综述

独脚金内酯调控植物根系发育的分子机制研究的进展

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摘要 独脚金内酯(strigolactones, SLs)是近年来发现的新型植物激素, 参与调控植物生长发育过程, SLs在调控根系形态方面具有重要的作用。该文重点综述了SLs对植物主根、侧根、根毛及不定根的调节, 特别是SLs与其他信号分子如生长素、乙烯、NO等的相互作用, 以及SLs在氮磷胁迫条件下对根系调控的研究进展, 为进一步深入了解SLs对植物生长和发育的调节奠定基础。

关键词 独脚金内酯; 根系; 植物激素; 营养胁迫; karrikins

Research Progress on Molecular Mechanism of Strigolactones Regulating Root Development

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Abstract SLs (strigolactones) are novel plant hormones that regulate the plant growth and development, and SLs plays an important role in regulating root architecture. This review focuses on the regulation of SLs on primary roots, lateral roots, root hairs and adventitious roots, especially the interaction between SLs and other signaling molecules such as auxin, ethylene and NO, and the regulation of SLs on roots under nitrogen and phosphorus stress, laying a foundation for further understanding the regulation of SLs on plant growth and development.

Keywords strigolactones; root system; plant hormones; nutrient stress; karrikins

根系是植物体吸收土壤水分和营养物质并运输到其他部位的重要器官。植物激素作为信号分子, 被认为在调控根系发育中发挥了重要作用[1]。独脚金内酯(strigolactones, SLs)是近年来发现的一种新型植物激素[2-3], 已被证明参与植物生长发育的多种过程, 如种子萌发、叶片衰老、茎分枝和根系发育等[4-5]。其中, SLs在调控根系生长方面(包括对主根、侧根、根毛及不定根的调控)发挥着重要作用, 并与

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表1　SLs生物合成和信号转导的同源基因

Table 1　Orthology of genes associated with strigolactone biosynthesis and signaling

类型 Type	拟南芥 *Arabidopsis thaliana*	水稻 *Oryza sativa*	大豆 *Glycine max*	番茄 *Solanum lycopersicum*	豌豆 *Pisum sativum*	在根系发育中的作用 Roles in root development	参考文献 References
Strigolactone biosynthesis	*AtD27*	*D27*	*GmD27*	–	–	–	[9-11]
	MAX3	*D17/HTD1*	*GmMAX3*	*SICCD7*	*RMS5*	Inhibition of LR density, promotion of PR elongation in *Arabidopsis thaliana*, promotion of RH elongation in *Glycine max*	[7-9,12-15]
	MAX4	*D10*	*GmMAX4*	*SICCD8*	*RMS1*	Inhibition of LR density, promotion of PR elongation in *Arabidopsis thaliana*, inhibition of AR formation in *Arabidopsis thaliana*, *Pisum sativum*, *Solanum lycopersicum*, inhibition of secondary lateral root formation, promotion of AR formation in *Oryza sativa*	[7-9,16-20]
	MAX1	*OsMAX1*	*GmMAX1*	–	–	Inhibition of LR density, promotion of PR elongation in *Arabidopsis thaliana*	[6,9,12,21]
Strigolactone signaling	*AtD14*	*D14*	*GmD14*	–	*RMS3*	Inhibition of LR density in *Arabidopsis thaliana*, *Hordeum vulgare*, inhibition of secondary lateral root formation in *Oryza sativa*	[9,19,22-28]
	MAX2	*D3*	*GmMAX2*	–	*RMS2*, *RMS4*	Inhibition of LR density and AR formation in *Arabidopsis thaliana*, promotion of PR elongation and RH elongation in *Glycine max*	[6,8,9,29-32]
	SMXL6/7/8	*D53*	*GmD53*	–	–	Inhibition of LR density and AR formation, promotion of root skewing in *Arabidopsis thaliana*	[9,33-35]

LR: 侧根; PR: 主根; AR: 不定根; RH: 根毛; –: 未确定。

LR: lateral root; PR: primary root; AR: adventitious root; RH: root hair; –: not determined.

其他激素互作形成复杂的调控网络[6-8]。SLs也能够通过关闭气孔, 刺激应激或光合基因表达, 增强抗氧化防御系统以及渗透调节和根系构型调节等参与植物胁迫应答, 尤其对根系结构的调整, 能够更好地响应植物氮磷缺乏[4]。不仅如此, SLs还能够与其他信号分子如NO和KARs(Karrikins)共同影响植物根系发育。本文中, 我们介绍了SLs的生物合成与信号转导, 并着重阐述了SLs关键酶基因及SLs与信号分子协同调控根系生长发育的机制, 以及SLs在氮磷胁迫下对根系调控的研究进展。同时, 为了清晰起见, 对于SLs的生物合成和信号转导基因, 我们主要使用拟南芥基因命名法, 有关其他植物中的同源基因见表1。

1　SLs生物合成及其关键酶基因对根系生长发育的调控

1.1　SL生物合成途径

SL的合成主要依赖于类胡萝卜素途径(图1)[36], 首先, AtD27蛋白通过作用于全反式-β-类胡萝卜素的C9-C10键将其可逆转化为9-顺式-β-类胡萝卜素, 在CCD7作用下, 9-顺式-β-类胡萝卜素裂解成为9-顺式-β-apo-10’-胡萝卜醛和β-紫罗兰酮, 之后CCD8催化前者, 将其转化为己内酯(carlactone, CL)[37]。CYP711A1蛋白通过连续氧化反应, 将CL转化为己内酯酸(carlactonic acid, CLA)[13], CLA在CYP722C和A2的催化作用下, 分别形成5DS、ORO和4DO, 即典型SLs, CLA

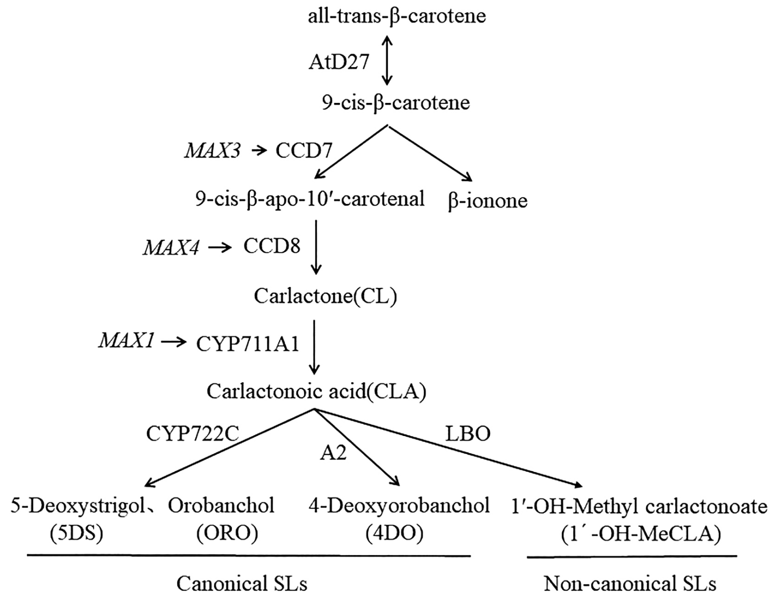

图1 SLs生物合成途径(根据文献[38]修改)

Fig.1 SLs biosynthetic pathway (modified from reference [38])

在LBO(lateral branching oxidoreductase)的催化作用下, 形成1’-OH-MeCLA, 即非典型SLs[38]。

1.2 SLs合成关键酶基因对根系生长发育的调控

SLs合成关键酶基因*MAX3*、*MAX4*和*MAX1*在调控植物根系发育中发挥了重要作用。因此, 本部分着重阐述了这些基因对植物根系发育的调控机制。

1.2.1 *MAX3*和*MAX4* 在SLs合成过程中, *MAX3*和*MAX4*分别编码的CCD7和CCD8蛋白能够进一步裂解和催化类胡萝卜素, 生成独脚金内酯前体CL[16-17,39]。研究发现, 与野生型相比, 拟南芥*max3*和*max4*植株均表现为侧根数量增加, 主根变短, 过表达*MAX3*植株主根长度恢复至与野生型相近, 根毛长度和密度增加[7-8]。对过表达*MAX3*的植株转录组的分析结果表明, *MAX3*的过表达下调了部分SLs生物合成和信号转导基因, 如*AtD27*、*MAX1*、*MAX4*和*MAX2*, 但*AtD14*和*SMXL6/7/8*的不同的拷贝表现出不同的增加或减少[9], 表明SLs在根系发育调控中发挥作用。另外, SLs也可以参与调控大豆根毛发育[9]。而在拟南芥中发现*MAX3*和*MAX4*突变对根毛的影响不大, 但是应用GR24(人工合成的SLs类似物)后, 突变体植株的根毛长度明显增加, 这表明植物根毛可能不是由内源SLs调控的[40]。

此外, 在应用GR24后, 拟南芥和豌豆*max4*植株的不定根数量增加且表现出剂量依赖性, 表明SLs会抑制不定根的形成[8]。研究人员对CYCLIN B1表达进行分析发现, SLs通过抑制建成细胞的第一次分裂进而抑制不定根的数量[8]。人们在番茄中也发现同样的现象, 在敲除*MAX4*基因后, 所有株系均出现了不定根数量增加的表型[17]。与这些植物不同的是, 与野生型相比, 水稻中*max4*植株会表现为不定根数量减少, 侧根数量差异不大[18-19,41]。应用GR24后, 不定根数量增加[18,41]。除此之外, *MAX4*突变还会诱导水稻产生二级侧根, 应用外源GR24会抑制该突变体植株侧根的形成[19]。

1.2.2 *MAX1* MAX1能够连续氧化CL的C19位, 最终合成SLs[12-13]。研究表明, 与野生型相比, 拟南芥*max1*植株主根变短, 侧根数量增加, 证实SLs对主根生长具有正调控作用, 对侧根具有负调控作用[6,9]。应用GR24能够引起拟南芥根尖分生组织细胞数量增加, 促进*max1*植株主根伸长; *max1*植株侧根原基V到VI期的发育会被GR24完全抑制, 因而造成侧根数量减少[6]。除此之外, 在应用较低浓度的GR24(1.25和2.50 μmol/L)时, 拟南芥*max1*植株并未表现出类似*max4*植株和野生型主根伸长的表型, 说明*max1*植株对GR24敏感性降低[6]。

2 SLs信号转导及其关键酶基因对根系生长发育的调控

目前, 人们共鉴定到3种主要的蛋白参与SLs

信号转导，包括AtD14、MAX2以及SMXL6/7/8。AtD14蛋白为SLs受体，它能够结合SLs并将其水解为中间分子CLIM(covalently linked intermediate molecule)，该分子被包裹在AtD14蛋白的催化中心，使得AtD14发生构象改变进而促进其与MAX2蛋白的互作[42]，形成SCF复合体，进一步招募SMXL6蛋白，形成D14-SCF^{MAX2}-SMXL6，引发泛素介导的SMXL6降解，解除了对*SMXL6/7/8*的转录抑制并激活其表达，新合成的SMXL6蛋白反过来又会抑制SMXL6/7/8的转录，形成负反馈回路，从而调控SLs信号响应[43]。下面重点叙述AtD14、MAX2和SMXL6/7/8对根系发育的调控。

2.1 *AtD14*

AtD14蛋白是α/β水解酶超家族成员，它能够利用催化三联体感知和失活SLs信号[44]。已有许多证据表明*AtD14*可抑制植物侧根发育[24-26,45]。相比于野生型，拟南芥和大麦*Atd14*植株侧根数量提高[24-26]。同时，*AtD14*还能够抑制水稻二级侧根的产生。与野生型相比，*Atd14*植株的二级侧根数量显著增加[19]。吴自明等[45]从水稻中分离得到*AtD14*等位基因突变体*htd4*，并发现该基因突变可导致SL合成和信号转导相关基因的变化：上调*MAX3*、*MAX4*、*AtD27*、*AtD14*和*MAX2*的表达；下调*SMXL6/7/8*的表达。这说明该基因突变导致SLs的生物合成增加，而抑制SLs的信号传递。

2.2 *MAX2*

MAX2属于F-box蛋白家族成员，这种蛋白可作为SCF(Skp1-Cullin-F-box)型泛素连接酶的亚基发挥作用[46]。*MAX2*基因在*SCR*(scarecrow)启动子的调控下，赋予侧根、根毛和分生组织细胞SLs敏感性[47]。SLs以MAX2依赖的方式负调控拟南芥侧根的发育。相较于野生型，*max2*植株的侧根数量增加，GR24处理*max2*植株后，对其侧根形成并无影响[6,40]。然而，与SLs信号转导类似，KARs信号也可以通过KAI2与MAX2互作影响根系发育，如果只应用*max2*突变体，而不与特定的突变体如*Atd14*突变体进行比较，就无法判断是哪种信号分子影响植物侧根发育[48]。*MAX2*突变也能够抑制大豆根毛和主根的发育，*MAX2*过表达则可以挽救这些表型，证实*MAX2*对根毛和主根的促进作用[31]。*MAX2*过表达和敲除对SLs合成和信号转导基因表达也有影响，*MAX2*过表达使*MAX1*和*MAX3*表达上调，*AtD14*、*SMXL6/7/8*和*AtD27*的表达下调，而敲除*MAX2*，可以使*MAX3*、*MAX4*、*AtD14*和*AtD27*的表达下调，*SMXL6/7/8*的表达上调，可见MAX2是一个重要的SLs信号组分，影响SLs的生物合成和信号转导[31]。此外，相较于*max2*和野生型，拟南芥*max3*和*max4*植株的侧根和不定根密度都介于二者之间，之前人们认为这可能是由于SLs能通过其他途径合成，或者即使在没有SLs情况下，SCF^{MAX2}仍然能够与MAX2相互作用传递SLs信号，现在人们也猜测这是由于SLs信号没有通过典型D14-SMXL6/7/8起作用，从而造成侧根和不定根减少[8,25,40,49]。

2.3 *SMXL6/7/8*

SMXL6/7/8属于SMXL蛋白家族成员，SMXL6能够与SCF^{MAX2}结合而在蛋白酶体中被降解，从而解除*SMXL6/7/8*的转录抑制，调控下游基因[50-51]。*SMXL6/7/8*主要在*MAX2*下游发挥作用，并能够明显抑制*max2*的根系表型，如抑制*max2*植株的侧根和不定根发育[34-35]。此外，当根生长在固体琼脂表面时，它的生长受到向重力性、负向光性、向触性和回旋运动的影响，由此造成根尖偏斜[35]。研究发现，*SMXL6/7/8*还参与促进根尖偏斜，*smxl6/7/8*植株根尖偏斜明显小于野生型[35]。

3 SLs在氮磷胁迫下对根系的调控

3.1 SLs与氮互作对根系的调控

氮是植物生长发育所需的主要矿质营养之一，其中铵态氮和硝态氮是植物从外界环境中吸收氮的主要矿物形式，但环境的波动和土壤内在的复杂性往往导致土壤氮分布发生巨大变化，进而影响植物根系发育[52]。有证据表明，SLs参与了缺氮条件下植物体根系的调控。在缺氮条件下，SLs的合成增加且通过MAX2通路促进水稻主根伸长，抑制侧根数量[53-54]；缺氮也能够诱导玉米根系分泌SLs并抑制侧根发育[55]。SLs也参与了硝态氮供应下对根系的调控。研究发现，在硝态氮供应下，SLs能够减少生长素在根中的运输，抑制水稻侧根的形成[56]，SLs也能够促进*PIN1b*的表达参与硝态氮调节的水稻根伸长[57]。硝态氮供应也能够抑制玉米中SLs的合成，诱导生长素产生，促进侧根发育[55,58]。这些实验表明，缺氮能够诱导SLs的合成与分泌；另外，SLs会与生长素共同参与硝态氮供应条件下对植物主根和侧根的调控。

3.2 SLs与磷互作对根系的调控

磷是植物生长发育所必需的营养物质之一，常

以磷酸盐的形式被植物吸收[59]。在缺磷条件下, SLs可以抑制番茄和拟南芥主根伸长, 增加侧根数量, 却促进水稻主根伸长, 降低其侧根数量[8,53,60]。这种在缺磷条件下根系的不同反应是SLs对生长素运输的作用不同造成的[78]。SLs也可以通过MAX2通路作用于生长素受体TIR1(transport inhibitor response 1)来调节拟南芥根毛对低磷胁迫的应答[61-62]。另外, 缺磷也可以影响SLs的合成和信号转导。缺磷条件下, 高粱、番茄和小麦等植物中SLs的合成增加[63-65]。番茄中SLs的信号基因*AtD14*被抑制, *SMXL6*的表达也被轻微抑制, 磷酸盐的供应可以恢复这些基因的表达[66]。可见, SLs能够与生长素互作, 参与缺磷条件下不同植物根系形态的调节, 缺磷也可以促进SLs的合成, 这些调节共同增强了植物对磷的吸收与利用。

4 SLs与其他激素和信号分子在根系调控中的互作

4.1 SLs-生长素

生长素可以介导植物侧根发育的各个阶段, 包括侧根的起始、侧根原基的形成与发育[67]。研究发现, SLs和生长素在调节植物侧根发育方面密切相关。应用GR24明显减少拟南芥的侧根数量, 且通过影响PIN的靶向定位和运输, 干扰生长素的动态平衡[6,68]。另外, GR24对拟南芥和油菜侧根形成表现出双重作用。低浓度GR24可促进侧根的形成, 而高浓度则抑制侧根形成。进一步研究发现, GR24的这种作用依赖于植物体的生长素水平变化, 较高剂量的GR24能够降低表皮细胞的生长素水平, 导致侧根启动减少[6,69]。可见, SLs能够通过抑制生长素水平, 从而抑制侧根的形成。

SLs也能够通过干扰生长素的运输调控植物不定根的发育。研究发现, SLs可能抑制生长素从上至下的运输, 进而抑制拟南芥和豌豆的不定根发育[8]。但二者也可能独立起作用, 因为在生长素含量升高的情况下, SLs仍然可以抑制拟南芥和豌豆不定根的形成[8]。在水稻和高茅草中, 应用GR24可以显著抑制PIN的表达, 促进不定根伸长[18,70]。不难看出, 生长素与SLs在调控不同植物不定根的发育过程中存在复杂的作用, 其精细调控机制仍然需要进一步研究。

SLs也可以通过抑制PIN活性抑制拟南芥和黄芪生长素运输, 促进主根的伸长[6,71]。这是由于GR24介导的PIN蛋白循环减少导致根和地上部维管组织中生长素运输能力的降低, 造成生长素在根分生组织积累, 进而使分生组织细胞数量和大小增多[6]。另外, SLs也能够通过调节PIN外流使表皮细胞中生长素水平增加, 促进拟南芥和番茄根毛的伸长[72-73]。总而言之, SLs能够通过调节PIN蛋白促进主根与根毛的伸长, 影响侧根和不定根发育。

4.2 SLs-细胞分裂素(cytokinin, CK)

CK和SLs在调控植物根系生长方面有着不同的相互作用。其中, 它们能够协同调控植物侧根发育。CK可以通过AHK3(arabidopsis histidine kinase 3)/ARR1(*Arabidopsis* response regulator 1)/ARR12/SHY2(short hypocotyl 2)通路影响GR24对拟南芥侧根的作用, 这可能与该通路可以下调PIN蛋白的表达有关, 从而影响GR24对侧根的作用[74]。CK和MAX2通路在调节主根生长和根毛发育方面作用相反, CK负调控主根和根毛发育, 而MAX2通路起到正调控作用[75]。研究发现, 拟南芥*ahk2 ahk3 max2*三突变体植株比*ahk2 ahk3*双突变体植株和*max2*突变体植株主根更长, 这表明CK和MAX2通路在调节主根伸长方面存在复杂的相互作用[75]。推测CK和SLs可能通过调节SHY2影响主根生长, 因为*shy2*突变体对GR24分生组织细胞不敏感, CK能够诱导SHY2的表达, 而*shy2*和*max2*突变体对CK的敏感性降低[76]。CK信号在调节根毛伸长方面具有AHK4依赖性, 且几乎不受MAX2功能丧失的影响, 说明CK和SLs在调控根毛发育方面相互独立[75]。此外, 虽然SLs和CK都能够抑制不定根的发育, 但是研究表明二者可能独立起作用[8]。

4.3 SLs-乙烯(ethylene, ET)

SLs和ET都能够促进植物根毛的发育, 且二者共同调控根毛生长。研究发现, SLs可以诱导ACS2(acc synthase 2)合成, 增加ET的含量, 促进拟南芥根毛伸长[40]。ET也可以与生长素互作调控根毛的发育, 暗示SLs、ET和生长素三种激素串扰, 共同调节根毛的发育[40,77]。ET也可以通过协调EIN3(ethylene insensitive 3)/EIL1(ein3-like 1)和RHD6(root hair defective 6)/RSL1(rhd6-like 1)独立起作用, 且应用GR24对*ein2*植株根毛无反应, 说明ET调控根毛发育并不总是需要生长素或SLs信号的[78-79]。另外, 虽然SLs和ET都能够抑制不定根的发育, 但是研究发现二者可能独立起作用[64]。

4.4 SLs-NO

SLs可以与NO共同调控植物主根发育, 但二者

之间的相互作用在不同植物间、不同条件下有所不同。正常条件下, SLs可以促进NO合成, 诱导拟南芥主根伸长[81]。而在低氮与硝态氮供应条件下, NO却作为SLs信号的上游调控因子发挥作用。在低氮条件下, NO正向调节SLs信号, 诱导水稻主根伸长[82-83]。而在硝态氮供应条件下, NO负向调节SLs信号, 诱导玉米早期根尖生长[84]。另外, 内源性和外源性SLs对NO也有不同的影响。与野生型相比, 拟南芥*max1*和*max2*根尖中NO的水平较高, 说明内源性SLs对NO有负面影响, 但外源GR24却能够诱导拟南芥根尖NO的产生[85]。

4.5 SLs-KARs

KARs是从野火烟中发现的一类小分子, 与SLs功能类似[86]。它能够通过KAR信号途径, 与SLs共同调控植物根系[25]。其中, 感知SLs和KARs的受体AtD14和KAI2互为同源蛋白, 并且都能够与F-box蛋白MAX2互作, 使SMXL家族的不同成员发生泛素化降解[87]。SLs和KARs在调控根毛发育方面并没有直接联系。但是, 如果KAI2缺失, 则可以触发AtD14信号来促进根毛的发育[25]。KAI2信号通路也可以与AtD14信号通路共同抑制拟南芥侧根的发育[25]。另外, SLs与KARs可以共同通过MAX2通路抑制拟南芥不定根的发育, 而且KARs通过KAI2/MAX2负向调节根尖偏斜需要SMXL6/7/8蛋白的参与, 说明KARs和SLs也可以共同影响根尖偏斜[35]。

5 展望

综上所述, SLs可以与信号分子互作抑制拟南芥侧根和不定根的形成, 促进主根和根毛的生长, 同时, SLs也可以参与氮磷胁迫条件下对主根和侧根的调控, 提高植物对水分和养分的吸收。作为近年来发现的新型植物激素, SLs与生长素、ET、CK等互作对根系的精细调控过程还需要进一步完善, 以及在SLs调控根系的过程中, 是否有更多的激素或信号分子(如赤霉素、油菜素内酯等)参与, 都需要进一步研究才能得出明确的结论。多项研究表明, 在长期进化过程中, SLs参与植物根系与丛枝菌根真菌共生关系的建立与维持, 使植物从土壤中获取氮、磷等元素, 但其所发挥的作用机制仍不清晰[88]。通过对SLs调控根系发育方面的深入研究, 可以逐渐完善根系发育机制的理论基础, 为提高农作物产量和品质提供科学依据。

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