综 述 Reviews

植物防御信号分子β-罗勒烯的研究进展

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摘要: 植物为了适应复杂的生活环境, 在长期的进化过程中, 发展起来了一套与动物免疫系统相似的、高度复杂的防御系统。研究表明, 众多的信号分子在调控植物防御反应中起着重要作用。β-罗勒烯是一种与植物防御启动密切相关的信号分子。本文综述了信号分子罗勒烯的结构组成、自然分布、化学合成、植物防御以及信号途径等方面的研究进展, 为其进一步的理论研究及农业应用提供了有益参考。

关键词: β-罗勒烯; 信号分子; 植物防御

Research Progress of Plant Defense Signal Molecule — β-Ocimene

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Abstract: To adapt to the complex environment, plants developed a highly sophisticated defense system, like the animal immune system during the long-term evolution process. It has been reported that diverse signal molecules play pivotal roles in defense response. In this paper, the structure, nature distribution, synthesis, the role in palnt defense and signalling of the β-ocimene are summarized, which provides good reference for the further basic study and agricultural application of the signal molecule.

Key words: β-ocimene; signal molecule; plant defense

在长期的进化过程中, 为了有效规避不利环境, 完成自己的生活周期, 植物进化出了一套自身特有的完善的防御系统。已有研究表明植物在受到生物胁迫以及非生物胁迫后, 会释放出一些活性物质, 如水杨酸(salicylic acid, SA)、茉莉酸(jasmonic acid, JA)、乙烯(ethylene, ET)和脱落酸(abscisic acid, ABA)等(Pichersky和Gershenzon 2002)。这些信号分子或激素能够启动植物的防御反应, 帮助植物直接应对环境的胁迫; 同时释放出的某些挥发物还能帮助其他植物直接远离攻击或吸引这些攻击者的天敌, 从而能完成对植物的间接的防御保护(Takabayashi和Dick 1998; Kessler和Baldwin 2001)。

现已了解到, 植物受节肢食草动物取食后能释放出一些挥发性物质。一些低分子量的萜类物质就是植物受食草动物取食后诱导释放的挥发性物质中的主要成分(Bohlmann等1998; Degenhardt和Gershenzon 2000; Arimura等2004)。像单萜类物质(E)-β-罗勒烯[(E)-β-ocimene]就是挥发物中的主要成分之一(Paré和Tumlinson 1999; Pichersky和

Gershenzon 2002)。研究表明(E)-β-罗勒烯是一种与植物防御启动密切相关的信号分子。它不仅能直接提高植物对某些病原菌及食草类昆虫的抗性, 如上调一些植株中JA和ET信号途径的表达水平; 同样也能充当植物之间的信号传递分子, 帮助受害植株周围的植株免遭伤害(Dicke等1990a, b, 1999; Arimura等2000, 2002)。
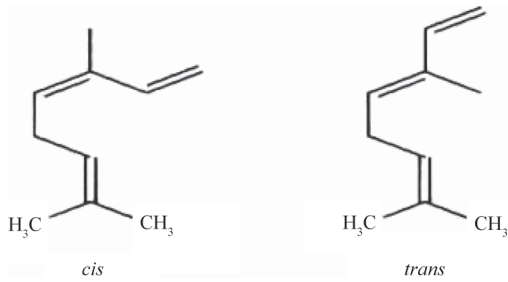
1 罗勒烯的结构与化学性质

罗勒烯是一种无环单萜类, 即3,7-二甲基-1,3,6-辛三烯, 自然界中存在顺式(Z, cis)和反式(E, trans)两种构型异构体(图1)。罗勒烯最早从罗勒油分离得到, 也存在于薰衣草油、龙蒿油等精油中, 与月桂烯属同分异构体。罗勒烯用钠和醇还原可产生二氢月桂烯, 加热时则异构化为别罗勒烯(allo-ocimene)。罗勒烯为无色液体, 溶于乙醇、乙醚等有机溶剂。

图1　Z-和E-β型罗勒烯的化学结构式

Fig.1　The chemical structural formula of cis-/trans-β-ocimene

2　罗勒烯在植物中的分布情况

　　现在已了解到许多植物体内含有罗勒烯, 它主要存在于植物叶片、果实以及花器官中(表1)。植物体本身含有的罗勒烯成分主要分布于植物各器官的挥发物及提取物中, 其中Duarte等(2008)通过对野生型丁香属植物*Eugenia dysenterica*不同成熟期果实进行研究发现, 果实中以(E)-β-罗勒烯为主要成分的单萜烯类的含量会随着果实的成熟呈现出下降趋势。现已了解到, 不仅在植物的地上部分如叶片和果实中含有罗勒烯成分, 在植物的根的提取物中也发现了罗勒烯的存在。Haghi等(2010)最近在伊朗中部地区发现了一种植物狭叶青蒿(*Artemisia dracunculus*), 利用GC/MS测定这种植物的根部提取物, 发现其中(E)-β-罗勒烯含量占11.0%, (Z)-β-罗勒烯占6.9%。这些证据都表明, 罗勒烯在不仅广泛分布于不同植物中, 而且其也广

泛存在于植物的各个部位中。

3　罗勒烯的生物合成研究

　　单萜合酶类是一个巨大的家族, 其能催化上千中萜类化合物的合成。β-罗勒烯是一种单萜挥发性有机物, 其生物合成受萜类合成酶调控, 其中单萜合酶(monoterpene synthases, monoTPS), 又称单萜环化酶(monoterpene cyclases), 是单萜生物合成的关键酶(Bohlm等1998)。萜类合酶起源于古萜类合酶, 以氨基酸序列相似度40%为基准将其分为TPS-a~TPS-g 7个亚家族。单萜合酶分布于TPS- b、TPS-d、TPS-f和TPS-g 4个亚家族(Bohlm等1998; Dudareva等2003)。单萜合酶基因表达受生物钟调节, 表达量以日为周期有节律的交替变换。如金鱼草月桂烯合酶、罗勒烯合酶, 拟南芥月桂烯和罗勒烯合酶基因的表达量和产物都呈现午后高、夜间低的昼夜交替规律(Lu等2002; Chen等2003)。

　　Aubourg等(2002)通过对拟南芥基因的序列分析发现拟南芥含有40个TPS类似基因, 并将这40个相似基因组成的家族命名为AtTPS家族。现有研究发现, 拟南芥中有2个相关的*AtTPS*基因——*AtTPS10*和*AtTPS03*能调控(E)-β-罗勒烯的合成。*AtTPS03*基因编码单萜合酶, 高度特异性催化香叶基二磷酸(GPP)生成β-罗勒烯(Jenny等2003)。研究发现, AtTPS10的合成产物中, (E)-β-罗勒烯的含量占20%; 而AtTPS03的合成产物主要为(E)-β-罗勒烯, 占到94%。*AtTPS03*更能特异性编码和调控

表1　罗勒烯在植物中的分布

Table 1　The distribution of ocimene in plant

植物种类	挥发油提取物成分	文献
Alpinia speciosa (月桃)	(Z)-β-罗勒烯	Ho等2010
Chrysanthemum coronarium (茼蒿)	(Z)-β-罗勒烯(5.2%)	Tawaha等2010
Limnophia aromatic (芳香沼类)	(Z)-β-罗勒烯(39.21%)	Bhuiyan等2010
Betula pendula (垂枝桦)	(E)-β-罗勒烯	Holopainen等2010
Brachanthemum (短舌菊)	(E)-β-罗勒烯(3.6%)	Shatar等2010
Citrus reticulate (柑橘)	(E)-β-罗勒烯	Kasali等2010
Cunila incana (百合属植物)	(E)-β-罗勒烯(10.36% +/- 0,48)	Agostini等2010
Artemisia dracunculus (狭叶青蒿)	(E)-β-罗勒烯(11.0%)	Haghi等2010
	(Z)-β-罗勒烯(6.9%)	
Tagetes zipaquinensis (万寿菊属植物)	(Z)-β-罗勒烯(18.8%)	Hernandez-Lo等2010
Salvia officinalis (药用鼠尾草)	(E)-β-罗勒烯(9.4 %)	Soleymani等2010
Machilus philippinensis (菲律宾樟树)	(Z)-β-罗勒烯(7.0%)	Ho等2010
Echinophora platyloba (具刺杜氏木属植物)	(Z)-β-罗勒烯(38.9%)	Hassanpouraghdam等2009
Eugenia dysenterica (丁香属植物)	(E)-β-罗勒烯(20.3%和21.7%)	Duarte等2008

(E)-β-罗勒烯的合成(Bohlmann等1998; Aubourg等2002)。我们对NCBI上公布的拟南芥TPS家族进行聚类分析(图2), 发现*AtTPS10*和*AtTPS03*被分在了同一个小亚组, 聚类结果与生物学意义相符。
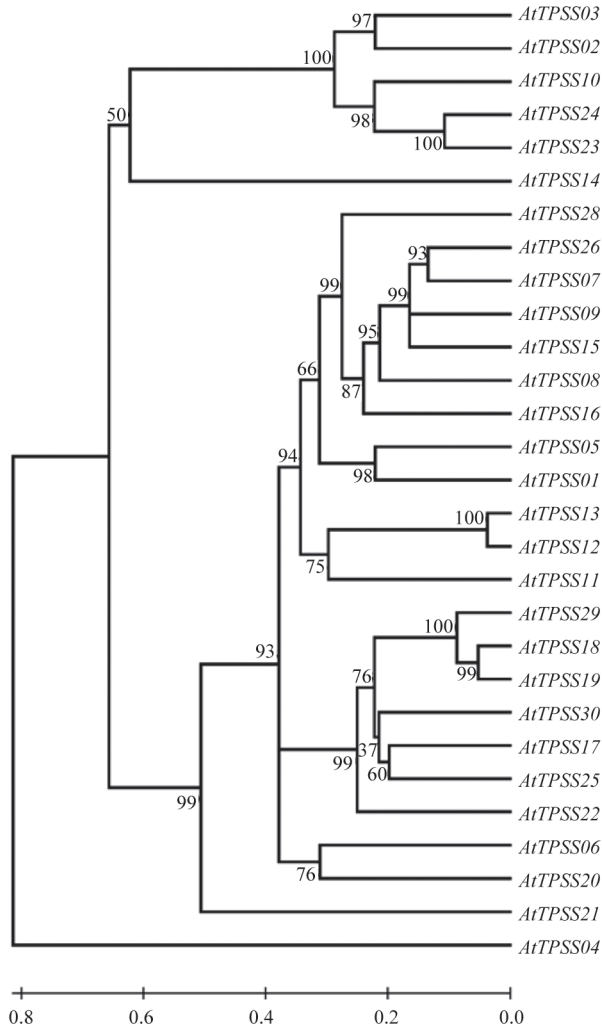

图2 拟南芥TPS家族基因聚类分析
Fig.2 Phylogenetic analysis of the TPS gene family
in *Arabidopsis thaliana*

4 罗勒烯在植物防御中的作用

　　(E)-β-罗勒烯是一种与植物防御启动密切相关的信号分子, 受节肢动物取食诱导释放。它能吸引食草动物的天敌, 使植株免受食草动物的伤害(Farmer 2001)。

4.1 植物在受到外界刺激时能释放罗勒烯

　　Arimura等(2004)通过对百脉根属植物*Lotus japonicus*的研究发现, LjE-β-OS (*Lotus japonicus* E-β-ocimene synthase)参与了由蜘蛛螨取食引起的百脉根的防御反应, 植物释放了(E)-β-罗勒烯, 在百脉根中, LjE-β-OS酶编码产生98% (E)-β-罗勒烯和2% (Z)-β-罗勒烯。叶片的机械损伤以及外施ALA都能瞬间增加LjE-β-OS的转录水平。这些都说明LjE-β-OS编码的(E)-β-罗勒烯参与了百脉根对外界的防御作用。Navia-Gine等(2009)发现, 被昆虫取食的蒺藜苜蓿(*Medicago truncatula*)叶片释放的(E)-β-罗勒烯比未损伤叶片的高出2倍。MtE-β-OS (*Medicago truncatul* E-β-ocimene synthas)在叶片中存在低水平的组成型表达, 但在花、茎、根中却毫无表达。其明显的昆虫诱导性表达特点以及相应的挥发物释放都揭示MtEBOS在蒺藜苜蓿对昆虫防御作用中起重要作用。Toome等(2010)运用willow-leaf rust system分析柳树树叶中营活体生活的真菌感染后挥发物的释放模式, 结果发现, 虽然总的单萜类化合物的释放量没有显著变化, 但作为压力信号分子的(Z)-β-罗勒烯在受感染后有显著上升。这说明, (Z)-β-罗勒烯参与了柳树对活体营养型真菌的防御抗性。此外, Opitz等(2008)在棉花(*Gossypium hirsutum*)研究中也发现, 萜类物质的累积过程实际上是一个正常的伤反应过程, 当植株受到机械损伤、虫害及茉莉酸处理后, E-β-罗勒烯的含量最高能增加15倍。

4.2 外施罗勒烯能提高植物的防御能力

　　大量实验表明, 外施罗勒烯也能启动植物防御机制, 增强抵抗外界刺激的能力。Kishimoto等(2006)研究发现, 在别罗勒烯处理的拟南芥叶片中, 穿刺到叶片表皮里的灰霉菌的菌丝生长受到抑制, 别罗勒烯还能诱导植物叶片的细胞壁和维管组织的木质化。别罗勒烯处理过的拟南芥叶片中木质化以及植物抗菌素累积的速度和强度都远高于未处理的对照叶片。此外, 拟南芥突变体*etr1-1*、*jar1-1*和*npr1-1*经别罗勒烯处理后, 能增强对灰霉菌的抵抗力。这些都表明别罗勒烯能诱导拟南芥的抗性反应。Godard等(2008)运用基因芯片分析以及定量PCR研究表明, 拟南芥经罗勒烯处理2 h后, MeJA在拟南芥组织中的含量增加, 拟南芥的*coi1*和*aoc*突变体表现出罗勒烯诱导的相关基因的表达降低。Arimura等(2000)利用(E)-β-罗勒烯处理利马豆, 发现诱导后的利马豆植株中许多与植

表2 植物受外界刺激后释放罗勒烯情况

Table 2 The release of ocimene in plant affected by external stimulation

植物种类	释放因素(取食动物/创伤)	文献
玉米(*Zea mays*)	寄生蜂(parasitic wasps)	Turlings等1990
棉花(*Gossypium hirsutum*)	甜菜夜蛾(*Spodoptera exigua*)	Loughrin等1994; Paré和 Tumlinson 1997
黄瓜(*Cucumis sativus*)	智利小植绥螨(*Phytoseiulus persimitis*)	Takabayashi等1994
利马豆(*Phaseolus lunatus*)	二斑叶螨(*Tetranychus urticae*)	Dicke等1999
	智利小植绥螨(*Phytoseiulus persimilis*)	Horiuchi等2001
地中海松(*Pinus pinea*)	创伤诱导	Loreto等2000
烟草(*Nicotiana tabacum*)	丁香假单胞菌(*Pseudomonas syringae*)	De Moraes等2001
拟南芥(*Arabidopsis thaliana*)	创伤诱导	Faldt等2003
百脉根(*Lotus japonicus*)	双斑螨(*Tetranychus urticae*)	Arimura等2004
三叶草(*Trifolium pratense*)	浅海小蚰(*Spodoptera littoralis*)	Kigathi等2009
番茄(*Lycopersicon esculentum*)	菜心虫(lervae of *Trichoplusia ni*)	Miresmailli等2010
桃树(*Prunus persica*)	桃蚜(*Myzus persicae*)	Staudt等2010

物抗性相关的基因得到诱导表达, 其中与SA途径启动紧密相关的PR1 (pathogen related 1)基因以及SA合成的关键基因PAL (phe ammonia lyase)的表达显著上升。

这都表明, 不仅植物受食草动物取食和病原菌感染后自身释放的罗勒烯能提高植物的抗性, 而且外施罗勒烯也能诱导植物启动防御机制, 提高植物的防御能力, 使植物更好地适应环境。

5 罗勒烯与植物其他防御信号途径的联系

植物不像动物一样能通过运动来有效规避不利环境的胁迫, 因而植物有其一套复杂完善的防御系统。在抵抗病原菌和食草动物取食时, 植物的防御反应主要依靠水杨酸(SA)、乙烯(ET)和茉莉酸(JA) 3条信号传导途径, 同时3条途径之间存在精细调控。在这三种植物激素中, SA是诱发系统获得抗性(systemic acquired resistance, SAR)的关键信号分子(Ryals等1996), JA和ET (JA/ET)是诱发诱导系统抗性(induced systemic resistance, ISR)的关键信号。SA依赖型的防御反应与抵抗活体营养型病原菌的侵染密切相关; JA/ET依赖型的防御反应与抵抗死体营养型原菌的侵染和昆虫取食密切相关(Gaffney等1994; Durner等1999; Glazebrook等2005; Howe和Jander 2008)。由SA、JA和ET信号分子诱导的信号传导途径之间存在复杂的交互调节(cross-talk)机制(Spoel和Dong 2008; Grant和Jones 2009; Pieterse等2009; Verhage等2010)。SA、JA和ET信号传导途径之间的交互调节是植

物免疫的重要调控机制。但是, 对于交互调节的作用至今存在着一定的争论, 某些信号途径之间的交互调节对于植物的防御到底是否有益有不同的理解。例如, 在拟南芥中的研究发现, SA防御信号途径的启动能抑制JA依赖途径的作用, 这样就降低了拟南芥对咀嚼类昆虫甜菜夜蛾(*Spodoptera exigua*) (Cipollini等2004)和粉纹夜蛾(*Trichoplusia ni*) (Cui等2005)的抵抗力; 然而Zarate等(2007)的研究发现, 一些食草性昆虫在取食时却能诱导出SA, 这样就抑制了取食时植物被激活的防御昆虫啃食的JA信号途径, 从而破坏了植物的创伤防御途径。

Arimura等(2000)在Nature上发表他们的研究成果, 证明β-罗勒烯能诱导与水杨酸有关的抗性基因的表达。Farmer等(2001)根据他们自己和他人的实验结果总结到受节肢动物取食激发植物叶片释放的挥发物中的β-罗勒烯是一种与植物防御启动密切相关的信号分子。在蒺藜苜蓿中的研究发现, 编码(E)-β-罗勒烯的酶能提升蒺藜苜蓿叶片对外施茉莉酸以及鳞翅目昆虫取食的反应。但是乙烯的合成前体ACC (1-aminocyclopropane-1-carboxylic acid)并不能提高MtEBOS的转录水平(Navia-Gine等2009)。Huang等(2010)用coronalon (一种人工合成的茉莉酸类似物, 作用与甲基茉莉酸类似)处理20~30 h后, 27个生态型的拟南芥中有20个生态型产生以(E)-β-罗勒烯为主要成分的挥发物, 其中产生量最高的是生态型*Ws*, 而*Col-0*生态

型产生的量最少。此外在利马豆植株中, 外施ACC能正调控3种与茉莉酸诱导相关的挥发物, 其中就包括(Z)-和(E)-β-罗勒烯(Horiuchi等2001)。拟南芥经罗勒烯处理2 h后, MeJA在拟南芥组织的含量增加; 拟南芥coi1和aoc突变体材料表现出罗勒烯诱导的相关基因的表达降低。Zhang等(2009)通过植物激素处理及基因表达分析揭示灰霉菌侵染和SA施用效果一样, 抑制了由蜘蛛满诱导相关的JA的产生, 同时也降低了2种JA调控的基因表达, 其中一种就是利马豆中的(E)-β-罗勒烯合成酶。这些研究都表明罗勒烯的信号途径可能与SA和JA/ET途径存在着紧密的联系, 这就为研究罗勒烯的信号途径提供了很好的思路。

为了更进一步明确β-罗勒烯与SA, JA/ET信号途径之间的联系, Liu等(2004)利用β-罗勒烯处理整株拟南芥后, 首次发现β-罗勒烯能诱导JA/ET途径的指示基因PDF1.2 (plant defensin 1.2)和SA途径的指示基因PR1同时表达。许多研究表明植物体内积累的SA对JA依赖的防御反应有拮抗作用, SA依赖型抗性抑制JA依赖型抗性(Pieterse等2001; Kunkel和Brooks 2002; Glazebrook等2003; Rojo等2003; Bostock 2005; Beckers和Spoel 2006; Koornneef和Pieterse 2008)。在拟南芥中, 外源SA的使用能高效抑制JA/ET信号途径标记基因PLANT DEFENSIN 1.2 (PDF1.2)和VEGETATIVE STORAGE PROTEIN 2 (VSP2)的表达(Koornneef等2008; Leon-Reyes等2009, 2010; Zander等2009)。在番茄和黄瓜中, SA的类似物acibenzolar-S-methyl (ASM)也与JA信号途径之间存在拮抗作用(Doherty等1988; Liu等2008)。Liu等的这一发现说明在植物中确有信号分子能够解除JA/ET与SA交互调节中的拮抗作用,但蕴涵在这一解除现象背后的机理尚需进一步研究。

6 展望

目前, 植物激素以及植物防御抗性的研究是十分热门的领域, 这一领域的研究也取得了很大的进展, 但是依旧存在着许多问题亟待解决。人们对JA/ET与SA途径之间拮抗作用形成的机制有较清楚的认识(Pieterse等2009; Verhage等2010)。但是, 人们对各信号分子之间的交互作用到底在植物防御功能中起什么作用, 以及还有哪些信号

分子能解除JA/ET与SA之间拮抗作用, JA/ET与SA间拮抗作用是如何解除等问题却了解得非常少。虽然已经有许多证据表明β-罗勒烯在植物防御功能上有一定的作用, 但这种作用是否能直接诱导植物的防御信号途径亦或是只是间接地参与植物防御信号途径尚有待证明。虽然我们也发现β-罗勒烯能诱导JA/ET途径的指示基因PDF1.2和SA途径的指示基因PR1同时表达, 证明确有信号分子能够解除JA/ET与SA交互调节中的拮抗作用, 但蕴涵在这一解除现象背后的机理是什么? 是否β-罗勒烯是通过一条相对独立的信号传递途径来激活植物防御系统, 同时使JA/ET依赖的抗性相关基因如PDF1.2和SA依赖的抗性相关基因如PR1表达? 这都是当前罗勒烯信号分子研究以及植物免疫领域急需解决的问题, 对于这些问题的深入研究将不断提高人们对植物防御信号分子的认识, 从而能更好的利用植物的防御体系网络为农业的无公害生产提供新的思路与理论指导。

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