

植物叶缘锯齿调控的研究进展

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摘要: 叶片是植物重要的营养器官, 叶缘锯齿(裂刻)在生产实践中有多种优势, 叶缘锯齿调控研究对作物育种、生产实践具有指导意义。本文梳理了叶缘锯齿形成的调控机制, 植物激素、基因表达、miRNA等协同作用调控叶缘锯齿形成。生长素(Auxin)在叶缘的不平衡积累能促进锯齿产生, 细胞分裂素(CK, cytokinins)依赖Auxin在叶缘的积累促进叶形复杂度, 而赤霉素(GA, gibberellin)负调控叶形复杂度。归纳了植物激素与基因参与叶缘锯齿形成的3条主要作用通路: TCP-CUC-PIN1-Auxin, KNOX-GA/CK, LMI1-CK。miR164、miR319、polycomb group表观遗传修饰和 α -1,2糖基转移酶等也参与叶缘锯齿形成。研究表明环境因子温度和光强通过KNOX-GA通路调控叶片发育, 高温和低光强均能降低叶形复杂度。不同植物控制叶缘锯齿性状的遗传机制存在较大差异。叶缘锯齿相关基因发掘以经济作物研究较多, 未来果树育种应着手推进赏食兼用研究。

关键词: 叶片发育; 叶缘锯齿; 植物激素; 调控机制; 遗传机制

Research Progress on the Regulation of Leaf Margin Serration Development in Plants

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Abstract: Leaves are important vegetative organs in plants, and the leaf margin serration (lobe) has many advantages in production practice. Disclosing the regulation of leaf margin serration has important guiding significance for plant breeding. This article reviews the regulation mechanism of leaf margin serration formation. Several factors such as plant hormones, gene expression, and miRNAs, are involved with roles in shaping leaf margins. Auxin unbalanced accumulation at the leaf margin can promote serration. Auxin-dependent cytokinins (CK) accumulation at leaf margin might result in the leaf shape complexity, while gibberellin (GA) negatively regulates leaf shape complexity. This review further summarizes three main pathways of plant hormones and genes involved in leaf margin serration formation: TCP-CUC-PIN1-Auxin, KNOX-GA/CK, LMI1-CK. The miR164, miR319, polycomb group (PcG) epigenetic modification and α -1,2-glucosyltransferase are known to be involved in leaf margin serration formation. The ambient temperature and light intensity regulate the leaf margin development through the KNOX-GA pathway. For instance, high temperature and low light intensity might decrease the complexity of leaf shape. The different genetic mechanisms on the regulation of leaf margin

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serration in plants are revealed. The genes that modulate or associate with the leaf margin serration are often reported in cash crops. In addition to fruit quality and resistance, ornamental character is one task with significant interest in future breeding of fruit trees.

Key words: leaf development; leaf margin serration; plant hormones; regulation mechanism; genetic mechanism

叶片是植物进行光合作用、蒸腾作用和吸收作用的重要场所,可辅助植物营养和土壤养分情况诊断,且叶片形态特征也是植物分类的重要依据。叶片类型简单分为单叶和复叶2大类,叶缘锯齿(裂刻)很大

程度上丰富了叶形的多样性,不论单叶或复叶,叶缘可分为全缘、锯齿和裂刻,裂刻可视为锯齿的极端型。复叶可以有不同的数量和排列的小叶,多为羽状和掌状^[1],复叶可视为是单叶叶缘深裂的极端类型(图1)。



图1 自然界叶形多样性^[1]

Fig.1 The range of leaf shapes found in nature^[1]

叶缘锯齿是植物对环境的一种适应,在实际生产中具有多种优势^[2-3]:辅助区分品种,同时观赏价值高^[4-5];更强的空间延展,竞争光源优势,净光合效率高,利于密植^[6-7];影响比叶面积,提高通风透气性^[8];抵御高温,增强耐旱性^[9];抵抗水分胁迫^[10]和冷害胁迫^[11]。甜瓜(*Cucumis melo* L.)裂叶型表现出对原叶型更强的白粉病抗性,占用土地空间小,适合密植,提高单位面积产量^[12]。鸡脚叶棉(*Gossypium hirsutum* L.)叶片裂刻深、裂片狭窄,通风透光性好,创造不利虫害生长环境。鸡脚叶棉具有早熟,生殖生长优势强,单株结铃数高、籽棉质量高,形态、生态和生理生化抗性相叠加等优点^[13]。叶缘形态变化研究对深刻认识植物环境适应性、作物遗传改良、指导农业生产具有重要实践价值,众多影响因素被发现鉴定,本文对叶缘锯齿的调控机制(环境因子、植物激素、调控因子)和遗传机制相关研究成果进行了综述,系统梳理复杂的调控网络,为叶缘锯齿在作物育种和生产实践的应用研究提供参考。

1 调控机制

植物叶形发育存在多种调控机制,植物激素、

调控因子、环境因子之间形成了复杂的调节网络,协同作用叶缘锯齿形成。

1.1 植物激素和调控因子

基于前人研究基础,本文归纳了植物激素与基因参与叶缘锯齿形成的3条主要作用通路:TCP-CUC-PIN1-Auxin、KNOX-GA/CK、LMI1-like(RCO)-CK。此外,miR164、miR319、PcG表观遗传修饰、 α -1,2糖基转移酶等也参与叶缘锯齿形成(图2)。

1.1.1 TCP-CUC-PIN1-Auxin 通路 叶缘锯齿位置与生长素(Auxin)高度聚集点有直接关联,生长素聚集点细胞生长快形成叶缘锯齿尖端,生长素浓度低的位置形成叶缘凹陷^[14]。生长素输入转运基因家族AUX1/LAX参与生长素由细胞外向细胞内运输过程,拟南芥(*Arabidopsis thaliana* (Linn.) Heynh.) *aux1lax1lax2*三突变体由于生长素转运紊乱导致叶缘裂刻减少^[15]。生长素在叶缘的梯度分布由生长素极性运输蛋白PIN1(PIN-FORMED1)调控^[16-17],苜蓿(*Medicago truncatula* Gaertn.)PIN1同源基因SLM1(SMOOTH LEAF MARGIN1)突变体叶缘锯齿减少,SLM1功能缺失导致生长素在叶缘弥漫性分布,表明PIN1在保持苜蓿叶缘锯齿发挥作用^[18]。双特异性磷酸酶IBR5(INDOLE-3-BUTYRIC ACID

RESPONSE5)通过负调控 *PIN1* 表达影响叶缘锯齿发育, *IBR5* 功能缺失突变体由于增加细胞面积表现出明显的锯齿叶形^[19]。转录因子 *NAM*(*NO APICAL MERISTEM*)/*CUC*(*CUP-SHAPED COTYLEDON1*)是叶缘锯齿发育调控的重要节点,调控 *PIN1* 的极性定位,拟南芥、番茄(*Solanum lycopersicum* L.)和菊科蓍草(*Achillea alpina* L.)等植物的 *NAM/CUC* 基因表达下调,叶缘锯齿程度减少^[16, 20-22]。叶绿体翻译起始因子 *SVR9/IF3*(*SUPPRESSOR OF VARIEGATION9*)通过抑制 *CUC2* 表达活性,打破叶缘生长素的稳态

平衡调控叶缘发育^[23]。拟南芥中介导囊泡运输解聚过程的关键蛋白 *AtNSF*(*N-ethylmaleimide-sensitive factor*)通过抑制 *CUC2* 介导的反馈回路调控 *PIN1* 运输的生长素聚集影响叶片的锯齿发育, *AtNSF* 的缺陷引起拟南芥叶缘锯齿增多^[24-25]。近期研究发现拟南芥 *B3* 家族 *NGAs*(*NGATHA-LIKEs*)亚家族转录因子通过抑制 *CUC2* 的转录负调控叶缘锯齿的形成,超表达拟南芥 3 个转录因子 *NGAL1-3* 都能够降低叶缘锯齿程度,功能缺失三突变体 *ngaltri* 表现为叶缘锯齿加剧^[26]。

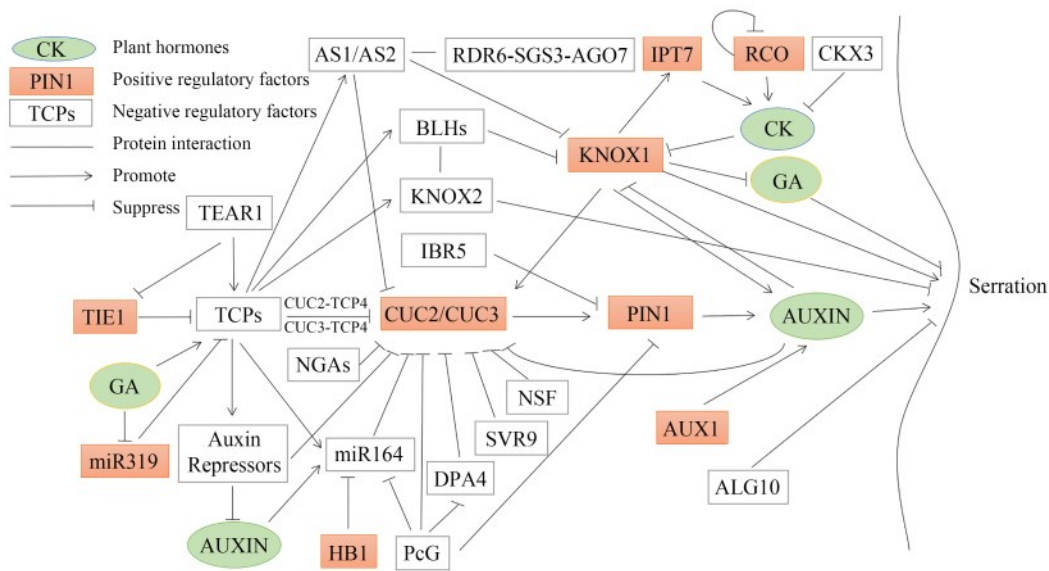


图2 叶缘形态发育调控网络图

Fig.2 Leaf margin morphological development regulation network

番茄 *CIN-clade TCP*(*TEOSINTE BRANCHED1/CYCLOIDEA/PCF*)类同源基因 *LA*(*LANCEOLATE*)活性加强,使复叶变成单叶, *TCP* 转录因子的活性调控对于植物叶片形态和大小的形成至关重要^[27]。拟南芥 *TCP4* 可以分别与 *CUC2* 和 *CUC3* 互作,抑制 *CUC2-CUC3* 二聚体形成,降低叶缘锯齿程度^[28]。 *TCPs* 直接激活 *miR164*、*ASI* 和生长素抑制基因 *IAA3/SHY2*(*INDOLE-3-ACETIC ACID3/SHORT HYPOCOTYL2*)、*SAUR*(*SMALL AUXIN UP RNA*)协同抑制 *CUCs* 表达^[29]。拟南芥 *TCP5* 通过激活 *KNAT3*(ClassII *KNOX*)和 *BEL*-like 基因 *SAW1* 表达从而抑制叶缘锯齿产生^[30]。拟南芥超表达 *TCP* 转录抑制子 *TIE1*(*TCP INTERACTOR-CONTAINING EAR MOTIF PROTEIN1*)突变体产生叶缘锯齿表型,研究发现 *TIE1* 通过招募共抑制因子 *TPL/TPRs* 在蛋白水平上抑制 *TCPs* 转录因子的活性,从而调控叶片发育^[31],与 *TIE1* 相互作用的含有 RING 结构域的 E3 泛素连

接酶 *TEAR1*(*TIE1-ASSOCIATED RING-TYPE E3 LIGASE1*),降低 *TEAR1* 及其同源基因的表达可使突变体叶片出现边缘过度生长和叶锯齿增多等表型^[32]。

1.1.2 KNOX-GA/CK 通路 赤霉素(GA, gibberellin)被认为负调控叶形复杂度,番茄发育的叶片外源施加赤霉素后叶形简单化且叶缘光滑,细胞分裂素(CK, cytokinins)可以抑制赤霉素对叶形调控,但不依赖赤霉素通路而能直接影响叶形发育^[33-34]。同源异性盒基因 *KNOX1*(ClassI *KNOX*: *STM/BP/KNAT1/KNAT2/KNAT6*)是调控叶片激素平衡的关键因子,分别正调控细胞分裂素和负调控赤霉素的生物合成,保持叶缘赤霉素含量在较低水平,同时可以激活细胞分裂素合成基因 *IPT7*(*ISOPENTENYL TRANSFERSASE7*),番茄超表达 *AtIPT7* 产生复杂的叶缘形态^[35]。超表达细胞分裂素降解基因 *CKX3*(*CYTOKININ OXIDASE3*)使番茄叶片中细胞分裂素含量降低,降低叶片复杂度和叶缘锯齿度,同时研

究发现细胞分裂素依赖生长素在叶缘实际积累来调控锯齿形成^[36]。拟南芥不同叶形品种的 *KNOX1* 同源基因 *STM* 的表达分析显示 *STM* 表达量与叶缘锯齿程度正相关,推测单叶品种拟南芥叶片 *STM* 的缺失表达可能是正向遗传选择结果^[37]。拟南芥中超表达鹅掌楸 (*Liriodendron chinense* L.) *KNOX1* 同源基因显著提高锯齿程度,表明 *KNOX1* 基因家族具有正向调控植物叶片复杂度的作用^[38]。莴苣 (*Lactuca sativ* L.) 上调表达 *KNOX* 基因家族转录因子 *LsKN1*, 由生长素、赤霉素和叶片背腹性等多条通路调控叶形使羽状缺刻转变为掌状裂刻,掌状裂刻亲本中 *LsKN1* 外显子存在 CACTA 转座子插入,显著提高了该基因的表达量。*LsKN1* 上调 *LsCUC2* 和 *LsCUC3* 表达, *LsKN1* 也能结合 *LsPID* 启动子促进生长素生物合成,抑制赤霉素生物合成促进掌状裂刻形成^[39]。*KNOX2* (*ClassIIKNOX: KNAT3/KNAT4/KNAT5/KNAT7*) 与 *KNOX1* 有相反的功能作用,激活或抑制 *KNOX2* 的基因功能分别产生叶缘光滑或锯齿表型^[40]。

拟南芥 *AS1* (*ASYMMETRIC LEAVES1*) 和 *AS2* 是叶片发育的重要调控因子,通过 *AS1*-Auxin 通路和 *AS* 蛋白家族直接或间接抑制 *KNOX1* 表达,促进叶片发育^[41-43]。*AS1*-*AS2* 和 *RDR6*-*SGS3*-*AGO7* 通路间的遗传互作协同调控 *KNOX1* 表达影响叶缘锯齿发育^[44]。拟南芥 *BLH* (*BEL1-LIKE HOMEODOMAIN*) 同源基因 *saw1saw2* 双突变体的叶缘裂刻明显加深,研究表明 *BLH* 蛋白通过抑制 *KNOX1* 表达调控叶缘发育^[45],进一步研究分析了 *SAW1* 的表达模式,发现 *SAW1* 只在叶片近轴端和叶表皮下部表达,不参与 Auxin-PIN1-CUC2 的叶缘调控模式,因为 *PIN1* 在叶表皮上部表达^[16],推测 *SAWs* 可能参与 TCP-NGA 通路^[46],或与 *KNOX2* 相似功能作用抑制叶缘锯齿形成^[47]。

1.1.3 LMII-like(RCO)-CK 通路 *RCO* (*REDUCED COMPLEXITY*) 基因是 *LMII* (*LATE MERISTEM IDENTITY1*) 串联复制的一部分,小叶的产生需要 *RCO* 调控,而拟南芥基因组缺失 *RCO* 基因,因此拟南芥叶形表现为单叶, *RCO* 转基因拟南芥叶缘出现锯齿^[48],拟南芥近源植物复叶碎米荠 (*Cardamine hirsute* L.) *RCO* 基因是自己的靶基因,通过低亲和连接位点转录抑制自身表达以及调控多种参与细胞分裂素生物合成与降解的基因,表明 *RCO*-CK 通路是复杂叶形成的条件之一^[49]。*LMII* 的修饰是陆地棉 (*G. hirsutum*) 产生不同叶片类型的原因, *VIGS* 沉默裂叶棉 *okra* 的 *LMII* 基因叶形裂刻程度恢复到正常^[50]。白菜 (*Brassica rapa* L.) 的 3 个 *LMII*-likes

基因在拟南芥中异源表达都能产生叶缘锯齿表型^[51]。研究人员构思了一种使单叶拟南芥向复叶碎米荠的叶形转变方式,例如使拟南芥叶片超表达 *STM* 和 *RCO* 基因, *STM* 基因使叶缘的叶脉伸长促进小叶形成, *RCO* 基因抑制叶缘局部成熟促进叶形复杂化,使单叶形成复叶^[52]。

1.1.4 miRNA 和 PcG 表观遗传修饰 研究表明拟南芥 miRNA 也参与调控叶缘锯齿产生,生长素通过激活 *miR164* 负调控 *CUC2* 表达, *miR164a* 功能缺失突变体叶缘深裂,而超表达 *miR164* 植株叶缘光滑^[16, 20]。研究发现拟南芥 HD-Zip I 亚家族成员 *AtHB1* (*Arabidopsis thaliana* HomeoBox1) 在叶缘光滑/锯齿转变存在功能作用, *AtHB1* 通过结合 *MIR164* 编码位点直接抑制 *MIR164* 表达进而增强 *CUC2* 表达水平,使 *AtHB1* 过表达植株叶缘锯齿化,反之抑制 *AtHB1* 表达叶缘光滑^[53]。拟南芥 *miR319A* 和 *miR319B* 单基因突变植株叶缘锯齿程度减弱,双突变体产生叶缘光滑的叶形, *miR319* 突变会增强 *cuc* 突变体锯齿程度,转录因子 *TCPs* 是 *miR319* 的靶基因, *miR319* 负调控 *TCPs* 降低叶缘锯齿程度^[54-55]。赤霉素通过抑制番茄 *miR319* 表达一定程度上调控 *TCPs* 活性^[56]。近期研究发现超表达 *miR319* 的杨树 (*Populus alba* × *Populus glandulosa*) 突变体产生矮化和叶缘裂刻表型^[57]。

此外表观遗传调节机制对拟南芥叶缘发育也有调节作用, *PcG* (Polycomb group) 通过在 *CUC2* 位点引入 H3K27me3 标记,从而抑制 *CUC2* 的表达参与叶缘锯齿发育的调控过程^[58]。除了 *CUC2*, *PcG* 的靶基因还包括 *miR164A*, *PIN1* 和 *DPA4* (*PcG TARGET IN THE APEX4*)^[59-60]。拟南芥 *DPA4* 通过 *PcG* 通路不依赖 *miR164* 调控,直接负调控 *CUC2* 表达抑制叶缘锯齿形成^[61]。

1.1.5 ALG10, α -1, 2 糖基转移酶 基于羽衣甘蓝 (*Brassica oleracea* L. var. *acephala*) 叶缘差异的 *F₂* 遗传分离群体,通过全基因组重测序与染色体精细定位,发掘到了叶缘差异性性状关键候选基因 *BoALG10*, 该基因编码 α -1, 2 糖基转移酶^[62]。通过互补转化、基因敲除等研究验证了 *BoALG10* 具有维持羽衣甘蓝叶缘光滑性状的功能^[63]。*ALG10* 变异造成 N-糖基化缺陷,此前研究显示 *AtALG10* 调控拟南芥产生更为短小的叶形^[64],而羽衣甘蓝则产生锯齿叶形。

1.2 环境因子

研究推测环境温度和光强通过 *KNOX*-GA 通路调控水生蔊菜 (*Rorippa aquatica* (Eaton) E.J. Palmer

& Steyerm)叶形。相较于低温,更高的环境温度诱导产生简单叶,15 ℃条件下形成羽状叶,30 ℃时形成叶缘光滑的单叶,而20 ℃和25 ℃时产生复叶。内源植物激素测定、基因表达共同验证了25 ℃下叶原基中具生物学活性的赤霉素分子GA₄含量和合成基因表达量均高于20 ℃条件,外源赤霉素处理简化了叶形复杂度^[65]。*KNOX1* 基因调控赤霉素生物合成以及KNOX1 蛋白直接调控 *GA₂₀OX* 基因表达^[66],进一步研究发现水生蔊菜*KNOX1* 同源基因*RaSTM* 和*RaBP*在20 ℃时表达量高于25 ℃^[65]。另一研究推测叶片可能起温度感应器的作用,水生蔊菜叶片在单叶控温装置30 ℃恒温处理下的叶形复杂度较20 ℃处理条件降低^[67]。

光强调控水生蔊菜叶形改变表现为90 μmol/(m²·s)高光强下产生叶缘复杂的裂叶,15 μmol/(m²·s)低光强下形成叶缘光滑的单叶。RNA-seq揭示了光强处理对叶片形成作用与冷处理一致,高光强处理下*RaSTM*表达量显著高于低光强条件^[65]。

2 遗传机制

植物控制叶缘锯齿性状的遗传机制存在较大

差异,多数研究认为叶缘裂刻有无属质量性状,而锯齿程度(数目)属数量性状。十字花科类作物研究较多,研究认为白菜锯齿性状由1对主效核基因和细胞质修饰基因控制^[68-69],另有研究认为是受一对显性基因控制的质量性状^[70-71]、锯齿数目受微效基因影响^[72],也有研究认为是由2对主基因加性效应和多基因显性效应控制^[73],同时存在基因gDNA拷贝数差异影响裂叶性状^[74]。甘蓝型油菜(*Brassica napus* L.)叶缘锯齿性状表现为质量性状,主要受1对显性基因控制^[75-77],也有研究认为受单显性基因控制^[78]以及受1对隐性基因控制^[79-80],可能是分离群体和调控基因的差异。羽衣甘蓝裂叶性状由细胞核内1对等位基因控制,裂叶对全叶为不完全显性,且裂叶性状还受微效多基因影响^[62]。芥菜(*Brassica juncea* L.)裂叶性状由1对不完全显性基因控制^[6, 81]。茼蒿、西瓜(*Citrullus lanatus* L.)裂叶性状为单基因显性性状^[82-83],甜瓜为单基因隐性性状^[84]。棉花和绿豆(*Vigna radiata* L.)为不完全显性基因控制^[85-87](表1)。桦木科桦树(*Betula pendula* Roth.)裂叶是受2对基因属叠加效应控制的隐性性状,基因型为ddbb^[88]。

表1 基于文献分析的植物控制叶缘锯齿性状的遗传机制

Table 1 Genetic mechanism of plant controlling leaf margin serrated traits based on literature analysis

物种 Species	杂交群体 Hybrid population	分离比例 Segregation ratio	遗传类型 Genetic types	候选基因 Candidate gene	基因功能 Descriptions	基因命名 Gene name	遗传差异 Genetic diversity	参考文献 References
芥菜 Mustard (<i>B. juncea</i>)	裂叶 LL×锯齿 叶 LSL	F ₂ ≈3:1; BC ₁ ≈1:1	不完全显性 基因	<i>BjuA040054</i>	HD-Zip I	<i>BjRCO</i>	—	[6]
甘蓝型油菜 Rapeseed (<i>B. napus</i>)	锯齿叶 Zhongshuang 9 (Z9)×裂叶 Tongling huaye (HY)	F ₂ ≈1:2:1; BC ₁ F ₂ ≈1:2:1	不完全显性 基因	<i>BnLLA10</i>	HD-Zip I	<i>BnLMII</i>	启动子区域2624 bp 片段插入	[75]
甘蓝型油菜 Rapeseed (<i>B. napus</i>)	圆叶 Zheyou 50×裂叶 Yuye 87	BC ₁ ≈1:2:1; F ₁ ≈1:1	不完全显性 基因	<i>Bra009510</i> 同源 基因	HD-Zip I	<i>LOBED- LEAF 1 (BnLLI)</i>	—	[76]
甘蓝型油菜 Rapeseed (<i>B. napus</i>)	圆叶 2205(P ₁)× 裂叶 1423(P ₂)	F ₂ ≈3:1; BC ₁ P ₁ ≈1:1; BC ₁ P ₂ ≈1:0	单隐性基因	<i>BnHB2205</i> (裂 叶); <i>BnHB1423</i> (圆叶)	HD-Zip I	—	8个氨基酸差异	[79]
羽衣甘蓝 Ornamental kale (<i>B. oleracea</i>)	羽状叶 F0819× 圆叶 S0835	F ₂ ≈1:2:1; BC ₁ ≈1:1	不完全显性 基因	<i>Bo9g184610</i>	<i>alpha</i> -1,2- glucosyltransf erase	<i>BoFL</i> (<i>BoALG10</i>)	3个SNP差异	[62]
羽衣甘蓝 Ornamental kale (<i>B. oleracea</i>)	裂叶 18Q2513 (P ₁)×非裂叶 18 Q2515(P ₂)	F ₂ ≈3:1; BC ₁ P ₁ ≈1:1; BC ₁ P ₂ ≈1:0	单显性基因	<i>BoLI-1</i> (<i>Bo9g18 1710</i>)	HD-Zip I	<i>BoLMIIa</i>	启动子区域1737 bp 缺失,92 bp插入, 1个SNP差异	[78]
白菜 Chinese cabbage (<i>B. rapa</i>)	裂叶 13XS199 H×叶全缘 13XS 198B	F ₂ ≈1:2:1	不完全显性 基因	<i>Bra009510</i>	HD-Zip I	<i>BrcLLI</i>	圆叶材料1个拷贝, 裂叶材料2个拷贝, <i>BrcLLI-a</i> 和 <i>BrcLLI- b</i> , <i>BrcLLI-b</i> 内含子有 245 bp缺失	[71, 74]

表 1 (续)

物种 Species	杂交群体 Hybrid population	分离比例 Segregation ratio	遗传类型 Genetic types	候选基因 Candidate gene	基因功能 Descriptions	基因命名 Gene name	遗传差异 Genetic diversity	参考文献 References
西瓜 Watermelon (<i>C. lanatus</i>)	'Lingxiu' F _{2:3} 自交系	F _{3:4} ≈3:1	显性等位 基因	ORF22 (<i>Cla018360</i>)	HD-Zip I	<i>CILL1</i>	InDel/在 LZ motif 24 bp 缺失	[83]
甜瓜 Melon (<i>C. melo</i>)	圆叶浅裂 Y8× 掌状裂叶 BM7; 圆叶 Jiashi×掌 状裂叶 BM7	F ₂ ≈3:1; BC ₁ ≈1:1	单隐性基因	MELO3C010784	ANT	<i>palmately lobed leaf (pll)</i>	—	[84]
陆地棉 Upland cotton (<i>G. hirsutum</i> L.)	正常叶 NC11- 2100×鸡脚叶 NC05AZ21	F ₁ ≈1:2:1	不完全显性 基因	<i>Gorai.002G24</i> 4000	HD-Zip I	<i>Late Meristem Identity1-D1b (GhLMII- D1b)</i>	InDel/第 3 外显子 8 bp 缺失	[85-86]
莴苣 Lettuce (<i>L. sativa</i>)	圆叶 PI491070× 裂叶 PI536760	F ₂ ≈3:1	单显性基因	LG3316063	HD-Zip I	<i>Lslobed</i>	SNP/1 个碱基(G/T) 差异	[82]
绿豆 Mungbean (<i>V. radiata</i>)	圆叶 Sulu×裂叶 AL127	F ₁ ≈1:2:1	不完全显性 基因	<i>Vradi03g04470</i>	A20/AN1	<i>lobed leaflet margins (LMA)</i>	—	[87]

—指文献中未有相关信息
— means no relevant information in the literature

3 总结与展望

叶片是植物重要的营养器官,叶缘形态不仅是植物多样性的体现,也是植物对环境的一种适应。叶缘锯齿在生产实践中有多种优势,如提高观赏性、增强抗逆性、适合密植,单位面积产量高等。叶缘锯齿调控研究对作物育种、生产实践具有指导意义,本文梳理了叶缘锯齿形成的调控机制,植物激素、基因表达、miRNA 和表观遗传调节机制等协同作用调控叶缘锯齿形成,生长素在叶缘的不平衡积累能促进锯齿产生,细胞分裂素依赖生长素在叶缘的积累促进叶形复杂度,而赤霉素负调控叶形复杂度。归纳了植物激素与基因参与叶缘锯齿形成的 3 条主要作用通路:TCP-CUC-PIN1-Auxin、KNOX-GA/CK、LMII-like(RCO)-CK。miR164、miR319、PcG 表观遗传修饰和 α-1,2 糖基转移酶等也参与叶缘锯齿形成。研究表明环境因子温度和光强通过 KNOX-GA 通路调控水生蔊菜叶形,高温和低光强均能降低叶形复杂度。不同植物控制叶缘锯齿性状的遗传机制存在较大差异,多数研究认为叶缘裂刻有无属质量性状,而锯齿程度(数目)属数量性状。

现有研究表明生长素、赤霉素和细胞分裂素参与叶缘锯齿发育,而其他植物激素脱落酸、油菜素内酯、乙烯等研究较少报道;叶缘锯齿候选基因的 QTL 位点研究已有相关报道^[89],据报道甘蓝型油菜的叶缘锯齿与耐盐性状连锁^[79],但其性状与其他农艺性状的连锁关系研究较少;未来叶缘锯齿基因参

与的生物或非生物胁迫调控机制也值得深入研究,为培育环境适应型作物提供参考。

叶缘锯齿相关基因发掘以拟南芥、羽衣甘蓝、棉花等研究较多,而果树开展此类研究较少。传统果树种植业在经济社会的快速发展的背景下陷入发展瓶颈,果树的观赏价值将成为产业发展的一个新增长点^[90]。近期研究报道了桃(*Prunus persica* (L.) Batsch)的 *PpLMII* 外显子中插入了一个 hAT 超家族(*mMoshan*)转座元件,产生与白粉病抗性相关的花外蜜腺的缺失或球形表型,说明 *PpLMII* 调控桃叶缘形态结构主要与花外蜜腺缺失有关,而对叶缘锯齿表型不明显^[91]。柑橘类橘枳叶形存在差异,三出复叶的枳(*Citrus trifoliata* L.)在-20 ℃不死亡,而单身复叶的橘在-6~-7 ℃就会冻死。三出复叶的枳和单叶的柠檬(*Citrus limon* (L.) Burm. F.)叶片各发育时期转录组数据显示 *KNOX* 基因家族成员 *CiKN1* 和 *CiKN6* 表达差异明显,*CiKN1* 和 *CiKN6* 存在蛋白互作,抑制 *CimiR164a* 表达,通过 miR164a-CUC2 通路调控叶片发育^[92]。未来,果树育种研究除了开展果实品质育种和抗性育种外,也应着手推进观赏性果树育种研究,发掘叶形发育相关基因为赏食兼用果树育种奠定基础,促成“城中有果园,果园在城中”的生态家园环境。

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