科学通报 2022 年 第 67 卷 第 33 期: 3964 ~ 3975

进 展

《中国科学》杂志社
SCIENCE CHINA PRESS

植物TCP转录因子研究进展

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2022-04-25 收稿, 2022-06-28 修回, 2022-06-29 接受, 2022-06-30 网络版发表
国家自然科学基金(31800504, 32000483)、中国农业大学生命科学实验教学中心能力提高项目和研究生教改项目(JG202209)资助

摘要 TCP(Teosinte branched1/Cycloidea/Proliferating cell factor)转录因子是植物特有的转录因子, 能够结合特定的启动子序列来调节其靶基因的表达水平. TCP为植物中保守和广泛存在的转录因子家族, 不同植物进化出多种方式精准调控其下游相关因子, 并且自身基因表达也被严格地调控. TCP不仅可以在植物根、茎、叶、花、果实和维管组织发育中起到重要调控作用, 还可以参与植物次生代谢、生物胁迫和非生物胁迫等重要生理学过程. 近年来, 有关TCP对植物生长发育调控机制的研究越来越多, 尤其是对上游调控因子及下游靶基因生物学功能的相关研究. 本文综述了TCP转录因子在维管组织发育、生命周期转变、植物逆境胁迫等过程中的调控机制, 以及miRNA-TCP、TCP与染色质重塑等相互作用调控网络的最新进展. 最后, 对目前TCP研究中存在的问题和未来的研究方向进行了讨论和展望.

关键词 TCP转录因子, 生物学功能, 逆境胁迫, 调控网络

在植物的整个生命过程中, 细胞代谢、组织形成、器官发育以及对不断变化的环境条件的适应都需要复杂而精确的基因表达调控. 转录因子与相应顺式作用元件之间的相互作用, 以及microRNAs(miRNAs)及其对靶基因的调控是转录和转录后水平上基因表达的主要决定因素.

转录因子(transcriptor factors, TFs)是植物中最重要的一类调节因子, 又称为反式作用因子, 是一种DNA结合蛋白, 在植物发育和响应非生物胁迫中起着重要的调控作用. TCP(Teosinte branched1/Cycloidea/Proliferating cell factor)转录因子是一类植物特有的转录因子家族. 目前, 在PlantTFDB(http://planttfdb.gao-lab.org/)数据库中, 已有149个物种鉴定出*TCP*家族基因[1]. 在高等植物中, *TCP*基因编码的蛋白分布数量逐渐增加, 且随着进化过程和分化过程, 基因的数量也逐渐增多, 例如在水稻(*Oryza sativa*)、玉米(*Zea mays*)和毛果杨(*Populus trichocarpa*)中都有大量*TCP*基因编码的蛋白[1~4]. 本文介绍TCP转录因子家族的系统分类, 并着重综述其功能及表达调控网络的最新进展.

1 TCP转录因子家族的系统分类及特点

TCP的名字由来自3个物种的3个基因的第1个字母组成, 即玉米中的*TEOSINTE BRANCHED 1*(*TB1*)、金鱼草(*Antirrhinum majus*)中的*CYCLOIDEA*(*CYC*)和水稻中的*Proliferating Cell Factor 1/2*(*PCF1/2*). *TCP*家族都含有非典型的碱性(basic)螺旋-环-螺旋(bHLH)结构[5](图1(a)), 根据其氨基酸序列的不同, 又被分为I和II两大类, 其中I类TCP的碱性区比II类TCP少4个氨基酸残基

引用格式: 唐羽翔, 高旭, 崔亚宁, 等. 植物TCP转录因子研究进展. 科学通报, 2022, 67: 3964–3975
Tang Y X, Gao X, Cui Y N, et al. Research advances in the plant TCP transcription factors (in Chinese). Chin Sci Bull, 2022, 67: 3964–3975, doi: 10.1360/TB-2022-0480

(图1(a)), 为PCF亚家族基; II类TCP根据碱性区和bHLH结构域氨基酸序列的不同, 进一步分为CINCINNATA (CIN)-like TCP(以下简称CIN)和CYC/TB1-like TCP(以下简称CYC/TB1)两类[11].

I类TCP编码蛋白结合序列为GGNCCCAC. 很早就有证据表明, PCF1/PCF2可以与增殖细胞核抗原(proliferating cell nuclear antigen, PCNA)基因调控序列结合[12]; TCP20能够通过结合CYCB1;1启动子改变细胞

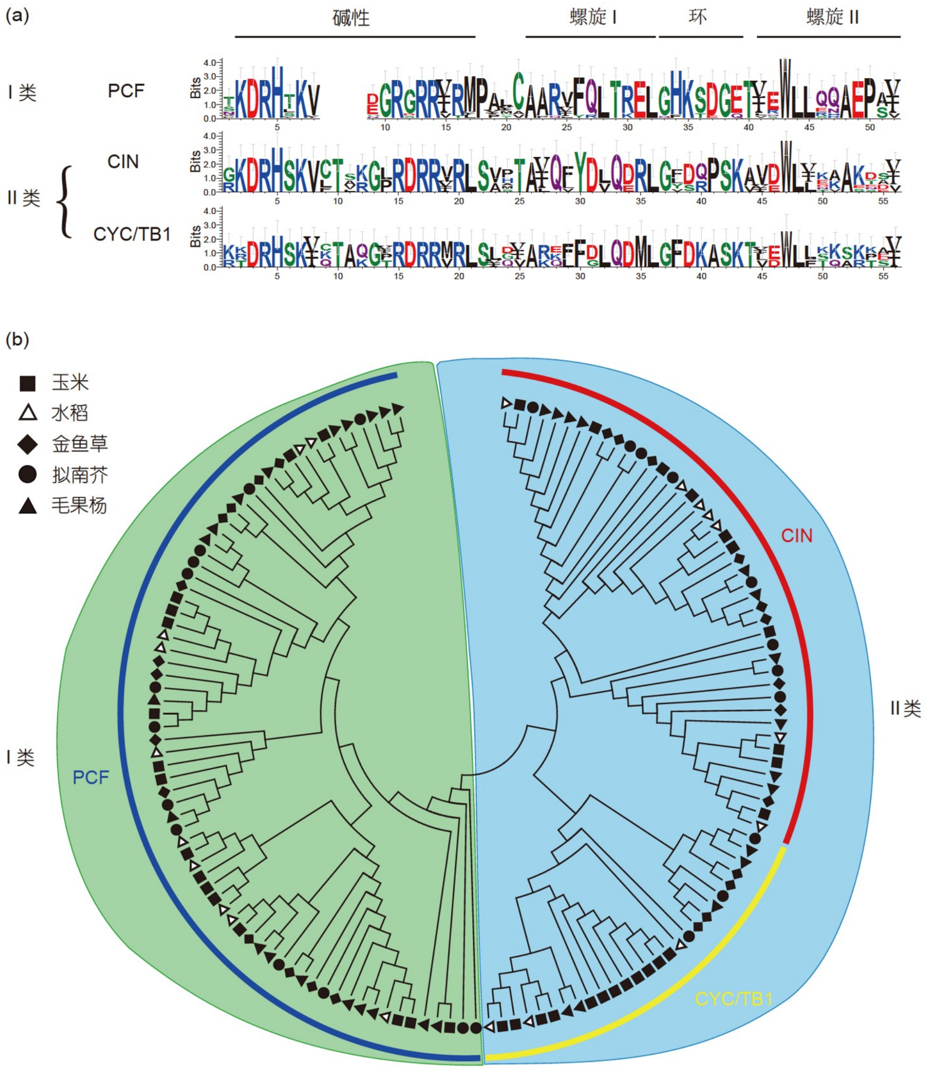

图 1 (网络版彩色)TCP蛋白家族的分类特征及进化关系. (a) TCP蛋白结构域序列标识图. 在拟南芥TCP结构域多序列比对的基础上, 使用WebLogo在线工具(http://weblogo.threeplusone.com/)[6]制作基因标识图. Bits代表比特分值, 表示序列中各个位置的信息含量. (b) TCP家族蛋白的系统发育关系. 无根系统发育树展示玉米(*Zea mays*)、水稻(*Oryza sativa*)、金鱼草(*Antirrhinum majus*)、拟南芥(*Arabidopsis thaliana*)、毛果杨(*Populus trichocarpa*)中TCP蛋白的进化关系. 其中金鱼草蛋白序列从Snapdragon Genome Database(http://bioinfo.sibs.ac.cn/Am/)下载[7], 其余物种蛋白序列来自PlantTFDB(http://planttfdb.gao-lab.org/)[1]. 使用HMMER[8]搜索TCP家族蛋白, 挑选$e<10^{-20}$的蛋白序列, 进而利用MEGA7软件[9], 通过邻接法构建系统进化树[10]. 仅使用TCP结构域进行分析

Figure 1 (Color online) The categorical feature and evolutionary relationship of TCP protein family. (a) Sequence logo of TCP domain. The sequence logo is generated by the Weblogo online tool (http://weblogo.threeplusone.com/)[6] based on the alignments of *Arabidopsis* TCP domains. Bits represents bit score, which indicates information content for each position in the sequence. (b) The phylogenetic relationship of TCP protein family. Unrooted phylogenetic tree shows the evolutionary relationship of the TCPs in *Zea mays* (*Zm*), *Oryza sativa* (*Os*), *Antirrhinum majus* (*Am*), *Arabidopsis thaliana* (*At*) and *Populus trichocarpa* (*Pt*). The protein sequence of AmTCPs is downloaded from the Snapdragon Genome Database[7] (http://bioinfo.sibs.ac.cn/Am/). TCP sequences of other species are downloaded from PlantTFDB (http://planttfdb.gao-lab.org/)[1]. HMMER[8] is used to search for TCPs, and $e<10^{-20}$ is chosen as a standard of compliant sequences. Then the phylogenetic tree is constructed using MEGA7 software[9] with Neighbor-joining method[10]. Note that only the TCP domains are used for the analysis

周期, 进而调节植物细胞增殖[13]. 此外, PCF还可以参与调控细胞生长、叶和花的发育等[14,15], 这一方面的研究将弥补之前对I类TCP基因作用机制探索的空缺. 由于I类TCP存在严重的基因冗余现象, 对I类TCP的研究并不如II类TCP充分[14,16,17], 但是近年来对I类TCP多基因突变体的研究正在丰富其功能机制的多样性.

II类TCP家族基因编码蛋白结合序列为G(T/C)GGNCCC[18]. CIN在植物叶形态[19~25]、根生长[26]、花瓣生长[27]以及花的对称形态形成等方面也都具有重要的调控作用[28~32]. *CIN*还具有加性效应和基因冗余现象[33], 这对开展这类转录因子的研究造成了困难. 此外, II类TCP中部分的CIN受到microRNA319的调控[34,35](表1).

为了明确了TCP家族的系统进化, 根据单子叶植物和双子叶植物中代表性模式植物TCP的蛋白序列, 我们构建了系统进化树. 从图1(a)可以看出I类和II类TCP, 以及不同类型II类TCP类型氨基酸序列的区别; 从图1(b)可以看出, TCP在多个物种都有分布, 并且基因多样性随着进化过程逐渐增加.

2 TCP转录因子参与植物发育调控

TCP家族蛋白主要在分生组织中调控植物的生长和发育过程, 以及各种生理生化反应的信号传导, 如维管组织的发育[26,37,38]、种子萌发和胚胎生长[35]、植物昼夜节律[55]等(图2).

2.1 TCP转录因子对维管组织发育的调控

TCP转录因子对维管组织发育有调节作用. Hou等人[50]对毛白杨(*Populus tomentosa*)的研究表明, *PtoTCP20*在茎和维管组织中的表达量高, PtoTCP20能够通过结合PtoWOX4a调控维管形成层细胞增殖, 并且通过激活*PtoWND6*的转录促进次生木质部细胞分化. 此外, NAC转录因子与TCP转录因子有着紧密联系, 既可以与TCP转录因子相互作用, 又可以作为其下游靶点, 共同参与植物维管组织发育调控. NAC(NAM、ATAF1/2和CUC2)转录因子包括SND1、NST1和NST2.

表 1 miR319参与调控的TCP家族蛋白及其生物学功能(改自文献[36])

Table 1 TCPs regulated by miR319 and their biological functions (modified from Ref. [36])

物种	靶基因	生物学功能	参考文献
拟南芥 (*Arabidopsis thaliana*)	*AtTCP24*	促进细胞壁木质化和次生细胞壁增厚	[37]
	AtTCP4	调控叶片细胞增殖	[38]
		调控茉莉酸生物合成, 加快叶片衰老	[39]
		调控叶片形态发生	[40]
		调控叶片成熟	[24]
		调控根发育	[26]
		调控花瓣宽窄	[27,41]
		木质部导管分化	[42]
		调控花瓣颜色	[43]
西伯利亚剪股颖(*Agrostis stolonifera*)	*AsPCF5*、*AsPCF6*、*AsPCF8*、*AsTCP14*	参与盐胁迫和干旱胁迫的应答	[44]
白菜(*Brassica rapa*)	*BrpTCP4*	调控白菜叶球形成	[45]
茶树(*Camellia sinensis*)	*CsTCP3*、*CsTCP4*	调控儿茶素生物合成	[46]
陆地棉(*Gossypium hirsutum*)	*GhTCP4*	促进棉纤维从细胞伸长到细胞壁增厚的转变	[47]
蒺苜蓿(*Medicago truncatula*)	*MtTCP3/4/10A/10B*	降低根瘤数量	[48]
毛白杨(*Populus tomentosa*)	*PtoTCP19*	调控毛状体形成, 提高昆虫防御能力	[49]
	PtoTCP20	调控次生维管组织发育	[50]
柳枝稷(*Panicum virgatum*)	*PvPCF5*	促进细胞壁生物合成, 提高生物量	[51]
番茄(*Solanum lycopersicum*)	*SlTCP3*	调控番茄的复叶发育	[52]
水稻(*Oryza sativa*)	*OsPCF5*、*OsPCF8*	提高低温驯化后的水稻幼苗耐冷性	[11]
	OsTCP21	负调控水稻分蘖数和产量	[53]
	OsPCF6/*OsTCP21*	增强水稻耐寒性, 提高活性氧清除能力	[54]

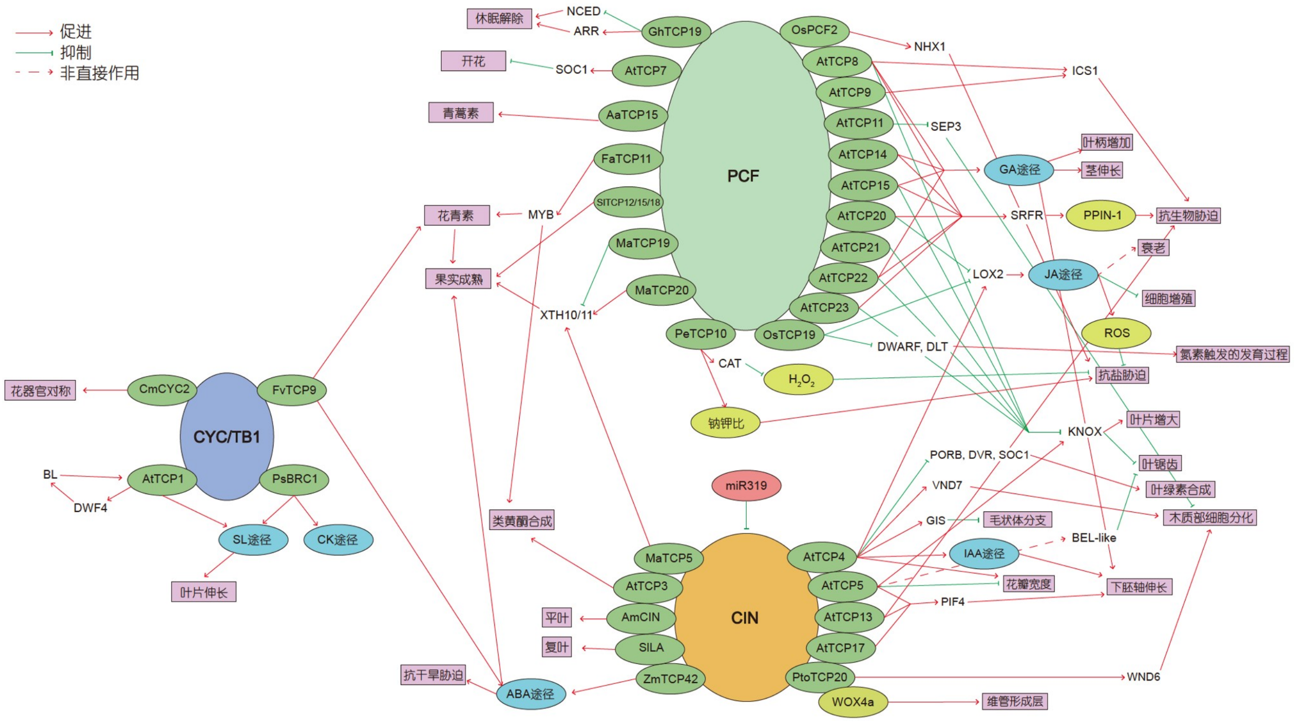

图 2 (网络版彩色)TCP转录因子的调控网络. TCP转录因子能够参与植物生长发育的各个方面, 在根、茎、叶、花、维管束等各个组织和器官的发育中起到重要作用. 此外, 其还能够直接或间接地参与调控植物次生代谢、抗逆境胁迫等多种重要的生理学过程. Am, 金鱼草; At, 拟南芥; Cm, 菊花; Fa, 草莓; Fv, 野草莓; Gh, 唐菖蒲; Ma, 小果野蕉; Os, 水稻; Pe, 毛竹; Ps, 豌豆; Pto, 毛白杨; Sl, 番茄

Figure 2 (Color online) Regulatory network of TCP transcription factors. TCP transcription factors can participate in all aspects of plant growth and development. They play an important role in the development of various tissues and organs, such as roots, stems, leaves, flowers and vascular tissues. Moreover, they can directly or indirectly participate in the regulation of plant secondary metabolism, resistance to stress and other important physiological processes. Am, *Antirrhinum majus*; At, *Arabidopsis thaliana*; Cm, *Chrysanthemum morifolium*; Fa, *Fragaria × ananassa Duch*.; Fv, *Fragaria vesca*; Gh, *Gladiolus hybridus*; Ma, *Musa acuminata Colla*; Os, *Oryza sativa*; Pe, *Phyllostachys edulis*; Ps, *Pisum sativum*; Pto, *Populus tomentosa*; Sl, *Solanum lycopersicum*

Koyama等人[56]对拟南芥的研究发现, AtTCP3能够抑制*CUC*基因的表达. 拟南芥TCP4与*VND7*的启动子结合而激活其表达, 激活次生细胞壁的生物合成, 从而调控各类木质部导管的分化[42,57]. 在拟南芥中, miR319过表达导致茎中*TCP4*丰度降低和次生细胞壁形成减少, *TCP4*的过表达可以促进次生细胞壁形成, 并且*TCP*家族基因的表达量增加能够提高*VND7*的转录, 表明miR319介导的*TCP4*可能通过激活*VND7*转录进行而参与了木质部导管分化, 控制发育过程中次生细胞壁形成[42]. miR319还可以调控*AtTCP4*的转录表达, 进而影响根的发育[26]. 此外, 拟南芥*TCP11*可能通过*SEP3*和*VND7*等下游基因, 参与了拟南芥维管束后生木质部导管分子的分化和形成[58].

2.2 TCP转录因子对植物叶形态及附属物形成的调控

TCP转录因子可以通过直接调控叶发育相关基因、miRNA、植物激素等参与叶形、叶片大小等的调控. AtTCP5、AtTCP8、AtTCP15、AtTCP21、AtTCP22、AtTCP23可以通过KNOX1通路调控叶的发育[17,21]. AtTCP5与BEL-like转录因子共同调节叶边缘形态[21]. Alvarez等人[59]研究发现, 拟南芥中NGATHA (NGA)与TCP有很强的功能冗余, 能够在叶片发育的多个阶段共同表达, 例如TCP3、TCP4、NGA1和NGA4在幼叶的远端表达, 将拟南芥叶分生组织的活动逐渐限制在边缘和基部区域, 它们的缺失会使子叶、叶片和花器官持续边缘生长. 另有研究报道, AtTCP4通过激活一种毛状体分支的负调控基因*GIS*来抑制叶片表面毛状体的分支[60]. 除此之外, 最新的研究表明, TCP4可以与GLABRA3(GL3)相互作用进而调控子叶毛状体的发育[61,62].

在拟南芥中, *AtTCP4*的mRNA为miR319的靶点之一, 受到miR319的调控, 对叶形态及叶发育起到重要作用[59,61]. 在番茄(*Solanum lycopersicum*)中, *LANCEOLATE*(*LA*)编码一个受miR319调控的CIN类TCP转录因

子. 在*La*缺失突变体中, 野生型的复叶变为单叶[52]. 在金鱼草中*cin*基因突变导致叶片由平叶向皱叶转化, 可能是幼叶中CIN通过改变细胞对阻滞信号的反应发挥作用, 进而调节细胞周期基因表达, 最终导致表达CIN的区域比不表达CIN的区域过度生长[63].

TCP能够参与多种植物激素途径调控叶片生长、叶片形态, 如生长素(3-indoleacetic acid, IAA)、细胞分裂素(cytokinin, CK)、茉莉素(jasmonate, JA)和独角金内酯(strigolactone, SL)等. 金鱼草的研究表明, *CIN*的缺失会导致叶边缘卷曲[19]. 此外, TCP可以通过IAA和CK途径调控叶片发育时的细胞增殖和分化[20]. 拟南芥*CIN*也有同样的功能[22]. AtTCP4和ATP酶BRAHMA(BRM)一同促进CK相应途径中抑制因子*AtARR16*的表达, 从而调控叶片的成熟[24]. Danisman等人[64]研究发现, JA合成基因*AtLOX2*是AtTCP20和AtTCP4的共同靶点, TCP20能够抑制*AtLOX2*表达, 而AtTCP4激活其表达, 并以此提出了基于TCP转录因子功能拮抗的JA控制叶片发育模型. 随着AtTCP4增加, 在叶片发育的后期, *AtLOX2*的表达量增加, JA的产量也随之增加. 在叶片发育的不同时间点, 叶片中JA含量的增加抑制了细胞增殖并诱导叶片后期衰老. 另有研究表明, *Attcp1*无义突变体的叶片长宽比较野生型更小, 且*TCP1*的表达在GR244DO(一种人工合成SL)处理后以D14(SL受体)依赖的方式被诱导, 表明TCP1可以介导SL调控叶片伸长的生理过程[65]. 在豌豆(*Pisum sativum*)中的研究发现, *Psbrc1*突变体表现出地上部分多分枝的表型, *PsBRC1*基因主要在腋芽中表达, 分别施加GR24(一种人工合成的SL)和CK能够促使其上调或者下调表达, 表明*PsBRC1*可能在SL和CK信号中发挥作用, 而SLs直接作用于腋芽内调控其生长[66].

2.3 TCP转录因子对植物花形态的调控

TCP转录因子对花的对称性发育、花瓣发育、花瓣颜色都有影响. 许多研究表明, CYC/TB1在形成花的对称形态方面起到重要作用[28~32]. Yuan等人[32]运用酵母双杂交实验以及BiFC实验证明, 菊花中CmCYC2-CmCYC2d、CmCYC2b-CmCYC2e、CmCYC2c-CMCYC2d蛋白之间可以形成异源二聚体, 并且运用酵母单杂交实验以及双荧光素酶报告基因检测证明, CmCYC2c可以与*CICYC2f*的启动子结合, 暗示着CmCYC2类的转录因子可能通过相互结合以及与启动子结合来调控菊花花器官的对称发育. 另外, CIN也对花瓣发育有影响, 例如, 拟南芥中*tcp5*缺失突变体比野生型有更宽的花瓣[67]. 与叶片形态调控类似, 受miR319调控的*AtTCP4*在花瓣发育过程中也起到关键作用. 研究表明, miR319a功能缺失的突变体花瓣比野生型窄, *AtTCP4*过表达则可以回补此表型[27,41].

TCP转录因子除了可以调控花的形态, 也影响开花时间. 拟南芥中, *tcp4*功能缺失突变体比野生型开花晚, 而*TCP4*过表达突变体(*TCP4:VP16-C*)较野生型开花早[68]. 进一步的研究表明, TCP4与PHYTOCHROME AND FLOWERING TIME 1(PFT1)结合激活转录因子*CONSTANS*(*CO*)转录, 促进拟南芥开花[69]. 此外, TCP7可以与CO和Nuclear Factor-γs(NFγs)相互作用激活*SOC1*表达以促进拟南芥开花[14].

最新的研究表明, 拟南芥TCP4可以通过抑制叶绿素合成调控花瓣颜色和花瓣颜色分布[43]. TCP4可以与叶绿素合成关键基因*PORB*、*DVR*以及正调控叶绿素合成*SOC1*的启动子区结合, 并抑制这些基因表达, 进而抑制绿色花瓣的形成[43].

2.4 TCP转录因子对植物果实发育的调控

TCP转录因子参与果实的成熟过程. 有研究报道, 柑橘(*Citrus reticulata*)全基因组共有编码20个TCP转录因子家族成员基因, 分别为*CsTCP1*~*CsTCP20*, 通过对不同组织、不同发育时期表达量分析, *CsTCP2*的表达量在果实中最高, *CsTCP5*、*7*、*8*、*10*、*11*、*15*~*17*的表达在野生型柑橘与晚熟突变体成熟期也具有明显差异, 表明TCP可能参与柑橘果实的成熟过程[70]. 另外, 在野草莓(*Fragaria vesca*)中, *FvTCP9*转录本积累水平在果实中很高, 其通过调节脱落酸(abscisic acid, ABA)信号转导相关基因(如*FaNCED1*、*FaPYR1*、*FaSnRK2*和*FaABI5*)的表达并与FaMYC1相互作用来调控花青素的合成, 促进果实成熟[71]. 小果野蕉(*Musa acuminata*)中, MaTCP20能够与MaTCP5结合形成二聚体, 促进*XTH10/11*(木葡聚糖内糖基转移酶/水解酶)的转录来使果实软化, 与MaTCP19结合形成异源二聚体抑制这种酶的转录[72]. 此外, 番茄中的研究也表明, SlTCP蛋白可能通过互相之间结合形成异源二聚体来参与调节番茄的生长发育[73].

2.5 TCP转录因子对植物发育的其他调控

TCP转录因子还可以参与茎伸长、休眠解除、温度感受等重要的生物学过程. Davière等人[74]对拟南芥

的研究发现，I类TCP转录因子与细胞周期相关基因直接结合，并且DELLA蛋白可以抑制TCP的作用. 此外，*tcp8tcp14tcp15tcp22*四突变体表现出极度矮化以及赤霉素(gibberellic acid, GA)不应的表型. 这些结果表明, I类TCP可以通过介导GA信号来调控植物高度[74]. 在唐菖蒲(*Gladiolus hybridus*)中的研究发现, GhTCP19通过抑制脱落酸(ABA)合成基因*GhNCED*的表达并且促进CK合成基因*GhIPT*以及信号转导基因*GhARR*来正向调控球茎休眠解除[75]. 近期，在马铃薯(*Solanum tuberosum*)中的研究表明，StBRC1b可以通过促进ABA信号转导, 使胞间连丝数量减少, 以抑制蔗糖和块茎化因子SP6A向芽中运输，进而促进气生腋芽的休眠而抑制块茎形成[76]. 研究人员通过对油菜素内酯生物合成中间体的定量分析(BR profile assay)，以及实时荧光定量PCR(quantitative real-time polymerase chain reaction, qRT-PCR)和染色质免疫共沉淀等实验，发现AtTCP1与BR合成关键基因*DWARF4*(*DWF4*)启动子中的两个GGNCCC基序互作, 调控*DWF4*的表达, 表明AtTCP1可以通过调节BR来调控植物生长和发育[77,78]. 在水稻中的研究表明，OsTCP19通过负调控对分蘖促进基因*DWARF*和*LOW-TILLERING*(*DLT*)的表达，来调控氮素触发的发育过程[79]. 另外，有研究报道，拟南芥转录因子AtTCP4对生长素合成限速酶编码基因光控*YUCCA5*表达是依赖的，在光信号通路与生长素调控下胚轴伸长过程中起着连接因子的作用[80].

3 TCP转录因子参与植物次生代谢物调控

TCP转录因子不仅可以参与调节植物的生长发育，而且在次生代谢物合成过程中起到重要的调控作用. 黄酮类化合物是多种多芳香族次生代谢产物，由一个15节碳骨架组成，是由苯基丙烷途径的一个分支形成. 目前有关TCP与苯丙烷代谢的研究主要集中在转录组分析方面[81]. 黄酮类化合物在植物中无处不在, 除了木质素和花青素，这些化合物通常与植物防御反应有关[82]. 在共生过程中, 植物分泌产生的类黄酮化合物多样性与决定根瘤菌反应的特异性有关[83]. Li和Zachgo[84]对miRJAW-resistant的*AtmTCP3*转基因植株和*AtTCP3*基因功能失活的*AtTCP3SRDX*突变体植株进行研究, 结果发现, *AtmTCP3*植物的幼苗和种子会过度积累黄酮醇、花青素和原花青素, 而*TCP3SRDX*植物中的原花青素水平略有下降，并且R2R3-MYB蛋白通过形成三元R2R3-MYB/bHLH(TCP3)/WD40(MBW)复合物激活晚期类黄酮生物合成基因，表明TCP具有促进类黄酮生物合成. 另外，草莓(*Fragaria* × *ananassa*) FaTCP11可能通过与MYB或bHLH家族转录因子互作，进而对草莓原花青素和黄酮醇的合成基因起到正调控作用[85].

4 TCP转录因子在植物逆境胁迫中的作用

4.1 TCP转录因子参与非生物胁迫过程

TCP家族基因可以通过调节细胞渗透压、改变细胞透性、减少有害物质和改变激素敏感性等方式，增加植物对逆境胁迫的响应.

OsNHX1是定位在液泡膜上最丰富的K^+-Na^+/H^+反向转运体，能够被盐、干旱和ABA所诱导. 转录因子OsPCF2能够结合*OsNHX1*的启动子, 并激活*OsNHX1*表达, 耐盐水稻(Hasawi)研究也表明, 经过盐胁迫处理后, OsPCF2在根中能够上调表达，表明其可能参与了耐盐[86].

干旱、高盐胁迫下，植物体内会产生如活性氧(reactive oxygen species, ROS)等有害物质, 对这类物质的清除是植物抵抗胁迫的一种重要调控方式. 在高盐条件下，与野生型拟南芥相比，转入*PeTCP10*的拟南芥通过促进过氧化氢酶(catalase, CAT)的活性来改善转基因拟南芥植物的抗氧化能力，并增强其对H_2O_2的耐受性[87]. 另外, 毛竹(*Phyllostachys edulis*)中的*PeTCP10*基因在拟南芥异源表达, 能够增加相对水含量, 减少电解质渗漏和Na^+积累[87]. 水稻*OsTCP19*在拟南芥异源表达, 能够减少植株失水和活性氧, 并且增加脂滴的积累, 最终提高转基因植株幼苗期和成熟植株的抗逆性[88]. 对于白桦(*Betula platyphylla*), BpTCP7转录因子可以通过清除活性氧，降低质膜损伤达到抗盐胁迫的生物学功能[89].

TCP也能够通过参与激素信号通路来调节植物的抗非生物胁迫能力. 譬如, 玉米中*ZmTCP42*在拟南芥中的过量表达改变种子萌发时对ABA过度敏感，进而增强其抗旱性[90]. 除此之外, TCP还可以参与对温度的响应调控机制. Zhou等人[91]发现, 低温条件下，蓝光受体AtCRYPTOCHROME 1(AtCRY1)能够与AtTCP17相互作用，降低AtTCP17的活性；相反，高温可以增加AtTCP17的稳定性，从AtCRY1-TCP17复合物中释放出来, 上调PHYTOCHROME-INTERACTING FACTOR 4 (PIF4)的表达，进而促进温敏性下胚轴的生长. 在高温

条件下，TCP14和TCP15能够与PIF4相互作用，诱导赤霉素生物合成以及植物生长相关基因的表达[91,92].

另外，有研究报道，黄花蒿(*Artemisia annua*)中AaTCP15转录因子能够参与JA和ABA双重响应调控，进而参与青蒿素生物合成[93].

4.2 TCP转录因子参与生物胁迫过程

在植物生长发育过程中，多样的病原菌能够对宿主造成严重的破坏，因此研究TCP参与调控生物胁迫过程十分重要．以往的研究已经鉴定出拟南芥TCP13能够与23个*Golovinomyces orontii*(*Gor*)、25个*Hyaloperonospora arabidopsidis*(*Hpa*)效应子和4个*Pseudomonas syringae*(*Psy*)效应子相互作用出现患病表型．相关家族成员TCP14、TCP15和TCP19能够被至少两个病原体的效应子所识别，表现出感染表型[94,95]．过量表达番茄(*Solanum lycopersicum*)*SlTCP14-2*能够增强植株对辣椒疫霉(*Phytophthora capsici*)的免疫，而SlTCP14-2与CRN12_997结合，又可以抵消这种免疫活性[96]．此外，拟南芥中I类TCP家族蛋白(TCP8、TCP14、TCP15、TCP20、TCP22和TCP23)与SRFR1(SUP PRESSOR OF rps4-RLD1)相互作用，调控SRFR1防御基因的表达，揭示植物发育与免疫调控机制[97]．在病原体攻击下，拟南芥*TCP8*及*TCP9*的表达模式与*Isochorismate Synthase 1* (*ICS1*)基本重叠．并且，在*tcp8tcp9*双突变体中，*ICS1*的表达量在免疫应答中显著降低．这些研究表明，TCP8和TCP9可能通过调节*ICS1*的表达来参与植物生物胁迫．TCP8和SARD1、WRKY28或NAC019之间，以及TCP8、TCP9和TCP20之间存在强烈相互作用，表明ICS1的表达有一个复杂的协调调节机制[98].

5 展望

TCP转录因子家族是一个植物特异性转录因子家族，通过结合特定的启动子序列来调节其靶基因的表达水平．TCP介导的调控模块在一个复杂的基因表达调控网络中发挥关键作用，并涉及植物生命过程中多个关键生物过程(图2).

在过去的几年中，对TCP转录因子的结构、生物学作用和分子机制有了一些了解：其可以通过与其他蛋白互作、结合增强子、调控染色质结构来调控基因表达，以影响植物生理和形态[62]．然而，以往关于TCP家族的研究主要集中在单一因素或单一途径，单个转录因子的过度表达可能促进或抑制大量下游基因，一个单一的基因可能受与其顺式元件结合的不同转录因子所调控，而且转录因子可能会对不同的逆境胁迫作出反应．面对植物中数以百万计的转录因子，如何在分子水平上对基因功能进行鉴定将是一个巨大的挑战[36].

此外，对TCP调控植物生长发育的分子机制、下游基因的分析以及其对环境适应的影响，目前还缺乏深入的研究，如TCP转录因子在植物免疫中的调控机制，有研究报道，TCP4作为miRNA的靶基因，可以与WRKY的启动子结合，直接激活与病原体相关的基因表达，提高芜菁(*Brassica rapa*)对茎腐病的抗性[99]；另有研究表明，WRKY转录因子与细胞周期相关基因CYCP3;1能够受到TCP的调节[100]．已有文献报道NAC、MYB等作为主要的调控因子直接诱导植物次生代谢物类黄酮类基因的表达，参与植物木质化的转录调控网络[101]，TCP与这些转录因子之间存在怎样的相互作用机制尚不清楚．因此，挖掘哪些基因是直接的TCP目标，WRKY-TCP、NAC-TCP等转录因子间相互调控，TCP对下游基因及miRNA的调控机制是什么，将是今后研究的一个重要方向.

TCP家族成员之间经常存在功能冗余，使得TCP因子的功能难以深入研究．尤其TCP蛋白质水平方面的调控机制尚不清晰．随着高分辨质谱技术的发展，非标记蛋白质组学技术成为研究植物细胞中蛋白质动态变化及其分子功能的重要技术手段[102]．因此，综合利用高通量测序技术、蛋白质组学技术和基因编辑等技术，全面系统地探讨TCP转录因子、TCP相关蛋白修饰在植物生长发育和胁迫响应中介导的转录调控网络及蛋白质层面的分子调控机制，将为作物遗传改良提供资源和方向.

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Summary for “植物TCP转录因子研究进展”

Research advances in the plant TCP transcription factors

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Transcription factors (TFs) are a group of protein molecules that can bind to a specific gene with a specific sequence specificity, thus ensuring that the target gene is expressed at a specific time and in space at a specific intensity. The plant-specific TFs of the TCP family (for Teosinte branched 1 in corn, CYCLOIDEA (CYC) in snapdragon (*Antirrhinum majus*) and PROLIFERATING CELL FACTOR 1/2 in rice) are characterized by an N-terminal non-canonical beta helix-loop-helix (bHLH) domain known as the TCP domain, and regulate the spatiotemporal expression of genes by binding to specific promoter sequences. TCP TFs play important roles in regulating the development of roots, stems, leaves, flowers, fruits, and vascular tissues, and participate in physiological processes such as plant secondary metabolism, plant immunity, and the responses to biotic and abiotic stress. The TCP TF family is conserved and widespread in plants. Based on the TCP domain sequence, TCP TFs are categorized into Class I and Class II; based on the amino acid sequence of the basic region and bHLH domain, the Class II TCP TFs can be further divided into CINCINNATA (CIN)-like TCPs (CIN) and CYC-like TCPs (CYC-C).

In recent years, increasing numbers of studies have shed light on how TCP TFs regulate plant growth and development, especially on the functions of upstream regulators and downstream target genes. Plants have evolved multiple ways to accurately regulate their downstream related factors, and their own gene expression is also strictly regulated. TCP genes have also been analyzed in various plants and found to take part in the regulation of circadian rhythms and the biosynthesis and signaling pathways of plant hormones, among other functions. Other studies have investigated the regulatory relationships between TCP TFs and microRNAs. Additionally, members of the TCP family are often functionally redundant, making it difficult to study their functions; therefore, gene-editing technology and high-throughput sequencing have opened up new avenues to study this TF family. Here, we summarize recent advances in our understanding of how TCP activity is translated to the dynamic spatiotemporal control of cell-fate determination, life-cycle transitions, dormancy release, seed germination, leaf development, outgrowth of shoot branches, growth-repressing microRNAs, and interactions with the chromatin remodeling machinery to modulate phytohormone responses. Furthermore, we discuss existing problems and future directions in TCP research, in particular the role of TCP-related protein modification in plant growth and development and stress responses. Finally, we provide perspectives on the future research that is needed to gain a deep understanding of the diverse regulatory networks of TCP TFs in plant growth and development.

TCP transcription factor, biological function, adversity stress, regulatory network

doi: 10.1360/TB-2022-0480