植食性昆虫的寄主选择机理及行为调控策略

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摘要：害虫是影响农作物生产的重要因素，过度使用化学农药已带来严重的“3R”问题。为了长期有效地控制害虫的危害，基于植食性昆虫寄主选择机制的行为调控策略已成为害虫治理研究的重要方向。天然植物资源（如驱避植物、诱集植物与诱集枝把）、物理模拟材料（如诱集色、驱避色与诱集模型）和人工合成物质（如引诱剂、驱避剂、刺激剂与抑制剂）等研发工作皆取得了突破性的进展。除单一措施的使用外，多种诱集措施协同利用的“诱集 + 诱集”策略、诱集措施与趋避措施结合使用的“排斥-诱集”策略也已被广泛应用。

关键词：植食性昆虫；寄主选择；行为；机理；害虫行为调控

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Host-plant selection mechanisms and behavioural manipulation strategies of phytophagous insects

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Abstract: Insect pest is one of the most important factors adversely affecting the development of crop production, and the control method intensively depending on insecticide application has brought serious 3R (residue, resistance and resurgence) problems. The novel control strategy based on the behavioral manipulation of phytophagous insects has become a main research field in recent decades for sustainable management of crop pests. Many trap and repellent techniques derived from the natural plant resources (e. g. trap crop, repellent crop and trap twig bundle), physical stimulant materials (e. g. trap color, repellent color and trap model) and synthetic compositions (e. g. attractant, repellent, stimulant, deterrent) have been developed successfully. Beside the single trap strategy, the pull-pull strategy combining different trap measures and the push-pull strategy integrating the utilization of trap and repellent measures, have been widely exploited for pest management in agricultural production.

Key Words: phytophagous insects; host-plant selection; mechanism; pest behavioural manipulation

昆虫行为生态学是一门新兴的边缘学科，虽然它的产生至今不过几十年的时间，但已在昆虫觅食、生殖、

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学习、社会等行为研究上取得了显著进展,同时对学科自身在害虫综合治理中的应用前景有了清楚认识[1]。理论上认为,任何时期昆虫的任何一个行为都可能被改变,这便为害虫的行为调控提供了可能[2]。随着昆虫行为及其机理研究的不断深入,迄今已发展形成了一系列的害虫行为调控措施。本文以植食性昆虫的寄主选择为题,全面总结其行为、机理以及应用方面的研究现状,深入阐述昆虫行为生态与害虫行为调控之间的密切联系,以期为我国这些领域的科学研究与技术开发提供参考。

1 昆虫寄主选择

1.1 寄主选择行为

对植食性昆虫而言,寄主植物分为两类:取食寄主与产卵寄主。植食性昆虫主要从取食寄主中获得生长所需的营养物质,而在产卵寄主上繁衍后代。一般来说,植食性昆虫的取食寄主与产卵寄主种类都是比较有限的,同时两者的范围往往也不一致。因此,植食性昆虫能够适时寻找到适合的取食、产卵寄主在其生命历程中尤为重要。在长期的进化过程中,植食性昆虫对寄主与非寄主植物之间的识别、对不同寄主植物之间的选择形成了一系列特殊的行为机制(图1-A)。有的非寄主植物含有一些特殊挥发性物质,对植食性昆虫表现出强烈的驱避作用;而另一些植物则对昆虫没有明显的驱避效应,但却因缺乏引诱物质或含有取食、产卵抑制物质而被昆虫放弃。对于不同的寄主植物,植食性昆虫表现出的喜好程度也不尽相同,往往对个别植物或植物的个别组织器官特别嗜好[3~6]。然而,当非寄主植物与寄主植物上的化学、物理信息极其相似时,有些昆虫也会被这些非寄主植物的"假象"所"蒙骗",从而做出错误判断,将卵产在自己或其后代不适合生存的非寄主植物之上[7~9]。

1.2 寄主选择机理

植食性昆虫的寄主选择行为常分为寄主的定向(远距离)、降落(近距离)和接触3个主要阶段。在这些行为过程中,昆虫的视觉、嗅觉、触觉和味觉发挥着关键作用(图1:B)。昆虫在接触植物前的定向、降落运动阶段,主要受植物的光学和气味特点的影响,因此其视觉和嗅觉起着主导作用。昆虫视觉器官包括有复眼和单眼,可以对寄主植物的颜色、形状、大小等进行识别。而触角、下颚须、产卵器等部位上发达的化学感受器能有效地探测到植物所挥发出来的气味,并做出相应的反应。当昆虫接触到寄主植物时,昆虫利用触角、跗足、口器、产卵器等部位上的接触性感受器对植物表面的形态结构和化学性质等进行评价。对于取食寄主的寻找,最后还需通过刺探、取食等方式利用味觉感受器来感受、判断植物内部的化学性质。昆虫利用上述不同的感觉器官来不断收集来自植物的各种信息,对正、负作用因素进行综合、评价,最后对植物做出取舍决定[3~6]。

2 害虫行为调控

伴随着对植食性昆虫寄主选择行为及其机理认识的不断深入,害虫行为调控技术的发展日新月异(图1:C)。早期基于对寄主选择行为的简单认识,形成了驱避植物、诱集植物、诱集枝把等天然植物资源的利用模式。随后,又将诱集色、驱避色、诱集模型等一些物理模拟材料用于害虫的行为调控。近年来,随着寄主选择行为机制研究的快速发展,大量的人工合成物质(如引诱剂、驱避剂、刺激剂、抑制剂等)被成功研制,并广泛应用。与此同时,诱集植物、诱集色等措施得到了新的发展,从而形成了当前较完整的害虫行为调控技术体系。

2.1 天然植物资源

2.1.1 驱避植物

有的非寄主植物能释放出一些特殊的气味,对某些害虫能产生明显的驱避作用。植物驱避作用的应用已有2000多年历史,迄今研究、应用最多的是植物的驱蚊作用[10]。对于植食性害虫也有一些报道,如番茄 *Lycopersicum esculentum* Mill 对小菜蛾 *Plutella xylostella* L. 成虫有很好的驱避作用,结球甘蓝 *Brassica oleracea* L. var. *capitata* L. 地间作番茄可有效地减轻其发生[11]。蔬菜地中胡萝卜茎蝇 *Psila rosae* Fabricius、葱种蝇 *Hylemya antique* Meigen、马铃薯甲虫 *Leptinotarsa decemlineata* Say、豌豆蚜 *Acyrthosiphon pisum* Harris 可分别通过种植洋葱 *Allium cepa* L.、胡萝卜 *Daucus carota* L. var. *sativa* DC、豌豆 *Pisum sativum* L. 和蓖麻 *Ricinus communis* L.

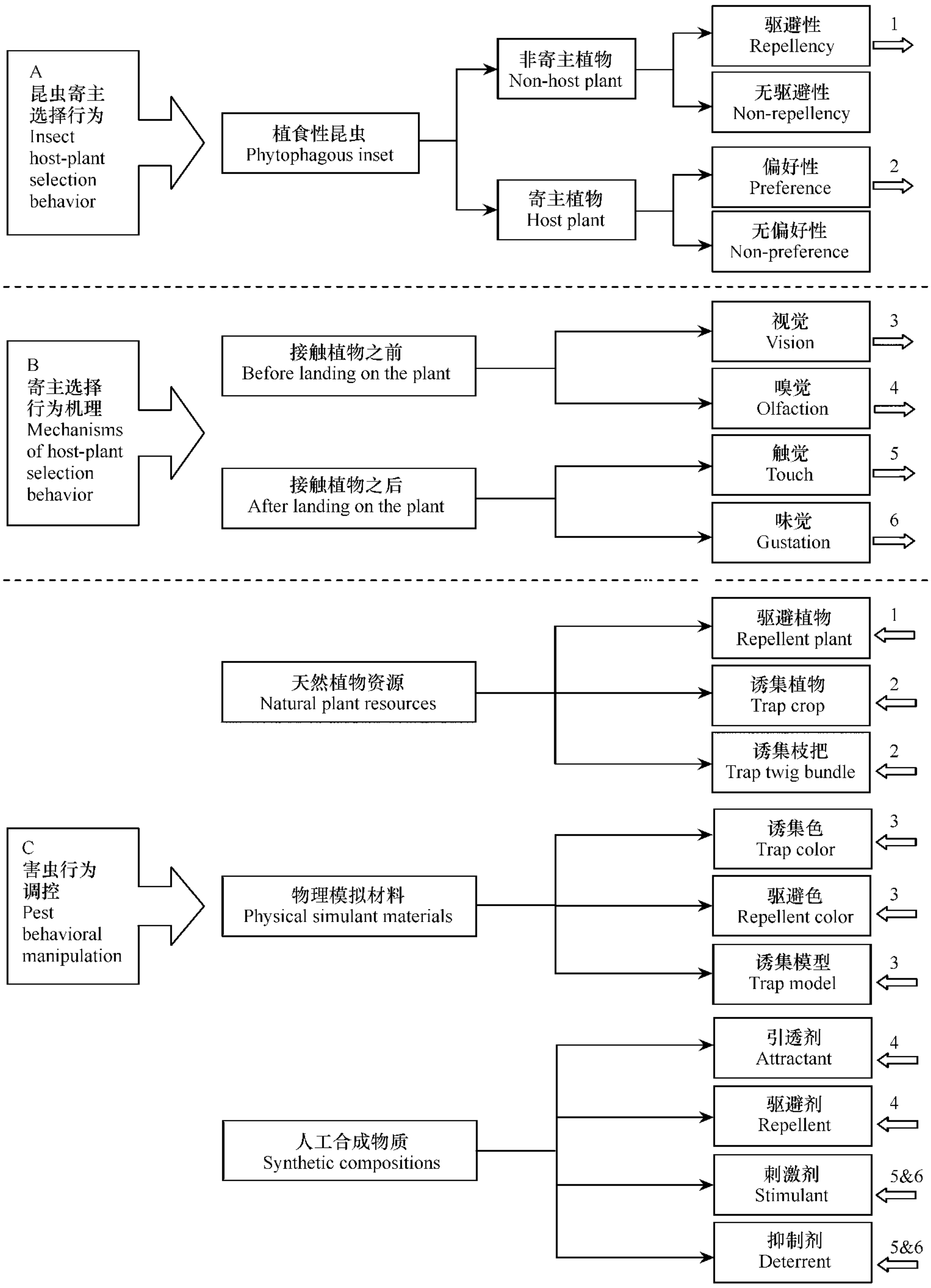

图 1　植食性昆虫的寄主选择行为、机理及其应用

Fig. 1　Host-plant selection behaviour of phytophagous insects, and its mechanisms and applications

来进行驱避防治[12]。另外,蚕豆 *Vicia faba* L. 地间作罗勒 *Ocimum basilicum* L. 或香薄荷 *Satureja hortensis* L. 能明显减少甜菜蚜 *Aphis fabae* Scopoli 成虫的侵入量[13]。

2.1.2　诱集植物

一些害虫对个别植物具有明显的嗜好性,合理种植这些植物可以吸引害虫来保护主栽作物免受为害,这类植物被称为诱集植物[14,15]。诱集作物的利用最早可以追溯到化学农药产生之前,这一技术迄今还广泛应用。在我国,生产上常利用玉米 *Zea mays* L.、高粱 *Sorghum bicolor* (L.) Moench 来诱集棉花 *Gossypium hirsutum* L. 田棉铃虫 *Helicoverpa armigera* Hübner 成虫产卵[16],利用苘麻 *Abutilon theophrasti* Medicus 来诱集棉

花、大豆 *Glycine max*（L.）Merr 田的烟粉虱 *Bemisia tabaci* Gennadius 成虫[17]等。国外报道，通过种植苜蓿 *Medicago sativa* L. 来诱集棉田豆荚草盲蝽 *Lygus hesperus* Knight[18]，种植高粱来诱集棉田谷实夜蛾 *Helicoverpa zea* Boddie[19]，种植向日葵 *Helianthus annuus* L. 诱集大豆蛀心虫 *Dectes texanus* LeConte[20]，种植菊花 *Dendranthema grandiflora* Tzvelev 诱集温室西花蓟马 *Frankliniella occidentalis* Pergande[21]等。一般来说，诱集植物的利用需结合杀虫剂的使用等其他防治措施来杀死诱集到的害虫，从而整体降低田间的害虫种群数量。当然，有一类特殊诱集植物就是因害虫"误判"而偏好的非寄主植物，害虫或其后代在这些植物上不能存活，因此无需其他害虫防治措施，常称这类诱集植物为致死性诱集植物（Dead-end trap crop）。如菽麻 *Crotalaria juncea* L. 可以直接诱杀扁豆实心虫 *Maruca testulalis* Geyer[22]、欧洲山芥 *Barbarea vulgaris* R. Br. 能成功诱杀小菜蛾[8,23]，香根草 *Vetiveria zizanioides*（L.）Nash 能直接诱杀斑禾草螟 *Chilo partellus* Swinhoe[24]等。这一目的也可通过转入杀虫基因等人为手段来达到。比如转 Bt 基因马铃薯 *Solanum tuberosum* L. 就可直接诱杀马铃薯甲虫 *Leptinotarsa decemlineata* Say[25]，转 *cry*1Ac 或 *cry*1C 的羽叶甘蓝 *Brassica oleracea* L. var. *acephala* DC 来直接诱杀小菜蛾[26]，Bt 玉米可直接诱杀甘蔗 *Saccharum officinarum* L. 上的非洲茎螟 *Eldana saccharina* Walker [27]等。

2.1.2 诱集枝把

诱集枝把与诱集植物都是基于昆虫对个别植物的嗜好性来诱集害虫，但两者之间存在着一定区别，前者的利用材料是离体植株，而后者利用的是完整的植物活体。诱集枝把在农业害虫的预报与防治中已有长期的应用。例如，利用半枯萎的杨树 *Populus* spp. 等枝把诱集棉铃虫成虫[16,28]，利用小谷草或稻草把诱集粘虫 *Mythimna separata* Walker 产卵[29]、利用榆树 *Ulmus pumila* L. 或杨树枝诱集金龟子[30]等。

2.2 物理模拟材料

2.2.1 诱集色

基于昆虫对个别颜色的偏好性，发展形成了粘性色板诱杀技术。如烟粉虱对黄色光具有很强的趋性[31]，因此生产上利用黄色粘虫板来诱杀、监测烟粉虱[32~34]。同时，色板诱集技术还在温室白粉虱 *Trialeurodes vaporariorum* Westwood、西花蓟马 *Frankliniella occidentalis* Pergande、豆带巢针蓟马 *Caliothrips fasciatus* Pergande、桔小实蝇 *Bactrocera dorsalis* Hendel 等多种同翅目、半翅目、双翅目害虫的防治中广泛应用，发挥着很好防治效果[35~39]。

2.2.2 驱避色

一些特定的颜色对某些昆虫对有着明显的驱避效应，这一特征在害虫行为调控中也有应用。最具代表性的就是银光避蚜效应。20 世纪中叶，国外就开始利用铝铂来驱避蚜虫[40]，随后我国开发了银色薄膜避蚜技术[41]。这些措施对农作物蚜害以及蚜传病害的防治效果比较理想，当前园林植物、烟草 *Nicotiana tabacum* L. 等生产上还广为应用[42,43]。

2.2.3 诱集模型

除了对特定的颜色表现出喜好或厌恶以外，个别的昆虫对植物形状也有明显的行为反应。如苹绕实蝇 *Rhagoletis pomonella* Walsh 的产卵场所为寄主植物的果实，经过长期的进化过程，苹绕实蝇便偏好于类似于果实形状的圆形物体，直径在 8cm 左右对其吸引力最强，而 8cm 以上的引诱力逐渐减弱。结合这一行为特征而研制的粘膜球形诱捕器在其诱集防治中广为应用[44]。此外，研究发现李象 *Conotrachelus nenuphar* Herbst[45]、西部樱桃实蝇 *Rhagoletis indifferens* Curran[46]、瓜小实蝇 *Bactrocera cucurbitae* Coquillett[47]等昆虫同样对不同形状、大小的诱集模型的喜好程度各不相同。

2.3 人工合成物质

2.3.1 引诱剂

在昆虫的寄主选择过程中，植物的特殊"指纹图谱"——挥发性物质常起着关键性的作用。因此，可以人工合成、应用其中的有效组分来进行害虫诱捕防治。例如，Bartelt 和 Hossain 利用植物挥发物 ethanol、2-

methyl-1-propanol、2-methyl-1-butanol、3-methyl-1-butanol、acetaldehyde、ethylacetate 配制成了一种取食引诱剂,广泛用于防治澳大利亚梨园甲虫 *Carpophilus davidsoni* Dobson[48]。Cruz-Lopez 等人对黄槟榔青 *Spondias mombin* L. 果实中的九种挥发物组分进行了合理配比,结果发现对西印度实蝇 *Anastrepha oblique* Macquart 的诱集效果明显[49]。Murai 等人则发现植物花的挥发物 methyl anthranilate 对黄胸蓟马 *Thrips hawaiiensis* Morgan 与色蓟马 *Thrips coloratus* Schmutz 有着明显的诱集作用[50]。

产卵引诱剂的应用在苹绕实蝇的防治上非常成功。该蝇产卵于寄主植物的果实,以果实形状及果实中挥发的特殊气味作产卵导向物。经鉴定,气味中对苹绕实蝇有产卵引诱作用的是丁醇己酸酯 butyl hexanoate,于是在小木球上涂以丁醇己酸酯,悬挂于果园四周,引诱苹绕实蝇将卵全部产在这些小球上,成功防止了苹绕实蝇的危害[51]。而梨树挥发性物质(Z)-3-hexen-1-ylacetate、(Z)-3-hexen-1-ol 与 benzaldehyde 按 4:1:1 进行配比,对已交配的东方果蛾 *Cydia molesta* Busck 有着很好的诱集作用[52]。松类植物中挥发性组分 alpha - pinene 与 Hodoron 则对雌性日本叶蜂 *Urocerus japonicus* Smith 的诱集效果明显[53]。榄仁树 *Terminalia catappa* L. 果实上几种挥发性组分进行混配后对桔小实蝇 *Bactrocera dorsalis* Hendel 雌成虫诱集效果很好,但对雄性个体的诱集效果较差[54]。

2.3.2　驱避剂

一些非寄主植物具有特殊的挥发性物质组分,能引起某些植食性昆虫负趋向运动或无定向移动,从而避免或抵御昆虫取食。利用这些特殊的挥发性组分来研制、开发害虫驱避剂有很多成功实例。比如,Poland 等人利用非寄主植物挥发物 1-hexanol, (Z)-3-hexen-1-ol, (E)-2-hexen-1-ol, 3-octanol 和马鞭烯酮 verbenone 进行合理配比,发现能有效地干扰纵坑切梢小蠹 *Tomicus piniperda* L. 对引诱剂 alpha-pinene 和寄主植物欧洲赤松 *Pinus sylvestris* L. 的选择[55]。Fettig 等人发现非寄主植物挥发性物质与马鞭烯酮 verbenone 混合能有效的干扰西部大小蠹 *Dendroctonus brevicomis* LeConte 对引诱剂的反应[56]。Erbilgin 等人发现苯乙酮 Acetophenone 对西部松大小蠹有很强的驱避活性,但对其捕食性天敌的影响较小[57]。

当然,有些趋避剂主要作用于昆虫的产卵行为。钟国华等人报道,闹羊花素-Ⅲ(Rhodojaponin-III)和黄杜鹃花 *Rhododendron molle* (Blume) G. Don 乙酸乙酯(EtOAc)萃取物对小菜蛾产卵有着明显的驱避作用[58]。Charleston 等人发现由苦楝 *Melia azedarch* L. 和印楝树 *Azadirachta indica* A. juss 内含物制成的生物农药也能有效地驱避小菜蛾产卵[59]。Seljasen 和 Meadow 则发现印楝素制剂 NeemAzal-T 与印楝种子的水提物均能有效地减少甘蓝夜蛾 *Mamestra brassicae* L. 在结球甘蓝上的产卵量[60]。

2.3.3　刺激剂

当昆虫接触寄主后,是否滞留主要取决于化学信息,而是否继续取食依赖于一定浓度的取食刺激剂。就植物来说,取食刺激剂可以是植物的营养物质如糖、脂肪、蛋白质,也可以是次生性化合物,如黑芥子苷、葫芦素等[3]。在实际应用中,取食刺激剂常与杀虫剂联合使用,即将害虫引向杀虫剂,并通过其大量取食,消灭害虫。Duan 和 Prokopy 在小木球表面涂以玉米糖浆,苹绕实蝇成虫在与木球的接触中导致其进一步的取食,被糖浆中混入的杀虫剂毒杀[61]。葫芦素可以刺激多种叶甲昆虫不由自主地取食,将杀虫剂与葫芦素和引诱剂混合制成毒饵,有效控制了多种食根叶甲的种群[62]。2006 年,Haribal 等人在茄科植物 *Solanum surattenses* 中分离出一种呋甾烷的衍生物,发现对甘蓝夜蛾 *Manduca sexta* Chitinase 有着明显的取食刺激作用[63]。

植物中同样存在着昆虫产卵的刺激物质,但人工开发的产卵刺激剂目前还未在害虫管理中得到应用。而 Unnith 和 Saxenna 的研究已显示了这一方法在害虫管理中应用的可能性。1990 年他们用高粱提取物刺激高粱秆蝇 *Atherigona soccata* Rondani 在其它寄主上产卵, 进而保护高粱免受危害[64]。近年来,产卵刺激物的研究上有了不少新进展。比如,研究发现黄樟 *Sassafras albidum* Nutt 中的 3-trans-caffeoyl-muco-quinic acid 对凤尾蝶 *Papilio troilus* L. 有着明显的产卵刺激作用[65],植物飞龙掌血 *Toddalia asiatica* L. 中(-)-(2S,4R)-4-hydroxy-1-methyl pyrrolidine-2-carboxylic acid 能刺激玉带凤蝶 *Papilio polytes* L. 的产卵[66],向日葵中 *ent*-kauran-16α-ol 和 *ent*-atisan-16α-ol 两种物质对向日葵条蛀螟 *Cochylis hospes* Walsingham 有明显的产卵刺激作用[67]。

2006 年,*Lee* 等人则发现辣椒 *Capsicum annuum* L. 中的(E)-capsaicin 对烟青虫 *Helicoverpa assulta* Guenee 产卵有着明显的促进作用,认为这是理想的接触性产卵刺激剂[68]。

2.3.4 抑制剂

一些植物次生代谢物质对昆虫的取食、产卵具有阻止和抑制作用。作用于昆虫取食行为的则称之为拒食剂,这方面已有一系列的成功实例[69]。印楝素是迄今为止人们发现的最强拒食剂,是拒食剂商业开发成功的典型例子。印楝素对多种鳞翅目、同翅目、直翅目等害虫有着很强的拒食作用[70]。川楝素也是一个很好的拒食剂,对菜青虫 *Pieris rapae* L. 、小菜蛾、亚洲玉米螟 *Ostrinia furnacalis* Guenée、斜纹夜蛾 *Prodenia litura* Fabricius 等多种害虫的拒食活性很强[71]。最近发现,漏芦属植物 *Leuzea carthamoides* Willd 中的提取物 20-hydroxyecdysone 能有效地抑制桃蚜 *Myzus persicae* Sulzer 和葡萄小卷叶蛾 *Lobesia botrana* Denis et Schiffermüller 幼虫的取食[72,73]。

昆虫产卵抑制剂方面研究最多的还是印楝素及其衍生物。据文献记载,印楝素对数十种害虫具有强烈的产卵抑制作用[74]。除此之外,已有数十种害虫的产卵抑制剂被相继报道[75]。具有代表性的有:从小花糖芥 *Erysimum cheiranthoides* L. 种子中分离出来的 erysimoside、erychroside 等物质对菜粉蝶 *Pieris rapae* L. 有着明显的产卵抑制活性[76],而 20-Hydroxyecdysone 对葡萄小卷叶蛾产卵具有抑制作用[73]。

2.4 几种措施的协同使用

2.4.1 "诱集 + 诱集"策略

"诱集 + 诱集"策略就是通过两种或两种以上的诱集措施结合使用来增加害虫行为调控效果。如在舌蝇 *Glossina spp.* 的防治中,色板诱集与引诱剂的使用都是常用方法,但将引诱剂喷布在色板上能有效地提高了其诱杀效果[77]。Martel 等则在诱集植物上喷施植物源引诱剂来提高害虫的诱杀效果[78]。Duan 和 Prokopy 则在粘膜球状诱捕模型在喷施产卵引诱剂来提高苹绕实蝇的诱杀效果[44]。也有报道同时组合利用几种不同诱集植物从而达到高效诱杀害虫的目的[79]。

2.4.2 "排斥-诱集"策略

"排斥-诱集"策略是通过结合使用驱避与诱集措施来协调治理害虫,Cook 等人对该策略做了全面综述[80]。结合利用诱集植物与驱避植物是其中一种形式,Khan 等人利用这一方法在玉米田斑禾草螟 *Chilo partellus* Swinhoe 等鳞翅目害虫的防治上取得了明显的效果[81]。而 Cowles 和 Miller 则利用诱集植物作为诱集源,产卵抑制剂作为排斥源,有效地控制住了葱地中种蝇 *Delia antique* Meigen 的为害[82]。这一模式在棉铃虫的防治上也取得了成功,其中排斥源是当前最有代表性的昆虫产卵抑制剂——印楝素[83]。此外,诱集植物与拒食剂[84]、诱集植物与驱避剂[85]、趋避剂与引诱剂[86]等组合模式也有一些探索研究。

3 研究展望

数十年来,人类一直被化学农药带来的抗药性、环境污染等问题所困扰,寻找可持续的害虫防控措施成为了大家关注的焦点,昆虫行为生态研究帮助其找到了一个新的突破口——害虫行为调控。基于对昆虫行为过程与行为机理的深入认识,利用某些行为特征来改变害虫的行为,进而调控其行为过程、减少其对保护对象(作物)的选择与为害。这类措施针对性强,防治效果可观,而且对其它生物以及环境没有负面影响。正因为如此,昆虫行为生态与害虫行为调控的研究引起了广泛关注。

植食性昆虫寄主选择行为是昆虫行为生态方面的研究热点,在几乎所有的主要农林害虫上都有不同程度的研究。但由于其过程复杂,涉及的机理众多,因此探明这一行为过程及相关的行为机理比较困难。而研究基础的不扎实往往会影响害虫行为调控技术的开发、利用,迄今昆虫寄主选择行为研究成果在害虫行为调控技术开发上的成功实例还相对有限[2]。为此,植食性昆虫寄主选择行为、机理的研究以及相关害虫行为调控技术的开发还有待加强。此外,近年来电生理技术与分子生物学技术在植食性昆虫寄主选择行为机理研究中广为运用[5,6,87,88],这将能更加完整地解释昆虫寄主选择行为机理,阐明其行为本质,为害虫行为调控措施的开发提供新的思路。

昆虫的行为可依环境条件及昆虫个体的经历不同而有所改变,这常被称为学习行为[89,90]。昆虫学习行为与害虫行为调控有着密切联系,例如原本在室内选择试验中引诱力较强的植物,当作为诱集植物种植在大片作物中时,它们并未能表现出明显的引诱作用,这可能就与害虫学习行为有关[91]。害虫对驱避源的学习适应也有相应的报道。如 Liu 等研究发现菊花 *Chrysanthemum morifolium* Ramat 粗提物对没有经历的小菜蛾雌成虫有着明显的驱避性,然而当雌蛾在羽化中短暂接触该粗提物后,以后就不再对该粗提物产生驱避反应[92]。印楝素原本是小菜蛾的产卵驱避、抑制剂,但经过学习小菜蛾对其反应也发生了改变,反而偏好在喷施印楝素的植株上产卵[93]。因此,在害虫行为调控措施研制到推广过程中,需综合考虑昆虫学习行为这一影响因素,从而确保害虫行为调控措施拥有真正的实践应用价值。当然,昆虫学习行为的合理利用也能促进害虫行为调控效果的提高。总之,昆虫学习行为研究在害虫行为调控技术的发展方面有着重要的意义。

在行为调控措施方面,不仅要巩固、发展现有技术形式,更要加强与转基因技术等新兴科技手段的结合。比如在明确植物-昆虫间化学通讯信号的生物诱导及其基因调控机制的基础上,通过转基因技术来调控作物自身释放的气味物质的产生,从而来控制害虫行为[94]。这一技术在拟南芥 *Arabidopsis thaliana* (L.) Heynh、玉米等植物上已有了突破[95,96]。同时,行为调控技术的合理组配也有着很好的发展潜力,"诱集 + 诱集"策略、"排斥-诱集"策略的探索和应用都取得了明显的进展,这是害虫行为调控措施应用层面上的发展与突破,当还有待进一步加强探索、应用。

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