Received: 23 November 2020 Revised: 16 January 2021 Accepted article published: 22 January 2021 Published online in Wiley Online Library: 6 February 2021

(wileyonlinelibrary.com) DOI 10.1002/ps.6289

Towards developing areawide semiochemical-mediated, behaviorally-based integrated pest management programs for stored product insects

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Abstract

With less emphasis on fumigation after harvest, due to the phase-out of methyl bromide and increasing phosphine resistance, diversified postharvest integrated pest management (IPM) programs are needed. Here, we synthesize knowledge on semiochemical-mediated, behaviorally-based tactics, wherein semiochemicals are deployed to manipulate pest behavior to protect commodities. We note that beyond monitoring, commercial use is limited to mating disruption targeting mostly moths. In total, behaviorally-based tactics have been attempted for eight species of stored product insects from two orders and six families. Eighteen challenges were identified that may have prevented robust implementation of semiochemicals for behaviorally-based management in stored products, including direct competition with ubiquitous food cues, and the diverse insect assemblages that colonize food facilities. Further, we discuss the scientific data and methods required to support stakeholder acceptance of semiochemicals at food facilities, including demonstrating that pests are not attracted from the landscape and minimal spillover around pheromones. We sketch a robust areawide behaviorally-based IPM program after harvest, and clarify properties for improving semiochemicals, including incorporating those that are broad spectrum, competitive with food cues, potent at low concentration, and exhibit dose-dependent attraction. The research gaps and testable hypotheses described here will speed developing behaviorally-based tactics at food facilities.

Supporting information may be found in the online version of this article.

Keywords: behavior; chemical ecology; attractants; food facilities; integrated pest management

1 CHALLENGES FOR FOOD FACILITIES IN THE 21ST CENTURY

1.1 Value and losses in the postharvest supply chain

Production for just corn, soybean, and wheat alone account for over \$86 billion USD each year, while value-added products like wheat flour amount to an economic worth of \$40 billion USD.[1] Last year in the United States, 16.5 billion bushels (≈ 427.8 million metric tons) of corn, soybean, and wheat were stored off and on-farm.[2] Despite the significant portion of the economy for which the postharvest supply (e.g. stored, transported, processed, marketed, and delivered to consumers) accounts, relatively less research attention and funding have been invested in it than in protecting commodities prior to harvest. Nonetheless, in this postharvest supply chain, significant losses in both quantity and quality of commodities can be incurred through attack by a large variety of insects. Each year global postharvest losses account for roughly \$100 billion USD,[3] and depending on the resources available to stakeholders, this may range between 2 and 60% losses of crops after harvest .[4,5]

1.2 Challenges in the IPM of stored products

For many food facilities, the insect pest species richness is abundant[6] and composition can vary unpredictably over time as well as due to the arrival of new infested raw or processed materials at a food facility, which may introduce or expand infestations.[7,8] For the sake of this contribution, a food facility is any facility involved in storing, processing, selling, or consuming food. Insects can also regularly immigrate into facilities from the surrounding landscape.[7] The relative contribution of insects from the landscape and those from receiving infested goods on infestation at food facilities likely varies among facilities and over time. However, captures outside a facility are often linked later with captures inside food facilities; *Trogoderma variabile* Ballion (Coleoptera: Dermestidae) marked outside facilities were later recaptured inside and marked individuals moved between 21 and 508 m.[9] Likewise, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) was found to have a diet that consisted of both starchy food and lignin-rich food, indicating frequent switching between woody hosts and stored maize when adjacent to food facilities.[10]

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Moreover, poor sanitation can increase the potential for infestation and spread.[11] Many stored product insect species are well-adapted to finding and exploiting very small amounts of food,[12] and may be distributed in small accumulations of food throughout a facility.[13] Colonization of packaged goods and movement of insects among infested packages in a facility may also contribute to pest problems.[14]

In addition to these system level constraints, for much of the 20th century, integrated pest management (IPM) programs for food facilities primarily relied on frequent fumigation with methyl bromide,[15,16] which was cheap, easy to apply, and highly effective, making it an attractive mitigation tactic. However, it is an ozone depleting substance and under the Montreal Protocol use of this fumigant was eliminated for most postharvest applications such as treating structures by the early 2000s. Historical overreliance on this strategy made it difficult to substitute novel IPM tactics at food facilities, but since this point, there has been a strong push by the industry to develop alternative tactics and compounds.[17]

Along with methyl bromide, another commonly used fumigant has been phosphine.[16] For the last couple decades, there has been an overreliance on phosphine for commodity treatments, and there are increasing challenges to its use. Top among these is increasing worldwide resistance to the compound by at least eight species of insects from 250 locations in 60 countries.[18] Rising resistance is threatening the continued efficacy of phosphine in places where it is primarily used such as bulk storage where there have been fewer attempts to significantly diversify IPM programs. This represents a potential opportunity to decrease reliance on phosphine in this area in order to preserve its efficacy as a tool of last resort. Phosphine is also not quite as versatile as methyl bromide, because it will readily corrode exposed copper wiring in facilities, which makes use in some structures difficult.[16]

Other fumigants that were readily available for use in food facilities during the 1980s are either no longer registered, or no longer produced due to a combination of health and environmental safety reasons.[16] To deal with the phase-out of methyl bromide and the drawbacks of phosphine, there has been a concerted attempt to develop replacements, including sulfuryl fluoride,[19] ethyl formate,[20] and others, but only sulfuryl fluoride has seen wide adoption to date and each alternative fumigant has its drawbacks. Meanwhile, there has been increasing demand by consumers for commodities that are insecticide-free or have reduced residues.[21] Consumers are even willing to spend more for such postharvest commodities, including cereals, flour, and others. These trends track with the exponentially growing organic industry, which has reached a value of $90 billion over two decades.[22]

1.3 Semiochemical-mediated, behaviorally-based management

The collective result of all these factors is a push to diversify IPM programs for food facilities away from the historical overreliance on a few fumigants. IPM is a holistic system of pest management that integrates control across types of tactics and commodities to manage pests in a cost-effective way below economic injury levels.[23] One way to diversify IPM programs is by investing in and developing semiochemical-mediated, behaviorally-based (hereafter, simply behaviorally-based) management tactics. For this contribution, the term behaviorally-based tactic encompasses a whole suite of techniques (Supporting Information Table S1) including five management tactics and one monitoring tactic that use various classes of semiochemicals to manipulate pest insect behavior to achieve a desirable outcome, usually the protection of commodities. The purpose of this review is to discuss the current state of the art in behaviorally-based management programs for stored product insects, as well as concretely extend the discussion by examining what robust implementation of behaviorally-based tactics may look like at a food facility. In particular, we discuss challenges to behaviorally-based tactics at food facilities, traits required of semiochemicals in such tactics, current research gaps, including the research needed to make tactics effective while minimizing risks that might be associated with use of attractants. We also highlight potential concerns in adoption of behaviorally-based tactics by stakeholders as well as examples of research data that is needed to assuage those concerns. While we focus on semiochemical-mediated tactics, we mention work with other kinds of stimuli (e.g. tactile, visual, sound, gustatory, etc.) where appropriate for successful implementation of tactics. It is our hope that this article generates testable hypotheses and renews momentum for developing behaviorally-based tactics to protect commodities after harvest.

2 EXISTING BEHAVIORALLY-BASED MANAGEMENT STRATEGIES AND CHALLENGES FOR STORED PRODUCTS

2.1 Overview

Monitoring and mass trapping results in tens of millions of USD in costs for lures and has been adopted on 10 million ha in preharvest agricultural systems, while attract-and-kill has been adopted on 1 million ha.[24] Meanwhile, pheromone-based mating disruption adoption has increased by 75% in recent years for many systems, especially preharvest agriculture covering over 750 000 ha globally.[25] Thus, in other agricultural systems, particularly high-value small fruit, pome fruit, and stone fruit crops, there has been significant work in developing behaviorally-based management strategies.[26–28] A considerable amount of attention has been paid in stored product entomology to the use of pheromones and incorporating pheromone-based technology,[29,30] with differing amounts of success. By far the most successful implementation of behaviorally-based strategies has been through the adoption of semiochemical-based monitoring programs and mating disruption at food facilities. Semiochemical-based monitoring programs have been extensively discussed elsewhere,[29,30] and will not be the focus of this contribution. Finally, while sterile insect technique through the release of irradiated males is a viable technique in other areas of entomology,[31] there has been no work done with this technology in stored products, stakeholder acceptance of releasing any type of insect (e.g. even beneficials) is low after harvest in many parts of the world, and it does not primarily rely on semiochemicals to manipulate pest populations, so we do not discuss this in the rest of our contribution.

2.2 Summary of behaviorally-based management in stored products

Other than semiochemical-based monitoring programs, there have been a number of semiochemical-mediated, behaviorally-based management tactics attempted for stored product protection. In total, different behaviorally-based management tactics have been evaluated for eight species of stored product insects from two orders and six families (Table 1). While attract-and-kill and mass trapping have been investigated in various contexts

Table 1. List of behaviorally-based management tactics for postharvest food facilities worldwide

Targeted species	Order	Family	Olfactory stimuli	Trapping system	Kill mechanism	CA[a]	Location(s)	Reference
Attract-and-kill								
Cadra cautella	Lep.	Pyralidae	(*Z*,*E*)-9,12-Tetradecadienyl acetate	Used but not listed	Cyfluthrin	No	Grain elevator	32
Ephestia kuehniella	Lep.	Pyralidae	(*Z*,*E*)-9,12-Tetradecadienyl acetate	Laminar dispensers	Cypermethrin	No	Large mills	33, 34
Lasioderma serricorne	Col.	Ptinidae	7-Hydroxy-4,6-dimethyl-3-nonanone	—	Timed Misters w/pyrethrin	No	Bakeries	32
Lasioderma serricorne	Col.	Ptinidae	7-Hydroxy-4,6-dimethyl-3-nonanone	Striped cross-panel	Micro-encapsulated permethrin	No	Tobacco processing facility	35
Multiple	Lep. & Col.	Multiple	Multiple pher. and kairo., SPB Tablet Lure, Insects Limited[b]	Spillage Traps	Deltamethrin insecticide netting	No	Commercial elevator, pilot-scale mill, pilot-scale warehouses	36
Plodia interpunctella	Lep.	Pyralidae	(*Z*,*E*)-9,12-Tetradecadienyl acetate	LastCall gel (IPM Tech) or Wax Panel	Permethrin, pyrethrin	No	Wind tunnel	37, 38
Plodia interpunctella	Lep.	Pyralidae	(*Z*,*E*)-9,12-Tetradecadienyl acetate	Pyrex Cake Pan	Granulosis virus	No	Simulated warehouse	39
Plodia interpunctella	Lep.	Pyralidae	(*Z*,*E*)-9,12-Tetradecadienyl acetate	Powder Tray Dispenser	*Beauveria bassiana*	No	Laboratory, wind tunnel	40–42
Prostephanus truncatus	Col.	Bostrichidae	Isopropyl (*E*)-2-methylpentenoate and isopropyl (2*E*,4*E*)-2,4-dimethyl-2,4-heptadienoate	Delta trap with oil fat pellet	*Beauveria bassiana*	No	Laboratory	43
Trogoderma glabrum	Col.	Dermestidae	(*E*)-14-Methyl-8-hexadecen-1-ol	Cardboard trap/ square	Pathogenic *Mattesia* spp.	No	Simulated warehouses, farmhouse	44, 45
Mass Trapping								
Cadra cautella	Lep.	Pyralidae	(*Z*,*E*)-9,12-Tetradecenyl acetate	Delta trap	Sticky glue	No	Large warehouse, confectionary factory	46
Ephestia kuehniella	Lep.	Pyralidae	(*Z*,*E*)-9,12-Tetradecadienyl acetate	Funnel trap	None Listed	No	Mills	47, 48

Table 1. Continued

Targeted species	Order	Family	Olfactory stimuli	Trapping system	Kill mechanism	CA[a]	Location(s)	Reference
Lasioderma serricorne	Col.	Ptinidae	7-Hydroxy-4,6-dimethyl-3-nonanone	Box trap, lasiotrap, multi-surface trap	Sticky glue	No	Bakeries, tobacco stores	49, 50
Plodia interpunctella	Lep.	Pyralidae	(*Z,E*)-9,12-Tetradecadienyl acetate	Delta trap	Sticky Glue	No	Storage room, food warehouses	51
Mating Disruption								
Cadra cautella	Lep.	Pyralidae	(*Z,E*)-9,12-Tetradecadienyl acetate	—	—	Yes	Storerooms (large), raisin warehouse	52, 53
Ephestia kuehniella	Lep.	Pyralidae	(*Z,E*)-9,12-Tetradecadienyl acetate	—	—	Yes	Flour mill, food and drug storage facility, chocolate factory	53–57
Lasioderma serricorne	Col.	Ptinidae	7-Hydroxy-4,6-dimethyl-3-nonanone	—	—	Yes	Mills	58
Plodia interpunctella	Lep.	Pyralidae	(*Z,E*)-9,12-Tetradecadienyl acetate	—	—	Yes	Storerooms, dried bean storage, food and drug storage, various warehouses	53, 56, 59
Sitotroga cerealella	Lep.	Gelechiidae	(*Z,E*)-7,11-Hexadecadien-1-ol acetate	—	—	Yes	Large boxes, simulated warehouses	60, 61
Repellency								
Many laboratory examples, but no field examples (see text for discussion)								
Push–pull								
Alphitobius diaperinus	Col.	Ten-ebrionidae	Assorted benzoquinones (push) and 6-component aggregation pher. (pull)[c]	Pitfall trap	None	No	Laboratory and poultry houses	62

[a] Abbreviations: CA – whether system is commercially-registered and available; Col. – Coleoptera; Lep. – Lepidoptera; Pher. – pheromone; Kairo. - kairomones.
[b] Proprietary blend from Insects Limited, but product states, 'lures contain a grain-oil food attractant and the pheromone for red flour beetles, confused flour beetles, cigarette beetles, warehouse beetles, and rice weevils.'
[c] Benzoquinones included 1,4-benzoquinone, 2-methyl-1,4-benzoquinone, and 2-ethyl-1,4-benzoquinone in a 1:249:750 ratio, while the six-component aggregation pheromone included (*R*)-limonene, (*E*)-ocimene, 2-nonanone, (*S*)-linalool, (*R*)-daucene, and (*E,E*)-farnesene in a 5.75:4:1:6.5:2:5.75 ratio[63].

for multiple species, there has been little adoption in the food industry.[64] Management of the same species using mating disruption has been much more successful, with commercial products available, and is regarded as highly effective (Table 1). It is interesting to note that four of the five species for which there are mating disruption tools are moths. Mating disruption may primarily target moths because adults are short-lived, whereas many stored product beetles are long-lived, presenting more opportunities for finding mates and thwarting mating disruption technology.[65,66] In addition to the biological limitations, there may be some regulatory considerations that have resulted in mating disruption only being available for pyralid moths in stored products. This is because the US Environmental Protection Agency (USEPA) includes an exemption for the class of moth pheromone used by some stored product moths that makes it significantly easier to obtain approval for commercial products.

Further, despite limitations of mating disruption with longer-lived species, there has been significant progress made with *Lasioderma serricorne* (F.),[58,66,67] and progress has been made in obtaining a registration for use of this technology by the USEPA, though it is already registered in Japan (Lindenmayer, pers. comm.). The main attractant for mating disruption of *L. serricorne* has been 7-hydroxy-4,6-dimethyl-3-nonanone (e.g. serricornin) (Table 1). Prior research has also found that other components of the species pheromone such as (2*S*,3*S*)-2,6-diethyl-3,5-dimethyl-3,4-dihydro-2H-pyran (e.g. anhydroserricornin) may also be attractive,[68] but recent research has called this into question when assessing the compound's ability to attract conspecifics to traps.[69] There has also been interest in developing mating disruption for *Trogoderma* spp.,[65] but there has not yet been any successful implementation. This may provide further impetus for why additional kinds of behaviorally-based tactics should be developed. Laboratory trials using simulated field conditions have been used for evaluating attract-and-kill of *Plodia interpunctella* (Hübner), but there has been no commercially adopted system. The overall lack of behaviorally-based tactics is in spite of 58 known pheromones for stored product insects (45 for Coleoptera and 13 for Lepidoptera).[70] By contrast, only 27 species have documented attraction to the currently available commercial lures,[70] which conforms to prior estimates of 20 to 30 pheromones available for stored product insects.[71]

There have been nine kill mechanisms evaluated in mass trapping and attract-and-kill (Table 1), including fogging machines, microencapsulated insecticide, insecticide-incorporated netting, and entomopathogenic agents. For example, timed misters were used to deliver pyrethrin to *L. serricorne* that were attracted to sprays with 7-hydroxy-4,6-dimethyl-3-nonanone (e.g. serricornin).[32] Later, attract-and-kill-based interception traps were evaluated at commercial food facilities in Kansas and Arkansas, and traps with long-lasting insecticide netting resulted in few to no progeny from insects that colonized the grain in the trap.[36] The entomopathogen *Beauveria bassiana* was used in an auto-dissemination attract-and-kill device where male *Plodia interpunctella* would pick up spores, then subsequently infect females.[40] The use of entomopathogens was particularly creative, because it employed a kill mechanism whose effects subsequently rippled out to other individuals in the same population with no prior contact to the device. Over recent years, there have been enormous strides forward in incorporating insecticides into other controlled release materials, such as insecticide-incorporated packaging,[72] and they are currently being evaluated in areawide suppression of pest populations in simulated warehouses. However, there has been an overall lack of research on including insecticide packaging or diatomaceous earths as kill mechanisms in behaviorally-based tactics. In particular, diatomaceous earth has been shown to have additive and/or synergistic effects when combined with other kill mechanisms like entomopathogens, and may be a suitable synergist for other insecticides.[42]

For repellents, there has been a lot of laboratory work with over 200 compounds and 160 plant extracts tested for activity on stored product insects, but there has been very little field efficacy work on repellency. There have been multiple reviews on the use of plant products for control of stored product insects, thus we have avoided extensive discussion of this work.[73,74] By contrast, there has been no work with push–pull strategies that we are aware of in stored products, and only one on the stored product insect, lesser mealworm, *Alphitobius diaperinus* (Coleoptera: Tenebrionidae), but in poultry houses.[62] In this single example, 1,4-benzoquinone, 2-methyl-1,4-benzoquinone, and 2-ethyl-1,4-benzoquinone was combined in a 1:249:750 ratio and acted as the 'push', while a six-component aggregation pheromone consisting of (*R*)-limonene, (*E*)-ocimene, 2-nonanone, (*S*)-linalool, (*R*)-daucene, and (*E*,*E*)-farnesene in a ratio naturally produced by males acted as the 'pull'. The push–pull system resulted in 5–12-fold more *A. diaperinus* captured in pitfall traps compared to a 'pull' system alone.[62]

2.3 Challenges and potential solutions to implementation of behaviorally-based management in stored products

We have aggregated low, moderate, and critical severity challenges (defined in Table 2) that may have slowed progress towards robust development of behaviorally-based tactics. Challenges were placed in these categories based on our joint expert opinion about (i) how easily they might be overcome; (ii) how pervasive a problem would be across food facilities in the postharvest supply chain; and (iii) the behavioral requirements for a particular behaviorally-based strategy, and whether abiotic, biotic, and logistical considerations in the postharvest supply chain would complicate the challenge further.

To summarize, we found that these challenges fell into four categories, including: (i) technological (33%); (ii) commercialization (22%); (iii) logistical (39%); and (iv) cultural (6%) (Table 2). Further, we acknowledge there may be some overlap in these categories, for example, with some logistical challenges also potentially being challenges to commercialization. However, in total 18 challenges with implementation were identified. Of those, 33 and 28% were classified as critical or moderate severity, respectively, while 39% were classified as low or variable severity.

2.3.1 Critical challenges

Among the critical challenges is encouraging stakeholder acceptance of using attractive semiochemicals in and around food facilities, which is discussed separately in a standalone section below because of its special importance. However, in brief, this is a complex topic, because this challenge consists of a combination of stakeholder concerns about attracting pests to their facility and a lack of definitive data that conclusively shows whether the use of these pheromones would increase immigration of insects into food facilities and cause infestations. More data are needed to determine whether these devices do not draw insects in from the field and whether they could result in increased infestations. Notably, this perception may be changing, because there has been widespread adoption of pheromone trapping and growing use of mating disruption.[65] Another critical severity challenge is

Table 2. List of potential challenges to implementing behaviorally-based tactics at food facilities, their severity, and some proposed solutions

ID	Tactic(s)	Type[a]	Challenge	Possible severity[b]	Potential solution(s)
1	All	Cul.	Stakeholder concern about attracting pests to sites of food production and storage	Critical	Data examining distance of attraction, area of aggregation, and proportion of attracted individuals that are killed/retained
2	Mass trapping, mating disruption	Log.	Regular immigration of insects into a food facility from the landscape	Critical	Incorporation of other integrated pest management (IPM) tactics such as residual insecticides and long-lasting insecticide netting; evaluate degree of impact of immigration on tactic and what levels are needed to negative impact success of tactic
3	Mass trapping, mating disruption	Log.	Regular arrival of already-infested commodities at a facility	Critical	Incorporation of other IPM tactics such as residual insecticides and long-lasting insecticide netting
4	All	Log.	Large diversity of insects invading food facilities	Critical	Lures will need to be broad spectrum in attraction or else multiple kinds of lures will need to be used
5	Attract-and-kill, push–pull, mass trapping	Tec.	Direct competition of attractants with ubiquitous food odors in environment	Critical	Incorporates a relatively unique (e.g. non-food), highly attractive stimulus
6	Push–pull, repellents	Tec.	Lack of long-distance repellents that will not impart off-odors to commodities	Critical	Deploy repellents near protected commodities but outside of facility; find repellents that humans cannot perceive, but which insects can, and which do not impact processing or end-use
7	All except mating disruption	Com.	Efficacy gap between behaviorally-based management and conventional tactics	Moderate	Direct comparisons in whole systems should be made for facilities under conventional compared to behaviorally-based management
8	All	Com.	Additional expenses to deploy tactics	Moderate	Target behaviorally-based management to value-added facilities or later in the postharvest supply chain; include lower cost attractive stimuli to decrease costs of lures, optimizing placement; evaluate duration of impacts to cost of implementation
9	All	Com.	Semiochemical lure longevity	Moderate	Improving lure dispenser or formulation
10	All	Log.	High pest population abundance	Moderate	Incorporation of other IPM tactics
11	Attract-and-kill, push–pull, mass trapping, repellents	Tec.	Ability of abundant food refugia as sites of reproduction (e.g. beyond olfactory stimuli) to undercut tactics	Moderate	Augmenting tactics with additional stimuli including gustatory; increased sanitation protocols
12	Attract-and-kill, push–pull	Com.	Dose-dependent increase in kill with additional stimuli	Low	Data on stimuli that scale with dose

Table 2. Continued

ID	Tactic(s)	Type[a]	Challenge	Possible severity[b]	Potential solution(s)
13	Mass trapping, mating disruption	Log.	Colonization by pest insects of sites of spillage, food dust accumulation, and refugia	Low	Better sanitation
14	All	Log.	Discrete enclosed environments (e.g. buildings, bins, and other structures at a food facility)	Low	Depending on tactic, could be deployed outside of enclosed space; tossed in; or hung from an opening
15	All	Log.	Unregulated abiotic conditions within facilities	Low	Improving lure dispenser or formulation or deploying outside of enclosed spaces
16	All	Tec.	Patchy distribution of pest species and individuals	Low	Data on plume reach; devices to actively disperse pheromone; targeting deployment of tactic to problem areas; or area-wide implementation
17	Attract-and-kill, mass trapping	Tec.	Differences in movement among species (walking *versus* flying, slow *versus* fast, etc.)	Low	Refining trap design so that it is behaviorally compatible with the targeted species
18	Mating disruption	Tec.	Permeation of environment with pheromone	Variable	Calculating pheromone plume dispersion and reach

[a] Types of challenges are classified as follows: technological (Tec.), cultural (Cul.), commercialization (Com.), and logistical (Log.).
[b] Severity levels defined as follows, low – challenge easily overcome or circumvented with little time or resources; moderate – with some investment of effort and research, challenge may be overcome; critical – a key challenge that will require a significant investment of time and research and that, if not overcome, may lead to a tactic not being successful; variable – severity depends on type of food facility.

the ubiquitous presence of already attractive food cues at many facilities. The background odors in an area may change behavior exhibited by insects that perceive a particular volatile.[75] More importantly, this challenge means that potential stimuli need to be even more attractive or be present in concentrations that are more attractive than the primary food source of these pest species to be effectively used in behaviorally-based tactics at food facilities. This may be difficult in some cases, because one of the most effective lures in many ground-based, commercial pitfall traps is a mix of grain oils.[76,77] However, some pernicious, but widespread species, like the red flour beetle, *Tribolium castaneum* (Herbst), may have inconsistent response to these stimuli depending on population or physiology (e.g. age or mating status).[78] A challenge for mating disruption and mass trapping may be the regular immigration of insects into a food facility. High immigration from surrounding areas may significantly decrease the efficacy of mating disruption in particular.[63] While the impacts of mating disruption on immigration are poorly understood in stored products, others[28,53,79] have pointed out that the use of mating disruption does not necessarily prevent the immigration of insects into a treated food facility, emphasizing the need for ongoing monitoring programs. In fact, high immigration of insects from the landscape also presents a threat to other IPM tactics such as fumigation, which is often viewed as a treatment of last resort. After fumigation, insect populations may quickly rebound after application through immigration.[80,81] However, one of the key advantages of deploying mating disruption in food facilities over in-field settings is the fact that most spaces are enclosed, which may at least reduce immigration relative to other systems. At least equally as important at food facilities is the arrival of new already-infested materials, which presents an additional critical challenge to the success of mating disruption and mass trapping.

To date, just a single push–pull system has been evaluated for a stored product insect species, but none in stored product environments. One of the critical challenges for a push–pull system or repellency will be identifying and testing repellent compounds that do not transfer off-odors into the commodities they are supposed to protect. While a large variety of compounds have been identified as repellents to stored product insects, these have been almost exclusively aromatic botanical oils,[82] and we are not aware of many attempts to characterize how they may affect the sensory properties of the commodities for end consumers. In addition, there are only infrequent attempts to characterize the specific chemical components involved in the repellency within the essential oil mixtures, and there are generally issues with botanical oil stability in other systems when deployed in the field.[83] Furthermore, botanical extracts often have to be applied in high concentrations to be effective,[84] have generally only been tested in a laboratory context,[82] may be repellent at some concentration but attractive at another, and/or they may only exhibit contact repellency,[84] and not long-distance repellency. Other possible sources of repellents include alarm pheromones (e.g. benzoquinones),[62] oviposition-deterring pheromones (such as those produced by *L. serricorne*, *Sitophilus* spp. or others), hormone analogs, or antifeedants. It is unlikely that hormone analogs would function as repellents in stored products. The most common juvenile hormone analog is S-methoprene, which is effective at disrupting development as a biorational insecticide, but has not shown evidence of repellency.[72] Regardless of whether plant compounds or these other cues are used, repellents must be identified that can be perceived by insects, but which do not affect processing of food products, and which are not detectable by humans in the final products. There has been some work to incorporate repellents into barriers for packaging, and these have shown promise in laboratory assays,[85] but may actually be less effective at repelling in the field when attractive odors are also around. Another alternative is to deploy repellents away from protected commodities, perhaps on the outside of a structure, while avoiding enclosed spaces with the commodities to avoid imparting off-odors.

Finally, the last critical severity challenge for most of the behaviorally-based tactics is that there is a large diversity of insects invading food facilities.[8] For example, traps with grain at commercial food facilities captured 14 stored product insect taxa.[36] These various taxa may have idiosyncratic responses to stimuli. For example, *Rhyzopertha dominica* males and females oriented differently (and inversely) to their pheromone, and while males showed no specific orientation to another male that was producing aggregation pheromone 1 day after emerging, they were actually repelled 2 days afterwards.[86] Taking these sort of patterns into account for 10 to 20 species when designing behaviorally-based tactics may be exceedingly difficult. To combat this, behaviorally-based strategies will need to use stimuli that are broad spectrum (e.g. are effective for multiple species), or at least specific combinations of species that are problematic for a given type of facility.

2.3.2 Moderate challenges

Additionally, there are five challenges classified as moderate severity (Table 2). One of these is potentially high local insect abundance around food facilities. It is well-known that behaviorally-based management tactics tend to break down under high population pressure.[87] However, behaviorally-based tactics should be implemented in the context of holistic IPM programs to provide multiple hurdles to pest infestation. Thus, incorporation of other types of tactics may ameliorate this issue. For example, structural fumigations and intensive sanitation programs could drive high population levels down, while proper sealing could reduce immigration, allowing behaviorally based programs to maintain low population levels and reduce new infestations. Another moderate challenge may be the additional expenses, knowledge, and time necessary to deploy behaviorally-based strategies and/or investment in education of stakeholders in how to effectively deploy tactics. While some pheromones are easy to synthesize, other types of pheromone lures (especially high dosage ones) can be expensive,[27] because it is difficult to isolate and purify specific stereoisomers for effective usage against pests as in the case of 7-hydroxy-4,-6-dimethyl-3-nonanone (e.g. serricornin).[88] However, costs for at least some species have come down significantly over time, though this is likely partially a function of pheromone chemistry. Larger compounds containing more stereoisomeric centers are often harder to purify. Other potential solutions are to replace some of the pheromones in a lure with lower cost attractive stimuli and/or target behaviorally-based strategies to value-added parts of the postharvest supply chain where facilities may have more money to spend on pest management, or where economic losses may be the greatest. In addition to costs associated with pheromone production, there is the inherent difficulty in the associated chemical analysis, as well as assessing insect physiology, and behavior in a suite of tests that often must span from laboratory to the field in an iterative approach. This process may delay advances by months or years.

Another moderate challenge may be that food sources at a facility where insects are feeding are in direct competition with any additional stimuli deployed at a facility.[11] In this case, lures could be augmented with additional stimuli such as gustatory, visual, or tactile cues. For example, it is known that *Tribolium castaneum*, *L. serricorne*, and some moths are positively phototactic.[89–91] Further, prior work has found that the most attractive wavelength of light to *Tribolium castaneum* was 390 nm, and that its inclusion increased trap capture by 19% over traps with just a pheromone lure.[92] Moreover, *Tribolium castaneum* were found to visit tall, dark, vertical silhouettes, and trap capture was elevated with traps placed against a dark compared to a white background.[93] Visual stimuli have also been evaluated for other stored product species, including psocids,[94] but there has generally been low adoption of light stimuli because of cumbersome cords, lack of electricity in some areas of food facilities, and the fact that some facilities keep their lights on permanently, reducing the effectiveness of light stimuli. As a result, adoption of light traps has been relatively low in the postharvest environment. However, new, smaller, more energy efficient light-emitting diodes (LEDs) are being released that have potential to renew the push for incorporating light stimuli. Alternatively, sanitation protocols could be more regular and improved at a facility so there are fewer food sources and sites of spillage or food dust accumulation.

Fürstenau and Kroos[95] recently discussed the efficacy gap between alternative and conventional tactics that must be overcome in order to increase adoption of biologically-based tactics, which we have included here and classified as a moderate challenge (Table 2). It is important that any behaviorally-based management approach be compared to the conventional system alternative in order to provide convincing data that alternative tactics are equally or more effective than existing management tactics. Finally, another moderate challenge is to improve the longevity of semiochemicals used in lures. It is important that behaviorally-based strategies be low maintenance, and if semiochemicals are in a slow release formulation, there will be fewer lure changes and reduced costs for stakeholders, which may improve adoption. This may be done by improving the lure matrix or dispenser functionality (e.g. timed misting, etc.). Specifically, semiochemicals can be extruded in a matrix that restricts diffusion according to the size of the specific pheromone, while for multi-component pheromones, two different matrices may be required to achieve appropriate release rates.

2.3.3 Low severity challenges

Lastly, six challenges were identified as low severity (Table 2), which may be easier to overcome than the ones mentioned earlier. For example, the temperature inside rice mills is generally 1 °C warmer than the surrounding environment, though this is significantly more during cooler times of the year;[77] nevertheless, activity of *Tribolium castaneum* inside rice mills generally correlates with the mean temperature outside the mill, and temperature differences may not always be consistent.[81] Over 5 years, the internal air temperature in flour mills was consistently warmer than the external air temperature, but the magnitude of this varied by season, with facilities separated by a few degrees in summer and 20–25 °C in winter.[80] By contrast, this may not be consistently true for other types of food facilities. Changes in temperature outside the facility may also modulate risk of immigration from the external environment, with correspondingly lower risk in winter, for example. However, these warmer inside temperatures may result in faster depletion of lures and more frequent maintenance for traps. Food facilities often consist of discrete enclosed environments, which may require that lures are deployed in multiple locations, or deployed in different ways depending on whether they are intended to protect bulk storage or structures. Air flow around different types of facilities may also be important for the dispersion of pheromone, and while it has been evaluated for at least a single species and trap type,[76] research should be expanded in this area, as it remains an important gap in knowledge about optimal placement of lures. Some facilities may have 'no entry' grain bins (e.g. where no access is permitted once the bin has been filled with commodity), which may prevent certain kinds of management. Clustered and patchy distribution of pests[96] may mean that lures must have a long plume reach, that devices to actively disperse the pheromone may be required, or that area-wide implementation of tactics may be needed.

3 POTENTIAL CONCERNS ABOUT USE OF ATTRACTANTS AND THEIR MITIGATION AT FOOD FACILITIES

3.1 Postharvest facilities as sources of food cues

Some stakeholders have expressed varying levels of concern that the use of attractants in facilities could draw insects into facilities and subsequently cause infestations that would not otherwise be there. This is a valid concern, and should be addressed directly by incorporating applicable experiments during the development and assessment of behaviorally-based strategies at food facilities. Nevertheless, our working hypothesis is that there are a variety of attractive odors already at facilities by virtue of handling food commodities (Fig. 1(A)). For example, in the main processing and bulk storage structures, there are an abundant amount of food kairomones emitted that may then drift outwards, attracting pests from the landscape. Most food postharvest storage structures, including grain bins, elevators, warehouses, and others are not airtight, and during windy days, even an attempted phosphine fumigation may fail, because wind blows it out from the structure.[97] Likewise, even food facilities with strict sanitation protocols may have sites of spillage, which emit their own blend of volatiles (Fig. 1(A)), and may contain a mix of food cues as well as microbially-produced volatiles with enhanced attractive properties to stored product insects.

Sites of spillage are not just emitting volatiles, but are also sites of reproduction for insects, which may colonize them, and then individuals may emit aggregation pheromones as in the case of many stored product beetles[70] (Fig. 1(A)). For example, *R. dominica* (F.), the lesser grain borer, emitted almost 20-times more aggregation pheromone and in a different ratio of stereoisomers when on a favorable host, such as those likely to be found at a food facility, when compared to a host found in a natural landscape.[98] When *R. dominica* males were seeded on hosts, many more conspecifics were attracted to the males producing aggregation pheromone on wheat than on wild hosts.[99] Thus, initial colonization of a spillage site by *R. dominica*, may result in subsequent colonization by more conspecifics, which may ultimately spill over into the protected commodities at food facilities.

With these abundant stimuli permeating the space around a food facility, it is still unknown from how far insects will be attracted to a location, or how frequently they are, but it is quite clear that some species disperse on the order of multiple to many kilometers,[100] and likely frequently.[101] While recent research has shown that walking insects can only respond to attractants from within a very short distance,[102] it is expected this may be farther for insects orienting while flying during long-range dispersal.[79] In addition, surrounding a food facility, there may also be hosts or field crop production in the environment that emit attractive volatiles and act as refugia for dispersing insects (Fig. 1(A)). The volatiles from the landscape are neither expected to be as attractive nor as abundant as those produced by food commodities at food facilities, and insect response is not expected to be as strong.[99] Thus, food facilities stand out as highly preferred areas in some landscapes where attractive semiochemicals (including food kairomones and insect pheromones) have, for all intents and purposes, already been deployed in large amounts from the insect's perspective.

3.2 Managing risk and addressing stakeholder concerns

The challenge in reassuring stakeholders with the deployment of additional semiochemicals lies in generating scientifically and economically valid data. Food facilities are already an attractive location for stored product insects, so the question becomes how that 'risk' should be managed. While sanitation and sealing may reduce risk, it will probably not eliminate it. An additional tactic may be to add more attractive odors in different locations at a facility to manipulate insect movement patterns and distribution to be more favorable to the protection of stored durable goods. Thus, food facilities have the opportunity to turn insect behavior against the pests by manipulating which populations move where and when.

However, this requires first generating, then presenting detailed information to stakeholders on a variety of topics in multiple ways to reassure managers at food facilities that they are not endangering their operations (Table 3). One of the top concerns by stakeholders may be bringing in insects in from the landscape that would not otherwise be there. This can easily be evaluated through mark-release-recapture studies[103] and a better understanding of factors that influence dispersal of insects around food facilities, pheromones, and traps. Another concern may be spillover of insects into a commodity near a pheromone source, which could be determined by assessing the zone of aggregation.[26] The spillover of individuals near a trap or pheromone may be the result of taxis to the stimulus being terminated when some threshold concentration of the stimulus is reached, as is common with aggregation pheromones.[26,70] These individuals may then encounter sites of spillage adjacent to the pheromone source or trap, decide to oviposit, and then produce progeny in the spillage as discussed with *R. dominica* earlier. Other stakeholders may be more concerned with progeny production in and near a trap, which could be determined by rigorously testing the kill mechanism in the trap.[104] When there is any discussion of odors diffusing and permeating a space, stakeholders will often want to ensure that there are no deleterious effects on finished products from the commodities. This could be performed for example by convening a sensory panel to evaluate any off-odors associated with products made by commodities exposed to such odors (e.g. as has been done with other pest management techniques[105]), though this may become very complex at large facilities where the sheer number of commodities managers deal with is large.

Importantly, the cost–benefit ratio of using behaviorally-based tactics needs to be considered in appropriate context for each food facility. For example, there may be less willingness to adopt intensive tactics for bulk storage or at points near the beginning of the supply chain, but more willingness if dealing with high-value

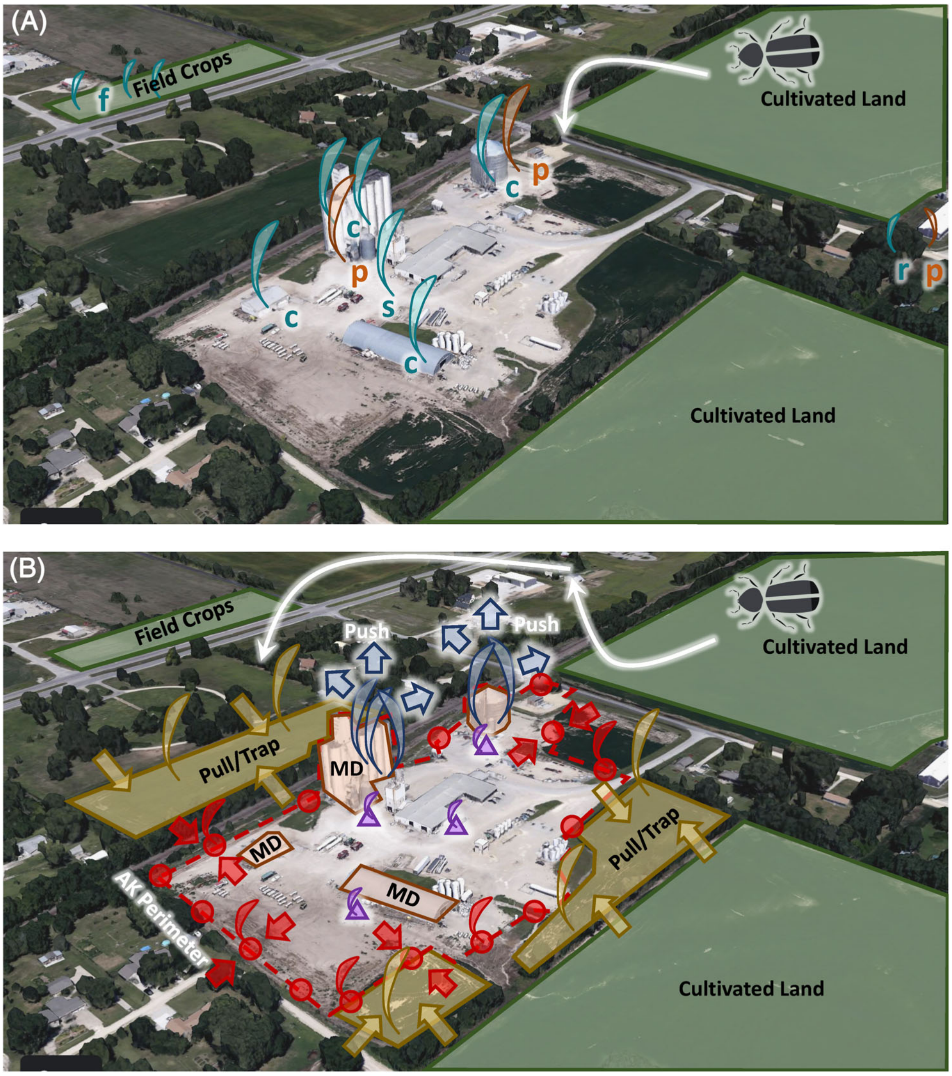

Figure 1. (A) Food odor plumes (kairomones, teal) in and around a food facility, including from the protected commodity (c), sites of food spillage (s), natural host refugia in the landscape (r), and preharvest commodities in the field (f); pheromones (orange) may also be produced by pest insects that have infested commodities (p). Size of the plume corresponds with expected strength of attraction by stored product insects. In an unguarded facility, pests are expected to directly be able to immigrate and infest commodities. (B) vision for a robustly implemented behaviorally-based IPM program, including mating disruption (MD) to protect the main commodity within structures (orange), attract-and-kill based interception traps at the perimeter of the facility (red), a repellent to 'push' away insects from the main buildings (blue), attractants deployed in adjacent areas or unused land to 'pull' pests that have been diverted (yellow), and semiochemical-baited traps for long-term monitoring of pest pressure at key parts of the facility (purple). The size of pheromone plume is proportional to reach of semiochemicals deployed. In a facility guarded by behaviorally-based tactics, pests are expected to be diverted away from protected commodities.

commodities subject to consumer complaints near the latter end. Another potential concern may be worker safety when in an enclosed space with a large amount of pheromone, for example dedicated to mating disruption or the safety of food in spaces that have been treated with large amounts of pheromone. However, Lepidopteran pheromones generally have negligible mammalian toxicity, and there is a strong track record of safety of mating disruption programs,[106] with the USEPA stating that up to 2001, there had been no safety incidents with pheromones by workers.[107] This is in stark contrast to existing tactics in stored products, such as fumigation with phosphine, which is comparatively much more hazardous to worker's health if mistakes are made in applications.

An important concern may be whether behaviorally-based tactics are equally effective against both phosphine-resistant and phosphine-susceptible populations. Recent research has demonstrated there may be consistent differences in some mobility parameters among phosphine-resistant and -susceptible populations.[108] For example, susceptible *R. dominica* were found to move significantly faster than resistant conspecifics, while susceptible *R. dominica* and *Tribolium castaneum* showed reduced climbing capacity compared to resistant strains. Moreover, susceptible *R. dominica* made more flight attempts than resistant conspecifics. By contrast, there were no consistent in most mobility parameters for *T. castaneum*.[108] These consistent differences in mobility among strains and species raise the possibility that behaviorally-based tactics may be more or less effective when targeting certain groups of insects. If resistant *R. dominica* are slower and less likely to initiate flight, then it is possible that a semiochemical-based trap may be less likely to effectively capture and remove them from the foraging population. Thus, when evaluating behaviorally-based tactics, evaluations should be made with both phosphine-resistant and -susceptible populations.

Table 3. A list of potential stakeholder concerns about deploying a behaviorally-based tactic at a food facility, and potential research to alleviate concerns

Concern	Proposed solution
Bringing in insects that would not otherwise be present	Evaluate distance of attraction by insects to a food facility, and identify environmental factors that affect plume reach and trapping area
Spillover of insects into commodity	Determine area of aggregation around pheromone source
Ability of insects to reproduce in or near trap	Consider progeny production in and near traps
Cost of deployment (time and money)	Ensure cost–benefit ratio makes sense; collaborate with agricultural economists
Semiochemicals imparting off-odors to commodities	Evaluate strategy with sensory panel to confirm no off-odors imparted on finished products
Safety profile of semiochemicals to workers and food safety	Assess safety of semiochemicals and treated commodities in animal models; where possible, use biorational semiochemicals or those with very low mammalian toxicity
Knowledge required to effectively deploy tactics by food facilities or pest control companies	Produce high quality outreach and extension materials, develop comprehensive education programs to communicate information
Education and adoption in distant or remote operations	Increase accessibility of extension materials, communicate in multiple formats, development of a mobile app for stored product integrated pest management (IPM)
Effectiveness of behaviorally-based tactics against phosphine-resistant insect populations	When collecting data on behaviorally-based tactics, include assessments of both phosphine-resistant and -susceptible populations

Lastly, rigorous, forward-looking, and comprehensive education programs will need to be undertaken to support adoption of new technology, both for direct stakeholders in the postharvest supply chain and for pest control operators who may be in charge of pest management programs at specific sites. This may involve the development of high-quality education and extension information delivered through multiple media to be able to reach remote locations. Multi-tiered, complex IPM programs are already being developed in high-value specialty crops such as for tree fruit,[109] thus it may be worthwhile for stored product entomology to look to other systems as a model for how to improve adoption of holistic IPM programs.

4 A VISION FOR ROBUST BEHAVIORALLY-BASED MANAGEMENT STRATEGIES FOR STORED PRODUCTS

Up to this point, there has been no clearly articulated vision for areawide implementation of behaviorally-based tactics at postharvest food facilities. However, in other systems, it is clear that a variety of tactics are possible and highly effective. As more information is developed about semiochemicals and their effectiveness in and around food facilities, it will become increasingly possible to deploy them singly or in concert to systematically manipulate pest populations and protect commodities, depending on the type of facility (Fig. 1(B)). For example, mating disruption, attract-and-kill, and push–pull could all be simultaneously deployed to provide multiple hurdles against pest infestation at a facility (Fig. 1(B)), and coupled with monitoring traps. This could work by protecting enclosed structures with commodities using mating disruption, assuming mating disruption can be expanded to other key species successfully. Central structures with commodities could additionally be protected with a repellent to 'push' immigrating insects away that could then be diverted (e.g. 'pulled') into adjacent plots with attractive stimuli and coupled with ways to remove individuals from the foraging population, or to at least retain them. On the perimeter of the area with the commodities, a line of attract-and-kill-based interception traps could be deployed to divert any insects not already captured by stimuli in adjoining areas. Finally, monitoring traps with small dosages of attractive stimuli could be deployed in key locations to provide long-term data on insect abundance within the perimeter of the facility to identify specific problem areas, as has been done already with commercial rice facilities, flour mills, and other facilities.[77,80,110] With multiple different stimuli, deployed in a variety of ways at different scales, and incorporating multiple types of kill mechanisms, these behaviorally-based tactics could significantly strengthen existing IPM systems. They may also function to help ameliorate pest problems brought into a facility from commodities that were infested elsewhere by redirecting where insects move once a commodity is stored. Their adoption may prevent the development of insecticide resistance, and might significantly decrease the need for fumigation, especially if implemented along with other IPM strategies, such as grain protectants, aerosols, residual sprays, fumigation,[15] and other novel tactics.[36,111] However, it is clear that behaviorally-based tactics must be tailored to individual food facilities, and only those tactics that are compatible with existing management efforts and facility operations should be used. Finally, this also means that the use of behaviorally-based management tactics cannot impede food quality or result in elevated measures of insect presence (e.g. insect-damaged kernels, insect fragments, etc.) during inspections after a shipment of commodity leaves a facility.

5 NEEDS FOR NOVEL STIMULI AND SYSTEMS IN FUTURE BEHAVIORALLY-BASED STRATEGIES FOR STORED PRODUCTS

5.1 The case for novel stimuli in stored products

Before this vision can come to fruition, currently known stimuli will need to be more available, and be used more efficiently. In addition, we also require more effective, novel stimuli. Fifty-eight pheromones are known from stored product insects, but commercially available lures only attract 27 species.[70] Increasing the number that are commercially available would be a good first step in allowing for the development and evaluation of behaviorally-based tactics. There is strong interest in developing behaviorally-based tactics for a variety of species, including for biosurveillance of the quarantined *Trogoderma granarium* (Everts)[112–114] and an emerging pest of concern to industry, red-legged ham beetle, *Necrobia rufipes* (De Geer).[115] In some cases, it may be not be commercially feasible to produce a particular kind of pheromone if there is not a robust market for it. However, increased and close collaboration among government,

Table 4. Summary of optimal stimuli, traps, and kill mechanisms for behaviorally-based management tactics

	Traits of optimal		
Tactic	Stimuli	Trap	Kill mechanism
Attract-and-kill	Attractive to a large diversity of species, long-lasting, inexpensive, attracts individuals to a very spatially restricted area with no spillover into commodity, dose-dependent attraction, range of attraction is around a food facility but does not bring in insects from farther away	Behaviorally-compatible with multiple species, compact, easily deployed without special equipment, impervious to weather or grain dust; alternatively, no trap needed, applied as gel	Knockdown and kill is immediate or rapid, contact ensures no progeny production, recovery unlikely, multiple active ingredients available to be able to rotate and prevent the development of resistance
Mating disruption	Effective against multiple species, large plume reach and good dispersion without human intervention, just one deployment necessary for a season, inexpensive to deploy, effective even at lower concentrations	None required	None required
Mass trapping	Attractive to a large diversity of species at low dosages, long-lasting, inexpensive, attracts individuals to just the trap with no spillover into commodity, range of attraction is around a food facility but does not bring in insects from farther away, low density of traps required	Trap consists of an effective existing commercially-available design that can also be used for monitoring	Knockdown and kill is immediate or rapid, contact ensures no progeny production, recovery unlikely, multiple active ingredients available to be able to rotate and prevent the development of resistance
Repellency	Repellent must be effective at low concentrations, not impart off-odors to commodities that they are protecting and/or have no deleterious effects on the sensory qualities of end products, and must repel at longer distances	None required	None required
Push–pull	Both attractant and repellent required. Attractant as for attract-and-kill above. Repellent must be effective at low concentrations, not impart off-odors to commodities that they are protecting and/or have no deleterious effects on the sensory qualities of end products, and must repel at longer distances	Trap only required for 'pull' part in adjacent location. Behaviorally-compatible with multiple species, easily deployed without special equipment, impervious to weather, dirt, or grain dust; alternatively, no trap needed, applied as gel, crop, or container of commodity	Kill mechanism only required for the 'pull' part. Knockdown and kill is immediate or rapid, contact ensures no progeny production, recovery unlikely, multiple active ingredients available to be able to rotate and prevent the development of resistance; alternatively, retention is permanent

academia, and industry will help leverage existing and new technology into strong, reliable behaviorally-based tools.[116]

Finally, there is still a need for novel, improved stimuli to manipulate the behavior of stored product insects. For some species, particular kairomones may range from strong attraction to no attraction at all, as in the case of *Tribolium castaneum*.[78] While the odors of intact or damaged grains have been found to be attractive to a variety of species,[117] and are suitable for use in monitoring traps,[76,80] they may not be ideal candidates in behaviorally-based tactics at food facilities, because of competition with background food odors (e.g. Challenge #5 in Table 2). We have compiled properties of optimal stimuli for use in a range of behaviorally-based tactics (Table 4). In some cases, the properties of optimal stimuli are similar among different behaviorally-based tactics, while in others, there may be unique properties that make a particular volatile more suitable for one approach over another. In focusing on novel stimuli, these traits should be prioritized and included in evaluations. Such novel stimuli may also serve to lure insects out of hiding in commodities or spillage and into the open or a trap inside a facility, where they can be managed better or eliminated from the foraging population.

5.2 Future directions

One promising suite of candidate compounds may be microbially-produced volatile organic compounds (reviewed in Davis *et al*.[118]). These microbial volatiles may originate primarily from bacteria and fungi present on commodities. Prior work has shown that microbial volatiles from fungi are attractive to a range of stored product cucujid beetles,[119] as well as other stored product species.[120] The ability of stored product insects to respond to microbial volatiles may be conserved across a range of stored product insect lineages as a result of their shared evolutionary history.[70] Many stored product insects originally fed on small animal (e.g. mammals, birds, insects, etc.) caches of food before the advent of anthropogenic agriculture; one cue that may have been present in most of these caches was the presence of microorganisms emitting volatiles, because caches were often in moist environments, and animals have been shown to frequently forget where they store their food.[121]

There has been ongoing work attempting to engineer plants to produce certain volatiles for the benefit of pest management,[122] and similar ecological engineering may be possible using microbes.[123] Optimizing microbial volatile emissions by a microbial species, while minimizing its detrimental effect on stored grain, may allow for the use of self-renewing volatile sources in a behaviorally-based trap that may have the potential to last longer and be more effective than conventional lure formulations. Unfortunately, little work has explored this potential avenue in the context of stored products.

Importantly, there may also be other novel classes of stimuli, such as those from wood volatiles. While some stored product insects evolved as feeders on animal caches, others such as *Prostephanus truncatus*,[10] originally evolved as pests of woody vegetation. Recent work has found volatile bouquets from the woody species, *Castanea crenata*, *Magnolia obovata*, *Paulownia tomentosa*, *Prunus jamasakura*, and *Zelkova serrata* were equally or more attractive to *Tribolium confusum* du Val than food cues, including various types of flour.[124] These volatiles may also be relatively unique at food facilities, and serve as useful new stimuli for inclusion in behaviorally-based tactics.

In order to identify promising bouquets, microbial species, or specific compounds, a streamlined chemical ecology workflow should be used. One way to comparatively more efficiently screen complex microbial (and other) blends of headspace volatiles for potential new attractive compounds may be to use a gas chromatograph coupled with an electroantennographic detector[125] to determine those compounds detected by a variety of stored product insects of different lineages, and then to follow-up with a subset of consensus compounds that are perceived by major species using rapid behavioral assays.[78] Some of these rapid assays may include 2-min trials per individual to assess taxis in a wind tunnel[36] or miniature wind tunnel,[112] as has been done in prior work for stored product insects. Finally, the most promising compounds with greatest attraction or repellency should be validated in realistic field tests. While this may not be a trivial amount of work, it is important to do in order to move the state of the art forward.

This contribution has laid out a framework for proceeding with the development of behaviorally-based tactics. Some of the key challenges, stakeholder concerns, and properties of ideal stimuli may be used as a starting point for further research on this topic. Whatever the specifics of new behaviorally-based tactics, it is clear that (i) they should be cost-effective for stakeholders, (ii) not endanger the protection of commodities in the postharvest supply chain, and (iii) be easy to implement with limited training or expertise. There has been an increasing recognition that you cannot uncouple the cultural systems responsible for agriculture from the biological components, and thus, obtaining stakeholder buy-in for these programs, and leveraging connections with other parts of the research enterprise will become increasingly important in the future. Furthermore, it will also become more important to evaluate behaviorally-based strategies in the context of other environmentally-friendly IPM tactics such as heat treatments, aeration,[126] and others in order to provide multiple hurdles against pest infestation. Overall, while there is still much work to do in developing behaviorally-based tactics for stored products, it is clear that these tactics have much potential to help alleviate the losses of key fumigants for protection of commodities.

ACKNOWLEDGEMENTS

This work was funded, in part, by a United States Department of Agriculture (USDA), National Institute of Food and Agriculture, Crop Protection and Pest Management Grant #2017-70006-27262. The use of trade names is for the purposes of providing scientific information only, and does not constitute endorsement by the USDA. The USDA is an equal opportunity employer.

SUPPORTING INFORMATION

Supporting information may be found in the online version of this article.

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