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UPWIND FLIGHT ORIENTATION TO PHEROMONE IN WESTERN PINE BEETLE TESTED WITH ROTATING WINDVANE TRAPS[1,2]

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Abstract—In the first trap design, a rotating windvane was connected to a 30 × 30 × 30-cm "square box" sticky trap enclosing a synthetic pheromone source (*exo*-brevicomin, frontalin, and myrcene) at the windvane's rotation axis. A second design used the windvane attached to two tubular (19-cm-diam. × 30-cm) sticky traps each suspended 120 cm from the same pheromone source and opposingly aligned "downwind" and "upwind" of the windvane. Significantly more beetles of each sex of *Dendroctonus brevicomis* LeC. (Coleoptera: Scolytidae) were caught on the downwind side compared to the upwind side of the square-box design. Even larger differences in catch, four times more males and 3.4 times more females, were found on the downwind tubular trap compared to the upwind one. The windvane trap design provides rigorous evidence that insects, especially bark beetles, orient upwind to pheromone sources (from at least 1.2 m downwind until reaching the source).

Key Words—*Dendroctonous brevicomis*, Coleoptera, Scolytidae, pheromone, anemotaxis, upwind orientation, *exo*-brevicomin, frontalin, myrcene.

INTRODUCTION

Upwind flight orientation by insects to pheromone has become a well-known fact or paradigm. This knowledge is based largely on correlative evidence be-

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[1] *Dendroctonus brevicomis* LeC. (Coleoptera: Scolytidae).

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tween wind direction and observations of flying insects or trap catches in the field. There are many studies on Lepidoptera and other insects orienting to pheromone sources in wind tunnels (Kellogg et al., 1962; Farkas and Shorey, 1974; Kennedy, 1977, 1983; Kennedy et al., 1980, 1981; Cardé, 1984). In some larger insects it is possible to correlate wind direction measurements using windvanes and simple observations of wing fanning (Elkinton et al., 1984). With many smaller insects, such as bark beetles, it is difficult to document their upwind flight orientation response to pheromone. Consequently, ''very little (olfactory) research has investigated orientation by flying beetles, nor has it addressed the intricacies of orientation behaviour'' (Borden, et al., 1985).

One reason this is so is that bark beetles have been difficult to fly in wind tunnels. Flight exercise is required in at least some bark beetles before they will take off flying upwind in pheromone-bearing wind (*Scolytus multistriatus:* Choudhury and Kennedy, 1980) or before they will ignore light and respond instead to attractant odors (*Trypodendron lineatum:* Graham, 1959). Even with flight exercise, preliminary studies (Byers, Schlyter, and Löfqvist, unpublished) on *Ips typographus* in a wind tunnel have been largely unsuccessful. The beetles fly towards lights and seem to have difficulty orienting upwind without leaving the plume and striking the side of the tunnel. The possibility that bark beetles are ''less accurate'' than moths when orienting to a pheromone source may be explained by differences in their requirements: male moths need to find females while bark beetles must find only an aggregation spread widely over a tree. Thus, it is possible that orientation mechanisms in flying bark beetles may be different from those in better-understood insects.

Due to the inherent difficulties of wind-tunnel experiments and flight observations on small beetles, close-range orientation studies have been done in the laboratory on walking bark beetles. The open arena bioassay has indicated they walk upwind and chemotactically orient to pheromone sources (Wood and Bushing, 1963; Birch and Wood, 1975; Byers and Wood, 1981) or to host odors (Byers et al., 1985). The beetles could also do so under natural conditions, although we have little or no evidence of this.

In the field, there are several studies on bark beetles that indicate, with various degrees of credibility, that beetles fly upwind to pheromone sources, presumably when stimulated by pheromone molecules within a plume. However, these studies were not truely rigorous, in that they relied on descriptive observation or they utilized correlations between wind direction and trap catches. For instance, McMullen and Atkins (1962) and Rudinsky (1963) observed that Douglas-fir beetles flew ''upwind'' and directly to a pheromone source although some ''flew by and circled back before landing.'' Gara (1963) stated *Ips paraconfusus* take off in all directions, but usually with the wind. Upon encountering pheromone-laden air, they oriented against the wind and flew back toward the source of attraction.

Later studies have attempted to quantify the orientation behavior by catching beetles in traps placed at or near a pheromone source (Chapman, 1962; Gara, 1963; Coster and Gara, 1968; Seybert and Gara, 1970; Gray et al., 1972; Tilden et al., 1979; Byers, 1983; Helland et al., 1984; Schlyter et al., 1987). The conclusions of these studies, however, were all dependent on correlations of trap catch with wind direction measured nearby (usually at one place) and time-averaged. Thus, sometimes the wind direction may not have been aligned with the "prevailing wind direction," and it was not known precisely what the relative frequencies of beetle attraction/wind direction were over certain periods during the test. Therefore, the objective of this study was to obtain direct evidence of upwind orientation to a pheromone source which was both quantitative and not dependent on correlative wind data. A pair of rotating traps on a windvane which aligns with the wind provides a novel design for testing anemotactic orientation to odor sources in insects. The hypothesis is that the "downwind" trapping surfaces will intercept and catch significantly more beetles than the control traps placed "upwind."

METHODS AND MATERIALS

A windvane was constructed that held either a box-type sticky trap or two tubular sticky traps suspended on opposing arms. A 5-mm metal shaft served as the axle which rotated inside two ball bearings fixed near the top of a 1.5-m metal pole that was driven vertically into the ground. A polycarbonate vane was attached to a support about 16 cm from the axle and counterbalanced by metal weights (Figure 1). The dimensions of the vane were approximately 2 mm thick × 15 cm top × 38 cm bottom × 39 cm and 45 cm sides. In the first trap design, a square box was constructed from four, 30 × 30-cm, 6.3-mm wire-mesh screens coated with Stikem Special,® Seabright Enterprises, Emeryville, California. The box rested on 4-mm fiber board and was aligned so that the downwind side was perpendicular to the vane (Figure 1).

In the second trap design, 19-cm-diam. × 30-cm-high tubular sticky traps were constructed from the same materials and suspended equidistant from the axle (120 cm) on the ends of a 2 × 2-cm wooden beam (Figure 2). The two opposing traps were aligned with the vane so that one trap would be consistently downwind while the other was upwind of the pheromone source. The pheromone components of *D. brevicomis*, *exo*-brevicomin and frontalin (both >96%), and the host component, myrcene (>98%), all from Chem. Samples Co., Cleveland, Ohio, were released individually from glass tubes (two for each component) inside a dispenser (Byers and Wood, 1980; Tilden and Bedard, 1985). The release rates varied significantly with temperature but were estimated to be about 3 mg/day of each component.

Beetles were collected from the sides of the box trap once or twice daily (seven replicates) during its placement in the Sierra National Forest near Bass

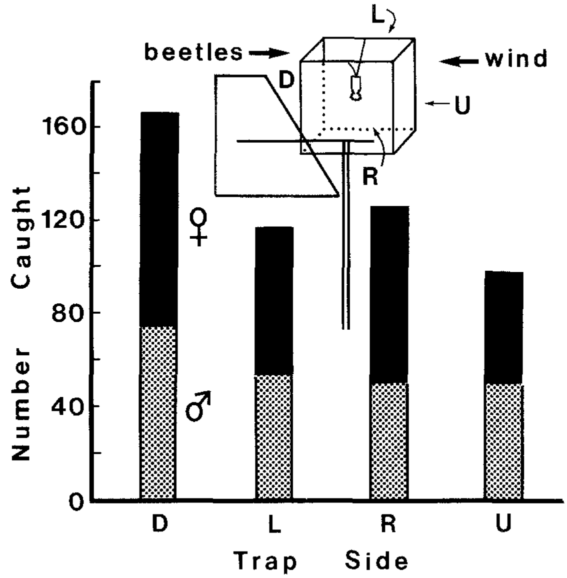

FIG. 1. Upwind orientation of *D. brevicomis* to a pheromone source within a "box" sticky trap (30 cm on a side) placed upon a windvane at 1.4 m height. The pheromone components, *exo*-brevicomin, frontalin and myrcene, were each released at 3 mg/day from within the box trap. Letters designate trap sides orientation: D = downwind, R = right and L = left of downwind, and U = upwind.

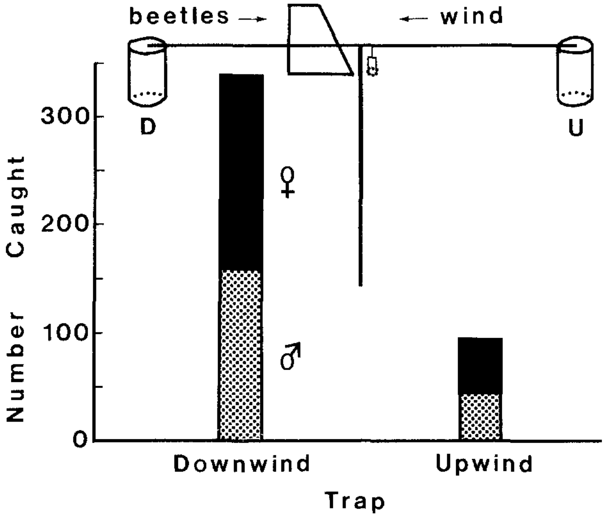

FIG. 2. Upwind orientation of *D. brevicomis* to a pheromone source placed at the rotation axis of a windvane (1.4 m height). Opposing tubular sticky traps (30 cm × 19 cm diam.) were aligned with the wind direction and each was 1.2 m from the rotation axis. The pheromone components, *exo*-brevicomin, frontalin, and myrcene, were each released at 3 mg/day in the forest.

Lake, Madera County, California, at 1000 m elevation (August 19-23, 1985). The opposing traps of the second design were similarly picked of beetles (six replicates) during testing in the same area (August 24–27, 1985). Wind speeds were measured with a fan anemometer for several 1-min periods during general alignment with the windvane in order to obtain an estimate of environmental conditions. Effects of position on the distributions of catch between the downwind side and the other three sides of the box trap and also between the opposing traps were determined with the Wilcoxon matched-pair test. Binomial confidence limits for sex ratios were calculated (Byers and Wood, 1980) and compared for significant differences with chi square.

RESULTS

The catches of *D. brevicomis* on the downwind, left and right of downwind, and upwind sides of the box sticky trap situated on the windvane are shown in Figure 1. As might be expected, if the beetles were flying upwind just prior to landing, the downwind side caught more beetles (32.3%) than either the left (22.8%) or right sides (25.7%) or the upwind side (19.3%), and the upwind side caught the fewest beetles. The downwind side caught significantly more males and females than did the upwind side (1.5 and 1.9 times more, respectively, ($P < 0.05$), and the sex ratios caught on the various sides were not significantly different (Table 1). It is apparent, however, that each of the four sides caught a significant proportion of the total catch.

TABLE 1. NUMBER OF *D. brevicomis* CAUGHT AND RATIOS (WITH 95% BINOMIAL CONFIDENCE LIMITS) ON WINDVANE TRAP WITH BOX TRAP OR OPPOSING TRAPS (SEE FIGURES 1 AND 2)

	Number caught		Sex ratio
	Male	Female	M/F[a] 95% BCL
Box trap			
Downwind side	74	92	0.80(0.59–1.09)
Left side[b]	53	64[c]	0.83(0.58–1.19)
Right side[b]	56[c]	76	0.74(0.52–1.04)
Upwind side	50[c]	49[c]	1.02(0.69–1.51)
Opposing traps			
Downwind trap	156	182	0.86(0.69–1.06)
Upwind trap	39[c]	53[c]	0.74(0.49–1.11)

[a] Sex ratios were not significantly different ($P > 0.05$, χ^2).

[b] When one is facing upwind.

[c] Wilcoxon matched-pair test showed trap surfaces had significantly different distributions of catch for a particular sex compared to the corresponding downwind side or downwind trap ($P < 0.05$).

In order to further test the anemotactic orientation hypothesis, two opposing traps were placed 120 cm from the pheromone source such that one trap was always aligned downwind while the other was upwind (Figure 2). Here it can be seen that the trap catches were even more different since four times more males and 3.4 times more females were caught on the downwind trap compared to the upwind trap (Figure 2). The differences in catch were statistically significant for both males and females ($P < 0.05$), while the sex ratios caught on each trap were not significantly different (Table 1). The wind was observed to change direction rather frequently (about once every minute) by as much as 180°. This was apparently more variable than observed earlier (Byers, 1983). Wind speeds varied between 0.5 and 1.5 m/sec with brief periods of calm (wind changing). All tests were conducted during favorable flight weather (warm and sunny, midday temperature 25–32°C).

DISCUSSION

The catches of *D. brevicomis* on the respective sides of the box sticky trap on the windvane indicate that both sexes orient upwind to pheromone sources, at least in the final landing stage. The fact that significant proportions apparently were caught on sides other than the downwind side can be explained in several ways. One possibility is that the wind direction changed more abruptly than could be followed by the windvane so that anemotactic beetles were caught by inappropriate sides. It is almost certain that the zigzag flight path of bark beetles as they traverse a narrowing plume (as in other insects, Kellogg et al., 1962; Traynier, 1968) would cause significant catches on the sides. The observation of earlier scientists also indicate that beetles that fly out of the odorous air attempt to turn and even circle back to the source, resulting in catches on the upwind side. After the experiments were concluded, I became aware of another example where a similar windvane trap (as in Figure 1) indicated that onion flies oriented upwind to host-plant odors, at least within 20 cm of the source (Dindonis and Miller, 1980). A box trap of much larger dimensions would have probably given much larger differences in catch among the sides.

Tests of anemotaxis on a larger dimension were attempted by separating the trapping surfaces about 120 cm from the source in both the downwind and upwind directions. The higher catches on the downwind trap indicated that beetles were responding anemotactically at least 1.2 m from the pheromone source. The fact that some beetles were caught on the upwind trap can be explained by: (1) the windvane may have sometimes lagged behind the change in wind direction and (2) not all anemotactic beetles were caught by the downwind trap and, when they were not trapped at the source, they dispersed at random on even continued more or less upwind until they were caught by the upwind trap. It would have been interesting to have compared these results with a test where a box trap was also placed over the source in order to reduce the possibility of the second explanation above. Of course, many trap configurations are possible in combination with the windvane concept.

Lindelöw and Weslien (1986) sum up our knowledge of *I. typographus* flight behavior during the dispersal flight: "when released, beetles always flew downwind for at least 10–15 m, after which time they were impossible to observe." However, it is sometimes possible to observe beetles a few meters before landing at a pheromone source during the late afternoon as sunlight is transmitted through their wings. Others have used white sheets to offer a contrast (Chapman, 1962; Seybert and Gara, 1970). These observations are not quantitative and are only correlated with wind direction, which is often imperfectly known.

Several quantitative studies have provided evidence for upwind orientation to attractive sources in bark beetles but one or more drawbacks are apparent: (1) the tests used marked beetles, often selected, that were subsequently released (unnaturally), (2) the tests were performed in unnatural settings (cages, grassland), (3) the tests used fixed-position traps that may not have been optimally aligned with the prevailing wind direction, (4) the wind direction was averaged and could only be correlated on a gross scale since instantaneous catch and wind direction were not determined, and (5) the wind measurements were usually only at one location and somewhat distant from the traps, and in some cases measurements were from weather stations several kilometers away.

Chapman (1962) found that more *Trypodendron lineatum* were caught on the downwind sides of sticky traps placed over attractive logs (drawbacks 3–5 above). Gara (1963) performed an interesting experiment in which a line of nine traps, placed parallel to the wind direction, released pheromones from each in increasing and then decreasing amounts. Marked *Ips paraconfusus* were then released at either the upwind or downwind areas of the line. The suggestion was that since the percent recoveries on the traps were virtually identical, this must mean that beetles released upwind flew with the wind until turning upwind in response to pheromone, while beetles released downwind flew immediately upwind in response to pheromone. Ignoring anemotactic theories and personal observation of flying beetles, however, one could argue that there is a more simple explanation of Gara's results. This is that beetles do not utilize wind direction when orienting to pheromone as their release either upwind or downwind made no difference on their distribution of recapture along the trap line. However, the windvane trap results presented here allow us to believe more strongly in Gara's explanation.

Coster and Gara (1968) released marked *D. frontalis* in a grassland area from four cardinal directions that were 30.5 m from a pheromone source. The beetles released from the downwind direction were recaptured in the highest proportion, but the numbers were probably too low for reliable statistics (drawbacks 1–5). Seybert and Gara (1970) found that caged *I. pini*, artificially induced to fly, flew proportionately more to the upwind wall (75%) when the cage was placed 6 m downwind of a pheromone source (no statistics, drawbacks 2–4). In a similar experiment with caged *D. ponderosae*, Gray et al. (1972) showed a statistically significant preference for upwind flight to attractants (drawbacks 2–4). Tilden et al. (1979) used sticky traps in four cardinal directions at 1.5- and 4.5-m distances from a pheromone source to monitor the attraction of *D. brevicomis*. They found that the downwind trap consistently caught more beetles than the upwind trap (drawbacks 3–5). Byers (1983) used three trap rows, each 21 m long of 15 sticky traps, placed perpendicular to the prevailing wind and each succeeding row was 4.6 m further downwind from a pheromone source in order to observe the upwind orientation of *I. paraconfusus*. Both sexes were caught in a narrowing and concentrating pattern as they approached the source, but the male catch at the source was significantly reduced compared to female catch (also compared to the sex ratios on the rows of traps), indicating that male orientation to pheromone is less focused than that of females (drawbacks 3–5).

Helland et al. (1984) released marked *I. typographus* in grassland from four cardinal directions either 12 or 20 m from a central pheromone source. Beetle catch was monitored in 64 traps, each capable of catching beetles from four cardinal directions with respect to the source, stationed in eight 24-m-long "spokes" radiating from the source. The pattern of catch was consistent with an upwind orientation to pheromone, for beetles released downwind, and there was evidence that beetles "swarmed" around the source and did not always move straight into the trap (drawbacks 1–5). In many respects their results are reminiscent of those obtained by Gara (1963) above. Schlyter et al. (1987) placed barrier traps in four cardinal directions each 3 m from a central pheromone source and found that *I. typographus* was again caught in a pattern consistent with upwind anemotaxis (although the wind measurements were taken several kilometers away from the experiment, drawbacks 3–5).

The present study provides a method for continuously integrating wind direction and flight intensity in a natural setting with naturally responding beetles. Thus, the method of coupling a windvane with beetle traps circumvents the five experimental drawbacks encountered in the past. However, much more remains to be understood about close-range flight orientation (observed here) and as well longer-range orientation that often was probed in the experiments discussed above.

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REFERENCES

BIRCH, M.C., and WOOD, D.L. 1975. Mutual inhibition of the attractant pheromone response by two species of *Ips* (Coleoptera: Scolytidae). *J. Chem. Ecol.* 1:101–113.

BORDEN, J.H., HUNT, D.W.A., MILLER, D.R., and SLESSOR, K.N. 1985. Orientation in forest Coleoptera: An uncertain outcome of responses by individual beetles to variable stimuli, pp. 97–109, *in* T.L. Payne, M.C. Birch, and C.E.J. Kennedy (eds.). Mechanisms in Insect Olfaction. Clarendon Press, Oxford.

BYERS, J.A. 1983. Sex-specific responses to aggregation pheromone: Regulation of colonization density in the bark beetle *Ips paraconfusus*. *J. Chem. Ecol.* 9:129–142.

BYERS, J.A., and WOOD, D.L. 1980. Interspecific inhibition of the response of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus*, to their pheromones in the field. *J. Chem. Ecol.* 6:149–164.

BYERS, J.A., and WOOD, D.L. 1981. Interspecific effects of pheromones on the attraction of the bark beetles, *Dendroctonus brevicomis* and *Ips paraconfusus* in the laboratory. *J. Chem. Ecol.* 7:9–18.

BYERS, J.A., LANNE, B.S., LÖFQVIST, J., SCHLYTER, F., and BERGSTRÖM, G. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. *Naturwissenschaften* 72:324–326.

CARDÉ, R.T., 1984. Chemo-orientation in flying insects, pp. 111–124, *in* W.J. Bell and R.T. Cardé (eds.). Chemical Ecology of Insects. Chapman and Hall, London.

CHAPMAN, J.A. 1962. Field studies on attack flight and log selection by ambrosia beetle *Trypodendron lineatum* (Oliv.) (Coleoptera: Scolytidae). *Can. Entomol.* 94:74–92.

CHOUDHURY, J.H., and KENNEDY, J.S. 1980. Light versus pheromone-bearing wind in the control of flight direction by bark beetles, *Scolytus multistriatus*. *Physiol. Entomol.* 5:207–214.

COSTER, J.E., and GARA, R.I. 1968. Studies on the attack behavior of the southern pine beetle. II. Response to attractive host material. *Contrib. Boyce Thompson Inst.* 24:69–76.

DINDONIS, L.L., and MILLER, J.R. 1980. Host-finding behavior of the onion fly, *Hylemya antiqua*. *Environ. Entomol.* 9:769–772.

ELKINTON, J.S., CARDÉ, R.T., and MASON, C.J. 1984. Evaluation of time-average disperson models for estimating pheromone concentration in a deciduous forest. *J. Chem. Ecol.* 10:1081–1108.

FARKAS, S.R., and SHOREY, H.H. 1974. Mechanisms of orientation to a distant pheromone source, pp. 81–95, *in* M.C. Birch (ed.). Pheromones. North Holland, Amsterdam.

GARA, R.I. 1963. Studies on the flight behavior of *Ips confusus* (LeC.) (Coleoptera: Scolytidae) in response to attractive material. *Contrib. Boyce Thompson Inst.* 22:51–66.

GRAHAM, K. 1959. Release by flight exercise of chemotropic response from photopositive domination in a scolytid beetle. *Nature* 184:283–284.

GRAY, B., BILLINGS, R.F., GARA, R.I., and JOHNSEY, R.L. 1972. On the emergence and initial behavior of the mountain pine beetle, *Dendroctonus ponderosae*, in eastern Washington. *Z. Angew. Entomol.* 71:250–259.

HELLAND, I.S., HOFF, J.M., and ANDERBRANDT, O. 1984. Attraction of bark beetles (Coleoptera: Scolytidae) to a pheromone trap: Experiment and mathematical models. *J. Chem. Ecol.* 10:723–752.

KELLOGG, F.E., FRIZEL, D.E., and WRIGHT, R.H. 1962. The olfactory guidance of flying insects. IV. *Drosophila*. *Can. Entomol.* 94:884–888.

KENNEDY, J.S. 1977. Olfactory responses to distant plants and other odor sources, pp. 67–91, *in* H.H. Shorey and J.J. McKelvey (eds.). Chemical Control of Insect Behavior. Wiley-Interscience, New York.

KENNEDY, J.S. 1983. Zigzagging and casting as a programmed response to wind-borne odour: A review. *Physiol. Entomol.* 8:109–120.

KENNEDY, J.S., LUDLOW, A.R., and SANDERS, C.J. 1980. Guidance system used in moth sex attraction. *Nature* 288:475–477.

KENNEDY, J.S., LUDLOW, A.R., and SANDERS, C.J. 1981. Guidance of flying male moths by wind-borne sex pheromone. *Physiol. Entomol.* 6:395–412.

LINDELÖW, A., and WESLIEN, J. 1986. Sex-specific emergence of *Ips typographus* L. (Coleoptera: Scolytidae) and flight behavior in response to pheromone sources following hibernation. *Can. Entomol.* 118:59–67.

MCMULLEN, L.H., and ATKINS, M.D. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. (Coleoptera: Scolytidae). *Can. Entomol.* 94:1309–1325.

RUDINSKY, J.A. 1963. Response of *Dendroctonus pseudotsugae* Hopkins to volatile attractants. *Contrib. Boyce Thompson Inst.* 22:23–38.

SCHLYTER, F., LÖFQVIST, J., and BYERS, J.A. 1987. Behavioural sequence in the attraction of the bark beetle *Ips typographus* to pheromone sources. *Physiol. Entomol.* 12:185–196.

SEYBERT, J.P., and GARA, R.I. 1970. Notes on flight and host-selection behavior of the pine engraver, *Ips pini* (Coleoptera: Scolytidae). *Ann. Entomol. Soc. Am.* 63:947–950.

TILDEN, P.E., and BEDARD, W.D. 1985. Field response of *Dendroctonus brevicomis* to *exo*-brevicomin, frontalin, and myrcene released at two proportions and three levels. *J. Chem. Ecol.* 11:757–766.

TILDEN, P.E., BEDARD, W.D., WOOD, D.L., LINDAHL, K.Q., and RAUCH, P.A. 1979. Trapping the Western pine beetle at and near a source of synthetic attractive pheromone: Effects of trap size and position. *J. Chem. Ecol.* 5:519–531.

TRAYNIER, R.M.M. 1968. Sex attraction in the Mediterranean flour moth, *Anagasta kuhniella:* Location of the female by the male. *Can. Entomol.* 100:5–10.

WOOD, D.L., and BUSHING, R.W. 1963. The olfactory response of *Ips confusus* (LeConte) (Coleoptera: Scolytidae) to the secondary attraction in the laboratory. *Can. Entomol.* 95:1066–1078.