

综 述 Reviews

独脚金内酯调控植物非生物胁迫响应的研究进展

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摘要: 独脚金内酯(strigolactones, SLs)是来源于类胡萝卜素合成途径的新型植物激素, 参与调节根系发育、分枝、生殖发育和叶片衰老等多种生物学过程。近年来, 研究发现SLs在植物响应养分、干旱和盐胁迫等方面发挥关键作用。本文主要对SLs信号及其作用机制的相关研究进行综述, 着重阐述SLs与脱落酸、生长素、细胞分裂素、赤霉素等激素交叉互作参与植物非生物胁迫响应调控机制, 为进一步明晰SLs信号参与抗逆调控提供新的研究思路。

关键词: 独脚金内酯; 信号转导; 激素; 非生物胁迫; 调控

植物在其整个生命周期中会遭遇包括生物和非生物在内的多种环境胁迫, 导致产量和品质下降, 严重威胁农业可持续发展和生态保护。植物感知胁迫信号后, 可通过调控自身抗逆信号途径重编程以应对不利条件。独脚金内酯(strigolactones, SLs)是近年来植物激素研究的热点之一, 在植物分枝和生长发育调控中起重要作用。SLs还可以作为根际信号分子, 诱导丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)的菌丝分枝, 刺激寄生杂草的种子萌发(Zwanenburg和Blanco-Ania 2018)。大量研究表明SLs广泛参与拟南芥(*Arabidopsis thaliana*)、水稻(*Oryza sativa*)、豌豆(*Pisum sativum*)、矮牵牛(*Petunia hybrida*)等植物根系统架构(root system architecture, RSA)、光形态建成、分枝、叶片衰老的调节(Urquhart等2015; Jia等2019)。近年来, 研究发现SLs在植物干旱、盐、营养缺乏等非生物胁迫响应中发挥关键作用(Zhuang等2017; Banerjee和Roychoudhury 2018), 相关研究正不断深入。本文概述了SLs的生物合成、转运和信号转导, 着重探讨SLs与脱落酸(abscisic acid, ABA)、生长素(auxin)、细胞分裂素(cytokinin, CK)、赤霉素(gibberlin acid, GA)等激素交叉互作参与植物非生物胁迫响应的机制, 以期今后SLs的相关研究提供一些参考。

1 SLs生物合成

SLs是一类来源于类胡萝卜素途径的脱辅基

类胡萝卜素(apocarotenoid)化合物, SLs的生物合成以类胡萝卜素为前体, 经脱氧、氧化等过程生成独脚金醇(strigol), 再由独脚金醇转化成具有生物活性的独脚金内酯类物质(Matusova等2005)。SLs可以分为典型(canonical)和非典型(noncanonical)两类, 典型SLs包含1个三环内酯(ABC环)和1个由烯醇醚键连接的单环内酯(D环), 而非典型SLs具有未闭合的BC环。多数典型SLs由4-脱氧邻苯二酚(4-deoxyorobanchol, 4DO)和5-脱氧三醇(5-deoxystrigol, 5DS)的衍生物组成, 二者分别具有邻苯二酚型和独脚金醇型SLs的最简结构(Yoneyama等2018)。研究表明类胡萝卜素异构酶D27 (DWARF 27)、类胡萝卜素裂解双加氧酶7 (carotenoid cleavedioxygenase 7, CCD7)和CCD8、细胞色素P450单加氧酶(cytochrome P450 monooxygenase, CYP450)及同源物(表1)参与SLs合成调控。D27、CCD7和CCD8将反式 β -类胡萝卜素转化为中间体己内酯(carlactone, CL) (Alder等2012; Seto等2014), 随后CL由MAX1 (MORE AXILLARY GROWTH1)编码的细胞色素P450单加氧酶及其同源物氧化生成CLA (carlactonoic acid) (Seto等2014; Brewer等

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表1 参与SLs生物和信号转导的相关基因及其编码蛋白功能

Table 1 Related genes and functions of their encoded proteins involved in SLs biology and signal transduction

类型		编码蛋白功能	基因来源及名称				参考文献
			拟南芥	豌豆	矮牵牛	水稻	
生物合成	β-胡萝卜素合成CL	类胡萝卜素异构酶	<i>AtD27</i>	—	—	<i>D27</i>	Lin等2009; Alder等2012
		类胡萝卜素裂解双加氧酶7	<i>MAX3</i>	<i>RMS5</i>	<i>DAD3</i>	<i>HTD1/D17</i>	Drummond等2009; Alder等2012; Abe等2014
		类胡萝卜素裂解双加氧酶8	<i>MAX4</i>	<i>RMS1</i>	<i>DAD1</i>	<i>D10</i>	Simons等2007; Alder等2012; Ligerot等2017
	CL合成SLs	细胞色素P450单加氧酶	<i>MAX1</i>	—	<i>PhMAX1</i>	<i>carlactone oxidase (Os01g0700900), orobanchol synthase (Os01g0701400), Os02g0221900, Os06g0565100</i>	Drummond等2012; Seto等2014; Zhang等2014
信号转导	信号感知	αβ折叠水解酶	<i>AtD14</i>	<i>RMS3</i>	<i>DAD2</i>	<i>D14/D88/HTD2</i>	Arite等2009; Hamiaux等2012; Nakamura等2013; Ligerot等2017
		F-box蛋白	<i>MAX2</i>	<i>RMS2</i> <i>RMS4</i>	<i>PhMAX2A</i> <i>PhMAX2B</i>	<i>D3</i>	Stirnberg等2007; Drummond等2012; Hamiaux等2012
	转录调节	抑制因子	<i>SMXLs</i>	—	—	<i>D53</i>	Jiang等2013; Zhou等2013
		转录辅阻遏物	<i>TPR2</i>	—	—	<i>TPL/TPR2</i>	Ke等2015; Jia等2018
		转录因子	<i>BRC1</i> <i>BRC2</i>	<i>PsBRC1</i>	—	<i>IPA1</i>	Soundappan等2015; Song等2017

—表示尚未报道。

2016)。后者再由甲基转移酶催化生成甲基化CLA (MeCLA), 最后由侧支化氧化还原酶(lateral branching oxidoreductase, LBO)催化生成类SLs化合物 (Brewer等2016)。然而, 水稻中CL在MAX1同源物CL氧化酶Os1400和SL异构酶Os900的连续作用后转化为列当醇(orobanchol), Os900和Os1400同属CYP711家族(Zhang等2014)。Wakabayashi等(2019)发现一种新型SLs合成关键酶细胞色素P450单加氧酶CYP722C, 液质联用分析的结果显示, CYP722C催化CLA中C-18位置的两步氧化生成18-oxo-CLA, 然后再通过BC环闭合反应合成邻苯二酚立体异构体。目前对SLs合成途径中CLA的下游调控机制仍不明确, 有待进一步研究。

2 SLs转运

SLs主要在根中合成, 茎、芽等组织中合成量极低(Visentin等2016)。根系SLs具有向芽远距离运输和向土壤分泌两种转运形式。Kohlen等(2011)研究发现拟南芥根系合成的SLs可通过木质部汁液转运到嫩芽; 而Xie等(2015)通过研究分析水稻木质部汁液列当醇和4DO水平, 认为上述两种SLs类似物可能通过其他途径由根转运到芽。根系SLs可通过短距离转运到土壤, 促进菌根形成, 增强根系养分吸收能力。转运蛋白在根系SLs转运或分泌过程中发挥关键作用, PDR1 (PLEIOTROPIC DRUG RESISTANCE 1)是第一个发现的胞内SLs

分泌转运体,属于ABC转运蛋白[ATP-binding cassette (ABC) transporter]超家族成员。研究表明,腋花矮牵牛(*Petunia axillaris*) *pdr1*突变体SLs分泌功能丧失,与真菌的共生作用减弱,突变体分枝增多,说明*pdr1*突变体SLs的转运分配功能受损(Kretzschmar等2012)。过表达*PDR1*上调根中*MAX1*和*DAD1*基因表达水平,显著促进侧根形成、根毛伸长、菌根形成,抑制叶片衰老(Liu等2017)。反之,外施SLs人工合成类似物GR24能上调*PDR1*的表达(Kretzschmar等2012; Sasse等2015)。细胞定位显示PaPDR1 (*P. axillaris* PDR1)蛋白具有特异性非对称特点,在根尖细胞中定位于下胚层细胞顶膜,可能介导SLs向芽快速转运;而在根尖以上部位主要存在于皮下通道细胞(hypodermal passage cells, HPCs)侧膜外层(Sasse等2015)。过表达*PaPDR1*抑制*PIN2* (*PIN-FORMED2*)表达,显著提高质膜*PDR1*/*PIN2*表达水平比例(Sasse等2015)。可见,PaPDR1极性定位有效调控SLs径向运输和根际外泌,PaPDR1蛋白与PIN2类似,可能具有多个细胞跨膜结构域,与PIN蛋白竞争靶向组分(Sasse等2015)。Shiratake等(2019)研究进一步证明PDR1蛋白可直接调节SLs短距离转运,而SLs长距离转运不直接依赖于PDR1,可能存在其他转运体。关于植物SLs长距离转运调控机制仍有待深入研究。此外,在烟草(*Nicotiana tabacum*)中存在一种与PaPDR1高度同源性的ABC转运蛋白NtPDR6,抑制NtPDR6表达会导致分枝增多,说明NtPDR6参与了调节SLs的转运(Xie等2014)。

3 SLs信号转导

SLs信号通路核心组分按功能分为激活因子和阻遏因子,分别包括MAX2/RMS4/D3、D14/D88/HTD2、TB1和D53/SMAXs(表1)。D3、D14/AtD14和MAX2主要起激活作用,D53和SMXL6/7/8(SUPPRESSOR OF MORE AXILLARY GROWTH2-LIKE 6/7/8)负调控SLs信号转导通路(Zhou等2013; Wang等2015)。SMXL6/7/8能与AtD14、MAX2以及TPR2 (TOPLESS-RELATED PROTEIN2)发生互作,抑制SLs早期响应基因*BRC1* (*BRANCHED1*)表达,且SMXL6/7与D14/AtD14相互作用受SLs及类

似物诱导(Wang等2015)。D14/AtD14是一种 α/β 水解酶受体,含有1个催化三联体形成的空腔,开放状态下可以绑定SLs信号分子(Arite等2009; Yao等2016)。D3蛋白是Skp-Cullin-F-box (SCF) E3泛素连接酶复合物关键组分,D53蛋白可与D14、D3互作,也可与转录辅阻遏物TPR发生相互作用,据此建立基于D14-D3复合物介导D53降解的SL信号转导核心模型(图1) (Jiang等2013; Zhou等2013)。D14/AtD14催化ABC环的去除反应,使D环与D14/AtD14的催化腔保持紧密且发生不可逆结合。同时,D14/AtD14构象改变使其处于“封闭状态”,与基于D3/MAX2的SCF (Skp1-Cullin-F-box)复合物互作形成D14-SCF^{D3/MAX2}复合体(Yao等2016),进而多泛素化转录阻遏物D53/SMXL6/7/8,再由D53-D14-SCF^{D3/MAX2}复合物触发26S蛋白酶体介导D53/SMXL6/7/8的降解,激活SLs信号转导途径(Yao等2016; Waters等2017)。

转录因子和转录调节因子是信号通路中的重要开关。目前有关SLs信号通路下游的调节因子尚不十分明确。已有研究表明TCP (TEOSINTE BRANCHED1/CYCLOIDEA/PROLIFERATING CELL FACTOR)家族转录因子在D53/SMXLs信号下游起作用(Zhao等2018)。SPL (SPOROXYTE-LESS)作为适配器样转录抑制因子,通过招募TPL/TPR (TOPLESS/TOPLESS-RELATED)共抑制因子来抑制TCP转录因子的活性(Wei等2015)。TCP功能缺失突变体分枝或分蘖增加,外施GR24无法使其恢复正常表型(Soundappan等2015)。拟南芥*max3 max2*突变体中*BRC1*表达水平下调,*smxl6 smxl7 smxl8*突变体的*BRC1*及靶基因*HB53*表达上调(Wang等2015)。最近在野棉花(*Anemone vitifolia*)中发现TIE1 (TCP interactor containing EAR motif protein 1)可与GhBRC1、GhBRC2和GhTCP13等转录因子发生互作,瞬时双荧光素酶检测表明GhTIE1抑制GhBRC1和GhTCP13蛋白活性,从而降低靶基因*GhHB21*、*HB40*和*HB53*的活性来调控分枝(Diao等2019)。TCPs与D53/SMXLs之间是否发生直接互作仍不清楚。IPA1 (ideal plant architecture 1)是SMXLs/D53下游转录因子,*IPA1*功能缺失突变体分蘖数增多,且对外施GR24不敏感,D53蛋白可

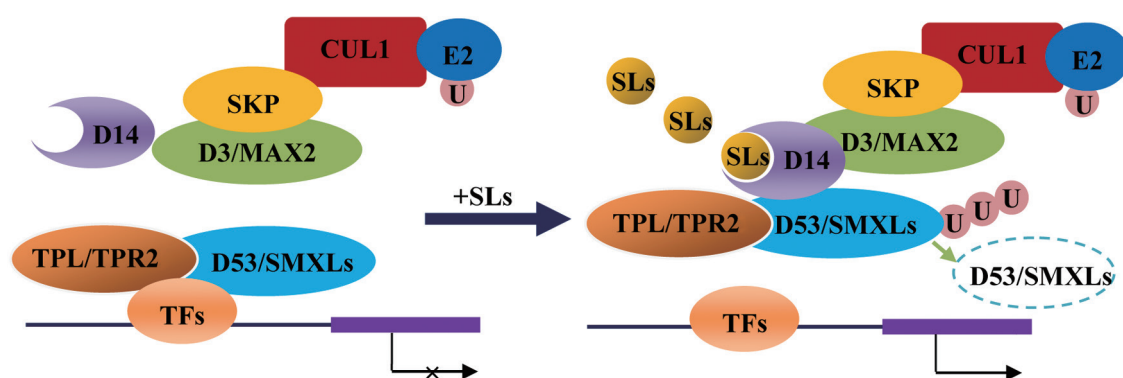


图1 独角金内酯信号转导途径核心模型

Fig.1 Core model of SLs perception and signaling pathway

参照Wang等(2015)和Jia等(2019)文献修改。转录抑制因子D53/SMXLs和辅抑制因子TPL/TPR2与SLs途径相关转录因子相互作用, 抑制其转录活性, 抑制下游靶基因的表达。SLs与受体D14的结合促进后者与D3/MAX2和D53/SMXLs进一步相互作用, 形成三元复合物, 使D53/SMXLs发生多泛素化, 最终被26S蛋白酶体降解, 从而解除D53/SMXLs对SLs信号转导的抑制, 激活SLs诱导的应答基因。

直接与IPA1蛋白相互作用, 抑制IPA1的转录激活活性, 从而抑制下游基因表达。IPA1也能直接结合D53的启动子并激活D53基因的表达, 从而形成负反馈调节(Song等2017)。另外, 科学家在独角金(*Striga hermonthica*)中发现一种与AtD14同源的ShHTL7 (hyposensitive to light)蛋白, ShHTL7被SLs及类似物感知, 将SLs及类似物水解为中间活性分子CLIM (a covalently linked intermediate molecule), 后者与ShHTL7共价结合启动SLs途径下游的信号转导(Yao等2017)。这种新型配体-受体互作方式为该领域研究开辟了新途径。

4 SLs通过与激素信号途径交叉互作响应非生物胁迫

4.1 与ABA互作

不同激素以及激素间的交叉互作在植物响应干旱、高盐或者低温等逆境胁迫的过程中发挥关键作用。近年来, 越来越多的实验证明SLs和ABA之间存在直接或间接互作, 共同调节植物非生物胁迫响应(图2)。

ABA影响植物体中SLs的生物合成。ABA生物合成限速酶NCED (9-*cis*-epoxycarotenoid dioxygenase)和CCD同属于类胡萝卜素裂解加双氧酶家族, CCD7和CCD8是SLs合成关键酶。López-Ráez等(2010)研究发现CCD抑制剂D2降低番茄

(*Lycopersicon esculentum*)根中SLs含量, 对ABA含量无影响; NCEDs抑制剂abamine SG可同时抑制ABA和SLs的合成。*notabilis/sitiens/flacca*突变体中的ABA和SLs含量显著减少, *SICCD7*和*SICCD8*基因表达下调, 说明NCEDs、AAO和钼辅因子(molybdenum cofactor, MoCo)可能参与调控SLs生物合成。ABA8'-羟化酶(ABA8'-hydroxylases, ABA8'-OH)通过氧化分解调节内源ABA水平, 抑制ABA8'-OH1/3活性, 显著促进ABA的积累, 并下调*D27*、*MAX1*、*CCD7*和*CCD8*基因的表达, 大幅降低根中SLs水平(Wang等2018)。反之, SLs通过反馈机制调控ABA水平。干旱胁迫下, 外施GR24可抑制百脉根(*Lotus japonicus*) *NCED*、*AAO*、*SDR1*等ABA生物合成相关基因的转录(Liu等2015), 同时激活ABA分解代谢相关基因*BGI*的表达, 抑制ABA转运蛋白基因*ABCG25*和*ABCG40*转录, 降低体内ABA水平(Ferrero等2018)。另有研究发现干旱胁迫下外施GR24可提高葡萄(*Vitis vinifera*)叶片*NCED1*、*CCD7*、*CCD8*及*BRC1*表达水平, 抑制*VvHYD1*和*VvHYD2*转录(Min等2019)。此外, Toh等(2012)发现热胁迫下外施GR24下调*NCED9*基因表达, 降低拟南芥种子内ABA水平。推测植物体中可能存在一种基于胁迫诱导的SLs与ABA水平调节机制。

SLs可作为气孔运动的调控因子, 与ABA共同

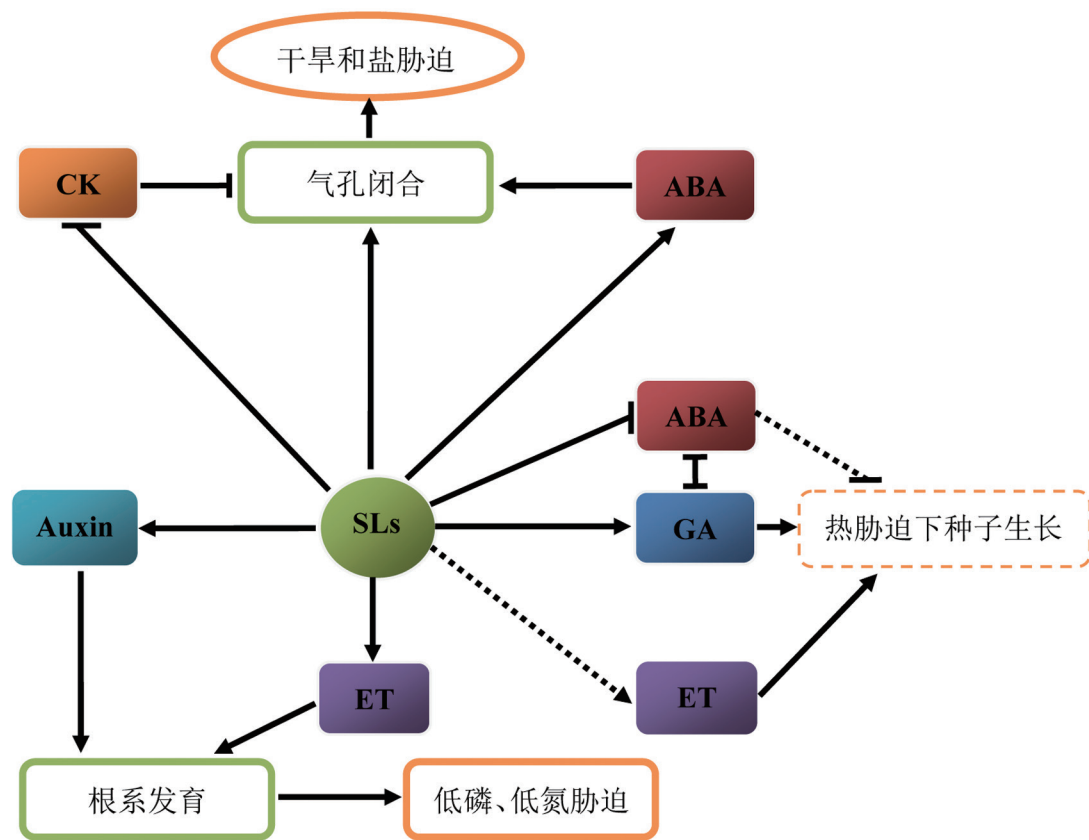


图2 独角金内酯与其他激素互作参与植物非生物胁迫的调控网络

Fig.2 Interaction of strigolactones with other hormones involved in the regulation network of plant abiotic stress

参照Mostofa等(2018)文献修改。SLs与ABA、CK协同调控植物气孔关闭响应干旱和盐胁迫; SLs与生长素和ET互作调节低磷或低氮胁迫下根的生长发育; SLs与ABA、GA和ET协同调控高温胁迫下种子的萌发生长。→和⊥分别代表激活和抑制作用。---→和⊥分别代表可能的激活和抑制作用。

调节水分胁迫下叶片的气孔关闭(Ha等2014; Liu等2015)。许多植物 sl 合成缺陷和信号转导突变体气孔闭合对ABA的敏感性下降, 而对于干旱胁迫高度敏感。干旱胁迫下拟南芥 $max2$ 突变体幼苗相比野生型气孔开度和气孔密度无变化, 角质层变薄, 但气孔闭合对ABA不敏感, 过表达 $MAX2$ 植株的表型无明显变化(Bu等2014)。 $max2$ 突变体中 $COR47$ 、 $RD29A$ 、 $RD29B$ 、 $KIN1$ 、 $RAB18$ 等受ABA诱导的干旱应答基因表达下调, 同时 $NCED3$ 、 $ABCG22$ 、 $ABII1$ 、 $HAB1$ 等ABA合成、转运和转导相关基因转录同样受抑制(Bu等2014)。在百脉根中, 与野生型相比 $LjCCD7$ 沉默植株气孔密度相当, 气孔导度增加, 气孔关闭对ABA的敏感性降低, 对PEG介导的渗透胁迫耐受性减弱(Liu等2015)。然而, 野生

型和 $LjCCD7$ 沉默植株ABA水平差异较小, 两者气孔对ABA敏感性的差异可能受ABA向保卫细胞转运能力影响。正常或胁迫条件下, 拟南芥 $max2$ 突变体叶片ABA转运相关基因 $ABCG22$ 和 $ABCG40$ 下调表达, 保卫细胞对外源ABA低敏感(Bu等2014; Ha等2014)。外施GR24预处理下调 $LjNCED2$ 的表达, 抑制渗透胁迫下野生型植株根ABA的生物合成。同时, $LjD27$ 、 $LjCCD7$ 、 $LjCCD8$ 、 $LjMAX1$ 和 $LjPDR1-226$ 表达水平也显著降低, 表明GR24负反馈调节SLs生物合成和转运(Mashiguchi等2009; Liu等2015), 外施GR24上调 $LjPDR1-295a$ 和 $LjPDR1-345$ 表达, 说明SLs转运受 $LjPDR1-295a$ 和 $LjPDR1-345$ 调控, 这与Kretzschmar等(2012)和Sasse等(2015)的结论一致。Visentin等(2016)研究发现 $SICCD7$ 基

因沉默使番茄植株根中SLs生物合成受抑制,降低了根中SLs水平。低水平SLs可能作为一种应激信号被传递至嫩芽,调节芽中*CCD7*和*CCD8*的表达,增强局部SLs的合成能力,显著提高气孔对ABA的敏感性,提升植株对干旱胁迫的耐受性,此过程可能与ABA长距离运输无关。此外,盐胁迫下SLs和ABA共同依赖H₂O₂、NO (nitric oxide)以及SLAC1 (slow anion channel associated 1)蛋白介导气孔关闭(Lü等2018),ABA主要依赖于气孔开放因子1 (stomatal opening factor 1, OST1)和MPK9/12 (MAP kinases 9/12)参与调节气孔运动,在植物逆境响应中扮演重要角色,OST1在SLs信号通路中是否发挥关键作用值得研究。

D27可能在SLs和ABA生物合成调控中扮演关键角色。研究发现干旱胁迫可同时诱导水稻根合成和积累SLs和ABA, *d3/d10/d17*突变体ABA水平显著高于野生型,而*d27*突变体叶片ABA水平不受干旱胁迫诱导,耐旱性较差;正常条件下,过表达*OsD27*显著提高根系ABA水平,而*d27*突变体与野生型接近(Haider等2018)。上述研究说明D27是SLs和ABA信号途径交叉互作的关键节点基因,深入研究不同类型胁迫下D27如何调控SLs和ABA水平,可为利用D27作为靶标基因进行作物抗逆分子改良提供参考。MAX2属F-box蛋白,为SL信号途径的重要组分,参与调控植物生长及胁迫响应。相比拟南芥*max3/max4*突变体, *max2*突变体对干旱胁迫高度敏感,而对ABA的敏感性明显低于野生型(Ha等2014)。推测MAX2可能在ABA信号及逆境胁迫响应调控中也发挥重要作用。进一步分析表明MAX2基因在ABA信号途径中ABI3和ABI5的上游起作用,在种子萌发期负向调节ABA途径,在幼苗期对ABA途径及干旱、渗透胁迫响应起正向调节作用(Bu等2014)。此外, karrikin信号途径KAI2基因也参与ABA信号及胁迫响应的调节(Bu等2014; Soundappan等2015; De Cuyper等2017), KAI是karrikin受体,干旱胁迫下, *kai2*突变体花色苷生物合成能力下降,气孔关闭对ABA不敏感,为KAI2和ABA信号途径交叉互作调控植物干旱胁迫响应提供相关证据(Li等2017),耐旱性分析显示,相比*d14/kai2*单突变体*d14 kai2*双突变体对干旱更

为敏感(Li等2017)。推测SLs、ABA下游信号元件之间可能存在复杂的互作关系。

此外, SLs和ABA参与类黄酮合成的调控,增强植物耐旱性(Ito等2015)。Ha等(2014)研究发现干旱胁迫下拟南芥*max2*突变体中*PAP1/MYB75*、*CHS*、*FLS1*、*DFR*等黄酮类合成相关基因表达水平下降,外施ABA不能恢复其野生型表现(Ha等2014),然而SLs和ABA在调控葡萄成熟期果实花色苷合成途径中表现强烈的拮抗效应(Ferrero等2018),说明SLs和ABA互作调控花色苷合成途径,推测SLs可能通过依赖或不依赖ABA途径调控非生物胁迫响应。此外,ABA信号通路的重要激活因子HY5 (elongated hypocotyls 5)的转录也受SLs调控(Tsuchiya等2015),HY5是否参与SLs-ABA交叉互作调控网络值得研究。

4.2 与生长素互作

SLs与生长素及CK协同控制植物的分枝或分蘖数量。Hayward等(2009)通过突变体嫁接试验发现生长素信号依赖AXR1 (auxin resistance 1)途径上调根中MAX3和MAX4基因表达,伴随极性运输中生长素水平的增加,芽基因型对MAX3和MAX4转录水平有一定程度影响。说明生长素和独角金内酯可相互调节含量和分布。Ligerot等(2017)发现RMS2介导豌豆从芽到根的反馈信号通路,生长素依赖RMS2途径上调表达SLs生物合成相关基因,SLs依赖RMS3和RMS4抑制生长素的生物合成和木质部介导的转运,据此形成一个内稳态的反馈回路,参与豌豆根系发育和分枝调控。另有研究表明水稻中SLs不改变生长素生物合成,但可负调控生长素转运抑制芽的生长(Zha等2019)。

SLs可作为生长素转运的重要调节因子或第二信使。PIN蛋白定位于质膜,介导生长素由胞内向胞外运输,决定植物中生长素浓度梯度分布。而SLs干扰生长素极性运输(polar auxin transport, PAT),并通过PIN介导的渠道运输机制调节生长素组织间的水平分布(Sun等2014)。热胁迫下,外施G24或NAA抑制剂NPA显著下调TIR1 (transport inhibitor response 1)、PIN1、PIN2、PIN5等生长素胞外转运标记基因的表达水平,与NPA相比外施G24显著影响PIN5基因的表达水平(Hu等2018)。NAA促进

SLs信号转导相关基因*D3*和*D14*的表达, 而NPA有显著抑制作用(Sun等2015; Hu等2018), 说明SLs通过抑制*PIN*基因表达破坏生长素向胞外转运和极性运输, 抑制芽生长激活, 促进根系发育。然而, 豌豆*sl*合成缺陷突变体中生长素运输受阻对侧芽发育没有抑制作用(Brewer等2015)。推测SLs可能通过不依赖PAT的途径调控腋芽的生长发育。

已有研究表明在氮、磷营养胁迫下, SLs与生长素协同调控植物根和芽的生长发育。SLs可调节局部组织的生长素水平, 并依赖于生长素分布状态发挥作用。低磷胁迫下GR24抑制根尖*PIN1*、*PIN3*和*PIN7*基因表达, 外施生长素可抵消GR24的抑制效应, 但不影响*PINs*基因的表达水平, 进一步分析表明SLs与生长素互作协同调节根冠比(Ruyter-Spira等2011)。此外, 外施GR24可恢复氮、磷营养胁迫下野生型、*d10/d27*突变体种子根的正常表型, 对*d3*突变体无明显作用, 低磷、低氮或外施GR24减少了 $[^3\text{H}]$ IAA的转运, 下调野生型和*d10/d27*突变体*PIN1a-b*、*PIN5a*、*PIN9*、*PIN10a*基因的表达, 说明低磷和低氮胁迫下SLs依赖于D3和生长素极性运输调控水稻根系发育(Sun等2014)。磷饥饿促进菊花(*Dendranthema grandiflorum*)根系合成SLs, 促进根系生物合成的SLs向顶侧运输(Xi等2015); 另外对茎段进行生长素和磷酸盐处理发现, 在无外源生长素的情况下, 磷酸盐激发SLs信号通路的局部响应, 上调*DgCCD7*、*DgCCD8*、*DgMAX2*和*DgBRC1*基因表达, 延迟或抑制腋芽生长, 外源生长素可拮抗磷酸盐的响应, 推测磷限制条件下SLs与生长素协同调节菊花分枝发育(Xi等2015)。在拟南芥中研究发现氮素形态和有效性影响拟南芥分枝, 低水平硝酸盐和铵根均能增加芽中生长素的输出量, 延迟腋芽激活, 在主茎中形成自上而下的生长素水平梯度, 进而抑制分枝生长(de Jong等2014)。而在低氮胁迫条件下*max1*突变体茎基部分枝数量增多, 地上部和根系生物量减少, 且根系减少量相对较小, 表明生物量分配由地上部向根系转移。进一步分析发现低氮条件下拟南芥通过依赖*AXR1*而不依赖*MAX1*的途径抑制芽的生长, 说明氮胁迫条件下*max1*突变体茎部生长素敏感性发生变化, 这与生长素向下运输受阻相关, 推

测SLs合成可能在维持质膜PIN1蛋白恒定水平上起关键作用, 维持生长素稳态(de Jong等2014)。Revalska和Iantcheva (2018)揭示了低磷和高磷胁迫下生长素与SLs之间的相互作用。低磷胁迫下, 相比野生型, 过表达*MtLAX3*和RNAi蒺藜苜蓿(*Medicago truncatula*)植株侧根数量增加, 主根长度减少, 生长素转运蛋白编码基因*MtLAX3*和SLs生物合成基因*MtMAX2*、*MtMAX3*上调表达, 而高磷胁迫抑制*MtLAX3*、*MtMAX2*和*MtMAX3*基因的表达。推测低磷胁迫信号激活*MtLAX3*表达, 并促进*MtLAX3*将生长素从细胞膜运输到细胞中, 激活磷酸盐级联反应, 刺激次生根生长, 抑制主根伸长。

4.3 与CK互作

CK与SLs间的相互作用具有植物组织特异性。CK与SLs在根中相互独立(Rasmussen等2012), 在腋芽激活和分枝生长中相互拮抗, 但在侧根发育调节中协同作用(Manandhar等2018)。研究表明CK可诱导SLs的生物合成, 而SLs相关基因介导CK的生物合成和转运, IPT3 (isopentenyltransferase 3)是CK生物合成限速酶, *max2/max4*突变体中*IPT3*基因的表达水平增加, 证明SLs负调控CK的生物合成过程, 而干旱胁迫促进*ahp2/ahp3/ahp5*突变体中*MAX3*和*MAX4*基因表达水平下调, 表明CK信号与SL生物合成相关(Nishiyama等2011)。这些发现支持激素间存在复杂稳态调节机制。

CK及其信号元件负调控植物干旱和盐胁迫响应。CK调控气孔密度是植物适应干旱的重要机制(Li等2019)。此外, CK信号抑制脂肪酸合成相关基因*FAD3/FAD8* (fattyacid desaturase 3/8)、蜡质生物合成相关转录因子SHN1/SHN3 (SHINE1/3) (Nishiyama等2011; Nguyen等2016), 提示CK信号可能通过减少角质层的形成而负调控干旱响应。SLs与CK在调控干旱胁迫响应中作用相反, *sl*缺失或信号转导突变体气孔密度、气孔开放程度均增加(Ha等2014; Visentin等2016; Zhang等2018)。相比*ck*突变体, *sl*突变体的ABA敏感性降低, 花青素合成减少, 分枝增加, 根长缩短(Ha等2014; Ito等2015)。研究认为CK氧化酶/脱氢酶基因*CKX1* (cytokinin oxidase/dehydrogenase 1)、*CKX2*、*CKX3*和*CKX4*与ABA响应相关(Nishiyama等2011)。然而,

干旱胁迫下*CKX1*、*CKX2*、*CKX3*、*CKX5*基因在*max2*突变体中下调表达(Ha等2014), 暗示SL与ABA和CK之间通过某种复杂的协同机制调控植物干旱胁迫响应。此外, 低磷胁迫下GR24增强*PIN*基因的表达, 同时*AHK3* (*ARABIDOPSIS HISTIDINE KINASE 3*)、*ARR1* (*ARABIDOPSIS RESPONSE REGULATOR 1*)和*ARR12*介导*SHY2* (*SHORT HYPOCOTYLS 2*)下调表达, 促进侧根生长发育(Goh等2012), 而*shy2/max2*突变体对CK的敏感性降低, CK促进*SHY2*表达, 而生长素抑制*SHY2*表达(Koren等2013)。因此*SHY2*可能作为生长素、CK和SLs信号整合的核心组分。

4.4 与GA互作

由于SL和GA信号转导均依赖于 α/β 水解酶和E3泛素连接酶介导的蛋白降解(Lopez-Obando等2015), SLs与GA信号转导的分子机制比较相似(Waters等2017)。活性GA和GID1 (gibberellin insensitive dwarf 1)结合促使GID1与SLR1/RGA互作, 形成的GID1-SLR1/RGA复合体被F-box蛋白GID2识别并结合, 再由SCF E3泛素化连接酶介导SLR1/RGA的降解(Daviere和Achard 2016)。而SL信号途径被D14激活, 与D3/MAX2共同作用促进D53/SMXLs降解(Jiang等2013; Soundappan等2015; Yao等2016)。GID1和D14均属于 α/β 水解酶, DELLA蛋白SLR1 (silender rice 1)可与SL受体D14相互作用, 调控SL信号途径, 而DELLA蛋白与SL受体结合抑制GID介导的GA信号转导(Nakamura等2013)。

SLs合成途径受GA调控。GA₁、GA₃、GA₄抑制根中SLs生物合成相关基因*D27*、*D10*和*D27*转录, 降低SLs类似物4DO的水平, 从而抑制寄生性杂草萌发(Ito等2017)。RNA-seq分析发现*gal1/max1/max3*突变体*GA2ox2* (gibberellin2 oxidase 2)、*BRC1*以及*SMXL8*的转录水平发生协同改变, GA与SLs在ABC转运蛋白合成调控中发生拮抗效应(Lantzouni等2017)。热胁迫下, SLs抑制拟南芥ABA合成和积累, 进而促进GA合成, 降低ABA/GA比例(Toh等2012)。进一步分析表明外施GR24增强野生型植株*GA3ox2*基因的表达, 显著提升GA₄水平, 但外施GR24不影响*max2*突变体的GA₄水平, 不能恢复*GA3ox2*基因的正常表达, 说明MAX2信

号是SLs-GA互作的关键调控因子, SLs参与GA信号调控涉及GA生物合成激活和代谢抑制(Toh等2012)。因此, 推测SLs可作为GA的调节信号, 促进热胁迫下寄生性或非寄生性种子萌发。然而, SLs是否与其他植物激素参与调控高温或热胁迫响应尚不明确。研究表明转录因子OSH1 (*Oryza sativa* homeobox 1)可与DLT (dwarf and low-tillering)协同负调控BR信号通路, 介导植物非生物胁迫响应, 平衡生长发育(Song等2018), GA缺陷和SL信号突变体中OSH1均参与调控水稻的分枝和分蘖(Lo等2008; Gao等2009), 为SLs-GA信号交叉互作提供了新思路, 但目前仍未发现GA与SLs信号下游组分间的直接分子联系。

5 展望

SLs作为一种新型植物激素, 已成为当前激素调控植物生长和发育领域的研究热点。研究者已分离鉴定了大量基本分子结构相同的SLs类化合物, 但其生物学功能存在差异, 因此, 研究SLs结构与生物学功能之间的相关性具有重要的意义。目前在SLs的生物合成和信号转导方面有较多的研究报道, D27和MAX1在SLs合成途径中的具体位置和作用仍不确定, 可能受不同物种的影响而导致功能出现差异。科学家已经成功构建了基于D14-D3复合物介导D53降解的SL信号转导核心模型, 然而具有SLs代谢活性的 α/β 水解酶D14如何与D3相互作用介导转录抑制因子D53的泛素化过程仍不十分明晰。转录因子在激素信号通路中起重要作用, 目前有关SLs信号通路下游的转录调节因子及其调控机制研究进展较慢, 已鉴定BRC1、BRC2、IPA1、TCP、TIE1等转录因子, 需加强新型转录因子的挖掘与鉴定研究, 转录抑制因子D53/SMAXs如何调控其下游转录因子介导SLs信号转导的分子机制仍不明确。SLs与ABA、生长素、CK、GA等植物激素交叉互作调节植物生长发育, 在干旱、低磷/氮、盐、高温等非生物胁迫响应中起重要作用。其中SLs与ABA互作研究较多, 且多集中于两者协同调节干旱或渗透胁迫下植物叶片气孔的闭合, 但仍有许多问题值得深入研究, 譬如胁迫条件下D27如何介导SLs和ABA生

物合成调控, OST1、HY5等转录因子如何在SLs和ABA信号通路协同发挥调控作用。由于SLs信号转导的“去抑制化激活”机制与生长素、赤霉素、茉莉酸等重要激素的信号转导激活机制类似,这必将加快SLs与其他激素之间的交叉互作研究。相信随着科研工作的深入和技术手段的进步,SLs的生物学功能必将更加明确,从而为植物生长发育的调控提供新的研究思路 and 理论指导。

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Advances in the regulation of plant abiotic stress response by strigolactones

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Abstract: Strigolactones (SLs) is novel plant hormone which derived from carotenoid synthesis pathway. It is mostly involved in regulating root development, branching, reproductive development, leaf senescence and other biological processes. In recent years, studies have also found that SLs plays a key regulatory role in plant response to nutrient, drought and salinity stress. Here, we summarized research progresses about SLs signal and its regulatory mechanism, especially the crosstalk of SLs and other plant hormone such as abscisic acid, auxin, cytokinin, gibberellin acid during the response to abiotic stress in plant. Understanding the network of SLs signaling might provide new insights to plant response mechanism to environment.

Key words: strigolactones; signaling transduction; hormone; abiotic stress; regulation

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