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ORIENTATION OF BARK BEETLES *Pityogenes chalcographus* AND *Ips typographus* TO PHEROMONE-BAITED PUDDLE TRAPS PLACED IN GRIDS: A NEW TRAP FOR CONTROL OF SCOLYTIDS

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Abstract—A puddle trap was designed that is simple to build and efficient in catching bark beetles (Coleoptera: Scolytidae). The trap is insensitive to wind and should be much easier to manufacture than the more complicated perforated pipe and barrier traps commercially available. A 7 × 7 grid of 49 puddle traps baited with aggregation pheromone components of *Pityogenes chalcographus* (chalcogran and methyl decadienoate) was placed at either 1.5-, 3-, 6-, or 12-m spacing between traps in the field for two or more replicates of one day length (June 1989, Torsby, Sweden). The resulting catches showed that beetles were trapped as they flew into the grid since the inner square-ring of 24 traps caught less beetles per trap than the outer square-ring trap average (36 traps) in most experiments. *Ips typographus* also landed in puddle traps primarily on the periphery of the grid (6-m spacing only) when traps were baited with its pheromone components, (*S*)-*cis*-verbenol and methyl butenol. Computer simulation of flying bark beetles in grids of traps of various spacings and catch radii estimated that the experimental pheromone traps had an effective catch radius of 1.3 m or less for *P. chalcographus*, depending on the spacing between traps. An effective catch radius of 2 m for *I. typographus* was found for the 6-m grid spacing. *P. chalcographus* beetles were increasingly disrupted in their orientation to pheromone at the closer trap spacings since the effective catch radius declined linearly with closer trap spacing. However, landing was still precise since unbaited puddle traps within the grid did not catch any bark beetles.

Key Words—Semiochemical, pheromone, pest control, insect trap, Scolytidae, Coleoptera, mass trapping, computer simulation, disruption, effective catch radius.

INTRODUCTION

The practical use of semiochemicals that disrupt the natural behavior and physiology of pest insects provides the economic foundation for studies of insect chemical ecology. Mass trapping using pheromone-baited traps is one of the primary strategies for control of pest insects (Silverstein, 1981). Bark beetle populations and their effects on tree mortality have been reduced by mass trapping. In 130-ha plots in California, tree mortality caused by the western pine beetle, *Dendroctonus brevicomis* LeC., was reduced to 10% that of former levels for several years following treatment (Wood and Bedard, 1977; Bedard et al., 1979; DeMars et al., 1980).

An epidemic of the European spruce engraver, *Ips typographus* L., occurred in the late 1970s in Norway and Sweden (Austarå et al., 1984). A control program using pheromone-baited traps was initiated in 1979, and in 1980 up to 5 billion *I. typographus* were trapped over extensive areas (140,000 km^2) (Bakke, 1985, 1988, 1989). The epidemic declined in 1981 and by 1982 in some areas it was hard to find Norway spruce, *Picea abies* (L.), killed by bark beetles. However, it is not known with certainty whether the mass trapping or other climatic and biological factors caused the decline. The trap used (N79 pipe trap with funnel) was relatively complex: consisting of a 1.35-m × 12-cm-diam. plastic tube with about 900 2-mm-diam. holes distributed over the surface, a 33-cm-diam. outer plastic funnel, a 12-cm-diam. inner plastic funnel and collection bottle, pheromone dispenser and holder, and a wooden stake for mounting the trap (Bakke et al., 1983; Regnander and Solbreck, 1981).

Like other pest bark beetles (Byers, 1989), *I. typographus* aggregates on host trees in response to an aggregation pheromone consisting of 2-methyl-3-buten-2-ol and (1*S*,4*S*,5*S*)-*cis*-verbenol (Bakke et al., 1977). Host-tree compounds are not effective in enhancing the attraction to pheromone components, and uninfested logs in the field are unattractive when beetles are known to be flying (Schlyter et al., 1987c). The smaller European spruce engraver, *Pityogenes chalcographus* L., is also attracted to a synergistic blend of the pheromone components, chalcogran (2-ethyl-1,6-dioxaspiro[4.4]nonane) and methyl (*E*,*Z*)-2,4-decadienoate (Francke et al., 1977; Byers et al., 1988, 1989, 1990b). Monoterpenes such as α-pinene from the host increase the attraction response to the pheromone components (Byers et al., 1988).

No studies have determined the effects of spacing many pheromone traps at different distances in a grid on the orientation of these two beetles. Computer simulation of bark beetle flight through a grid of traps of various diameters also has not been attempted. The objectives of the present study were: (1) to investigate orientation of flying *P. chalcographus* and *I. typographus* in a grid of 49 pheromone-baited traps at different spacings, (2) to simulate reductions of catch as beetles fly through a grid of traps and compare these results to catches in the field traps in order to determine effective catch radii for the pheromone-baited traps under different conditions, and (3) to construct a simple and, therefore, inexpensive trap that would be easy to set up in the field and be about as effective as the pipe trap above in catching bark beetles.

METHODS AND MATERIALS

Pheromone-Baited Puddle Traps for Control of Bark Beetles. The puddle trap is constructed from 1.5-mm wire looped into a 28-cm-diam. ring to form the rim of the "swimming pool" (Figure 1). After joining the wire to form the loop, the wire is arched to the opposite side of the ring (with a 1-cm loop at the top for attachment of dispensers and rain/sun shield) and twisted several times to strengthen the wire skeleton. A 0.5 × 0.5-m white polyethylene trash bag is cut to obtain a plastic sheet that is stretched over the ring, around the arching wires, and then under itself, whereupon the trap is placed in a scooped-out depression in the soil. Water is poured over the stretched plastic which sags slightly forming a pool with sloping plastic sides. The weight of the water and the low profile keep the trap from blowing away even under windy conditions. The final step is to attach a plastic cup or aluminum rain and sun shield that contains pheromone dispensers.

Dispensers can be taped inside plastic cups (Figure 1) that are covered with aluminum foil to shield chemicals from the sun and rain. In the present experiments, however, aluminum foil formed into a 5 × 5-cm-diam. cup was used

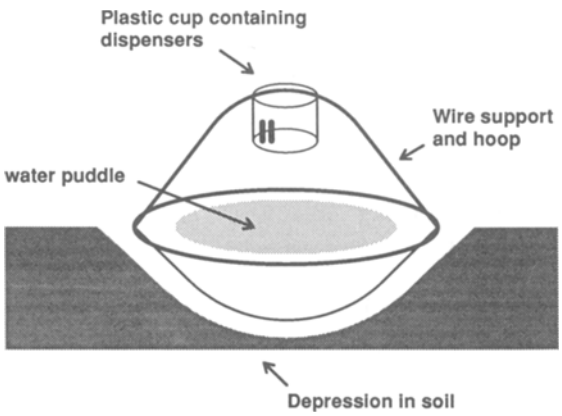

FIG. 1. Puddle trap constructed of wire hoop for support of plastic sheet containing water pool and wire arch for holding a plastic cup (covered with aluminum foil) containing pheromone dispensers. A depression, as indicated, is dug in the forest duff to form and support the water pool held by the plastic sheet (see text for details).

to shield a glass vial containing a mixture of pheromone components. For *P. chalcographus*, open 3.2 × 1.1-cm-diam. glass vials (0.525-cm-diam. opening) were used, one per trap, containing 50 μl of a stock mixture of 200 μl chalcogran (46:54 *E*:*Z*, 98% pure from W. Francke, University of Hamburg, Germany), 200 μl methyl (*E*,*Z*)-2,4-decadienoate (99.5% pure, Shell Agrar), and 2.6 ml (−)-α-pinene ($[\alpha]_D^{22} = -42°$).

The diffusion–dilution equation for obtaining predicted semiochemical release rates (Byers, 1988a) by dilution with solvent:

$$ml_s = fw_s * (g_{sem}/fw_{sem} - f_{sem} * g_{sem}/fw_{sem})/f_{sem}/g_s \quad (1)$$

can be solved for the mole fraction of the chemical (equal to the fraction of the release rate when neat):

$$f_{sem} = 1/(fw_{sem} * ml_s * g_s/(fw_s * g_{sem}) + 1) \quad (2)$$

where f_{sem} = mole fraction of semiochemical or the proportion of the release rate when neat; fw_{sem} = formula weight of semiochemical; ml_s = milliliters of solvent; g_s = grams solvent per milliliter (density); fw_s = formula weight (or molecular weight) of solvent; and g_{sem} = grams of semiochemical. Weighted averages can be used for a mixture of solvents.

Based on the release rates for a similar length tube and neat chemicals (Byers et al., 1988), ratio of the areas for dispenser openings (2.53), and the rearranged diffusion–dilution equation 2 above, the expected release (milligrams per day per dispenser) was about 0.15 mg for chalcogran, 0.003 mg for methyl (*E*,*Z*)-2,4-decadienoate, and 31 mg for (−)-α-pinene. For attraction of *I. typographus*, (1*S*,4*S*,5*S*)-*cis*-verbenol was released at 1 mg/day/trap and 2-methyl-3-buten-2-ol at 50 mg/day/trap from dispensers described previously (Schlyter et al., 1987c).

Trapping of Bark Beetles with a 7 × 7 Grid of Pheromone-Baited Puddle Traps. Grids of 49 puddle traps, as described above, were placed in two relatively flat clear-cut areas of Norway spruce (plots 1 and 2) about 1 km apart and 7 km south of Torsby, Sweden. Plot 1 was approximately 120 × 90 m and the grid (6 m between trap lines) was placed at least 15 m from the forest edge. Experiments were conducted with *P. chalcographus* on June 7, 10, and 11, and with *I. typographus* on June 15–17, 1989. Plot 2 was larger (150 × 200 m), and the 49 traps in the grid, baited with *P. chalcographus* pheromone components, were placed at 12-m spacings on June 10–12. The traps were at least 20 m from the forest edge. The spacing was changed to 3 m for experiments on June 13 and 14, and then to 1.5 m on June 15–17, 1989. Beetles that had been caught the previous day were counted the following morning before the flight period as they floated in the puddle traps. The beetles and other debris were removed by straining the water with a fine screen.

Data from the catches of puddle traps in the 7 × 7 grids were presented graphically with a personal computer program (QuickBASIC 4.5 and Adobe PostScript command language). Contouring of the catch data was achieved with the algorithm presented by Dixon and Chapman (1980). However, a three-dimensional view was effected by plotting the x coordinate after adding to the x coordinate the corresponding y coordinate multiplied by a fixed scaling value (0.6) and plotting the y coordinate by multiplying the y coordinate by a fixed scaling value (0.45).

Computer Simulation of Trapping as Bark Beetles Immigrate into a 7 × 7 Grid of Traps. The trap grids probably would catch flying beetles as they immigrated (or were attracted) into the area. The catch per trap on traps in the outer ring (24 traps on the periphery of the grid) should thus be higher than on the 16 traps in the inner ring (traps just within the outer ring). Catches of each species per trap for the outer ring of traps, the inner ring traps, and the center-ring traps (8 traps surrounding the center trap) were averaged for each grid spacing on several dates. Ratios were calculated for the catch per trap for traps in the outer-ring trap to the inner-ring. These ratios served as a comparison to the ratios found in a computer simulation model, modified from a mass trapping simulation model (Byers, 1993) that is based on a mate-finding model (Byers, 1991). The program code is available upon request.

In the simulation model, the trap and pheromone plume radius, analogous to the effective attraction radius (Byers et al., 1989), can be independently varied as well as the x and y axes, the number of beetles, their step size and turning angles, and the number of traps and their spacing in the grid. Beetles were "released" at random only on the periphery of the area. Since they are not allowed to move outside the rectangular boundaries, the beetles rebound at random angles back toward the grid of traps (i.e., they immigrate into the grid as in nature). The simulation area enclosed grids of 49 traps of different spacing, and the simulation ended when all beetles were caught. A record of which traps (outer, inner, or central rings) caught beetles was kept so that ratios could be compared to the catch ratios from the field in order to calculate theoretical, effective catch radii.

RESULTS

Pheromone-Baited Puddle Traps for Control of Bark Beetles. Both *Ips typographus* and *Pityogenes chalcographus* were caught readily by the puddle traps (Figures 2–6). A comparison of several trap types (June 11, 1989), each baited with methyl butenol and *cis*-verbenol at the rates above from different experiments within 200 m of each other indicated that the puddle trap (Figure 1) is efficient in catching bark beetles. This trap (with plastic cup) caught 110 *I. typographus*, while four tubular sticky-screen traps at 1.5-m height (30 cm long × 30 cm diam.; Byers et al., 1990a) averaged 81 ± 63 (±SD). Two pipe traps with funnel (Bakke et al., 1983) caught 32 ± 13, and three cross-pane window traps (Schlyter et al., 1987b) averaged 28 ± 8. It was found that detergent (for lowering the water surface tension) was not necessary to drown the beetles. In pure water, beetles would continue to move on the surface for many hours but none could leave due to their inability to climb out of the water and up the plastic sheet. Eventually beetles would sink and drown; rain caused relatively more to sink.

Observations indicated that beetles of both species oriented with a casting and/or circling flight to the trap and then either struck the plastic cup that shielded the dispensers and fell into the water or landed directly in the water or on surrounding plastic. Although white plastic traps were used in the present experiments, black plastic traps also caught the beetles. The black color worked even without water when it was sunny as beetles that landed could not find a perch to initiate flight and died within seconds from extreme heat.

Trapping of Bark Beetles with a 7 × 7 Grid of Pheromone-Baited Puddle Traps. The catch of *Pityogenes chalcographus* in puddle traps spaced 6 m apart in plot 1 on June 7 totaled 4086 and was highest along one edge of the grid nearest the forest (Figure 2A). A few days later, on June 10, a similar pattern was evident (Figure 2B) with a total catch of 2367. The next day, however, the catch of 11,974 was more uniformly spread throughout the grid of traps (Figure 2C). A second grid of traps at 12 m spacing was set up in plot 2 on June 10 (Figure 3A) and the total catch of 132 was much less than in plot 1. The next day 1136 beetles were caught (Figure 3B), and the distribution was more uniform than on the previous day. On June 12, 4794 beetles were caught in a distribution similar to June 10 in the same plot (Figures 3A and 3B).

The 12-m spacing was reduced to 3 m so that the new grid was well inside the former area. This grid caught 1216 *P. chalcographus* (Figure 4A) but the next day only 224 (Figure 4B), although the patterns were similar. The grid size was further reduced in plot 2 to a 1.5-m spacing. The catch totaled 238 on June 15 (Figure 5A), and 643 from 0900 to 1500 hr, and 323 from 1500 to 2100 hr on June 16 (Figure 5B and 5C). In all experiments, two additional traps without pheromone were placed in each grid equidistant between the diagonal corners of the inner-ring traps and the center-ring traps. None of these controls caught any bark beetles during the tests.

Since the high catches of *P. chalcographus* in plot 1 on June 11 were taxing my ability to count them, the baits were removed and replaced with those for *I. typographus*. On June 13 and 14, the pattern of catch was quite similar (total catches of only 77 and 58, respectively, Figure 6A and 6B). On June 15, a small shift in catch took place, but most still were caught closest to the forest (along the bottom edge of the figures, total of 47, Figure 6C); on June 16 a

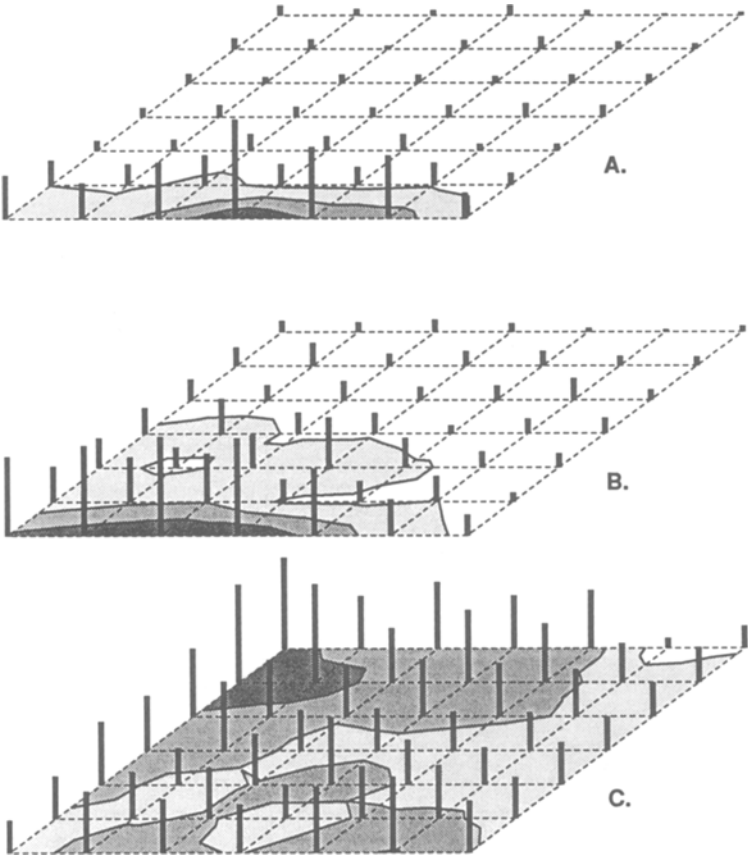

FIG. 2. (A) Catches of bark beetle *Pityogenes chalcographus* (June 7, 1989) in 49 puddle traps baited with synthetic pheromone components (see text) and placed in a grid of 6-m spacing (plot 1, Torsby, Sweden). Contour lines represent increments of 25% of the maximum trap catch (largest bar = 476). (B) Same experiment on June 10, 1989 (largest bar = 178). (C) Same experiment on June 11, 1989 (largest bar = 465).

significant proportion was caught on the side farthest from the forest (total catch of 53, Figure 6D).

Computer Simulation of Trapping as Bark Beetles Immigrate into a 7 × 7 Grid of Traps. The simulation model is represented pictorially in Figure 7, where "traps" of radius 1.3 m (for example) are shaded circles placed at a 6-m spacing. The tracks of 60 simulated beetles are shown entering the periphery of the area at random and flying in the area until caught (Figure 7). The fact that "beetles" were not allowed to leave the simulation area is equivalent to intro-

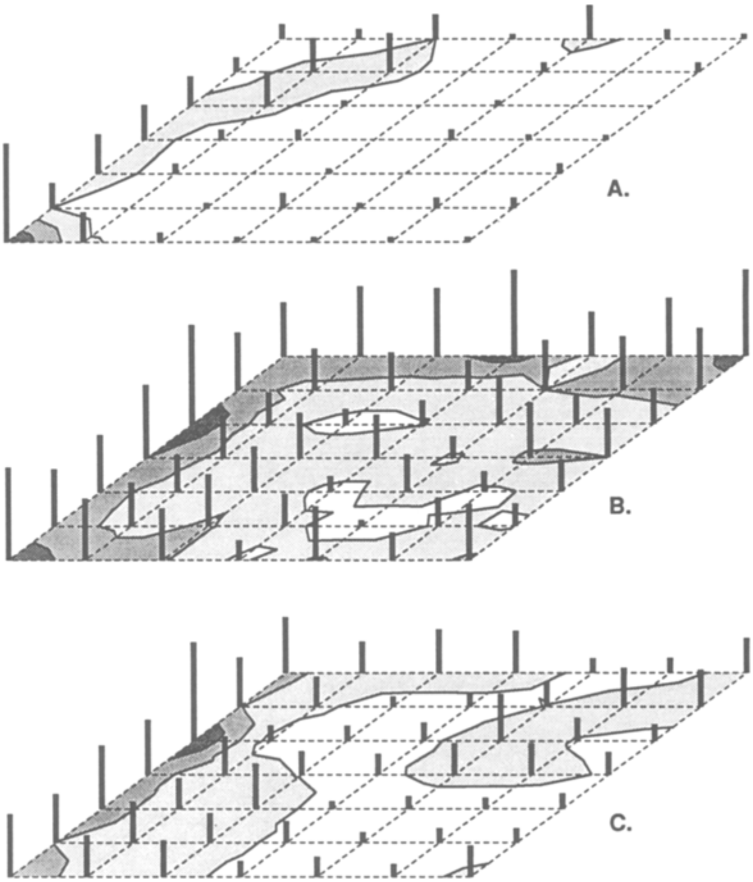

FIG. 3. (A) Catches of bark beetle *Pityogenes chalcographus* (June 10, 1989) in 49 puddle traps baited with synthetic pheromone components (see text) and placed in a grid of 12-m spacing (plot 2, Torsby, Sweden). Contour lines represent increments of 25% of the maximum trap catch (largest bar = 20). (B) Same experiment on June 11, 1989 (largest bar = 50). (C) Same experiment on June 12, 1989 (largest bar = 319).

ducing a new beetle when one leaves, and thus all catch ratios of inner to outer traps are based on the same number of beetles. In the actual simulations, the distribution of trap catches of 4000 beetles at each trap radius (Figure 8) was used to obtain ratios of inner to outer trap catches.

For a grid of 49 traps at 6-m spacing, as the simulated trap radius (effective catch radius) is changed from nearly 0 to a maximum of 3 m, the ratio of catch for the trap catch average on the outer ring of 24 traps to that on the inner ring of 16 traps increases from one to nearly infinite (Figure 8). The curve could not

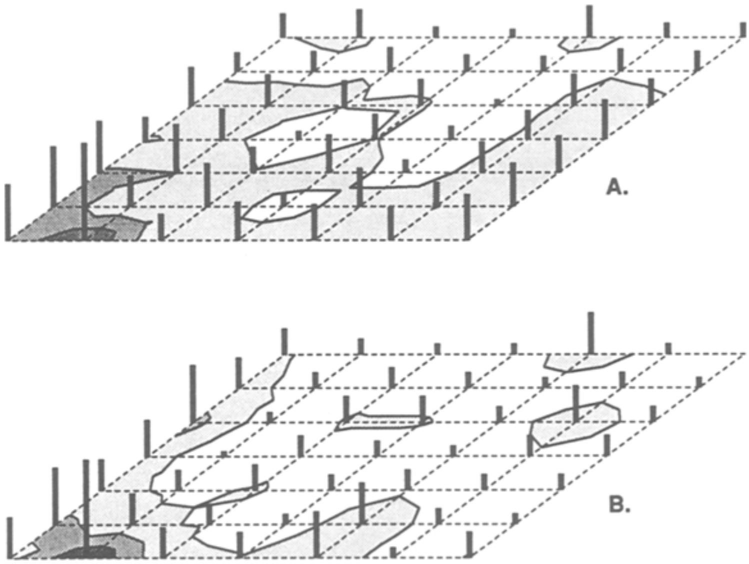

FIG. 4. (A) Catches of bark beetle *Pityogenes chalcographus* (June 13, 1989) in 49 puddle traps baited with synthetic pheromone components (see text) in a grid of 3-m spacing (plot 2, Torsby, Sweden). Contour lines represent increments of 25% of the maximum trap catch (largest bar = 82). (B) Same experiment on June 14, 1989 (largest bar = 19).

be fit by standard curvilinear equations (exponential, logarithmic, geometric, or quadratic). However, the reciprocal of the ratio (i.e., catch per trap on the inner ring divided by the catch per trap on the outer ring) gave a relationship that was fit perfectly by the quadratic equation $Y = aX^2 + bX + c$ ($r^2 = 0.999$). The best fitting equation used $a = 0.0694$, $b = -0.56$, and $c = 1.015$. Thus the equation for the relation between the trap radius and the outer/inner catch ratio is then the reciprocal of the quadratic equation. To solve for X given Y, the equations are solved in terms of Y. Therefore, a catch ratio (inner/outer) of $Y = 0.3$ yields an effective catch radius of $X = 1.59$ m for a trap as found from the equation:

$$X = \frac{-b - \sqrt{b^2 - 4a(c - Y)}}{2a} \tag{3}$$

Similarly, a catch ratio (outer/inner) of $Y = 9$ yields an effective catch radius of $X = 2.23$ m as found from the equation:

$$X = \frac{-b - \sqrt{b^2 - 4a[c - (1/Y)]}}{2a} \tag{4}$$

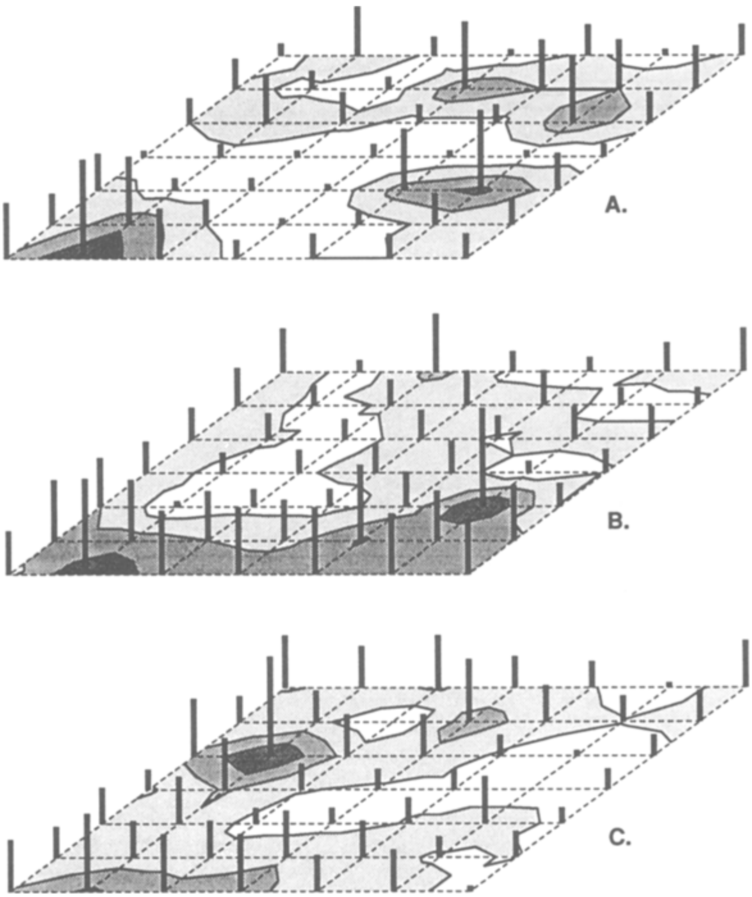

FIG. 5. (A) Catches of bark beetle *Pityogenes chalcographus* (June 15, 1989) in 49 puddle traps baited with synthetic pheromone components (see text) in a grid of 1.5-m spacing (plot 2, Torsby, Sweden). Contour lines represent increments of 25% of the maximum trap catch (largest bar = 16). (B) Same experiment on June 16, 1989, between 0700 and 1500 hr (largest bar = 34). (C) Same experiment on June 16, 1989, between 1500 and 2100 hr (largest bar = 19).

For comparison to the field catches either equation 3 or 4 can be used to solve for the effective catch radius in the field, assuming the field conditions are simulated appropriately by the model. Simulations at spacings of 1.5 m and different trap radii gave best fitting quadratic coefficients of $a = 0.8788$, $b = -2.042$, and $c = 0.97$; similarly, for 3-m spacings: $a = 0.2067$, $b = -1.026$,

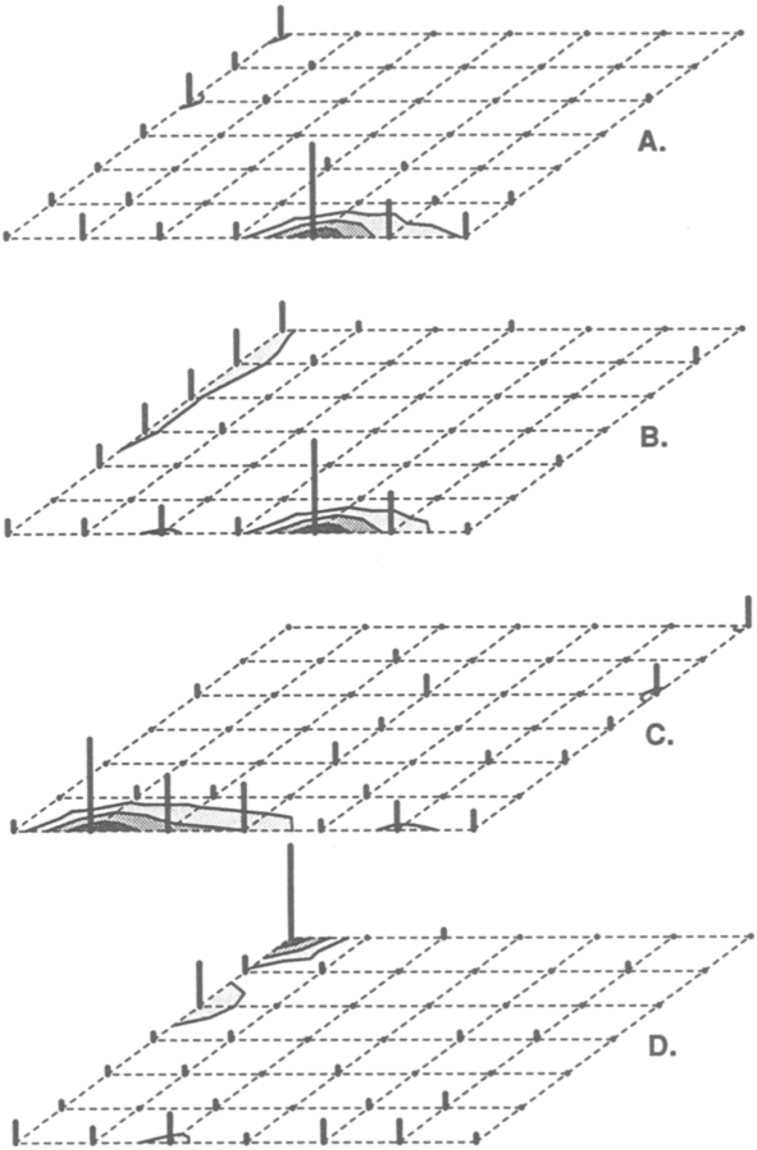

FIG. 6. (A) Catches of bark beetle *Ips typographus* (June 13, 1989) in 49 puddle traps baited with synthetic pheromone components (see text) in a grid of 6-m spacing (plot 1, Torsby, Sweden). Contour lines represent increments of 25% of the maximum trap catch (largest bar = 21). (B) Same experiment on June 14, 1989 (largest bar = 14). (C) Same experiment on June 15, 1989 (largest bar = 10). (D) Same experiment on June 16, 1989 (largest bar = 13).

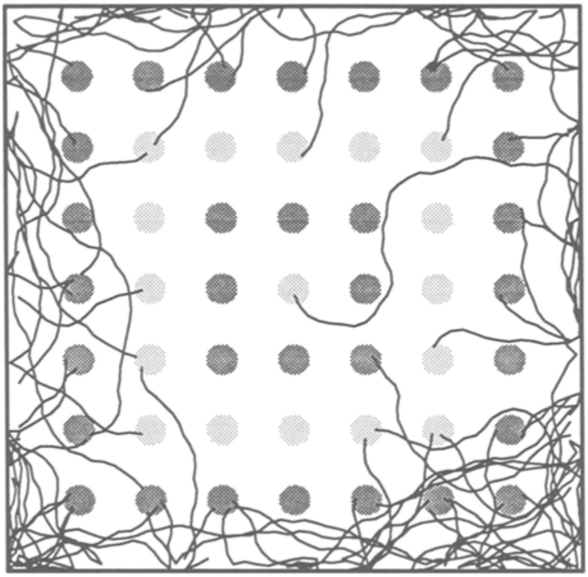

FIG. 7. Paths (wavy lines) of 60 "bark beetles" during simulation of their flight into a grid of 49 traps of effective catch radius equal to 1.3 m. The simulation area was 48 × 48 m with 6-m spacing between traps. Beetles were released at random along the edges of the area and they were not allowed to leave. The movements employed a maximum turn angle of 30° and steps of 1 m. In simulations that varied the effective trap radius, a ratio was obtained that compared the average catch per trap on the outer ring of 24 traps to the average per trap in the next inner ring of 16 traps.

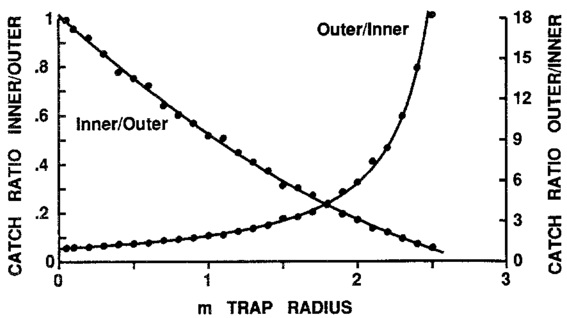

FIG. 8. Quadratic relationship between the simulated trap radius (see Figure 7) and the ratio of catch per trap on the inner ring of 16 traps and the outer ring of 24 traps (Inner/Outer) and the reciprocal quadratic relationship between the trap radius and the simulated catch ratio of the outer 24 traps and the inner 16 traps (Outer/Inner). Each point represents results from an average of four simulations each using 1000 "beetles" with model parameters as in Figure 7 (see text for details).

and $c = 1$; and for 12-m spacings: $a = 0.0242$, $b = -0.311$, and $c = 0.992$ ($22 \geq N \leq 26$ and $r^2 \geq 0.99$ for each regression).

Table 1 reports the outer/inner catch ratios (from Figures 2–6) and the corresponding expected trap radii using equation 4 for each of the quadratic equations at the 1.5-, 3-, 6-, and 12-m trap spacings. The average effective catch radius for *I. typographus* was 2.04 ± 0.66 m (±95% CL) at the 6-m grid spacing. The relationship between the spacing of traps in the grid and the effective catch radius for *P. chalcographus* is shown in Figure 9. Thus, the effective catch radius in the field was very small when traps were closely spaced at 1.5 m apart but increased linearly as the distance between traps was increased. This

TABLE 1. AVERAGE CATCHES AND CATCH RATIOS OF *Pityogenes chalcographus* AND *Lps Typographus* PER TRAP FOR TRAPS IN VARIOUS RINGS (SEE FIGURE 7) OF 7 × 7 TRAP GIRD (VARIOUS SPACINGS AND DATES, 1989).[a]

	Average Trap catch				Effective catch radius (m)
P. chalcographus	Outer ring	Inner ring	Center ring	Outer/inner catch ratio	
12-m spacing					
Figure 3A, June 10	3.7	2.3	0.9	1.65	0.81
Figure 3B, June 11	28.8	18.5	15.9	1.56	0.73
Figure 3C, June 12	118.5	77.5	80.4	1.53	0.71
6-m spacing					
Figure 2A, June 7	108.4	62.7	54.8	1.73	0.87
Figure 2B, June 10	55.5	40.8	42.9	1.36	0.54
Figure 2C, June 11	246.0	248.8	236.8	0.99	0.01
3-m spacing					
Figure 4A, June 13	28.7	23.5	16.4	1.22	0.37
Figure 4B, June 14	5.5	3.7	3.9	1.48	0.66
1.5-m spacing					
Figure 5A, June 15	4.9	5.8	3.3	0.86	0.00
Figure 5B, June 16	14.9	13.0	8.5	1.14	0.26
Figure 5C, June 16	7.0	7.0	5.0	0.99	0.02
lps typographus					
6-m spacing					
Figure 6A, June 13	2.9	0.3	0.4	9.20	2.24
Figure 6B, June 14	2.3	0.1	0	18.67	2.48
Figure 6C, June 15	1.5	0.3	0.5	4.93	1.90
Figure 6D, June 16	1.8	0.6	0.2	3.11	1.53

[a]The ratio of the outer ring ($N = 24$) catch average divided by the inner ring ($N = 16$) catch average was used in the reciprocal quadratic equation 4, as determined by simulations, to find the effective catch radius.

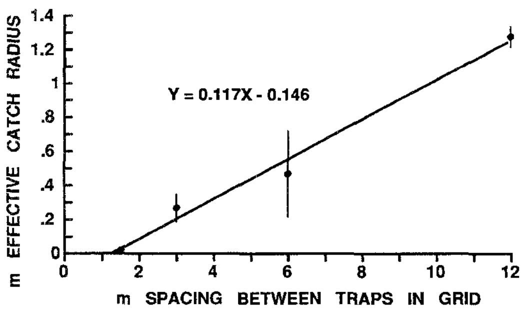

FIG. 9. Linear relationship between the spacing distance between field traps in the grid and the size of the effective catch radius for *Pityogenes chalcographus*. The effective catch radius, X, is found from equation 4, where the coefficients were obtained from simulations at the respective spacings, and Y is the ratio of catch on the outer-ring–inner-ring traps in the field. Each point represents the average from Table 1 ($\pm$SEM).

indicates that at closer trap spacings, there was significant competition between traps in attracting beetles since in principle the effective catch radius should be constant for a specific pheromone release rate.

DISCUSSION

One of the earliest traps to be used to catch bark beetles is the barrier or window trap (Chapman and Kinghorn, 1958), and many modifications of this type of trap have been used (Schlyter et al., 1987b; Tunset et al., 1988). Several large funnels at various heights in the forest canopy were used by Gara (1963) to catch *Ips paraconfusus*. A series of several funnels (the multiple-funnel trap) each directly above the other serves as both a barrier and collecting apparatus (Lindgren, 1983). The pipe trap described earlier and used in the mass trapping program in Scandinavia (Bakke et al., 1983) has served as the standard experimental trap in several subsequent studies (Schlyter et al., 1987a–c; Byers et al., 1988). The bucket trap with small holes, and similar designs, derives from the pipe trap where beetles must enter holes as if they were seeking mates and host tissue (Moser and Browne, 1978; Byers, 1983a).

The pipe trap can be used without a funnel but relatively less beetles are caught since the funnel collects falling beetles that strike the pipe barrier (Bakke et al., 1983; Regnander and Solbreck, 1981). Relatively more males of *I. typographus* are caught by pipe traps when they have a funnel since males are relatively less attracted compared to females when the concentration of aggregation pheromone increases (Schlyter et al., 1987a,b), a phenomenon found also for *I. paraconfusus* and *P. chalcographus* (Byers, 1983b; Byers et al., 1988).

Barrier traps work rather well for larger scolytids such as most *Ips* species since they often can not recover their flight ability after striking the barrier. However, for smaller scolytids such as *P. chalcographus* (2 mm long) the insects have less momentum and can more often recover after striking the barrier. Electrostatic forces at the surface of plastic barriers also can affect small insects more so than larger ones.

The sticky trap has been commonly used in semiochemical experiments for catching all sorts of scolytids and associated insects (Bedard and Browne, 1969; Browne, 1978; Byers, 1983b; Byers et al., 1989). The problem with sticky traps, of course, is that they must be picked by hand (laborious and time consuming) or cleaned with a solvent (thus the trap must be replaced). Furthermore, heavy rain, which occurs often in Scandinavia, soon reduces the trapping efficiency of Stikem Special. The problem with pipe traps, multiple-funnel traps, and window traps is that they are relatively complex to construct. Field olfactometers, consisting of a fan and formed sheet metal (Vité and Gara, 1962; Gara, 1963), mechanical rotary nets (Chapman and Kinghorn, 1958; Vité and Gara, 1962), wind-vane traps (Byers, 1988b), and mechanical, slow-rotation sticky traps (Byers et al., 1990a) are even more complex. This complexity (and expense) is appropriate for certain kinds of experimental purposes but it is a disadvantage for larger-scale experiments and control programs.

The puddle trap (Figure 1) is simple, easy to set up, and inexpensive compared to pipe (Scandinavia), multiple-funnel (U.S.A./Canada), or schlitzfalle (Germany) traps. Puddle traps are also easily transported, being constructed of wire and plastic sheeting. The traps can be reused after each replicate by simply straining the insects from the water. Rain has little effect on the trap since beetles are pounded down to the bottom, and later if the rains continue, water overflows the edges without taking the insects. Due to the low profile and heavy weight of the water pool, even strong winds of several meters per second have no effect on the trap. The puddle trap could be constructed as a broad conical dish of polypropylene and have a floating pheromone dispenser. This design would allow stacking of traps for transport and make them easy to manufacture so that many more traps could be employed in control programs for the same cost, thus increasing the prospects of success.

In the experiments reported here, synthetic chalcogran was released at about 0.15 mg/day from each trap [46% racemic *E* isomer of which half is the bioactive (2*S*,5*R*) enantiomer; Byers et al., 1989]. This could be equivalent to the release from 208 males feeding in a log [360 ng chalcogran/male/day released of which 46% is (2*S*,5*R*); Schurig and Weber, 1984; Byers et al., 1989, 1990b]. The release of methyl (*E*,*Z*)-2,4-decadienoate from *P. chalcographus* has not been determined, but in the abdomen it is present at about 10% that of chalcogran (Birgersson et al., 1990). Assuming proportional release rates for the two components, then a release of methyl (*E*,*Z*)-2,4-decadienoate of 2.4 μg/

day from the trap is equivalent to the release from 67 beetles. Individual male *I. typographus* feeding in Norway spruce trees released an average of 0.16 mg 2-methyl-3-buten-2-ol per day (Birgersson and Bergström, 1989) so the traps that released 50 mg/day were equivalent to 312 beetles. Release of *cis*-verbenol at 1 mg/day from the traps was equivalent to 178 *I. typographus* feeding in trees, while release of α-pinene at 31 mg/day corresponded to release from about 39 entrance holes (Birgersson and Bergström, 1989).

It is difficult to compare the catches in grids of the same size and plot but on different dates since the wind and temperature, as well as the population density would be expected to vary with time. Different sizes of grids on the same plot may vary in catch patterns not only due to time but also due to changes in spatial dimensions. Figures 2–6 illustrate the variation in trap catch and, presumably, the densities of flying beetles as affected by microclimate and wind patterns. In spite of the catch variation, the outer ring of 24 traps caught proportionally more per trap than the inner ring of 16 traps, and these usually caught more than a trap on the center ring (Table 1). This pattern is consistent with the expectation that beetles entering the grid would be attracted to the first traps they encountered, while the proportion not caught (due to chance and going between traps) would fly until encountering the next ring of traps where they have yet another chance of being attracted and trapped. The likelihood of beetles passing the outer ring of traps on their way through the grid is dependent on the effective size of the traps, i.e., higher pheromone releases would effectively create a larger trap. This hypothesized "filtering" effect is also evident in the results of Bakke et al. (1983), where the number of *I. typographus* caught per trap declined towards the center in a hexagonal grid of 91 pipe traps spaced 20 m apart.

The simulation model (Figure 7) varied the size of the effective catch radius from very small, so that all traps would catch about the same and thus the catch ratio of outer–inner traps would be 1, to very large, so that the ratio would become infinite (Figure 8). By comparing the catch ratio from the field trapping at a particular grid spacing to the simulation results, it is possible to estimate a theoretical effective catch radius for the field traps for each bark beetle species (Table 1). The estimated effective catch radius for *I. typographus* of 2.04 m (at the 6-m grid spacing) corresponds remarkably closely to the effective attraction radius (EAR) of 1.9 m reported earlier at the same pheromone release rate (Byers et al., 1989).

The four different spacings of traps in the grids and their catches can be used in a simulation model to estimate four effective catch radii for these traps on *P. chalcographus* (Figures 7–9). In principle, the same effective catch radius should be calculated from field catches regardless of the grid spacings of traps, as long as the true catch radii do not overlap. At the largest spacings between traps, the calculated effective catch radius was largest (Figure 9), indicating that beetles were experiencing the least difficulty orienting to these traps. At even greater spacing between traps (not tested here), the effective catch radius should stabilize in magnitude since pheromonal interactions between traps would not occur. Thus, this estimated value should remain constant for a given pheromone release rate, regardless of the population density. Since the estimate of the catch radius decreased with closer spacing of traps, and was nearly zero at 1.5-m spacing (Figure 9), this indicates that beetles were increasingly disrupted in orientation to pheromone at closer trap spacings. The pheromone plumes from these traps probably intermingled to the extent that a significant proportion of beetles orienting first to one trap might not land but follow a coalescing plume to another trap. However, even at the 1.5-m spacing between traps, there was apparently no confusion as to where to land since the control traps (only 1.06 m from four other pheromone traps) caught no beetles.

The simulation model above was derived from another that represents graphically the movement of insects in an area where mass trapping is ongoing (Byers, 1993). The model parameters for the mass trapping are: (1) the x and y dimensions of the area, (2) the number of traps, (3) the trap's effective catch radius, (4) the placement of traps at random with a minimum spatial separation or in uniform rows and columns, and (5) the test duration. The model parameters for the insects are: (1) the number of insects, (2) the average speed, (3) the step size, and (4) the maximum angle of deviation within which a random angle is taken from the former direction at each step. Initial directions and turning angles at each step are random for each insect. The model led to discovery of iterative equations that can predict the mass trapping efficiency of a particular set of model parameters above and provide a basis for the design of mass trapping experiments and control programs (Byers, 1993).

Tilden et al. (1981) tested the effects of release of synthetic pheromone from a 7 × 7 grid of 49 release points (but no traps) at a 15-m spacing on the orientation of the bark beetle, *D. brevicomis*, to a center trap and pheromone source. They found that the many pheromone sources disrupted the orientation to the source, since 97% fewer beetles were caught at the center trap than in the control without many release points. A transect of six traps through the grid caught more beetles on the outer traps than on the inner traps. It is not certain whether beetles were experiencing sensory adaptation or were wasting time flying to one or more of the many pheromone sources (cf. Cardé, 1981; Sanders, 1981; Baker et al., 1988). In the experiments presented here, however, the wasting of time investigating sources of synthetic pheromone (false trail following) was at least partly precluded since beetles would usually be trapped. Thus, the shrinking effective catch radius with closer bait spacing might be due to sensory adaptation (Baker et al., 1988). However, the pheromone plumes (trails) at the closer spacings would also intermingle more and tend to mask or camouflage the locations of the pheromone sources.

The effective attraction radius (EAR), as well as the effective catch radius discussed above, can be used to describe the strengths of semiochemical signals within and between species, irrespective of the population level or environmental conditions (Byers et al., 1989). While calculation of the EAR uses a formula that compares the catch of the pheromone trap with that of a noninteracting, passive trap in the same area (Byers et al., 1989), the estimation of the effective catch radius compares catches on a grid of pheromone traps to results from simulations using equation 3 or 4 above. However, the two concepts of attraction strength are essentially the same, i.e., a physical trapping radius that catches all insects by interception. This does not mean that these radii describe the way a plume looks or the distance that insects are attracted, but means that a passive trap in effect must have the specified radius to catch the number it did when it was baited with pheromone. The EAR should be calculated for a release rate of semiochemical from a trap that is not in competition with other sources nearby, while the effective catch radius requires a grid of pheromone traps. However, to calculate a more accurate effective catch radius, one must space the traps sufficiently apart to minimize interactions between pheromone plumes, otherwise the radius will be underestimated.

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