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昆虫取食诱导的植物间的通信作用综述

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摘要:昆虫取食不仅能诱导植物本身产生防御反应,还能诱导邻近健康植物产生防御反应,这就是植物间通信作用。植物受到昆虫取食后,会释放出一系列的挥发性化合物,已经证明昆虫取食诱导的植物挥发性化合物在植物通信中起作用。本文总结昆虫取食诱导的挥发性化合物在植物通信中的作用及其机制,这有利于增加植物抗虫性找到害虫综合防治的新途径。

关键词:昆虫取食;植物间通信;挥发性化合物

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昆虫取食不仅能诱导植物本身抗虫性增加,还能诱导邻近健康植物的抗虫性增加,这就是植物间的通信作用。植物间的通信首先是由 Rhoades 在 1983 年提出来的^[1],他在田间发现被毛虫取食的树很少有毛虫再来取食,令人惊讶的是邻近健康的树也是只有很少的毛虫取食。目前室内和田间试验已经在至少 30 种植物中证实植物通信作用的存在^[2-3]。Rhoades 还提出受害植物和邻近植物间空气中的交流能引起邻近植物抗性水平的增加^[1]。严格控制实验室条件的结果可以表明植物间是通过空气交流的。番茄植物与剪枝的山艾一起放在小的密闭容器内可以增加番茄蛋白酶抑制剂的含量^[4],蛋白酶抑制剂可以减少昆虫的取食^[5]。其他密闭容器中的试验支持并且扩展了这个结论^[6-8]。田间植物间的距离大于 60 cm,同时有植物间空气的流通条件,邻近植株的抗性也会增加^[9]。当阻止空气流通后,包括树枝间和植物间的系统诱导抗性都不能检测到。如果山艾受害植株和健康植株离得更近,则山艾间的通信作用更有效^[10-11]。植物通信对于信息的传递者和接收者都是非常有益的。研究植物通信的作用及机理,对于害虫-植物-植

物-天敌之间的相互关系具有重要的意义,可为害虫综合治理提供重要的理论依据。

1 昆虫取食诱导的挥发性化合物在植物通信中的作用

昆虫取食能诱导植物产生一系列的挥发性化合物(volatile organic compounds, VOCs),这些化合物不仅能激活间接防御反应以吸引天敌,而且能作为伤害信号诱导系统性防御反应。昆虫取食杂交杨(*Populus deltoides* × *nigra*)的叶片能敏化没有导管连接的邻近叶片防御反应;未受害的叶片暴露于同一茎秆的受害叶片释放的挥发性化合物中,与未接收挥发性化合物的叶片相比,对舞毒蛾(*Lymantria dispar* L.)取食的防御作用提高了^[12]。当维管的连接受限制时,挥发性化合物信号有利于系统防御反应的发生,同时在短距离的植物间也发现这种现象的存在。受害诱导利马豆叶片释放的挥发性化合物能诱导和敏化未受害的植株和同一植株的未受害部分花外蜜露 EFN 的分泌^[13]。这个研究不仅证明了在自然界中受害植物释放的挥发性化合物的质和量都足以激发未受害植株的间接防御反应,还证明了 VOCs 是快速和有效的植物间通信的信号。

目前关于植物通信的研究大部分都集中于一些模式系统如野生烟草和利马豆^[14]。以利马豆为例,应用离体利马豆叶片和 RT-PCR 技术研究表明,未被二斑叶螨侵染的利马豆叶片暴露在叶螨侵染叶片释放的挥发性气体中时,未被侵染叶片和被侵染叶片中脂氧合酶(十八烷途径中的关键酶)活性升高到几乎相同的程度,被侵染叶片中检测到 6

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个基因的转录物,包括基本病原菌相关蛋白基因 PR-2(1,3-葡糖糖化酶)和 PR-3(几丁质酶)、酸性病原菌相关蛋白基因 PR-4(酸性几丁质酶)、十八烷途径中的脂氧合酶(LOX)基因、苯丙烷类代谢途径中的苯丙氨酸解氨酶(PAL)基因以及异戊二烯合成途径中的法呢基焦磷酸合成酶(FPS)基因。暴露在二斑叶螨诱导的挥发性气体中 1 d 后的利马豆叶片中,检测到 6 个防御基因中 5 个基因的转录物。暴露在机械损伤诱导物中的利马豆叶片中只检测到 PR-2 基因转录物。完整利马豆植株与离体利马豆叶片不同,完整利马豆植株暴露在二斑叶螨侵染的利马豆释放的挥发性气体中,只检测到 PR-2、PR-3 和 PAL 转录物的积累^[15-17]。

2 昆虫取食诱导的挥发性化合物在植物通信中的作用机制

昆虫取食诱导的植物挥发物能影响邻近植物的防御策略^[1,18]。例如暴露于昆虫取食诱导的植物挥发物的植物,诱导抗虫性增加^[11,19-22];植物避免遭受昆虫的取食^[23-25];诱导抗性相关化合物的增加和抗性基因的表达^[4,6,17,26];还有敏化植物的防御反应^[27-28]。植物挥发性化合物通过表皮吸收或激活生理反应影响邻近植物,有很多试验证据表明表皮吸收和生理反应的作用^[27]。

虽然许多昆虫取食诱导植物产生挥发性化合物成分已经确定^[29-33],但是很少有研究证明哪种挥发物在植物通信中起作用^[34]。目前已经证明茉莉酸甲酯可以激发邻近植物的防御反应。茉莉酸甲酯是艾属植物产生并且释放的非常高浓度的一种挥发性化合物。番茄植物在密闭容器内暴露于山艾释放的 MeJA,能使蛋白酶抑制剂的含量以剂量依赖的形式增加^[4]。

为了证明昆虫取食诱导植物挥发性化合物中诱导抗性的关键化合物,目前许多试验是使植物暴露于相对高浓度人工合成的纯化合物。这些研究表明除了茉莉酸甲酯,萜类化合物和 C₆ 绿叶挥发物也能激活依赖于茉莉酸的植物防御反应^[15,26,35-37]。然而,这种 VOCs 诱导的防御反应剧烈程度比茉莉酸甲酯或昆虫激发子激发的反应要弱得多。Engelberth 等研究发现,甜菜夜蛾(*Spodoptera exigua*)取食玉米诱导产生的 VOCs 不能直接诱导防御反应,但是可以敏化植物对以后受到的伤害和昆虫激发子产生防御反应,只可以被外源性 3 种绿叶

挥发物(Z)-3-己烯醇,(Z)-3-己烯醛或(Z)-3-己烯乙酸酯的应用所模拟。相反,暴露于昆虫激发子的植物释放的 VOCs 仅有微量的绿叶挥发物,不能激发邻近植物的反应,表明绿叶挥发物是毛虫诱导 VOCs 中有活性的化合物^[28]。与这些结果相反,烟草天蛾侵染烟草不能敏化邻近的烟草植株^[38]。奇怪的是,这些化合物(绿叶挥发物和萜类化合物)先前证明能敏化其他种植物的防御反应^[28,36]。另外一方面,山艾的离体叶片释放的 VOCs 能敏化烟草,烟草夜蛾取食能提高烟草蛋白酶的活性^[39]。这就证明了剪枝的山艾释放的 VOCs 含有敏化-诱导的化合物,而这些化合物是烟草天蛾取食烟草诱导释放的化合物中所没有的。因此 VOC-诱导敏化是植物界中普遍存在的现象,只是敏化-诱导的化合物因不同种植物而不同。

Ton 等从分子化学和行为角度证明了 VOC-诱导敏化反应能增强玉米的直接和间接抗虫性。用差式杂交的方法研究灰翅夜蛾(*Spodoptera littoralis*)取食玉米诱导的防御基因,确定了 10 种防御相关基因对茉莉酸或昆虫激发子作出反应^[40]。暴露于取食诱导的 VOCs 不会直接激活这些基因,但是具有敏化作用,当遇到昆虫袭击时,使它们更快更强地作出反应,能增加芳香族和萜类化合物的释放,在 VOCs 释放最多的时候,敏化的植物能显著吸引更多的寄生蜂。这个试验还证明 VOC-诱导敏化的目标是特定茉莉酸诱导基因的一部分,在分子水平联系这些反应来提高直接和间接抗虫性。

诱导抗性的空间范围包含有各种各样的机制。例如,造瘿昆虫取食植物后,植物产生高度敏感反应,阻止虫瘿的生成,然后杀死入侵的昆虫^[41-42]。这种高度定位反应包括营养物质的损失和围绕植物受伤地方的细胞坏死。其他的诱导反应是系统的并且包含同等的信号在整个植株中移动。例如咀嚼毛虫取食后,番茄植株产生系统素,一种信号分子,能使破坏迅速从受害叶片扩散到整个韧皮部^[43]。系统素或其他信号分子诱导蛋白酶抑制剂和其他化学物质的合成,使得含有导管联系的植株上的咀嚼性昆虫很难存活^[44-45]。系统抗性只有在山艾植株的树枝间检测到,挥发性信号在树枝间传导。这个信号还没有确定,许多挥发性化合物包括茉莉酸甲酯是由受害植物释放出来的并且作为空气传播的信号物质^[39,46-47]。

目前,有关植物通信及诱导抗性集中于基因表达、次生代谢物质、酶活性和诱导释放的挥发物^[48],

而一些其他的影响如时间、位置、来源、诱导程度和昆虫种类都能影响植物的防御反应,还会间接影响取食者^[49]。目前的试验都是将取食植物和健康植物放在密闭容器中进行的^[50],或植物暴露于挥发性物质^[11]。但是在自然的条件下,昆虫取食的时间、空间可能对低样本的数据产生错误或者强大影响。还有一些其他影响因子需要长期研究^[14]。

3 结论与展望

人们早就意识到诱导抗性能作为一种工具应用于在农业中,主要研究集中于利用昆虫取食诱导的植物来操纵害虫的捕食性和寄生性天敌而不是利用寄主植物本身的抗性^[51-53]。研究人员更多地关注利用间接防御开发害虫防治策略,较少地关注增加寄主植物抗性^[54]。到目前为止,利用挥发性物质最成功的是非洲许多农民使用的用于保护玉米和其他作物的“push-pull”系统^[52],这个系统通过有价值的作物与另一释放趋避害虫信号的物种间作,使害虫远离该作物,同时沿田间边种植了第3个物种,以吸引害虫,将它们从田间“拉出”并远离作物。因此,研究昆虫取食诱导植物间的通信作用及其机制,有利于通过增加植物抗虫性找到害虫综合防治的新途径。

参考文献:

- [1] Rhoades D F. Responses of alder and willow to attack by tent caterpillars and webworms: evidence for pheromonal sensitivity of willows [M]//Plant resistance to insects. Washington D C; American Chemical Society, 1983.
- [2] Heil M, Karban R. Explaining evolution of plant communication by airborne signals [J]. Trends in Ecology & Evolution, 2010, 25 (3): 137 - 144.
- [3] Karban R, Wetzel W C, Shiojiri K, et al. Deciphering the language of plant communication: volatile chemotypes of sagebrush [J]. New Phytologist, 2014, 204 (2): 380 - 385.
- [4] Farmer E E, Ryan C A. Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves [J]. Proceedings of the National Academy of Sciences of the United States of America, 1990, 87 (19): 7713 - 7716.
- [5] Broadway R M, Duffey S S. Plant proteinase inhibitors: mechanism of action and effect on the growth and digestive physiology of larval *Heliothis zea* and *Spodoptera exiqua* [J]. Journal of Insect Physiology, 1986, 32 (10): 827 - 833.
- [6] Shulaev V, Silverman P, Raskin I. Airborne signalling by methyl salicylate in plant pathogen resistance [J]. Nature, 1997, 385 (6618): 718 - 721.
- [7] Qi Q, Shi X Y, Liang P, et al. Induction of phenylalanine ammonia-lyase and lipooxygenase in cotton seedlings by mechanical wounding and aphid infestation [J]. Progress in Natural Science, 2005, 15 (5): 419 - 423.
- [8] Lyu M, Kong H L, Liu H A, et al. Induction of phenylalanine ammonia-lyase (PAL) in insect damaged and neighboring undamaged cotton and maize seedlings [J]. International Journal of Pest Management, 2017, 63 (2): 166 - 171.
- [9] Karban R, Shiojiri K, Huntzinger M, et al. Damage-induced resistance in sagebrush: volatiles are key to intra- and interplant communication [J]. Ecology, 2006, 87 (4): 922 - 930.
- [10] Karban R, Shiojiri K, Ishizaki S, et al. Kin recognition affects plant communication and defence [J]. Proceedings: Biological Sciences, 2013, 280 (1756): 20123062.
- [11] Karban R, Yang L H, Edwards K F. Volatile communication between plants that affects herbivory: a meta-analysis [J]. Ecology Letters, 2014, 17 (1): 44 - 52.
- [12] Frost C J, Appel H M, Carlson J E, et al. Within-plant signalling via volatiles overcomes vascular constraints on systemic signalling and primes responses against herbivores [J]. Ecology Letters, 2007, 10 (6): 490 - 498.
- [13] Heil M, Silva Bueno J C. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature [J]. Proceedings of the National Academy of Sciences of the United States of America, 2007, 104 (13): 5467 - 5472.
- [14] Grof - Tisza P, Karban R, Pan V S, et al. Assessing plant-to-plant communication and induced resistance in sagebrush using the sagebrush specialist *Trirhabda pilosa* [J]. Arthropod - Plant Interactions, 2020, 14 (3): 327 - 332.
- [15] Arimura G I, Ozawa R, Shimoda T, et al. Herbivory-induced volatiles elicit defence genes in Lima bean leaves [J]. Nature, 2000, 406 (6795): 512 - 515.
- [16] Arimura G I, Tashiro K, Kuhara S, et al. Gene responses in bean leaves induced by herbivory and by herbivore-induced volatiles [J]. Biochemical and Biophysical Research Communications, 2000, 277 (2): 305 - 310.
- [17] Arimura G I, Ozawa R, Horiuchi J I, et al. Plant-plant interactions mediated by volatiles emitted from plants infested by spider mites [J]. Biochemical Systematics and Ecology, 2001, 29 (10): 1049 - 1061.
- [18] Baldwin I T, Schultz J C. Rapid changes in tree leaf chemistry induced by damage: evidence for communication between plants [J]. Science, 1983, 221 (4607): 277 - 279.
- [19] Karban R, Maron J, Felton G W, et al. Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants [J]. Oikos, 2003, 100 (2): 325 - 332.
- [20] Ninkovic V, Ahmed E, Glinwood R, et al. Effects of two types of semiochemical on population development of the bird cherry oat aphid *Rhopalosiphum padi* in a barley crop [J]. Agricultural and Forest Entomology, 2003, 5 (1): 27 - 33.
- [21] Karban R. Plant behaviour and communication [J]. Ecology Letters, 2008, 11 (7): 727 - 739.
- [22] Heil M. Herbivore-induced plant volatiles: targets, perception and

- unanswered questions[J]. *New Phytologist*, 2014, 204(2): 297–306.
- [23] Ninkovic V, Olsson U, Pettersson J. Mixing barley cultivars affects aphid host plant acceptance in field experiments[J]. *Entomologia Experimentalis et Applicata*, 2002, 102(2): 177–182.
- [24] Glinwood R, Pettersson J, Ahmed E, et al. Change in acceptability of barley plants to aphids after exposure to allelochemicals from couch – grass (*Elytrigia repens*) [J]. *Journal of Chemical Ecology*, 2003, 29(2): 261–274.
- [25] Glinwood R, Ninkovic V, Pettersson J, et al. Barley exposed to aerial allelopathy from thistles (*Cirsium* spp.) becomes less acceptable to aphids[J]. *Ecological Entomology*, 2004, 29(2): 188–195.
- [26] Arimura G I, Ozawa R, Nishioka T, et al. Herbivore – induced volatiles induce the emission of ethylene in neighboring Lima bean plants[J]. *The Plant Journal*, 2002, 29(1): 87–98.
- [27] Choh Y, Shimoda T, Ozawa R, et al. Exposure of Lima bean leaves to volatiles from herbivore – induced conspecific plants results in emission of carnivore attractants: active or passive process? [J]. *Journal of Chemical Ecology*, 2004, 30(7): 1305–1317.
- [28] Engelberth J, Alborn H T, Schmelz E A, et al. Airborne signals prime plants against insect herbivore attack[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2004, 101(6): 1781–1785.
- [29] de Moraes C M, Lewis W J, Pare P W, et al. Herbivore – infested plants selectively attract parasitoids[J]. *Nature*, 1998, 393(6685): 570–573.
- [30] Rasman S, Turlings T C J. First insights into specificity of belowground tritrophic interactions [J]. *Oikos*, 2008, 117(3): 362–369.
- [31] Clavijo M A, Unsicker S B, Gershenzon J. The specificity of herbivore – induced plant volatiles in attracting herbivore enemies [J]. *Trends in Plant Science*, 2012, 17(5): 303–310.
- [32] Xiao Y, Wang Q, Erb M, et al. Specific herbivore – induced volatiles defend plants and determine insect community composition in the field[J]. *Ecology Letters*, 2012, 15(10): 1130–1139.
- [33] Rowen E, Kaplan I. Eco – evolutionary factors drive induced plant volatiles; a meta – analysis [J]. *The New Phytologist*, 2016, 210(1): 284–294.
- [34] Moreira X, Nell C S, Katsanis A, et al. Herbivore specificity and the chemical basis of plant – plant communication in *Baccharis salicifolia* (Asteraceae) [J]. *New Phytologist*, 2018, 220(3): 703–713.
- [35] Farag M, Paré P W. C6 – Green leaf volatiles trigger local and systemic VOC emissions in tomato[J]. *Phytochemistry*, 2002, 61(5): 545–554.
- [36] Ruther J, Kleier S. Plant – plant signaling; ethylene synergizes volatile emission in *Zea mays* induced by exposure to (Z) – 3 – hexen – 1 – ol [J]. *Journal of Chemical Ecology*, 2005, 31(9): 2217–2222.
- [37] Yan Z G, Wang C Z. Wound – induced green leaf volatiles cause the release of acetylated derivatives and a terpenoid in maize[J]. *Phytochemistry*, 2006, 67(1): 34–42.
- [38] Paschold A, Halitschke R, Baldwin I T. Using ‘mute’ plants to translate volatile signals[J]. *Plant Journal*, 2006, 45(2): 275–291.
- [39] Kessler A, Halitschke R, Diezel C, et al. Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata* [J]. *Oecologia*, 2006, 148(2): 280–292.
- [40] Ton J, D’Alessandro M, Jourdie V, et al. Priming by airborne signals boosts direct and indirect resistance in maize [J]. *Plant Journal*, 2007, 49(1): 16–26.
- [41] Fernandes G W. Hypersensitivity: a neglected plant resistance mechanism against insect herbivores [J]. *Environmental Entomology*, 1990, 19(5): 1173–1182.
- [42] Fernandes G W. Hypersensitivity as a phenotypic basis of plant induced resistance against a galling insect (Diptera: Cecidomyiidae) [J]. *Environmental Entomology*, 1998, 27(2): 260–267.
- [43] Pearce G, Strydom D, Johnson S, et al. A polypeptide from tomato leaves induces wound – inducible proteinase inhibitor proteins[J]. *Science*, 1991, 252(5022): 895–897.
- [44] Orians C M, Jones C G. Plants as resource mosaics: a functional model for predicting patterns of within – plant resource heterogeneity to consumers based on vascular architecture and local environmental variability[J]. *Oikos*, 2001, 94(3): 493–504.
- [45] Orians C M. Herbivores, vascular pathways, and systemic induction: facts and artifacts[J]. *Journal of Chemical Ecology*, 2005, 31(10): 2231–2242.
- [46] Karban R, Baldwin I T, Baxter K J, et al. Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush[J]. *Oecologia*, 2000, 125(1): 66–71.
- [47] Preston C A, Laue G, Baldwin I T. Methyl jasmonate is blowing in the wind, but can it act as a plant – plant airborne signal? [J]. *Biochemical Systematics and Ecology*, 2001, 29(10): 1007–1023.
- [48] Kant M R, Jonckheere W, Knegt B, et al. Mechanisms and ecological consequences of plant defence induction and suppression in herbivore communities[J]. *Annals of Botany*, 2015, 115(7): 1015–1051.
- [49] War A R, Paulraj M G, Ahmad T, et al. Mechanisms of plant defense against insect herbivores[J]. *Plant Signaling & Behavior*, 2012, 7(10): 1306–1320.
- [50] Karban R, Baldwin I T. Induced response to herbivory [M]. Chicago: Chicago University Press, 1997.
- [51] Stenberg J A, Heil M, Åhman I, et al. Optimizing crops for biocontrol of pests and disease[J]. *Trends in Plant Science*, 2015, 20(11): 698–712.
- [52] Pickett J A, Khan Z R. Plant volatile – mediated signalling and its application in agriculture: successes and challenges [J]. *New Phytologist*, 2016, 212(4): 856–870.
- [53] Turlings T C J, Erb M. Tritrophic interactions mediated by herbivore – induced plant volatiles: mechanisms, ecological relevance, and application potential[J]. *Annual Review of Entomology*, 2018, 63(1): 433–452.
- [54] Karban R. The ecology and evolution of induced responses to herbivory and how plants perceive risk[J]. *Ecological Entomology*, 2020, 45(1): 1–9.