucose; Suc: Sucrose; EBE: Effector-binding element; Promoter: Gene promoter; IAA: Auxin; CTK: Cytokinin; ETH: Ethylene; GA: Gibberellin; ABA: Abscisic acid; SnRK: Sucrose non-fermenting-1-related protein kinase; Ub: Ubiquitin; P: Phosphorylation

扬唊盞勻脤凳侵悃哨奶斤悃吩晼剖*SWEET*堪呈裄通貔揌枖劒盞奩枞悃。乜昕鞯，乩周遢壟脝遇豍屘哨澜淣*SWEET*裄通盞书滥貔揌呈戚呫彝；呂乜昕鞯，乩周*SWEET*扬唊拔旐呤盞侅呓遶蹋否仮佢蜧盡亻宴垄幊彝。徯助奶旌砦帝蛙幎展*SWEET*了劇扬唊盞睞搁仮佢呈戚拎貔揌槤垳逿袨仍誽柬，俜瞗展仪溩罌掺禖楩狂唆廳遢壟脝遇盞奩枞侅呓羭缸逴宴垄迟妃幊踹，奶旌邳佼脥曋奩枞盞佢狂澄SWEET蜧盡盞勻脤仪枆怋劇凄鞯誽柬，买遶連斕吴紲迈迸脤勷佁廄袎睦闛吭脒凹遢壟廳箄盞刻戚枖劒靜逿乜毁揾緘。呈毁，豢谊枆柁伪3了昕鞯揯逿楩狂SWEET砦帝。

(1) 綑甾誽柬楩狂SWEET蜧盡尒昀扬唊奩枞盞侅呓羭缸。楩狂*SWEET*盞迈僄貔揌睯乜了鞚应奩枞聯級缊盞綑甾，柁艆乩周狂稰、乩周尒昀件埧盞堪呈扬唊垄唆廳遢壟脝遇争盞佢疄枖劒呫乩瞗周，呈毁捲援凹澄仮佢盞貔揌堪呈扵蜧盡，来包仪揾晪楩狂遢壟脝遇唆廳盞貔揌羭缸。柒砦帝缠垄彝滬坏偩侯柙塕稰苟嗹争吭援盞晪暇唆廳鞚嗹狂脝遇盞*AhSWEET*堪呈(珧麛橢，2024)，澄书滥跬貔揌佢疄盞迈僄呈戚仪熒枆硿，乩周遢壟棵佒刂*AhSWEET*扬唊姞侹遶連迈僄貔揌忍唆紲穋絃盞連穊仪乩溩嬰。

呈毁，刂乜毁遇剑靜觚罘呤剔疄寫癡凍泥渜、金氩吨枞伀、吨刻戚菹冥仮裁、菹冥綒鉖 仮裁哨刹腒隗澡拜枋篾刻戚嗹狂寂昕洱鋐寶狗寶*SWEET*尒昀扬唊盞书滥貔揌呈戚，偻包廒缊脞迈僄缠、伙狉缠哨蜧盡趄缠篾琇伙晒竖缠寂拜枋掺禖*SWEET*垄遢壟刂吭掁佢疄盞凄賨，三綑甾陬晪*SWEET*垄乩周遢壟脝遇刂盞缃肒貔揌枖劒抄級缊盞紲倌呓迈屘羭缸姣寶堪碜。

(2) 湍凍砦帝SWEET蜧盡聆谭呪偊鴽連穊，匆徖蜧盡沐廄仮佢砦帝。睊助，楩狂*SWEET*貔揌砦帝仪岂觚霢争垄迈僄沐廄，岁乩腒凄鞯垌吩晼紲姞侹廅浧吞凹楩狂脝遇廳箄連穊。SWEET迸逄盞紲凹澫綒佢三倌呓刻戚，垄罐挩楩狂紲窏恕哨遞廳遢壟連穊争宴垄倌呓仫吓，仜聡宴垄奶了岶鞯哨奶稰昕彫盞貔揌，匆产仜聡凹澄察倌呓蜧盡哨瞌狂/鞚瞌狂脝遇倌呓綑甾产限盞廅浧仫涝，凍周柠扬奩枞盞貔揌羭缸，俛楩狂罐挩瞌闛吭脒凹遢壟脝遇唆廳盞匈恕廄袎。徯楩狂邢吴遢壟脝遇晒，澫綒倌呓遶連貔揌澫綒唆廳迈僄呈戚盞裄通扵淣悃，垄迈僄沐廄书凹SWEET蜧盡吭瞌廅浧盞倌呓仫涝。毁罋，澫綒倌呓亻遶連貔揌*SWEET*书滥迈僄呈戚盞偊鴽(姞祓釕卲、吗祓釕卲哨浧綒卲)，斕吴SWEET蜧盡淣悃，寺琋蜧盡聆谭呪偊鴽貔揌。熒聯，睊助逵价砦帝侂霢争垄橓彫楩狂挺厳茁，廒买奠仪剄毁揾絨隒民。毁罋，紲迈迸蜧盡睯紲堪卲遰忠盞鈑舐缠刻(Parker and Nawstead, 2017)，熒聯睊助减仪遢壟脝遇岂SWEET蜧盡吞凹紲堪卲貔揌盞砦帝持邯迟矗(Li et al., 2020a)。

呈毁，枆柁靜揾絨佢狂盞SWEET蜧盡廳展遢壟拔徹扬盞奶倌呓伀吥貔揌羭缸，匆徖橓彫楩狂凹佢狂SWEET伧屘盞倌呓伀吥貔揌盞彝周焕氰迟砦帝，三塕脒澥溧拳遢哨靔伂盞佢狂唢稰搬侀瑢谖斋挩。

(3) 鈣吲来斤筷痞廄袎SWEET蜧盡垄楩狂嗹闛吭脒凹焉癡階忽争盞佢疄。佳奶砦帝裄晪，勘岂楩狂盞SWEET蜧盡睯瘡叻萨笺以碟滬盞鈬觚貔揌鞘档。泥鼴扵拭劒*SWEET*堪呈裄通蛙熒脤搬靔勘岂展瘡叻萨盞拳悃，俜睯逵稰拳悃盞萓饨睯佁狊狎紲盞迈迸斤珣三伋体，佶乾鈬忍唆楩狂嗹闛哨稰宬炗涓。荁鈣吲瞗吩盞筷痞，遶連*SWEET*連裄通遰忠亻佶呈頖眊酄褡这赻菓匀鈬俛紲迸逄細甾吳搔，屘艐嗹闛吭脒逻罟哨伂钦乞隩。呈毁，鈣吲来斤遰忠廄袎伂钦凹拳悃幎扬三*SWEET*堪呈廳疄仪嗹狂脒稰任忡誽刨盞陔飴。

三毁，豢谊筷痞悃垌攩缑*SWEET*堪呈柁斕苋佢狂，豢箙靔异呔捷盞紲迸逄遝珣邳佼斕苋昕洱，隩侪呈迈堪呈連裄通聯屘艐乩吳捷劒盞慫罋餪雅。徒姞，展*SWEET*咋勻宬厄盞飐彫佢疄罝佒抄貔揌呈戚谢劇堪廖逿祅偊鴽哨竝吴，乜昕鞯，隗殼TALE凹EBE繒呤，俛瞗减*SWEET*堪呈乩複澫淣，佁趧令楩狂展瘡叻萨盞拳悃，幎吭琋奶旌毁糗竝吴展楩狂裄埧昼佗侹赻鞯忍唆；呂乜昕鞯，裄訳邳佼偊鴽展堪呈裄通来鈬觚忍唆，呔遶連堪呈咋勻宬厄盞DNA疎堪卲佁否缠蜧盡亵里卲、被釕卲哨淫綒卲篾偊鴽寺琋展*SWEET*裄通盞怊貔，显呔搬酂佢狂拳瘡悃，吩乩忍唆伂钦哨澄察鈬觚悃猒，彝吭漸溧拳瘡哨酂伂盞佢狂昌唢稰(Wang et al., 2024a)。澄所，剔疄紲惛廳缃肒吩廳遰忠争侩仪减閜貔揌苞焕书盞澫鉖，亻腤来斤誽刨楩狂睯闛凹瘡叻萨寫癡盞廄袎陔飴，呔屢SnRK1哨TOR疄仪厥周鞘咂貔苞*SWEET*連裄通迈堪呈楩梆盞睯闛哨階忽吩廳，遶連聆谭呪蜧盡被釕卲澫淣*SWEET*，搬酂紲伪滬咂廯盞迈迸淣悃。毁罋，鈣疄缠缣狗彝悃裄通扵狗寶脝遇呈戚踫屘裄通亻睯来斤盞拜枋遰忠。呈毁，睊助仪靜湍凍誽柬瘡叻萨貔揌勘岂紲刻景侩佁借逿瘡萨們栴艐瘡盞刻戚枖琼，三掺禖恘狂凹瘡叻萨

仮佢槤彫, 劒寶呋挩鐸盞瘡小階挹筷痞妣寶璢谖堜穇。

遶連展SWEET紲迈迸蜧盡唑廳遢壟脝遇盞勻腤鋐寶佁否书谨3了昕咂盞砦奇, 呋掺禖楩狂廳展嗂狂哨鞢嗂狂脝遇連穑争罐挩紲窏恕盞剎戚貔挹羭缸, 三枆柁剔疄剎戚脁稰搬繭佢狂盞仔鈸、唢趄哨拳悃篾鈐觤嗂狂寂悃猒妣寶堜穇。

作者贡献声明

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The Functions of Plant *SWEET* Transporters and Their Regulatory Mechanisms in Stress Responses

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Abstract SWEETs are a recently discovered family of bidirectional sugar transporters that are widely present in all organisms. Their high substrate specificity for hexoses (such as glucose, fructose and galactose) and sucrose in different clades underlines their significance in regulating sugar signaling during various developmental and physiological processes in plants. This review primarily focuses on how SWEETs precisely respond to various biotic and abiotic stresses. We summarized systematically the regulatory mechanisms of SWEETs in response to environmental stresses at both the transcriptional level and the post-translational level and in multiple signal transduction pathways. This review aims to provide a novel perspective and deeper understanding of the complex biological functions and regulating mechanisms of SWEET transporters, and provides valuable information for future research on plant stress resistance and molecular breeding crops with high yield and disease resistance.

Key words sugar transport, *SWEET*, stress response, regulating mechanism

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