

植食性昆虫产卵诱导寄主植物 抗虫机制研究进展*

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摘 要 植食性昆虫产卵作为生物诱导因子能刺激植物产生一定程度的诱导抗性, 相对于取食危害, 诱导抗性研究仍处于初级阶段, 目前的研究成果主要集中在国外。为了促进该领域在国内的研究, 本文主要从产卵诱导激发子、植物体的结构防御、化学防御、防御基因表达及间接防御等方面综述了昆虫产卵诱导植株产生抗性的各种防御机制, 并对产卵诱导抗性未来的研究方向进行了探讨。作为诱导植物防卫反应的分子, 认识和掌握激发子应是产卵诱导抗性研究的第一步。产卵诱导的结构防御主要通过改变植物细胞壁结构, 另外使产卵部位产生赘生物或组织坏死以及超敏反应。化学防御通过诱导产卵植株产生趋避产卵的挥发物降低产卵植株或邻近植株的产卵量, 并且通过受害植株叶片的营养物质和次生代谢物质含量的改变进而增加孵化幼虫的死亡率来提高防御能力。从分子层面上, 产卵诱导了防御蛋白的合成和抗性基因的上调表达, 对于相关的通路研究主要集中在 JA、SA 和乙烯等信号分子的转导途径上。生态或间接防御主要是借助植株间挥发物的释放来传递防御信息, 通过利用和促进三级营养关系来保护植物。有较多研究报道了产卵诱导所产卵植株及邻近植株挥发物的改变, 从而吸引捕食性和寄生性天敌来进行间接防御。目前对于产卵诱导抗性的研究仍多集中在理论层面上, 开发应用于主要农林害虫防治实践的产品和技术还很少。利用植株的诱导抗性对虫害进行生态调控是未来害虫管理的研究方向, 相关防御机制研究为其提供科学的理论依据。

关键词 植食性昆虫; 产卵; 诱导抗性; 防御机制; 激发子

Advances in the development of oviposition-resistant plants

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Abstract Oviposition by herbivorous insects can stimulate plants to produce a certain degree of resistance. Compared to research on resistance to insect feeding, research on oviposition resistance is still in its infancy in China and most results are from overseas. To promote domestic research in this field, this paper reviews various aspects of oviposition-induced plant resistance, including the elicitor, structural defense, chemical defense, defensive gene expression and indirect defense. The future direction of research on oviposition-induced resistance is also discussed. Identifying and understanding the elicitor

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mechanism should be the first step in research in this area. Structural defense occurs mainly through changes in the plant cell wall structure, growth of the oviposition site, tissue necrosis and hypersensitivity. Chemical defenses includes the production of volatiles that deter further egg deposition on a chosen plant or neighboring plants. It also includes changes in nutrients and secondary metabolites in the leaves of affected plants that increase larval mortality. At the molecular level, oviposition can induce the synthesis of defensive proteins and the up-regulation of genes associated with resistance. Studies of related pathways mainly focus on the transduction pathways of signal molecules, such as JA, SA and ethylene. Ecological or indirect defense is mainly induced by transmitting information via the release of volatiles between plants, thereby promoting a tertiary trophic relationship that protects plants in the same location. There has been a relatively large amount of research conducted on the release of volatile compounds by plants to attract natural enemies, such as predators and parasitic wasps for indirect defense. Currently, research on oviposition induced resistance is still mainly theoretical, and there are few products or techniques available for the control of agriculture or forestry pests. Induced plant resistance is, however, likely to be an important way of controlling pests in the future, and further research on plant defensive mechanisms is, therefore, essential to provide a theoretical basis for this.

Key words plant feeding insect; oviposition; induced resistance; defence mechanism; elicitor

植物抗虫性是植物以各种机制抵御昆虫侵害的能力,早在 1951 年 Painter 和 Reginald 提出植物抗虫性的三大机制: 抗性、耐害性和驱避性 (Painter and Reginald, 1951)。个体抗虫性从防御来源可分为先天性的组成抗性和后天被危害后的诱导抗性 (Howe and Jander, 2008)。组成抗性包括植物先天存在的物理结构和理化物质减少植食性昆虫取食 (杨乃博等, 2014)。诱导抗性是植物在遭受虫害及病菌等外来因子影响时,通过改变自身的生理生化特点而具有的防御反应 (Haukioja, 1991; Zangerl, 2010), 这种反应可在被诱导的部位产生局部抗性,也可在非诱导部位产生系统抗性 (Sticher *et al.*, 1994; 张鹏翀等, 2008)。植物能够进化出诱导防御是因为它们承担比基本抗性特征更低的资源分配成本,在调节昆虫和微生物的相互关系中起着重要作用 (Bonello *et al.*, 2006; Bolton, 2009)。

诱导防御机制包括直接的和间接的,如结构防御、化学防御、防御蛋白合成、生态防御和耐受防御等,且各种防御间是相互协调统一的。例如,在针叶树中,防御机制无论属于哪个类别,都有可能作为一种高度整合和协调的反应被生物和非生物因素所调节 (Bonello *et al.*, 2006)。植食性昆虫的产卵行为作为早期预警信号能诱导寄主产生一系列的直接或间接的防御反应 (Hilker and Fatouros, 2015)。本文在以往产卵

防御机制相关综述 (Hilker and Meiners, 2006, 2010, 2011; Reymond, 2013; Hilker and Fatouros, 2016) 的基础上,结合最新的研究成果,对该领域的研究进行总结、分析和探讨。

1 产卵激发子的研究现状

诱导子 (激发子) 是能够诱导植物产生局部抗性 or 系统抗性的生物或非生物物质,包括物理、化学和生物因子 (王万能等, 2010)。生物诱导因子包括活菌体、菌体细胞提取物、菌体培养滤液以及植食性昆虫的产卵或取食等生物源物质 (陈晨等, 2010)。目前对于昆虫取食能给植物损伤组织注入特异性激发子的研究较多 (李新岗等, 2008), 其中包括从昆虫口腔分泌物中获得的,例如甜菜夜蛾 *Spodoptera exigua* 口腔分泌物中发现的第一个激发子 N-17-羟基亚麻酰基-L-谷氨酰胺 (Alborn *et al.*, 2000; Yoshinaga *et al.*, 2005)、菜粉蝶中的 β -葡糖苷酶 (Yoshinaga *et al.*, 2005)、美洲棉铃虫 *Helioverpa zea* 中的葡萄糖氧化酶和烟草天蛾 *Manduca sexta* 中的脂肪酸-氨基酸钼合物 (Musser *et al.*, 2002)。对于产卵危害的激发子研究较少,已发现在豆象 *Callosobruchus maculatus* 的产卵液中存在激发子豆象素 B、C 和 D (BruchinB, C 和 D), 是由长链二元醇与 3-羟基丙酸单酯或双酯化而成

(Doss *et al.*, 2000); 在榆叶甲 *Xanthogaleruca luteola* 和松叶蜂 *Diprion pini* 的中输卵管中也有产生诱导植物防御反应的激发子 (Meiners and Hilker, 2000; Hilker *et al.*, 2002)。而对于卵粒物质成分的研究也较少, 在几种鳞翅目昆虫的卵里发现了比植物组织中浓度高的茉莉酸 (Jasmonic acid, 简称 JA), 卵壳中也含有少量的 JA (Tooker and De Moraes, 2005), 并且 15 种非鳞翅类昆虫的卵粒里均含有 JA、水杨酸 (Salicylic acid, 简称 SA) 及其代谢前体物之一苯甲酸 (Tooker and De Moraes, 2007)。激发子作为能诱导植物防卫反应的分子, 认识和掌握激发子应是产卵诱导抗性研究的第一步, 但目前的研究还十分有限, 对其诱导的机制研究还不够深入。

2 产卵诱导的结构防御及超敏反应

植物在受到昆虫攻击后, 可以通过改变细胞壁结构来进行局部防御, 细胞壁组成主要通过酚类化合物、木质素、木栓质或二氧化硅的沉积, 以及与富含羟基脯氨酸的糖蛋白浓缩而成 (Hammerschmidt and Nicholson, 1999)。产卵部位能产生赘生物或组织坏死, 从而挤压卵的生长或使其脱落, 还能诱导合成杀卵物质。例如, 卵块可诱导叶表面形成瘤状物, 将卵从植物表面升高, 使暴露的卵很容易从叶片脱落 (Doss *et al.*, 2000), 又可形成坏死组织使卵粒脱离, 降低幼虫孵化的存活率 (Shapiro and Devay, 1987; Balbyshev and Lorenzen, 1997)。水稻植物甚至会产生一种杀卵物质, 杀死白背飞虱 *Sogatella furcifera* (Horváth) 的卵 (Seino *et al.*, 1996; Suzuki *et al.*, 1996; Yamasaki *et al.*, 2003)。

另一方面, 有研究表明植食性昆虫的产卵行为作为植物防御的早期信号能诱导产卵部位产生超敏反应。这种由卵诱导的反应类似于植物对病原的超敏反应 (Hypersensitive response), 即 HR 反应 (Reymond, 2013), 即感染后细胞的快速死亡反应 (Mur *et al.*, 2008)。细胞死亡反应之前会有一系列的生化 and 细胞信号, 包括活性氧

(ROS)、胼胝体积累与病原相关蛋白的爆发 (Coll *et al.*, 2011)。类似超敏反应已被证实也能由半翅目 (Hemiptera)、鳞翅目 (Lepidoptera) 和鞘翅目 (Coleoptera) 昆虫在植物上产卵引起。如单子叶植物水稻 *Oryza sativa* (Yang *et al.*, 2014) 和各种双子叶植物 (十字花科的拟南芥 *Arabidopsis thaliana* 和芸苔属植物 *Brassica* spp.) (Little, 2007; Fatouros *et al.*, 2014; Pashalidou *et al.*, 2015)、豆科的菜豆 *Phaseolus vulgaris* (Garza *et al.*, 2001)、夹竹桃科的催吐白前 *Vincetoxicum hirundinaria* (Kalske *et al.*, 2014)、茄科的茄属 *Solanum* sp. 和灯笼草属 *Physalis* sp. (Balbyshev and Lorenzen 1997; Petzold-Maxwell *et al.*, 2011)。但木本植物的相关研究还很少, 如作为主要造林树种的杨树还未见报道, 可以深入开展产卵诱导结构防御及超敏反应的研究。

3 产卵诱导化学防御

植物在受到昆虫侵袭时, 包括取食和产卵危害均可通过调节体内化学物质的组成和数量来降低其营养水平, 从而对昆虫的为害产生拮抗 (Haukioja, 1991; 王杰等, 2018), 这些化学物质包括蛋白质、糖、氮和叶绿素等生理物质 (Mcclure, 1980; Kogan and Paxton, 1983)。营养物质和次生代谢物质是植物化学防御系统的重要屏障, 已经在多种寄主与害虫间被证实。例如, 昆虫产卵诱导受害寄主的营养成分降低及部分次生代谢物质含量增加, 从而降低孵化幼虫的取食能力 (Hilker and Fatouros, 2015)。

3.1 诱导营养物质含量降低

昆虫产卵能降低植物的营养质量从而提高对幼虫取食的防御能力 (Hilker and Fatouros, 2015)。研究表明幼虫取食产卵的松树、榆树、各种油菜科植株和烟草植物会使其体重增加量减少, 有些甚至比以无卵植物为食的幼虫死亡率更高 (Beyaert *et al.*, 2012; Geiselhardt *et al.*, 2013; Pashalidou *et al.*, 2013; 2015; Bandoly *et al.*, 2015; 2016; Austel *et al.*, 2016)。郭丽

等 (2019) 研究表明杨小舟蛾 *Micromelalopha sieversi* 产卵危害后, 两种黑杨无性系的产卵植株及邻近植株叶片中的可溶性糖、全 N 和游离氨基酸的含量均有不同程度降低。

3.2 诱导次生代谢物质含量增加

次生代谢物也是化学防御的重要物质, 由外界刺激诱导产生的次生物质能使植物获得抵御部分侵害的能力。研究发现酚类化合物的氧化作用会产生活性氧, 从而导致昆虫中肠组织的氧化应激 (Barbehenn *et al.*, 2007), 其亲氧化剂活性直接与抗虫性相关 (Ruuhola *et al.*, 2008)。已证实植食性昆虫产卵能诱导酚类化合物的形成 (Bandoly *et al.*, 2015; 2016; Austel *et al.*, 2016)。例如, 榆树 *Ulmus minor* 在受榆树叶甲 *Xanthogaleruca luteola* 产卵后会诱导叶片酚类物质 (刺槐素) 的增加从而增强对幼虫取食的抗性 (Austel *et al.*, 2016)。又如, 杨小舟蛾 *M. sieversi* 产卵后 108 杨和 111 杨叶片中的单宁和总酚的含量均升高 (郭丽等, 2019)。但也有研究表明, 松叶蜂 *D. pini* 在松树 *P. sylvestris* 上产卵后, 松枝的总酚类化合物浓度没有显著变化 (Beyaert *et al.*, 2012)。对于重要食叶害虫产卵诱导主要寄主的各种次生代谢物质含量变化还有待深入研究。

4 产卵诱导防御蛋白和防御机制

4.1 诱导防御基因表达

可溶性病原相关蛋白 (Pathogenesis-related proteins, 简称 PR 蛋白) 家族是植物在遭受病原菌感染或特定化合物处理后产生的一类诱导防御蛋白质 (Edreva, 1990; 2004), 与植物系统获得性抗性和过敏性坏死反应关系密切 (王静等, 2012)。研究发现植食性昆虫产卵除能诱导挥发物释放和内含物含量改变外, 还能诱导产卵植株相关抗性基因的表达 (Roda and Baldwin, 2003)。如: 植物抗霉素生物合成 (Cooper and Goggins, 2005), 芥子油苷生物合成 (Geiselhardt *et al.*, 2013), 生成蛋白酶抑制剂 (Kim *et al.*,

2012), 或萜类化合物生物合成 (Leopold and Degrugillier, 1973; Köpke *et al.*, 2010; Beyaert *et al.*, 2012)。欧洲粉蝶 *Pieris brassicae* 在拟南芥 *A. thaliana* 的叶片上产卵后, 包括防御和压力相关的基因被诱导表达, 并且造成局部细胞死亡 (Bruessow and Reymond, 2007)。涂抹欧洲粉蝶压碎卵粒的脂质部分在拟南芥上, 还能诱导叶片的 PR-1 基因和病原体相关分子模式 (PAMP) 响应基因的表达 (Gouhier-Darimont *et al.*, 2013)。并且, 欧洲粉蝶与菜粉蝶 *P. rapae* 的卵粒沉积物能诱导 PR1 基因表达在卵粒沉积部位和周围的叶片组织中显著提高 (Little *et al.*, 2007)。又如, 棉铃虫 *Helicoverpa zea* 在番茄 *Solanum lycopersicum* 上产卵后会诱导蛋白酶抑制剂 (*Pin2*) 基因的表达和积累茉莉酸 (JA) 以应对接下来的幼虫取食 (Kim *et al.*, 2012); 甜菜夜蛾 *Spodoptera exigua* 在沙漠烟草 *Nicotiana attenuata* 上产卵, 会诱导两种防御性状, 苯丙类化合物和蛋白酶抑制剂活性, 以响应幼虫的摄食, 从而减少取食危害 (Bandoly and Steppuhn, 2016)。茄属植物 *Solanum dulcamara* 在甜菜夜蛾 *Spodoptera exigua* 产卵位置能产生肿瘤和绿化组织, 并积累活性氧 (ROS) 诱导防御基因和蛋白质的产生来应答 (Geuss *et al.*, 2017)。杨小舟蛾产卵危害后, 2 种黑杨无性系的产卵和邻近叶片中与 PR 蛋白、先天免疫调节和生物胁迫反应等功能相关的防御基因分别上调表达, 但具体基因存在差别, 而与光合活性相关基因全部显著下调表达 (Guo *et al.*, 2020)。

4.2 防御通路研究

植物的诱导防御反应是包括 SA、JA、乙烯和过氧化氢等在内的多种信号分子联合作用的结果 (Arimuru *et al.*, 2005; Bodenhausen and Reymond, 2007)。但目前相关研究仍多集中在植食性昆虫取食危害后, 产卵危害的报道较少。例如, SA 在卵块沉积的下方大量聚集, 许多水杨酸反应基因是通过产卵诱导产生的 (Little *et al.*, 2007; Buchala, 2010)。欧洲粉蝶在拟南芥上产卵后, SA 在卵块部位积聚 (Bruessow *et al.*,

2010)。并且已经证实了在拟南芥中 SA 通路应对卵块激发子的重要性 (Gouhier-Darimont *et al.*, 2013)。同时, 在榆树和豌豆中发现榆黄叶甲 *Xanthogaleruca luteola* 产卵后能够诱导 JA 生物合成基因表达 (Doss *et al.*, 1995; Büchel *et al.*, 2012)。另外, 松叶蜂 *Diprion pini* 的产卵分泌物能够系统诱导乙烯的释放 (Schröder *et al.*, 2007)。

目前研究表明, JA 通路在产卵过程中伴有叶片损伤的情况下较为明显, 而 SA 通路表现为在卵粒只沉积于植物表面而无明显损伤的情况下参与 (Reymond, 2013)。与叶片损伤相关的产卵行为可能会诱导 JA 应答基因的转录, 在幼虫开始取食时促进 JA 应答及创伤诱导的防御基因的转录增强 (Erb *et al.*, 2012)。现阶段产卵对 JA 反应及 JA 水平的精确影响仍是未知的。尽管发现 SA 调节和 JA 调节在植物间的许多相互作用是拮抗的, 但同时二者也存在中性甚至协同作用 (Corné *et al.*, 2012), 这种相互作用取决于所处阶段和顺序及施加外源激素的剂量 (Caarls *et al.*, 2015)。例如, 植物最先处于由病原诱导的 SA 中, 如产卵侵染, 再处于幼虫取食的 JA 诱导, 发现 SA 通路和 JA 通路均无拮抗作用。相反, 以前被病原感染的植物对幼虫的抵抗力有所提高 (Oosten *et al.*, 2008; Hilfiker *et al.*, 2015)。另外, 酚类物质与 SA 共享共同的生物合成中间体 (Lattanzio *et al.*, 2008), 酚类物质合成的前体可能是由产卵诱导的 SA 通路提供的。Guo 等 (2020) 研究发现 2 种黑杨无性系在杨小舟蛾产卵后上调表达的防御基因包括抗菌基因, 可能二者均启动了水杨酸防御系统, 可以进一步分析产卵叶片的过氧化氢含量, 验证是否真正启动了过氧化氢和 SA 信号转导途径。

5 产卵诱导的生态或间接抗性

5.1 通过三级营养关系间接防御

植物诱导的生态防御主要是植物在遭受害虫侵扰后通过释放挥发物在植株内及植株间进行信息传递而获得抗性 (姜永根和程家安, 2000;

王国昌等, 2010)。间接防御是通过利用和促进三级营养关系来保护植物, 植物挥发物作为植物之间以及植物和昆虫天敌之间交流的信息化物质 (Bukovinszky *et al.*, 2009), 通过吸引天敌如捕食者和寄生蜂来间接防御 (Hunter, 2002)。植物在受植食动物侵袭时, 其释放出的挥发物可能在数量和质量上都与未损伤的植物不同 (Dicke and Loon, 2000), 这种信息介导的间接抗性有可能增加对害虫天敌 (捕食性和寄生性) 的吸引 (Meiners and Hilker, 1997; Wegener *et al.*, 2001; Hilker *et al.*, 2002; Colazza *et al.*, 2004; Kessler and Heil, 2011)。樟子松 *P. sylvestris* 的松针在有卵块沉积后释放的挥发物能吸引松叶蜂寄生蜂 (Hilker *et al.*, 2002), 带有卵块的松枝释放的(E)- β -法尼烯显著增加, 能够吸引卵寄生蜂 *Chrysonotomyia ruforum* (Mumm *et al.*, 2003)。卵寄生蜂赤眼蜂 *Trichogramma brassicae* 利用欧洲粉蝶和菜粉蝶的卵块沉积物诱导的寄主挥发物准确定位卵块位置 (Pashalidou *et al.*, 2010)。相似的三级营养关系在榆树 *Ulmus* spp. (Meiners and Hilker, 1997; 2000) 和菜豆 *Phaseolus vulgaris* (Colazza *et al.*, 2004) 上都已发现。这种诱导反应并不只局限于产卵部位, 靠近产卵部位的无卵叶片也能释放出对寄生蜂有吸引力的挥发物, 表现出系统性诱导抗性 (Meiners and Hilker, 2000; Hilker *et al.*, 2002; Colazza *et al.*, 2004)。利用特殊的挥发物成分开发植物源性保护剂也将为主要农林害虫的生物防治提供新思路和新方法。

5.2 诱导抗性对目标卵的专一性及时效性

研究发现由卵诱导的植物抗性对目标卵具有专一性。例如, 专食性的欧洲粉蝶在芸苔 *Brassica nigra* 上产卵能吸引不同种类的赤眼蜂 *Trichogramma* sp., 而广食性的甘蓝夜蛾 *Mamestra brassicae* 和甜菜夜蛾 *Spodoptera exigua* 产卵则不能吸引卵寄生蜂 (Fatouros *et al.*, 2012; Cusumano *et al.*, 2015)。与之相反的是, 有些植物的防御反应是专门针对特定昆虫种类而吸引特定卵寄生蜂的 (Meiners and Hilker,

2000; Mumm *et al.*, 2005)。同时, 产卵诱导的间接抗性的时间范围是有差别的。例如, 甘蓝 *Brassica oleracea*、卷心菜斑色蛾 *Murgantia histrionica* 和沟卵蜂 *Trissolcus brochymenae* 的诱导反应时间都小于 24 h (Conti *et al.*, 2010)。当大豆受美洲蟥 *Euschistus heros* 产卵危害后, 其卵寄生蜂黑卵蜂 *Telenomus podisi* 能对大豆诱导的挥发物快速作出反应 (Moraes *et al.*, 1998)。欧米啮小蜂 *Oomyzus gallerucae* 是榆树叶甲的主要卵寄生蜂, 在植食动物产卵 3 h 后, 就能对带有卵块的榆树叶片释放的挥发物作出反应 (Meiners and Hilker, 1997; 2000)。又如, 松叶蜂 *D. pini* 的卵寄生蜂 *Chrysonotmyia ruforum* 不会被产卵 1 d 的松针所吸引, 产卵 3 d 后松枝的挥发物才能吸引卵寄生蜂 (Hilker and Meiners, 2002)。同样, 赤眼蜂 *T. brassicae* 寄生 3 d 卵粒的成功率为 80%, 对于新鲜卵粒和 1 d 卵粒的寄生比率分别为 40% 和 50% (Fatouros *et al.*, 2005)。杨小舟蛾分别在 2 种黑杨无性系产卵后 24 h, 各自与产卵植株邻近的植株再接虫的产卵量均显著降低 (Guo *et al.*, 2019)。

5.3 植物挥发物对产卵行为的影响

植食性昆虫产卵是保证种群数量和维持种群稳定的重要行为。产卵反映了植食性昆虫与寄主植物间的相互适应关系及昆虫种群的建立和维持机制 (张茂新等, 2003)。在某种程度上, 植食性昆虫的产卵选择行为反映了昆虫对寄主植物的利用方式, 从而影响其种群的繁衍和进化 (钦俊德, 1987)。例如, 亚洲柑橘木虱 *Diaphorina citri* 雌成虫对柑橘嫩芽具有明显的产卵偏好性 (李皓等, 2018), 而黑腹果蝇 *Drosophila melanogaster* 则对高盐具有明显的产卵驱避性 (高露等, 2019)。通常的产卵行为包括寄主的搜寻和定位, 识别与选择 (接受/拒绝), 最终完成产卵 (唐宇翀等, 2010)。植食性昆虫在搜寻和定位寄主植物的过程中, 化学信号起着先决和主导作用。这些化学信号包括寄主植物、昆虫本身或两者共同散发的挥发性化学物质 (张

贺贺等, 2015)。其中植物挥发物的作用最大, 这些物质主要包括烃类、醛类、醇类、酯类、酸类、酮类、萜烯类和芳香族类等经代谢过程产生的短链碳氢化合物及其衍生物, 它们以特定比例构成该种植物的化学指纹图谱 (樊慧等, 2004)。研究发现, 植物挥发物在亚洲玉米螟 *Ostrinia furnacalis* 雌蛾寻找产卵寄主过程中的作用非常重要 (张文璐等, 2018)。毛茛叶甲 *Pyrrhalta maculicollis* 雌虫相比于严重危害的叶片更喜欢在未侵染的叶片上产卵 (Meiners *et al.*, 2005)。粉纹夜蛾 *Trichoplusia ni* 交配后的雌蛾首先选择在未受损伤的棉花植株和甘蓝植株上产卵 (Landolt, 2011)。甘蔗螟虫 *Diatraea saccharalis* 的产卵会导致繁殖期水稻植株对同一物种的进一步产卵产生抗性 (Hamm and Stout, 2010)。

5.4 植物挥发物在植株间的信号传递

一些植物利用挥发物信号来协调体内系统的反应以及植株间的信息传递。诱导的植物挥发物可以作为植物间的化学信号传递给相邻的、未损伤或未受侵染的植物 (Dicke and Bruin, 2001)。通过空气传递实验证实了挥发物在植物间信息交流的作用 (Karban *et al.*, 2010)。挥发物可以快速地在植物内部进行交流, 这种交流比任何植物内部化合物更快地从一个植物器官转移到另一个植物器官 (Heil and Bueno, 2007)。已有实验证实与产卵叶片邻近的未产卵叶片确实表现出了系统性的诱导抗性 (Meiners and Hilker, 2000; Hilker *et al.*, 2002; Colazza *et al.*, 2004)。例如在榆树 (Wegener *et al.*, 2001)、豆科植物 (Colazza *et al.*, 2004) 和松针 (Mumm and Hilker, 2006) 上出现卵块后萜类挥发物的数量和种类都会发生变化。当马尾松 *P. massoniana* 的松针释放高浓度的 β -蒎烯时, 能显著降低松毛虫 *Dendrolimus punctatus* 雌虫的产卵量 (Zhao *et al.*, 2003)。杨小舟蛾产卵后, 108 杨和 111 杨的产卵和邻近植株均表现出了诱导抗性, 3-蒎烯和 β -蒎烯作为植株间传递的化学信号显著降低了邻近植株上的产卵量 (Guo *et al.*, 2019)。

6 产卵诱导抗性未来的研究方向

产卵诱导抗性是整个诱导抗性研究中的重要一环,然而,相对于取食诱导抗性,其研究比较薄弱。本文针对目前产卵诱导抗性机制进行了概述和总结,发现其中仍存在诸多空白领域和需要深入研究的方面,结合研究领域将未来可能的研究方向列举出来供大家参考。

(1) 植食性昆虫种类繁多,目前已研究产卵抗性的种类还较少,所以针对主要农林害虫的产卵诱导抗性需要分别进行研究,包括产卵诱导抗性作用及其机制、开发应用等问题。

(2) 目前对于产卵危害的激发子研究还较少,认识和掌握激发子应是诱导抗性研究非常重要的一步。需要研究其主要成分、作用机制等,利用激发子开发化学合成激活剂可作为植物保护剂提高其自身诱导抗虫性,为农林害虫的生物防治提供新思路和新方法。

(3) 产卵的诱导抗性研究需在传统诱导抗性研究的现有理论上拓宽和深入,比如防御酶活性、信号通路转导等分子机制,产卵诱导抗性在植株间信号传递,结合已有的三级营养关系和挥发物化学信号传递的相关成果探讨有效抗性的传递距离、地上地下信号传递等问题。

(4) 植食性昆虫产卵作为取食危害的第一步,对后续幼虫期抗性的影响及其机制也缺乏研究,是未来需加强研究的重要方向。

(5) 自然界的物种之间通过长期的进化形成了多样而复杂的相互关系和调节机制,自然界的害虫往往不只一种,只有充分认识不同害虫危害之间的相互关系,才能更好地对其进行生态调控。所以不同害虫产卵后相互之间的作用及其机制也是需要深入研究的重要方向。

(6) 诱导抗性功能作为一种多层的、高度集成的防御系统,可以持久有效地抵御各种害虫和病原体的侵害 (Vallad and Goodman, 2004)。它们的应用可以从抗性物质和杀虫剂研制到害虫生物控制和管理措施,对环境友好,具备广阔的发展前景。产卵诱导抗性的应用还十分缺乏。未来应在产卵诱导抗性机制研究的基础上,从害虫

防御剂和抑制剂的研究及其应用技术,到利用诱导抗性的生态学技术等多方面加强相应的应用技术研究。

综上所述,产卵诱导抗性的研究将是植株自身抗虫性研究的重要内容,对其的深入研究,将会完善和补充相关诱导抗性研究的理论体系和相应的应用技术。

7 结语

植物的诱导抗性是一种普遍存在的现象,其抗性机制及在植物保护中的潜在应用价值应得到足够重视。随着研究方向的拓展和更全面抗性机理的发现,为植物病虫害的防治开辟了一条新的途径。目前诱导抗性研究多集中在植食性昆虫取食危害上,而产卵作为早期预警信号诱导植株产生抗性的相关研究较少,认识产卵诱导植株的抗性机制具有重要意义。林木自身的诱导抗性具有广普性、稳定性及无污染等优点,虽然目前诱导抗性的应用还不能与现代成熟的植保技术相竞争,但认识植物能够有效地通过诱导而得到保护的概念及相关机制的研究将为病虫害防治提供理论指导。

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