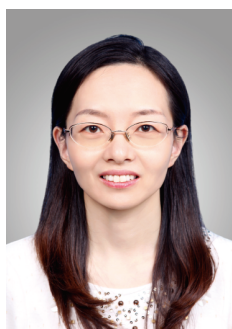


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独脚金内酯在植物中的功能及其农业应用

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摘要: 独脚金内酯(strigolactones, SLs)是一类由 β -胡萝卜素衍生而来的植物激素,在植物中广泛存在,在调控植物生长发育与环境适应性中发挥关键作用。SLs通过转运蛋白调控其分布及分泌过程,通过信号转导途径发挥抑制植物分枝发育、调节根系构型、响应多种非生物胁迫等功能,同时也是植物与菌根真菌、寄生植物互作过程中的重要根际信号。因其在农业生态系统中的多重功能,SLs成为作物改良和可持续农业领域的研究热点。本文系统综述了SLs的生物合成、运输及信号通路,探讨了其在作物株型改良、环境适应性提升、共生互作调控和寄生杂草防控中的应用潜力及未来研究方向。

关键词: 独脚金内酯;植物激素;生物合成;转运;信号转导;农业应用

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Functions and agricultural applications of strigolactones

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Abstract: Strigolactones (SLs) are a class of phytohormones that play an important role in plant growth, development, and responses to environmental stress. They also function as rhizosphere signalling molecules that modulate interactions with arbuscular mycorrhizal fungi and parasitic plants. SL biosynthesis originates from all-*trans*- β -carotene and proceeds through a series of conserved enzymatic reactions to generate the core intermediate, carlactone (CL). Cytochrome P450 oxidases and methyltransferases then catalyse CL to produce a range of structurally diverse SLs, including both

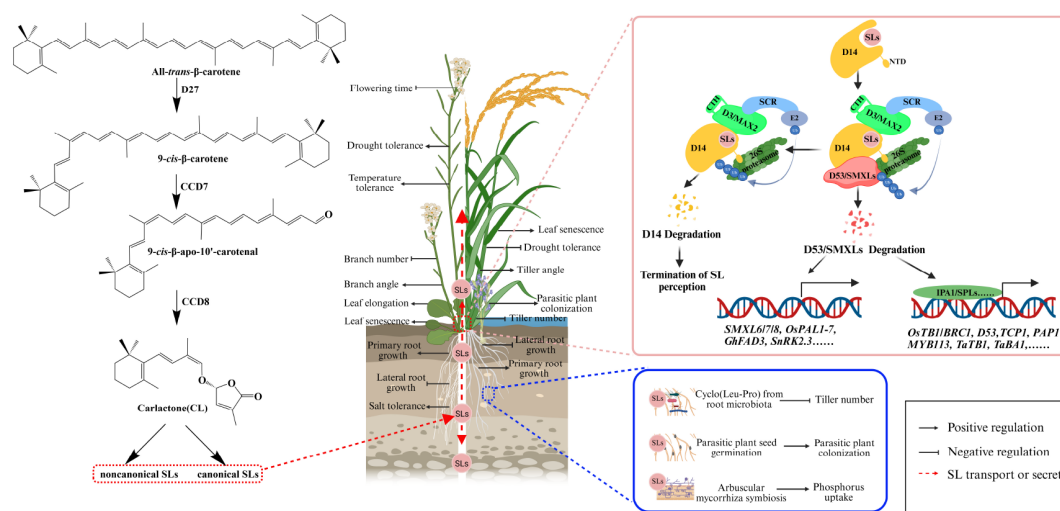
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canonical and noncanonical SLs. Specific ABCG family transporters regulate the SL distribution within plants and their secretion into the rhizosphere. SL perception relies on the formation of a complex composed of the receptor D14, the F-box protein D3/MAX2, and the transcriptional repressors D53/SMXLs. The D3/MAX2 protein promotes the degradation of D53/SMXLs, thus activating the signal transduction. Subsequently, D3 mediates the ubiquitination and degradation of D14, thereby triggering the termination of signal perception. These dual roles enable D3 to precisely regulate the intensity and duration of SL perception. SLs inhibit branch number, promote branch angle, and regulate internode elongation and leaf development, thereby optimizing shoot architecture. SLs promote primary root elongation and inhibit lateral root formation, thus modulating root architecture. Moreover, the SL pathway is involved in responses to abiotic stress, primarily by regulating the antioxidant enzyme activities, stomatal movements, anthocyanin accumulation, and interactions with other hormones. Furthermore, the biosynthesis and secretion of SLs play an indispensable role in establishing the symbiosis with arbuscular mycorrhizal fungi and triggering seed germination of parasitic plants. This article provides a systematic review of the biosynthesis, transport, and signalling pathways of SLs and discusses their potential applications in optimizing crop architecture, enhancing environmental adaptability, promoting symbiosis, and controlling parasitic weeds. It also outlines directions for future research.



Key words: strigolactones; plant hormones; biosynthesis; transport; signal transduction; agricultural applications

独脚金内酯(strigolactones, SLs)是由类胡萝卜素衍生的一类萜类内酯,在植物生长发育以及根际信号传递中发挥重要作用。SLs最初在棉花(*Gossypium hirsutum*)根际分泌物中被发现,并被证实能够促进独脚金(*Striga*)等寄生植物种子萌发^[1],促进丛枝菌根真菌(arbuscular mycorrhizal fungi, AMF)分枝和菌根共生^[2],因此被鉴定为一种根际信号。随后,研究人员在对一系列多分枝突变体如豌豆(*Pisum sativum*)的*ramosus(rms)*突变体、拟南芥(*Arabidopsis thaliana*)的*more axillary growth(max)*突变体、水稻(*Oryza sativa*)的*dwarf(d)*和*highly-tillering dwarf 1(htd1)*突变体、矮牵牛(*Petunia hybrida*)的*decreased apical dominance(dad)*突变体的研究中发现,SLs具有抑制植物分枝/分蘖的内源功能^[3-7],且在极低浓度下即可在体内发挥高效的调控作用,因而于2008年SLs被正式认定为一种新的植物激素^[8,9]。

1 独脚金内酯生物合成

1.1 独脚金内酯的保守合成途径

在鉴定出棉花分泌物中SL分子的化学结构与构象后^[10,11],不同结构的SLs陆续从多种物种中被分离出来^[12,13]。部分SLs具有完整的ABC环,而另一类则不具备完整的ABC环,但二者均保留与生物活性密切相关的烯醇醚桥和D环结构。基于这种结构特征,SLs可分为两类:具有完整ABC环的经典SLs与ABC环不完整的非经典SLs;同时,根据C环立体异构的不同,又可分为β-构型的独脚金醇型与α-构型的列当醇型^[12,13]。

尽管在不同物种中SLs结构有非常大的差异,它们的初始合成路径是保守的,所有SLs具有相同的合成前体:全反式-β-胡萝卜素^[12,14,15]。首先,β-胡萝卜素异构酶DWARF27(D27)将全反式-β-胡萝卜素异构为9-顺式-β-胡萝卜素^[16]。随后,类胡萝卜素裂解双加氧酶7(carotenoid cleavage dioxygenase 7,

CCD7)和CCD8顺序反应将9-顺式- β -胡萝卜素转化为己内酯(carlactone, CL)^[16]。不同的物种中后续参与催化反应的酶不同,从而造成了不同物种中SLs的多样性(图1)。

1.2 独脚金内酯的物种特异性合成途径

水稻中有5个拟南芥MAX1(more axillary growth 1)的同源蛋白(Os900、Os1400、Os1500、Os1900、Os5100),可催化CL生成CLA,随后Os900催化CLA生成4-脱氧独脚金醇(4-deoxyorobanchol, 4DO), Os1400能够将4DO转化成为列当醇(orobanchol, ORO), 4DO和ORO均属于经典SL(图1A)^[17,18]。水稻Os900和Os1400的突变显著减少了根系分泌物中经典SLs的含量,而茎秆高度与野生型类似,且水稻分蘖甚至更少,暗示经典SLs可能在根际微环境中发挥外源信号作用,其他具有SL活性的分子具有调控水稻分蘖的功能(图1A)^[19]。此外,水稻细胞色素P450氧化酶OsCYP706C2催化CL形成非经典SL:4-oxo-MeCLA(图1A), *Oscyp706c2*突变系没有矮化多分蘖表型,但侧根数量减少,根浸出液不会影响独脚金种子的萌发,但会抑制菌根真菌的共生^[20],暗示4-oxo-MeCLA在调控不同的株型特征以及共生、寄生关系上存在特异性。

在番茄(*Solanum lycopersicum*)中,拟南芥MAX1的同源基因SIMAX1同样能够催化CL在C-19位发生连续氧化生成CLA^[21],随后细胞色素P450氧化酶CYP722C催化CLA转化为列当醇^[22],而另一细胞色素P450氧化酶CYP712G1则进一步催化列当醇生成三种二脱氢列当醇异构体(图1B)^[23]。尽管已有研究提出生成茄内酯醇(solanaol)的假设模型^[23,24],但具体每一步催化的酶和产物仍待进一步明确。有意思的是,豇豆(*Vigna unguiculata*)中的细胞色素P450氧化酶CYP722C同样具有催化CLA转化为列当醇的功能;而在百脉根(*Lotus japonicus*)和棉花中,CYP722C催化CLA生成5-脱氧独脚金醇(5-deoxystrigol, 5DS)^[22,25,26]。

在拟南芥中,细胞色素P450氧化酶CYP711A1(MAX1)把CL的C-19位甲基氧化为羧基,催化CL转化为CLA(carlactonoic acid)(图1C)^[27]。CLA目前已知有三条转化路径。首先,CLA甲基转移酶(CLA methyltransferases, CLAMT)对CL的C-19位进行进一步甲基化修饰,将CLA转化为MeCLA(methyl carlactonoate)^[28], MeCLA进一步被侧枝氧化还原

酶(lateral branching oxidoreductase, LBO)氧化成非经典SLs:1-OH-MeCLA(图1C)^[29,30]。其次,最近有新的研究通过导入植物SLs生物合成的核心通路建立微生物SLs表达体系,鉴定出拟南芥中一种新型非经典SL:16-OH-CLA;其合成途径显示,细胞色素P450单加氧酶CYP722A以及单子叶植物中特有的CYP722B催化CLA的C-16位氧化生成16-OH-CLA,之后在CLAMT的催化下生成16-OH-MeCLA(图1C),随后16-OH-MeCLA被LBO代谢生成未知的活性物质,调控拟南芥分枝^[31]。最后,系统发育分析发现CYP722A活性位点单氨基酸残基的突变能够催化CLA的C-18位发生氧化生成18-OH-CLA,并进一步转化为经典SLs(图1C)^[31]。该发现有可能为进一步研究种子植物中介导根际信号传递的非经典SLs的进化提供线索。

在玉米(*Zea mays*)中存在两条平行的SLs生物合成通路。一条通路由细胞色素P450氧化酶ZmMAX1b催化CL氧化生成CLA,随后ZmCLAMT1进一步催化CLA生成MeCLA, ZmCYP706C37将MeCLA氧化为3-oxo-MeCLA,最终形成玉米内酯(zealactone)(图1D)^[32]。在另一条通路中, ZmCYP706C37首先催化CL在C-3和C-19位同时氧化,生成3-oxo-19-OH-CL,进而转化为玉米内酯醇(zealactol),随后ZmMAX1b催化玉米内酯醇C-19位氧化生成玉米内酯酸(zealactonoic acid, ZA),最后ZA在甲基转移酶ZmCLAMT1的催化下被转化为玉米内酯(图1D)^[32]。然而,关于玉米内酯如何进一步转化为玉米吡喃内酯及其他衍生化合物目前尚不清楚,有待深入探索。

2 独脚金内酯的转运

SLs可作为内源植物激素从根系转运至地上部分,进而调控植物生长发育。嫁接实验表明,野生型砧木能够恢复多种SLs生物合成缺陷突变体接穗的多分枝表型,例如拟南芥max突变体、豌豆rms突变体以及矮牵牛dad突变体作为接穗嫁接在WT砧木上,分枝数量明显减少;而嫁接在对应的突变体砧木上的突变体接穗分枝数量没有变化,表现为多分枝表型;嫁接在突变体砧木上的WT接穗分枝数量与WT类似,这说明SLs可从根部运输至地上部分,并在调控植物分枝发育中发挥关键作用^[33-35]。另外,不同类型的SLs合成突变体嫁接实验进一步说明

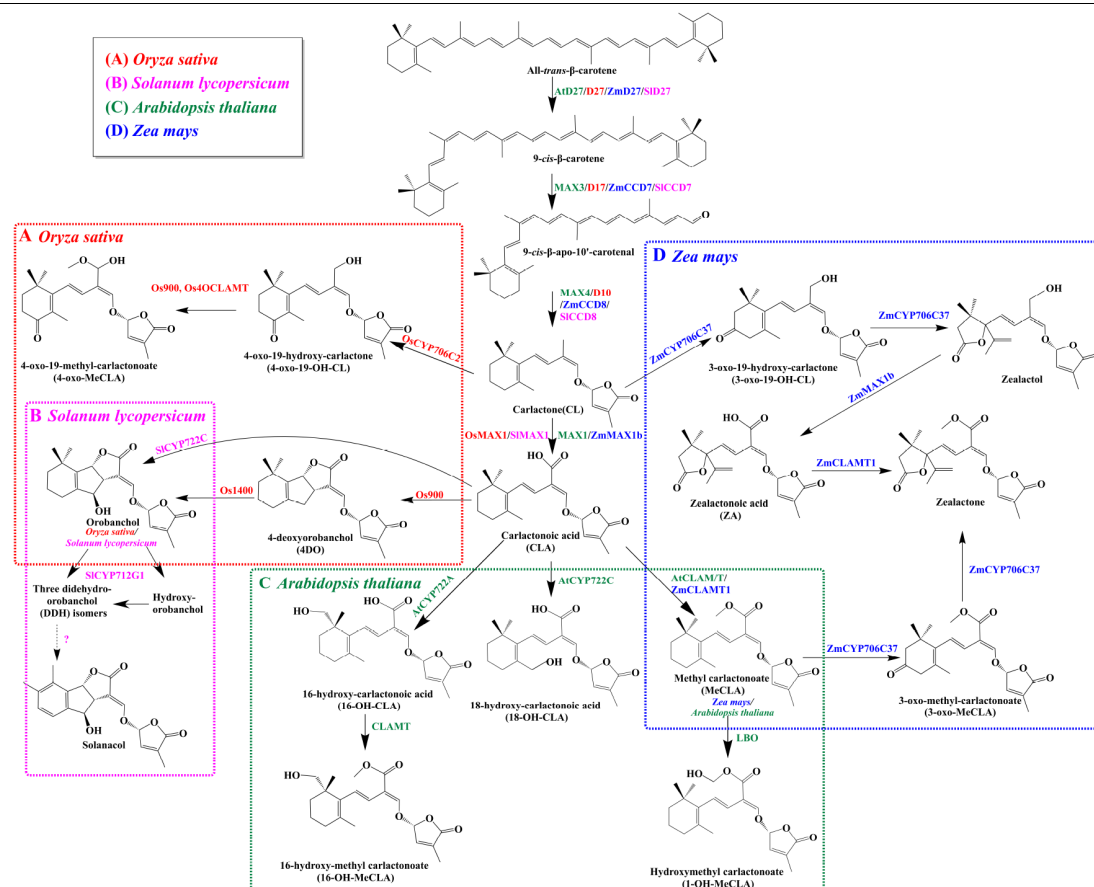


图1 独脚金内酯生物合成通路

共同途径:全反式-β-胡萝卜素通过D27、CCD7和CCD8酶的连续催化反应转化为己内酯(carlactone, CL),随后以CL为底物,在不同物种中分化出不同的独脚金内酯(strigolactones, SLs)合成路径。(A)水稻中有两条SLs合成路径:其一,OsMAX1将CL氧化成CLA,Os900进一步催化CLA生成4DO,随后Os1400催化4DO生成经典SL列当醇(orobanchol, ORO);其二,OsCYP706C2催化CL形成非经典SL——4-oxo-MeCLA。(B)在番茄中,CL经过SIMAX1和CYP722C的连续催化氧化生成ORO,CYP712G1催化ORO生成三种二脱氢列当醇异构体,最后以目前未知的机制转化为茄内酯醇(solanacol)。(C)在拟南芥中,细胞色素P450氧化酶MAX1催化CL转化为己内酯酸(carlactonic acid, CLA),CLA通过三条路径分别转化为16-OH-MeCLA、18-OH-MeCLA以及1-OH-MeCLA。(D)玉米中也有两条SLs合成路径:其一,CL经过ZmMAX1b和ZmCLAMT的连续催化生成MeCLA,随后ZmCYP706C37通过连续氧化将MeCLA转化为3-oxo-MeCLA,最终生成玉米内酯(zealactone);其二,ZmCYP706C37催化CL生成3-oxo-19-OH-CL,进而转化为玉米内酯醇(zealactol),随后ZmMAX1b催化玉米内酯醇氧化生成玉米内酯酸(ZA),最后ZmCLAMT1催化ZA生成玉米内酯。

Figure 1 Strigolactone biosynthetic pathway

Common pathway: All-*trans*-β-carotene is converted to carlactone (CL) via sequential catalysis by D27, CCD7, and CCD8. CL serves as a common precursor for species-specific strigolactone (SL) biosynthesis pathways. (A) Rice. Two SL biosynthesis pathways operate in rice. (i) OsMAX1 oxidizes CL to CLA and Os900 catalyzes CLA to 4DO; Os1400 converts 4DO to the canonical SL orobanchol (ORO). (ii) OsCYP706C2 converts CL to the non-canonical SL 4-oxo-MeCLA. (B) Tomato. CL is sequentially oxidized to ORO via SIMAX1 and CYP722C. CYP712G1 converts ORO into three didehydro-orobanchol isomers, which are then converted to solanacol via an unknown mechanism. (C) *Arabidopsis*. MAX1 catalyzes the conversion of CL to carlactonic acid (CLA). CLA is channeled into three pathways, producing 16-OH-MeCLA, 18-OH-MeCLA, and 1-OH-MeCLA. (D) Maize. Two SL biosynthesis pathways exist in maize. (i) CL is sequentially converted to MeCLA via ZmMAX1b and ZmCLAMT; ZmCYP706C37 then catalyzes the successive oxidation of MeCLA to 3-oxo-MeCLA, and finally zealactone. (ii) ZmCYP706C37 converts CL to 3-oxo-19-OH-CL, leading to zealactol; ZmMAX1b oxidizes zealactol to ZA, and ZmCLAMT1 converts ZA to zealactone.

CL、CLA、MeCLA等SLs前体可能发生转运^[29]。

同时,SLs也能从根系分泌到土壤中,作为外源根际信号,诱导AMF共生并决定寄生植物的寄生过

程^[15]。2012年,研究者利用反向遗传学方法在矮牵牛中首次鉴定出一种SLs转运蛋白PDR1 (pleiotropic drug resistance 1),该蛋白属于G型ABC转运蛋白

(ATP-binding cassette subtype G transporters)家族^[36]。PhPDR1主要定位于根尖下皮层通道细胞的顶膜及根尖以上部位下皮层通道细胞的外侧膜,这种极性分布暗示其可能参与SLs向上运输至地上部分以及向外分泌到土壤中的过程^[36,37]。Phpdr1突变体表现为根系分泌物中SLs含量和AMF共生显著减少,地上部分枝增多,根浸出液诱导的分枝列当(*Phelipanche ramosa*)种子萌发减少^[36]。此外,相较于野生型,放射性同位素标记的GR24在Phpdr1突变体中从根系向地上部运输和向外分泌更慢,而在PhPDR1过表达株系中从根系向外分泌更快^[36,37]。这些结果证明PhPDR1参与SLs向地上部的转运和向土壤的分泌。

列当科寄生植物种子可响应SLs信号而萌发,进而寄生在玉米、高粱(*Sorghum bicolor*)、番茄等寄主植物上,通过摄取寄主的水分、养分和其他营养物质,最终造成作物显著减产^[32,38,39]。早期防治的分子策略主要围绕抑制寄主植物体内SLs合成,以阻止寄生植物种子萌发,但该方法会因SLs缺乏而影响寄主本身的生长发育与产量形成。例如,在高粱中,与水稻CCD7同源的基因*Non-dormant Axillary Bud 1(NABI)*发生突变后,SLs合成被阻断;与野生型相比,nab1突变体的粒宽、粒厚、粒长、千粒重以及单株产量均显著下降^[40]。为此,挖掘并改造SLs转运蛋白,在不影响其生物合成的前提下,选择性调控SLs的运输与分泌过程是更好的策略。

在番茄中,矮牵牛PhPDR1的同源蛋白SIABCG44和SIABCG45^[39,41]定位于细胞质膜,能够介导SLs向地上部分转运和向土壤分泌^[39]。在缺磷条件下,番茄中NSP(nodulation signaling pathway)家族蛋白SINSP1和SINSP2能够直接结合到SIABCG44和SIABCG45的启动子上,诱导其表达上调^[39]。值得注意的是,与SLs合成缺陷突变体*Slccd8*相比,*Slabcg44*和*Slabcg45*突变体对植物整体发育影响相对较弱,但是向根系分泌的SLs显著减少,对列当的抗性增强^[39]。

此外,在高粱中也鉴定到两个属于G型ABC转运蛋白家族的SLs转运蛋白,分别命名为SbSLT1和SbSLT2^[38]。这两种蛋白定位在根表皮细胞的细胞膜上,通过异源酵母表达和蛙卵表达系统实验证实了它们具有SLs转运活性及底物特异性,并进一步鉴定出对转运功能至关重要的高度保守氨基酸残

基,即SbSLT1中的F693和SbSLT2中的F642^[38]。此外,*Sbslt1*和*Sbslt2*突变体植株表型与WT没有差异,但其根系分泌SLs的能力降低,对独脚金的抗性增强^[38]。然而,目前关于转运蛋白的组织特异性、在细胞中的极性分布以及底物特异性的认识仍不清晰,有待深入研究。

3 独脚金内酯信号途径

SLs的信号感知依赖于SL受体DWARF14(D14)、F-box蛋白D3/MAX2以及转录抑制因子D53/SMXLs形成的复合体,该复合体中的F-box蛋白可特异性识别并标记靶蛋白,使其发生泛素化修饰,进而被26S蛋白酶体降解,启动下游信号传递^[42-45]。与其他激素信号通路的受体不同,SLs受体具有水解酶活性,能够水解SLs分子,并与水解产物共价结合,激活下游SLs信号转导(图2)^[12,14,46]。

3.1 信号感知机制

SLs的信号转导依赖于精密的分子识别机制与蛋白质互作网络。拟南芥*Atdl14*突变体、水稻*Osd14*突变体以及矮牵牛*dad2*突变体均表现出多分蘖表型,并对SLs处理不敏感,提示D14蛋白参与SLs的信号感知过程^[47-49]。与此相似,拟南芥*max2*突变体、水稻*d3*突变体以及豌豆*rms4*突变体同样呈现多分蘖与SLs不敏感表型,说明这些基因也参与SLs的信号感知与转导途径^[8,9,48]。

尽管不同植物中SLs的结构存在多样性,但其受体在不同物种间比较保守。D14属于 α/β 蛋白水解酶超家族,兼具酶催化活性与受体功能,不同于大多数植物激素受体,该蛋白具有一个保守的催化三联体Ser-His-Asp,其三维结构中含有一个配体结合口袋及由四个 α 螺旋组成的盖子结构域^[46,49]。当D14与SLs结合时,D14水解SLs生成羟甲基丁烯内酯与三环内酯,随后D14与D环衍生的共价连接中间体(CLIM)形成共价键,受体蛋白D14从开放构象转变为闭合构象,进而促进其招募F-box蛋白D3/MAX2,共同形成SCF E3泛素连接酶复合物^[46],抑制蛋白D53/SMXLs(suppressor of MAX2-like)能够与D14和D3形成三元复合体,随后发生泛素化和降解,启动下游信号转导^[42-45]。D14水解SLs的反应速率偏低,但下游抑制蛋白D53/SMXLs却能在SLs处理后的5~30 min内迅速降解^[42-45]。再者,缺乏酶催化活性的AtD14^{D218A}突变体仍然能以SLs依赖性方

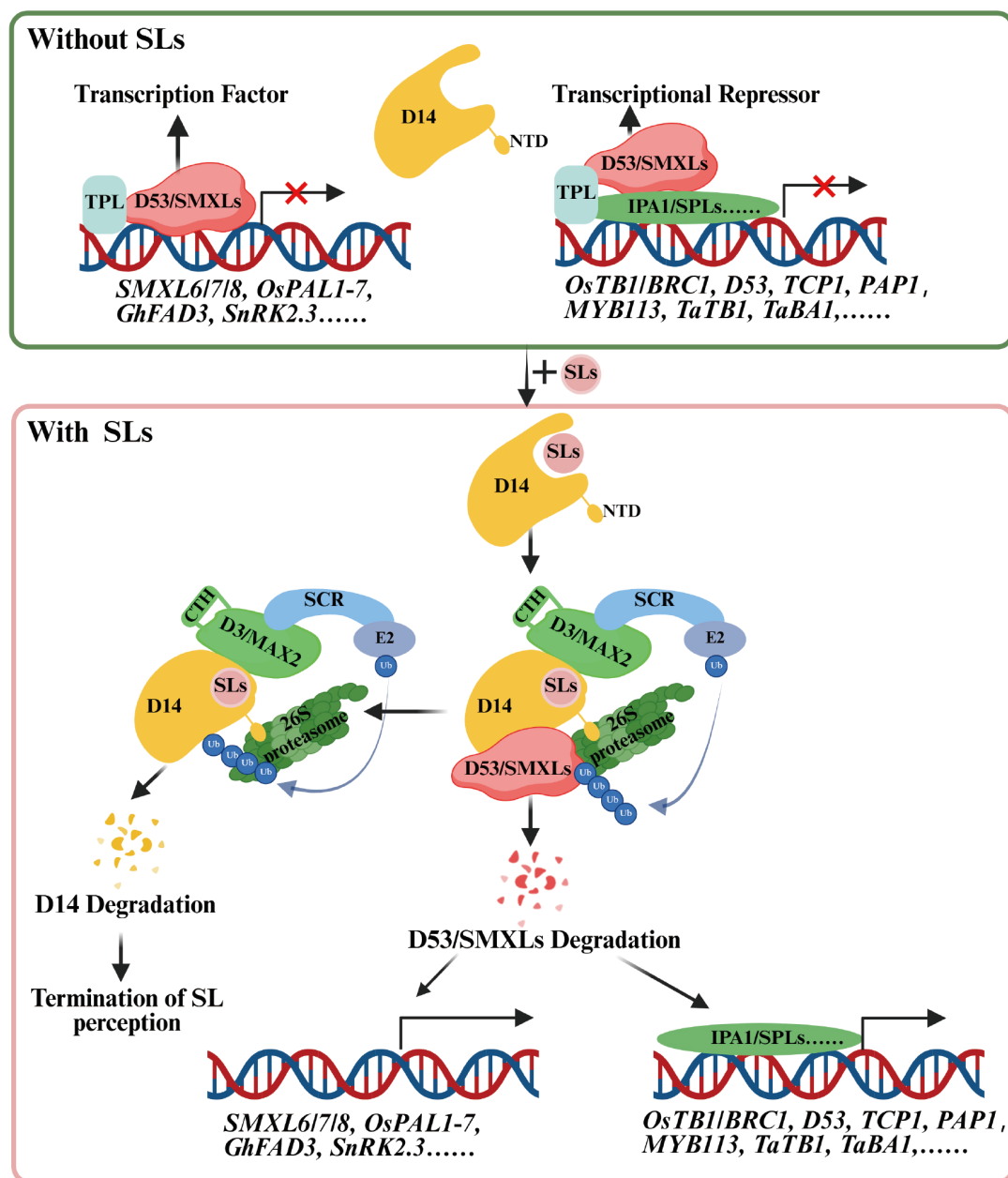


图2 SLs信号感知、转导、终止机制模型

在缺乏SLs的条件下,D53/SMXLs和TPL直接结合在SMXLs等靶基因的启动子上,抑制其转录;同时,SMXLs与转录因子形成复合物,结合在下游基因的启动子上,抑制其转录。当D14受体感知到SLs后,构象发生变化,并招募F-box蛋白D3/MAX2和D53/SMXLs,形成D14-SCF^{D3/MAX2}-D53/SMXLs复合物,诱导D53/SMXLs的泛素化和降解,解除对下游靶基因的抑制,启动下游基因的表达。D53被降解后,水稻OsD14以D3依赖性方式泛素化和降解,而拟南芥AtD14以MAX2不完全依赖性方式降解,从而终止SL信号感知。

Figure 2 Mechanisms of signal perception, transduction and termination of SLs

In the absence of strigolactones (SLs), D53/SMXLs and TPL directly bind to the promoters of target genes, such as *SMXLs*, and repress their transcription. Meanwhile, SMXLs form complexes with transcription factors, which associate with the promoters of downstream target genes to inhibit their transcription. Upon perception of SLs by the D14 receptor, D14 undergoes a conformational change and recruits the F-box proteins D3/MAX2 and D53/SMXLs, forming the D14-SCF^{D3/MAX2}-D53/SMXLs complex. This complex induces ubiquitination and degradation of D53/SMXLs, leading to de-repression of downstream target genes and activation of their expression. Following degradation of D53, OsD14 in rice (*Oryza sativa*) is ubiquitinated and degraded in a D3-dependent manner, whereas AtD14 in *Arabidopsis thaliana* is degraded in a MAX2-partially dependent manner, thereby terminating SL signal perception.

式回补 $atd14$ 突变体表型^[50]。此外,对SLs不敏感的 $d14-5$ 突变蛋白虽然与D3的相互作用显著减弱,但其SLs水解活性反而高于野生型D14^[46],表明D14的酶催化功能与其信号转导角色在机制上可以发生解偶联^[12]。

SLs信号感知在翻译后调控与转录后修饰两个层面均受到精细调控。随着D3-ASK1复合物以及D14与D3的C末端 α 螺旋(C-terminal α -helix, CTH)基序复合物结构的鉴定,研究发现D3的CTH基序存在脱离状态(dislodged state)与结合状态(engaged state),两种构象状态的变化能够动态调控SLs信号感知^[51,52]。缺失CTH基序的MAX2 ^{Δ CTH}株系以及在 $max2$ 株系中过表达CTH基序处于非结合状态的蛋白MAX2^{D693K}均表现出多分枝表型^[53],说明D3-CTH基序以及构象变化对于SLs信号感知都是必需的。利用系统的生化和遗传实验进一步鉴定出了一系列独脚金内酯感知过程中关键的D14、D3氨基酸残基,其在D14-D3相互作用、D53的泛素化修饰、D53蛋白质降解以及水稻分蘖抑制等过程中发挥重要作用。另外,过表达D3-CTH基序会抑制SLs信号转导,导致分蘖增加,这种负调控效应可能源于两种机制:一是CTH基序通过竞争性干扰D3-D14-D53复合物的形成产生显性负效应;二是脱离状态的CTH可能使D14处于“钝化”状态,从而削弱SLs感知,并抑制D53的泛素化及其降解^[52]。因此,该研究提出了一个新的SLs感知模型:SLs信号诱导受体D14与CTH基序处于结合状态的D3以及抑制蛋白D53形成复合物,激活D53的泛素化修饰及降解过程,启动SLs信号转导,抑制植物的分枝或分蘖发育;如果D14与CTH基序处于脱离状态的D3结合,则会使D14进入“钝化”状态或者干扰D14-D3-D53信号感知复合物的形成,阻碍D53的降解,减弱SLs信号感知(图2)^[52]。在转录后调控方面,水稻 $dwarf$ and $high$ tillering 1($dht1$)突变体表现出与SLs信号突变体类似的表型: $DHT1$ 编码一个单子叶植物特有的hnRNP样蛋白,可通过剪接D14的前体mRNA来保证其正常表达;而 $DHT1$ 突变后,对D14前体mRNA的剪接效率下降,导致D14的表达受到抑制^[54]。

3.2 信号转导机制

水稻D53基因的鉴定源于一个对SLs不敏感的显性功能获得性突变体 $d53$,该突变体表现出与 $d14$ 和 $d3$ 相似的表型,分蘖数增多并且植株内SLs含量

升高^[42,43]。拟南芥中水稻D53的同源基因的功能缺失三突变体 $smxl6/7/8$ 完全抑制了 $max2$ 突变体的多分枝表型^[44,45]。D53及其在拟南芥中的同源蛋白SMXL6/7/8是一类具有核定位功能的转录抑制蛋白,结构上表现出与I类Clp ATP酶相似的特征。在SLs存在时,D53和SMXL6/7/8能够直接与D14及D3/MAX2互作并被降解;而在缺乏SLs的条件下,它们通过与共抑制因子TOPELESS (TPL)及其相关蛋白(TPR)结合,进而抑制下游转录因子的活性(图2)^[42-45]。D53及其同源蛋白SMXL6/7/8在转录调控中具有双重功能:一方面可与转录因子结合,进而抑制下游基因的转录,发挥转录抑制子功能,目前已鉴定出多个受D53/SMXLs调控的转录因子靶标,例如TOE1和IPA1^[55,56];另一方面,能够直接识别并结合靶基因的启动子区域并抑制其表达,发挥转录因子功能(图2)。例如,在拟南芥中,SMXL6和SMXL7能够直接结合SMXL6/7/8启动子区域,SMXL8能够结合SMXL7启动子区域,进而抑制基因表达,在信号的负反馈抑制中发挥关键作用(图2)^[57];在水稻中,D53可直接结合到7个苯丙氨酸解氨酶基因($OsPAL1\sim7$)的启动子上,抑制它们的表达进而调控稻瘟病抗性^[58]。在棉花中,GhD53不仅能够直接结合到脂肪酸去饱和酶(fatty acid desaturase, GhFAD)编码基因 $GhFAD3-2$ 和 $GhFAD3-4$ 的启动子上,也能够与SL相关转录激活因子(SL-related transcriptional activate factor, GhSLRF)互作,防止GhSLRF结合到 $GhFAD3$ 的启动子上,两种机制同时抑制 $GhFAD3$ 的转录表达(图2)^[59]。SLs的信号转导同样存在翻译后修饰。一类植物特异性I类酪蛋白激酶(AELs)能够在拟南芥中磷酸化SMXL6/7/8蛋白,抑制其与MAX2的相互作用,进而抑制SLs诱导的SMXL6/7/8泛素化修饰,增强SMXL6/7/8的蛋白质稳定性,抑制SLs信号转导并促进植物分枝形成^[60]。

3.3 感知和转导的终止机制

激素作为关键的内分泌性信号分子,在浓度升高时,能够迅速启动下游信号转导以响应刺激;而在刺激消失后,信号反应逐步衰减,从而维持通路的动态平衡,避免引发生理紊乱。对于SLs而言,其信号终止机制主要包括信号感知的终止和信号转导的终止。

在终止信号感知层面,SLs通过调控其受体D14的降解来防止信号过度响应(图2)。水稻D14的降

解依赖于其与D3的直接互作,同时也需要其N端无序基序(N-terminal disordered,NTD)与26S蛋白酶体亚基OsRPN9b直接结合^[52]。然而,在双子叶植物(如拟南芥)中,AtD14缺乏NTD基序,AtD14的降解在拟南芥*max2-1*突变体中减少但未被完全阻断,说明拟南芥AtD14的降解不完全依赖于MAX2,具体降解机制有待进一步研究^[61]。因此,D3在SLs信号调控中具有“油门-刹车”双重功能:在SLs信号感知的5~30 min内,D3能够招募D53并促进其泛素化降解,从而激活下游信号通路,发挥类似“油门”的功能;而在SLs信号感知1~3小时内,D3主要介导受体D14的泛素化降解,终止信号传递,起到类似“刹车”的作用(图2)。这一“油门-刹车”机制有助于精确调控植物体内SL信号的持续时间与强度,维持SL信号响应的动态平衡^[52]。

在终止信号转导层面,SMXL6/7/8可与自身启动子结合并抑制转录,SMXL6/7/8降解后可解除对自身转录的抑制,快速翻译产生新的抑制蛋白(图2)^[57],这一反馈机制有助于重建SMXL6/7/8对下游转录因子及靶基因启动子的抑制作用,维持信号通路的稳态调控^[44,45]。此外,SLs信号终止可能与信号分子的降解相关,拟南芥羧酸酯酶15(*Arabidopsis* carboxylesterase 15,AtCXE15)及其在不同物种中的同源蛋白均具有SLs水解酶活性,过表达AtCXE15能够增强对SLs的降解,进而促进植物分枝^[62]。

4 独脚金内酯的农业应用前景

植物无法移动,为适应不断变化的环境条件,进化出了复杂的调控网络,用以感知养分可利用性、协调资源分配、调节生长可塑性、响应胁迫信号并执行多种适应性反应^[63]。SLs作为一类重要的植物激素,能够在多个层次调控植物的生长发育,尤其在形态建成方面发挥核心作用,例如调节分枝/分蘖数目、叶形发育及开花时间等(图3)^[55,57]。在农业应用中,SLs展现出重要的应用潜力,既可用于防控寄生病害,也能促进植物与菌根真菌的共生关系,因而具有广阔的应用前景(图3)^[15]。

4.1 调控作物生长发育

SLs在调控植物发育中发挥的核心功能是抑制分枝/分蘖(图3)。分枝/分蘖的数目、角度和着生位置直接影响植物的整体株型和最终产量。目前,关于SLs调控植物分枝/分蘖的机制存在两种主要模

型。其一,SLs直接调控转录因子branched 1(BRC1)进而抑制分枝/分蘖的发育。BRC1/TB1(*teosinte branched 1*)是抑制腋芽生长的关键调控因子,拟南芥SMXL6/7/8能够直接靶向SPL等蛋白家族,并通过依赖于EAR结构域的方式抑制BRC1的表达,促进侧芽伸长(图2)^[44,45,56,57]。在水稻中,D53可直接结合水稻株型关键调控因子IPA1,抑制其转录激活活性,从而降低OsTB1的表达水平(图2)^[56]。在小麦(*Triticum aestivum*)中,TaD53同样直接与TaSPL3和TaSPL17结合,抑制其下游靶基因TaTB1和空秆基因1(*barren stalk 1*,TaBA1)的表达,调控小麦的分蘖和小穗发育(图2)^[64]。植物中也存在不依赖于BRC1的调控途径。例如在拟南芥和豌豆中,*brc1*突变体与SL合成或信号突变体的分枝数量存在差异,在拟南芥中还表现出明显的加性效应^[65];另外,BRC1在水稻和玉米中的同源基因的表达量在SL突变体中降低不明显,过表达OsTB1仅能部分挽救*d3*突变体的多分蘖表型,暗示在SL途径中可能存在BRC1以外的分枝调控机制^[66,67]。另一种模型是经典的生长素渠化模型,SLs通过调控生长素运输蛋白PIN1在细胞膜上的分布来抑制分枝/分蘖发育。研究表明,SLs能够以网格蛋白依赖性方式诱导PIN1蛋白的降解^[68]。在拟南芥*smxl6/7/8 max2*突变体中,PIN1蛋白积累减少,生长素转运和植物分枝/分蘖受到抑制^[44],而且*pin1*突变能够抑制拟南芥*d14*突变体和*max2*突变体的多分枝表型^[69]。此外,植物的分蘖也会受到根际微生物群落的影响。最近研究发现根际细菌来源的环二肽cyclo(Leu-Pro)能够直接与水稻中的受体OsD14结合并激活SL信号,抑制水稻分蘖,说明根际微生物可以通过合成及分泌模拟激素功能的小分子调控植物发育(图3B)^[70]。

根系对于植物吸收水分和养分是极其重要的,调控植物根系形态建成是SLs调控植物发育的另一个典型的作用(图3)。SLs促进主根和冠根生长,而抑制侧根的发育,水稻SLs生物合成突变体*d10*、*d17*、*d27*和SLs信号感知突变体*d14*和*d3*的冠根变短,对野生型水稻进行缺磷处理会增加其冠根长度^[71]。在缺磷条件下,水稻NSP1、NSP2信号通路促进SLs合成相关基因的表达,提高植物体内SLs水平,抑制CRL1基因的表达,降低水稻侧根密度^[72]。正常生理条件下,低浓度外施GR24会增加拟南芥主

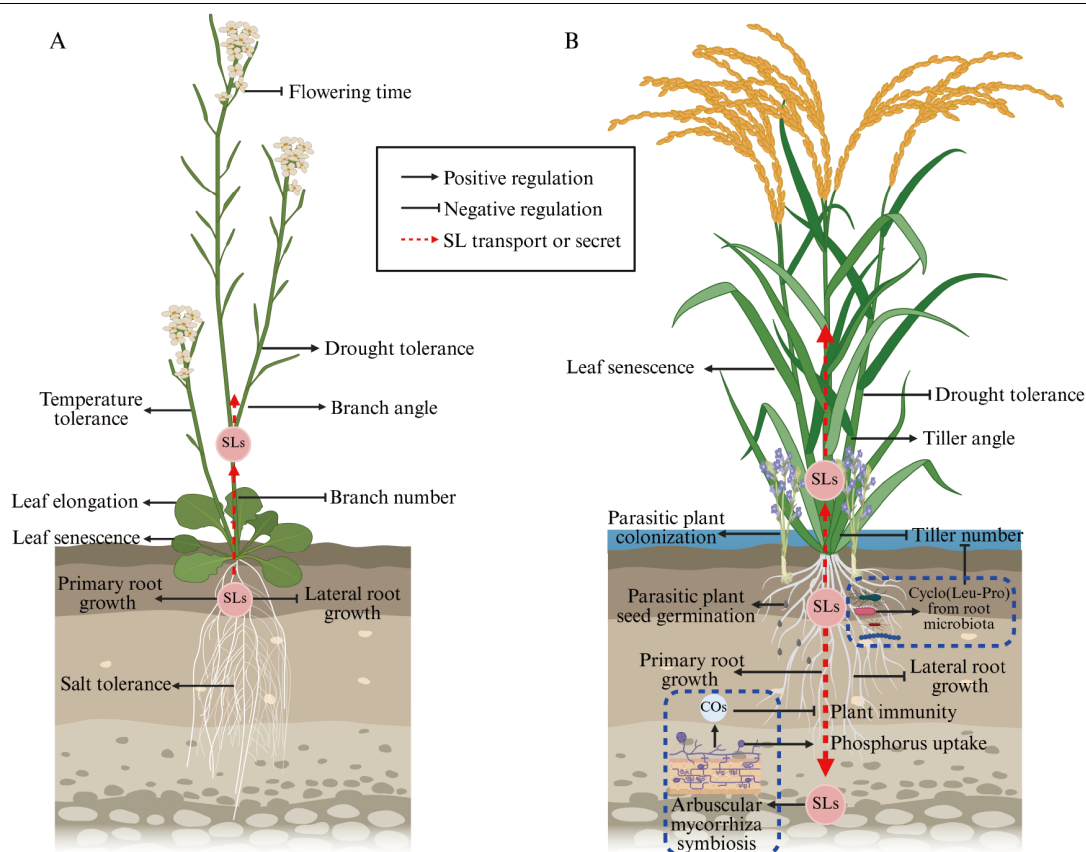


图3 独脚金内酯在拟南芥、水稻生长发育和胁迫响应中的作用

(A)在拟南芥中,SLs仅发挥内源性激素分子作用,促进主根生长、叶片伸长、叶片衰老,同时提高拟南芥对非生物胁迫(如干旱、盐碱、冷热胁迫等)的耐受性,在侧根生长、分枝形成、分枝夹角、开花时间等方面起抑制作用。(B)在水稻中,SLs同时发挥内源性激素分子和根际信号分子的作用:促进主根生长、叶片伸长、叶片衰老,增大分蘖夹角;抑制侧根生长、分蘖形成,负调控水稻对干旱的耐受性;同时,促进菌根真菌(AMF)的共生,刺激寄生植物种子的萌发及定殖。

Figure 3 The roles of strigolactones in the growth and development and stress response of *Arabidopsis* and rice

(A) In *Arabidopsis thaliana*, strigolactones (SLs) act solely as endogenous hormones to promote primary root growth, leaf elongation, and leaf senescence, while enhancing tolerance to abiotic stresses (e.g., drought, salinity, cold, and heat stresses). In contrast, SLs inhibit lateral root growth, branch formation, and branch angle, and delay flowering time. (B) In rice (*Oryza sativa*), SLs function both as endogenous hormones and rhizosphere signaling molecules: they promote primary root growth, leaf elongation, and leaf senescence, and increase tiller angle, but inhibit lateral root growth, tiller formation, and negatively regulate drought tolerance of rice. In addition, SLs facilitate symbiosis with arbuscular mycorrhizal fungi (AMF) and stimulate the germination and colonization of parasitic plant seeds.

根长度,同时伴随分生区和过渡区的扩大以及侧根的减少,而高浓度外施GR24则会抑制主根生长^[73]。同时,SLs对侧根发育的影响也受到根中生长素水平的调控:在低浓度生长素条件下,GR24抑制侧根形成;但在高浓度生长素条件下,GR24的施用能够显著增强侧根的起始^[73]。

SLs能够调控叶形(图3A)。SMXL6以EAR依赖性方式靶向调控叶发育的基因*TCPI*(图2),GR24^{4DO}以D14依赖性方式诱导*TCPI*表达上调;*TCPI*的表达在*smxl6/7/8*突变体中显著上调,突变体叶片长宽比显著升高;在*max3*突变体中,*TCPI*表达水平显著下

调^[57]。SLs也能够促进叶片衰老(图3),拟南芥SLs的生物合成和信号突变体*max1*、*max3*、*max4*、*Atd14*和*max2*均表现出延缓衰老的表型;此外,对拟南芥进行暗处理或乙烯处理强烈诱导SLs合成基因*MAX3*和*MAX4*的表达,促进叶片衰老期间的SLs积累^[74]。在拟南芥中,SLs受体AtD14和MAX2能够直接与叶片衰老关键抑制蛋白SPX1/2互作,并介导SPX1/2的泛素化和降解,解除对转录因子*WRKY75*的抑制作用,激活编码水杨酸生物合成限速酶基因*SA induction-deficient 2 (SID2)*的转录,促进水杨酸(SA)的生物合成,从而促进叶片衰老^[75]。

SLs还参与调控植物开花时间(图3A)。拟南芥SLs生物合成突变体 $max3$ 和信号突变体 $Atd14$ 和 $max2$ 表现为早花表型,而阻遏蛋白 $smxl6/7/8$ 突变体则表现为晚花表型^[55]。核定位的AtD14采用双重策略增强AP2转录因子TOE1的功能:一方面,AtD14以依赖于SLs的方式直接结合转录因子TOE1,提高其稳定性,抑制 FT 基因转录;另一方面,AtD14感知SLs后介导SMXL7的降解,解除SMXL7对TOE1转录活性的抑制,TOE1进而抑制 FT 表达,植株表现出延迟开花的表型^[55]。

此外,花青素水平在 $smxl6/7/8$ 突变体中显著升高,在 $max3$ 突变体中略有下降。研究发现,SLs能够通过诱导SMXLs的降解,促进调控花青素合成的转录因子 $production\ of\ anthocyanin\ pigment\ 1\ (PAP1)$ 、 $PAP2$ 、 $MYB113$ 和 $MYB114$ 的表达(图2),提高花青素的积累^[57]。

4.2 环境适应

氮和磷是植物生长发育所必需的大量元素,对于提高作物产量具有重要意义。低氮和低磷条件能够诱导SLs关键合成基因 $D17$ 和 $D10$ 表达上调,促进SLs的生物合成^[76]。在缺磷条件下,水稻磷饥饿响应关键转录因子OsPHR2(*Oryza sativa* phosphate starvation response 2)诱导结瘤信号通路蛋白NSP1和NSP2的表达,NSP1和NSP2形成异源二聚体直接结合到多个SL生物合成基因的启动子上,显著促进SLs的生物合成^[72]。在缺磷条件下,SLs主要行使两方面的功能^[12,15,63,72]:一方面,调控植物形态建成,发挥内源性激素信号分子的作用,抑制植物分枝/分蘖,减少养分需求,同时优化根系结构,促进水分和养分的吸收;另一方面,作为根际信号促进菌根真菌共生,扩大磷的来源。在低氮条件下,水稻一方面增加SLs生物合成,另一方面其D14的NTD结构域被磷酸化,增强了D14稳定性,从而起到延长和放大SLs信号的作用,确保对分蘖发育的持续抑制^[52]。此外,SL信号通路与多种激素信号通路之间存在相互作用,共同协调植物对养分缺乏的响应。例如,SL可作为生长素的第二信使,参与调控分蘖对低氮胁迫的应答过程^[77,78]。在低氮条件下,SLs的积累促进D14与关键抑制因子D53的互作,诱导D53降解,促进赤霉素(GA)信号通路中抑制蛋白SLR1的部分降解,从而解除对GRF4的竞争性抑制,激活氮响应基因的表达,进而增强植物对低氮环境的适应能

力^[79]。另一方面,低氮环境诱导D14的N端结构域发生磷酸化,增强D14的稳定性,提高SLs信号感知能力,进而抑制水稻的分蘖发育^[52]。

干旱胁迫会诱导叶绿素降解,减弱光合作用,诱导活性氧(reactive oxygen species, ROS)的迸发,限制植物生长和发育,甚至导致植物死亡。SLs生物合成和信号突变体 $max2$ 、 $max3$ 、 $max4$ 的气孔密度增大, $d14$ 突变体气孔孔径增大,导致突变体失水速率增加,对干旱和盐胁迫敏感^[80,81]。外施SLs能够挽救拟南芥SLs合成缺陷突变体的干旱敏感表型,增强野生型拟南芥的耐旱性^[81]。拟南芥 $smxl6/7/8$ 三突变体植物叶片温度升高,角质层透性降低,水分流失和细胞膜损伤减少,花青素合成增多,表现为植物耐旱性提高^[82]。有研究表明,SMXL6/7/8能直接结合到ABA途径重要蛋白激酶 $snf1-related\ protein\ kinase\ 2.3\ (SnRK2.3)$ 的启动子上,抑制其转录表达,负调控拟南芥ABA响应以及耐旱性^[83]。SLs还能通过调控根系形态建成,调控植物的耐旱性。如GR24外施促进小麦干旱条件下的根系生长^[84],调控象草(*Pennisetum purpureum*)中光合作用相关基因 $PpPEPCK$ 、 $PpRuBPC$ 、 $PpPGK$ 、 $PpGAPDH$ 、 $PpFBA$ 和 $PpSBPase$ 以及根系发育相关基因 $PpACAT$ 、 $PpMFP2$ 、 $PpAGT2$ 、 $PpIVD$ 、 $PpMCCA$ 和 $PpMCCB$ 的表达^[85],促进葡萄(*Vitis vinifera*)中抗氧化酶基因 $CAT1$ 、 $GSHPX1$ 、 $GSHPX2$ 、 $POD42$ 、 $APX6$ 和 $SODCP$ 的表达^[86]。此外,在干旱条件下,外施GR24能够提高中国辣椒(*Capsicum chinense*)的叶绿素含量,增强抗氧化酶POD、CAT以及SOD的活性,减少 H_2O_2 的积累,缓解氧化损伤,缓解干旱导致的气孔密度下降和气孔开度降低,增强中国辣椒的耐旱性^[87]。值得注意的是,与其他植物不同,SLs负调控水稻耐旱性(图3B),水稻SLs生物合成 $d10$ 、 $d17$ 突变体以及信号突变体 $d3$ 中ABA含量高于野生型,水稻存活率显著提高,水稻耐旱性增强^[88]。

土壤盐碱化会导致植物生长被抑制、叶片失绿萎蔫、生物量下降,造成作物严重减产,是农业的一大难题。在盐胁迫条件下,拟南芥SLs生物合成突变体 $max3$ 、 $max4$ 与信号突变体 $max2$ 存活率显著下降^[81]。在NaCl处理条件下,外施GR24能够提高番茄叶绿素含量,促进光合作用,提高抗氧化酶SOD、CAT和POX的活性,增加脯氨酸含量,减少 H_2O_2 和丙二醛(MDA)积累,缓解氧化损伤,增强番茄的耐

盐性^[89];外施GR24能够提高面包小麦的抗氧化酶APX、POX的活性,减少H₂O₂和MDA积累,提高叶片中K⁺/Na⁺的比值,降低离子毒性,增强面包小麦的耐盐性,提高产量^[90]。这些发现表明,SLs通过调节植物形态建成、抗氧化酶活性、光合作用、离子稳态等促进植物对盐胁迫的适应,但其中的分子机制仍待进一步研究。

热胁迫和冷胁迫对植物的危害主要源于其对细胞结构与生理过程的直接破坏,造成作物产量损失,严重威胁农业生产和可持续发展,而SLs则在提高植物对热胁迫和冷胁迫的耐受性方面发挥重要的作用(图3A)。热胁迫和冷胁迫能够诱导番茄中*CCD7*、*CCD8*、*MAX1*和*MAX2*的表达,增加SLs的积累^[91]。在热胁迫和冷胁迫条件下,SLs以ABA依赖性方式促进转录因子CBF1(C-repeat binding factor 1)、抗氧化酶和热休克蛋白HSP70的表达,并提高抗氧化酶(SOD、APX、GR、MDAR、DHAR)的活性,以提高番茄对冷热胁迫的耐受性^[91]。拟南芥SLs合成突变体*max1*和信号突变体*max2*对热胁迫更敏感,而外施GR24能够增强SLs合成突变体*max1*和*max3*对热胁迫的耐受性^[92]。拟南芥转录因子*AtMYBS1*能够与*MAX1*基因的启动子结合抑制其表达及SLs的合成,负调控拟南芥的耐热性,而*Atmybs1*突变体则能够增强SLs合成和植物耐热性^[93]。同样,拟南芥SLs合成突变体*max1*、*max3*、*max4*和信号突变体*max2*、*d14*对冷胁迫更敏感,而*smxl6/7/8*三突变体耐冷性更强,外源施加GR24^{DS}能够挽救SLs合成缺陷突变体的冷敏感表型。转录因子WRKY41直接与CBFs基因的启动子区域结合抑制其表达,而F-box蛋白MAX2能使WRKY41泛素化并降解,解除对CBFs基因的抑制,促进其表达^[94]。同时,SLs介导的SMXLs的降解促进了花青素的生物合成,可能对植物耐冷性提高有一定贡献^[57,94]。此外,冷胁迫能够增加番茄中泛素化蛋白的积累,而SLs合成缺陷突变体表现为泛素化蛋白积累增加,对冷胁迫更加敏感^[95]。外施GR24会诱导自噬相关基因(*ATGs*)的表达,另外,SLs能够诱导*HY5*的表达,*HY5*进一步激活*ATG18a*的转录,增强自噬,减少泛素化蛋白的积累;同时,*HY5*能够直接结合SLs生物合成基因*CCD7*、*CCD8*、*MAX1*上游的启动子并促进其表达,促进SLs积累,提高植物耐冷性^[95,96]。最近的研究发现了一个整合乙烯和SLs信号的转录因子

MdGLK1,正调控苹果耐冷性;乙烯能够抑制E3泛素连接酶MdEBF1介导的MdGLK1的泛素化和降解,提高其稳定性;而SLs可解除MdSMXL8对MdGLK1-MdBZR1复合体的抑制,激活下游MdCBFs基因的表达,协同提高苹果的耐冷性^[97]。

4.3 促进共生

AMF能与超过70%的陆生植物形成共生关系(图3B),显著促进植物对矿物质特别是磷元素的吸收^[98]。根系分泌的SLs可诱导AMF产生一系列反应,包括孢子萌发、菌丝生长与分枝、线粒体代谢增强、有丝分裂活跃、效应基因表达上调以及几丁质寡聚糖释放等,从而促进其与植物的共生互作^[2,99,100]。值得注意的是,水稻SLs信号突变体*d14*表现出更高的AMF定殖量,这可能源于其SLs分泌增加;而*d3*突变体则显示出定殖减少,提示D3在AMF共生中具有关键作用^[101]。缺磷条件能激活磷酸盐饥饿响应转录因子PHR,通过特异性结合到靶基因启动子区的P1BS基序来调控*OsRAM1*、*OsPT11*等与共生建立、磷吸收过程相关基因的表达^[102]。此外,缺磷条件还能诱导地钱(*Marchantia paleacea*)体内SLs的生物合成与分泌,分泌到环境中的SLs刺激AMF分泌短链几丁质寡聚体(shortchain chitin oligomers,CO)4和CO5,进而抑制植物免疫,促进AMF的共生和磷的获取(图3B)^[99]。*OsSMAX1*通过抑制SLs生物合成及与AMF共生相关基因的表达来负调控共生建立,水稻*d14l*突变体与*d3*突变体表型相似,两者AMF定殖均显著减少;而*Ossmax1*突变能够恢复*d14l*和*d3*突变体的定殖水平^[103]。最新研究发现,AMF接种能够通过D14L依赖的方式降解Karrikin通路抑制蛋白SMAX1,激活水稻Karrikin信号通路,从而激活响应基因*D10*、*D17*、*D27*、*Os900*等的表达,促进SL合成与分泌,进而促进AMF与水稻根系共生过程的建立^[104]。这些结果共同说明,AMF共生与由D14L介导、依赖F-box蛋白D3并诱导SMAX1蛋白降解的信号通路密切相关。

4.4 控制寄生

寄生性杂草给农业生产造成巨大损失,其防控已成为SLs研究的热点方向^[63]。这类杂草能够感知寄主根系分泌的化学信号物质(如SLs)而萌发,进而建立寄生关系(图3B)。基因组分析显示,寄生植物中的KAI2/HTL受体经历了多次基因复制,系统发

育研究表明不同寄生植物之间出现了趋同进化,这些受体也因此进化出感知SLs的新功能^[105]。结构分析进一步揭示,与拟南芥AtKAI2相比,寄生植物如ShKAI2d/HTL的配体结合口袋更大,对多种SLs具有亲和力,并且具备水解SLs的活性^[106,107]。此外,将寄生植物来源的KAI2d/HTL回补至拟南芥*kai2*突变体中,可使其恢复对SLs的特异性萌发反应:例如ShHTL7对多种SLs表现出广谱响应,甚至能感应皮摩尔级别的SLs浓度^[105,106,108]。由于寄生植物遗传操作较为困难,其SLs信号响应通路的具体机制仍需进一步研究。

减少寄生植物寄生的方法之一是抑制寄主植物合成SLs。虽然SLs合成缺陷的寄主植物对寄生植物具有显著的附着前抗性,但会对农艺性状造成不利影响。例如,高粱中水稻*D17*的同源基因*Sbnab1*的突变破坏了SLs的生物合成,导致SLs缺乏,有效抑制了独脚金种子萌发,但造成了矮生多分蘖表型以及产量的严重下降^[21,38]。通过抑制SLs向根际的分泌,可有效规避上述对寄主农艺性状的不利影响^[38,39]。矮牵牛中首次报道的SLs转运蛋白——ABCG家族的PDR1在该过程中发挥关键作用:该基因突变后,植株根系分泌物中SL含量显著降低,分枝列当种子的萌发也因此受到明显抑制^[36]。近期,研究人员在番茄和高粱中分别鉴定出两个G型ABC转运蛋白家族的SLs转运蛋白SlABCG44/45与SbSLT1/2,均定位于细胞膜。在*Slabcg45*与*Sbslt1/2*功能缺失突变体中,SLs向根际的分泌减少,抑制寄生植物种子萌发,减少列当和独脚金的侵染与寄生,同时对寄主作物的农艺性状几乎无负面影响,显著提升了寄生植物侵染环境中的作物产量,为寄生植物防治提供了新策略^[38,39]。

由于寄生植物中的KAI2/HLT受体对不同结构的SLs具有选择性识别能力,因此,通过调控寄主植物根系分泌物中SLs的组成,可有效提升其对寄生植物的抗性。例如,通过抑制玉米细胞色素P450氧化酶ZmCYP06C37、ZmMAX1b及甲基转移酶ZmCLAMT1的活性,或在高粱中突变磺基转移酶基因*low germination stimulant 1 (LGS1)*,以及在珍珠粟中缺失两个CLAMT基因的功能,均可改变根系分泌物中SLs的种类与比例,从而显著降低独脚金的萌发率并抑制其寄生^[32,109,110]。

此外,人工合成的SLs类似物及模拟物(如GR24、

Nijmegen-1、MP1和MP3等)有望在农业中被用作“自杀性萌发剂”,可有效减少土壤中独脚金种子的积累^[111]。例如,在高粱和珍珠粟田间施用Nijmegen-1、MP16和MP3后,高粱田间的独脚金出苗率分别下降60%、11%和52%,珍珠粟田间的独脚金出苗率分别降低43%、41%和33%^[112],但目前仍存在效果不稳定、成本极高、实用性不强等问题,亟待解决。另外,培育能够合成与分泌更多SLs,且分泌的SLs能够更强地诱导寄生种子萌发的“诱捕作物”,并将其作为轮作或与易感作物间作的品种,可进一步诱导寄生植物种子发生“自杀性萌发”,从而减轻其危害,也是一种有应用潜力的生物防治策略^[12,113]。

5 总结与展望

自SLs被确立为植物激素以来,短短十余年间该领域已取得一系列重要突破。从基于突变体鉴定SLs合成与信号通路关键基因,到利用转录组等多组学技术系统解析其下游调控网络及转运蛋白功能,SLs不仅作为内源性激素精密调控植物重要的生长发育过程,提升植物对营养缺乏与非生物胁迫的适应能力,同时还作为关键的根际信号分子,在调控植物建立共生与寄生关系中发挥核心作用。

SLs能精细调控分蘖数量、株高、叶型及根系构型等关键农艺性状,深入解析其协同调控网络,不仅有助于阐明株型建成的分子基础,还可为培育适应密植、抗倒伏、高效利用光能与土壤资源的理想株型作物提供重要理论指导。作物可通过优化形态结构,保持光合效率,提高抗氧化酶积累及活性以减少氧化损伤,调节气孔行为、促进渗透调节以减少水分散失等一系列措施,提高对营养缺乏、非生物胁迫等不利环境的适应性,其底层分子机制值得进一步研究和探索。SLs作为植物根系分泌的关键信号分子,能够启动并增强植物与AMF的共生,显著提升作物养分吸收与抗逆能力,在减少化肥依赖、培育高效共生作物方面具有重要农业应用价值。SLs对于控制寄生也有重要的指导意义,SLs转运蛋白的鉴定为培育抗寄生作物提供了新思路,深入解析SLs转运的调控机制及底物特异性将有利于深入理解寄生过程并开展高效防控,具有广阔的农业应用前景。

综上所述,对SLs作用机制的深入解析为株型改良、抗逆育种、寄生防治奠定了理论基础。多组学、人工智能、基因编辑等技术的快速迭代,必将加速

SLs在农业生产中的应用,为可持续农业发展提供新的解决方案。

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