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· 专题论坛 ·

生物和非生物逆境胁迫下的植物系统信号

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摘要 复杂多变的自然环境使植物进化出许多适应策略, 其中由局部胁迫引起的系统响应广泛存在, 精细调节植物的生长发育和环境适应能力。植物系统响应的诱导因素首先引起植物从局部到全株范围的信号转导, 这类信号称为系统信号。当受到外界刺激时, 植物首先在受刺激细胞内触发化学信号分子的变化, 如茉莉酸和水杨酸甲酯等在浓度和信号强度方面发生变化; 进而, 伴随着一系列复杂的信号转换, 多种信号组分共同完成系统响应的激活。植物激素、小分子肽和RNA等被认为是缓慢系统信号通路中的关键组分, 而目前也有大量研究阐释了由活性氧、钙信号和电信号相互偶联组成的快速系统信号通路。植物系统信号对其生存和繁衍至关重要, 其精确的转导机制仍值得深入研究。该文综述了植物响应环境的系统信号转导研究进展, 对关键的系统信号组分及其转导机制进行了总结, 同时对植物系统信号传递的研究方向进行了展望。

关键词 系统信号, 茉莉酸, 水杨酸, RNA, 活性氧

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植物的生长发育时刻受到外界环境的影响。面对环境的变化, 植物进化出复杂的响应机制来应对不同种类的胁迫(Kosová et al., 2011)。当植物局部细胞感受到外界环境变化时, 能产生全株性的适应性反应, 称为系统响应(Szczegielniak et al., 2012)。植物系统响应广泛存在, 根据其诱导因素的不同, 可以分为应对病原菌产生的系统获得抗性(systemic acquired resistance, SAR)、应对非生物胁迫产生的系统性获得适应(systemic acquired acclimation, SAA)以及应对创伤和植食性动物啃咬的系统性创伤响应(systemic wound response, SWR) (Durrant and Dong, 2004; Gaupels et al., 2017; Szechyńska-Hebda et al., 2017)。这些系统响应使植物既能够及时、高效地应对环境变化或生物侵扰, 又能够产生广谱抗性, 并通过跨代遗传而得以保留(Rasmann et al., 2012)。植物系统响应影响深远, 对植物生长发育和环境适应至关重要。

在植物系统响应中, 不同组织和器官之间的远距离沟通称为植物系统信号(plant systemic signaling) (Karpinski et al., 1999; Konert et al., 2013; Tsutsui and Notaguchi, 2017)。对于植物而言, 系统信号通路被激活后诱导未受胁迫的植物组织基因表达, 而胁迫信号的系统性转导机制十分复杂精妙。那么植物系统信号通路是怎样被激活的? 系统信号又是以何种形式贯穿整株植物进行转导呢? 研究表明, 不同的胁迫诱导植物局部细胞产生不同的化学信号。例如, 机械损伤或植食动物啃食诱导创伤部位产生茉莉酸(jasmonic acid, JA) (McConn et al., 1997; Smirnova et al., 2017); 病原菌侵染诱导植物受感染部位细胞内水杨酸(salicylic acid, SA)含量升高(Fu and Dong, 2013; Niu et al., 2016); 昆虫啃食诱导被啃食部位生长素(auxin)积累(Machado et al., 2016)。这些化学信号在产生后可能直接向植物其它组织传输或与其它信号发生协同作用而进行系统传输, 也可能以进一步激发电信号等广谱信号网络的方式来传递系统信号(Hilleary and Gilroy, 2018)。研究表明, 在系统信号通路中有几类关键组分, 包括: (1) 植物激素、RNA、蛋白质或多肽以及小分子代谢物等具有特异性的分子, 它们可能通过响应不同的胁迫调节系统响应, 或担任信号分子, 在植物维管组织内进行长距离运输

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(Le-Brasseur et al., 2002; Shah et al., 2014; Coppola et al., 2017; Zhang and Hu, 2017; Han et al., 2018); (2) 由钙离子、电信号和活性氧相互偶联形成的快速系统信号，这类信号具有很高的传输速度(>1 mm·s^{-1})，且能响应多种胁迫，被认为是一种通用信号网络(Choi et al., 2014, 2016; Gilroy et al., 2016); (3) 离子通道(ion channel)、谷氨酸受体类似物(glutamate receptor-like, GLR)和呼吸爆发氧化酶同系物(respiratory burst oxidase homologue, RBOH)等具有信号转化和调节作用的信号元件(Miller et al., 2009; Mousavi et al., 2013; Choi et al., 2016)。

越来越多的研究表明，系统信号的复杂通路很可能由不同信号通路交互组成，因此，尽管已报道了一些关键的信号组分，但系统信号转导的精确机制还需要深入研究。本文阐述了植物系统信号的研究现状，总结了植物系统信号通路中的一些关键组分及系统信号转导机制(表1)，进而讨论并展望了系统信号通路研究领域的重点和热点方向。

1 缓慢系统信号

1.1 茉莉酸和水杨酸

植物激素对植物的生长发育起着至关重要的调控作用。已有许多研究表明，响应创伤和植食动物啃食的茉莉酸(JA)和响应病原菌侵染的水杨酸(SA)在系统信号通路中作用最为重要。此外，油菜素甾醇(brassinosteroid, BR)、乙烯(ethylene, ET)和脱落酸(abscisic acid, ABA)等也参与调控系统信号通路(Xia et al., 2011; Gorecka et al., 2014; Caarls et al., 2015; Li et al., 2017; Takahashi et al., 2018)。

大量研究表明，JA是植物响应创伤和寒冷等非生物胁迫的重要激素(Ding et al., 2002; Koo et al., 2009; Vashegyi et al., 2013)。创伤或昆虫啃食使JA及其代谢物JA-异亮氨酸(JA-isoleucine, JA-Ile)等在植物创伤部位和其它健康组织中积累(Koo et al., 2009; VanDoorn et al., 2011; Yan et al., 2013); 维管束中也存在JA，据此推测JA可能是维管束系统信号分子的潜在候选者(Vlot et al., 2008)。然而，JA在植物体内被认为采用重头合成(*de-novo* synthesis)途径，表明远距离植物组织中的JA可能不是从创伤位点运输而来(Koo and Howe, 2009)。综上，JA很可能与其它信号通路存在交互作用，从而系统性地传导创伤信号，即JA在创伤位点的积累激活电信号和钙离子信号等快速系统信号通路，并在传递到其它组织后进一步激活JA的重头合成。

SA是一种酚类物质，主要通过异分支酸合酶(isochorismate synthase, ICS)途径合成(Chen et al., 2009)。SA在植物免疫反应中起至关重要的作用。例如，蜡样芽孢杆菌(*Bacillus cereus*)及丁香假单胞菌(*Pseudomonas syringae*)活体营养型病原入侵后，激活SA调控的SAR信号通路，增强植物抗病性(Song et al., 2015; Niu et al., 2016)。SA的积累进一步诱导植物抗病基因的表达及相关物质积累。例如，在大麦(*Hordeum vulgare*)中，SA诱导超氧化物歧化酶(superoxide dismutase, SOD)和谷胱甘肽还原酶(glutathione reductase, GR)等防御反应调节相关酶的活性升高，同时也有助于植物保持活性氧(ROS)的动态平衡(Ananieva et al., 2004)。NPR1 (nonexpressor of pathogen-related gene 1)作为SA受体，是激活SAR的关键调控因子，在SA处理和病原菌侵染后，其基因表达量上调(Mou et al., 2003; Lee et al., 2015; Niu et al., 2016; Ali et al., 2017)，其过表达植株对黑斑病菌(*Alternaria brassicae*)和十字花科白粉菌(*Erysiphe cruciferarum*)的抗性显著增强(Lee et al., 2015)。

植物通过精确调节其内源激素水平以对病原体进行有效防御，JA和SA之间的平衡也对系统抗性至关重要(Van der Does et al., 2013)。在一些特定的防御响应中，JA和SA以相互拮抗的方式来调控防御反应(Yuan et al., 2017)。如在哈茨木霉菌(*Trichoderma harzianum*)菌株T-78的定殖过程中，NPR1、谷氧还蛋白GRX480和WRKY转录因子等SA信号元件都能够对JA信号产生抑制作用，反之JA信号通路的激活也能削弱SA对T-78定殖水平的抑制作用(Yuan et al., 2017)。在拟南芥(*Arabidopsis thaliana*)中，转录因子ANAC032在上游调控JA/SA通路互作，如可通过抑制*NIMIN1*的作用来激活SA通路，从而抑制*PDF1.2A*等JA响应基因的表达(Allu et al., 2016; He et al., 2017; Yuan et al., 2017; Betsuyaku et al., 2018)。因此，研究JA和SA之间相互拮抗作用中的关键因子能

表1　植物系统信号中的重要组分

Table 1　Important components of plant systemic signaling

信号组分			作用方式	参考文献
缓慢系统信号	激素类	茉莉酸(JA)	响应创伤、寒冷和昆虫啃食等, 在植物体内发生系统性积累	Koo et al., 2009; VanDoorn et al., 2011; Yan et al., 2013
		水杨酸(SA)	响应病原菌侵染, 调控植物免疫反应	Mou et al., 2003; Lee et al., 2015; Ali et al., 2017
		油菜素甾醇(BR)	与系统信号组件互作, 调控系统响应, 如活性氧	Xia et al., 2011, 2015
	RNA		响应多种胁迫, 作为基因表达产物在维管束中系统性转运	Yoo et al., 2004; Suzuki et al., 2015
	小分子肽	系统素	广泛存在于茄科植物中, 提高植株对植食性动物的抗性	Scheer et al., 2003; Coppola et al., 2017
		环二肽	增强植物对病原菌和病毒侵害的抵抗力, 诱导活性氧累积及Ca^{2+}信号转导	Wu et al., 2017
	其它小分子代谢物	氨基酸代谢物	在维管束中, 如壬二酸和哌啶酸, 引起SA的积累, 诱导植物对病原菌的抗性	Jung et al., 2009; Shah et al., 2014
		MeSA	在维管束中, SA的代谢产物, 是重要的系统信号分子	Park et al., 2007
快速系统信号	活性氧		迅速产生并响应多种胁迫, 是从胞间信号到系统信号转导的重要信号形式	Dat et al., 2000; Hancock et al., 2001; Czarnocka and Karpinski, 2018
	Ca^{2+}		迅速产生并响应多种胁迫, 细胞内重要的第二信使, 具有信号转导迅速和分布广泛的特征	Ranty et al., 2016; Zhu, 2016
	电信号		响应创伤和昆虫啃咬等, 以高效的信息传递功能与其它机制及信号体系发生联合	Vincill et al., 2012; Gilroy et al., 2016; Hedrich et al., 2016; Szechyńska-Hebda et al., 2017
其它	离子通道		如GLR和TPC, 调控电信号和Ca^{2+}等快速信号的胞间传递, 也为多种信号的偶联提供可能	Miller et al., 2009; Choi et al., 2016; Gilroy et al., 2016
	RBOH		是调控活性氧信号转导的关键酶类	Miller et al., 2009; Mittler, 2017
	NPR1		SA受体, 是SA信号通路的关键组分	Mou et al., 2003; Niu et al., 2016; Ali et al., 2017

够为揭示系统信号通路的精确机制提供有力的证据。

1.2　小分子肽

系统素(systemin)是一种从番茄(*Lycopersicon esculentum*)中分离出来的18肽。用系统素处理番茄植株不仅能提高模式识别受体、信号酶和转录因子的表达水平, 显著提高植株对植食性动物的抗性, 而且能够诱导合成具有生物活性的挥发性有机物, 使相邻植株间能够进行系统性交流(Scheer et al., 2003; Coppola et al., 2017; Xu et al., 2018)。环二肽是由2个氨基酸分子通过环化脱水形成的小分子肽, 具有多种生物活性。在烟草(*Nicotiana tabacum*)中施加环二肽能够减轻烟草疫霉病菌(*Phytophthora nicotianae*)和烟草花叶病毒(*Tobacco mosaic virus*)的侵害程度, 并诱导气孔关闭、ROS累积以及保卫细胞胞浆中的Ca^{2+}和NO产生(Wu et al., 2017)。

1.3　各类RNA

被子植物的维管束内含有种类众多的RNA, 数千种mRNA从源器官向分生组织转运, 使得RNA具有传递系统信号的潜力(Ham and Lucas, 2017)。核糖核蛋白复合体在RNA转运过程中起着稳定RNA的作用, 有证据表明RNA的系统性转运影响植物发育和作物产量(Ham and Lucas, 2017)。对南瓜(*Cucurbita maxima*)等植物的韧皮部提取液进行分析, 证实了其中miRNA (单链/双链)的存在, 发现其中RNA结合蛋白PSRP1能与25核苷酸单链RNA类相结合, 进而调控该类RNA的胞间转运(Yoo et al., 2004)。近期有研

究证实mRNA可以进行系统性转运。施加强光胁迫后, 拟南芥植株内mRNA含量在20–60秒内发生变化, 累积的mRNA中有20%能触发ROS和ABA相关响应(Suzuki et al., 2015)。在创伤响应中, 番茄系统素及前系统素(prosystemin)为系统信号通路中的上游组件, 其中番茄前系统素的mRNA被证实在番茄、烟草和拟南芥的维管束中都能进行系统性转运(Zhang and Hu, 2017; Zhang et al., 2018)。

1.4 小分子代谢物

尽管JA和SA在系统响应中起着至关重要的调控作用, 但其却被认为不是系统信号传递的直接物质。在植物维管束中还存在一些小分子代谢物质, 被推测是传递长距离信号的信号分子, 如水杨酸甲酯(MeSA)、赖氨酸分解代谢物哌啶酸(pipecolic acid)及壬二酸(azelaic acid) (Shah et al., 2014)。Park等(2007)以烟草为材料, 通过基因沉默等技术手段证明了MeSA在植物中的信号传递作用。壬二酸是一种九碳二羧酸, 在拟南芥维管束中被发现。对拟南芥施加壬二酸能够引起SA的积累, 从而诱导拟南芥对丁香假单孢菌的抗性, 壬二酸及其诱导基因*AZI1*表达的蛋白被证明是植物系统性免疫响应中的启动元件(Jung et al., 2009)。

2 快速系统信号

除了多肽、RNA、小分子代谢物和激素之外, 植物体内传递系统信号的化学调节物质还有一类更加迅速的信号网络。它们独立于化学信号的传递, 以超过1 mm·s^{-1}的速度传遍整个植株, 由ROS波动、Ca^{2+}信号通路以及电信号网络共同组成, 称为快速系统信号(Gilroy et al., 2014; Choi et al., 2017)。

2.1 活性氧

活性氧在生物有机体中广泛存在, 在动植物的信号通路中起着至关重要的作用(Zandalinas and Mittler, 2018)。作为一种新陈代谢的重要产物, ROS在所有细胞隔间大量产生。在健康细胞中ROS含量保持稳定状态(Gechev et al., 2006), 但是在受到胁迫部位的细胞中ROS呈瞬间或持续增长, 且增长剧烈, 被称作氧化迸发(oxidative burst) (Dat et al., 2000; Hancock et al., 2001)。当植物体受到生物胁迫(如昆虫、寄生虫、微生物及病毒入侵), 或经受非生物胁迫(如过度光照、紫外辐射、臭氧、干旱、洪涝或不适宜的温度影响)时, 细胞中氧化还原反应扰动被诱发, 在接收胁迫信号的细胞内, 不同细胞器或非原质体产生ROS (Czarnocka and Karpinski, 2018)。ROS的局部产生触发信号的级联放大(Van Breusegem et al., 2008), 细胞间的信号交流形成ROS波且在不同的组织间传递, 携带相关信号进行长距离传输(Mittler et al., 2011)。ROS通常作为新陈代谢反应的副产物, 但高等植物可以自主产生ROS, 并将其用作信号分子来调控一系列生理过程(Kadota et al., 2015)。对病原菌的响应或ROS形式的系统信号转导依赖于呼吸爆发氧化酶同系物(respiratory burst oxidase homologue, RBOH), 在拟南芥*rbohd*突变体中, ROS相关的快速系统信号转导受到抑制(Miller et al., 2009; Mittler, 2017)。植物通过ROS诱导的ROS释放(ROS-induced ROS release, RIRR)过程进行胞间信号交流, 单个细胞中的ROS含量升高触发邻近细胞释放ROS, 这种ROS生产状态(ROS production state)沿着邻近细胞在植物体不同器官之间进行传递。植物中的RIRR主要用于描述胞间交流水平(Zandalinas and Mittler, 2018)。ROS在植物中是通用的信号分子, 直接或间接与其它信号通路的活化相联系(Czarnocka and Karpinski, 2018)。在与激素的互作中, ROS通过活化植物激素调节植物的胁迫耐受性(Xia et al., 2015; Tian et al., 2018)。

2.2 钙离子

Ca^{2+}是植物必需的矿质元素, 同时也是植物生长发育的重要调节因子及植物细胞壁的重要组成部分(Hepler, 2005)。Ca^{2+}在植物细胞内充当重要的第二信使, 联系植物对外界胁迫的感受与植物的适应性反应, 而Ca^{2+}感受器(Ca^{2+} sensor)是植物应对生物与非生物胁迫响应的关键性枢纽(Ranty et al., 2016)。渗透性胁迫(如盐、寒冷和高温), 以及氧化胁迫、重金属和ABA, 都能引起胞浆内游离Ca^{2+}浓度升高(Zhu, 2016)。有证据表明, Ca^{2+}不仅调控植物细胞间信号交流, 而且可能也调控植物长距离信号交流及生理反应(Kudla et al., 2018)。植物体内拥有基于Ca^{2+}波动的系统快速信号, 该信号通过表皮和内胚层细胞传遍整

个植株, 速度达400 μm·s^{-1}。Ca^{2+}信号的传递依赖于液泡离子双孔通道(two pore channel, TPC)系统, TPC1在靶器官引起的分子响应有利于提高植株的胁迫耐受性(Choi et al., 2014)。胞内Ca^{2+}浓度在距离遥远细胞中的时空分布表明Ca^{2+}可能是植株内调控不同种类胁迫的一种通用信号(Kudla et al., 2018)。

除ROS和Ca^{2+}之外, 植物细胞内的第二信使, 如NO和磷脂酸(phosphatidic acid, PA)也被认为具有传递快速系统信号的潜力。在干旱和盐等非生物胁迫下, NO能够在邻近植物细胞之间传递胁迫信号; 在受到病毒侵染时, 植物激素BR能够调控NO的积累(Zou et al., 2018)。PA是一类具有信号转导功能的磷脂分子, 在植物应对冷害、冻害、创伤及盐碱等多种非生物胁迫响应中起重要作用(Welti et al., 2002; Wang et al., 2006; Kooijman and Burger, 2009; Bourtsala et al., 2018)。

2.3 电信号

电信号对于高等植物的胞内和胞间信息交流、生长发育以及胁迫响应都是必需的。在SAA和SAR中, 电信号不具备SAA和SAR所需要的信息特异性, 但却能以高效的信息传递功能与其它机制及信号体系发生联合。在对光合作用的调控中, 细胞氧化还原电位、Ca^{2+}和液压波动、激素通路和气孔调节都被认为是重要的信号组件(Szechyńska-Hebda et al., 2017)。韧皮部的电信号传播与创伤响应紧密相关, 机械损伤和昆虫啃食伤害均能够诱导电信号的传播(Gilroy et al., 2016)。在捕蝇草(*Dionaea muscipula*)中, 电信号可能由触须感觉到的机械刺激或叶中脉感知到的化学刺激所引发, 随后的动作电位能以10 m·s^{-1}的速度在捕蝇草体内传导(Volkov, 2019)。在感受到外界刺激时, 植物细胞膜的膜电势会发生迅速改变, 这种信号将会以波浪的形式进行传导: 电势的波状变化以离子穿过细胞膜或细胞器膜为驱动, 随后沿着相邻的细胞或细胞器进行传导, 同时反馈影响胞内电活动, 从而调控细胞自身的代谢; 短距离胞间电信号可以维持局部细胞的响应, 而长距离胞间电信号则引起系统响应(Szechyńska-Hebda et al., 2017)。电信号的传播伴随着一系列氧化还原反应的发生, 通常与Ca^{2+}和ROS信号相偶联, 共同完成快速系统信号的转导(Choi et al., 2017)。据报道, GLR (glutamate receptor-like)离子通道家族在快速系统信号中起重要调控作用, 决定电信号和Ca^{2+}信号的转导方式和速度(Stephens et al., 2008; Vincill et al., 2012; Hedrich et al., 2016)。然而, 在*glr3.3*/*glr3.6*双敲除突变体中, 创伤引起的电信号依然可以在韧皮部中进行传播, 因此推测可能还存在更多的调控因子, 这需要更广泛深入的研究来阐明快速系统信号的组分(Hedrich et al., 2016)。

3 维管组织在系统信号转导中的作用

一直以来, 维管系统都被认为是信息传递的高速通道, 为植物组织间的长距离信号传输提供系统性互联。维管组织由木质部、韧皮部和薄壁细胞组成(Lucas et al., 2013), 其内皮层细胞特化的细胞壁允许分子进行系统运动(Ramachandran et al., 2018)。木质部的导管细胞由细胞程序性死亡后保留下来的细胞壁增厚所形成, 为水分和营养物质的传输提供保障; 相反, 韧皮组织由一系列活细胞组成, 包括成熟的筛管分子及其邻近伴细胞, 将光合作用同化产物由成熟叶片转移到生长中的幼嫩组织(Notaguchi and Okamoto, 2015)。

植物维管组织中物质的丰富性是系统性信号传递的基础。植物激素(如JA)响应创伤后在维管束中积累, 营养元素(如磷元素)在维管束中转运(Tsutsui and Notaguchi, 2017)。氧化还原反应动态变化影响系统信号的传递。尽管目前对贯穿植物整株的信号路径知之甚少, 但对维管束的研究提示我们在维管束内可以完成氧化还原反应信使的合成、信号放大和系统转运(Gaupels et al., 2017)。通过对维管束内流动物质的分析, 发现维管组织转运着种类繁多的基因产物, 为植物长距离通信提供分子基础; 对木质部伤流的分析证实蛋白质可随木质部蒸腾流转运。此外, 有研究表明, 韧皮部转移系统中包含蛋白质和一系列RNA。因此, 植物维管系统很可能在系统信号传递中起主要作用(Notaguchi and Okamoto, 2015)。

4 研究展望

目前, 关于系统信号的研究已初步阐释了植物感知外界环境所引起的系统信号及其传递途径。基于缓慢系统信号的研究成果, 快速系统信号的发现为我们提供

了新的思路和方向，即应深入研究植物不同组织间的沟通方式。一方面，植物维管束中的物质丰富性暗示着系统信号能够贯穿植株根和地上部分进行长距离传输，木质部的多肽、韧皮部的蛋白质和RNA都可作为特定的信号进行长距离传递(Chiou and Lin, 2011; Notaguchi and Okamoto, 2015; Xuan et al., 2017)。有研究者分析了韧皮部中RNA结合蛋白，揭示了RNA的特异性(Gilroy et al., 2014; Ham and Lucas, 2017)。这些发现提示我们，维管系统中分子的功能和性质以及它们的传输机制仍需要大量工作来阐明。另一方面，不同种类的刺激能够引起不同种类的系统信号转导。已有大量研究阐释了不同环境下的系统信号转导。例如，在营养和水分运输中根与地上部分的系统信号转导；在机械损伤和病原体入侵时JA和SA等抗病激素信号的活化；以及在强光胁迫下的电信号系统转导。在植物体应对病虫侵害和机械损伤等胁迫时，JA和SA对系统响应起重要的调控作用；在一些非生物胁迫，如荫蔽胁迫和盐胁迫下，生长素、赤霉素、脱落酸和油菜素甾醇等激素起重要的调控作用(Casal, 2012; Caarls et al., 2015; Shu et al., 2017, 2018; 帅海威等, 2018)。那么，植物激素是否也调控植物的系统信号通路？植物激素及其相关代谢产物是否也能作为系统信号分子，在植物组织之间传递系统信号，进而调控植物系统性响应非生物胁迫？这些信号通路之间是否存在交互作用？植物又是如何完成不同信号之间的转化？以上问题值得深入探讨。

目前，随着荧光生物传感器技术的开发，让难以捉摸的系统信号分子日渐趋于可视化，并使实时检测信号分子的系统性转运变得可行，这为进一步揭示系统信号的广泛性和特异性创造了条件(Zhang and Hu, 2017; Takahashi et al., 2018)。

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Plant Systemic Signaling Under Biotic and Abiotic Stresses Conditions

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Abstract Plants have evolved numerous strategies to adapt to complex and changing surroundings. Plants have a wide range of systemic responses induced by local stresses to precisely regulate plant growth, development and adaptability to environments. Plant systemic responses induce whole-plant signaling transmission at first, called systemic signaling. When subjected to local stresses, plants trigger chemical molecules in local cells, such as biosynthesis and/or signaling transduction of the phytohormones jasmonic acid and methyl salicylate. Accompanied by a series of complex signal cascades, multiple signal components work together to activate the systemic response. In the past several years, pioneer studies demonstrated that phytohormones, small peptides and several types of RNAs are considered key components of slow-moving systemic signaling, and rapid systemic signals include reactive oxygen species, calcium signals and electrical signals. Plant systemic signaling is essential for plant growth, development and adaptation to the environment, and the precise transmission mechanism is worthy of further investigation. In this review, we describe the research progress in plant systemic signaling transmission and response to the environment and summarize several key systemic signal components and their transmission mechanism. Finally, the potential challenges of future research in this research field are discussed.

Key words systemic signaling, jasmonic acid, salicylic acid, RNA, reactive oxygen species

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