

番茄 *SELF-PRUNING* 基因家族及株形调控功能研究进展

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摘要: 番茄 *SP* (*SELF-PRUNING*) 基因调控植株的有限型生长习性, 其与金鱼草 *CEN* (*CENRORADIALIS*) 基因和拟南芥 *TFL1* (*TERMINAL FLOWER 1*) 基因同源, 属于调控植物生长习性和开花的同一类基因。目前已报道了番茄 *SP* 基因家族 8 个成员 (*SP*、*SP9D*、*SP2I*、*SP3D*、*SP5G*、*SP6A*、*SIGI* 和 *SPGB*), 该基因家族能直接或间接调控番茄植株的生长习性, 影响其株形。对番茄 *SP* 家族基因结构特征、亲缘关系、表达特性以及株形调控功能等研究进展进行综述, 以期调控番茄生长习性, 获得紧凑型株系、实现均一化和现代机械化采收提供有效的技术支撑。

关键词: 番茄; *SELF-PRUNING*; 基因; 株形; 调控; 生长习性

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Advances in Research of the *SELF-PRUNING* Gene Family and Plant Architecture Regulatory Functions in Tomato

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Abstract: The *SELF-PRUNING* (*SP*) gene belongs to a class of genes that regulate plant growth habits and flowering, it has been found in tomato to regulate the determinate of growth habits. Furthermore, it is homologous to the *CENRORADIALIS* (*CEN*) gene in *Antirrhinum majus* L. and the *TERMINAL FLOWER 1* (*TFL1*) gene in *Arabidopsis thaliana*. At present, eight members of *SP* gene family (*SP*, *SP9D*, *SP2I*, *SP3D*, *SP5G*, *SP6A*, *SIGI*, and *SPGB*) have been reported. The studies have shown that the family genes should directly or indirectly regulate the growth habits and affect the shoot architecture of tomato plants. Therefore, in this paper, the research on the genetic structure features, genetic relationships, expression characteristics, and plant architecture regulation of the *SP* family in tomato is reviewed, in order to regulate for growth habits of tomato, obtaining compact strains, achieve homogenization and modern mechanized harvesting, and agronomic traits and provide effective technical support.

Keywords: tomato; *SELF-PRUNING*; gene; shoot architecture; regulatory; growth habit

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植物株形的多样性是基于两种基本分枝模型 (Bell & Hemsley, 1992) 变异的结果。一种是以金鱼草 (*Antirrhinum majus*) 和拟南芥 (*Arabidopsis thaliana*) 为代表的单轴分枝模型, 初级枝条顶端分生组织呈无限生长, 营养器官由侧芽产生, 但在开花诱导后其营养器官被侧生的生殖器官取代, 并且叶腋发生的侧枝也表现出生殖功能, 在营养生长与生殖生长阶段之间有明显的区别, 所以该模式表现出明显的顶端优势, 主干粗壮而挺直。另一种是以番茄 (*Solanum lycopersicum*) 为代表的合轴分枝模式, 其根据茎顶端形成的花穗情况, 分为有限生长与无限生长两种类型。有限生长类型, 又称为自封顶型, 植株产生 2 ~ 3 个花穗后, 花穗下方腋芽分化形成花芽, 不再长成侧枝, 主轴停止生长, 整个植株不再向上生长, 通常表现为植株矮小、熟性早、成熟期集中、产量相对较低 (斋藤隆和片冈节男, 1981; 徐鹤林和李景富, 2007; 李景富 等, 2011; 毛秀杰 等, 2018)。无限生长类型, 植株长至第 6 ~ 12 片真叶时, 主茎顶端分生组织停止营养生长, 分化为花的分生组织, 形成第 1 个顶花穗 (焦志成, 2018), 主茎通过侧枝继续生长, 一系列的侧枝连接在一起形成合轴主茎, 每个侧枝产生 3 片叶和 1 个顶花穗, 这样重复多次循环呈规律性地向上生长形成复合主枝 (Atherton & Harris, 1986; Samach & Lotan, 2007), 整个植株高大, 生长期长。番茄作为典型的合轴分枝模型植物, 同时具有有限生长和无限生长两种类型, 这两种类型在生长期、成熟期和产量等方面具有明显不同 (Kinet, 1977)。因此, 对于番茄生长习性的研究一直受到关注, 近年, 对调控番茄生长习性的相关基因研究取得了新的进展。

番茄 SP (*SELF-PRUNING*) 基因家族调控着植株的生长习性。对番茄 SP 基因家族成员构成、结构特点、基因表达模式及其功能差异进行了综合论述, 阐明了其家族成员之间相互关系, 以及不同物种间同源基因的进化关系, 为深入研究其对植株生长习性的调控机理, 以及在番茄株形改良中的应用提供理论依据。

1 番茄 SP 基因家族及同源基因进化分析

1.1 番茄 SP 同源基因家族进化分析

尽管合轴分枝模式植物番茄与单轴分枝模式植物金鱼草和拟南芥的分枝方式存在很大差异, 调控番茄分生组织由营养生长到生殖生长转换的开关基因 (Carmel-Goren et al., 2003) 与调控金鱼草和拟南芥顶端分生组织呈无限生长的基因属于同一家族基因, 且亲缘关系较近。金鱼草 *CEN* (*CENRORADIALIS*) 基因 (Bradley et al., 1996a, 1996b, 1997) 与拟南芥 *TFL1* (*TERMINAL FLOWER 1*) 基因均能调控顶端分生组织进行无限生长 (Shannon & Meeks-Wagner, 1991; Bradley et al., 1996a; Wickland & Hanzawa, 2015)。目前报道的拟南芥 *TFL1* 基因有 6 个家族成员: *TFL1*、*FT*、*MFT* (*MOTHER OF FT AND TFL1*)、*ATC* (*ARABIDOPSIS THALIANA CENTRORADIALIS HOMOLOG*)、*TSF* (*TWIN SISTER OF FT*) 和 *BFT* (*BROTHER OF FT AND TFL1*) (Schoentgen & Jolles, 1995; Ohshima et al., 1997; Amaya et al., 1999; Kardailsky et al., 1999; Kobayashi et al., 1999; Lee et al., 2008; Lee & Lee, 2010; Blumel et al., 2015)。拟南芥另一类转录因子编码基因 *CO* (*CONSTANS*) 与 *FT* 基因的表达十分密切, 也为同一类家族基因 (Fornara et al., 2009; Tiwari et al., 2010; Song et al., 2012)。辣椒 (*Capsicum annuum* L.) 作为番茄的同科植物, 在其克隆的 *CaSP* 基因 (Dong et al., 2006; Elitzur et al., 2009) 与 *SP* 同源, 而且发现辣椒 *CaSP* 同源基因较番茄 *SP* 调控更加明显 (Jeifetz et al., 2011; Cohen et al., 2012)。另外, 在禾本科植物水稻 (Chardon & Damerval, 2005)、玉米 (Danilevskaya et al., 2008)、高粱 (Paterson et al., 2009) 和谷子 (Bennetzen et al., 2012) 中发现的 PEBP

(phosphatidylethanolamine-binding protein) 家族基因, 以及棉花中发现的 5 个 *TFL1* 同源基因, 包括 *SELF-PRUNING GhSP*、2 个 *TFL1-like* 和 2 个 *BFT-like* (*BROTHER OF FT-like*) 基因 (Prewitt et al., 2018) 等, 均属于一类同源家族基因。

笔者从 NCBI 数据库 (<http://www.ncbi.nlm.nih.gov/>) 和茄科基因组数据库 (<http://solgenomics.net/>) 中检索了番茄 (*Solanum lycopersicum/S. pennellii*)、辣椒 (*Capsicum baccatum/C. chinense/C. annuum/C. frutescens*)、甜瓜 (*Cucumis melo*)、小米 (*Setaria italica*)、水稻 (*Oryza sativa japonica/O. brachyantha*)、玉米 (*Zea mays*) 和高粱 (*Sorghum bicolor*) 的 SP 同源蛋白序列, 以及拟南芥 (*Arabidopsis thaliana/A. lyrata*) *FTL1*、*CO*、*FT* 蛋白序列和金鱼草 (*Antirrhinum majus*) *CEN* 蛋白序列, 共计 25 个蛋白序列, 利用 MEGA 7.0.26 软件 (<http://www.megasoftware.net/>) 邻接法进行聚类分析, 并构建系统进化树 (图 1)。这些蛋白分为 5 组, 中国辣椒和浆果状辣椒 SP 蛋白单独聚为一类 (Group 5)。其中番茄 SP 蛋白家族分属于 4 个组, 普通番茄 SP2G、SPGB 和 SIG1 与琴叶拟南芥转录因子编码蛋白 *CO* 归为一组 (Group 1), 除 SP2G 外, SPGB、SIG1 和 *CO* 蛋白均属于一类响应调节蛋白; 普通番茄 SP5G、SP6A、SP3D、SFT 与拟南芥 *FT* 和 *TSF* 蛋白聚为一组 (Group 2), 其中 *FT* 与 *SFT* 蛋白同源; 普通番茄、潘那利番茄 SP 和一年生辣椒、灌木状辣椒 SP 蛋白与金鱼草 *CEN* 蛋白聚为一组 (Group 3), 表明属于同茄科的番茄和辣椒 SP 蛋白结构相似, 亲缘关系相近, 并且可与金鱼草 *CEN* 蛋白共同进行研究探讨; 普通番茄 SP9D 与拟南芥 *TFL1* 以及禾本科 SP 蛋白聚为一组 (Group 4)。对番茄 SP 蛋白家族进行聚类及进化关系的分析, 可为进一步研究番茄 SP 基因家族提供有效的参考依据。

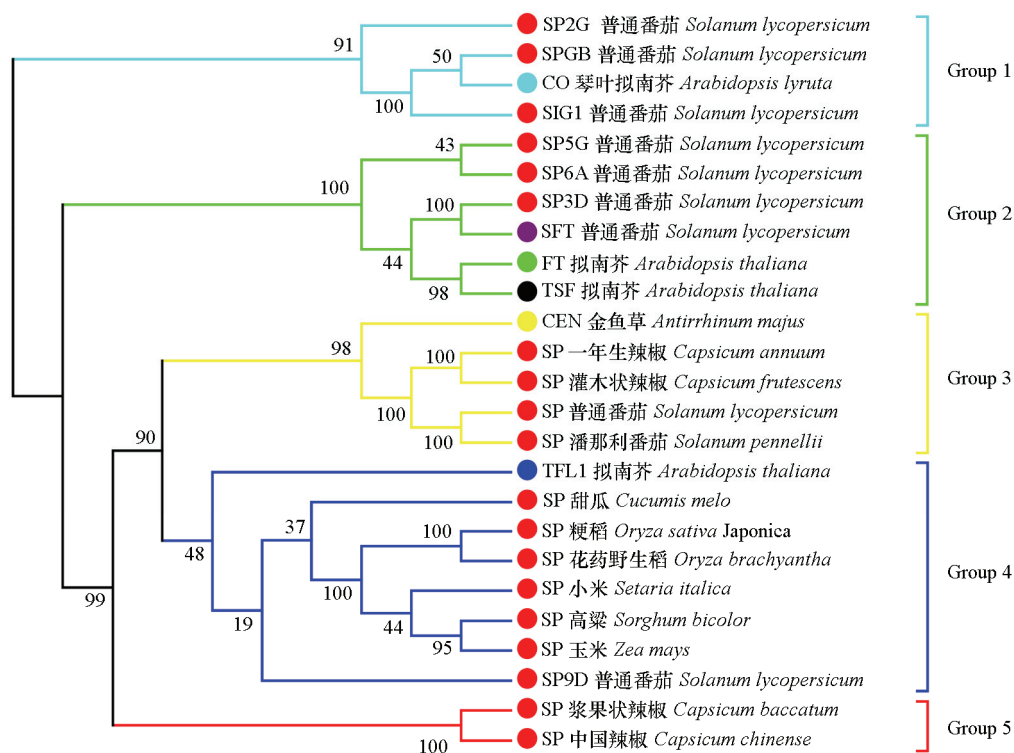


图 1 番茄 SP 与同源家族蛋白系统发生树分析

Fig. 1 Phylogenetic analysis of SP in tomato and homologous family proteins in other species

1.2 番茄 SP 基因家族成员进化分析

1998 年, 番茄 *SP* 基因被克隆, 且精细定位于 6 号染色体上 (Pnueli et al., 1998), 全长 2 267 bp, CDS 蛋白质编码区包含 175 个氨基酸序列 (Aoki et al., 2010)。2001 年, Pnueli 等 (2001) 采用 *SP* 基因 cDNA 全长诱导活化野生型番茄茎尖 RNA 结构域筛选法获得 2 个 *SP* 互作蛋白 SIG1 (SP-interacting protein 1) 和 SPGB (SP G-box protein), 并利用 Swiss-Prot 数据库经过同源序列比对构建了 *SP* 基因的三维蛋白结构模型。Carmel-Goren 等 (2003) 通过构建 26 个不同 cDNA 文库, 利用拟南芥同源基因 *TFL1*, *FT* 和 *MFT* cDNA 探针技术对番茄 *SP* 基因家族的 6 个成员 *SP*、*SP9D*、*SP2I* (*SP2G/MFT*)、*SP3D* (*SFT*)、*SP5G* 和 *SP6A* 进行鉴定, 并成功克隆, 分别精细定位于番茄 6、2、3、5、6 和 9 号染色体上。目前已经发现番茄 *SP* 基因家族成员 8 个, 包括 *SP*、*SP9D*、*SP2I* (*SP2G/MFT*)、*SP3D* (*SFT*)、*SP5G*、*SP6A*、*SIG1* 和 *SPGB*。

笔者从 NCBI 数据库和茄科基因组数据库中检索获得 8 个番茄 (*Solanum lycopersicum*) *SP* 基因家族成员基因序列, 并利用 MEGA 7.0.26 软件邻接法和 GSDS 2.0 在线软件 (<http://gsds.cbi.pku.edu.cn/>) 进行聚类及基因作图 (图 2), 发现 *SIG1* 不含内含子, 由 5'、3' 两端 UTR 和一段 CDS 区构成; *SPGB* 由 3 个 CDS、2 个内含子和 3' 端 UTR 区构成, 5' 端没有 UTR 区; *SIG1* 和 *SPGB* 聚在一起, 亲缘关系较近。其余 6 个基因 (*SP3D*、*SP6A*、*SP5G*、*SP*、*SP9D* 和 *SP2G*) 均由 4 个外显子和 3 个内含子构成。其中 *SP2G* 的 5' 端没有 UTR 序列, 3 个内含子区域较另外 5 个基因 (*SP3D*、*SP6A*、*SP5G*、*SP* 和 *SP9D*) 长, 单独聚为一类; *SP6A* 和 *SP9D* 的 5' 和 3' 端均没有 UTR 序列, 但亲缘关系较远, 而 *SP9D* 与 *SP* 聚为一类, 表明二者亲缘关系较近; *SP3D*、*SP5G* 和 *SP* 包含完整的两端 UTR 区、4 个外显子和 3 个内含子, 但并未聚在一起, 而是 *SP3D*、*SP6A* 和 *SP5G* 聚为一类; *SP3D* 较以上基因包含很长的 2 个内含子区域, 结构差异明显 (Shalit et al., 2009, Krieger et al., 2010)。

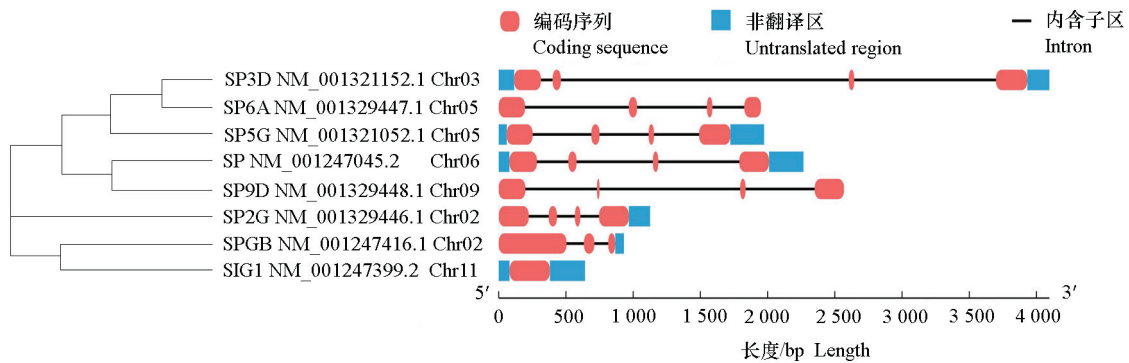


图 2 番茄 SP 基因家族同源关系及结构

Fig. 2 Homologous relationship and structure analysis of SP gene family in tomato

2 番茄 SP 基因家族的表达

番茄 *SP* 基因家族 8 个成员中, 因结构不同, 在其表达功能上也存在明显差异。在野生的有限生长型纯合番茄材料中, *sp* 为隐性等位基因, 编码有限生长蛋白, 调控植株的有限型生长, 主要表现为番茄合轴茎逐渐变短, 产生两个连续的花穗后停止生长 (Martí et al., 2006; Thouet et al., 2008)。 *SP* 基因首先在幼苗期 2~3 叶时在茎尖和叶中表达, 之后在 8~10 叶时出现的第 1 个顶花芽和合轴

顶点分生组织、腋芽和花原基中表达, 另外, *SP* 基因在植株整个生长阶段产生的叶原基和花器官原基中均有表达 (Pnueli et al., 1998; Carmel-Goren et al., 2003); *SP3D* (*SFT*) 基因编码单花束调控蛋白, 调控番茄初生芽花期、合轴组织生长习性和花形态, 主要在花器官 (如茎尖、花瓣、子房和雌蕊) 中表达, 而在营养器官中的表达非常低, 尤其在根中不表达 (Lifschitz & Eshed, 2006; Krieger et al., 2010); *SP5G* 基因编码 SELF PRUNING 5G 蛋白, 主要功能为抑制番茄开花, 参与番茄光周期调控, 仅在子叶和叶片中表达 (Carmel-Goren et al., 2003; Soyk et al., 2017), 且在植株形成第 1 花穗 (8 ~ 9 叶) 前叶中表达量最高 (Shalit et al., 2009); *SP6A* 基因编码一类开花位点蛋白, 在植株发育的各个阶段并未检测到表达情况 (Carmel-Goren et al., 2003); *SP9D* 基因仅在营养器官 (根、茎和茎尖) 表达 (Fridman et al., 2002); *SP2G* (*MFT*, *SP2I*) 基因的表达较为特别, 在植株整个发育组织器官中均被检测到 (Aoki et al., 2010), 可能参与合轴组织生长习性的调控; *SIG1* 基因编码 *SP* 基因的响应蛋白, 通过与 *SP* 蛋白互作调控番茄株形结构及花期 (Pnueli et al., 2001); *SPGB* 基因编码的蛋白包含 1 个特殊的 G-box (CCACGTGG) 结合蛋白结构域 (Giuliano et al., 1988; Menkens et al., 1995), 通过磷酸化/去磷酸化方式 (Harter et al., 1994) 参与 *SP* 蛋白互作, 进而调控番茄花期, 主要在开花前期的叶和顶芽中表达 (Pnueli et al., 2001; Lifschitz et al., 2006)。

3 番茄 *SP* 基因家族对番茄株形的影响

植物株形是通过侧枝、节间生长和茎封顶来维持植株有限生长和无限生长的重要农艺性状 (王艳芳, 2006; Wang & Li, 2008; 周慧, 2015), 也是增产增收非常重要的因素 (冯辉 等, 2008; 鲁博 等, 2008)。目前对株形性状的研究已有诸多发现。在番茄 (Pnueli et al., 1998) 和普通豆类作物 (Repinski et al., 2012) 中植株茎的自封顶生长是自然驯化导致的。番茄 *sp* 基因调控植株有限生长, 使得主茎缩短, 植株变得紧凑, 花期提前, 果实提早成熟 (Samach & Lotan, 2007)。*SP* 基因抑制番茄植株开花, 过表达 *SP* 后会延长合轴茎的营养生长, 花穗的部分花被叶取代, 使得花穗间叶片和花穗枝条本身的叶片数量增加, 抑制营养生长向生殖生长转变, 植株整体变矮且叶片浓密 (Pnueli et al., 1998; Carvalho et al., 2011); 而将野生无限生长型番茄 *SP* 基因突变后, 突变体 *sp* 植株花期提前, 合轴茎的叶片数也逐渐减少, 主茎缩短, 并最终出现两个连续的花穗而停止生长, 使得植株由无限生长转变为有限生长 (Marti et al., 2006; Kobayashi et al., 2014; Lifschitz et al., 2014), 且整个植株果实成熟期提前 (Yeager, 1927; Pnueli et al., 1998; Samach & Lotan, 2007), 该突变体植株已被广泛应用于番茄育种中 (Samach & Lotan, 2007)。因此, 在番茄生长发育阶段 *SP* 基因对株形的影响起到不可或缺的作用。

SP3D 与拟南芥 *FT* 基因同源, 为成花素基因, 参与植株花期调控, 影响植株构型。将 *SP3D* 基因功能缺失后, 花期延长, 而其双突变体表现花穗、花和果实减少, 株形变大; 利用双突变杂合有限生长型番茄 (*sp/sp*) 材料对 *SP3D* 基因功能缺失后, 植株叶片、花穗以及每一花穗花的数量均明显增多, 增产 60% 以上 (Krieger et al., 2010; Jiang et al., 2013), 但利用双突变纯合有限生长型番茄 (*sp/sp*) 材料对 *SP3D* 基因功能缺失后, *sp3d* 突变体植株产生无限生长型花穗, 果实产量下降 (Molinero-Rosales et al., 2004; Lifschitz et al., 2006; Shalit et al., 2009); 利用有限生长型番茄材料 Micro-Tom 构建的杂合 *sp3d* 突变体 (*sft/+*), 植株株形较单突变体 *sft* 矮, 花期提前, 果实产量明显增加 (Thouet et al., 2012; Vicente et al., 2015), 表现亚有限生长型株系 (Fridman et al., 2002; Carmel-Goren et al., 2003; Krieger et al., 2010)。另外, 通过 *SP* 和 *SP3D* 的位置比率分析发现, *SP3D*

能促使提前开花, 而 *SP* 调控植株的有限型生长 (Park et al., 2014), 所以 *SP/SP3D* 基因结构模型是增加作物产量和改善植株构型的有效目标组合 (McGarry & Ayre, 2012; Zsögön et al., 2017)。

SPGB 和 *SIG1* 基因作为一类 *SP* 蛋白互作调控响应因子, 对番茄株形也起到非常重要的作用。通过对番茄 *SPGB* 基因的突变体株系 *ssp* (*suppressor of sp*) 分析发现, 植株花期推后 (Park et al., 2014), 进一步通过酵母杂交试验表明 *SPGB* 蛋白与 *TFL1*、*FT* 和 *SP* 蛋白间均有互作关系, 而且 *SP3D* 也与 *SP* 和 *SPGB* 蛋白间互作, 三者共同调控番茄植株花期、植株结构和果实产量 (Lozano et al., 2009; Jiang et al., 2013); 过表达 *SIG1* 基因会部分恢复功能缺失突变体 *sp* 的表型, 与 *SP* 基因互作共同调控番茄的植株构型 (Pnueli et al., 2001)。

SP5G 基因调控番茄光周期敏感性, 能使植株增高而延迟开花, 相邻花穗间的叶节间数量增多, 是影响植株生长习性重要的调控基因。*SP5G* 功能缺失后, 植株失去光周期敏感性, 花期明显提前 (Soyk et al., 2017; Cao et al., 2018)。但对 *SP5G* 和 *SP* 基因进行双突变后, 番茄植株果实成熟明显提前, 且株形矮化变为紧凑株形, 较 *sp* 突变体植株更加紧凑, 有助于提高番茄产量 (Soyk et al., 2017; Zhang et al., 2018)。另外, 利用有限生长型番茄 (*Solanum pennellii*) 材料对 *SP5G/SP9D* 基因进行双突变后, 会导致突变体植株茎节间伸长, 相邻花穗间叶节间数增多, 主茎封顶时间延长 (Fridman et al., 2002; Jones et al., 2007); 含纯合 *spsp* 基因有限型株系与含杂合 *SP9D* 基因的株系杂交后代表现为亚有限生长型株系, 而含纯合 *spsp* 基因与纯合 *sp9dsp9d* 基因株系杂交后代则表现有限生长型株系 (Fridman et al., 2002), 从而说明 *SP9D* 与 *SP* 基因共同参与番茄生长习性的调控, 影响其株形。对于 *SP6A* 和 *SP2G* 基因对番茄株型影响的细致研究还未见报道, 但从番茄 *SP* 基因家族同源性可预测 *SP6A* 和 *SP2G* 基因有可能与其他成员进行互作调控, 共同调控番茄生长习性。

此外, 近期的研究表明, *sp* 突变体使得离体的下胚轴向地性弯曲和伸长, 可改变生长素的极性运输以及响应机制, 同时游离的生长素水平和生长素基因表达模式也被改变, 表明 *SP* 蛋白可以通过影响生长素转运和响应机制来影响番茄部分生长习性 (Silva et al., 2018)。番茄的自封顶现象在农业生产中十分重要, 可将多年生作物驯化培育为一年生作物, 大大缩短生产周期, 提早果实上市。并且, 培育矮化株形好的番茄品种, 可适用于加工番茄的大田栽培机械采收 (Rick, 1978; Atherton & Harris, 1986; Stevens & Rick, 1986), 大大提高生产效率。

4 展望

近年来有关番茄 *SP* 家族基因相关的研究受到重视, 利用番茄 *SP* 同源基因调控作物株型的相关报道陆续增多, 如辣椒 (Jeifetz et al., 2011; Cohen et al., 2012; Qin et al., 2014)、水稻 (Harter et al., 1994; Mayu et al., 2002) 和棉花 (McGarry et al., 2016; Prewitt et al., 2018; Si et al., 2018) 等。其中, 对棉花植株的株形结构研究较多, 着重研究 *CETS* (*CENTRORADIALIS/TERMINAL FLOWER I/SELF-PRUNING*) 家族基因, 通过调控无限生长和有限生长间的平衡来影响植株的株形结构 (Prewitt et al., 2018; Si et al., 2018), 进而提高棉花产量和采收一致性。另外, 番茄 *sp* 突变体与 *sft*、*sp5g* 突变体杂交组合表现出较好的农艺性状, 但 *SP* 蛋白是如何具体与 *SFT*、*SP5G* 蛋白之间互作的, 调控通路以及互作机理, 目前尚不清楚。番茄 *SP* 家族基因与植物激素间的调控关系目前报道还很少, 外界环境的调节作用如何综合影响 *SP* 基因的表达等, 都是亟需深入研究解决的问题。相信, 通过上述问题的进一步研究, 对番茄株形改良、培育轻简化品种, 实现均一化和现代机械化采收方面将会带来积极的作用。

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