

水稻挥发物在调控害虫中的作用及其应用前景*

林娜** 吕静 娄永根***

(浙江大学农业与生物技术学院昆虫科学研究所, 杭州 310058)

摘要 植物挥发物作为生态系统中各生物间信息传递的载体在影响生物进化及生物群落组成中发挥着重要作用。剖析植物挥发物的主要化学组分及其生态学功能, 不仅能从一个侧面揭示生物间的协同进化, 而且可为害虫的可持续治理提供有效的绿色防控技术。为此, 本文围绕水稻挥发物主要组分与合成途径、虫害诱导水稻挥发物合成的调控机理、水稻挥发物的生态学功能及应用前景等方面, 对国内外的最新研究成果进行综述, 提出了今后的研究方向, 并推动水稻挥发物在害虫防控中的应用。

关键词 水稻挥发物; 害虫; 天敌; 生态学功能; 应用

Prospects for the application of rice volatiles in pest control

LIN Na** LÜ Jing LOU Yong-Gen***

(Institute of Insect Sciences, College of Agriculture and Biotechnology,
Zhejiang University, Hangzhou 310058, China)

Abstract Plant volatiles, transmit information between taxa and thereby play an important role in evolution and community composition. Deciphering the main chemical components of plant volatiles and their ecological functions can not only reveal the co-evolution of organisms, but also identify potentially effective, environmentally-friendly, compounds for sustainable pest management. This paper summarizes the latest progress in research on rice volatiles, mainly focusing on their components and biosynthesis pathways, the regulatory mechanism underlying the biosynthesis of herbivore-induced volatiles, their ecological function and prospects for their application in pest control. Directions for research future are suggested to promote the application of rice volatiles in pest control.

Key words rice volatiles; insect pests; natural enemies; ecological functions; applications

在自然界中, 植物不同于动物, 动物可以通过较强的行动力传递信号, 但植物通常以化学等方式与周围环境进行信息交流, 挥发物便是植物与外界信息交流的重要媒介之一。植物挥发物中不仅存在引诱植食性昆虫的利它素(Kairomone)或趋避植食性昆虫的利己素(Allomone)成分, 在开花期还可能会释放引诱授粉者的互益素

(Synomone)成分(Dudareva *et al.*, 2013; Ayelo *et al.*, 2021a; Zhou and Jander, 2022)。当受到植食性昆虫为害时, 植物挥发物组成(组分或组成比例)会发生变化, 这些变化除了能被同种或异种植食性昆虫感知, 从而对它们产生引诱或趋避外, 也可能被植食性昆虫天敌和(或)周围其他同种或异种植物所利用, 使得植食性昆虫天敌

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**第一作者 First author, E-mail: lin_na@zju.edu.cn

***通讯作者 Corresponding author, E-mail: yglou@zju.edu.cn

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发现寄主或猎物以及邻近植物启动相关防御反应 (Hare, 2011; Schuman and Baldwin, 2016; Bouwmeester *et al.*, 2019), 分别发挥互益素或类似于昆虫种内报警信息素 (Alarm pheromone) 的作用。除了发挥能影响其他生物行为或生理的信息化合物 (Infochemicals) 的作用外, 植物挥发物也可能对植食性昆虫的生长发育和繁殖产生直接的有利或不利影响, 起到防御化合物或有益化合物的作用 (Dudareva *et al.*, 2013; Nishida, 2014)。因此, 鉴定植物挥发物主要种类, 并深入剖析其调控植物、植食性昆虫及其天敌互作关系的作用及其合成与调控机制, 不仅可深入理解昆虫与植物的互作关系与机理, 而且可望开发害虫绿色防控技术。例如, 利用对害虫有趋避作用的挥发物组分可以开发植食性昆虫趋避剂, 利用对害虫天敌有吸引作用的挥发物组分可以开发天敌引诱剂, 也可以将能够诱导植物产生“防御警备”的挥发物制备成相关产品, 提高植物的防御能力; 此外, 可以通过遗传改良改变植物挥发物以提高植物抗虫性等等 (Ayelo *et al.*, 2021a, 2021b; Wang *et al.*, 2022)。

水稻 *Oryza sativa* 是世界上最重要的粮食作物之一, 全球一半以上人口以稻米作为主要食物。水稻在整个大田生长期中, 受到多种植食性昆虫为害, 其中主要包括鳞翅目害虫二化螟 *Chilo suppressalis*、三化螟 *Tryporyza incertulas*、稻纵卷叶螟 *Cnaphalocrocis medinalis* 以及半翅目害虫褐飞虱 *Nilaparvata lugens*、白背飞虱 *Sogatella furcifera* 和灰飞虱 *Laodelphax striatellus* 等 (程家安和祝增荣, 2017; Zhao *et al.*, 2020)。至今, 有关水稻挥发物在调控害虫及其天敌互作关系中的作用已有很多研究报道 (刘芳等, 2002; Xiao *et al.*, 2012; Hu *et al.*, 2020; Li *et al.*, 2020; Liao *et al.*, 2022), 并鉴定了一批具有活性的挥发物, 揭示了一些挥发物的合成与调控途径, 但有关如何利用水稻挥发物防控害虫则研究得较少。本文综述国内外有关水稻挥发物及其在调控害虫中作用的最新研究成果, 并提出今后的研究方向, 以期促进这一方面相关内容的研究, 并推动水稻挥发物在害虫防控中的应用。

1 水稻挥发物主要组分及其生物合成途径

植物挥发物包括植物在正常情况下释放的组成型挥发物 (Constitutive plant volatiles) 和在受到生物或非生物逆境胁迫时释放的挥发物, 如植食者为害诱导的植物挥发物 (Herbivore induced plant volatiles, HIPVs)。植物挥发物种类很多, 包括绿叶挥发物、萜类化合物、酚类、苯类、含氮和含硫化合物等 (娄永根和程家安, 2000; Hare, 2011; Tholl *et al.*, 2021)。迄今为止, 在水稻植株中已经鉴定了超过 50 种挥发物, 包括绿叶挥发物、萜类化合物、烷烃类及其他物质 (莫晓畅和娄永根, 2016; Hu *et al.*, 2020)。

1.1 绿叶挥发物及其生物合成

绿叶挥发物 (Green leaf volatiles, GLVs) 是一类由 6 个碳骨架构成的醇、醛和酯 (Matsui and Engelberth, 2022)。这些化合物来源于植物脂肪酸, 通过脂氧合酶 (Lipoxygenase, LOX) / 过氧化氢裂解酶 (Hydroperoxide lyase, HPL) 途径合成。植物体内脂肪酸 (α -亚麻酸、亚油酸) 通过脂氧合酶催化生成脂质过氧化氢, 随后经过过氧化氢裂解酶裂解生成 C6 醛和十二碳烯酸, 部分 C6 醛被还原为 C6 醇, 并可在酯酰辅酶 A 酰基转移酶的催化下进一步转化为酰基酯 (D'Auria *et al.*, 2007; Nakashima *et al.*, 2013; Tanaka *et al.*, 2018; Matsui and Engelberth, 2022)。植物绿叶挥发物主要有正己醛、正己醇、(E)-2-己烯醛等 9 种 (Scala *et al.*, 2013; Matsui and Engelberth, 2022)。值得一提的是, 脂氧合酶途径也是植物茉莉酸 (Jasmonic acid, JA) 合成途径, 在植物体内通过调控不同的脂氧合酶, 使得 GLVs 和 JAs 的合成维持稳态 (Tyagi *et al.*, 2016; Mwenda *et al.*, 2017)。

目前, 水稻中报道的绿叶挥发物主要有正己醛、(Z)-3-己烯-1-醇、(Z)-3-己烯醛、(E)-2-己烯醛、(E)-2-己烯-1-醇和 (Z)-3-己烯乙酸酯等 (表 1) (汪鹏和娄永根, 2013; Sun *et al.*, 2014; Hu *et al.*, 2020)。未受胁迫时, 植物释放的 GLVs 处于较低

水平, GLVs 被储存在植物细胞或组织器官中, 一旦遭受生物或非生物逆境胁迫则迅速引起胁迫部位绿叶挥发物的大量释放, 因此 GLVs 是临近植物和其他生物体感知到的重要信号之一 (Mochizuki *et al.*, 2016; Matsui and Engelberth, 2022)。

1.2 萜类化合物及其生物合成

萜类化合物是植物诱导型挥发物中最丰富的一类物质, 主要包括单萜、倍半萜及其衍生物。植物体内萜类化合物的合成通过两条途径: 一是胞质的甲羟戊酸 (Mevalonate, MVA) 途径, 二是质体的甲基赤藓糖醇-4-磷酸 (2-methyl-D-erythritol-4-phosphate, MEP) 途径; 两条途径分别在多种酶的调控下独立生成共同的萜类化合物前体——异戊烯基焦磷酸 (Isopentenyl diphosphate, IPP)。MVA 途径中 IPP 与其异构体二甲基丙烯焦磷酸 (Dimethylallyl pyrophosphate, DMAPP) 生成前体——法尼基焦磷酸 (Farnesyl pyrophosphate, FPP), 进而生成倍半萜和三萜; MEP 途径中二者缩合形成牻牛儿基焦磷酸 (Geranyl diphosphate, GPP) 和牻牛儿牻牛儿焦磷酸 (Geranylgeranyl pyrophosphate, GGPP), 进一步生成单萜、二萜和四萜 (Dewick, 2002; Cheng *et al.*, 2007a; Tholl, 2015)。目前, 已报道的害虫为害水稻诱导的主要挥发性萜类化

合物已超过 20 种 (表 1), 包括单萜 6 种, 倍半萜类 17 种 (娄永根等, 2002; 杜孟浩等, 2005; 闫锋等, 2010; Zhuang *et al.*, 2012; Wang *et al.*, 2018; Hu *et al.*, 2020); 萜烯同系物 (Homoterpene) 2 种: (E)-4,8-二甲基-1,3,7-壬三烯, [(3E)-4,8-dimethyl-1,3,7-nonatriene, DMNT]和(3E,7E)-4,8,12-三甲基十三-1,3,7,11-四烯, [(3E,7E)-4,8,12-trimethyltrideca-1,3,7,11-tetraene, TMTT]。

1.3 其他挥发物

水稻挥发物还包括多种烷烃类以及除绿叶挥发物和萜类挥发物之外的醛、醇、酮、酯类化合物 (表 1)。水稻中烷烃类挥发物主要有 9 种, 包括正十三烷、正十四烷、正十五烷等 (娄永根等, 2002; 杜孟浩等, 2005; 闫锋等, 2010)。除此之外, 还包括 2-庚酮、2-庚醇、辛醛、异弗尔酮、吲哚和水杨酸甲酯等 (Zhuang *et al.*, 2012; 刘晓丽和娄永根, 2018; Hu *et al.*, 2020)。这些化合物中, 吲哚和水杨酸甲酯是通过莽草酸途径合成的 (Zhuang *et al.*, 2012; Boba *et al.*, 2017); 异弗尔酮是类胡萝卜素的 C₉ 降解产物 (Izumi *et al.* 2021), 类胡萝卜素是一种四萜类化合物, 因此, 异弗尔酮可能是通过萜类化合物生物合成途径产生的。其他一些化合物的生物合成途径还有待进一步研究。

表 1 水稻挥发物主要组分
Table 1 Main components of rice volatiles

编号 No.	挥发物类别 Volatile species				
	绿叶挥发物 GLVs	萜类化合物 Terpenoids			其他挥发物 Others
		单萜类 Monoterpenes	倍半萜类 Sesquiterpenes	萜烯同系物 Homoterpenes	
1	正己醛 n-Hexanal	α-侧柏烯 α-Thujene	α-古巴烯 α-Copaene	DMNT	正十三烷 n-Tridecane
2	(E)-2-己烯-1-醇 (E)-2-Hexen-1-ol	α-蒎烯 α-Pinene	α-雪松烯 α-Cedrene	TMTT	正十四烷 n-Tetradecane
3	(Z)-3-己烯-1-醇 (Z)-3-Hexen-1-ol	月桂烯 Myrcene	倍半萜侧柏烯 Sesquithujene	—	正十五烷 n-Pentadecane
4	(Z)-3-己烯醛 (Z)-3-Hexenal	(+)-柠檬烯 (+)-Limonene	β-榄香烯 β-Elemene	—	正十六烷 n-Hexadecane
5	(E)-2-己烯醛 (E)-2-Hexenal	(E)-氧化芳樟醇 (E)- linalool oxide	α-香柠檬烯 α-Bergamotene	—	正十七烷 n-Heptadecane

续表 1 (Table 1 continued)

编号 No.	挥发物类别 Volatile species				其他挥发物 Others
	绿叶挥发物 GLVs	萜类化合物 Terpenoids			
		单萜类 Monoterpenes	倍半萜类 Sesquiterpenes	萜烯同系物 Homoterpenes	
6	(Z)-3-己烯乙酸酯 (Z)-3-Hexenyl acetate	芳樟醇 Linalool	β-石竹烯 β-Caryophyllene	—	正十八烷 n-Octadecane
7	—	—	(E)-α-香柑油烯 (E)-α- bergamotene	—	正十九烷 n-Nonadecane
8	—	—	倍半香桉烯 Sesquisabinene	—	正二十烷 n-Eicosane
9	—	—	β-法尼烯 β-Farnesene	—	正二十一烷 n-Henicosane
10	—	—	α-葎草烯 α-Humulene	—	2-庚酮 2-Heptanone
11	—	—	α-长叶蒎烯 α-Longipinene	—	2-庚醇 2-Heptanol
12	—	—	α-姜黄烯 α-Curcumene	—	辛醛 Octanal
13	—	—	α-姜烯 α-Zingiberen	—	异弗尔酮 Isophorone
14	—	—	(+)-雪松醇 (+)-Cedrol	—	吲哚 Indole
15	—	—	β-甜没药烯 β-Bisabolene	—	水杨酸甲酯 Methyl salicylate, MeSA
16	—	—	β-倍半水芹烯 β-Sesquiphellandren e	—	—
17	—	—	(E)-γ-甜没药烯 (E)-γ-Bisabolene	—	—

2 害虫为害诱导水稻挥发物生物合成的调控机理

受到植食性昆虫为害后,植物可以通过细胞膜表面模式识别受体感知植食性昆虫的为害信号,启动膜电位去极化、胞质钙离子内流、活性氧迸发以及丝裂原活化蛋白激酶(Mitogen-activated protein kinase, MAPK)级联途径激活等一系列早期事件,并由此而激活由茉莉酸、水杨酸(Salicylic acid, SA)、乙烯(Ethylene, ET)等植物激素介导的信号转导网络,最终导致植物转录组的重构以及防御化合物,包括挥发物的合

成(Li *et al.*, 2013; Wasternack and Hause, 2013; Lu *et al.*, 2014; Erb and Reymond, 2019; Zhou and Zhang, 2020)。

与很多植物中报道的一样,茉莉酸信号途径在调控水稻挥发物的生物合成中起着重要作用。一方面,水稻在受害虫为害时,能迅速积累茉莉酸及其生物活性形式茉莉酸异亮氨酸(Jasmonic acid-isoleucine, JA-Ile);伴随发生的是水稻挥发物释放量的显著增加(Howe *et al.*, 2018; Xu *et al.*, 2021)。另一方面,当 JA 合成通路关键酶丙二烯氧化物合酶(Allene oxide synthase, AOS)基因, OsAOS1 和 OsAOS2 被反义抑制时,二化螟为害诱导的水稻挥发物总量及 2-庚醇、α 蒎烯、

正十四烷和(E)- β -石竹烯等挥发物含量显著降低(Zeng *et al.*, 2021)。在缺乏丙二烯氧化物环化酶(Allene oxide cyclase, AOC)基因的茉莉酸缺陷突变体中,水稻组成型挥发物和诱导型挥发物的含量都显著减少(Mujiono *et al.*, 2021; Xu *et al.*, 2021)。另外,外用茉莉酸处理水稻,大多数水稻挥发物释放量显著增加,其中包括2-庚酮、2-庚醇、柠檬烯、芳樟醇、(E)- α -香柑油烯、(E)-橙花叔醇(E)-Nerolidol)、 β -石竹烯和水杨酸甲酯等(Lou *et al.*, 2005; Taniguchi *et al.*, 2014)。

除了茉莉酸信号途径以外,水杨酸与乙烯途径也在调控水稻挥发物生物合成中发挥重要作用。如外用水杨酸处理水稻,可增加水稻 β -蒎烯、(+)-3-蒎烯[(+)-3-Carene]、2-乙基己醇(2-Ethyl-1-hexanol)、甘菊蓝(Azulene)和水杨酸甲酯等挥发物的释放量(Stella De Freitas *et al.*, 2019)。Li等(2013)研究发现,SA响应基因OsNPR1(Non-expressor of pathogenesis-related genes1)反义抑制后,提高二化螟诱导的水稻体内JA和乙烯含量,相应的挥发物释放水平特别是萜类挥发物的含量亦显著提高。乙烯由1-氨基环丙烷-1-羧酸(1-Amino-1-cyclopropanecarboxylic acid, ACC)通过ACC合成酶(1-aminocyclopropane-1-carboxylic acid synthase, ACS)和ACC氧化酶(1-aminocyclopropane-1-carboxylic acid oxidase, ACO)生成。反义抑制水稻中乙烯生物合成基因OsACS2,降低植株乙烯释放量及二化螟取食诱导的挥发物,但褐飞虱为害反而增加了反义品系挥发物的释放(Lu *et al.*, 2014)。外源乙烯处理抑制了劳氏粘虫*Mythimna loreyi*口腔分泌物诱导的水稻体内芳樟醇、(E)- β -法尼烯和(Z)-3-己烯-1-醇的含量(Mujiono *et al.*, 2020)。由此可见,害虫为害诱导的水稻挥发物的生物合成主要受到茉莉酸、乙烯以及水杨酸等信号途径的调控。至于这些信号途径具体是如何调控这些挥发物的生物合成的,则目前尚不清楚。

3 水稻挥发物的生态学功能

植物生态系统中的各种生物都是植物挥发

物的潜在利用者和(或)被影响者。因此,植物挥发物不仅可能影响植食性昆虫及其天敌的行为与生长发育繁殖,还可能影响生态系统中其他同种与异种的植物、授粉者以及微生物等(如植物病原菌、昆虫致病真菌、根际微生物、植物与昆虫等各种共生微生物)。

3.1 水稻挥发物对植食性昆虫的影响

水稻挥发物能明显影响害虫的行为,并且这种影响受水稻受害程度、为害水稻的害虫种类以及水稻生育期等影响。例如,当水稻植株受为害程度较轻时,褐飞虱和白背飞虱都表现出对异种飞虱为害水稻的偏好性;当植株受为害程度加重后,两种飞虱均趋向选择健康水稻苗(刘芳等, 2002)。斜纹夜蛾*Spodoptera litura*为害水稻产生的多种萜类挥发物对褐飞虱具有驱避作用(Xu *et al.*, 2002)。二化螟幼虫为害水稻对二化螟和稻纵卷叶螟雌成虫具有趋避作用,稻纵卷叶螟幼虫为害水稻只对二化螟雌成虫表现出趋避作用(陈华才等, 2004; 魏丹等, 2013; Sun *et al.*, 2014)。与分蘖期不同,水稻抽穗扬花期的挥发物吸引条赤须盲蝽*Trigonotylus caelestialium*、中稻缘蝽*Leptocoris chinensis*等多种蝽类(Fujii *et al.*, 2010)。

剖析水稻挥发物中影响害虫行为的活性组分,发现不同挥发物组分对同种害虫或同种挥发物组分对不同害虫发挥着不同作用(表2)。例如,(S)-芳樟醇对褐飞虱的寄主选择和产卵均有趋避作用,发挥了利己素的作用,但(S)-芳樟醇对稻纵卷叶螟似乎有引诱作用,发挥着利它素的作用(Xiao *et al.*, 2012)。另一种萜类挥发物—— β -石竹烯,不仅能够吸引褐飞虱取食和产卵,而且对飞虱的发育也有调控作用。如沉默石竹烯合成酶基因OsCAS的水稻植株上,稻飞虱种群数量明显减少,并且延缓了褐飞虱若虫的发育(Xiao *et al.*, 2012)。此外, β -石竹烯也是吸引水稻抽穗期害虫条赤须盲蝽为害的关键化合物,且具有剂量效应,低浓度时对条赤须盲蝽雌成虫有吸引作用,高浓度则趋避(Fujii *et al.*, 2010)。水稻中的GLVs也能调节稻飞虱的行为及其生长繁

殖, 如(Z)-3-己烯醛能够吸引白背飞虱的产卵且有利于其生长, (Z)-3-己烯-1-醇含量下降后不仅吸引褐飞虱雌成虫和若虫, 也促进褐飞虱卵的发育 (Tong *et al.*, 2012; Hui *et al.*, 2015)。此外, 2-庚酮、2-庚醇和水杨酸甲酯对褐飞虱的取食和产卵也有一定的趋避作用, 2-庚酮、 α -法尼烯和(+)-柠檬烯等对白背飞虱有较强的吸引作用,

(Z)-法尼烯、橙花叔醇和雪松醇对灰飞虱有明显的引诱作用(周强等, 2003; 刘芳等, 2009; Tong *et al.*, 2012; Hui *et al.*, 2015; Hu *et al.*, 2019; Liao *et al.*, 2022)。Chen 等 (2022) 研究发现, 稻纵卷叶螟对(E)-2-己烯醛、3-己醇 (3-Hexanol) 和(Z)-3-己烯乙酸酯和(E)-2-己烯醇表现出一定的偏好性。

表 2 水稻挥发物组分对害虫的影响
Table 2 Effects of rice volatiles on pests

挥发物 Volatiles	害虫种类 Species of insect pests				
	褐飞虱 <i>Nilaparvata lugens</i>	白背飞虱 <i>Sogatella furcifera</i>	灰飞虱 <i>Laodelphax striatellus</i>	稻纵卷叶螟 <i>Cnaphalocrocis medinalis</i>	条赤须盲蝽 <i>Trigonotylus caelestialium</i>
2-庚酮 2-Heptanone	趋避取食和产卵 (Liao <i>et al.</i> , 2022)	吸引 (Hu <i>et al.</i> , 2019)	—	—	—
2-庚醇 2-Heptanol	趋避取食和产卵 (Liao <i>et al.</i> , 2022)	—	—	—	—
(S)-芳樟醇 (S)-Linalool	趋避取食和产卵 (Xiao <i>et al.</i> , 2012)	—	—	吸引 (Xiao <i>et al.</i> , 2012)	—
水杨酸甲酯 Methyl salicylate	趋避 (周强等, 2003)	—	—	—	—
(Z)-3-己烯醛 (Z)-3-Hexenal	趋避取食和产卵 抑制卵的发育 (Tong <i>et al.</i> , 2012)	吸引产卵 促进若虫发育 (Hui <i>et al.</i> , 2015)	—	—	—
(E)-2-己烯醛 (E)-2-Hexenal	趋避 (周强等, 2003)	吸引产卵 促进若虫发育 (Hui <i>et al.</i> , 2015)	—	吸引 (Sun <i>et al.</i> , 2014)	—
(Z)-3-己烯-1-醇 (Z)-3-Hexen-1-ol	趋避取食和产卵 抑制卵发育 (Tong <i>et al.</i> , 2012)	吸引产卵 促进若虫发育 (Hui <i>et al.</i> , 2015)	—	吸引 (Sun <i>et al.</i> , 2014)	—
β -石竹烯 β -Caryophyllene	吸引取食与产卵 促进若虫发育 (Xiao <i>et al.</i> , 2012)	—	—	—	低浓度吸引, 高浓度趋避 (Fujii <i>et al.</i> , 2010)
(Z)-3-己烯乙酸酯 (Z)-3-Hexenyl acetate	—	—	—	吸引 (Sun <i>et al.</i> , 2014)	—
(Z)-法尼烯 (Z)-Farnesene	—	吸引 (Hu <i>et al.</i> , 2019)	吸引 (刘芳等, 2009)	—	—
(+)-柠檬烯 (+)-Limonene	—	吸引 (Hu <i>et al.</i> , 2019)	—	—	—
橙花叔醇 Nerolidol	—	—	吸引 (刘芳等, 2009)	—	—
雪松醇 Cedrol	—	—	吸引 (刘芳等, 2009)	—	—

3.2 水稻挥发物对害虫天敌的影响

在稻田生态系统中, 常见的寄生性天敌主要有稻虱缨小蜂 *Anagrus nilaparvatae*、二化螟盘绒茧蜂 *Cotesia chilonis* 及螟蛉绒茧蜂 *Apanteles ruficrus* 等, 捕食性天敌包括黑肩绿盲蝽 *Cyrtorhinus lividipennis*、拟环纹豹蛛 *Pardosa pseudoannulata*、拟水狼蛛 *Pirata subpiraticus* 等。害虫为害诱导的水稻挥发物对害虫天敌具有明显的引诱作用。如稻飞虱为害诱导的水稻挥发物对其卵期寄生蜂, 稻虱缨小蜂具有显著的引诱作用 (Xiang *et al.*, 2008; Liu *et al.*, 2021)。分析水稻挥发物中活性组分发现, 2-庚酮、(E)- β -石竹烯、(S)-芳樟醇、DMNT、水杨酸甲酯、(Z)-3-己烯醛、(E)-2-己烯醛和(Z)-3-己烯乙酸酯是对稻虱缨小蜂具有明显的引诱作用 (Cheng *et al.*, 2007b; Hu *et al.*, 2020; Li *et al.*, 2020; Liao *et al.*, 2022) (表 3); 并且几种组分的混合物也具有引诱作用, 如水杨酸甲酯与(Z)-3-己烯醛的混合物, (Z)-3-己烯醛、(Z)-3-己烯乙酸酯和芳樟醇的混合物, MeSA、(Z)-3-己烯醛、(Z)-3-己烯乙酸酯和芳樟醇的混合物 (汪鹏和娄永根, 2013)。除了稻虱缨小蜂外, 稻纵卷叶螟、东方粘虫 *Mythimna separata* 和草地贪夜蛾 *Spodoptera frugiperda* 为害后的水稻挥发物均能吸引相应的寄生性天敌, 如黄眶离缘姬蜂 *Trathala flavo-orbitalis*、螟蛉瘤姬蜂 *Itopectis naranyae*、中红侧沟茧蜂 *Microplitis mediator* 和 *Cotesia marginiventris* (Yuan *et al.*, 2008; Liu *et al.*, 2017; Shi *et al.*, 2019)。二化螟盘绒茧蜂和螟蛉绒茧蜂一类的鳞翅目幼虫专性寄生蜂, 在寄主定位过程中则更多是综合利用了植物挥发物、寄主昆虫本身及其排泄释放的混合化学信号 (陈华才等, 2002, 2003)。水稻挥发物组分中的芳樟醇、DMNT 和 TMTT 对二化螟盘绒茧蜂具有吸引作用, 水杨酸甲酯则对二化螟盘绒茧蜂表现出低浓度趋避, 高浓度吸引的作用 (Li *et al.*, 2021; Yao *et al.*, 2022)。水稻受两种蜡象 *Tibraca limbativentris* 和 *Glypheidemia spinosa* 为害后产生的萜类挥发物在组分和比例上都存在较大差异, 前者诱导水稻释放(E)- β -法尼烯、杜松-1,4-二烯 (Cadina-1,4-diene) 和牻牛

儿烯-D-4-醇 (Germacrene-D-4-ol), 后者诱导水稻产生更多的柠檬烯、 β -月桂烯和多种倍半萜烯, 这些混合挥发物可以吸引两种蜡象的寄生性天敌黑卵蜂 *Telenomus podisi* (Ulhoa *et al.*, 2020)。水稻挥发物与捕食性天敌的关系研究及其与寄生性天敌关系的研究广泛而深入。研究表明, (S)-芳樟醇一方面趋避褐飞虱, 另一方面能够强烈吸引多种捕食褐飞虱的蜘蛛, 2-庚酮和水杨酸甲酯也能吸引多种蜡类和蜘蛛 (Xiao *et al.*, 2012; Li *et al.*, 2020; Liu *et al.*, 2022)。

值得一提的是, 在水稻的这些挥发物中, 有些组分对天敌具有趋避作用 (表 3)。如 2-庚酮、2-壬酮 (2-Nonanone)、肉豆蔻酸异丙酯 (Isopropyl myristate)、2-十三烷酮 (2-Tridecanone)、(E)-乙酸-2-庚烯酯[(E)-Hept-2-enyl acetate]、 α -姜烯、(+)-柠檬烯和 α -蒎烯等对稻虱缨小蜂具有趋避作用, TMTT 则对稻虱缨小蜂表现出低浓度吸引, 高浓度趋避的作用 (Xiao *et al.*, 2012; 汪鹏和娄永根, 2013; 莫晓畅和娄永根, 2016; Hu *et al.*, 2020; Li *et al.*, 2021)。这可能与天敌寻找最适宜寄主等有关 (Lou *et al.*, 2005; Li *et al.*, 2020)。

3.3 水稻挥发物对微生物的影响

除了能调控植物-植食性昆虫-天敌三级营养层互作关系外, 植食性昆虫诱导的植物挥发物也能够影响昆虫共生菌与致病菌、植物病原菌、根际微生物等多种微生物。水稻中, 挥发物对微生物影响的研究目前主要集中在水稻挥发物对水稻病原微生物的影响。卢凯等 (2010) 对 7 种虫害诱导水稻挥发物研究发现, 绿叶挥发物 (E)-2-己烯醛、(Z)-3-己烯-1-醇和(E)-2-己烯-1-醇及萜类挥发物, 芳樟醇、柠檬烯、 β -石竹烯和橙花叔醇在离体条件下均对稻瘟病菌和水稻纹枯病菌的生长具有一定抑制作用。白背飞虱诱导的水稻 (E)-2-己烯醛能直接抑制白叶枯病菌的体外生长; 尽管芳樟醇对白叶枯病菌的生长没有直接抑制作用, 但水稻体内过量表达芳樟醇合成酶基因能够提高防御相关基因的表达, 进而增强植株对白叶枯病菌的抗性 (Gomi *et al.*, 2010; Taniguchi *et al.*, 2014)。也有研究发现虫害诱导挥发物有

表 3 水稻挥发物组分对害虫天敌的影响
Table 3 Effects of rice volatiles on natural enemies

挥发物 Volatiles	天敌种类 Species of natural enemies		
	稻虱缨小蜂 <i>Anagrus nilaparvatae</i>	二化螟盘绒茧蜂 <i>Cotesia chilonis</i>	黑卵蜂 <i>Telenomus podisi</i>
2-庚酮 2-Heptanone	吸引 (Hu <i>et al.</i> , 2020)	—	—
(S)-芳樟醇 (S)-Linalool	吸引 (Hu <i>et al.</i> , 2020)	吸引 (Yao <i>et al.</i> , 2022)	—
β -石竹烯 β -Caryophyllene	吸引 (Hu <i>et al.</i> , 2020)	—	—
DMNT 3E-4,8-dimethyl-1,3,7-nonatriene	吸引 (Hu <i>et al.</i> , 2020)	吸引 (Yao <i>et al.</i> , 2022)	—
TMTT (E,E)-4,8,12-trimethyl-1,3,7,11-tridecatetraene	低浓度吸引高浓度趋避 (Hu <i>et al.</i> , 2020)	吸引 (Li <i>et al.</i> , 2021)	—
(E)-2-己烯醛 (E)-2-Hexenal	吸引 (Hu <i>et al.</i> , 2020)	—	—
水杨酸甲酯 Methyl salicylate	吸引 (Hu <i>et al.</i> , 2020)	低浓度趋避 高浓度吸引 (Yao <i>et al.</i> , 2022)	—
(Z)-3-己烯醛 (Z)-3-Hexenal	吸引 (汪鹏和娄永根, 2013)	—	—
(Z)-3-己烯乙酸酯 (Z)-3-Hexenyl acetate	吸引 (汪鹏和娄永根, 2013)	—	吸引 (Ulhoa <i>et al.</i> , 2020)
2-壬酮 2-Nonanone	趋避 (Hu <i>et al.</i> , 2020)	—	—
肉豆蔻酸异丙酯 Isopropyl myristate	趋避 (Hu <i>et al.</i> , 2020)	—	—
2-十三烷酮 2-Tridecanone	趋避 (Hu <i>et al.</i> , 2020)	—	—
(E)-乙酸-2-庚烯酯 (E)-Hept-2-enyl acetate	趋避 (Hu <i>et al.</i> , 2020)	—	—
(+)-柠檬烯 (+)-Limonene	趋避 (Hu <i>et al.</i> , 2020)	—	吸引 (Ulhoa <i>et al.</i> , 2020)
α -姜烯 α -Zingiberene	趋避 (Li <i>et al.</i> , 2020)	—	—
α -蒎烯 α -Pinene	趋避 (Hu <i>et al.</i> , 2020)	—	—
2-庚醇 2-Heptanol	趋避 (Hu <i>et al.</i> , 2020)	—	—
β -法尼烯 β -Farnesene	—	—	吸引 (Ulhoa <i>et al.</i> , 2020)
β -月桂烯 β -Myrcene	—	—	吸引 (Ulhoa <i>et al.</i> , 2020)

利于昆虫病原真菌的生长,如水杨酸甲酯是促进蜡蚧轮枝菌的菌丝生长和产孢,增强该病原真菌对昆虫的致病毒力的关键物质(Lin *et al.*, 2017)。

3.4 水稻挥发物对邻近植物的影响

害虫为害诱导的植物挥发物也会影响其邻近的同种或异种植物,使得邻近植物产生“防御警报”、间接防御或防御抑制。植物“防御警报”是指在受到某些生物或者非生物因子刺激后,植物提前启动体内防御系统,从而使植物在受到后续相关生物胁迫时产生更快和更强的防御反应;间接防御则是邻近植物在接收挥发物信号后,改变自身挥发物的释放以吸引寄生或捕食性天敌应对可能发生的虫害胁迫(Mauch-Mani *et al.*, 2017; Takabayashi and Shiojiri, 2019)。植物挥发物除了有利于邻近植物防御启动外,有时也会抑制邻近植物的防御反应,加重植物的受损程度(Mérey *et al.*, 2011)。

绿叶挥发物、部分萜类挥发物以及吲哚已被证明能够对邻近植物产生影响。如(Z)-3-己烯醇、(Z)-3-己烯醛、(Z)-3-己烯乙酸酯等多种绿叶挥发物在玉米、小麦等禾本科作物中能够启动健康植株的防御反应,提高植物对病虫害的抗性(Engelberth *et al.*, 2004)。对萜类挥发物的研究表明, α -蒎烯、 β -蒎烯等单萜能够触发拟南芥 *Arabidopsis thaliana* 中水杨酸相关的先天免疫(Riedlmeier *et al.*, 2017); β -石竹烯能够通过调节茉莉酸信号途径影响植物抗性(Nagashima *et al.*, 2019; Frank *et al.*, 2021); β -罗勒烯(β -ocimene)诱导邻近北京白菜 *Brassica pekinensis* 体内水杨酸和茉莉酸相关基因的表达和芥子油苷的积累,从而影响桃蚜 *Myzus persicae* 的生长发育(Erb *et al.*, 2015; Kang *et al.*, 2018)。虫害诱导的吲哚不仅促进邻近玉米叶片释放芳樟醇、DMNT、(Z)-3-己烯乙酸酯等多种挥发物,而且显著提高虫害诱导后玉米植株体内茉莉酸、茉莉酸异亮氨酸和脱落酸的含量(Erb *et al.*, 2015)。

在水稻中,发现吲哚处理激活水稻 MAPK 级联途径和过氧化氢积累,进而在水稻受病原菌感染后,更快更强地提高病程相关蛋白

(Pathogenesis resistance protein, PR 蛋白)基因、茉莉酸和植物抗毒素生物合成基因以及抗氧化酶基因的转录水平,提高了水稻对稻瘟病菌的抗性(Shen *et al.*, 2018)。与此类似,吲哚预处理水稻植株,能够直接诱导水稻类受体蛋白激酶 OsLRR-RLKs 的表达,从而使水稻在受草地贪夜蛾幼虫为害时,迅速激活丝裂原激活蛋白激酶 OsMPK3,上调下游 WRKY 转录因子 OsWRKY70 和几个茉莉酸生物合成基因转录水平,导致茉莉酸含量更高积累,最终提高水稻对草地贪夜蛾的抗性(Ye *et al.*, 2019)。受二化螟为害后的水稻挥发物被邻近水稻植株感知后,提高了水稻对二化螟的直接抗性和间接抗性。一方面挥发物诱导了茉莉酸相关基因的表达,促进了茉莉酸和茉莉酸异亮氨酸的积累,并且经挥发物预处理的水稻在受到二化螟为害后,体内胰蛋白酶抑制剂(Trypsin protease inhibitors, TrypPIs)相关基因的表达更快,TrypPIs 的积累更多;另一方面,挥发物处理后的水稻对二化螟盘绒茧蜂的引诱作用显著提高(Yao *et al.*, 2022)。

4 水稻挥发物在害虫防控中的作用及其应用前景

如前所述,植物挥发物中的很多组分都发挥着信息化合物、防御化合物或有益化合物的作用(表 2, 表 3),这些作用都可以直接或间接地影响到植食性昆虫的种群动态。合理地开发利用这些信息化合物或防御化合物,就能达到防控害虫的目的。植物挥发物在害虫防控中主要应用在以下方面:1)利用一些挥发物组分对害虫的引诱作用,结合害虫性信息素和聚集信息素等,应用于害虫预测预报(Reddy and Guerrero, 2010; Onge *et al.*, 2018);2)利用一些挥发物组分对天敌的引诱作用,开发天敌引诱剂(Ayelo *et al.*, 2021b);3)利用一些挥发物组分对天敌和害虫的引诱作用或驱避作用,改良作物品种(Xiao *et al.*, 2012; Pickett and Khan, 2016);4)开发害虫驱避剂和引诱剂,然后利用推-拉策略,防控害虫(Pickett *et al.*, 2014; Brill *et al.*, 2019)。

目前,水稻挥发物在害虫防控中的应用还不多,但一些具有较好应用潜力的措施或技术正在被开发。例如,在田间应用(Z)-3-己烯醛、(Z)-3-己烯乙酸酯和芳樟醇组成的混合物或由水杨酸甲酯、(Z)-3-己烯醛、(Z)-3-己烯乙酸酯和芳樟醇组成的混合物,可以显著提高褐飞虱卵的被寄生率(汪鹏和娄永根,2013)。在田间种植芳樟醇合成酶基因沉默的突变水稻品系,褐飞虱种群密度远高于对照植株,褐飞虱卵的被寄生率和蜘蛛种群密度也显著降低,而在石竹烯合成酶沉默水稻品系上,田间害虫和天敌的种群密度都显著降低(Xiao *et al.*, 2012);因此,通过在水稻中过量表达芳樟醇合成酶基因或沉默石竹烯合成酶基因,可以达到控制稻飞虱的目的。在水稻中过表达萜类合成酶基因 *OsTPS46*,增加了柠檬烯、(E)- β -法尼烯、芳樟醇、(E)- β -石竹烯、水杨酸甲酯、 α -甜没药烯、(E)- α -香柑油烯和 α -葎草烯 8 种挥发物的释放,提高了水稻对禾谷缢管蚜 *Rhopalosiphum padi* 的抗性(Sun *et al.*, 2017)。Li 等(2020)研究表明水稻萜类合成酶基因 *OsCYP92C21* 调控水稻中两种同萜类挥发物 DMTT 和 TMTT 的生物合成;将该基因与豇豆中的萜类合成酶基因 *PITPS4* (可以将 FPP 和 GGPP 分别转换成合成 DMTT 和 TMTT 的前体化合物, (E)-橙花叔醇和香叶基芳樟醇[(E,E)-geranylinalool])一同转入水稻,可以显著提高水稻挥发物中 DMNT 和 TMTT 的释放量,并对二化螟盘绒茧蜂有显著的引诱作用。这些工作体现了利用水稻挥发物防控害虫的很好潜力。

5 结论与展望

20 多年来,有关水稻挥发物主要组分、合成途径、调控机理及其生态学功能等都取得了很大研究进展。从这些研究结果中可以看出,水稻挥发物是一种复杂的混合物,涉及的化学组分多,其合成途径及影响其合成的因子也很多。此外,水稻挥发物的生态学功能也很复杂,不仅能影响水稻、害虫及其天敌、微生物等的生理、行为和(或)适合度,而且影响每一种生物的组分不同、同一活性组分对不同生物的生态学效应也

可能完全不同。这些不仅反映了植物挥发物作为生态系统中各生物间信息传递的载体在影响生物进化及生物群落组成中的重要作用,而且也说明了要利用植物挥发物防控害虫还需要开展深入与系统的研究。首先,要进一步鉴定水稻挥发物组分。尽管目前已鉴定了相当数量的水稻挥发物,但综合多年来的研究结果发现,还有一些受害虫为害诱导的水稻挥发物组分是未知的。同时,挥发物组分的鉴定还取决于捕集挥发物的材料以及分离鉴定挥发物的仪器的灵敏度。一些现有仪器不能检测到的挥发物组分可能具有重要的生物学功能(Turlings and Erb, 2018)。因此,进一步分离鉴定水稻挥发物组分将是今后的一项重要工作。第二,要深入剖析水稻挥发物的合成途径及其调控机理。尽管目前对挥发物主要组分,如萜类化合物、绿叶挥发物等的总体生物合成途径有了一个比较清楚的认识,但对某一种特定挥发物的生物合成过程尚不清楚。此外,对于挥发物生物合成的调控机理,目前更是缺少了解。这对于希望利用遗传改良改变植物挥发物组成,进而达到控制害虫的目的还是远远不够的。第三,在室内与室外深入全面揭示水稻主要挥发物组分的生态学功能。如上所述,同一挥发物组分对生态系统中不同生物可能有完全不同的生态学效应。因此,必须对水稻主要挥发物组分的生态学功能开展全面系统的研究,以便从中选择比较合理的挥发物组分用于害虫防控,避免产生不良的生态学后果。第四,揭示昆虫和水稻识别挥发物的机理,包括昆虫的嗅觉机理以及植物识别挥发物的受体等等。这方面的深入研究,有利于进一步发掘与拓展害虫防控新技术。随着上述工作的深入开展,相信能够在阐明水稻挥发物相关功能、揭示挥发物在驱动生物间协同进化的同时,开发害虫绿色防控技术,实现水稻害虫的可持续治理。

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