甘蔗分蘖发生及成茎的调控研究进展

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摘要: 甘蔗是以收获地上茎为主的重要糖料作物, 蔗糖分储藏在蔗茎节间, 而分蘖是甘蔗有效茎形成的关键, 因此促进甘蔗分蘖成茎是提高甘蔗产量的最有效途径之一。目前, 水稻分蘖机理的研究取得了突破性进展, 甘蔗也具有禾本科植物特殊的分蘖特性, 但相关研究相对滞后, 尤其是分子调控机制。本文详细阐述了甘蔗分蘖的生物学特性及现实意义, 从栽培技术与管理、环境条件、植物生长调节剂(植物激素)和遗传因素等方面阐述甘蔗分蘖发生及其生长发育的研究结果, 为深入研究甘蔗分蘖调控的分子机理提供新视角, 也为甘蔗高产栽培技术及分子辅助育种提供理论依据。

关键词: 甘蔗; 分蘖; 有效茎数; 植物激素; 化学调控

甘蔗(*Saccharum officinarum*)是热带和亚热带地区普遍种植的重要糖料作物, 对我国民经济的可持续发展具有重要意义。近年来, 世界食糖供给大部分来源于甘蔗糖, 而甘蔗种性退化、宿根性差及单产不高严重影响了我国甘蔗糖业的可持续发展(李杨瑞和杨丽涛2009)。甘蔗茎是蔗糖分储藏和收获的重要部位, 可见甘蔗增产实则是提高单位面积蔗茎产量(即单产)。有效茎是甘蔗产量构成要素, 而促进分蘖是增加单位面积有效茎数的关键 (Punia等1983; Tena等2016)。

分蘖是水稻(*Oryza sativa*)、小麦(*Triticum aestivum*)、大麦(*Hordeum vulgare*)、高粱(*Sorghum bicolor*)、甘蔗等禾本科植物在生长发育过程中形成的一种特殊的发育生物学现象, 且分蘖通过影响茎穗数的多少并进而影响作物单产(McSteen和Leyser 2005)。甘蔗单产=单位面积有效茎数×单茎重, 其中有效茎来源于甘蔗分蘖成茎, 是蔗茎产量的主体(Tena等2016), 由此可见, 促进有效分蘖对甘蔗增产具有直接关系(Smiullah等2013; Zhao等2017)。在植株生长发育过程中, 无效分蘖会对有效分蘖产生植株营养分配上的竞争, 从而降低作物对土壤养分资源的有效利用率, 最终造成作物产量下降(Fischer 1975; Jones和Kirby 1977; Xing和Zhang 2010)。因此, 在确保一定主茎正常生长前提下, 促进分蘖成茎是增加甘蔗单位面积有效茎数的最有效途径。宿根蔗是甘蔗生产的重要组成部分, 其种植面积占相当大的比重, 一般占总种植面积的70%~80%, 且甘蔗的分蘖率与其宿根性呈极显著正相关, 分蘖率越强的甘蔗品种宿根性越好。由此可见, 调控分蘖成茎对甘蔗高效高产栽培具有重要指导意义。

目前, 分蘖机理已经成为植物发育生物学和合理群体结构建成的研究热点, 属于多基因控制的数量性状, 其表型变化受多种内部因素和外部环境条件的共同调控和影响(Li等2003; Mitchel等2013; Hussien等2014)。现今国内外甘蔗科研多侧重于产量、糖分、抗旱、耐寒、抗病等方面的研究, 但一直难有较大突破, 尤其在产量方面(Singh等2010; Henry和Kole 2010; Manners 2011)。分蘖成茎是甘蔗产量形成的关键, 目前针对甘蔗分蘖的研究主要集中在品种栽培及其分蘖力评价(黄福珠2005; 唐仕云等2016; 黄家雍等2016)、茎蘖消长模型(蒋菊生等1993)、影响和调控分蘖的生理生化等方面(吴凯朝2005; 叶燕萍2006; 王威豪等2007)等方面, 而分蘖分子调控机理方面的研究则相对薄弱和匮乏。本文详细分析了甘蔗分蘖生长

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发育的生物学特性和意义, 在此基础上, 从甘蔗栽培技术与管理、环境条件、植物生长调节剂(主要为植物激素方面)、遗传因素等方面总结甘蔗分蘖特性的研究成果, 旨在通过定向调控分蘖成茎, 为实现甘蔗高效高产栽培技术提供理论参考, 也为深入研究甘蔗分蘖机理提供新视角。

1 甘蔗分蘖的生物学特性及其意义

分蘖起源于甘蔗植株主茎地下基部未伸长节间的侧芽萌发, 并形成不定根系, 最终脱离主茎而独立发育为成熟个体。甘蔗的生长发育一般经历萌芽期、幼苗期、分蘖期、伸长期和成熟期5个阶段, 幼苗期是甘蔗分蘖的准备阶段, 而分蘖期是增加单位面积有效茎数的关键时期, 经历了分蘖芽的发生和形成、分蘖苗的消长及分蘖成茎(李杨瑞2010)。甘蔗分蘖的发生经历2个过程: 地下基部腋芽形成和侧芽生长; 一般情况下, 当幼苗出现3~4片真叶时, 地下基部未伸长节间的侧芽开始萌动(图1), 在第7~8片真叶时分蘖芽开始出土并形成分蘖苗, 并于第10~12片真叶时达到分蘖高峰期, 同时地上部主茎开始伸长, 随后分蘖开始减少甚至停止, 期间伴随着不定根的生长, 它有助于分蘖苗吸收水分和养分, 进而提高分蘖存活力及成茎率(李杨瑞2010)。和其他禾本科作物一样, 甘蔗分蘖也有有效分蘖和无效分蘖之分, 其中发育成熟后蔗茎长度达1 m以上的分蘖为有效分蘖, 反之, 则为无效分蘖; 一般早期发生的分蘖基本能长成有效茎, 而后期分蘖多为无效的。

因此, 甘蔗分蘖的意义主要体现如下: (1)分蘖茎是构成产量的主体部分。甘蔗单位面积上的有效茎数由主茎和分蘖茎共同组成, 分蘖茎所占的比例因品种基因型、种植密度、栽培技术、环境条件等而有所差异; (2)分蘖是甘蔗苗期高产管理的重要指标。根据分蘖率、根系大小、蔗茎糖分、叶、蘖发生的相关性等判断其苗情, 以壮、弱、旺等进行不同分类管理; (3)群体结构的自我调节功能。甘蔗群体的健壮与否, 可通过分蘖进行合理调控, 是适应其外界环境的一种自我保护机

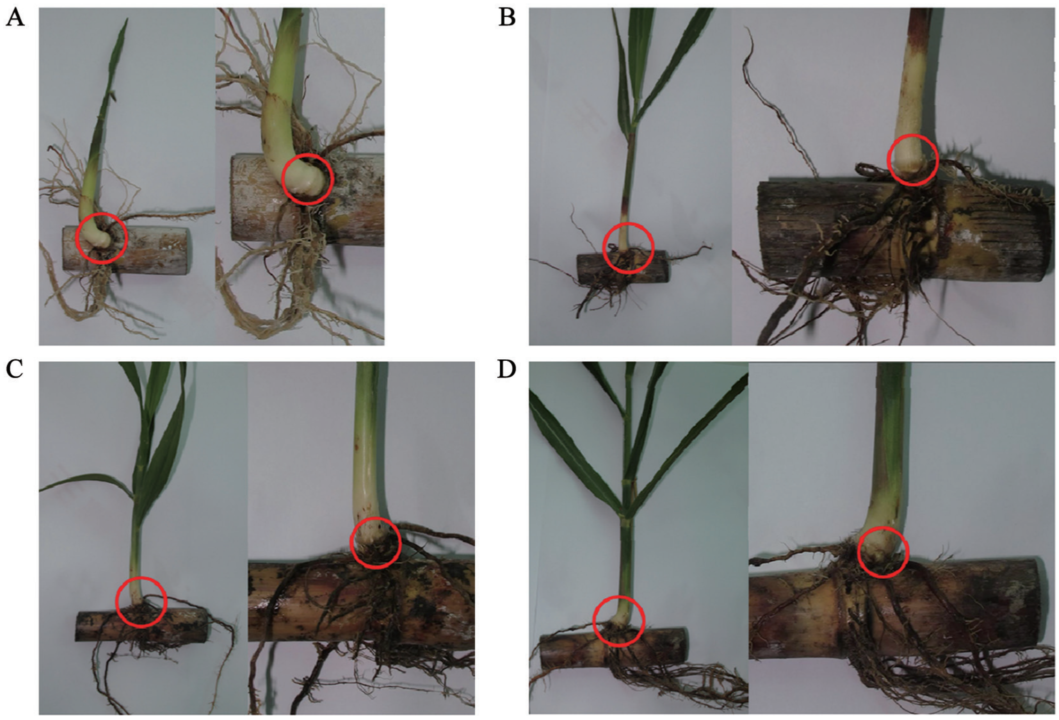

图1 水培条件下甘蔗分蘖发生的动态过程

Fig.1 The dynamic process of tillering formation in hydroponic sugarcane

A: 1~2叶龄的甘蔗苗, 基部未出现腋芽; B: 3叶龄的甘蔗苗, 基部腋芽基已隐约可见(即分蘖始发); C: 4叶龄的甘蔗苗, 基部腋芽基清晰可见, 并微突起(即分蘖发生中); D: 5叶龄甘蔗苗, 基部腋芽基完全凸起形成分蘖芽(即分蘖形成)。

制; (4)分蘖可再生能力, 是甘蔗宿根性强弱的体现。在分蘖期, 甘蔗在分蘖节处产生许多不定根和形成分蘖芽, 以确保在各种环境条件中自身的生存和繁衍。由此可见, 甘蔗分蘖发生及成茎比例的研究势必成为高产优良品种选育的重点关注。

2 栽培技术对甘蔗分蘖的影响

甘蔗分蘖与栽培技术及其管理措施密切相关, 通过集成各种栽培技术和改善管理措施可提高土壤肥力和改善其理化特性, 提高甘蔗根系对营养物质的利用效率, 进而促进甘蔗分蘖, 并提高其成茎的比例以增加有效茎数, 实现增产(周承圣1965; 李杨瑞等2014)。叶燕萍等(1995)、廖青等(2010)、覃凤兰(2014)等的研究结果说明, 机械深耕深松技术增加了甘蔗地下部分蘖节的数量, 进而显著提高甘蔗分蘖率和有效茎数; 而且现今其他适用的栽培技术和种植模式也一定程度影响甘蔗出苗及分蘖, 从而实现不同程度的增产(苏天明等2009; 邓军等2017; 周灵芝等2017)。也有研究指出, 适当调节甘蔗种植的株行距, 可促进分蘖生长成茎, 获得合理群体结构, 实现产量最大化(罗俊等2012; 陈建国等2014)。近年来, 基于种源、成本和效益等问题, 配套栽培技术对甘蔗新品种的推广和应用极其重要, 用种量是甘蔗栽培首要考虑的要素。许多研究表明, 针对不同地区和不同品种栽培上的差异, 通过合理密植可提高甘蔗分蘖率和成茎率, 增加有效茎数, 达到增产目的(陆建勋等2010; 段维兴等2012; 罗晟昇等2015; 陆文娟等2015), 是从栽培技术上寻找提高甘蔗单产的突破口(陈玉水等2008)。此外, 不同播种时间也会对甘蔗分蘖产生影响, 一般春夏交际时期种植的甘蔗分蘖及成茎比例最高, 也会因品种而出现一点差异(徐林等2010; 毛玲荣等2017)。还有, 甘蔗的田间管理措施对甘蔗分蘖的影响也不可忽视(Vasantha 2012, 2014; Singh等2017), 一般认为, 甘蔗苗期合理的水肥管理(Mary等2016; 刘亚男等2017)及病害(Schaker等2016; Joshi等2016)、虫害(Silva等2017)、草害(Begum和Bordoloi 2016; Shrivastava等2017)等的综合防治有利于甘蔗分蘖, 促进有效分蘖生长成茎。

3 环境因素对甘蔗分蘖生长发育的影响

植物的生长发育与环境息息相关, 环境因子的改变会影响甘蔗分蘖及其成茎率, 最终导致产量的差异(Marchiori等2010), 因此可根据不同甘蔗品种分蘖的生态表型进行合理布局、调整种植结构, 促使优势茎蘖形成合理的群体结构以提高甘蔗产量。研究表明, 甘蔗分蘖率与有效茎数呈正比(Soopramanien等1983), 且分蘖密度是较单茎重和株高更为重要的产量决定因素(Mebrahtom等2016; Tena等2016), 但分蘖的消长易受环境条件的影响, 20°C是甘蔗发生分蘖的最低临界温度, 而28~30°C是甘蔗分蘖及其成茎的最适环境温度, 温度过低或过高均不利于甘蔗分蘖(陈尚洸1978)。在不同的生育周期中, 甘蔗的需水量也有很大的差异, 分蘖期和成熟期需水量较低, 伸长期需水量较高(罗维钢等2016), 可见蔗田水分的控制对甘蔗分蘖的生长发育也至关重要(莫建飞等2015; 粟世华2015)。甘蔗属高光效的C_4类禾本科作物, 充足光照条件是甘蔗分蘖生长发育的首要因素(陈尚洸1978), 弱光条件或者光资源(包括时空分布、光强和光质)受限均可引起甘蔗分蘖进程的停滞, 也不利于甘蔗的生长发育(丘立杭等2017)。土壤条件是甘蔗赖以生存的环境基础。在不同生长阶段, 甘蔗吸收氮、磷、钾等大量元素和肥料浓度参数存在较大差异(王秀林和阳代天1994; 谭宏伟等2016)。前人研究表明, 通过合理施用硅钙磷肥和有机肥可提高酸化蔗地的土壤肥力, 并明显对甘蔗分蘖、株高、有效茎及产量产生积极的影响(邢颖等2016)。此外改善和提高土壤有效态中微量元素即可提高新植甘蔗出苗率与分蘖率, 还能促进宿根蔗发株(崔雄维等2011; Mellis等2016), 但低氮水平的土壤条件对甘蔗分蘖和有效茎数的不利影响较大(王伦旺等2010; Vasantha等2014); 提高旱坡地土壤温度和含水量也能显著提高甘蔗分蘖率, 实现增产(杨善等2016)。也有研究表明, 通过改善有益微生物群落可调理土壤理化特性以增加土壤肥力, 进而提高甘蔗对养分的利用效率, 促进甘蔗萌芽、分蘖、株高和有效茎数等产量农艺性状向有利的方向发展, 实现高产(陈廷速等2013; 高欣欣等2016; Meesilp等2016); 但是病原微生物的浸染会抑制甘蔗分蘖及其生长发育(Wayne 2010)。综上可知, 外部环境主要通过改变土壤的理化特性和微生物群落来调控和影响甘蔗分蘖及其生长发育, 病虫草害也对甘蔗分蘖特性造成一定程度上伤害。

4 植物生长调节剂对甘蔗分蘖发生、成茎特性的影响

植物激素在植物生长发育的各个过程中发挥着重要的调控作用。目前, 在水稻、玉米、小麦等禾本科作物上的研究表明, 分蘖特性除了容易受环境因素的影响外, 植物激素也精密地调控分蘖的发生和发育过程; 一般认为, 外部因素是通过改变植物体内激素的含量及其平衡来影响分蘖发生和成茎的(Li等2003)。众所周知, 利用植物生长调节剂可影响植物内源激素系统, 进而调控作物朝着利于人们预期的方向生长发育。生长素类似物2,4-二氯苯氧乙酸(2,4-Dichlorophenoxyacetic acid; 2,4-D)是第一种应用于甘蔗生产的植物生长调节剂(Beauchamp 1950); 随后, 植物生长调节剂的相关研究和应用受到了世界各产糖国的高度重视, 并取得了一系列相关研究成果(Moore等1989; Solomon等2004)。目前, 乙烯利是应用最为广泛的甘蔗生长调节剂, 它不仅能增糖, 还能促进分蘖芽萌发及生长成为有效茎(潘有强等1997; 李永健等2002; Terefe等2017), 可能由于乙烯利能够破除IAA的顶端优势对侧芽的抑制作用(Harrison和Kaufman 1982; Wang等2006); 也可能是乙烯利影响了甘蔗内源激素系统的平衡导致(周传凤2004), 进一步研究发现, 生长素(IAA)和细胞分裂素(CTK)在甘蔗分蘖芽(侧芽)的萌动和生长过程中起重要作用(周传凤等2007a, 2007b)。因为乙烯利明显引起了甘蔗根区CTKs含量和CTKs/IAA比值的增加, 赤霉素(GA_3)和ABA含量也较高; 虽然IAA含量变化相对较小, 但其含量仍然高于对照的; 相关性分析表明, CTKs和CKTs/IAA是甘蔗分蘖发生的直接原因, 且基部CTKs是甘蔗分蘖发生的关键内源激素, ABA以分子信号形式通过激素间互作调控无效分蘖衰亡, GA_3则在乙烯利促进分蘖成茎中起重要作用(叶燕萍2006)。李和平等(2014)认为高浓度内源IAA和CTK与甘蔗组培苗后代具有过强分蘖力密不可分, 可能是组培中残留的6-BA导致的; 也可能是2,4-D和NAA残留引起(Sardar等2016)。罗明珠等(2002)等的研究结果表明, 分蘖期甘蔗叶片中较高含量的IAA和$GA_{1/3}$及较低含量的ABA和ZRs是分蘖成茎高产的内因, 因为GA_3可通过诱发IAA的合成或抑制IAA氧化酶的活性而间接影响顶端优势对分蘖的抑制作用(Phillips 1975), GA_3/ABA、IAA/ABA和ZRs/ABA的平衡对甘蔗分蘖生长发育至关重要, 且GA_3/ABA比值的升高是分蘖成茎的关键(丘立杭等2017), 但是提高内源ABA的含量可导致分蘖死亡(Vasantha等2012)。因此, 喷施一定浓度的外源GA_3和吲哚丁酸(IBA)可促进甘蔗分株和分蘖, 增加有效茎数(林韶湘和苏广达1984; Terefe等2017)。刘俊仙等(2016)利用多效唑浸种提早了甘蔗分蘖的发生及生长发育, 并认为与苗期甘蔗叶片中CTK和ABA含量的增加及IAA和GA_3含量的下降紧密相连; 但不同甘蔗品种间的IAA、GA_3、ZR和ABA的含量差异较大(郭家文等2007); 此外独角金内酯也可能参与了甘蔗分蘖的调控(吴转娣等2016)。由此可见, 甘蔗分蘖的发生不仅受单一激素绝对含量的影响, 还取决于多种激素间相对含量的动态, 并通过激素间的互作形成复杂的调控网络(图2); 内源激素含量及其平衡可能是影响甘蔗分蘖及分蘖成茎的直接原因, 外部因素对分蘖的影响主要是通过改变甘蔗体内激素含量及其平衡进而引发一系列生理生化效应来实现的。

5 甘蔗分蘖特性的遗传因子研究

甘蔗分蘖与品种的种性密切相关, 性状的遗传力越大, 受环境制约越小, 反之, 受环境影响越大; 可见遗传因子从本质上决定了甘蔗分蘖的强弱及与环境的关系。甘蔗杂交后代有效茎数性状的广义遗传力差异大(杨荣仲等2016), 这暗示甘蔗分蘖的遗传力变化范围也较大, 容易受环境影响, 是由多基因控制的数量性状。Ming等(2002)首先定位到了有效茎数(与甘蔗分蘖成茎呈正相关的农艺性状)的数量性状位点(quantitative trait locus, QTL), 但其连锁图谱覆盖的基因组非常低。Hoarau等(2002)进一步鉴定了42个产量性状QTL, 分别为11个有效茎数QTL、16个茎径QTL和15个茎长QTL, 而且这些QTL的等位基因之间存在互作, 并解释了30%至51%这些性状的表型变异。Pribil等(2007)获得了63个可能表达了水稻或者甘蔗*TB1*基因的甘蔗转基因株系, 甘蔗*TB1*基因过量表达的株系分蘖有下降趋势, 但未达到显著水平; 此外, 转了*GA 2-oxidase*基因的甘蔗栽培品种的株高表型与其分蘖发生呈负相关性; 但转了*MAX3*基因的所有株系均表现出侧芽生长受抑制和株高下降的结果。目

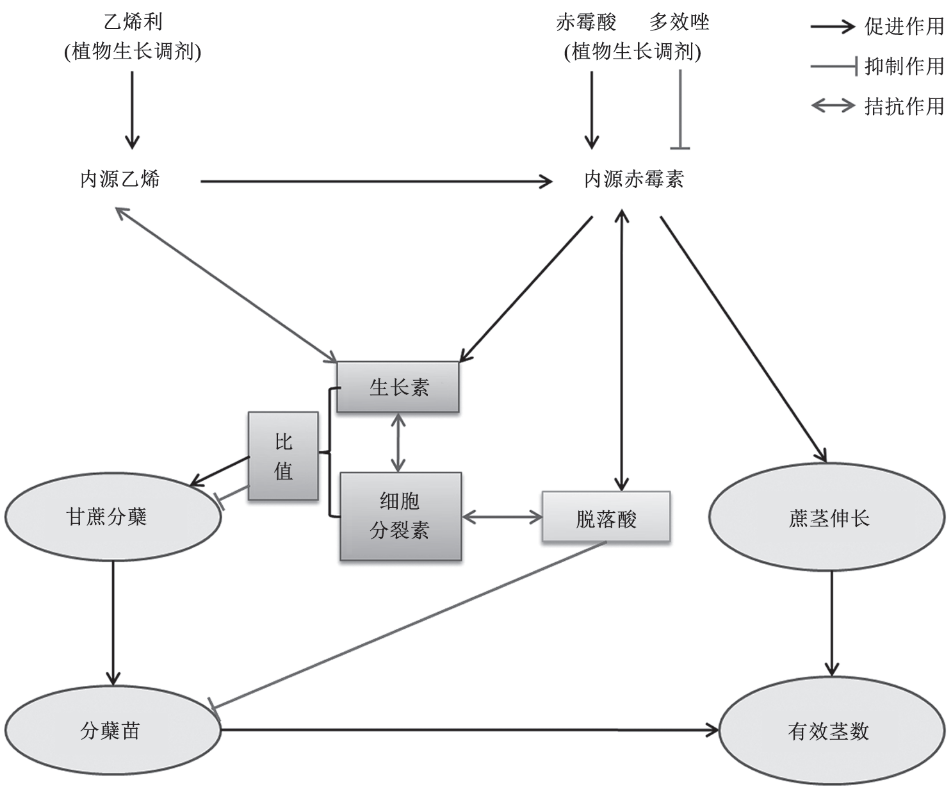

图2 植物激素调控甘蔗分蘖及成茎的臆想网络图

Fig.2 Phytohormone regulatory networks of tillering formation and stem forming from available tillers in sugarcane by conjecturing

前, 在禾本科作物上, *TAD1*、*D14*、*TB1*、*MOC1*、*FC1*等多个调控分蘖的重要基因已经被克隆和鉴定, 研究发现这些基因的功能主要分为3种, 一种是属于转录调控因子, 主要通过调控其他基因的转录来发挥作用; 一种是调控内源激素生物合成途径的关键基因, 通过调节植物激素含量及其平衡来发挥作用; 还有一种就是编码可在植物体内长距离运输的信号及次生代谢物质来起调节作用(刘杨等2011)。

目前, 在甘蔗上, 国内有研究报道, 通过RT-PCR和RACE技术克隆到了一些调控分蘖的同源基因, 比如甘蔗*KNOX*、*TB1*、*TAD1*和*MOC1*基因(李旭娟等2015a, 2015b, 2017a, 2017b)、*ScHTD2*和*ScF-box*基因(吕爱丽等2016, 2017)、*CCD8*基因(吴转娣等2016), 但仅对这些同源基因做了表达分析研究。Aitken等(2008)通过QTL定位, 并利用SSR和SNP标记作图, 鉴定认为甘蔗*TB1*基因并非控制甘蔗分蘖的主要基因, 它发挥着次要或者不确定性的作用。综上可知, 甘蔗分蘖与禾本科模式植物水稻的分蘖特性相似, 也是由多基因控制的数量性状, 而品种间的分蘖差异可能来源于这些基因间的表达情况及互作效应, 也有可能是基因与环境互作的结果。

6 展望

分蘖机理的研究对以收获茎、穗为主的禾本科作物生产实践的可持续发展具有重大的指导意义。分蘖期甘蔗分蘖数的多少在很大程度上决定了有效茎数, 而有效茎数是甘蔗产量的关键构成因素。随着禾本科模式植物水稻分蘖调控基因*MOC1*的成功克隆, 标志着分蘖的植物激素调控机理取得了突破性进展。

目前, 甘蔗分蘖在种植方式和栽培条件上的系统研究相对较成熟, 尤其是优良品种的配套栽培技术及管理措施; 在生理生化研究上也取得了一些研究成果(叶燕萍2006)。同时也同源克隆了一些甘蔗分蘖基因, 它们大多为独脚金内酯生物合成和信号传导途径中的组分, 仅进行了基因表

达分析研究, 但对基因的生物学功能验证缺乏进一步的探索, 且关于独脚金内酯在甘蔗中的合成、转运以及信号转导途径更是空白。不仅如此, 植物激素对甘蔗分蘖及其成茎的研究深度不够, 缺乏系统性分析。比如, 内源激素含量及平衡如何影响甘蔗分蘖芽的萌发及分蘖苗生长成茎; 激素间的互作在其中发挥着怎样的作用, 植物激素又如何与外界环境互作共同调控甘蔗分蘖的形成与生长发育, 尤其是光照、温度或者水分等环境因子怎样调控植物激素的信号途径还不清楚。随着现代分子生物学的快速发展, 有望通过现今先进的实验技术手段和生物信息学分析, 从转录组学、蛋白组学和代谢组学方面全面地阐述植物激素在甘蔗分蘖的发育过程中发挥了怎样的作用, 挖掘激素间互作的信号转导和代谢通路, 找出激素调控甘蔗分蘖的重要分子网络图谱。因此, 通过深入研究植物激素调控甘蔗分蘖的分子机理, 明确以上研究问题, 可指导利用植物生长调节剂定向调控甘蔗分蘖的发生及生长成茎, 促进形成合理的群体结构, 进而增加有效茎数, 提高甘蔗产量。

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Advances of regulation study on tillering formation and stem forming from available tillers in sugarcane (*Saccharum officinarum*)

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Abstract: Sugarcane is an important sugar crop mainly harvested stems which be above the ground, and sugar is stored in the internode of cane stems. Tillering is the key to the formation of millable canes in sugarcane. Therefore, it is one of the most effective ways to improve sugarcane yield through promoting tillering and accelerating stems development from tillers. At present, research on tillering mechanism has made breakthrough progress in rice. Sugarcane is also of the tillering character because tiller is a special type of branches in poaceae, but the relative researches of sugarcane tillering lag behind, especially the molecular regulation mechanism. In this paper, we particularly described the biological character of tillering and its current significance, as well as, summarized the results of tillering formation and growth and development of available tillers involving the aspects of cultivation techniques and related management, environmental conditions, plant growth regulators (phytohormones) and genetic factors in sugarcane. This work not only provides a new perspective for insight into the tillering regulation molecular mechanism of sugarcane, but also provides a theoretical basis for the high-yield cultivation technologies and molecular-assisted breeding in sugarcane.

Key words: *Saccharum officinarum*; tillering; number of millable canes; phytohormone; chemical regulation

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