

Dispersal and flight behaviour of *Ips sexdentatus* (Coleoptera: Scolytidae) in pine forest

H Jactel

INRA, Centre de Recherches d'Orléans, Station de Zoologie Forestière, Ardon, 45160 Olivet, France

(Received 30 October 1990; accepted 6 March 1991)

Summary — The dispersal range and the flight behaviour of *Ips sexdentatus* in pine forest were studied using mark-recapture experiments. 9 614 beetles were marked by the elytra engraving method and released just after emergence. They were caught at different distances in pheromone baited traps. Less than 10% of the beetles failed to take off. Flyers were captured at distances up to 4 km. The main dispersal occurred during the first day. When wind speed rose > 3 m/s, beetles were mainly caught in the upwind direction at the shortest trapping distances and mainly in the downwind direction at the longest trapping distances. For the same trap density, the number of beetles captured increased with trapping distance. This was interpreted as a flight exercise requisite prior to chemotropic orientation. The trapping attraction radius was estimated at 80 m. These findings bring into question the use of the pheromone trapping system for the control and prognosis of *Ips sexdentatus*.

***Ips sexdentatus* / bark beetle / pine / mark recapture / dispersal / flight behaviour / pheromone attraction**

Résumé — Dispersion et comportement de vol d'*Ips sexdentatus* (Coleoptera: Scolytidae) en forêt de pin sylvestre. Des expériences de lâcher-recapture ont permis d'étudier la dispersion et le comportement de vol d'*Ips sexdentatus* en forêt de pin sylvestre. Neuf mille six cent quatorze scolytides ont été marqués par gravage des élytres et lâchés juste après émergence. Ils ont été recapturés, à distances croissantes, par un nombre égal ou croissant de pièges à phéromone. Trois à dix-huit pour cent des scolytides se sont révélés incapables de s'envoler (tableau 1). Les autres ont été recapturés jusqu'à 4 km du point de lâcher. Plus de 80% des captures ont été enregistrées dans les 6 h suivant le moment du lâcher. Pour une même densité de pièges, supposée optimale, le nombre d'insectes recapturés augmente avec la distance de piégeage (fig 2). Les scolytes ne deviendraient donc sensibles à l'attraction de la phéromone qu'après une certaine durée de vol obligatoire. Un modèle est présenté qui tient compte de ce comportement et du rayon d'action des pièges à phéromones (fig 3) pour calculer les taux de recapture en fonction de la distance de piégeage (fig 4). Le rayon d'attraction des pièges a été estimé à environ 80 m. Ces résultats remettent en question l'utilisation de la technique de piégeage phéromonal pour le contrôle ou la prognose d'*Ips sexdentatus*.

***Ips sexdentatus* / scolytite / pin sylvestre / lâcher-recapture / vol / déplacement / comportement / phéromone / piège**

INTRODUCTION

The dynamics of bark beetle populations depend largely on 2 factors: beetle population density and tree resistance (Berryman, 1972; Christiansen *et al*, 1987). Population density represents the effective number of insects which are able to find suitable host trees. Several authors have pointed out that, for their first flights, up to 40% mortality can occur at the insects' take off (Schmid, 1970; Schmitz, 1979; Wollerman, 1979; Shore and McLean, 1988; Salom and McLean, 1989). Because the food supply of bark beetles is often scarce, transient, and widely dispersed, beetle success may depend on flight capacity. Numerous studies suggest that flights over long distances (up to tens of km) are common for many species of scolytids (Gara, 1963; Koponen, 1980; Botterweg, 1982; Nilssen, 1984). Lastly, Boren *et al* (1986) made a list of Scolytidae species in which flight exercise could trigger an attraction to pheromones: *Dendroctonus frontalis*, *Dendroctonus pseudotsugae*, *Ips typographus*, *Pityogenes chalcographus*, *Scolytus multistriatus* and *Trypodendron lineatum*.

Therefore, in order to understand the spatial and temporal dynamics of *Ips sexdentatus* populations, investigations into their dispersal and flight pattern become necessary. Unfortunately the literature on the dispersal of this species is very scarce (Termier, 1970; Forsse, 1989) and as yet no field experiment has been carried out. In north central France, *Ips sexdentatus* can produce 2 generations and numerous sister-broods (up to 7) in a year (Vallet, 1982). A flight precedes each settlement and occurs when the temperature rises to 18 °C (Bakke, 1968; Vallet, 1982). Consequently, the flight activity of *Ips sexdentatus* is almost continuous from April to October.

The objectives of this study were the following: i), How far can the beetles fly, and how do wind speed and wind direction influence the orientation of the flight? ii), What is the real number of *Ips sexdentatus* which are able to fly? iii), What are the consequences of the flight behaviour on beetles response to pheromones?

MATERIALS AND METHODS

Studies employing 2 release-recapture experiments were made in the Forest of Orléans, north central France, during the summers of 1989 and 1990. They were conducted in pure stands of Scots pine, *Pinus sylvestris* (L), 35–75 yr old. When the size of an experimental plot overstepped the limits of these stands, some traps were set in mixed stands of Scots pine of the same age and Durmast oak, *Quercus petraea* (Mattus) Liebl. The experimental plots were chosen to be as similar as possible and with the least amount of competitive host material (logs or windfalls) which might have a strong influence on rate of beetle recapture.

All the mark-recapture experiments were set up on the same principle. Marked beetles were released in the central point of a single ring of trap locations. Several radii of trap rings (*ie*, minimum distances of flight) were tested, but only 1 ring was set up per plot.

Experiment 1 was designed to study the proportion of flyers and their range of dispersal. It consisted of 5 plots, at least 5 km apart from one another. In each plot, 4 traps were set up in a ring in 4 cardinal directions. The first plot had a radius of 50 m, the others 100, 200, 500, and 1 000 m respectively. This experiment was replicated 3 times during the summer of 1989, but only the 3 shortest distances were tested the first time.

Experiment 2, consisting of 4 plots, was designed to investigate the need of flight exercise prior to pheromone attraction. The first plot had its traps located in a ring of 100 m radius, the second 200, the third 400 and the last 600 m. In each ring, the traps were 200 m apart from each other. Consequently, the 4 plots had 3, 6, 12 and 18 traps respectively, but the same number of traps per circumference section. This experi-

ment was replicated 3 times during the summer of 1990.

In the present study, barrier-traps with flat funnels of the Röchling model were used. They were hung from support posts 1.5 m high. They were placed away from tree shadows and had no herbaceous plants under them. They were baited with Stenoprax® dispensers (Shell Agrar) containing the *Ips sexdentatus* synthetic pheromone, a mixture of methyl butenol, ipsdienol and α -pinene. This dispenser has a very short duration of efficiency (Malphettes, personal communication). Thus the traps were baited 2 h before the release of the beetles and the dispensers were removed on the evening of the next day. A paper saturated with lindane was put into the trap collector in order to prevent the beetles from escaping and to eliminate their predators.

The release point was set at the center of each trap ring in a sunny clearing. It consisted of a wooden platform (17 x 17 cm) set into a plastic box (25 x 25 cm). This box was fixed on a 1.3-m support and sheets of paper covered its base. Beetles that failed to take off from the platform fell into the box. They could then either slide over the sides of the box or swarm over the stands of the platform and try to fly again. Definitive non-flyers, which had died during release or which were unable to fly were recovered from the box.

Tested beetles were of 2 different origins. For experiment 2 and the second replication of experiment 1, they were collected from trap trees in the Forest of Orléans just before emergence. They were held in bags containing bark and stored in a cold chamber for several weeks. For the other releases, the beetles came from laboratory breedings (Jactel and Lieutier, 1987). All the insects belonged to the second generation (offspring) except for the first replication of experiment 2, which utilised overwintering beetles. According to the literature, the response to pheromone attraction could be linked with a flight exercise. Thus, in order to compare recapture percentage, we had to use emerging beetles prior to any flight. Cold storage in a black chamber ensured lowest beetle activity between emergence and release.

Upon emergence, insects were collected and marked by the elytral engraving procedure (Lieutier *et al.*, 1986). Because the beetles might mix their tags in the trap collector, we preferred to use the engraving method rather than fluorescent powder (Gara, 1963) or radioactive (Moore

et al., 1979) marking technique. Lieutier *et al.* (1986) reported that a slight mortality is observed with the elytra engraving method, but that the flight of surviving beetles is not affected. The beetles were marked according to their date of emergence in experiment 1, and according to their release point in experiment 2. The insects which emerged at a given day were distributed at random in to 4 or 5 groups, each corresponding to an experimental plot. Thus each plot received the same number of beetles of the same age and origin. Just after tagging, they were stored in damp tissues in a cold chamber for 1–10 d until the day of release.

On the flight day, beetles were put one by one on to the release platform when the temperature was $> 20^{\circ}\text{C}$. The release lasted about half an hour per plot, so total release duration was ≈ 3 h, between 10 am and 1 pm. At least 3 h later, non-flyers were removed. Traps were checked in the late afternoon of the day of release and the following day.

In order to determine how the wind influenced the catch, data from a meteorological station were used which recorded wind speed and wind direction every 3 h. This station was in an open field, 40 km from the experimental plots.

All statistical analyses were carried out using the SAS software (SAS Institute 1985).

RESULTS

Experiment 1

5 978 marked beetles were released and the percentage of non-flyers averaged 5.5% (table I). $81.6 \pm 7.5\%$ of the total capture occurred on the first day and the percentage did not vary significantly between the different trapping distances ($P = 0.68$, F test).

The percentages of recapture were significantly different between the different trapping distances ($P = 0.0018$, F test). For the 3 replications (fig 1), the highest recapture level was obtained at 100 m. Despite a lower trap density, it had a significantly higher recapture level than at 50 m.

Table I. Percentage of non-flyers in the marked beetles released in experimented 1 and 2.

	Experiment 1			Experiment 2		
	Replication			Replication		
	1	2	3	1	2	3
No of beetles released per plot	661	369	430	400	255	254
% Non-flyers	6.1 ± 2.2	3.3 ± 1.4	7.0 ± 0.5	2.9 ± 3.2	7.2 ± 3.7	18.4 ± 4.0

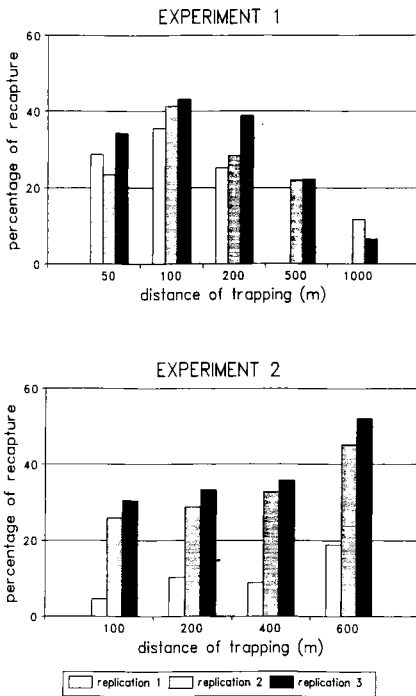


Fig 1. Percentage of recapture of the flying marked beetles according to the distance of trapping. In experiment 1, the plots present equal numbers of traps (increasing distances between 2 nearby traps with increasing distances of trapping). In experiment 2, the plots present equal densities of traps (same distances between 2 nearby traps with increasing distances of trapping).

Since > 80% of the capture occurred on the first day, the speed and the direction of the wind were only taken into consideration during only the first 9 h of the experiment to calculate the relative rate of capture in each trap of a plot, *i.e.* in each direction (fig 2). Catches were observed in all the directions, but their distribution was not uniform. Captures were more important in the upwind direction at the shortest trapping distances (50 and 100 m) but more important in the downwind direction at the longest distances (500 and 1 000 m). This irregularity was more accurate when the wind rose > 3 m/s (replications 1 and 3).

Experiment 2

In the 1990 experiment, the percentage of non-flyers was still low, but varied from 3–18% (table I).

The recapture rates obtained with the overwintering beetles in the first replication were consistently lower than those obtained with the offspring beetles in the last 2 replications (fig 1). The percentage of recapture increased with trapping distance. Since the experiment was conceived using a distance of 200 m between 2 nearby traps in all the plots, the probability of flying in a trap attraction zone was supposed

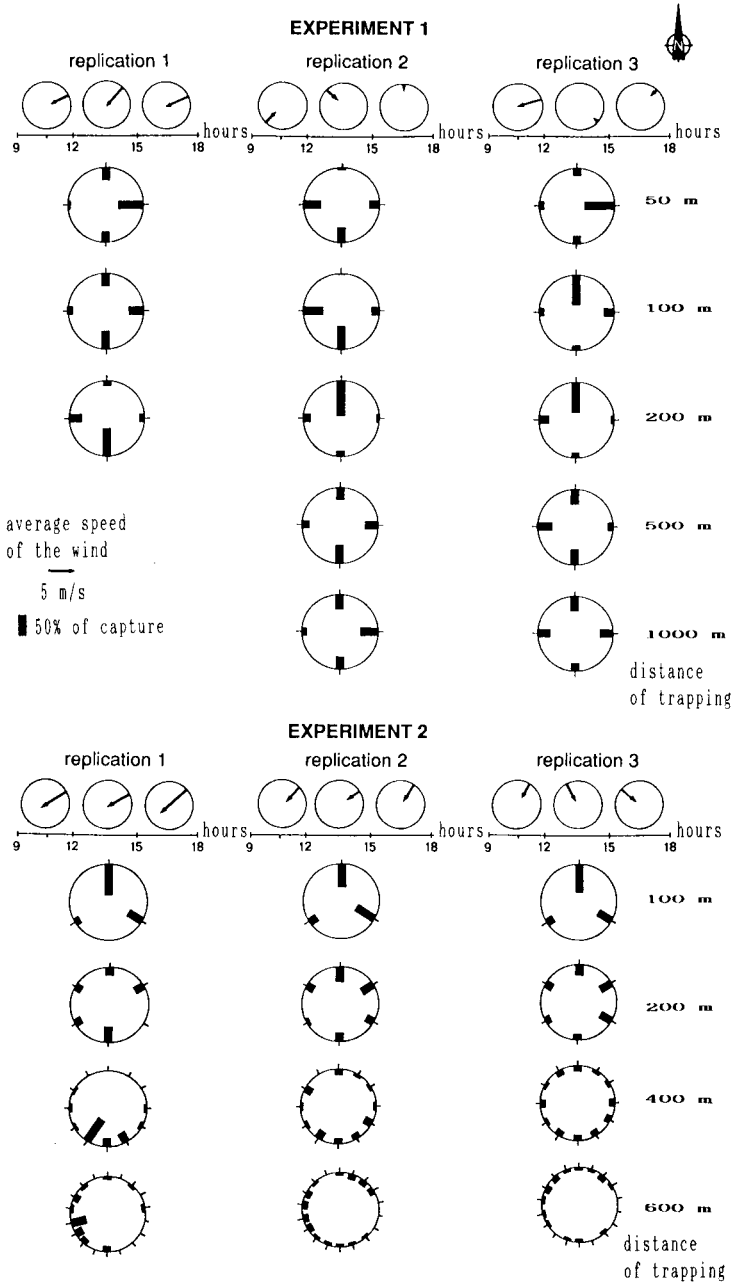


figure 2

Fig 2. Effect of wind speed and wind direction on the flight orientation of *Ips sexdentatus*. Relative proportions of recapture in the traps of each plot in experiments 1 and 2.

to be equal in all the plots. Consequently, the recapture percentage would be proportional to the percentage of insects sensitive to the pheromone attraction at this distance. Thus the number of insects responsive to the pheromone attraction seemed to increase with their flight distance.

As observed in experiment 1, when the wind speed increased beyond 3 m/s in experiment 2 (1st replication) upwind traps caught more beetles at 100 m, whereas downwind traps caught more beetles at 400 and 600 m (fig 2).

DISCUSSION

Non-flyers

The percentage of *I sexdentatus* non-flyers was constantly low, but varied from 3–18%. This variation could be linked to differences between populations since the released beetles were of several origins and since the confidence interval of each mean was narrow. Likewise, with *Scolytus multistriatus*, Wollerman (1979) recorded from 1–50% non-flyers for the same treatment. For *Trypodendron lineatum*, the proportion of non-flyers can vary from 14% (Salom and McLean, 1989) to 43% (Shore and McLean, 1988). Schmitz (1979) assumed that physiological conditions or the presence of parasites can affect flight capacity, but Forsse (1987) proved that the presence of endoparasitic nematodes does not affect the flight duration of *Ips typographus*. In flight mill studies, an increase of the non-flyer numbers was observed as the intraspecific competition for food increased during larval development (Jactel, in preparation). These findings suggest that the non-flyer factor must be taken into account for population dynamics and thus needs more investigation.

Flight distance

The percentage of recapture was almost 10% at 1 000 m from the release point. Twenty-four marked beetles were recovered from colleagues' pheromone traps that were 3 km from the present study. Moreover, as beetles were tagged according to their plot in the second experiment, it was possible to follow flights from one plot to another. Forty-six *I sexdentatus* were found which belonged to a different plot; this corresponded to flight distances from 1.5–4 km. Thus *I sexdentatus* can fly over long distances in forests like many other scolytids. According to Gara (1963) *Ips confusus* can fly up to 1 km and *Dendroctonus frontalis* 2 km. Likewise *Trypodendron lineatum* can fly 1 km (Shore and McLean, 1988), and *Ips typographus* from 20–60 km (Nilssen, 1984; Forsse and Solbreck, 1985). With such a dispersal range, bark beetles can widely explore their natural habitat. Consequently, the spatial distribution of infestation foci may radically change after each major flight.

Dispersal speed

The dispersal *I sexdentatus* appears to occur rapidly. Including the longest distances, almost 80% of the marked beetles were caught on the release day, *ie* during the 6 h following the first take-off. Within the same amount of time Wollerman (1979) obtained 70% of total recapture of *Scolytus multistriatus* and Lindelöw and Weslien (1986) and Salom and McLean (1989) found 90% respectively with *Ips typographus* and *Trypodendron lineatum*. These findings are consistent with the flight speed recorded on flight mills. All of them are almost 4 km/h (Atkins, 1961; Gara, 1963; Jactel, 1991). This means that the dispersal of scolytids occurs over a

short time period, thus providing more opportunity to avoid unfavorable weather and predators. The beetles caught later might have failed to take off several times (Schmid, 1970) or might have dispersed in steps.

Flight behaviour

If one assumes that the attraction zone of any trap had the same surface on the same days, we could suppose that the probability of flying into any of these zones should decrease as the trapping distance increased. Since the percentages of recapture at the trapping distance of 200 m were always lower than those obtained at 100 m in experiment 1, we can assume that the attraction zone of the traps might have a radius of ≈ 100 m (if this radius were 200 m, the decrease in the rate of recapture would have begun at 500 m). Consequently, the probability of flying in 1 of the 4 zones of trap attraction would equal 1 when the beetles were released at < 100 m from the traps and would decrease for longer distances. Secondly, since the percentages of recapture were always higher at 100 than at 50 m in experiment 1, we can suppose that a factor might exist which increased the probability of trapping as the distance of recapture increased. This factor could be in the form of a flight exercise requisite prior to pheromone attraction; as the trapping distance increased, the number of beetles which had performed their necessary exercise would increase, as would the attraction and rate of recapture.

The first hypothesis assumes that the attraction zone could be regarded as a disc of radius R for each trap. The most widely accepted model for the pheromone dispersion in forests is the plume model (Fares *et al*, 1980). Taking into account this theory, the equiprobability zones of

capture around a pheromone trap could be represented by concentric ellipses (McClendon *et al*, 1976). The long axes of these ellipses are directed with the wind and approximate discs for the highest probabilities of capture. In this study, since the percentage of recapture was the sum of the 4 traps caught in the 4 directions, the R radius could have been interpreted as the average size of the capture ellipses.

The second hypothesis of the model assumed that a flight exercise might be required prior to pheromone attraction. In experiment 2 traps were placed in an order so that their attraction zones were contiguous, assuming in a first approximation that the trap attraction radius equalled 100 m. Thus the probability of flying in an attraction zone should have tended to be 100% in all the plots. An increase of the recapture rate was found with trapping distance. If no flight exercise was necessary prior to trap attraction, we would have expected to have found the same or perhaps a decreasing percentage of recapture at the different distances due to the losses increasing as the insects keep on flying. In a laboratory experiment, Graham (1959) observed that the response behavior of *Trypodendron lineatum* is at first phototactic and later chemotropic only after a certain flight duration. This phenomenon was observed for many other bark beetles such as *Dendroctonus pseudotsugae* (Atkins, 1966; Bennett and Borden, 1971), *Tomicus piniperda* (Perttunen *et al*, 1970), *Scolytus multistriatus* (Choudury and Kennedy, 1980), *Dendroctonus frontalis* (Andryszak *et al*, 1982) and *Ips typographus* (Gries, 1985; Schlyter *et al*, 1987). Moreover, several mark-recapture procedures with concentric rings of traps obtained significant captures in the outer rings. Such is the case for *Scolytus multistriatus* (Lanier *et al*, 1976) and *Trypodendron lineatum* (Salom and McLean, 1989). Some authors argue that the beetles are able to respond to

pheromone attraction as soon as they emerge (Gara and Vité, 1962; Gara, 1963; Gray *et al*, 1972; Lindelöw and Weslien, 1986). But this objection is not inconsistent with the main theory. It is likely that a part of the population can have a chemotropic response at the very beginning of its dispersal (Atkins, 1966; Francia and Graham, 1967; Andryszak *et al*, 1982). According to the current theory, the flight threshold corresponds to the consumption of a certain part of the insect's lipid supply, which varies among the individuals in a population (Atkins, 1969; Borden *et al*, 1986). In a same manner, Borden (1967), Birch (1974) and Botterweg (1982, 1983) found overwintering beetles much less responsive to pheromones than the summer generation and attributed this to the greater lipid content in the overwintering generation (Hagen and Atkins, 1975). This could explain the lower rate of capture obtained in the first replication of the experiment 2.

According to these assumptions, a mathematical model was set up to calculate the percentage of recapture at the different distances of trapping in the first experiment. It was founded on 2 assertions:

– When D (the distance of trapping) is shorter than $R \sqrt{2}$ (with R the radius of the trap zone of attraction), the percentage of recapture would equal the proportion of beetles which have flown the requisite exercise (fig 3a). Because this rate corresponds to a cumulative percentage of beetles, it might follow a logistic curve with the following formula:

$$\frac{\exp(aD + b)}{1 + \exp(aD + b)} \quad (1)$$

– When D is longer than $R \sqrt{2}$, the recapture percentage would be the product of the previous formula multiplied by the probability of flying in 1 of the 4 attraction

zones of a plot. Each beetle was supposed to fly roughly in the same direction. Consequently its location on the plot surface might be determined by the dispersal angle in which it had flown since the takeoff (fig 3b). So, the probability of flying in a trap attraction zone would take the following form:

$$\frac{8\alpha}{360} \quad \text{where } \alpha = \arcsine(R/D) \quad (2)$$

and the rate of recapture might equal the following formula:

$$\frac{8 \arcsine(R/D)}{360} \times \frac{\exp(aD + b)}{1 + \exp(aD + b)} \quad (3)$$

This model of 3 parameters (a , b and R) was fitted to the field data (fig 4) according to the NLIN procedure (SAS, 1985). It converged for a R radius of 79.4 m. This effective trapping/attraction radius multiplied by

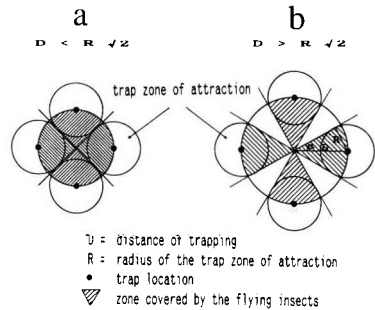


Fig 3. Schematic representation of probability of flying in a trap zone of attraction (resembling a disc) in experiment 1. a) When the trapping distance D is shorter than $R \sqrt{2}$, this probability equals 1. b) When D is longer than $R \sqrt{2}$, this probability equals 8α with $\alpha = \arcsine(R/D)$.

360

(the linear distance between 2 nearby traps equals $2R \sqrt{2}$).

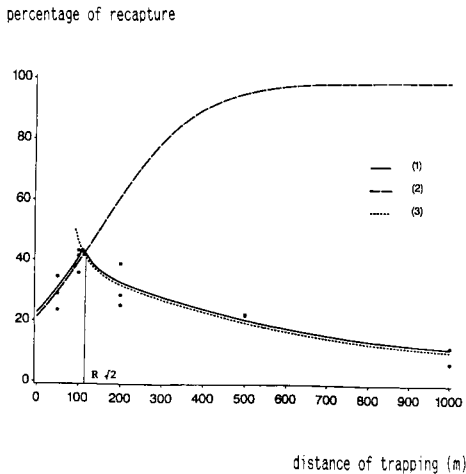


Fig 4. Model predicting the percentage of recapture in 4 traps according to the distance of trapping, in experiment 1. 1) Percentage of recapture of the flying marked beetles in 4 pheromone traps (1) = (2) when $D < R \sqrt{2}$; (1) = (3) when $D > R \sqrt{2}$. 2) Cumulative percentage of beetles responsive to the pheromone attraction after flight exercise. 3) Cumulative percentage of beetles responsive to the pheromone attraction multiplied by the probability of flying in a trap zone of attraction. Parameters of the model with their asymptotic 95% confidence interval: $a = 0.009 \pm 0.006$; $b = -1.32 \pm 0.57$; $R = 79.4 \pm 23.9$.

$\sqrt{2}$ equals 112 m. This value is consistent with the fact that the recapture decrease from a trapping distance of 100 m in experiment 1. It is also close to the 100 m calculated by McClendon *et al* (1976) in a pheromone trapping system applied to *Anthonomus grandis*. Likewise Anderbrant and Schlyter (1987) indicated that the attraction range of baited sticky traps is 50 m or less when applied to *Scolytus scolytus*.

According to this model, $\approx 20\%$ of the *I. sexdentatus* flyers were sensitive to the pheromone attraction at take-off and almost 100% after 1 000 m of flight. These results were higher than those obtained in

experiment 2. The disparity could be due to a difference between the lipid supply of the insects in 1989 and 1990. Since this disparity increased with the flight distance, it could also be due to an increasing "loss" of beetles with the distance of flight. Indeed, the number of insects attacked by predators or definitively settled on a tree should increase with the distance of flight.

Influence of wind speed and wind direction

Numerous authors have observed that scolytids first fly with the wind (Helland *et al*, 1984; Lindelöw and Weslien, 1986; Schlyter *et al*, 1987) but after a certain amount of flight, and in the vicinity of a pheromone source, they fly upwind (Seybert and Gara, 1970; Gray *et al*, 1972). Choudury and Kennedy (1980) demonstrated that insects can locate an attractive source of odour by flying against an air flow in the presence of the odour. As we did in our experiments, Salom and McLean (1989) observed an inversion of the preferential directions of capture for the longest distances of trapping. These results could thus be interpreted as follows: i), in the plots with short trapping distances (50 and 100 m), the beetles were already in the pheromone plume when they took off. So they flew against the wind to locate the pheromone source and they were caught preferentially in the upwind traps. This behavior is consistent with a trapping attraction radius of 79.4 m ($79.4 \sqrt{2} = 112$ m); ii), in the plots with long trapping distances (400–1 000 m), the beetles took off in air with no pheromone and then flew with the wind. They were later attracted by a trap in its vicinity so the main captures were observed in the downwind direction.

We noticed such an orientation of the flight direction when the speed of the wind rose > 3 m/s. This value is more important

than *Ips sexdentatus* speed of flight recorded on the flight mill (Jactel, 1991). Since we used meteorological data recorded in an open field far from the forest, we might have overestimated the real speed of the wind in the experimental plots.

CONCLUSION

Ips sexdentatus can disperse over long distances in pine forest (at least 4 km). Flying with the wind, it can widely explore its habitat, searching for scarce suitable hosts. The response of *I. sexdentatus* to pheromone attraction seems to be released by flight exercise which varies in duration among the individuals of a population. Such an internal feed-back causes the insects to move from their brood area where the food supply has been reduced. The variable threshold of response to pheromone attraction favours the interbreeding of beetles with other populations and decreases the chance of intraspecific competition for food. Flying upwind to locate the pheromone source, the beetles can benefit from a local aggregation before the mass attack of the host tree. If the orientation response is really under fuel-dependent flight control, the determination of the fuel content profile of a population could lead to predictions of its dispersal distribution.

In addition to the short life of the pheromone dispenser, the attraction radius of the pheromone traps does not exceed 100 m. Since the proportion of responsive beetles does not reach 100% before at least 1 000 m, a very large number of traps would be required to intercept all the beetles of an infestation focus. Determining the number of wild beetles caught by a trap in a plot appears to be impossible. According to the flight capacity of *I. sexdentatus* and its flight-dependent pheromone re-

sponse, a trap can catch beetles coming from another plot, but inversely cannot catch all the beetles of its own plot. So, according to the dispersal range of the bark beetles, prognosis and mass-trapping could not find a reliable response in a pheromone trapping system, unless applied on a forest scale.

ACKNOWLEDGMENTS

The author thanks the Office National des Forêts for permitting him to carry out this study in the Forest of Orléans. He also thanks Mr Pidoux and Forêt-Assistance for providing the pheromone dispensers, and F Lieutier for advice during the study and help in reviewing this manuscript.

REFERENCES

- Anderbrant O, Schlyter F (1987) Ecology of the Dutch elm disease vectors *Scolytus laevis* and *Scolytus scolytus* (Coleoptera: Scolytidae) in Southern Sweden. *J Appl Ecol* 24, 539-550
- Andryszak NA, Payne TL, Billings PM, Benenati JM (1982) Effect of flight activity on laboratory response of the southern pine beetle to an attractant. *J Georgia Entomol Soc* 17, 456-460
- Atkins MD (1961) A study of the flight of the Douglas fir beetle, *Dendroctonus pseudotsugae* Hopk (Coleoptera: Scolytidae). III. Flight capacity. *Can Entomol* 93, 467-474
- Atkins MD (1966) Laboratory studies on the behaviour of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. *Can Entomol* 98, 953-991
- Atkins MD (1969) Lipids loss with flight in the Douglas fir beetle. *Can Entomol* 101, 164-165
- Bakke A (1968) Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris* L) in Norway with particular reference to influence of temperature. *Medd Nor Skogforsoksves* 21, 443-602

- Bennett RB, Borden JH (1971) Flight arrestment of tethered *Dendroctonus pseudotsugae* and *Tripodendron lineatum* in response to olfactory stimuli. *Ann Entomol Soc Am* 64, 1273-1286
- Berryman AA (1972) Resistance of conifers to invasion by bark beetle-fungus associations. *Bio Sciences* 22, 598-602
- Birch MC (1974) Seasonal variation in pheromone-associated behaviour and physiology of *Ips pini*. *Ann Entomol Soc Am* 67, 58-60
- Botterweg PF (1982) Dispersal and flight behavior of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Z Angew Entomol* 94, 466-489
- Botterweg PF (1983) The effect of attack density on size, fat content and emergence of the spruce bark beetle *Ips typographus* L. *Z Angew Entomol* 96, 47-55
- Borden JH (1967) Factors influencing the response of *Ips confusus* to male attractant. *Can Entomol* 99, 1164-1193
- Borden JH, Hunt DWA, Miller DR, Slessor KN (1986) Orientation in forest Coleoptera: an uncertain outcome of responses by individual beetles to variable stimuli. In: *Mechanisms in Insect Olfaction* (Payne, Birch, Kennedy, eds) Clarendon Press, Oxford
- Choudury JH, Kennedy JS (1980) Light versus pheromone-bearing wind in the control of flight direction by bark beetles, *Scolytus multistriatus*. *Physiol Entomol* 5, 207-214
- Christiansen E, Waring RH, Berryman AA (1987) Resistance of conifers to bark beetle attack: searching for general relationship. *For Ecol Manage* 22, 89-106
- Fares Y, Sharpe PJH, Magnuson CE (1980) Pheromone dispersion in forests. *J Theor Biol* 84, 335-359
- Forsse E (1987) Flight duration in *Ips typographus* L: intensivity to nematode infection. *J Appl Entomol* 104, 326-328
- Forsse E (1989) Flight duration of eleven species of bark beetles (Scolytidae) and observations of aerial height distribution. In: *Migration of Bark Beetles with Special Reference to the Spruce Bark Beetle Ips typographus*. Dissertation, Sverige Lantbruksuniversitet, Uppsala
- Forsse E, Solbreck Ch (1985) Migration in the bark beetle *Ips typographus* duration, timing and height of flight. *Z Angew Entomol* 100, 47-57
- Francica FC, Graham K (1967) Aspect of orientation behavior in the ambrosia beetle *Tripodendron lineatum*. *Can J Zool* 45, 985-1002
- Gara RI (1963) Studies of the flight behavior of *Ips confusus* in response to attractive material. *Contrib Boyce Thompson Inst* 22, 51-66
- Gara RI, Vité JP (1962) Studies on the flight patterns of bark beetles in second growth Ponderosa pine forest. *Contrib Boyce Thompson Inst* 21, 275-289
- Graham K (1959) Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. *Nature (Lond)* 184, 283-284
- Gray B, Billings RF, Gara RI, Johnsey RL (1987) On the emergence and initial flight behavior of the mountain pine beetle, *Dendroctonus ponderosae*, in eastern Washington. *Z Angew Entomol* 71, 250-259
- Gries Von G (1985) Zur Frage der Dispersion des Buchdruckers (*Ips typographus* L.). *Z Angew Entomol* 99, 12-20
- Hagen BW, Atkins MD (1975) Between generation variability in the fat content and behavior of *Ips paraconfusus*. *Z Angew Entomol* 79, 169-172
- Helland IS, Hoff JM, Anderbrant O (1984) Attraction of bark beetles (Scolytidae) to a pheromone trap. *J Chem Ecol* 10, 723-752
- Jactel H (1991) A preliminary study of the dispersal potential of *Ips sexdentatus* Boern. (Coleoptera: Scolytidae) with an automatically recording flight mill. *J Appl Entomol* (in press)
- Jactel H, Lieutier F (1987) Effects of attack density on fecundity of the Scots pine beetle *Ips sexdentatus* Boern (Coleoptera: Scolytidae). *J Appl Entomol* 104, 190-204
- Koponen M (1980) Distribution of *Ips amitinus* (Eichoff) (Coleoptera: Scolytidae) in Finland in 1974-1979. *Notul Entomol* 60, 223-225
- Lanier GN, Silverstein RM, Peacock JW (1976) Attractant pheromone of the European elm bark beetle (*Scolytus multistriatus*): isolation, identification, synthesis, and utilization studies. In: *Perspectives in Forest Entomology* (Anderson, Kaya, eds) Academic Press, NY, 149-175

- Lieutier F (1984) Impact économique des scolytides : voies de recherches. *CR Acad Agric Fr* 70, 835-843
- Lieutier F, Ham R, Ham M, Garcia J (1986) Une méthode de marquage individuel des coléoptères scolytides pour les études de laboratoire. *Agronomie* 6, 773-776
- Lindelöw A, Weslien J (1986) Sex specific emergence of *Ips typographus* (Coleoptera: Scolytidae) and flight behavior in response to pheromone sources following hibernation. *Can Entomol* 118, 59-67
- McClendon RW, Mitchell EB, Jones JW, Mc Kinion JM, Hardee DD (1976) Computer simulation of pheromone trapping systems as applied to boll weevil population suppression: a theoretical exemple. *Envir Entomol* 5, 799-806
- Moore GE, Taylor JF, Smith J (1979) Tracing dispersion of southern pine beetles from felled brood trees with phosphorus 32. *J Georgia Entomol Soc* 14, 83-87
- Nilssen AC (1984) Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera: Scolytidae and Curculionidae) in northern Finland. *Ann Entomol Fenn* 50, 37-42
- Perttunen V, Oksanen H, Kangas E (1970) Aspects of the external and internal factors affecting the olfactory orientation of *Blastophagus piniperda*. *Contrib Boyce Thompson Inst* 24, 293-297
- Pesson P, Chararas C (1969) Les scolytides, insectes ravageurs mondiaux des forêts de conifères. *Année Biol* 8, 683-733
- Salom SM, McLean JA (1989) Influence of wind on the spring flight of *Trypodendron lineatum* (Olivier) (Coleoptera: Scolytidae) in a second-growth coniferous forest. *Can Entomol* 121, 109-119
- SAS Institute (1985) *SAS User's Guide: Statistics, Version 5*. SAS Institute, Cary, NC
- Schlyter F, Löfqvist J, Byers JA (1987) Behavioral sequence in the attraction of the bark beetle *Ips typographus* to pheromone source. *Physiol Entomol* 12, 185-196
- Schmid JM (1970) Dispersal studies with radioactively tagged spruce beetles. *USDA For Ser Rocky Mountain For and Range Exp Stat Res Note RM* 178
- Schmitz RF (1980) Dispersal of pine engraver beetles in second growth Ponderosa pine forest. In: *Proc 2nd IUFRO Conf, Dispersal of Forest Insects* (Berryman, Safranyik, eds) 41-50
- Seybert JP, Gara RI (1970) Notes on flight and host selection of the pine engraver *Ips pini*. *Ann Entomol Soc Am* 63, 347-350
- Shore TL, McLean JA (1988) The use of mark-recapture to evaluate a pheromone-based mass trapping program for ambrosia beetles in a sawmill. *Can J For Res* 18, 1113-1117
- Termier M (1970) Essai d'interprétation du vol des Coléoptères. *CR Acad Sci Paris* 270, 1157-1160
- Vallet E (1982) Données bio-écologiques récentes sur trois insectes ravageurs responsables du dépérissement du pin sylvestre en région centre: *Tomicus piniperda*, *Ips acuminatus* et *Ips sexdentatus*. *Bull Inst Ecol Appl* 9, 3-41
- Wollerman EH (1979) Attraction of European elm bark beetles, *Scolytus multistriatus*, to pheromone-baited traps. *J Chem Ecol* 5, 781-793