The Use of Push-Pull Strategies in Integrated Pest Management

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Abstract

Push-pull strategies involve the behavioral manipulation of insect pests and their natural enemies via the integration of stimuli that act to make the protected resource unattractive or unsuitable to the pests (push) while luring them toward an attractive source (pull) from where the pests are subsequently removed. The push and pull components are generally nontoxic. Therefore, the strategies are usually integrated with methods for population reduction, preferably biological control. Push-pull strategies maximize efficacy of behavior-manipulating stimuli through the additive and synergistic effects of integrating their use. By orchestrating a predictable distribution of pests, efficiency of population-reducing components can also be increased. The strategy is a useful tool for integrated pest management programs reducing pesticide input. We describe the principles of the strategy, list the potential components, and present case studies reviewing work on the development and use of push-pull strategies in each of the major areas of pest control.

INTRODUCTION

IPM: integrated pest management

Biological control (or biocontrol): the use of natural enemies of the pest in pest management

Semiochemical: chemicals that convey a signal from one organism to another so as to modify the behavior of the recipient (also known as behavior-modifying chemicals)

Conservation biocontrol: habitat management to provide conditions that promote biological control

The term push-pull was first conceived as a strategy for insect pest management (IPM) by Pyke et al. in Australia in 1987 (115). They investigated the use of repellent and attractive stimuli, deployed in tandem, to manipulate the distribution of *Helicoverpa* spp. in cotton, thereby reducing reliance on insecticides, to which the moths were becoming resistant. The concept was later formalized and refined by Miller & Cowles (97), who termed the strategy stimulo-deterrent diversion while developing alternatives to insecticides for control of the onion maggot (*Delia antiqua*). In this review, we retain the original terminology. We describe the principles and components of the push-pull strategy, summarize developments over the past 20 years since the term was coined, and discuss how the strategy may contribute to addressing the global demand for the reduction of toxic materials in the environment as part of IPM strategies in the future.

PRINCIPLES OF THE PUSH-PULL STRATEGY

Push-pull strategies use a combination of behavior-modifying stimuli to manipulate the distribution and abundance of pest and/or beneficial insects for pest management. Strategies targeted against pests try to reduce their abundance on the protected resource, for example, a crop or farm animal. The pests are repelled or deterred away from this resource (push) by using stimuli that mask host apparency or are repellent or deterrent. The pests are simultaneously attracted (pull), using highly apparent and attractive stimuli, to other areas such as traps or trap crops where they are concentrated, facilitating their elimination (**Figure 1**). Most work on push-pull strategies has targeted pest behavior, so this review relates mostly to pests, rather than to the manipulation of beneficial organisms. However, the latter case aims to establish a concentrated population on the protected resource to promote biological control, and although stimuli similar to those utilized in the former case are used to achieve this, they act to push the beneficials out of the surrounding area and pull them to where they are required for control. The strategies therefore comprise a two-pronged mechanism to direct the movement and affect the distribution and abundance of the insects (push-pull). Because the stimuli used to achieve this generally act by nontoxic mechanisms, integration with population-reducing methods is also usually needed when the strategies are targeted at pests.

Push-pull strategies bring together various elements of different pest management tactics and provide a framework for their effective deployment. Behavioral manipulation methods for insect pest management have been previously reviewed (50). Behavior-modifying stimuli for use in push-pull strategies primarily include visual and chemical cues or signals. These are discussed in the following section and summarized in **Figure 1**. Chemical stimuli, in particular semiochemicals, have the most versatility and potential for use in pest management and have also been well reviewed (1, 2, 38, 55, 110). Habitat diversification strategies (intercropping and trap cropping) have attracted much interest as pest management strategies (5, 62, 127). These also work through behavioral manipulation, and in this review we consider them methods of delivering various behavior-modifying stimuli. For example, trap crops can be plants of a preferred growth stage, cultivar, or species that divert pest pressure from the main crop because they are more attractive (62, 127). The mechanisms underlying differential pest preference usually involve certain visual or semiochemical stimuli. Trap crops can therefore be used to deliver attractive pest-behavior-modifying stimuli. Biological control and especially conservation biocontrol are additional important strategies in IPM (31, 81, 131, 139) and can be used with push-pull strategies as population-reducing methods and are also discussed below.

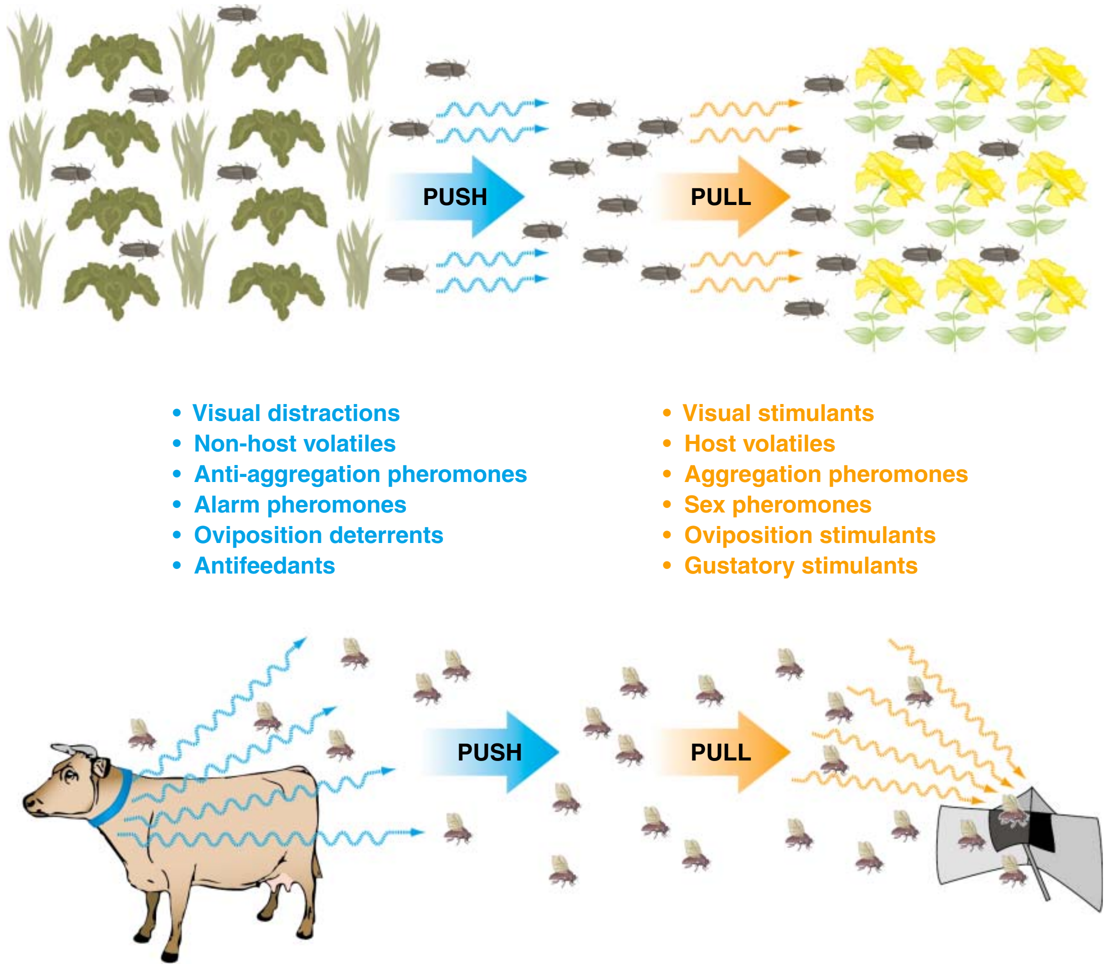

Figure 1

The push-pull strategy: diagrammatic representation of the components and generalized mode of action.

The principles of the push-pull strategy are to maximize control efficacy, efficiency, sustainability, and output, while minimizing negative environmental effects. Each individual component of the strategy is usually not as effective as a broad-spectrum insecticide at reducing pest numbers. However, efficacy is increased through tandem deployment of push and pull components (36, 47, 89, 97, 100, 115). By concentrating the pests in a predetermined site, the efficiency and efficacy of population-reducing methods can also be maximized. Population reduction by biological control methods or highly selective botanicals is preferred to broad-spectrum, synthetic insecticides. The use of renewable sources, particularly plants, for the production of semiochemicals is encouraged and is becoming possible even for insect-produced semiochemicals (10b, 18, 24, 63, 103). In agricultural systems, the goal is to maximize output from the whole system while minimizing cost, and harvestable intercrops or trap crops, rather than sacrificial crops, should be used wherever possible (74).

The development of reliable, robust, and sustainable push-pull strategies requires a clear scientific understanding of the pest's

Pheromone: a semiochemical that conveys information between members of the same species, usually with mutual effects for both the emitter and receiver

Antifeedant (feeding deterrents): a chemical that prevents or interrupts feeding activity by contact chemoreception or by postgustatory effects

DEET: *N*,*N*-diethyl-3-methylbenzamide (or *N*,*N*,diethyl-*m*-toluamide)

biology and the behavioral/chemical ecology of the interactions with its hosts, conspecifics, and natural enemies. The specific combination of components differs in each strategy according to the pest to be controlled (its specificity, sensory abilities, and mobility) and the resource targeted for protection.

COMPONENTS OF THE PUSH-PULL STRATEGY

The function of push components of the push-pull strategy is to make the protected resource hard to locate, unattractive, or unsuitable to the pest. This is achieved through the use of stimuli that effect natural enemy avoidance behaviors and negatively influence host location and host acceptance (feeding and reproduction). These stimuli may act over the long or short range and ultimately lead to the pest being repelled or deterred from the resource or not even approaching it. Long-range stimuli represent the first line of defense: preventing or reducing infestation in the first place. Stimuli that act over the short range, however, can be powerful tools in preventing specific pestiferous behaviors. In pull components of push-pull strategies, attractive stimuli are used to divert pests from the protected resource to a trap or trap crop. The stimuli used to achieve this act mostly over a long distance. However, short-range stimuli can be useful additions to arrest and retain the pests in a predetermined place to facilitate the concentration of their populations and to prevent them from returning to the protected resource. The stimuli can be delivered in a variety of ways.

Stimuli for Push Components

In this section, we list and discuss the stimuli that can be used as push components of the push-pull strategy. The stimuli have been grouped according to whether they are visual or chemical cues, whether they are synthetic or plant- or insect-derived semiochemicals, and whether they are usually used to affect host recognition and selection over a relatively long range (visual cues, synthetic repellents, nonhost volatiles, host volatiles, antiaggregation pheromones, and alarm pheromones) or shorter-range host acceptance (antifeedants, oviposition deterrents, and deterring pheromones).

Visual cues. Manipulation of host color, shape, or size to inhibit host orientation and acceptance behaviors of pests in IPM has rarely been used, as these traits usually lack specificity and are often impractical to change in hosts (50). However, by understanding how pests use visual stimuli, these aspects can at least be minimized or even disrupted (6, 32, 114).

Synthetic repellents. Repellents such as MNDA (*N*-methylneodecanamide) and DEET (*N*,*N*-diethyl-3-methylbenzamide, often referred to as *N*,*N*,diethyl-*m*-toluamide) are commercially available and may be used in push-pull strategies against cockroaches and invasive lady beetles (100, 104, 120). DEET is considered the most effective commercial repellent available and is used primarily to repel hematophagous insects. However, there are concerns over its safety and alternatives are sought. 2-(2-Hydroxyethyl)-1-piperidinecarboxylic acid 1-methylpropyl ester (picaridin, also known as KBR 3023) has recently been approved by the Centers for Disease Control and Prevention in the United States as an alternative repellent for mosquitoes.

Nonhost volatiles. Volatiles derived from nonhosts can be used to mask host odors or evoke nonhost avoidance and repellent behaviors. Plant essential oils such as citronella and eucalyptus are commercially produced as repellents against hematophagous insects (50a). PMD (*p*-menthane-3,8-diol), isolated from lemon eucalyptus oil of *Eucalyptus citriodora*, has been registered by the U.S. Environmental Protection Agency for use against mosquitoes and provided similar protection to repellents containing low levels of DEET

(10a). Camphor showed potential as a repellent for a push-pull strategy developed for the multicolored Asian lady beetle (*Harmonia axyridis*), an introduced aphid biocontrol agent in the United States that has become a nuisance pest in buildings in its overwintering aggregative phase (121). There is also interest in developing essential oils as repellents in push-pull strategies against phytophagous pests (24, 91). Although these oils are relatively nontoxic and safe, the duration of their effect is often limited (64, 50a, 121). Nonhost plant rejection, mediated by specific nonhost volatiles, has been demonstrated using synthetic volatiles: green leaf volatiles and specific bark volatiles from angiosperm trees reduced colonization of conifer hosts by bark beetles (10, 58, 147).

Host-derived semiochemicals. Insects recognize suitable hosts by using key volatiles that are often present in specific ratios (26). Directed host orientation ceases if host odors are presented in inappropriate ratios, as demonstrated for the Colorado potato beetle (*Leptinotarsa decemlineata*) (144). Repellent behaviors may be elicited if the host odors signal poor-quality hosts. For example, the codling moth (*Cydia pomonella*) was repelled by the odors of apple at inappropriate phenological stages (142). Also, herbivore-induced plant volatiles (HIPVs) can deter plant utilization by subsequent herbivores as indicators of competition or induced defenses (17, 40, 42). HIPVs are produced by the plant as indirect defenses that attract natural enemies of the herbivore (see pull section), in addition to an increase in direct physical and chemical defenses that affect herbivore performance (7, 28). For example, methyl salicylate and (*Z*)-jasmone are HIPVs repellent to aphids when released in the field (17, 106).

Antiaggregation pheromones. Antiaggregation pheromones control the spatial distribution of insects and reduce intraspecific competition for limited resources (113). These, and multifunctional pheromones that are attractive at low concentrations but repellent at high concentrations (i.e., in crowded conditions), are produced by several species of bark beetles to optimize host use (22). Formulations of these volatiles can be used in push-pull strategies to control these pests (84, 126).

Alarm pheromones. Some insect species, when attacked by natural enemies, release alarm pheromones, causing avoidance or dispersal behavior in conspecifics (60a, 88, 133). The alarm pheromone for many pest aphids is (*E*)-β-farnesene (*E*βf) (60a, 108). It can be applied to the main crop to repel aphids in the field (24). *E*βf also functions as a kairomone pull for natural enemies of aphids (60a, 108). Increased dispersal can improve efficacy of population-reducing components (57, 122), but because in a push-pull strategy these components would usually be applied to the trap crop, any repellent effects would be counterproductive, highlighting the need for a full understanding of the action of components in the strategy for robustness.

HIPV: herbivore-induced plant volatile

***E*βf:** (*E*)-β-farnesene

Kairomone: an allelochemical of benefit to the receiving species and not the emitter

Antifeedants. Most antifeedants are plant-derived, and their use in IPM has been reviewed previously (50, 64, 67). Several antifeedants, including azadirachtin (the primary active component of neem, derived from *Azadirachta indica*), have toxic effects at normal treatment rates. The drimane dialdehydes polygodial, first isolated from the waterpepper (*Polygonum hydropiper*), and warburganal, isolated from *Warburgia ugandensis*, show repellent activity against several agricultural and some domestic (urban) pests (51, 94, 95). For less mobile pests, a combination of nonsystemic antifeedants and population-reducing agents could be effective (56). A relatively unexplored additional benefit of antifeedants may be that the effectiveness of population-reducing agents is increased by antifeedant-induced stress (67, 98).

Oviposition deterrents and oviposition-deterring pheromones. Oviposition deterrents and oviposition-deterring pheromones

ODP: oviposition-deterring pheromone

Attracticide: combined use of attractive pheromones or host volatiles with biocides, usually insecticides (also known as lure and kill)

(ODPs) are compounds that prevent or reduce egg deposition and so have the potential in push-pull strategies to control species that cause damage through this process or whose imagoes are pestiferous (36, 97, 115). Numerous botanical deterrents isolated from nonhosts have deterred oviposition by pests, and of these, neem-based formulations have been the most studied (47, 86, 89, 115, 119). Petroleum oil sprays and some natural enemy food supplements also deter oviposition by some phytophagous pests (92, 93). ODPs are another class of spacing pheromones that enable female insects to avoid laying eggs on previously exploited hosts, thereby reducing intraspecific competition (83, 102, 113, 146). Application of synthetic ODP of the European cherry fruit fly (*Rhagoletis cerasi*) [*N*-[15-(β-D-glucopyranosyl)-8-hydroxypalmitoyl]taurine] in field trials showed that it can successfully protect cherry trees (*Prunus avium*), and the authors suggested that if 1 in every 10 trees were left untreated and baited with visually attractive sticky traps, the strategy would be more effective (4). This represents a simple push-pull strategy.

Stimuli for Pull Components

In this section we list and discuss the stimuli that can be used as pull components of the push-pull strategy. They are grouped in a manner similar to that used for the push stimuli in the previous section.

Visual stimulants. Visual stimuli are rarely the sole method used to attract pests to traps or trap crops, but they can enhance the effectiveness of olfactory stimuli. Blue and black traps, approximating the size of a mammalian host, are used to control cattle tsetse fly (*Glossina* spp.). Crucial to the development of efficient traps was the finding that black stimulates landing (52). In plant-based strategies, the visual cues related to the plant growth stage can be important (33, 112a). Red spheres (7.5 cm in diameter) mimicking ripe fruit attracted sexually mature apple maggots, *Rhagoletis pomonella* (112a). These traps, coated with either sticky material or contact insecticides and baited with synthetic host odors, have been used successfully in IPM strategies for this pest (114a, 114b).

Host volatiles. Host volatiles used in host location can be used to bait traps for monitoring, mass-trapping, or in attracticide strategies. Hematophagous dipterans are attracted to mammalian-associated volatiles such as CO_2, 1-octen-3-ol and acetone from the breath, and a mix of body odors (52). Using knowledge of host specificity and preferences, the attractiveness of synthetic host odor blends can be maximized. These odors show promise in strategies against various mosquito species and the Highland biting midge (*Culicoides impunctatus*) (14). Host plant odors can also be used in traps or to increase the effectiveness of trap crops (2, 11, 90, 114a, 114b).

HIPVs are often reliable indicators of the presence of hosts or prey to predators and parasitoids and are therefore attractive (pull) to these beneficials (17, 28, 40, 41, 138). Specific HIPVs such as methyl salicylate and (*Z*)-jasmone are attractive to predators and parasitoids and lead to the reduction of pest abundance in the field (17, 65). HIPVs can also be attractive to some herbivores, particularly specialists, although they may be repellent for others, particularly generalists (40, 82).

Sex and aggregation pheromones. Insects release sex and aggregation pheromones to attract conspecifics for mating and optimizing resource use. Both types of pheromones are increasingly important components of IPM, particularly in pest monitoring. Traps baited with these pheromones have a lower detection threshold than other methods and can help in push-pull strategies to determine the timing of stimuli deployment and population-reducing interventions. Male-produced pheromones that attract females over a long range are most useful in direct control strategies. Male-produced sex pheromones from the sandfly (*Lutzomyia longipalpis*) have been identified and synthetically produced and may be used for the control of leishmaniasis in Latin America (63, 130). Aggregation pheromones represent the primary pull stimulus used in push-pull strategies for forest pests (15, 84, 126). Host plant odor can enhance or synergize the attraction of herbivores to sex and aggregation pheromones (21, 44, 84, 117).

Gustatory and oviposition stimulants. Trap crops may naturally contain oviposition or gustatory stimulants, which help to retain the pest populations in the trap crop area. Gustatory stimulants, such as sucrose solutions, have also been applied to traps or trap crops to promote ingestion of insecticide bait (114b, 115). Food supplements may also help to establish populations of natural enemies and influence their distribution (131).

Delivery of Push and Pull Stimuli

Various methods are available to deliver the stimuli used for behavioral manipulation of pests within a push-pull strategy. We list and discuss the most commonly used in this section.

Natural products or nature-identical synthetic analogs. The semiochemicals used are natural products and can be extracted from plants (e.g., essential oils) or insects. Extraction of pheromones from insects, however, is usually impractical beyond experimental purposes. Most commercially used semiochemicals are synthetic but nature identical. Synthetic production of semiochemicals, and their formulation as sprays or in slow-release dispensers, ensures standardization and contributes to the robustness of the strategies. Nevertheless, on occasion the structures are complex and synthesis is uneconomical or impossible on commercial scales. For insect-derived pheromones, production from plants or through plant genetic manipulation is possible (10a, 18, 24, 63, 103) and represents a more sustainable route than synthesis.

Vegetative diversification: intercropping and trap cropping. In plant-based systems, naturally generated plant stimuli can be exploited using vegetation diversification, including intercropping and trap cropping. Push stimuli can be delivered by intercropping with nonhost plants that have repellent or deterrent attributes appropriate to the target pest. Intercropping reduces pest density in crops, principally by disrupting host location through reducing the visual apparency of the host plant (48), by repellent or deterrent semiochemicals in the nonhosts, or both (75, 78). Enhanced natural enemy abundance in diversified systems may also lead to increased herbivore mortality through predation and parasitism (70, 71, 79). Molasses grass (*Melinis minutiflora*) and silverleaf desmodium (*Desmodium uncinatum*), which release repellent HIPVs, are used as intercrops in a push-pull strategy for maize in Africa (70, 74). Intercropping strategies may be economically impractical in temperate systems at present, and success has been highly variable (5, 135). We suggest that this is because, in many cases, the intercropping partners have been selected without *a priori* knowledge of the actual mechanisms of action. The planting arrangement also needs to be carefully designed, with consideration for the colonization ability and mobility of the pest (8, 111).

The host plant stimuli responsible for making a particular plant growth stage, cultivar, or species naturally more attractive to pests than the plants to be protected can be delivered as pull components by trap crops (33, 36, 47, 97, 115). The effectiveness of trap crops can be enhanced further by the application of additional attractive semiochemicals, or these can be applied to part of the main crop so that it can act as a trap crop. This approach has recently been termed semiochemically assisted trap cropping (127) and has been used in several plant-based push-pull strategies (11, 13, 15, 84, 89, 90, 126). Trap crops therefore

Allomone: a semiochemical that favors the emitter and not the recipient

represent a key element of plant-based push-pull strategies. However, the relative attractiveness of the trap crop compared with the main crop, the ratio of the main crop given to the trap crop, its spatial arrangement (i.e., planted as a perimeter or intercropped trap crop), and the colonization habits of the pest are crucial to success and require a thorough understanding of the behavior of the pest (8, 111).

Antixenotic cultivars. Antixenosis represents plant traits that modify herbivore behavior conferring nonpreference. These plant resistance properties are exploited in nonhost intercrops but could also be used to deliver push stimuli in the main crop. Trichomes of wild potato release the aphid alarm pheromone component *E*βf, in which it acts as an allomone and repels aphids at short distances (53). Trichomes of tomato provide mechanical disturbance to small herbivores or produce sticky or toxic exudates (128). Introducing such traits from wild species into cultivated crops has its possibilities, although the effects of these traits on natural enemies need consideration (128).

Plant induction. Plant defenses, including HIPVs, elicited naturally by herbivore damage can be artificially induced by chemical elicitors such as the plant hormones salicylic acid and jasmonic acid (7, 28). The same elicitor may induce resistance in some plant species and increase susceptibility in others (87), and different elicitors can induce different responses in the same plant species (46, 77). Generalist insects may be repelled by induced plants, whereas specialists are attracted (28). A thorough understanding of elicitors' effects on pests and beneficials is therefore important for robustness and could lead to induction of the trap crop to make it more attractive to pests and induction of the main crop to make it less attractive. HIPVs such as the methylated hormones methyl salicylate, methyl jasmonate, and the related (Z)-jasmone can also induce defense in intact plants (17, 25, 46, 82, 134). Such elicitors could be used to switch on plant defense (109). Also, there is evidence that the activation of defenses of plants neighboring induced plants occurs via HIPVs (7, 29, 101, 109); this could pioneer a new aspect in push-pull strategies by exploiting these effects using intercropping and mixed-seed systems.

Traps. Traps used in mass-trapping or attracticide strategies can deliver visual pull stimuli and can be used for releasing olfactory baits that help them compete effectively with the surrounding environmental stimuli. Trap design and positioning are important and can be maximized by adopting a systematic approach in which the behavior of the insect is closely observed (107, 140).

INTEGRATION OF PUSH-PULL STRATEGIES WITH POPULATION-REDUCTION METHODS

The push-pull strategy can easily be incorporated directly into IPM strategies involving generic insecticides (15, 90, 90a, 100, 115, 118, 129). However, less environmentally harmful and more intrinsically benign alternatives are preferred. Insect growth regulators, and botanical insecticides such as neem, have potential use in push-pull strategies (56, 89, 115, 129). The endotoxins of *Bacillus thuringiensis* (Bt) and spinosyn (spinosad) isolated from *Saccharopolyspora spinosa* are commercially available as insecticides, as are genetically modified crop plants expressing the gene for the Bt toxin. Biological insecticides based on entomopathogenic nematodes, fungi, bacteria, and viruses are used in IPM (139), but to date few push-pull strategies have used them (47).

In plant-based strategies, antibiosis can be exploited. Plants that are highly attractive to pests, but upon which they or their larvae are unable to survive, can be used as dead-end trap crops, killing either adult pests or their progeny (73, 127, 143).

Predators and parasitoids can make valuable contributions to biological control in IPM and many are commercially available for inundative release (31, 131). Their use as a population-reducing component in push-pull strategies has been limited so far, but predators of thrips have been tested to improve control in a strategy to protect chrysanthemums in greenhouses (11, 12), and parasitoids contribute to the population reduction of stem borers in maize (70, 71). The importance of population reduction by natural enemies in push-pull strategies is likely to increase in the future as strategies for their behavioral manipulation are developed.

Advances in elucidating the chemical ecology of predators and parasitoids (60, 105, 108) and understanding their habitat requirements (79, 81) may lead to the development of push-pull strategies to manipulate their abundance and distribution for improved biocontrol. For example, natural control of aphids by their parasitoids often fails if the parasitoids do not come into the field sufficiently early to prevent the exponential increase in aphid populations. The aphid sex pheromone component nepetalactone, and aphid HIPVs including (*Z*)-jasmone, to which aphid parasitoids are attracted, can be used to pull parasitoids into the field (112). To push the parasitoids from surrounding areas to crops where they are needed, the recently discovered lady beetle footprint pheromone, tricosane and pentacosane, that is used by the aphid parasitoid *Aphidius ervi* to avoid intraguild predation by the sevenspotted lady beetle (*Coccinella septempunctata*) has potential for use (99).

DEVELOPMENT AND USE OF PUSH-PULL STRATEGIES

In this section, we review a series of push-pull case studies that are under development or used in practice in the major areas of insect pest control (also see **Supplemental Table 1**; follow the Supplemental Material link from the Annual Reviews home page at **http://www.annualreviews.org**). We do not include push-pull strategies in stored-product pest management, as no complete strategies are yet ready for testing (38). In all cases below, the strategy is targeted mainly at the pest itself, although we have included behavioral manipulation of beneficials where appropriate.

Push-Pull Strategies in Subsistence Farming

The most successful push-pull strategy, indeed the only example currently used in practice, was developed in Africa for subsistence farmers. Although directed at resource-poor farmers, lessons can be learned and applied to organic or low-input agricultural systems.

Control of stem borers in maize and sorghum. Maize (*Zea mays*) and sorghum (*Sorghum bicolor*) are principal crops for millions of the poorest people in eastern and southern Africa, and lepidopterous stem borers, e.g., *Chilo partellus*, *Eldana saccharina*, *Busseola fusca*, and *Sesamia calamistis*, cause yield losses of 10% to 50% (69, 74). Agricultural advisory services in the region recommend the use of chemical pesticides, but this is uneconomical and impractical for poor, small-scale farmers (74).

Thousands of farmers in east Africa are now using push-pull strategies to protect their maize and sorghum (74). The strategies involve the combined use of intercrops and trap crops, using plants that are appropriate for the farmers and that also exploit natural enemies. These plants were selected following trials in Kenya of potential host and nonhost plants (70, 71, 75). Stem borers are repelled from the crops by repellent nonhost intercrops, particularly molasses grass (*M. minutiflora*), silverleaf desmodium (*D. uncinatum*), or greenleaf desmodium (*D. intortum*) (push), and are concentrated on attractive trap plants, primarily Napier grass (*Pennisetum purpureum*) or Sudan grass (*Sorghum vulgare sudanense*) (pull).

Molasses grass, when intercropped with maize, not only reduced stem borer infestation, but also increased parasitism by *Cotesia sesamiae* (70, 71). Coupled gas chromatography-electroantennography of stem borers with volatiles from molasses grass showed attractive compounds similar to those found from maize but, in addition, identified five other compounds including (*E*)-β-ocimene and (*E*)-4,8-dimethyl-1,3,7-nonatriene (75, 78). These had already been identified from herbivore-damaged plants (138) and were repellent to stem borers in oviposition assays (70). Desmodium intercrops also produce these compounds, together with large amounts of other sesquiterpenes (75), and furthermore, when intercropped with maize or sorghum, suppress the parasitic African witchweed (*Striga hermonthica*), a significant yield constraint of arable land in the savannah region (72, 72a, 76, 137).

A trap crop of Sudan grass also increased the efficiency of stem borer natural enemies (71). Although stem borers oviposit heavily on Napier grass, it produces a gummy substance that restricts larval development, causing few to survive (73, 143). Six host volatiles were attractive to gravid stem borers: octanal, nonanal, naphthalene, 4-allylanisole, eugenol, and (*R*,*S*)-linalool (75). Recent studies have indicated that the differential preference of moths between maize and sorghum and Napier grass trap crops is related to a large burst of four electrophysiologically active green leaf volatiles released from the trap crop plants within the first hour of the scotophase, the time at which most oviposition occurs (30).

The push-pull strategy has contributed to increased crop yields and livestock production, resulting in a significant impact on food security in the region (74, 76). However, wherever these approaches are developed for the specific needs of local farmers, it is essential that the scientific basis of the modified systems is elucidated (75).

Push-Pull Strategies in Intensive Arable Agriculture

Development of push-pull strategies has been directed mainly at pest problems in intensive agricultural systems, yet owing to the continued reliance on cheap insecticides, at present none are used commercially. However, push-pull strategies are beginning to be seriously considered as plausible pest control solutions that help to manage insecticide resistance threats or negate altogether the need for insecticides.

Control of *Helicoverpa* in cotton. *Helicoverpa* species are polyphagous lepidopterous pests of a wide range of crops. The potential of combining the application of neem seed extracts to the main crop (push) with an attractive trap crop, either pigeon pea (*Cajanus cajan*) or maize (*Z. mays*) ('pull') to protect cotton (*Gossypium hirsutum*) crops in Australia from *Helicoverpa armigera* and *H. punctigera* has been investigated (115). Trap crop efficiency was increased by application of a sugar-insecticide mix. Trap crops, particularly pigeon pea, reduced the number of eggs on cotton plants in target areas and remained effective throughout the trial, although the degree of efficacy varied with growth stage. In trials, the push-pull strategy was significantly more effective than the individual components alone and reduced the number of eggs three days after application of the bait by 92%, 40%, and 78%, respectively, against the untreated control when pigeon pea was at its most attractive stage. The potential of this strategy was supported by a recent study in India. Neem, combined with a pigeon pea or okra (*Abelmoschus esculentus*) trap crop, was an effective strategy against *H. armigera* (47). The nuclear polyhedrosis virus of *H. armigera* was tested on the trap crop in place of insecticides, but this had little effect. Although the authors suggested that such a strategy could be used to manage insecticide resistance in

H. armigera, further studies are needed to verify this.

In future studies in this system, the ability of *H. armigera* to learn should be considered. Because the trap crop represents a small portion of the cropping area, moths are likely to first encounter cotton and subsequently learn to prefer it (39). Experience-induced preferences for plants treated with repellents and deterrents have also been shown in moths (85, 86). More understanding is needed to mitigate this potential limitation; the positioning of the trap crop may be imperative and methods to maximize the preference differential are needed. New products may help in this respect. Recently identified ODPs may become available (83, 146). Natural enemy food supplements that attract and sustain natural enemies in target areas for control are already commercially available. One such product, Envirofeast®, also has oviposition-deterring properties and could provide a combined push and beneficial pull in push-pull strategies (92).

Control of *Sitona lineatus* in beans. *Sitona lineatus*, the pea leaf weevil, is a pest of field legumes in Europe, the Middle East, and the United States. Adult feeding reduces leaf area, while larvae damage the nitrogen-fixing root nodules. Commercially available neem antifeedant (push) and synthetic aggregation pheromone 4-methyl-3,5-heptanedione (21) released from polythene dispensers (pull) were tested as components of a push-pull strategy for *S. lineatus* in field trails using fava beans (*Vicia faba*) (129). Both components altered the abundance and distribution of weevils as predicted. The neem antifeedant was as effective as the insecticide control treatment in reducing the abundance of weevils, but repeated applications were necessary to maintain efficacy. The crop perimeter treated with the aggregation pheromone could be used as a semiochemically assisted trap crop. Alternatively, field margins incorporating clover and other Leguminosae, currently promoted in agri-environment schemes, may be utilized (and would also act as a refuge for predators of *S. lineatus*). In either case, the aggregated population must be controlled with sufficient speed to prevent the adults from redistributing into the crop and producing pheromones to compete with the treatment pheromones.

Control of the Colorado potato beetle in potatoes. The Colorado potato beetle (*L. decemlineata*) is a pest of solanaceous crops, particularly potato (*Solanum tuberosum*), in the United States and mainland Europe. It is attracted to host plant volatiles (42, 43, 82, 144), and early-planted potato trap crops sprayed weekly with a slow-release formulation of an attractant comprising (*Z*)-3-hexenyl acetate, (*R*,*S*)-linalool, and methyl salicylate had significantly more adult beetles, eggs, and larvae than did untreated trap crops (90). Yields of plots bordered by such trap crops did not differ significantly from conventionally treated plots, but they did require 44% less insecticide (90). There is potential for further development of this semiochemically assisted trap cropping tactic within a push-pull strategy.

In greenhouse studies, potato plants treated with a neem-based antifeedant were significantly less preferred by the Colorado potato beetle when deployed in tandem with attractant-treated plants (89). In field studies, rows treated with the attractant were sandwiched between rows treated with the antifeedant within a perimeter trap crop, while the center of the plot remained untreated. This novel arrangement of push and pull stimuli effectively manipulated the distribution of the insects, and the combination of the attractant with insecticide (attracticide) maintained yield compared with conventionally treated plots (90a). The strategy could be further improved by using the Colorado potato beetle aggregation pheromone (*S*)-3,7-dimethyl-2-oxo-6-octene-1,3-diol (45), which recently showed potential in the field and is synergized by the synthetic blend of host volatiles (as above) (44, 80). The synthetic blend could also be used to enhance attraction and subsequent biocontrol by predators such as the spined soldier bug (*Podisus maculiventris*) (41), for which an aggregation pheromone has also been identified (3).

Control of the pollen beetle in oilseed rape. A push-pull strategy based on an attractive trap crop is being developed to protect oilseed rape (*Brassica napus*) from its specialist pests. Turnip rape (*Brassica rapa*) is a preferred host for several oilseed rape pests (9, 33). Simulations using a spatially explicit individual-based model indicated that a perimeter trap crop was the most appropriate arrangement (111). In field trials, a perimeter turnip rape trap crop significantly reduced the abundance of the pollen beetle (*Meligethes aeneus*) in spring-sown plots of oilseed rape compared with plots without a trap crop (34). Growth-stage-related visual and olfactory stimuli were at least partly responsible for the preference for turnip rape by *M. aeneus* (33). Less preferred cultivars of oilseed rape with low proportions of alkenyl glucosinolates (which release low amounts of the volatile isothiocyanates most attractive to pests) were selected as the main crop (33). As push components, nonhost plant volatiles (lavender, *Lavandula angustifolia*) deterred *M. aeneus* in laboratory and field bioassays (91), but antifeedants were ineffective (55). Insecticides can be used to reduce pest populations in the trap crop (9). Parasitoids of the pests also respond to host plant stimuli (68), and their behavior could be manipulated similarly to augment biological control in the trap crop. The entomopathogen *Metarhizium anisopliae* also shows promise for use with the trap crop (27).

Push-Pull Strategies in Horticulture

Push-pull strategies possibly have the most potential in horticultural production because of the relatively confined areas used in operation and the high value of the produce. However, this potential is far from being realized, with only two examples of strategies (for onions and chrysanthemums) in development.

Control of onion maggot on onions. *Delia antiqua* is an important pest of onion (*Allium cepa*) in northern temperate regions, including Canada, Europe, and the United States. Onion culls (small or sprouting unmarketable bulbs) have been used as trap crops to divert oviposition from seedling onions, and the mechanisms for success have been elucidated (36). However, unless fly densities are unusually low, this strategy alone is unlikely to provide adequate control, and a push-pull strategy has been suggested (97). Cinnamaldehyde was selected as a promising oviposition deterrent (37), and a push-pull strategy comprising potted cull onions as trap plants and seedlings treated with cinnamaldehyde (50%, formulated in activated charcoal) was tested in the greenhouse, (36, 97). Each component reduced oviposition significantly after two days, but they had the greatest effect when combined together as a push-pull treatment. There was strong evidence that this was a multiplicative rather than an additive effect, although the strategy still remains to be tested in the field.

Control of thrips on chrysanthemums. Western flower thrips (*Frankliniella occidentalis*) are a serious pest of greenhouse-grown chrysanthemums; they cause feeding damage and transmit viruses, and their presence is unacceptable in flowers for market. The predatory mite *Amblyseius cucumeris* is used in IPM strategies but preys only on first-instar larvae, and control is not always maintained. The predatory bug *Orius laevigatus* has potential for controlling thrips on flowers, and the predatory mites *Stratiolaelaps* (*Hypoaspis*) *miles* and *Gaeolaelaps* (*Hypoaspis*) *aculeifer* showed potential for controlling ground-dwelling thrips stages (11, 12). To make such a combination of predators economical, a push-pull strategy is being developed to push thrips from target plants and concentrate them onto trap plants where the predators are released or maintained.

Volatiles of the nonhost plant rosemary (*Rosmarinus officinalis*) showed potential to be used in this strategy as thrips repellents, but they were also repellent to the predatory bug *O. laevigatus* (11). Negative effects of push-pull components on beneficials should be minimized, so the antifeedant polygodial (extracted from *Tasmannia stipitata*) was selected for use as a push in this system (13). For practical reasons, a pull based on preferred cultivars of chrysanthemum was sought by growers, and a bronze-colored cultivar Springtime was found to be most attractive (11) and provided pollen for the maintenance of predators in the absence of thrips. Trap plants were effective when baited with the attractive host plant volatile *E*βf, reducing infestations on the antifeedant-treated main crop (11, 13). The full push-pull strategy, including the predators, has not been tested.

The thrips alarm pheromone decyl and dodecyl acetate (133) and the recently identified aggregation pheromone (*R*)-lavandulyl acetate and neryl (*S*)-2-methylbutanoate (59) may be suitable as additional push and pull components, respectively. The alarm pheromone increased take-off and decreased landing rates in adults (88), induced larvae to fall from plants, and also reduced oviposition (133). Predators and parasitoids may use these compounds as host-finding kairomones (132), which could further improve predator efficiency.

Push-Pull Strategies in Forestry

Plant protection in forests represents possibly the greatest control challenge for push-pull strategies because of the large and often inaccessible areas involved. However, pheromone-based strategies to control bark beetles (Scolytidae) in conifers were suggested (23, 61) and have shown considerable promise.

Control of bark beetles on conifers. Bark beetles are serious pests of coniferous trees in many northern temperate regions, including Canada, Europe, and the United States. Several species exist and their chemical ecology has been reviewed (22). Aggregation pheromones are in operational use for monitoring purposes, in mass-trapping, and in strategies that concentrate pest populations on trap trees that are then destroyed (22). Antiaggregation pheromones that induce dispersal from existing infested areas and exclude beetles from environmentally or socially important areas are being investigated (22).

A combination of both aggregation and antiaggregation pheromones was used in a push-pull strategy based on mass-trapping to control an infestation of *Ips paraconfusus* that was decimating a stand of rare Torrey pine trees (*Pinus torreyana*) in California (126). Lindgren funnel traps baited with slow-release formulations of the commercially available aggregation pheromones (*R*,*S*)-ipsenol, *cis*-verbenol, and ipsdienol as (*S*) isomer (97%) were placed on dead trees in a row opposite the stand of trees to be protected. Trap placement on dead trees reduced the risk of spillover infestation onto healthy trees and provided suitable visual cues for additional attraction of the beetles. The antiaggregation pheromones (*R*,*S*)-ipsdienol and verbenone as (*S*) isomer (86%) were released from dispensers placed inside the uninfested stand, parallel to the funnel traps. More than 330,000 *I. paraconfusus* were caught over the period of operation, and tree mortality was eliminated.

In a similar study, the antiaggregation pheromone 3-methylcyclohex-2-en-1-one (push) and traps baited with aggregation pheromones (frontalin, seudenol, and 1-methylcyclohex-2-en-1-ol with ethanol) (pull) reduced populations of the Douglas-fir beetle (*Dendroctonus pseudotsugae*) in treated plots of Douglas-fir (*Pseudotsuga menziesii*), but it could not be determined if this effect was due to push, pull, or the push-pull effect.

This study also highlighted the disadvantages of mass-trapping strategies, i.e., the potential for spillover attacks and trapping the pests' natural enemies (123).

Lindgren & Borden (84) conducted a trial aimed at reducing infestations of the mountain pine beetle (*Dendroctonus ponderosae*) in a target plot of lodgepole pine trees (*Pinus contorta*) and concentrating them into flanking subplots. The antiaggregation pheromone verbenone as (*S*) isomer (84%) deployed in slow-release dispensers was tested as a push within the target plots, and attractive baits comprising *trans*-verbenol as (*S*) isomer (83%), *exo*-brevicomin, and the host kairomone myrcene were tested as a pull, deployed from two flanking subplots. The verbenone push treatment significantly reduced the percentage of attacked trees in target plots, but the addition of the pull treatment did not further reduce attacks in the center plots. However, the ratio of attack distribution was higher than expected in the flanking subplots and was only consistently altered when both components were added (84). Similarly, the direction of the spread of southern pine beetle (*Dendroctonus frontalis*) infestations was successfully reversed by applying verbenone as (*S*) isomer (66%) to infested trees and buffering trees around the leading edge of the expanding infestation, in addition to deploying the aggregation pheromone frontalin from baited trees in a predetermined trap area (15). Large-scale trials are required to test whether this strategy could become operational. In future tests, the efficacy of verbenone could be improved by combining it with other pheromones (22), nonhost plant volatiles (58, 147), or both.

Push-Pull Strategies for Control of Veterinary and Medical Pests

Knowledge of host preferences, both between (54) and within (16, 35, 118) species, is being exploited in push-pull strategies for hematophagous and other carnivorous flies, which are the most destructive veterinary and medical pests.

Control of muscid flies. The horn fly (*Haematobia irritans*) is an obligate blood-feeding pest of pastured cattle in many parts of the world; it causes disease, reproductive failure, and reduced milk and meat yields. Studies have revealed that fly load differs among individual heifers within herds, and the feasibility of a push-pull approach to fly control was demonstrated by introducing fly-resistant or fly-susceptible cattle to different herds, significantly reducing or increasing the total number of flies in the herd, respectively (66). The mechanisms for this differential attraction are due partly to differences in volatile semiochemicals emanating from the hosts (16). Bioassay data implied that cows with low fly loads produce additional volatiles that mask attractive volatiles or actively repel flies. Repellents, naphthalene, propyl butanoate, and (*R*,*S*)-linalool, and attractants (*R*,*S*)-1-octen-3-ol, 6-methyl-5-hepten-2-one, and (*R*,*S*)-3-octanol, were identified. Preliminary field trials showed that heifers treated with attractants had reduced rather than increased fly load, but that significant redistribution of the fly load within the herd could be achieved (16). Further work on identifying the correct concentrations of chemicals to produce a predictable distribution of flies is in progress, to enable flies to be pushed from most of the herd and pulled to individual cows baited with insecticides or to traps.

Control of mosquitoes and midges. Push-pull strategies may control disease-transmitting flies of medical importance, such as mosquitoes and biting midges, by exploiting natural differential attractiveness within a host species (35) or using botanical repellents (10a, 20, 50a) as push stimuli and attracticides based on host odors (14) or attractive pheromones (19) as pull stimuli. However, these strategies have yet to be tested.

Push-Pull Strategies in Control of Urban Pests

Control of domestic (urban) pests that infest our homes, workplaces, hospitals, and other public buildings relies heavily on the use of chemical insecticides. The use of toxic chemicals in these places, particularly schools and hospitals, is often impractical or undesirable. Push-pull strategies may offer effective, nontoxic solutions to control some of these pests (100, 121).

Control of cockroaches. Cockroaches of several species pose a significant risk to human health, as they transmit diseases and produce allergens. Aggregation in the German cockroach (*Blattella germanica*) is induced by pheromones contained in their frass. The pheromones comprise volatile attractants (several alkylamines and (*R*,*S*)-1-dimethylamino-2-methyl-2-propanol) and contact-chemoreceptive arrestants (blattellastanoside-A and -B, derived from β-sitosterol) (124, 125). Attractants and pheromones are used commercially in attracticide traps for cockroaches. A push-pull strategy comprising the insect repellent *N*-methylneodecanamide and a feces (i.e., pheromone-containing)-contaminated surface as an attractant with an insecticide-based food bait has been evaluated (100). Dual-choice tests between untreated shelters and shelters treated with the attractant or repellent were offered to cockroaches in association with nonbaited and insecticide-baited food near the shelters. The push-pull treatment was more effective than the individual components and the control in influencing cockroach distribution, bait intake, and the percentage and speed of mortality. This strategy could be improved. Biopesticides based on the entomopathogen *M. anisopliae* are registered for cockroach control in some countries. Also, chemicals derived from the catnip plant (*Nepeta cataria*) are being developed as botanical repellents and could replace synthetic repellents as the push component in this strategy; in laboratory tests, catnip essential oil performed better than DEET in repelling cockroaches (104).

ADVANTAGES AND DISADVANTAGES OF PUSH-PULL STRATEGIES

Advantages

The use of push-pull strategies has several advantages over conventional pest control regimes and the use of individual components in isolation. These advantages are listed and discussed below.

Increased efficiency of individual push and pull components. Individual elements may fail because their effects are not strong enough to effect control on their own. For example, trapping strategies using attractive baits may have a significant impact on species with low reproductive rates but fail for species with high reproductive rates. By adding another component with negative effects on host selection, the preference differential is increased and the additive effects may reduce pests to below economic thresholds. Furthermore, the efficiency of push and pull behavior-controlling elements is often not only additive but synergistic (36, 47, 89, 97, 100, 115).

Improved potential for use of antifeedants and oviposition deterrents. The use of these tactics in IPM is often limited or ineffective because of habituation, or host deprivation, in the absence of more suitable hosts (4, 67). By adding pull stimuli, a choice situation is created and alternative feeding or ovipositional outlets are provided, which can mitigate these effects (116).

Increased efficiency of population-reducing components. As the pest populations are concentrated in predetermined areas (either traps or trap crops), less chemical or biological control material is required to treat the pest population (56, 90), thereby reducing costs. Leaving areas untreated also provides an enhanced opportunity for the conservation of natural enemies and other nontarget organisms.

Resistance management. Because the behavior-modifying stimuli used in push-pull strategies are used in combination and are not highly effective when used alone, the components do not select strongly for resistance. The strategy is generally compatible with the use of conventional insecticides, and the reduction in the amounts required for control reduces the opportunity for pests to develop insecticide resistance. In some cases, noninsecticidal components can replace the need for insecticides; cessation of use over time may lead to a reduction in the proportion of the population that are insecticide resistant, particularly if there are fitness costs to resistance (47, 49). Push-pull strategies could also contribute to resistance management of Bt crops (74, 96).

Disadvantages

The use of push-pull strategies has some disadvantages over conventional pest control regimes. These disadvantages are common to mostly all alternative pest control strategies.

Limitations to development. A good understanding of the behavioral and chemical ecology of the host-pest interactions and the effects of the strategies on beneficials is essential but requires considerable research effort. If knowledge is insufficient, control may break down and robustness and reliability are reduced. Development of semiochemical components is often limited by formulation and delivery technology.

Registration. Owing to a small and specialized market, the cost of semiochemical registration is often high. Registration of semiochemicals in North and South America has been discussed elsewhere (64, 122a). Europe, particularly the United Kingdom, lags behind the United States and many other countries in devising appropriate registration arrangements for semiochemicals. This problem must be remedied, or Europe will fall behind in the use of push-pull strategies as replacements for broad-spectrum insecticides.

Limitations to adoption. An integrated approach to pest control is more complex, requiring monitoring and decision systems, and currently incurs higher operational costs than does the sole use of insecticides. This, and the comparatively variable efficacy that comes with incomplete knowledge of the biological operation of the whole strategy, has limited uptake. So far, only two strategies have been used successfully on a commercial scale (**Supplemental Table 1**). However, in the event that the continued spread of insecticide resistance and the withdrawal of insecticides due to legislation leave few other alternatives, adoption would increase.

FUTURE PROSPECTS

The push-pull strategy is a powerful and effective IPM tool. However, its potential has been underexploited. There is increasing interest in the strategy: during the course of researching literature for this review, we came across more than 100 papers that mention the push-pull strategy. However, many of these were from the same few research groups. After 20 years since the term was coined, there are little more than a handful of push-pull strategies making progress toward commercial use (**Supplemental Table 1**). We hope that this review increases awareness of the strategy and stimulates research for further development and widespread use.

Several new technologies may help develop and improve future push-pull strategies. Because we better understand the behavior of pest and beneficial insects, enabled by advances in analytical techniques, synthesis procedures, and formulation science, we may have a larger and more effective armory of semiochemicals and other stimuli for future use. In plant-based strategies, the use of induced defenses and plants that produce the desired semiochemicals themselves, rather than applying them to the plant, would help make the strategies more sustainable and available, especially for resource-poor farmers. Improved understanding of the spatial-scale effects on pest and natural enemy population dynamics, coupled with increased capability of spatially explicit computer models, will enable us to deploy more accurately components of the strategy in terms of the quantities needed and their spatial distribution. Push-pull strategies targeted at predators and parasitoids, which enable the manipulation of their distributions for improved biological control, are just around the corner. This prospect will allow these strategies to be applied in novel ways and increase their use in IPM in the future.

SUMMARY POINTS

1. The push-pull strategy is a behavioral manipulation method that uses repellent/deterrent (push) and attractive/stimulant (pull) stimuli to direct the movement of pest or beneficial insects for pest management.
2. Stimuli used for behavioral manipulation in push-pull strategies include visual and semiochemical cues or signals that work by nontoxic mechanisms. Strategies are therefore integrated with other population-reducing methods. Sustainable and environmentally sensitive components are favored, and the use of insecticides can be reduced.
3. Push-pull strategies targeted at pest insects are being developed in all major areas of pest management. However, their use is currently underexploited.
4. Changing attitudes toward replacing broad-spectrum insecticides with new technologies, particularly semiochemical tools, to manipulate the behavior of natural enemies for improved biological control will enable improved push-pull strategies to be developed and used more widely in the future.

NOTE ADDED IN PROOF

Where compounds are chiral, indication of the enantiomeric composition is given where unambiguously apparent in the primary publications

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