Modelling push-pull management of pest insects using repellents and attractive traps in fruit tree orchards

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Abstract

BACKGROUND: Push-pull with semiochemicals in pest management uses repellents to reduce response of pests to food-mate resources (push) and attractive traps to reduce populations (pull). Simulation models of push-pull can aid understanding of plant-insect interactions in nature and suggest hypotheses for field tests that improve management. A previous model indicated advantages of push-pull for controlling ambrosia beetle, *Euwallacea fornicatus*, pest of avocado trees. However, the simulated behavior of repellency was inconsistent with field observations.

RESULTS: We simulated individual-based movement of insects in push-pull to reveal relationships between parameters of radii (strength) of attractive traps, pest aggregations, and repellents with densities of each in an avocado orchard to visualize and understand the interactions and significance. Simulations indicated placement of traps along a 1-ha area periphery as a barrier resulted in similar trapping and mating as when traps were in a grid, either when insects originated randomly inside the plot or came from outside the plot. However, when insects originated from outside, both arrangements caught slightly more than when insects originated within the plot.

CONCLUSION: There were no differences in capture rates whether traps were spaced in a barrier along the plot's periphery or in a grid covering the plot. Push-pull was more effective than pull (mass trapping) alone. Repellent behavior of individuals when encountering a repellent radius was modelled by approximate 90° turns (right or left at random) when about to enter an infestation, consistent with earlier observations of effects of repellents on bark beetles orienting to aggregation pheromone. © 2022 Society of Chemical Industry.

Keywords: orientation behavior; ambrosia beetles; bark beetles; nonhost plants; inhibitors; trapping

1 INTRODUCTION

Push-pull strategies to protect crops are represented by two types: (i) intercropping with repulsive non-crop plants (or with flowering non-crop plants attracting natural enemies of pests) combined with attractive trap crops,[1–8] and (ii) semiochemical repellents combined with attractive pheromone traps.[9–11] There can be hybrids of the two types but here we will explore the second type of push-pull with semiochemicals based on some research on bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae). Pest management strategies of semiochemical push-pull seek to protect crops by use of repellents that cause pests to avoid the crop (push) while at the same time attracting pests to pheromone dispensers in traps that remove the pests before they find mates or hosts (pull).

The use of pull tactics was clearly a goal in early studies when aggregation pheromones were used in mass trapping experiments of forest bark beetles in the decade following the late 1960s.[12–14] Pest management with attractive semiochemicals such as sex pheromones can involve detection (determining pest distribution), monitoring (assessing pest populations), and control using mass-trapping or mating disruption.[15–19] Probably all insects, especially common pest insects, use attractive sex/aggregation pheromones and other host semiochemicals to find mates and food resources.[20] There are other types of insect pheromones such as anti-aggregation

pheromones and repellent allomones (colloquially termed inhibitors or repellents) that signal negative consequences of colonizing potential food and breeding resources.[9,21–23] Other non-host plant allomones aid the searching insect to avoid non-hosts and find appropriate hosts.[24–27]

Shortly after the early experiments on mass-trapping, the utility of push was suggested when inhibitors (repellents) such as verbenone and *trans*-verbenol were found to have allomone and pheromone effects that reduced response of bark beetles *Ips paraconfusus* and *Dendroctonus brevicomis* to their aggregation pheromones.[21,22] They suggested that the inhibitors 'may prove useful as behavior modifying chemicals that would inhibit the aggregation phase of host colonization and perhaps reduce tree mortality'. It was also suggested that at close-range the repellents allowed individuals of both species to avoid colonized bark of either species and thus avoid intra- and interspecific

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competition, and as a cue that the host had become unsuitable.[23,28] In the following years, a meta-analysis of 31 push-pull treatments with aggregation pheromone and repellents showed a mean reduction in tree mortality of 59% for two major bark beetle species.[29]

Models of pull with mass-trapping (encounter rate models) have been successfully developed for individual-based movement of insects regarding attractive pheromone traps and competitive natural attraction of females, males, and host plants by using the effective attraction radius (EAR) or circular EAR (EARc) in two dimensions.[11,18,30–33] However, only one previous simulation model of semiochemical push-pull of insects has been developed, namely for the polyphagous shot hole borer (PSHB), *Euwallacea fornicatus* (Eichhoff), an ambrosia beetle attacking avocado trees in California, Israel, and South Africa.[33] The model relied on pull strengths of attractive traps based on effective attraction radii measured for sticky traps either releasing odors from natural aggregations or attractant quercivorol. The push part was based on experiments where decreasing distance between verbenone inhibitor and traps releasing quercivorol resulted in declining captures of PSHB. The model simulated repellency after encountering a repellent radius by causing the beetle to ignore natural aggregations for three flight steps of 0.5 m each. However, this type of behavioral response to a repellent has not been documented in the field. We aim to model a more realistic push-behavior based on field observations of bark beetles in nature avoiding aggregation pheromone sources that included a repellent.[27]

The present model will allow variation in numbers of repellents, attractive traps, and attractive natural aggregations in different spatial arrangements, as well as numbers of searching pest individuals originating anywhere or from outside the 1-ha simulation area. Additionally, the model will incorporate variable attractive strengths of the semiochemical traps and natural aggregations, as well as strength of repellents. Simulations should aid understanding of the key parameters for successful push-pull such as trap density and placement (pull), sources of natural attraction and distribution (competing pull), and repellent strength, density and placement (push). Although the push-pull model here is presented in relation to chemical ecology of PSHB in avocado orchards, the simulation approach can accommodate other pest systems with attractive and repellent semiochemicals.

2 MATERIALS AND METHODS

2.1 Development of parameters describing pull methods

In pest detection, monitoring, and mass-trapping, the trap's capture rate is due to the following factors: (i) trap size and efficiency, (ii) trap's blend of attractive volatiles, (iii) their release rates, (iv) population density of flying pest insects, and (v) competitive sources of natural attraction.[11] A strongly attractive lure-trap might catch few at low pest population density and erroneously appear ineffective, while a weak lure-trap could catch many at high pest density and wrongly appear effective. Thus, it is important to use the effective attraction radius (EAR) as a measure of an attractive trap's capture strength regardless of pest density.[30–34] For example, given a catch of an insect species by a pheromone trap and a second catch by a blank sticky trap 20 m away, then the EAR of the pheromone trap is equivalent to the radius of an unattractive sticky sphere that would catch the same number as the pheromone trap.[32,35] The calculation of EAR requires comparison of attractive trap catch (C_a) to nearby passive (blank) trap catch (C_b), and the passive trap's silhouette interception area (S),

which is the mean interception area of the trap at all viewing angles. The passive trap must have a high capture efficiency such as a sticky-screen cylinder, while the attractive trap can be of any type. Simulations have shown the EAR equation, $[C_a \times S/(C_b \times \pi)]^{0.5}$, gives a consistent value for a specific baited-trap strength regardless of pest density.[30]

The size of the spherical EAR relates to its strength and can serve as a substitute for pheromone traps in simulations in three dimensions. However, less complex models in two dimensions are obtained by converting an EAR to a circular EARc using the standard deviation (SD) of the pest's vertical flight distribution as estimated by catches on traps at several heights above ground.[34] The SD was estimated as 0.88 m for PSHB at a mean flight height of 1.24 m.[31] An EAR is converted to EARc with the equation: $EARc = \pi \times EAR^2/[2 \times SD \times (2 \times \pi)^{0.5}]$.[31] Byers *et al.*[32] calculated that the average EARc of avocado limbs infested with PSHB ranged from 0.25 m (less infested, N = 7) to 0.98 m (more infested, N = 7). This is less than a 2.86 m EARc for a relatively high release rate of attractant quercivorol (10× rate or 1.26 mg day^{-1} at 25 °C) from a sticky-screen trap (28 cm diam. ×33 cm high cylinder, S = 0.0924 m^2). In simulations presented subsequently we kept EARc of traps at 2.8 m unless varied, and EARc of PSHB aggregations at 0.5 m unless varied.

2.2 Development of parameters describing push methods

The use of a number of EARc in an area to describe mass-trapping (pull) and competing sources of natural aggregation is well established.[30–35] On the other hand, insect behavior regarding repellents (push) is poorly known and therefore difficult to model. Volatiles are termed inhibitors if they reduce response of insects to attractants such as pheromones.[21,27,36] The behavioral mechanism of inhibitors resulting in lower trap catch seems to involve repellency (turning away) near the odor source. For example, bark beetles have been observed in late afternoon sun flying several meters directly upwind into a trap releasing aggregation pheromone, but when inhibitors were added to this trap, beetles still flew directly upwind until 0.5 to 1 m from the trap and then turned left or right to avoid the trap.[27]

Verbenone is a well-known inhibitor of scolytine beetles that likely evolved for avoiding unsuitable host trees emitting this volatile.[10,21,23,28,36–39] The inhibitors verbenone and piperitone (hereafter also called repellents) as they were moved closer than 2 m from a quercivorol trap became increasingly effective in reducing attraction of PSHB to this trap.[33] In similar experiments,[35] verbenone (0.8 mg day^{-1}) was moved increasingly closer to a quercivorol trap, and at 2 m separation the fitted curve [catch = 264.4–212(exp(−X))] estimated a mean catch of 236 while at 0 m separation the mean catch was 52.4 (reduction to 22%). Solving for X at 50% of the catch at 2 m separation gives X = 0.6 m. In addition to separation distance between repellents and attractants, the release rate of the repellent affects catch. Increasing tenfold doses (0.01–10×) of verbenone released from 1× quercivorol traps caused a sigmoidal kinetic–decay relationship in catch.[35] In this test, verbenone at 1× rate (0.8 mg day^{-1}) reduced attraction to 17%, and at 8 mg day^{-1} to 6.5%. Recent work indicates that verbenone-SPLAT® (ISCA) released at about 1 mg day^{-1} from points every 40 cm along the major avocado trunks reduced PSHB aggregation densities by half and the aggregations were about half the size compared to those on adjacent control trees.[11] However, the efficacy of verbenone-SPLAT was

likely reduced because the repellent treatments were not initiated at the beginning of flight season.

We have not found a precise way to measure the size of a repellent's circular effective repellent radius (ERRc) for use in models because observed repellent effects are in conjunction with attractant-releasing traps. Theoretically, an ERRc would likely depend on (i) repellent release rate and (ii) the pest's subsequent ill-defined avoidance behavior of attractive sources. The coordinates of the ERRc give the location of the effect, and the ERRc magnitude would be correlated to the pest's response to repellent release rate, but the repellent effect also seems to depend on the particular pest's avoidance behavior. Thus, if a simulated insect approaches EARc of a natural aggregation while still within the repellent radius, then it may turn randomly either right or left to avoid the aggregation as observed earlier.[27] In our simulations, the ERRc coordinates, densities, and radius (relative strength) were varied.

2.3 Modelling push-pull methods

Computer software programmed in Java 1.6 (https://chemical-ecology.net) simulated individual-based movements of PSHB beetles in an avocado orchard and encounters with attractive quercivorol traps, attractive PSHB aggregations on avocado branches, and repellents using algorithms described earlier.[31–33] Beetles were either released anywhere in a 100 × 100 m (1-ha) area at random or in other simulations at random along the plot's perimeter (Fig. 1). In each simulation, 1000 initial beetles individually moved in a correlated random walk with steps of 0.5 m s^{-1}, in which their forward direction could vary at each step by an angular deviation randomly selected from a normal distribution with a standard deviation of 6°. Beetles wandered up to 14 400 flight steps (4 h) until nearly all encountered either a trap or an aggregation.

Simulated avocado trees were spaced 4 m apart within a row, with parallel rows 6 m apart, and the radius of each tree was 2 m. Thus, in a 1-ha area 400 trees could be placed (25 rows of 16 trees). A set number of repellents (usually 3/tree) were evenly spaced around a circle of 1-m radius from the center of each tree, and PSHB aggregations were randomly distributed among the trees at a random distance within 1 m from a tree's center (Fig. 1). When beetles encountered ERRc of a repellent they continued their random walk. However, if they encountered an aggregation EARc while still within the repellent radius, they remained in their current position and turned 90° either right or left at random. On the next step they moved in this new direction (with slight deviation due to random walk), which caused them to avoid the aggregation and move through the ERRc.[27] Beetles within ERRc that entered trap EARc did not turn because such traps in practice would be placed greater than 2 m from repellents in trees.

In each simulation, the coordinates for each trap (in grid or on periphery), repellents per tree, and the PSHB aggregations were selected as described above. The simulation then gave each of the 1000 PSHB (x,y) coordinates at random in the area, as well as an initial angular direction at random. For each step, and for each individual, the following process occurred: a step was taken by the first individual of 0.5 m to a provisional polar coordinate (p,q), if this new coordinate was outside the area then repeated random angles were tried until the (p,q) coordinate was inside the area. Based on the step segment of (x,y)-(p,q) then an algorithm tested whether any trap EARc was penetrated by the step, if so, the individual was captured.[30] Otherwise, the step segment was

compared to determine if any repellent ERRc was penetrated with the same algorithm. If the beetle penetrated a repellent ERRc and if the beetle's next step would enter an aggregation EARc then the beetle does not step but turns left or right at random as described above. Otherwise, the beetle's step segment is checked with each aggregation EARc and if one is penetrated then the individual is removed because it has joined an aggregation and reproduced. If the beetle did not encounter either a trap or an aggregation, then the (p,q) coordinate becomes the (x,y) coordinate and the simulation moves to the second beetle for the same procedure until all remaining beetles have moved. Beetles continue to move until all are caught by traps or join an aggregation, or when 4 h of flight elapsed.

In the first set of simulations, the effects on the percentages of the population trapped or finding aggregations were explored using different arrangements of traps. Twenty-five traps (EARc = 2.8 m) were placed either in a 5 × 5 trap grid that covered the plot (Fig. 1) or in a barrier along the plot's perimeter (traps fully within plot). Various simulations estimated percentages of initial population that were captured by traps or found aggregations in a push-pull system compared to mass-trapping alone when
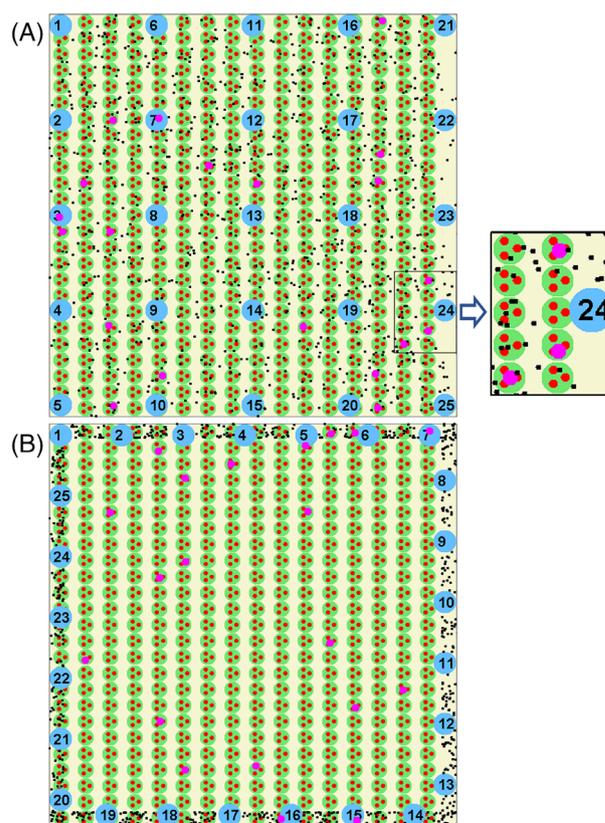

Figure 1. Screen-captured images of simulations in 100 × 100 m plots with black dots representing 1000 initial PSHB beetles that had moved seven steps of 0.5 m length in an orchard of 400 avocado trees (25 × 16 green disks), each tree with three repellents (red dots) of 0.6 m ERRc. Beetles were caught by 25 larger blue disks representing attractive traps of 2.8 m EARc (numbered 1–25) or beetles found medium-sized purple disks (1 m EARc) depicting 20 conspecific aggregations distributed at random on trees. (A) Beetles originated anywhere within the plot at random and were caught by traps in a 5 × 5 grid (image portion at right enlarged ×2). (B) Beetles originated at random on the periphery of the plot and immigrated inward to intercept 25 traps spaced evenly along the inside of the plot's perimeter.

varying strengths and densities (number per ha) of verbenone repellent ERRc, attractive aggregation EARc, and 10x quercivorol sticky-trap EARc. When these parameters were varied, all other variables remained constant unless varied (0.6 m for repellent ERRc and three per tree, 20 PSHB aggregations each 0.5 m EARc, and nine quercivorol traps each 2.8 m EARc). After each simulation, the population percentages trapped or finding aggregations and the mean number of steps taken by individuals before removal was recorded (each variable increment was mean of eight simulations and 95% CI). Non-linear, least-squares fitting software was used to iteratively find equations that fit the relationships best (TableCurve 2D version 5.01, Systat Software Inc., Chicago, USA).

3 RESULTS

In an avocado orchard, eight simulations of 1000 beetles each searched in a 1-ha area of 400 trees to estimate mean population percentage that was captured by 25 quercivorol traps (EARc = 2.8 m) or mean percentage joining 20 aggregations on avocado branches (EARc = 1 m). The repellents had 0.6 m ERRc and either none or three per tree. The first set of simulations used $2^3 = 8$ combinations of (i) none or three repellents, (ii) 5 × 5 grid or 25 peripheral traps, and (iii) beetles originating inside at random or outside along the periphery at random (Table 1). The use of push with three repellents per tree (insects originating inside) caused about 90% of the population to be trapped and only 10% found aggregations, compared to only 80% of the population trapped and 20% finding aggregations when there were no repellents (Table 1). The same relative effects were seen when comparing peripheral traps with no repellents and three repellents (insect origin inside). However, there was a slight 4–5% increase in trapping when the insects originated from outside of the area compared to inside, for both grid traps and peripheral traps (Table 1). Interestingly, with three repellents per tree, the 5 × 5 grid of traps compared to the 25 peripheral traps caught essentially the same proportions when insects began search anywhere inside the area (89.6% vs. 88.4%, respectively), and grids and peripheral traps also had the same proportions when insects came from outside the area (91.9 ± 1.2% vs 93.5 ± 1.0%, with overlapping 95% CI, Table 1). Based on these results, simulations explored the effects of varying numbers of repellents per tree and radius of repellents on population percentages trapped and finding aggregations.
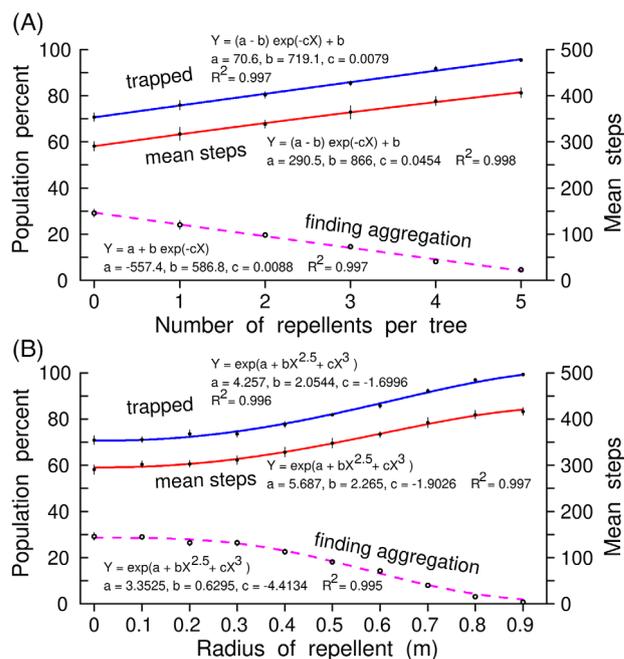

Figure 2. Relationships between varying two repellent parameters on mean percentages of 1000 simulated insects (originating anywhere) in a 1-ha area that were either (i) trapped by nine attractive traps (2.8 m EARc in 3 × 3 grid) or (ii) finding 20 aggregations placed at random, each of 0.5 m EARc, and the mean number of steps taken by individuals (N = 8 simulations each mean ± 95% CI). (A) Number of repellents (0.6 m ERRc) varied from 0 to 5 per tree (400 trees in area). (B) Radius of repellent (ERRc) varied from 0 to 0.9 m (three repellents per tree).

The number of repellents (0.6 m ERRc) per tree was varied to simulated push such that insects within an ERRc avoided nearby aggregations of 0.5 m EARc. Increasing the number of repellents from 0 to 5 per tree caused the population percentage trapped on 9 traps of 2.8 m EARc to increase linearly from 71% to 96%, and conversely the percentage finding 20 aggregations decreased from 29% to 4% (Fig. 2(A)). The variation in mean percentages and steps per individual was very small as indicated by 95% CI (N = 8), giving confidence for the curve-fits of the various linear transformed and non-linear functions (Figs 2 and 3). Most insects were caught in traps or found aggregations long before the maximum 4-h flight period of 14 400 steps (c.f. mean steps in Fig. 2 and 95% CI). Simulations (see Fig. 1(A), N = 8) with

Table 1. Mean percentages (±95% CL, N = 8 simulations) of initial populations of 1000 insects per simulation that were either trapped by 25 pheromone traps each with effective attraction radius (EARc) of 2.8 m or found one of 20 aggregations each of 1 m EARc in a 1-ha area

Repellents per tree	Trap placement	Insect origin	Mean % trapped	Mean % found aggregation
0	Grid	Inside area	79.9 ± 1.4	20.1 ± 1.4
3	Grid	Inside area	89.6 ± 0.8	10.4 ± 0.8
0	Grid	Outside area	84.5 ± 1.3	15.5 ± 1.3
3	Grid	Outside area	91.9 ± 1.2	8.1 ± 1.2
0	Periphery	Inside area	77.1 ± 1.3	22.9 ± 1.3
3	Periphery	Inside area	88.4 ± 0.9	11.6 ± 0.9
0	Periphery	Outside area	86.7 ± 1.1	13.3 ± 1.1
3	Periphery	Outside area	93.5 ± 1.0	6.5 ± 1.0

Repellents had an effective repellent radius (ERRc) of 0.6 m and either none or three repellents were placed on each of 400 trees (see Methods for details of insect movement, repellence model, trap placement, and insect origin).
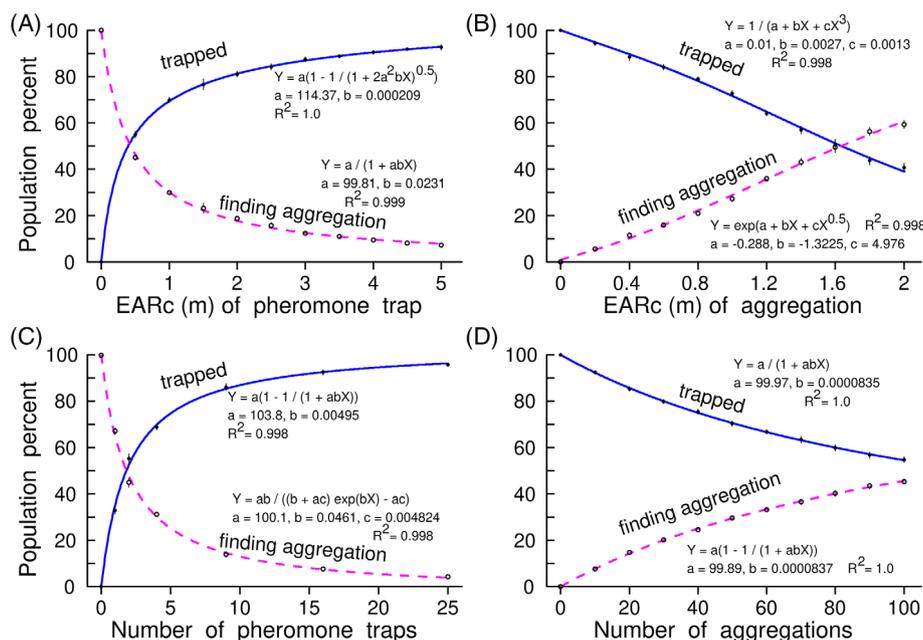
Figure 3. Effect of varying numbers and strengths of pheromone traps or varying numbers and attractive strengths of aggregations in a 1-ha area on the percentage of 1000 PSHB (originating anywhere at random) trapped by attractive traps or finding aggregations. Unless varied, other parameters were held constant at nine traps in grid (each trap of 2.8 m EARc), 20 aggregations (each of 0.5 m EARc) placed at random, and three repellents per tree of 0.6 m ERRc. Each point represents mean of 8 simulations with vertical lines 95% CI. (A) Relationship between varying EARc of trap and mean percentages of insects either trapped or finding aggregations. (B) Relationship between varying EARc of aggregations and mean percentages of insects either trapped or finding aggregations. (C) Relationship between number of traps and mean percentages of insects either trapped or finding aggregations. (D) Relationship between number of aggregations and mean percentages of insects either trapped or finding aggregations.
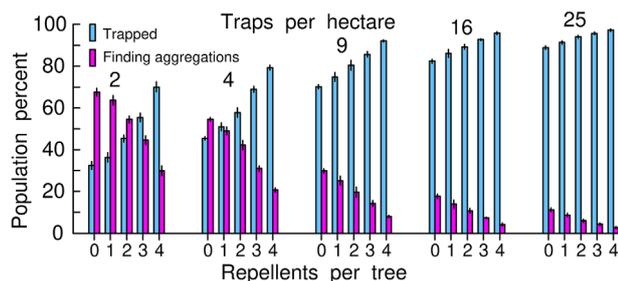
maximum flight durations of either 0.5 h (≤900 m) or 4 h (≤7200 m) suggest identical proportions are trapped or join aggregations (≤900 m: 90.1 ± 1.1% trapped and 9.9 ± 1.1% join; ≤7200 m: 89.6 ± 0.8% trapped and 10.4 ± 0.8% join). However, at shorter 0.1 h flights (≤180 m: 86.4 ± 0.4% trapped and 9.8 ± 0.6% join) with 3.8% left exhausted.

Varying the radius of repellents (ERRc) from 0 to 0.9 m (three repellents per tree) gave similar sigmoid exponential curves of population percentages trapped or finding aggregations (Fig. 2 (B)). The percentage of the population trapped increased from 71% at 0 m repellent radius (same as if no repellents were used) to about 99% at a repellent radius of 0.9 m (Fig. 2(B)). Further increases in repellent radius (data not shown) caused an overlap of the spaced repellents in trees such that beetles could not

Figure 4. Mean percentages of initial populations of 1000 simulated beetles that were trapped by increasing numbers of traps in grids (2.8 m EARc for traps, blue bars) or found one of 20 aggregations (0.5 m EARc, purple bars) in a 1-ha avocado orchard of 400 trees. Repellents had a radius of 0.6 m and were placed on all trees (see Methods for details). Each bar a mean of eight simulations, and vertical error lines represent 95% CI (bars are significantly different if error lines do not overlap).

encounter aggregations. The curve for mean number of steps taken by an individual before being caught/find aggregations ranged from 295 steps (at 0 m ERRC or no repellents) to about 420 steps at 0.9 m ERRc.

In another set of simulations, the repellent radius of 0.6 m was kept constant while varying either (a) EARc of traps, (b) EARc of aggregations, (c) number of traps, or (d) number of aggregations (Fig. 3). The percentage of beetles trapped increased dramatically from 0 to 93% as the trap's EARc was varied from 0 to 5 m, while concomitantly the percentage finding aggregations (EARc = 0.5 m) declined from 99.8% to 8% (Fig. 3(A)). These relationships giving percentage trapped or finding aggregations were very similar to simulations when numbers of quercivorol traps (EARc = 2.8 m) were increased from 0 to 25 (Fig. 3(C)). When the trap EARc was held constant at 2.8 m and nine traps, and the EARc of aggregations was increased from 0 to 2 m (20 aggregations per ha), then a declining sigmoid relationship resulted in percentage trapped (from 99.7% at 0 m down to 39% at 2 m). Conversely, an increasing sigmoid relationship was shown for percentage finding aggregations (from 1% at 0 m up to 61% at 2 m; Fig. 3(B)). An increase in the number of aggregations from 0 to 100 per ha caused the percentage trapped to decline from 100% in a concave curve down to 54.5%, and the percentage finding aggregations to increase in a convex curve from 0% up to 45.6% (Fig. 3(D)).

Simulations that varied both number of repellents from 0 to 4 per tree and the number of traps from 2 to 25 per ha, two parameters that can be manipulated readily by managers, show combinations that result in effective control (Fig. 4). When there were no repellents and only mass-trapping occurs, about 68% of the population joined aggregations at two traps, which then decreases to only 11% at 25 traps. At 2 traps/ha, increasing the number of

repellents per tree from 0 to 4 caused percentages finding aggregations and reproducing to decline from 68% to only 30% (Fig. 4). Similarly, increases in density of traps/ha gave decreasing proportions finding aggregations.

4 DISCUSSION

In our models of push-pull using semiochemicals, the pull part focuses on attractive semiochemicals to lure pests into traps. The most potent lures are usually sex and aggregation pheromones, while host plant volatiles can also be attractive as indicated by EAR/EARc.[18,19,30-36] Mass-trapping simulations of pull using correlated random walks of individuals and EARc of pheromone traps in competition with naturally attractive entities (host plants, sex pheromones) has been simulated in several studies.[11,18,30-34] On the other hand, the push part of push-pull has only been modelled once by varying both number of traps (2, 4, and 16) and number of repellents per tree (0, 1, and 3) to see effects on the population proportions of PSHB trapped or finding aggregations.[33] The earlier push-pull model simulated repellency by a repellent radius that when contacted caused the individual's next three steps to ignore any intercepted aggregation. The location and radius of the repellents does spatially reflect dose effects, but the essential number of discrete steps while ignoring aggregations was arbitrary, and contrary to the avoidance of attractants with repellents observed with other bark beetles in the field.

In the present study, a repellent behavior was modelled that has been observed for bark beetles approaching repellent volatiles released with aggregation pheromone.[27] In simulations, beetles moving inside ERRc that would have penetrated an aggregation EARc on their next step, instead turned right or left at random and then on their next step proceeded in the new direction away from the aggregation. When PSHB originated anywhere in the plot, about 10% more PSHB were caught by 25 traps when repellents were used on trees (push) than without repellents (Table 1). Conversely, about 10% less beetles found aggregations with repellents than without. The same trends occurred when beetles originated from the outside, but the proportions of trap capture were a few percent higher and finding aggregations were a few percent lower than when insects originated inside the plot. Most significantly, whether the attractive traps were placed in a grid or along the plot's periphery (Fig. 1) made no difference in total insects trapped or finding aggregations when the insect origin was the same (inside or outside, Table 1). These results indicate there is no compelling rationale to place traps on an area's periphery as a barrier to protect crops as suggested earlier[40-45] compared to the same number of traps in a grid covering the area (Fig. 1), at least for the areas modelled and trap EARc. This result may seem counter-intuitive since field studies have shown that pheromone traps along the edges of a grid catch more insects per trap than inner traps, indicating emigration into the plot.[11,46] However, in our simulations only total catches for all traps were compared between trap configurations. Since both trap arrangements appear equivalent, then implement whichever is convenient. However, choice of the trap arrangement may depend on the pest's flight preferences in relation to the crop.

As the number of ERRc repellents per tree increased, the catches on nine traps increased linearly and the number joining aggregations decreased linearly (Fig. 2(A)). However, these linear trends were not extended past five repellents per tree since eventually their radii overlap, while in nature increasing repellent densities is likely to have asymptotic effects. For example, catch of PSHB on quercivorol-baited trap decreased asymptotically with increasing numbers of repellent piperitone dispensers placed 0.75 m away (cf. Fig. 2 in Byers et al.).[35] An increase in the radius of a repellent (three repellents per tree) caused sigmoidal curves of increasing numbers trapped and mirrored sigmoid curves of decreasing population finding aggregations (Fig. 2(B)). The curves changed most between 0.3 to 0.7 m repellent radii, and at 0.9 m the three repellents overlapped and precluded beetles from finding aggregations and thus they could only be trapped (Fig. 2(B)).

A push-pull system in a plot with 20 aggregations and trees with three repellents each was simulated with increasing EARc of attractive traps, or an increase in numbers of traps. The percentage of PSHB trapped increased rapidly with increasing trap EARc before becoming asymptotic, while the curve for populations finding aggregations was the inverse, declining rapidly before becoming asymptotic (Fig. 3(A), (C)). The convex asymptotic nature is not due to overlap of EARc as it was increased, nor due to too many traps, because the traps never overlapped (Fig. 1). The diminishing returns in trapping with increases in trap EARc or number of traps has been shown earlier,[31] and is due to increasingly larger traps competing for the progressively lower density of insects by the end of the simulation period. The relationship between number of traps/ha and population captured is consistent with similar convex curves of increasing density of pheromone traps and moth captures in the field.[47-50] Using data of increasing densities of codling moth pheromone traps and total relative catch,[47] we found a good fit ($R^2 = 0.95$) with the 2d-order kinetic formation equation: $Y = a(1-1/(1 + abX))$ used in Fig. 3(C). An increase in EARc of aggregations gave slightly sigmoidal curves of populations trapped or finding aggregations (Fig. 3(B)), suggestive of the stronger sigmoidal curves of increasing repellent radius (Fig. 2(B)). In both cases as radii are enlarged they may increasingly overlap and cause sigmoidal relationships. An increase in numbers of aggregations caused the percentage trapped to follow a 2d-order kinetic decay function (Fig. 3(D)) that also fit the percentage finding aggregations with increasing trap radius (Fig. 3(A)). The percentage finding aggregations conversely followed a 2d-order kinetic formation function (Fig. 3(D)) that also fit the percentage trapped as pheromone trap number increased (Fig. 3(C)).

The pest manager would need to balance the costs of several baited traps with costs of placing repellents on crop plants and determine if control is feasible. This analysis would be based on costs of the attractants, repellents, dispensers and traps at various densities. It is apparent that benefits are realized with small increases in EARc of traps (Fig. 3(A)) and small increases in the density of traps (Fig. 3(C)). There are natural limits on EARc of traps with attractants that depend on the behavior of the pest species. The dose–response curve for quercivorol traps and EARc of PSHB shows a sigmoid hyperbolic function that for 10x dose (1.26 mg day^{-1}) gave EARc = 2.8 m, and the highest dose of 100× (12.6 mg day^{-1}) gave EARc = 3.4 m.[35] The EARc of the aggregation is not under the control of the manager, but it is smaller at the start of the colonization season and this is when push-pull is more effective in control of PSHB. Likewise, the number of aggregations is also not under control of the manager, but for bark beetles the densities are initially low for incipient infestations. The density of aggregations might remain low with an effective push-pull treatment. In many cases repellents are not known for pest species that would preclude push-pull, although new push compounds are continually being discovered.[11,51] Insects exhibit circadian rhythms of pheromone release and response[52] that compete with trap pull and interact

with push. Smart dispensers of push and pull semiochemicals could save costs by dispensing only during pest activity.[52]

The use of EARc to represent aggregations and attractive traps is reasonable in models. However, use of ERRc for repellents is questionable, although the size theoretically can be adjusted to reproduce reality. The problem is that little is known about behavior of insects regarding inhibitors and repellents. Inhibitors when released together with an attractant will lower the capture rate of responding insects compared to attractant alone. Likely repellents will do the same. However, repellents strictly are defined to cause a change in orientation toward an attractant such that the insect generally moves away. This appears to be the case for inhibitors with attractants in the field as mentioned above where bark beetles veered away when within about 1 m from the source of aggregation pheromone. The active inhibitory range (AIR) was proposed as the distance at which a repellent begins to reduce the flux of orienting insects as they pass through passive trap rings encircling a trap releasing aggregation pheromone and repellents.[37] The AIR for a mix of inhibitors for bark beetle *Ips typographus* L. was between 1 to 2 m (similar to observations). A different approach mentioned earlier for PSHB separated verbenone repellent at decreasing distances from the aggregation pheromone with effects also at 1–2 m. This latter approach also was used on *I. typographus* to show that effects of repellents became apparent within about 1 m.[53] This indicates that repellents at the rates tested affect behavior at relatively close range. There may be other ways to model repellency with porous ERRc in which a probability <1 of avoiding landing for several steps. But this approach will not replicate the avoidance behavior of insects affected by repellents while orienting toward an attractive source of pheromone.

Simulations show that more traps with powerful attractants and more potent repellent sources are desired for maximum push-pull effects. While research may find increased dosages and blends of attractants can marginally increase trap EARc, and repellent blends might also increase ERRc of the repellent, these variables are largely fixed in managing control programs. However, the number of attractant-baited traps and number of repellents are easily manipulated by pest managers to achieve better control. Depending on whether repellents or attractive traps cost more, the simulations indicate that to achieve less than approximately 8% of beetles finding infestations and reproducing in 1-ha avocado orchard there should be four repellents and 9 or 16 traps (8% or 4.3%), or three repellents and 16 or 25 traps (7.3% or 4.4%), or two repellents and 25 traps (6%, Fig. 4). These numbers of repellents are suggestive and may require several repellent dispensers per larger avocado tree branches. Only field experiments varying numbers of attractive traps and repellents on trees will indicate whether damage can be reduced as balanced by costs.[11]

The push–pull models here were designed for exploring control of PSHB aggregating on avocado limbs. However, the models with little modification are applicable to bark beetles and other pests with aggregation pheromones and at least one known inhibitor. The model can also accommodate pests with sex pheromones that mate once. For pests attracted to aggregations in food resources such as PSHB, competing traps should be placed a few meters from host trees in clearings. Repellents need attachment on avocado trunks just before flight season begins in May to counter attraction to single female attacks on bark and reduce growth of aggregations. It is generally accepted that mass-trapping with pheromones is more effective at lower pest population densities.[15–17,31,54] PSHB populations can be lowered by removal of infested avocado limbs and alternative hosts within orchards, a practice that is complementary to a push–pull system. Natural enemies of PSHB are not known to be affected by push–pull with quercivorol or by repellent dispensers containing verbenone or piperitone. A heat-sealed 0.15-mm film polyethylene bag (flat 2 × 2 cm) filled with 250 mg verbenone releases about 1 mg day^{-1} at 25 °C, which should last over the 6-month field season.[11] Mass-trapping of PSHB where the egg-laying females are targeted has an advantage over mating disruption or mass-trapping of male-searching species (most moths) in which only males respond. The areal size of the push-pull should be large enough to reduce influx of immigrants since mass-trapping has been considered more successful with isolated pest populations.[19,55] The simulations here may suggest how pilot tests in the field can be made successful when conducted by commercial entities.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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