



西花蓟马与植物互作中的诱导 防御与适应性研究进展*

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摘要 西花蓟马 *Frankliniella occidentalis* 通过取食、产卵和传播植物病毒对园艺和农业作物生产构成了严重威胁。利用植物诱导防御反应以抵抗西花蓟马危害是作物保护最具生态效益的方法。在植物与西花蓟马的互作中, 虫伤、外源植物激素、微生物及其他一些非生物因子均可诱导植物产生防御反应, 且植物次生化合物、Ca²⁺、防御酶及防御信号通路相关基因在植物诱导抗性中起着重要作用。而西花蓟马也形成了一系列解毒代谢和行为适应等反防御机制适应寄主植物的防御反应。本文综述了植物诱导防御反应对西花蓟马抗性、及西花蓟马对植物防御反应的适应性研究进展。

关键词 西花蓟马; 诱导防御; 解毒及代谢适应; 行为适应

Review of induced plant defenses against the western flower thrip and adaptations by thrips to counter these

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Abstract The western flower thrip (WFT), *Frankliniella occidentalis* pose a serious threat to horticultural and agricultural crops by feeding and ovipositing on plants, and by transmitting plant viruses. Plant induced defense responses are the most environmentally friendly method of protecting crops from the WFT. In the interaction between plants and the WFT, herbivore damage, exogenous plant hormones and microorganisms, and abiotic factors, can all enhance plant defensive responses. In addition, plant secondary compounds, intracellular Ca²⁺, defensive enzymes and signaling pathway-related genes, all play an important role in the induction of plant resistance. The WFT adapts to plant defenses by a series of detoxification processes and behavioral adaptations. In this article, we review progress in research on induced plant defense response against the WFT and adaptations of the WFT to counter these responses.

Key words *Frankliniella occidentalis*; plant defense response; detoxification and metabolic adaptations; behavioral adaptations

在植物与昆虫长期的互作过程中, 植物形成了一系列的组成型和诱导型防御机制, 昆虫则进化出相应的生理生化适应和行为适应的反防御机制 (Kant *et al.*, 2015; War *et al.*, 2018; Erb and

Reymond, 2019)。植物防御反应和昆虫反防御适应性因昆虫口器类型、昆虫种类和寄主植物类别而存在不同程度的差异 (Zhu-Salzman and Zeng, 2008; Stam *et al.*, 2014; Schuman and

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Baldwin, 2015)。咀嚼式口器和刺吸式口器昆虫取食诱导的植物防御反应及昆虫的适应性机制已有许多报道(张海静等, 2012; Kant *et al.*, 2015; Basu *et al.*, 2018; War *et al.*, 2018; Erb and Reymond, 2019)。近年来, 对锉吸式口器且为世界性重要入侵害虫西花蓟马 *Frankliniella occidentalis* (Pergande) 的有关研究也越来越多 (Maharijaya *et al.*, 2012; Steenbergen *et al.*, 2018; Escobar-Bravo *et al.*, 2019)。利用植物防御反应以减轻西花蓟马危害是一种极具潜力的防治方法 (Steenbergen *et al.*, 2018)。本文综述了诱导植物产生防御反应的方式, 以及西花蓟马对植物防御反应的解毒代谢和行为适应研究进展, 以期利用植物防御反应防控锉吸式口器害虫的研究与应用提供参考。

1 植物诱导防御反应对西花蓟马的抗性

诱导防御反应以增强植物对西花蓟马抗性的方式, 主要包括虫伤诱导、外源植物激素及其衍生物、次生代谢物及挥发物、微生物等生物因子和光照、紫外线 (UV) 和 CO₂ 等非生物因子的诱导等, 植物次生化合物、Ca²⁺、防御酶及防御信号通路基因等在植物防御反应中也起重要作用。

1.1 虫伤诱导的植物防御反应

虫伤诱导是通过昆虫取食和产卵造成损伤, 并伴随其口腔分泌物和产卵液等相关因子作用于植物而诱导产生的防御反应 (Bruessow *et al.*, 2010; Schmelz, 2015)。虫伤诱导植物防御反应抵抗西花蓟马主要包括两种类型: (1) 西花蓟马预先取食诱导植物产生的防御反应, 对后取食的西花蓟马或其他害虫产生防御作用; (2) 其它昆虫预先取食诱导的植物防御反应以抵抗西花蓟马。如西花蓟马和烟青虫 *Heliothis virescens* 预先分别取食或共同取食, 诱导烟草植株产生防御反应可抑制后取食西花蓟马的取食和产卵 (Delphia *et al.*, 2007)。鄧军锐等 (2016) 研究亦证实西花蓟马或二斑叶螨 *Tetranychus urticae* 预先取食

可诱导菜豆植株产生防御反应, 从而影响后取食者的生理酶活性。杂食性天敌昆虫无毛小花蝽 *Orius laevigatus* 取食可诱导甜椒产生防御反应, 提高了天敌对西花蓟马的生防效果 (Bouagga *et al.*, 2018)。被西花蓟马取食的黄瓜对无毛小花蝽也具有吸引作用 (Venzon *et al.*, 1999), 而对二斑叶螨则具有排斥作用 (Angelo *et al.*, 1997)。

西花蓟马取食可诱导植物激活茉莉酸 (JA) 信号网络和调控植物专化性代谢物 (Maharijaya *et al.*, 2012; Steenbergen *et al.*, 2018), 诱导 JA、水杨酸 (SA) 和乙烯 (ET) 途径标记基因表达 (Abe *et al.*, 2008; Abe *et al.*, 2009), 调控植物防御酶活性以实现直接或间接防御。研究表明西花蓟马取食可诱导菜豆叶片过氧化物酶 (POD)、过氧化氢酶 (CAT) 和超氧化物歧化酶 (SOD) 活性发生明显变化 (岳文波等, 2018), 也可显著诱导脂氧合酶基因 *LOX*、苯丙氨酸解氨酶基因 *PAL* 和 β -1,3-葡聚糖酶基因 *PR-2* 表达, 诱发系统抗性 (张宇羽等, 2017)。但西花蓟马取食诱导的植物防御反应因植物品种不同而异 (Maharijaya *et al.*, 2012; Escobar-Bravo *et al.*, 2017a)

1.2 外源物质诱导的植物防御反应

内源植物激素及其衍生物外源合成后作用于植物可增强植物对西花蓟马的抗性。西花蓟马受外源 JA 诱导植物抗性的明显影响, 如外源 JA 处理番茄 (Thaler *et al.*, 2001)、辣椒 (Sandeep *et al.*, 2019)、大白菜和不同基因型拟南芥 (Abe *et al.*, 2009) 均可增强植株抗性, 抑制西花蓟马在寄主上的种群繁衍。但与 JA 作用方式不同的类胡萝卜素 α -Ionone 也可诱导植物增强对西花蓟马的抗性 (Murata *et al.*, 2020)。JA 可诱导菜豆产生对西花蓟马有驱避作用的挥发物 (E)-2-己烯醛和对南方小花蝽具有引诱作用的 (E)-2-乙酸叶醇酯 (李顺欣等, 2016)。且 JA 诱导菊花对西花蓟马的抗性因 JA 作用部位的不同而存在明显差异 (Chen *et al.*, 2020)。

JA 和 SA 衍生物也可诱导寄主植物产生防御反应, 抑制西花蓟马在寄主上的取食、产卵及种群繁殖。如水杨醛和水杨酸甲酯 (MeSA) 施

用于大豆和黄瓜叶片,可导致西花蓟马在叶片上停留的时间明显缩短,显著阻止西花蓟马产卵并降低取食损伤 (Koschier *et al.*, 2007)。外源物质对寄主植物的影响存在浓度和时间效应,茉莉酸甲酯 MeJA 和顺式茉莉酮 (Cis-jasmone) 2 种 JA 衍生物处理菜豆叶片可驱避西花蓟马 2 龄若虫,且浓度为 1% 的顺式茉莉酮处理可以减少西花蓟马的取食损伤 (Egger *et al.*, 2014)。将 MeJA、顺式茉莉酮和烯丙基苯甲醚 3 种植物次生化合物按两两 1:1 混合处理菜豆植株,对西花蓟马的取食和产卵抑制作用明显增强 (Egger *et al.*, 2014)。另外,顺式茉莉酮和 MeJA 两类化合物处理菜豆植株后对西花蓟马的抑制作用可长达 96 h (Egger *et al.*, 2016)。

1.3 其他方式诱导的植物防御反应

昆虫和螨类携带的植物病毒和细菌等微生物对调控植物防御反应也具有一定的作用 (Schausberger, 2018)。西花蓟马不仅可传播植物病毒 (Rotenberg *et al.*, 2015),也携带欧文氏菌 (*Erwinia*) 和泛菌 (*Pantoea*) 等共生菌 (Facey *et al.*, 2015)。这些共生微生物对蓟马诱导的植物防御反应存在潜在的影响 (Dutta *et al.*, 2016)。此外,植物致病性丁香假单胞杆菌番茄变种 DC3000 (*Pst*) 及其侵染衍生的植物冠菌素 (Coronatine),亦可激活番茄 JA 防御途径增强对西花蓟马的抗性 (Chen *et al.*, 2018)。

此外,紫外光 UV-B、光量、光质、温度、CO₂ 和干旱胁迫等非生物因子也可诱发植物防御反应以抵抗植食性昆虫危害 (Escobar-Bravo *et al.*, 2017b)。对 VI 型毛状体缺乏型番茄突变体 (od-2) 植株和野生型植株的研究表明,高光合活性辐射 (Photosynthetically active radiation, PAR) 可介导毛状体相关的化学防御作用以抵抗西花蓟马 (Escobar-Bravo *et al.*, 2018a)。UV 介导增强番茄对西花蓟马的抗性与 JA 信号通路的激活有关,而与植物次生代谢或毛状体相关的性状无关 (Escobar-Bravo *et al.*, 2018b)。Escobar-Bravo 等 (2019) 进一步研究证实 UV 辐射可调节植物对西花蓟马的抗性,但受剂量和植物基因型的影响。CO₂ 浓度升高也影响菜豆的防御反应

及西花蓟马的适应能力 (Qian *et al.*, 2018)。

1.4 植物次生化合物对西花蓟马的抗性作用

植物次生代谢产生的各种物质在抵抗植食性昆虫为害中起着重要作用 (Johnson, 2011; Gols, 2014)。如生物碱类 (Alkaloids)、苯并噁嗪 (Benzoxazinoides)、氰基葡萄糖苷 (Cyanogenic glucosides)、芥子油甙 (Glucosinolates)、非蛋白质氨基酸 (Nonprotein amino acids)、酚类 (Phenolics)、萜类 (Terpenoids)、单宁 (Tannins) 及类黄酮 (Flavonoids) 等 (War *et al.*, 2012, 2018; Fürstenberg-Hägg *et al.*, 2013)。浓度 0.1% 的麝香草酚 (Thymol) 及 1% 的香芹酚 (Carvacrol) 两个单萜酚类物质处理菜豆叶片后造成西花蓟马偏好性明显下降 (Peneder and Koschier, 2011)。Liu 等 (2017) 研究表明 6 种吡咯里西啶生物碱 (Pyrrolizidine alkaloids, PAs) 也可有效降低西花蓟马存活率,但不同 PAs 之间作用有明显差异。

植物挥发物是一类小分子的植物次生化合物 (李军, 2016),在植物诱导抗虫反应中也起重要作用。植食性昆虫攻击植物可诱导植物产生驱避害虫或吸引天敌定位寄主的挥发性防御化合物 (James, 2005; Das *et al.*, 2013)。如无毛小花蚜取食诱导甜椒产生的萜类化合物、(Z)-3-己烯酯、MeSA 和其他一些未知化合物可吸引西花蓟马天敌以起到间接防御的作用 (Bouagga *et al.*, 2018)。而其他一些挥发物如邻氨基苯甲酸甲酯不仅可以吸引植食性西花蓟马,对捕食性蓟马 *Ceraninus menes* 也具有吸引作用 (Murai *et al.*, 2000)。烟草被取食诱导释放的挥发物尼古丁可能是影响西花蓟马对寄主植物取食和产卵选择性的关键挥发物 (Delphia *et al.*, 2007)。

蛋白酶抑制剂 (Protease inhibitors, PIs) 是蛋白质与蛋白酶形成复合物并抑制其蛋白水解活性的物质。植物可利用 PIs 减轻植食性昆虫的取食和产卵,如将重组马铃薯半胱氨酸蛋白酶抑制剂和马匹抑素 (Equisatin) 饲喂西花蓟马雌成虫 5 d 时,产卵率降低 45% (Annadana *et al.*, 2002)。利用多结构域半胱氨酸蛋白酶抑制剂处理温室中的马铃薯,亦可对西花蓟马产生抗性 (Outchkourov *et al.*, 2004)。

1.5 外源 Ca^{2+} 的间接调控作用

Ca^{2+} 在植物诱导防御反应中充当第二信使的作用。昆虫取食可诱导植物胞质 Ca^{2+} 浓度增加从而激活多种钙感应蛋白 (War *et al.*, 2012; Erb and Reymond, 2019), 促进植物防御物质 JA 的生物合成 (Yan *et al.*, 2018) 进而调控植物的防御反应。喷施 CaCl_2 可导致西花蓟马取食后的菜豆植株脂氧合酶 (LOX)、丙二烯氧化物合成酶 (AOS)、苯丙氨酸解氨酶 (PAL) 及 β -1,3-葡聚糖酶 4 种防御酶活性发生明显变化, 并明显激活 JA 通路相关基因 *LOX* 和 *AOS* 及 SA 通路相关基因 *PAL* 和 *PR-2* 的表达 (刘勇, 2016)。Zeng 等 (2020) 研究也证实西花蓟马取食预先外施 CaCl_2 处理的菜豆植株可提高 LOX、PAL 和 β -1,3-葡聚糖酶的活性, 增强菜豆植株对西花蓟马的抗性。

1.6 防御酶及防御信号通路基因的调控作用

植物防御酶活性及防御信号通路基因的表达是调控植物防御反应的关键因子, 但也因作物种类、诱导处理方式以及昆虫的取食行为而存在一定差异。菜豆植株 POD、CAT 和 SOD 活性变化对西花蓟马取食诱导产生的系统防御反应具有调控作用 (岳文波等, 2018); 此外, 多酚氧化酶 (PPO)、LOX、PAL、 β -1,3-葡聚糖酶及蛋白酶抑制剂 (PIs) 等也可通过不同程度的表达变化响应西花蓟马取食、机械损伤及外源 MeSA 和 JA 诱导的菜豆防御反应 (从春蕾等, 2014)。JA 通路基因 (*VSP2* 和 *LOX2*)、JA/ET 通路基因 (*chiB* 和 *PDF1.2*) 以及 SA 通路基因 (*PR1* 和 *BGL2*) 的表达量变化在调控西花蓟马取食诱导拟南芥产生防御反应方面具有重要作用 (Abe *et al.*, 2008)。JA 信号通路基因 *PIN2* 和 SA 通路基因 *PR1* 和脱落酸 ABA 通路基因 *ASR* 在调控甜椒防御西花蓟马中也起着重要作用 (Bouagga *et al.*, 2018)。

2 西花蓟马对植物防御反应的适应性

2.1 解毒及代谢适应

解毒及代谢适应是昆虫生理生化适应的具

体体现, 其解毒代谢相关酶及其基因是调控昆虫适应植物防御反应的关键因子。昆虫利用口腔中的唾液蛋白酶和中肠中的解毒酶、消化性蛋白酶或同工酶、肠道酸碱水平、围食膜以及昆虫解毒代谢相关基因调控等对植物防御化合物进行解毒代谢及消化吸收 (Kant *et al.*, 2015; War *et al.*, 2018; Erb and Reymond, 2019; 赵婵等, 2019)。西花蓟马通过调节体内微粒体多功能氧化酶 (MFO)、乙酰胆碱酯酶 (AChE)、胱甘肽-S-转移酶 (GSTs) 和羧酸酯酶 (CarE) 的活性来适应西花蓟马或二斑叶螨预先取食诱导产生防御反应的菜豆植株 (鄧军锐等, 2016), 亦能通过调节解毒酶适应外源 JA 诱导的菜豆防御反应 (李顺欣等, 2017)。西花蓟马体内的解毒酶对其取食和外源物质诱导的番茄植株产生明显的响应 (蒲恒浒等, 2018a), 且也能调控对植物次生物质辣椒素的适应 (侯晓琳等, 2018)。西花蓟马体内保护酶 (如 POD、CAT 和 SOD) 和消化酶 (如胰蛋白酶、胰凝乳蛋白酶和淀粉酶) 在调控自身适应植物防御反应方面也具有一定的作用 (鄧军锐等, 2016; 姜丽娜等, 2017; 李顺欣等, 2017; 蒲恒浒等, 2018b)。此外, 昆虫解毒及代谢相关基因如细胞色素 P450 酶基因 *CYP6AE14*、*CYP6B4* 和 *P6AB60* (Mao *et al.*, 2007; Kumar *et al.*, 2014; Sun *et al.*, 2018)、唾液蛋白酶基因 *COO2* (Elzinga *et al.*, 2014)、GSTs 基因 *SIGSTE1* 等 (Zou *et al.*, 2016) 等在调控昆虫适应植物防御化合物中起着重要作用。抗药性研究表明, 西花蓟马细胞色素 P450 酶、GSTs 和丝氨酸蛋白酶 (Tps) 等基因具有一定的解毒及代谢作用 (Cifuentes *et al.*, 2012; Gao *et al.*, 2020), 但其在调控西花蓟马适应植物防御反应方面的作用机制有待进一步研究。

2.2 行为适应

昆虫对植物防御反应的行为适应是由昆虫对植物次生代谢物和挥发物等防御化合物及其植物毛状体等特殊物理结构做出识别, 然后调控昆虫行为, 使其对寄主植物做出定位、取食、产卵、避开有毒化合物以及躲避天敌等反应。西花

蓟马响应植物防御化合物而做出的取食和产卵选择性行为是其主要的行为适应方式, 如 Delphia 等 (2007) 研究发现西花蓟马对诱导释放防御性挥发物的烟草植株的取食和产卵偏好性降低。MeJA、顺式茉莉酮和烯丙基苯甲醚 3 种植物次生化合物也造成西花蓟马取食产卵的偏好性下降 (Egger and Koschier, 2014), 且增加西花蓟马 2 龄若虫转移到土壤中化蛹以避免 MeJA 和顺式茉莉酮的胁迫 (Egger and Koschier, 2014)。但西花蓟马持续暴露在顺式茉莉酮和 MeJA 环境中, 会出现类似于抗药性的驯化适应, 减弱植物次生化合物对自身的威慑作用 (Egger *et al.*, 2016)。此外, 西花蓟马传毒行为也能增强其对植物防御反应的适应能力 (Abe *et al.*, 2012)。

3 小结与展望

西花蓟马寄主范围广, 隐匿性极强, 极难防治, 根据诱导防御相关原理开发抗性作物是防控西花蓟马极具生态效益的方法之一。西花蓟马主要受植物 JA 防御网络的影响, 同时也受其他防御通路的影响, 但相关的作用机制因作物种类而存在一定差异, 有待进一步的明确。西花蓟马对植物防御反应的适应机制的研究中, 对于解毒酶调控的生理适应和挥发物等调控的行为适应已取得一定进展, 但其适应性分子机制, 如西花蓟马适应有毒植物次生化合物的功能基因尚不明确。另外, 对于西花蓟马产卵诱导的植物防御反应以及西花蓟马产卵是否对植物防御反应也存在抑制作用等问题尚未明确。

未来的研究中, 结合分子生物学手段进一步分析西花蓟马响应植物防御反应的组学特征, 挖掘响应植物防御反应的关键基因和效应子, 沉默或敲除西花蓟马适应植物防御反应的关键基因, 恢复其对植物防御反应的敏感性, 从而恢复植物对西花蓟马的抗性, 进而实现防控目的; 或者利用西花蓟马取食诱导植物防御反应的相关原理进一步开发抗性作物以控制西花蓟马, 亦或是将植物防御反应与“推-拉”策略相结合利用生态调控手段控制西花蓟马亦是可行的研究方向。

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