

茶树害虫挥发性化学信息物质的研究进展*

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摘 要 植食性昆虫利用种内化学信息物质进行求偶和交配, 从而维持其田间的种群数量; 植物在识别植食性昆虫的为害后, 可产生直接和间接防御反应来抵御植食性昆虫的为害。相应地, 植食性昆虫亦可利用植物的虫害诱导化学信息物质选择嗜好寄主, 从而提高其生长适应度。茶树是多年生常绿木本经济作物, 常年病虫害发生严重。据不完全统计, 茶树病虫害每年给茶叶带来的经济损失就高达 20%-50%, 严重影响茶产业的绿色、健康和可持续发展。近 20 年, 科研工作者在调控茶树害虫行为和种群动态的主要化学信息物质、作用方式及调控机理等方面展开了较为系统的研究, 取得了一些研究成果。本文着重从茶树害虫性信息素的种类及其特异性、寄主和非寄主植物挥发物对害虫种群的调控作用等方面对目前的研究进展进行了综述, 并对利用挥发性化学信息物质构建茶树害虫的生态调控技术进行了展望, 以期茶树害虫化学信息物质的研究提供参考。

关键词 茶树; 害虫; 昆虫性信息素; 虫害诱导茶树挥发物

Progress in research on volatile semio-chemicals of insect tea pests

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Abstract Herbivorous insects use intraspecific semio-chemicals for courtship and mating whereas plants can produce direct and indirect chemical defenses after detecting the damage caused by insect pests. Herbivorous insects can also use these defensive chemicals produced by plants to identify hosts. Tea is a perennial, evergreen, woody, cash crop that is adversely affected by disease and insect pests throughout the year. The economic losses to tea production caused by diseases and pest insects are as high as 20%-50% per annum, which seriously hinders the development of a sustainable and environmentally-friendly tea industry. In the past 20 years, researchers have carried out systematic research on the main semio-chemicals, their modes of action and the mechanisms that regulate the behavior and population dynamics of tea pest insects. This paper mainly reviews current progress in the identification and utilization of tea pest insects' sex pheromones, the role of host and non-host plants in the regulation of pest insect populations, and discusses prospects for the ecological regulation of insect tea pests using pheromones.

Key words tea; pest insects; insect sex pheromone; herbivore-induced tea volatiles

在自然界, 植食性昆虫利用挥发性化学信息物质进行种内与种间的交通讯联系。已知的这

些挥发性化学信息物质主要包括植食性昆虫信息素和植物挥发物。其中, 由植食性昆虫合成与

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分泌的信息素不仅在昆虫种内的取食、交配、报警、聚集和防御等方面发挥着重要作用,也在昆虫种间以利己素、利它素和互利素的形式调节昆虫与其他节肢动物之间的关系,而且还可被植物所感知,从而引起植物的防御警备反应(杜家纬, 2001; Helms *et al.*, 2017)。大量研究结果表明,植物在遭受植食性昆虫攻击后所释放的挥发物(Herbivore-induced plant volatiles, HIPVs)无论是种类还是数量都会较健康植株发生显著的改变。HIPVs已证明可被植食性昆虫、天敌、临近同种植物以及周围其他有机体所利用,进而直接或间接地调节植物与昆虫群落之间的互作关系(Schuman and Baldwin, 2015; Jing *et al.*, 2021)。非寄主植物挥发物也会为植食性昆虫提供嗅觉和味觉相关的化学信息,同样在植食性昆虫的寄主定位过程中发挥着重要作用(贾志飞等, 2022; 吕金言和孟昭军, 2022)。因此,在深入剖析植食性昆虫种内与种间化学通讯联系、感受机制及其调控机理的基础上,利用化学信息物质的作用特点建立靶标害虫的种群监测和调控策略,则有望实现害虫的绿色防控。

茶树是多年生常绿木本经济作物,多种植在暖温带、亚热带和热带地区,常年病虫害发生严重。据不完全统计,茶树病虫害每年给茶叶带来的经济损失就高达 20%-50%,严重影响茶产业的绿色、健康和可持续发展(尚怀国等, 2022)。近 20 年,科研工作者深入研究了调控茶树害虫行为和种群动态的主要化学信息物质、作用方式及调控机理,并尝试使用上述化学信息物质开发害虫种群调控技术,以期扭转茶树虫害治理主要依赖化学农药的格局。基于此,本文着重从茶树害虫性信息素的鉴定和利用、寄主和非寄主植物挥发物对害虫种群密度的调控作用等方面对目前的研究进展进行较为详尽的综述,希望可为茶树害虫化学信息物质的研究提供参考。

1 昆虫源化学信息物质

昆虫性信息素一般由雌成虫的特殊腺体合成并分泌于体外,用来引诱雄成虫前来交尾从而达到种群繁衍的目的,也有少数昆虫的性信息素

由雄成虫分泌引诱雌成虫。昆虫性信息素具有种内特异性,一般来说只调控种内异性成虫个体的求偶和交配行为,从而起到生殖隔离的作用。与传统的化学药剂防治相比,利用性信息素结合诱捕器田间诱杀成虫具有特异性、高效性、不引起害虫抗性、对天敌及有益生物安全和不污染环境等优点,已越来越多地被用于害虫的绿色防控中(Reynolds *et al.*, 2016; Rizvi *et al.*, 2021)。

茶树是一种具有保健功效的饮料作物,质量安全问题一直备受关注。截止目前,已有 18 种茶树重要害虫的性信息素得到了分离和鉴定,包括 14 种鳞翅目害虫、3 种半翅目害虫和 1 种鞘翅目害虫。其中,茶小卷叶蛾 *Adoxophyes honmai* Yasuda、褐带长卷叶蛾 *Hornona coffearia* Neitner、茶细蛾 *Caloptilia theivora* Walsingham、茶毛虫 *Euproctis pseudoconspersa* Strand、茶尺蠖 *Ectropis obliqua* Prout、艾尺蠖 *Ascotis selenaria cretacea* Butle 以及茶蚕 *Andraca bipunctata* Walker 等 12 种害虫性信息素的研究已有较为详尽的描述(孙晓玲和陈宗懋, 2009; 罗宗秀等, 2016)。本文仅对近年来茶树害虫性信息素的研究进展,以及各信息素成分之间的有效配比加以补充和完善。具体害虫对应的性信息素成分、功能及有效配比等相关信息详见表 1。

如前所述,昆虫性信息素通过调节种内异性成虫的求偶和交配行为从而发挥其生殖隔离的作用,并且这种生殖隔离现象也普遍存在于同种昆虫的不同地理种群之间(刘万才等, 2022)。研究发现茶尺蠖和灰茶尺蠖之间存在着不完整的隔离交配系统,表现为灰茶尺蠖雄成虫的交配干扰能力显著强于茶尺蠖雄成虫,杂交后雌成虫的产卵量较种内自交雌成虫的产卵量显著下降,卵的孵化率显著降低,杂交子一代(F_1)生长发育异常且存活率低(席羽等, 2014; Zhang *et al.*, 2016; Wang *et al.*, 2019)。进一步的研究发现,茶尺蠖性信息素成分顺-3,9-环氧-6,7-壬二烯介导了茶尺蠖和灰茶尺蠖之间的交配前生殖隔离(Luo *et al.*, 2017),而顺-3,6,9-十八碳三烯和顺-3,9-环氧-6,7-十八碳二烯是茶尺蠖两个近缘种共有的性信息素成分(Ma *et al.*, 2016; Luo *et al.*, 2017)。由此推测两个近缘种在田间可能存在生

表 1 18 种茶树害虫性信息素的组成、有效配比和生态功能
Table 1 Composition, effective ratio and ecological function of sex pheromones of 18 tea pest insects

目 Order	科 Family	种 Species	化学成分 Component	比例 Ratio	生态功能 Ecological function	参考文献 Reference
鳞翅目 Lepidoptera	卷蛾科 Tortricidae	茶小卷叶蛾 <i>Adoxophyes honmai</i> Yasuda	顺-9-十四碳烯乙酸酯	未见明确报道 Not reported	引诱交尾 Induce copulation	Ishiwatari <i>et al.</i> , 1977; Tamaki <i>et al.</i> , 1971,1984
			<i>cis</i> -9-tetradecen-1-ol acetate			
			顺-11-十四碳烯乙酸酯			
			<i>cis</i> -11-tetradecen-1-ol acetate			
			反-11-十四碳烯乙酸酯			
			<i>trans</i> -11-tetradecen-1-ylacetate			
			十二烷基乙酸甲酯			
			10-methyl dodecyl acetate			
			顺-9, 反-12-十四烷二烯乙酸酯			
			<i>cis</i> -9, <i>trans</i> -12-tetradecadienyl acetate			
		茶卷叶蛾（日本） <i>Homona magnanima</i> Diakonoff	顺-11-十四碳烯乙酸酯	30 : 3 : 1	引诱交尾 Induce copulation	Noguchi <i>et al.</i> , 1979
			<i>cis</i> -11-tetradecenyl acetate			
			顺-9-十二碳烯醇乙酸酯			
			<i>cis</i> -9-dodecenly acetate			
			11-十二碳烯乙酸酯			
			11-dodecenly acetate			
			反-9-十二碳烯乙酸酯			
			<i>trans</i> -9-dodecenyl acetate			
			1-十二烷醇			
			1-dodecanol			
		褐带长卷叶蛾（东南亚） <i>Homona coffearia</i> Neitner	乙酸十二烯基酯	未见明确报道 Not reported	引诱交尾 Induce copulation	Kochansky <i>et al.</i> , 1978
			1-dodecyl acetate			
			反-11-十六碳烯醛			
			<i>trans</i> -11-hexadecenal			
			顺-11-十六碳烯醛			
			<i>cis</i> -11-hexadecenal			
			10, 14-二甲基十五碳醇异丁酸酯			
			10, 14-dimethylpetadecyl isobutyrate			
			14-甲基十五碳醇异丁酸酯			
			14-methylpentadecyl isobutyrate			
	细蛾科 Gracillariidae	茶细蛾 <i>Caloptilia theivora</i> Walsingham	反-11-十六碳烯醛	未见明确报道 Not reported	引诱交尾 Induce copulation	Ando <i>et al.</i> , 1985
			<i>trans</i> -11-hexadecenal			
			顺-11-十六碳烯醛			
			<i>cis</i> -11-hexadecenal			
			10, 14-二甲基十五碳醇异丁酸酯			
			10, 14-dimethylpetadecyl isobutyrate			
			14-甲基十五碳醇异丁酸酯			
			14-methylpentadecyl isobutyrate			
			10, 14-二甲基十五碳醇正丁酸酯			
			10, 14-dimethylpentadecyl n-butyrate			
	毒蛾科 Lymantriidae	茶毛虫 <i>Euproctis pseudoconspersa</i> Strand	10, 14-二甲基十五碳醇异丁酸酯	50 : 3 : 3	引诱交尾 Induce copulation	Wakamura <i>et al.</i> , 1994
			10, 14-dimethylpetadecyl isobutyrate			
			14-甲基十五碳醇异丁酸酯			
			14-methylpentadecyl isobutyrate			
			10, 14-二甲基十五碳醇正丁酸酯			
			10, 14-dimethylpentadecyl n-butyrate			

续表 1 (Table 1 continued)

目 Order	科 Family	种 Species	化学成分 Component	比例 Ratio	生态功能 Ecological function	参考文献 Reference
鳞翅目 Lepidoptera	毒蛾科 Lymantriidae	黄尾毒蛾 <i>Euproctis similis</i> Fuessly	顺-7-十八碳醇-2-甲基丁酸酯	未见明确报道 Not reported	引诱交尾 Induce copulation	Yasuda <i>et al.</i> , 1994
			<i>cis</i> -7-octadecenyl-2-methylbutyrate			
			反-7-十八碳醇-2-甲基丁酸酯			
			<i>trans</i> -7-octadecenyl-2-methylbutyrate			
			顺-7-十八碳醇异戊酸酯			
			<i>cis</i> -7-octadecenyl isovalerate			
			顺-9-十八碳醇-2-甲基丁酸酯			
			<i>cis</i> -9-octadecenyl-2-methylbutyrate			
			顺-9-十八碳醇异戊酸酯			
			<i>cis</i> -9-octadecenyl isovalerate			
			顺-7-十八碳醇异丁酸酯			
			<i>cis</i> -7-octadecenyl isobutyrate			
			顺-7-十八碳醇丁酸酯			
			<i>cis</i> -7-octadecenyl butyrate			
			10, 14-二甲基十五碳异丁酸酯			
			10, 14-dimethylpentadecyl isobutyrate			
		折带黄毒蛾 <i>Artaxa flava</i> (Bremer)	14-甲基十五碳醇异丁酸酯	10 : 3	引诱交尾 Induce copulation	Wakamura <i>et al.</i> , 2007
			14-methylpentadecyl isobutyrate			
			顺-16-甲基-9-十七烷基异丁酸酯			
			<i>cis</i> -16-methyl-9-heptadecenyl isobutyrate			
		台湾黄毒蛾 <i>Euproctis taiwana</i> Shiraki	16-甲基十七烷基异丁酸酯	3 : 1	引诱交尾 Induce copulation	Yasuda <i>et al.</i> , 1995
			16-methylheptadecyl isobutyrate			
			顺-3,9-环氧-6,7-十八碳二烯			
			6,7-epoxy- <i>cis</i> -3,9-octadecadiene			
		茶尺蠖 <i>Ectropis obliqua</i> Prout	顺-3,6,9-十八碳三烯	4 : 2 : 4	引诱交尾 Induce copulation	Yang <i>et al.</i> , 2016
			<i>cis</i> -3,6,9-octadecatriene			
			顺-3,9-环氧-6,7-壬二烯			
			6,7-epoxy- <i>cis</i> -3,9-nonadecadiene			
	尺蛾科 Geometridae	灰茶尺蠖 <i>Ectropis grisescens</i> Warren	顺-3,9-环氧-6,7-十八碳二烯	4 : 6	引诱交尾 Induce copulation	Ma <i>et al.</i> , 2016
			6,7-epoxy- <i>cis</i> -3,9-octadecadiene			
			顺-3,6,9-十八碳三烯			
			<i>cis</i> -3,6,9-octadecatriene			

续表 1 (Table 1 continued)

目 Order	科 Family	种 Species	化学成分 Component	比例 Ratio	生态功能 Ecological function	参考文献 Reference
鳞翅目 Lepidoptera	尺蛾科 Geometridae	艾尺蠖 <i>Ascotis selenaria cretacea</i>	顺-6,9-环氧-3,4-十九碳二烯 3,4-epoxy- <i>cis</i> -6,9-nonadecadiene 顺-3,6,9-十九碳三烯 <i>cis</i> -3,6,9-nonadecatriene	未见明确报道 Not reported	引诱交尾 Induce copulation	Ando <i>et al.</i> , 1997; Ohtani <i>et al.</i> , 2001
		茶蚕 <i>Andrcwa bipunctata</i> Walker	反-11,反-14-十八碳醛 <i>trans</i> -11,14-octadecadienal 十八碳醛 n-octadecanal 反-11-十八碳烯醛 <i>trans</i> -11-octadecenal 反-14-十八碳烯醛 <i>trans</i> -14-octadecenal	未见明确报道 Not reported	引诱交尾 Induce copulation	Ho <i>et al.</i> , 1996
	刺蛾科 Limacodidae	丽绿刺蛾 <i>Parasa lepida</i> Cramer	顺-7,9-癸二烯-1-醇 <i>cis</i> -7,9-decadien-1-ol	未见明确报道 Not reported	引诱交尾 Induce copulation	Wakamura <i>et al.</i> , 2007
		茶蚜 <i>Toxoptera aurantii</i> Boyer de Fonscolombe	荆芥内酯 (4 <i>aS</i> ,7 <i>S</i> ,7 <i>aR</i>)-nepetalactone 荆芥醇 (1 <i>R</i> ,4 <i>aS</i> ,7 <i>S</i> ,7 <i>aR</i>)-nepetalactoll	4.3-4.9 : 1	引诱交尾 Induce copulation	Han <i>et al.</i> , 2014
半翅目 Hemiptera	蚜科 Aphididae	绿盲蝽 <i>Aploygus lucorum</i> Meyer-Dür	4-氧代-反-2-己烯醛 4-oxo- <i>trans</i> -2-hexenal 丁酸己酯 hexyl butyrate 丁酸-反-2-己烯酯 <i>trans</i> -2-hexenyl butyrate	雌性 Female: 5 : 5 : 83 雄性 Male: 5 : 87 : 8	引诱交尾 Induce copulation	张涛, 2011
	盾蚧科 Diaspididae	桑盾蚧 <i>Pseudaulacaspis pentagon</i> Targioni-Tozzetti	顺 3, 9-二甲基-6-异丙烯-3, 9- 癸二烯丙酸酯 <i>cis</i> -3, 9-dimethyl-6-isopropenyl-3, 9-decadien-1-ol propionate	未见明确报道 Not reported	引诱交尾 Induce copulation	Heath <i>et al.</i> , 1979
	象甲科 Curculionidae	茶丽纹象甲 <i>Mylocherinus aurolineatus</i> Voss	正二十五烷 pentacosane	未见明确报道 Not reported	性别识别 Induce copulation	Sun <i>et al.</i> , 2017

殖错配的现象。与性信息素组分数量相对应,基因组水平上的研究发现了茶尺蠖拥有更为复杂的生殖和识别系统,从而使茶尺蠖在生殖识别上更具特异性,最终导致两个物种的非对称生殖干扰现象(程梓淇等,2022)。此外,早前的研究发现顺,顺-6,9-环氧 3,4-十九碳烷二烯的手性异构体是引起艾尺蠖以色列种和日本亚种之间生殖隔离的重要因素(Cossé *et al.*, 1992; Ando *et al.*, 1997; Witjaksono *et al.*, 1999)。

昆虫性信息素的生物活性和田间诱集效果不仅受到性信息素多组分配比的影响,而且也受到化合物化学结构的影响(罗宗秀等,2022)。昆虫性信息素通常由 1-2 个主要组分和若干个微量组分构成,主要组分和微量组分之间的协同作用是影响性信息素生物活性的关键因素之一。研究发现,添加茶毛虫性信息素次要成分 14-甲基十五碳醇异丁酸酯可以提高主要组分 10, 14-二甲基十五碳醇异丁酸酯的引诱效果。顺-9-十四碳烯-1-醇乙酸酯和顺-11-十四碳烯-1-醇乙酸酯是茶小卷叶蛾性信息素的主要组分, 10-甲基十二烷基乙酸酯和反-11-十四碳烯-1-醇乙酸酯是其微量组分,四者以 63 : 31 : 2 : 4 混合的田间诱集效果显著高于仅含有两种主要组分的诱芯(Tamaki *et al.*, 1971, 1983, 1984)。同样地,化合物化学结构影响性信息素活性的现象在茶树害虫性信息素中广泛存在。研究发现,茶小卷叶蛾、茶毛虫、茶细蛾、茶尺蠖和艾尺蠖等害虫的主要性信息素成分均有手性结构。环氧化合物顺-6,9-环氧-3,4-十九碳烷二烯的 3R,4S 构型对以色列种艾尺蠖雄蛾的诱集效果优于 3S,4R 手性异构体(Ando *et al.*, 1997); 11-十六碳烯醛是茶细蛾性信息素的重要活性成分之一,其反式异构体无引诱活性,当反式与顺式异构体按照一定比例混合则对雄蛾具有较好的引诱活性(Ando *et al.*, 1985); 9-十四碳烯-1-醇乙酸酯是茶小卷叶蛾性信息素的主要成分,该化合物顺式异构体 Z9-TDA 对茶小卷叶蛾雄成虫具有较强的引诱活性,而反式异构体却具有驱避作用。因此,正确和完整地鉴定害虫性信息素的成分和结构是有效利用的前提。

2 植物源挥发性化学信息物质

植食性昆虫对来自寄主和非寄主植物的刺激会产生视觉、机械、味觉及嗅觉等一系列相关反应(Sharma *et al.*, 2020)。其中,植物挥发物提供的嗅觉信号在大多数植食性昆虫寄主定位过程中发挥着至关重要的作用(Xu and Turlings, 2017)。也有研究结果表明,植物间的合理间作或套作亦可通过改变植物挥发物而提高植物的抗虫性(Mutyambai *et al.*, 2019, Barnes *et al.*, 2020)。例如,当玉米 *Zea mays* Linn. 与绿叶山蚂蝗 *Desmodium intortum* (Mill.) Urb.间作时,二者通过根系的化学通讯交流显著提高了玉米植株挥发物的释放种类和释放量,从而有效地保护玉米植株免受鳞翅目害虫的为害(Yeboah *et al.*, 2021)。传统常规茶园的单一种植模式导致茶园生态系统抗性降低,近年来科研人员尝试通过提高茶园生态系统中的生物多样性来提高其自然控害能力,目前已经取得了一些研究进展。

2.1 虫害诱导挥发物

寄主植物挥发物为植食性昆虫的寄主定位提供化学信息(Bruce *et al.*, 2005)。通常情况下,健康植物仅释放少量的挥发物,只有在遭受到生物或非生物胁迫后,植物挥发物的释放种类和数量才会显著增加,从而为周围的生物有机体提供丰富的化学信息集合(Lin *et al.*, 2021)。大量的研究表明,HIPVs 的组成特征不仅具有植物种类、品种、生育期和部位的特异性,而且还具有植食性昆虫种类、虫龄、为害程度/方式和其他一些环境因子的特异性(Turlings and Erb, 2018; Doudareva, 2019)。HIPVs 可被植食性昆虫、天敌、临近同种植物以及周围其他有机体所利用,从而直接或间接地规范多个有机体间的相互作用关系(Murali-Baskaran *et al.*, 2022)。

茶尺蠖、茶丽纹象甲、假眼小绿叶蝉 *Empoasca onukii* Matsuda、神泽氏叶螨 *Tetranychus kanzawai* Kishida 和咖啡小爪螨 *Oligonychus coffeae* Nietner 等害虫为害诱导茶树释放挥发物的种类、时空动态、生理和生态功能等方面已有较为详尽

的报道 (Maeda *et al.*, 2006; Ishiwari *et al.*, 2007; 蔡晓明, 2009; Sun *et al.*, 2010, 2014; Cai *et al.*, 2013; Rahman and Babu, 2021)。这些 HIPVs 既有组成型的, 也有诱导型的, 还有新生成的。通过比较分析发现, 不同害虫为害诱导茶树释放的挥发物种类既有共有的成分, 也有特有的成分, 这些虫害诱导挥发物对不同茶树害虫行为的规范及其调控模式已有较多报道 (张瑾等, 2022)。例如, 已有研究发现茶尺蠖幼虫诱导茶树释放的 HIPVs 具有如下生态功能: 1) 对茶尺蠖幼虫的寄生性天敌-单白绵绒茧蜂 *Parapanteles hyposidrae* Wilkinson 具有显著的引诱作用; 通过田间喷施茉莉酸甲酯诱导茶树释放与茶尺蠖幼虫为害相似的挥发物组成可提高田间茶尺蠖的被寄生率 (桂连友等, 2004; 王国昌, 2010); 2) 可为茶尺蠖交配和产卵场所的定位提供有效化学信息; 其中, 顺-3-己烯基乙酸酯、顺-3-己烯丁酸酯和顺-3-己烯醛为雌蛾产卵场所的定位提供化学信息, 顺-3-己烯基乙酸酯、苯甲醇、顺-3-己烯基丁酸酯和顺-3-己烯醛 4 种物质联合为交配场所的选择提供信息 (Sun *et al.*, 2014, 2016); 3) 可作为化学信号物质被周围健康茶树所感知, 从而激活/诱导临近茶树防御警备/反应; 在这些化合物中, 顺-3-己烯醇、芳樟醇、 α -法尼烯和萜烯同系物 DMNT 可通过激活茉莉酸信号途径、乙烯信号途径以及钙离子信号通路提高茶树的直接和间接防御反应 (Xin *et al.*, 2016, 2019; Jing *et al.*, 2018, 2021), 而吲哚和萜烯同系物 DMNT 则依赖茉莉酸信号途径激活茶树的防御警备反应 (Jing *et al.*, 2020; Ye *et al.*, 2020)。此外, 假眼小绿叶蝉、神泽氏叶螨、咖啡小爪螨和茶蚜 *Toxoptera aurantii* (Boyer de Fonscolombe) 等害虫为害诱导茶树释放的 HIPVs 对它们的捕食性和寄生性天敌具有显著的引诱能力 (赵冬香, 2001; 韩宝瑜和周成松, 2004; Maeda *et al.*, 2006; Ishiwari *et al.*, 2007; 潘铖等, 2016; Rahman and Babu, 2021), 实现了茶树的间接防御功能。利用害虫的行为特点, 科研工作者基于 HIPVs 已经开发出了一系列茶树害虫的化学生态防控技术, 如茶丽纹象甲引诱剂、茶尺蠖雄成虫引诱剂、假眼小绿叶蝉

Empoasca onukii Matsuda 成虫引诱和茶树诱导抗虫剂等 (孙晓玲和陈宗懋, 2013; 孙晓玲等, 2017; 辛肇军等, 2018; 韩宝瑜等, 2021)。

2.2 非寄主植物挥发物

植食性昆虫避开选择非寄主植物的原因可能是由于非寄主植物缺乏寄主植物的化学信息特征谱, 也可能是由于非寄主中含有某些驱避的化学成分。非寄主植物体内的有毒次生化合物也可引起植食性昆虫离开、拒绝取食, 甚至被毒杀。传统茶园种植模式由丛栽到单一矮化密植再到条栽的转变, 导致茶园生境日趋简单。因此, 合理间作或套作非寄主植物可在一定程度上干扰茶园害虫寄主定位, 也可为天敌昆虫提供庇护所, 从而整体提升茶园生态系统的控害水平。白三叶草 *Trifolium repens* Linn、圆叶决明 *Chamaecrista rotundifolia* (Pers.) Greene 等非寄主植物与茶树间作对茶树害虫和天敌种群数量和动态的影响已有大量报道, 详见表 2。

至今, 也有一些研究对非寄主植物释放的功能性挥发物进行了分析和鉴定。例如, Zhang 等 (2014a) 通过对一系列芳香植物的筛选发现罗勒草 *Ocimum basilicum* Linn、迷迭香 *Rosmarinus officinalis* Linn 释放的挥发物可掩盖茶树提供的化学信息, 对茶尺蠖的寄主定位具有显著的干扰效应。并且, 发现了薰衣草 *Lavandula pinnata* Lundmark、迷迭香和柠檬桉 *Eucalyptus citriodora* Hook.f. 对假眼小绿叶蝉亦具有明显的驱避作用 (张正群, 2013; Zhang *et al.*, 2014a; Cai *et al.*, 2019)。研究发现, 当薰衣草在与茶树间作时, 所释放 α -蒎烯和 1,8-桉烯释放的季节动态与茶园中的叶蝉种群动态具有一定的伴随性, 由此推测在茶园中合理间作薰衣草可以持续且有效地控制叶蝉的寄主选择行为 (Zhang *et al.*, 2014b)。Cai 等 (2019) 从 8 种芳香植物挥发物中挖掘出二甲基二硫醚和 1,8-桉树脑对假眼小绿叶蝉具有显著的驱避作用, 二者以一定比例混合可以作为假眼小绿叶蝉的驱避剂在田间使用。然而, 非寄主植物与茶树间作提高茶园生态系统抗虫能力的机理研究尚不够系统和深入。今后, 可从非寄主植物挥发物对茶树害虫和天敌昆虫寄主选

表 2 非寄主植物与茶树间作对茶树害虫的影响
Table 2 Effects of intercropping of non-host plants and tea plants on tea pest insects

序号 No.	非寄主植物 Non-host plant	靶标害虫 Target pest insect	作用 Effect	功能挥发物 Functional volatile	文献 Reference
1	白三叶草 <i>Trifolium repens</i> Linn.	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda 茶蚜 <i>Toxoptera aurantii</i> (Boyer de Fonscolombe)	为天敌提供蜜源和庇护所, 降低叶蝉种群密度 Nectar source and shelter of natural enemy, reduce the population density of leafhopper	反-3-己烯醇 <i>trans</i> -3-hexenol 丁酮 2-butanone 2-丙酮 2-propanone	宋同清 <i>et al.</i> , 2006, Massei <i>et al.</i> , 2007
2	铺地木蓝 <i>Indigofera hendecaphylla</i> Jacq	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	李慧玲 <i>et al.</i> , 2016a, 2016b
3	猪屎豆 <i>Crotalaria pallida</i> Aiton	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	李慧玲 <i>et al.</i> , 2016a, 2016b
4	丁香罗勒 <i>Ocimum gratissimum</i> L. var. suave (Willd.) Hook.f.	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda 绿盲蝽 <i>Aplyogus lucorum</i> Meyer-Dür	为天敌提供蜜源、引诱绿盲蝽, 趋避叶蝉 Nectar source of natural enemy, lure <i>Aplyogus lucorum</i> Meyer-Dü and avoid <i>Empoasca onukii</i> Matsuda	桉叶油醇 Eucalyptol 十二烷 Dodecane 柠檬烯 Limonene 1-辛烯-3-醇 1-octen-3-ol 罗勒烯 Ocimene 松油醇 Terpineol	陈泽军, 2021
5	薰衣草 <i>Lavandula pinnata</i> Lundmark.	茶尺蠖 <i>Ectropis obliqua</i> Prout 假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源、驱避叶蝉, 干扰寄主定位 Nectar source of natural, repelling and interfering	α -蒎烯 α -pinene 1,8-桉叶素 1,8-cineole	潘斌, 2015; 张正群, 2013; Zhang <i>et al.</i> , 2014b
6	迷迭香 <i>Rosmarinus officinalis</i> Linn	茶尺蠖 <i>Ectropis obliqua</i> Prout 假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	驱避茶尺蠖、叶蝉, 干扰寄主定位 Repelling and interfering	γ -松节油 γ -terpinene 芳樟醇 Linalool (<i>S</i>)-顺式马鞭草烯醇 (<i>S</i>)- <i>cis</i> -verbenol 樟脑 Camphor 马鞭草烯酮 Verbenone	张正群, 2013; Zhang <i>et al.</i> , 2013
7	柠檬桉 <i>Eucalyptus citriodora</i> Hook.f.	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	驱避叶蝉, 干扰寄主定位 Repelling and interfering	未见明确报道 Not reported	张正群, 2013

续表 2 (Table 2 continued)

序号 No.	非寄主植物 Non-host plant	靶标害虫 Target pest insect	作用 Effect	功能挥发物 Functional volatile	文献 Reference
8	芸香 <i>Ruta graveolens</i> Linn	茶尺蠖 <i>Ectropis obliqua</i> Prout	驱避叶蝉, 干扰寄主定位 Repelling and interfering	未见明确报道 Not reported	张正群, 2013
9	罗顿豆 <i>Lotononis bainesii</i> Baker	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	李慧玲 <i>et al.</i> , 2016a, 2016b
10	圆叶决明 <i>Chamaecrista rotundifolia</i>	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	李慧玲 <i>et al.</i> , 2016a 胡桂萍 <i>et al.</i> , 2021;
11	平托花生 <i>Arachis pintoi</i> Krapov. & W.C.Greg.	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	李慧玲 <i>et al.</i> , 2016a
12	樱花 <i>Cerasus</i> sp.	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	提高天敌功能团群落多样性 Improve the diversity of natural enemy functional groups	未见明确报道 Not reported	胡桂萍 <i>et al.</i> , 2021
13	百喜草 <i>Paspalum notatum</i> Flugge	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	Chen <i>et al.</i> , 2019
14	藿香蓟 <i>Ageratum conyzoides</i> Linn	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	刘双弟, 2012
15	决明子 <i>Cassia tora</i> Linn	假眼小绿叶蝉 <i>Empoasca onukii</i> Matsuda	为天敌提供蜜源和庇护所 Nectar source and shelter of natural enemy	未见明确报道 Not reported	刘双弟, 2012
16	罗勒草 <i>Ocimum basilicum</i>	茶尺蠖 <i>Ectropis obliqua</i> Prout	驱避茶尺蠖, 干扰寄主定位 Repelling and interfering	未见明确报道 Not reported	李慧玲 <i>et al.</i> , 2016a; 李慧玲 <i>et al.</i> , 2016b

择行为的调控作用,以及非寄主植物与茶树之间通过根系或地上部分进行化学信息交流的模式与机制等方面展开深入研究。

3 总结与展望

植食性昆虫种内化学信息物质和虫害诱导植物挥发物是植食性昆虫种内、植食性昆虫与植物,以及植物与植物之间进行化学通讯的主要媒介。植食性昆虫利用种内化学信息物质进行求偶和交配,从而维持其田间的种群数量;植物在识别植食性昆虫的为害以后,可产生直接和间接防御反应来抵御害虫的为害。相应地,植食性昆虫亦可利用植物的虫害诱导化学信息物质选择嗜好寄主,从而提高其生长适应度。目前,植食性昆虫性信息素和虫害诱导挥发物均被发现可引起植物的防御警备反应(Helms *et al.*, 2013; Erb *et al.*, 2015)。此外,植物间的合理间作或套作亦可通过改变植物挥发物而提高抗虫性(Mutyambai *et al.*, 2019; Barnes *et al.*, 2020; Nboyine *et al.*, 2021)。例如,当柑橘 *Citrus reticulata* Blanco 与番石榴 *Psidium guajava* Linn. 间作时,番石榴挥发物可激活柑橘植株中茉莉酸(JA)的生物合成,以及蛋白酶抑制剂、萜类、苯丙类和黄酮类防御化合物生物合成的相关通路,从而提高了柑橘对柑橘木虱 *Diaphorina citri* Kuwayama 的抗性(Ling *et al.*, 2022)。利用植物与植食性昆虫之间的化学通讯物质开发害虫的生态调控技术,是有效且可持续调控田间害虫种群密度的重要途径(娄永根等, 2018)。

茶树起源于中国西南茶区,茶产业是我国传统优势产业和绿色生态产业,有力支撑了我国脱贫攻坚和乡村振兴战略的实施。尽管我们在主要茶树害虫种内化学信息物质的鉴定和利用、虫害诱导挥发物的生态功能等方面已经取得了一些研究进展,但是与水稻和玉米等模式研究系统相比,还具有很大差距。基于茶树害虫挥发性化学信息物质的研究进展,今后可从以下方面开展茶树害虫种群密度的生态调控:1)基于生态工程原理,通过合理间作非寄主植物来提高茶园生态系统的抗性;2)基于性信息素,构建标准化的

重大茶树害虫种群监测和大量诱杀技术;3)基于茶树诱导抗性,进一步挖掘茶树诱导抗虫剂并加以合理使用,以提高茶树的自身抗性;4)基于寄主和非寄主植物的挥发物,筛选其中具有引诱和驱避作用的重要功能成分,从而获得高效 Push-Pull 单元,并建立田间配套使用技术。

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