Recapture of *Ips typographus* L. (Col., Scolytidae) with attractants of low release rates: localized dispersion and environmental influences

Anne J. Franklin*†‡, Catherine Debruyne* and Jean-Claude Grégoire*§

*Laboratoire de Biologie Animale et Cellulaire, Université Libre de Bruxelles, CP 160/12, 50 av. F.D. Roosevelt, B-1050 Brussels, †Centre Luxembourgeois de l'ULB, 19 rue de la Fontaine, B-6870 Saint-Hubert, ‡Fonds pour la Formation à la Recherche dans l'Industrie et l'Agriculture, and §Fonds National de la Recherche Scientifique, 5 rue d'Egmont, B-1000 Brussels, Belgium

Abstract

1 The dispersal of *Ips typographus* L. (Col., Scolytidae) was studied using a mark–release–recapture approach in a grid of traps equipped with pheromone lures of release rates of about 8.4 mg/day of 2-methyl-3-buten-2-ol (MB) and 0.29 mg/day of (*S*)-*cis*-verbenol (cV) in experiment 1, and 1.2 mg/day of MB and 0.04 mg/day of cV in experiment 2.

2 We investigated whether beetle dispersal reflected the simple diffusion pattern observed in previous *I. typographus* experiments, for which attractant release rates generally approached 50 mg/day of MB and 1 mg/day of cV. We also examined how environmental parameters (wind) and human activities (felling) could influence the beetles' flight.

3 The recapture percentage was higher in experiment 1 than in experiment 2: respectively, 7.0% (with 64 traps) and 2.3% (with 100 traps) of the beetles that took off were caught in the traps.

4 With the higher release rate (experiment 1), trap catches decreased with increased distance, whereas with the lower release rate (experiment 2), trap catches rose between 50 and 100 m then decreased with increasing distance.

5 Flight was little orientated by prevailing wind directions, a feature probably explained by the low wind speeds (0–1.2 m/s) observed throughout the study.

6 High trap catches of unmarked beetles close to areas undergoing thinning activities suggest that the presence of freshly cut spruce and larch material could have an influence on dispersal, attracting the beetles into the felling area. Spatial analyses show that capture patterns were autocorrelated up to distances of about 250 m.

Keywords Dispersal, environmental influences, host attraction, *Ips typographus*, release–recapture, Scolytidae.

Introduction

The interplay between dispersal and the environment is an important aspect of bark beetle population ecology. Its study not only helps to understand the dynamics of infestations but also to develop strategies of pest control and forest management. Most information available on *Ips typographus* dispersal comes from mark–recapture experiments using traps or rings of traps equipped with commercial pheromones (Weslien & Lindelöw,

1990; Zumr, 1992; Zolubas & Byers, 1995; Duelli *et al.*, 1997). Such pheromones were primarily developed for mass trapping and have high release rates that probably influence the insects' dispersal, as they attract beetles that fly quite far away from the traps. Experiments deploying strong diffusion traps close to the release point would then capture a high proportion of marked beetles that could otherwise have reached more distant traps (Byers, 1999).

The objective of our experiments was to study *I. typographus* dispersal through a network of evenly spaced, live, standing, trap-carrying trees equipped with lures of low diffusion rates. Our aim was to minimize trap influence and to recreate flight

conditions as close as possible to natural dispersal. Data obtained in this study were related to earlier release–recapture experiments (see Byers, 1999, for a synthesis). The following questions were addressed: (1) Is the pattern of simple diffusion obtained in previous experiments replicated with low diffusion lures? (2) Does *I. typographus* disperse randomly from its emergence site or is its flight influenced by environmental factors such as wind or forest composition? In addition, the spatial distribution of captures of unmarked beetles was investigated in relation to environmental parameters.

Materials and Methods

Study site

The study was conducted in 1998 and 1999 in a planted conifer forest at Wellin, southern Belgium, where spruce monocultures dominate most of the study area; other conifers consist of Douglas fir and larch. A mixed deciduous forest borders the south of the experimental plot (Fig. 1A). Altitude averages 400 m a.s.l. No attacked trees were found on site before the experiments; only one tree – not part of the trapping grid – became attacked close to the north-western limit of the plot during the summer of 1998.

Traps and lures

A regular, evenly spaced trapping grid was chosen over a concentric grid (radiating trap lines) in order to analyse the effects of dispersal direction as well as dispersal distance (Turchin, 1998). This set-up, together with attractants of low release rates, was designed to interfere as little as possible with dispersal of the beetles and to obtain a good estimate of their spatial density, capturing only individuals flying at close proximity to the traps while still having a recapture rate high enough for statistical analyses.

In 1998, a grid of 64 traps spaced out regularly every 50 m was set up in the spruce stand (Fig. 1). The trapping system consisted of small barrier-traps (13 cm wide × 24 cm high, ending in a funnel connected to a collecting jar) attached to the tree trunks, facing the centre of the plot. The set-up was adapted from Raty *et al.* (1995) and Franklin & Grégoire (1999), using lighter PVC collectors that could be more easily handled. A major difference was that the lures were fixed on the trap 10 cm above the collecting funnel, not on the tree. Insecticide treatment was applied to the trap-carrying trees as described by Franklin & Grégoire (1999). Trap-trees were georeferenced in an X, Y coordinate system centred on the release platform.

Each collector was baited just before the flight period began with dispensers. Each dispenser consisted of two polyethylene bags, one for 2-methyl-3-buten-2-ol (MB) and one for (*S*)-*cis*-verbenol (cV), the major components of the *I. typographus* aggregation pheromone (Bakke *et al.*, 1977). Ipsdienol was not used, as it did not prove essential for *I. typographus* capture (Schlyter *et al.*, 1987a, b). Release rates (estimated at $20 \pm 2\,°C$) were about 8.4 ± 0.7 mg/day of MB and 0.29 ± 0.07 mg/day of cV, approaching the ideal ratio of about 50 MB : 1 cV quoted by Schlyter *et al.* (1987c). This experiment was replicated six times during the beetles' second flight period (August 1998).

The second experiment was carried out in 1999 at the same site but 36 trap-carrying trees were added in order to increase the potential recapture distance (Fig. 1). Release rates were about seven times lower than in 1998 and were 1.2 ± 0.2 mg/day of MB and 0.04 ± 0.01 mg/day of cV. This experiment was replicated 10 times, with six replicates occurring during the first flight period (May) and four replicates during the second flight period (July–August).

Release–recapture

The release and capture procedures were the same for both experiments. Bark was collected from infested trees in spring and summer and placed under emergence tents (Lindelöw & Weslien, 1986) at the experimental plot just before flight started. Releases took place when the temperature rose above $18\,°C$, the flight threshold for *I. typographus* (Annila, 1969). As soon as beetles emerged from the tents, they were collected and marked with fluorescent powder (Radglo®, Radiant Color N.V., Belgium), through gentle shaking in a vial with a small amount of dust. In 1999, the colour of the powder was changed for each day of release. From earlier experiments (Anderbrant, 1985; Salom & McLean, 1989; Dubois, 1992), it was assumed that the marking process did not significantly affect the flight behaviour of the beetles.

As soon as marked, the beetles were allowed to fly away from the release platform (a plastic container placed on a wooden board fixed to a 1.5-m high post) at the centre of the experimental plot. To prevent walking beetles from escaping, the sides of the container were treated with Fluon® (Fluon GP1, De Monchy Int., Rotterdam). Beetles that did not fly were excluded from the experiment. Only freshly emerging beetles were used, and, therefore, beetles emerging between release periods were discarded from the trials.

The collecting funnels were emptied 24 h after the release and were checked a few days later in order to see whether additional marked beetles were caught in the traps. Marked and unmarked beetles were counted, with confirmation of identification of marked individuals under a UV lamp. Beetles were sexed in 1999 by the method of Schlyter & Cederholm (1981) and doubtful cases were confirmed by observation of the genitalia.

Weather data

Temperature was recorded on site every hour with an electronic thermograph (Optic StowAway Temp®, Onset Computer Corporation, Pocasset, MA, U.S.A.). Wind direction data were collected with the use of a compass and a thread allowed to hover freely in the wind. Wind speed was measured with a hand-held anemometer (Testovent® 4200, Testoterm S.A., Belgium). Both wind parameters were assessed every hour during releases, with four measurements carried out during a time interval of 5 min.

Analysis

Beetle catches were mapped using a geographical information system (Surfer v.7, Golden Software, Golden, CO, U.S.A.), and wind direction data were summarized in the form of rose
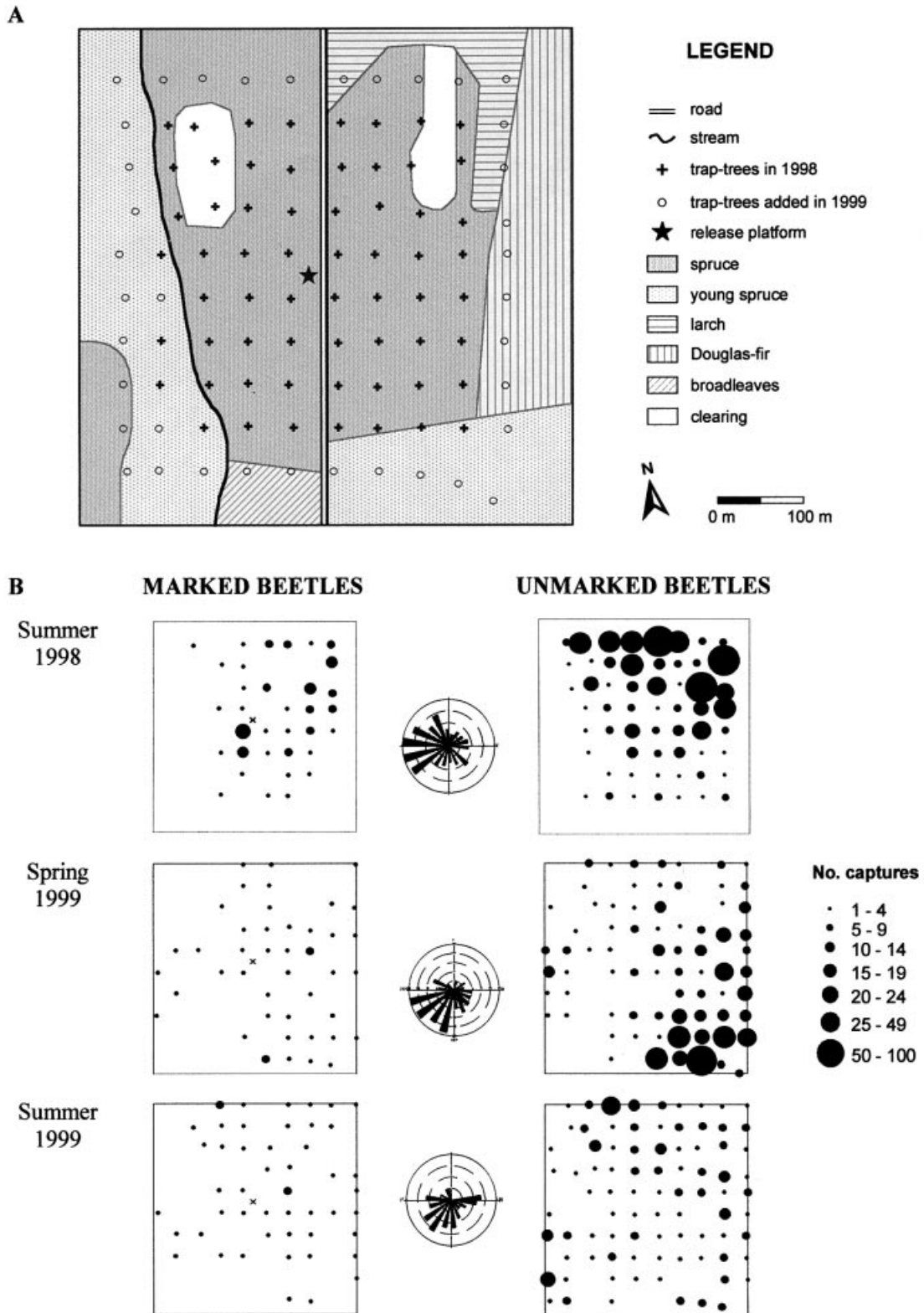
A

B

Figure 1 Maps showing the study site at Wellin, with localization of traps (A) and distribution of total catches of marked and unmarked *Ips typographus* for the three flight seasons, together with wind rose diagrams showing the dominant winds (B). 'Young spruce' corresponds to spruce less than 40 years old.

diagrams (Oriana v.1.06, Kovach Computing Services, Pentraeth, Wales, U.K.).

Analyses of circular data were based on statistical procedures described by Fisher (1993) and Zar (1996). The data for each circular distribution were subjected to the Rayleigh test for randomness, which determines if the distribution is random or can be considered as directed. To test whether the beetle flight direction (θb) was the same as the wind direction (θw), a one-sample test, analogous to a one-sample t-test for data on a linear scale, was conducted using wind direction as a pre-assigned angle to be tested against the beetle flight direction. The null hypothesis was tested by observing whether θw lay within the $1 - \alpha$ confidence interval for θb. If θw lay outside the interval, then H_o was rejected (Zar, 1996).

The spatial structure of catches of unmarked beetles was investigated using geostatistics (Variowin 2.2., Pannatier, 1996). These methods help to characterize the degree of autocorrelation among the measured data points and to interpolate values between observations based on the degree of autocorrelation encountered. A good introduction to their application to ecological data is provided by Rossi *et al*. (1992) and Liebhold *et al*. (1993). In this study, autocorrelation was evaluated using the semivariogram (or variogram), which calculates the variability among observed data points as a function of their separation distance. This was done by computing the average squared difference between paired observations separated by a common lag:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i = 1}^{N(h)} [z(xi) - z(xi + h)]^2$$

where $z(x)$ represents the measured sample value (number of beetles caught) at the location x, $z(x + h)$ is the sample value at the location $x + h$; $N(h)$ is the number of data pairs separated by distance h and $\gamma(h)$ corresponds to the estimated variogram value at this distance. The variogram is represented graphically by $\gamma(h)$ as a function of h and its shape describes the degree of autocorrelation present: small variogram values at short lags correspond to data that are highly autocorrelated or spatially continuous, whereas larger values at greater lags indicate that the data are more dissimilar or more spatially discontinuous; constant variogram values imply that the variance between values does not change with distance (Rossi *et al*., 1992). Standardization was carried out for comparison purposes and was obtained by dividing the variogram values by the sample variance.

Results

Marked beetles

Data on releases and recaptures for 1998 and 1999 are presented in Table 1. Take-off percentages averaged 83%. The low take-off rate of 41% corresponds to a day when temperatures did not quite reach the 18 °C flight threshold.

The recapture percentage, based on the number of beetles that flew away, showed a strong variation between replications (Table 1). This variation was partly due to temperature differences, as a higher proportion of beetles was recaptured with increasing temperatures (1998: arcsine (%catches) $= 0.022 *$ avg.temp. $- 0.14$, $R^2 = 0.88$, $P < 0.01$; 1999: arcsine (%catches) $= 0.020 *$ avg.temp. $- 0.18$, $R^2 = 0.88$, $P < 0.01$). No significant relationship was found between catches and wind speed.

Recaptures were higher in 1998 than in 1999: on average, about 7.0% of the beetles were recaptured in 1998, with 64 traps, whereas only 2.3% were recaptured in 1999, with 100 traps. Differences were statistically significant after allowing for temperatures: the regressions between the arcsine of %catches and temperature showed similar slopes ($t_{obs} = 1.44$, d.f. $= 12$, $P > 0.05$) but significantly different elevations ($t_{obs} = 7.84$, d.f. $= 13$, $P < 0.001$).

Most beetles were caught within 24 h of their release but the 1999 experiment showed that about 10% (16 beetles) were caught between 24 and 48 h after taking off.

The distribution of the total catches is presented in Fig. 1B. Maps are presented by flight season, as environmental conditions differed greatly for each season. In 1998, thinning in the larch plantation to the north-east of the experimental plot took place during the release days, and during spring 1999, selective cutting occurred in the young spruce plantation to the south of the plot. No forest management operation took place during the summer of 1999.

To examine the patterns of *I. typographus* distribution across our grid, distance classes of 50 m intervals were established from the centre of the experimental plot. As the number of traps varied for each interval, we calculated the percentage of beetles caught per trap for each distance class and we averaged the results for all release days. A plot of these data is shown in Fig. 2. Two distinctive patterns emerge: in 1998, the percentage recaptures decreased with increasing distance, whereas in 1999 a rise in captures was observed between the 50 m and 100 m distance classes then recapture rates decreased at higher distances. Data were pooled for spring and summer releases in 1999, as no statistical differences were detected between flight periods.

As indicated by the error bars, there was considerable variation among the trapping days. A two-way analysis of variance performed on the recapture data showed that the percentage recaptures differed significantly between years and between distance classes (years: $F_{1,81df} = 11.4$, $P = 0.01$, distance: $F_{6,81df} = 3.7$, $P = 0.03$, years $\times$ distance: $F_{4,81df} = 6.8$, $P < 0.01$). Regression analysis was then used, as multiple-comparison procedures are not recommended for treatments forming progressive series (Perry, 1986). For 1998, the model $Y = aX^b$ was used to describe how the percentage recapture per trap (Y) decreased with increasing distance (X). Parameter estimation gave $Y = 0.69 * X^{-0.77}$ ($R^2 = 0.90$, $P = 0.01$). No simple model could be applied to the 1999 data, but it was observed that after the initial increase of captures, the percentage recaptures decreased linearly with increasing distance (arcsine $Y = -0.0003 * X + 0.144$, $R^2 = 0.79$, $P = 0.02$).

The directional component of our data was addressed using circular statistics. Mean wind direction and mean angles of beetle catch from the release point are presented in Table 2, and maps of daily catches and wind rose diagrams are illustrated in Fig. 3. On one day only was the wind direction variable according to Rayleigh's test, and about half of the beetles'

Table 1 Results of *I. typographus* release–recapture experiments of 1998 and 1999. Diffusion rates of attractants were 8.4 mg/day MB and 0.29 mg/day cV in 1998, and 1.2 mg/day MB and 0.04 mg/day cV in 1999. N/A = not available.

| | | | | Captured beetle totals | | | | |
| | | | | Marked | | | Unmarked | |
Release no.	Date	No. released that flew	% that flew	No.	% of no. that flew	Sex ratio (M/F)	No.	Sex ratio (M/F)
98–1	27 July	277	70	7	2.5	N/A	197	N/A
98–2	5 August	236	60	6	2.5	N/A	60	N/A
98–3	6 August	378	93	15	4.0	N/A	55	N/A
98–4	7 August	522	94	48	9.2	N/A	122	N/A
98–5	8 August	526	91	49	9.3	N/A	190	N/A
98–6	9 August	236	88	27	11.4	N/A	124	N/A
Totals 1998		2175	84	152	7.0		748	
99–1	7 May	1015	73	13	1.3	1.17	217	1.07
99–2	23 May	406	41	0	0.0	–	0	–
99–3	26 May	1279	92	9	0.7	0.80	41	0.64
99–4	27 May	1462	91	29	2.0	0.71	129	0.52
99–5	28 May	608	91	13	2.1	0.86	147	0.47
99–6	29 May	419	91	11	2.6	0.83	152	0.62
99–7	30 July	485	96	20	4.1	0.43	194	0.27
99–8	31 July	502	98	19	3.8	0.36	74	0.30
99–9	1 August	403	97	24	6.0	0.33	67	0.26
99–10	2 August	348	96	18	5.2	0.50	57	0.27
Totals 1999		6927	83	156	2.3		1,078	
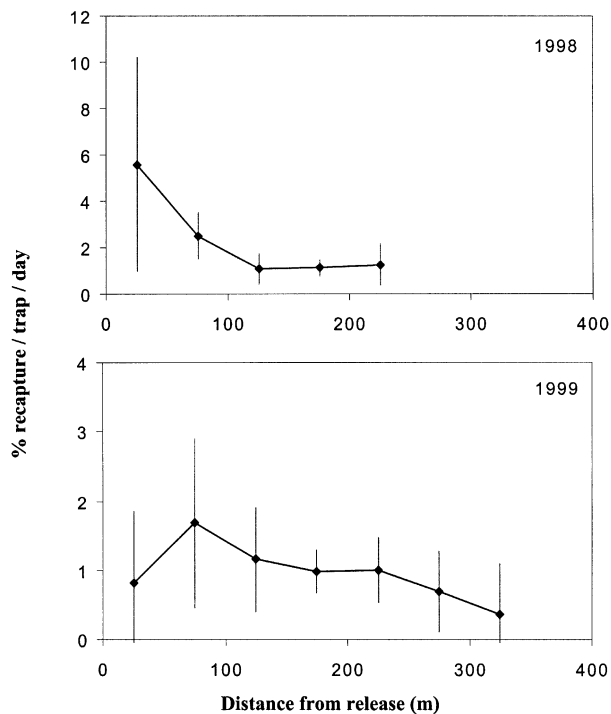
Figure 2 Average percentage of marked *I. typographus* recaptured per trap per day in 50 m wide distance classes from the release point, $n = 6$ in 1998 and $n = 9$ in 1999 (replicate 99–2 excluded from the data). Error bars represent the standard deviation. Data were pooled for spring and summer releases in 1999, as no statistical differences were detected between flight periods.

recapture data were determined as random. Only replicates for which directions were significant were analysed further. One-sample tests were used to compare mean flight directions to wind directions. On all occasions, beetle flight differed significantly from upwind direction. However, as illustrated by Figs 1 and 3, at least a few beetles were caught in traps upwind close to the release platform for each 1998 replicate. This phenomenon was not observed in 1999. Two of the 1999 replicates (99–1 and 99–9) showed a significant downwind movement of the beetles.

Unmarked beetles

Catches of unmarked *I. typographus* are summarized in Table 1. As for marked beetles, they were higher in 1998 than in 1999: they averaged 1.95 beetles/trap/day in 1998, 1.14 beetles/trap/day in spring 1999 and 0.98 beetles/trap/day in summer 1999. Differences in catches between 1998 and 1999 were not significant when compared with a one-way analysis of variance ($F_{1,14 \, \text{d.f.}} = 4.41$, $P = 0.054$). No significant relationships were found between catches and temperature.

The distribution of total catches is presented in Fig. 1B, and daily catches are illustrated in Fig. 4. More beetles were captured by outer traps than by central traps in 1998 and spring 1999, when selective cutting was underway in stands peripheral to the study plot. In summer 1999, catches were made uniformly over the study area. There were no management activities during those replicates.

Some 'daily highs' can be observed in the catches. For example, on replicate 98–1, most captures were observed to the north of the plot. These might be explained by the attack of a spruce in that vicinity, as an infested tree was detected at the end

of the 1998 season. During the last three 1998 replicates (98–4 to 98–6), high numbers of beetles were caught at the north-east of the experimental set-up. At the time, timber harvesting took place in the larch plantation close to those traps. On the first replicate of spring 1999, high catches at the south of the plot were observed close to a spruce that was felled the day before. On 28 May 1999 (replicate 99–5), more than 50 beetles were caught in one trap localized in the spruce stand undergoing selective thinning. On that day, a small processing machine was removing the branches of felled trees less than 5 m from the trap-carrying tree.

The degree of autocorrelation and spatial structure of catches were fairly similar for replicates within the same flight period and therefore further analyses were made on pooled data. Figure 5 presents the experimental semivariograms for the different flight seasons. For 1998, variogram values not surprisingly showed a linear increase, reflecting the strong south-western–north-eastern gradient in captures observed in Fig. 1B. In 1999, catches were spatially structured. In spring, there was a strong autocorrelation among samples less than 265 m apart, whereas observations separated by more than 265 m appeared independent of one another. The spatial structure of catches was less marked for the summer flight season, with low autocorrelation existing up to about 250 m.

Sex ratio

The sex ratio of recaptured beetles was determined in 1999 (Table 1). Except for replicate 99–1, more females were caught than males. This bias was twice as large during the second flight period, with an average male/female sex ratio of 0.41, whereas in spring it was equal to 0.87. The variation of the sex ratio as a function of distance was computed for each release season but no significant relationships were observed.

The 1999 sex ratio of unmarked beetles showed the same trend as for the marked beetles (Table 1). A larger number of females were caught, with a stronger bias during the second flight period: the spring sex ratio averaged 0.66 males per female, whereas the summer sex ratio averaged 0.28. Both sex ratios were lower than those found for marked beetles.

Discussion and conclusion

Three principal features appeared when we examined the data from our experiments. In the first place, with the lowest release rate, beetle dispersal did not decrease regularly with increasing distance. Secondly, flight seemed little orientated by prevailing winds. Thirdly, trap catches of unmarked beetles suggest that the presence of felled material could have an influence on dispersal.

Recapture rate and strength of the lure

The percentage recapture was low for both experiments 1 and 2, amounting to less than 10% of the released beetles. This was possibly due to the low pheromone concentrations of the lures, as a greater proportion of *I. typographus* was recaptured at the higher release rate: lures were about seven times as strong in 1998 as in 1999 and led to beetle catches about three times higher, with trap number and temperature variations taken into

Table 2 Relationships of flight direction of *I. typographus* to wind parameters for the two experiments in 1998 and 1999 and comparisons between mean flight direction and mean wind direction.

Release No.	Date	Flight direction $\theta b \pm 95\%$CI *	Wind direction $\theta w \pm 95\%$CI *	Upwind flight θb vs. θw ‡	Downwind flight θb vs. θw-180° ‡	Wind speed Average (m/s)	Range (m/s)
1998							
98–1	27 July	Variable	N/A	–	–	N/A	N/A
98–2	5 August	Variable	277 ± 21	–	–	0.6	0.0–2.7
98–3	6 August	Variable	263 ± 18	–	–	0.6	0.2–2.1
98–4	7 August	86 ± 29	297 ± 13	$P \leqslant 0.05$	$P \leqslant 0.05$	0.6	0.1–1.5
98–5	8 August	88 ± 21	170 ± 43	$P \leqslant 0.05$	$P \leqslant 0.05$	0.6	0.1–1.8
98–6	9 August	81 ± 24	Variable	–	–	1.2	0.2–2.1
1999							
99–1	7 May	47 ± 48	190 ± 14	$P \leqslant 0.05$	NS	0.4	0.1–0.8
99–2	23 May	–	243 ± 16	–	–	0.4	0.1–0.7
99–3	26 May	134 ± 40	222 ± 31	$P \leqslant 0.05$	$P \leqslant 0.05$	0.2	0.1–0.5
99–4	27 May	Variable	223 ± 26	–	–	0.3	0.1–0.9
99–5	28 May	117 ± 32	238 ± 08	$P \leqslant 0.05$	$P \leqslant 0.05$	0.6	0.2–1.3
99–6	29 May	Variable	245 ± 17	–	–	0.6	0.2–1.2
99–7	30 July	Variable	217 ± 28	–	–	0.2	0.0–0.8
99–8	31 July	38 ± 46	129 ± 46	$P \leqslant 0.05$	$P \leqslant 0.05$	0.1	0.0–0.5
99–9	1 August	39 ± 30	226 ± 32	$P \leqslant 0.05$	NS	0.2	0.0–1.5
99–10	2 August	Variable	210 ± 33	–	–	0.2	0.0–1.2

* θb = mean flight direction of beetles, θw = mean wind direction. N/A = not available; variable = random distribution as determined by the Rayleigh test ($P > 0.05$).‡ Comparisons assessed using a one-sample test for the mean directional flight angle. If $P \leqslant 0.05$, the flight direction differs significantly from the wind direction. NS therefore indicates similar flight and wind directions.
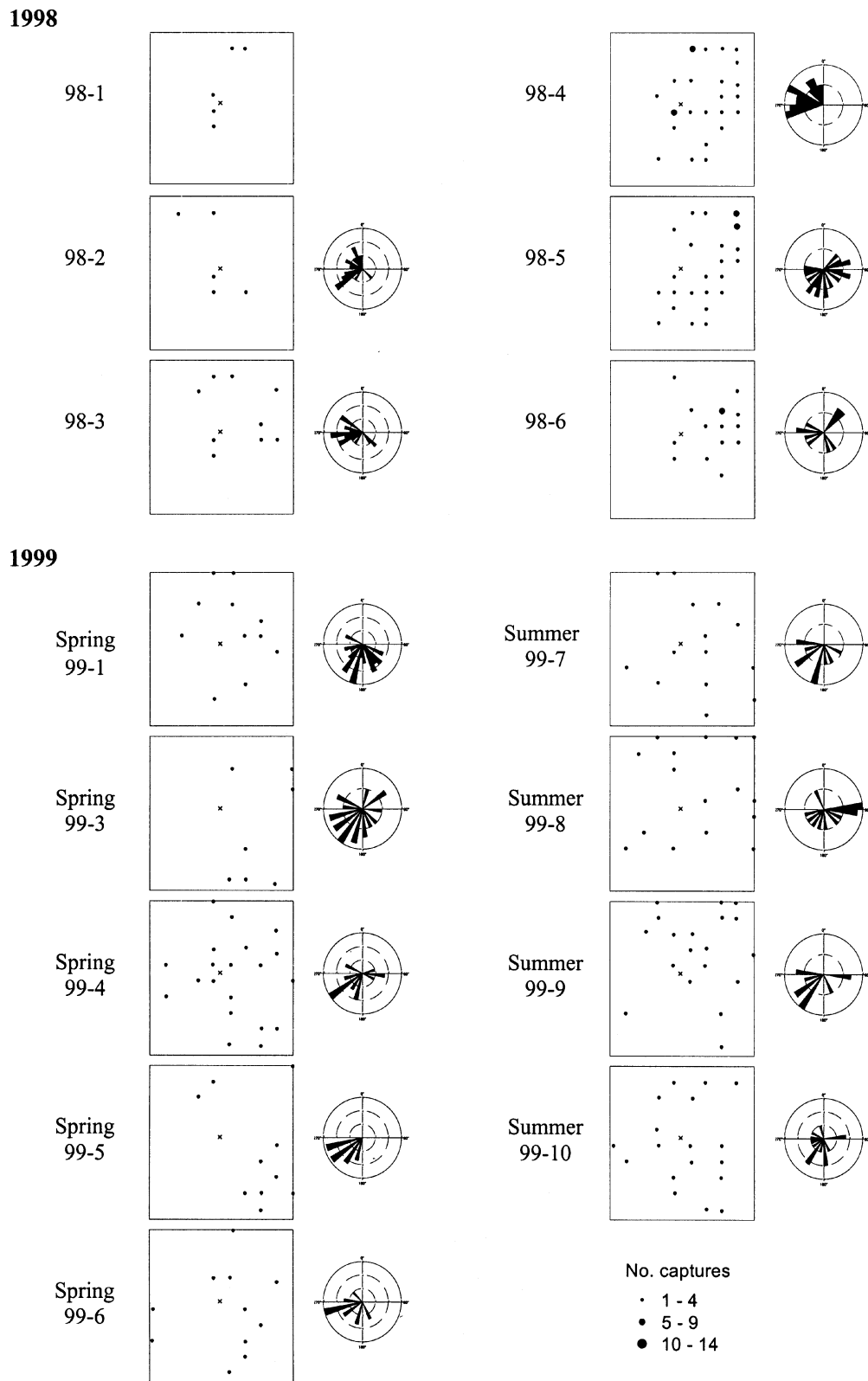
Figure 3 Localization of daily recaptures of marked beetles and daily wind rose diagrams for 1998 and 1999 experiments. 1998 replicates correspond to the second flight of *I. typographus*, whereas 1999 replicates comprise first (spring) and second (summer) flights. The cross marks the point of release.
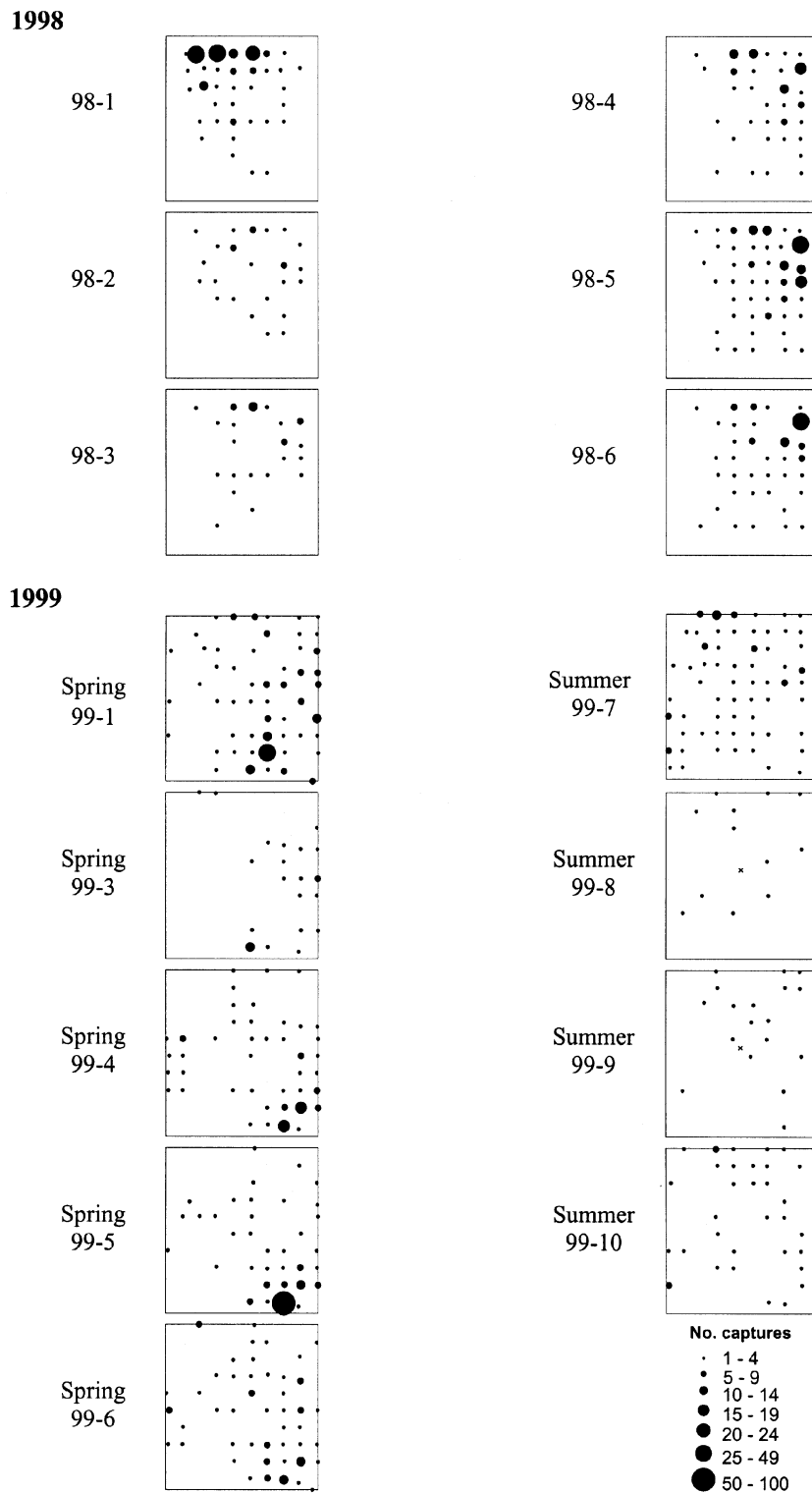
1998

98-1

98-2

98-3

98-4

98-5

98-6

1999

Spring
99-1

Spring
99-3

Spring
99-4

Spring
99-5

Spring
99-6

Summer
99-7

Summer
99-8

Summer
99-9

Summer
99-10

No. captures
- 1 - 4
- 5 - 9
- 10 - 14
- 15 - 19
- 20 - 24
- 25 - 49
- 50 - 100

Figure 4 Localization of daily catches of unmarked *I. typographus* for 1998 and 1999.

consideration. These differences in attraction are similar to results from Schlyter *et al.* (1987c), who obtained an increased beetle response with increasing release rates of MB and cV.

Another interpretation could be that most of the beetles left the area in an adaptive dispersal flight, and that we only recaptured the fraction of beetles that was reacting to
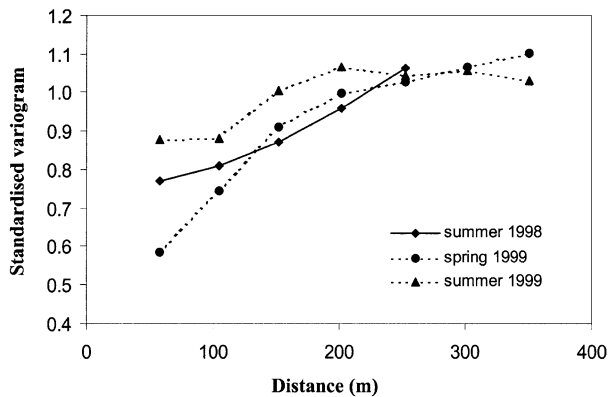
Figure 5 Standardized semivariograms for catches of unmarked beetles for 1998 and 1999 experiments. A linear trend in the data was observed in 1998, whereas a spatial structure occurred for in 1999. Spherical models applied to the data yielded the following parameters: range = 265 m, nugget = 0.36, sill = 0.70 for spring 1999 and range = 250 m, nugget = 0.76, sill = 0.29 for summer 1999.

the pheromones rapidly after emergence (see below and Duelli *et al.*, 1997).

Distance of dispersal

Movement of the beetles can either be approximated by a model of simple passive diffusion (Kareiva, 1983; Turchin, 1998) or, more simply, be described by empirical models that attempt to fit the data to a regression curve (Taylor, 1978).

Depending on the strength of the attractant, different recapture patterns were observed. With the strongest lure, the mean number of *I. typographus* per trap decreased with increasing distance. This is consistent with previous experiments with several bark beetle species, including *I. typographus* (Botterweg, 1982; Weslien & Lindelöw, 1990; Zumr, 1992; Zolubas & Byers, 1995; Duelli *et al.*, 1997), *Dendroctonus frontalis* (Turchin & Thoeny, 1993), *D. ponderosae* (Safranyik *et al.*, 1992) and *Scolytus multistriatus* (Wollerman, 1979).

The equation $Y = 0.69 * X^{-0.77}$ was used to describe how the percentage recapture per trap decreased with distance. This model is based on the hypotheses that the marked beetles spread radially in an increasingly large area and that there is no competition between traps. Similarly to observations by Weslien & Lindelöw (1990), the rate at which recaptures declined with distance was slower than expected by a model assuming pure dilution of the released beetles (b = − 1), suggesting that the responsiveness to pheromones in *I. typographus* increases with flight distance.

When lower release rates were used in experiment 2, the recapture pattern differed: percentage recaptures first rose from 50 to 100 m, then decreased linearly with increasing distance. This behaviour, observed for both spring and summer generations, suggest that responsiveness to pheromones appears at greater distances than with the higher release rates.

Variations in patterns could be explained by lower competition between traps in our 1999 experiments than in previous studies. Most experiments with *I. typographus* used either

Ipslure® or Pheroprax®, commercial attractants releasing about 50 mg/day of MB and 1 mg/day of cV (Schlyter *et al.*, 1987a, c; Byers, 1999). In those cases, traps could have interfered with each other at the shortest distances from the release centre. Indeed, preliminary observations (Franklin and Grégoire, in preparation) suggest that the attraction radius for Pheroprax lures approaches 25 m, half the intertrap distance of this study, whereas the low release rate attractants we used in 1999 show a much smaller attraction range.

Behaviour could be modulated by the amount of pheromones at the release point. If the air is saturated with pheromones, for example where there is no shortage of susceptible hosts, more emerging beetles will explore nearby areas and will be responsive at short distances, and we obtain the pattern of diffusion observed in previous experiments. By contrast, if no source of attraction is present at take-off, the beetles will spend less time flying close to their emergence site and will move rapidly away. A greater proportion beetles will then disperse before responding to pheromones, therefore performing a true migration flight, which can take them to new potential breeding sites (Duelli *et al.*, 1997).

Directionality of dispersal

Wind direction and velocity have been reported to influence bark beetle dispersal in several studies, with long distance flights (several hundred metres) tending to be downwind (Botterweg, 1982; Safranyik *et al.*, 1989; Salom & McLean, 1989, 1991; Jactel, 1991) and upwind responses usually occurring close to the release point (5–50 m) (Salom & McLean, 1989, 1991; Jactel, 1991). During our experiments, the released beetles showed little tendency for wind directed movement: in no cases was the flight direction correlated to upwind direction, and it was correlated to downwind direction on two occasions only (Table 2). However, the wind speed was always much lower than 2 m/s, the estimated limit over which *I. typographus* is not able to direct its flight (Gries *et al.*, 1989; Byers, 1996). Moreover, our study was conducted on a relatively limited scale, possibly under the range where wind influence on dispersal is perceptible. Upwind flight was apparent only when data were pooled for all releases in 1998, showing that upwind traps close to the release site somewhat influenced initial dispersal during the experiments with the higher release rate attractants. Such capture patterns were not observed when lower release rates were used.

Forest composition did not seem to influence initial *I. typographus* dispersal, as beetles were caught in mature spruce stands as well as in areas with young spruces, other conifers such as larch and Douglas fir, and mixed deciduous trees.

Influence of felling activities

The beetle's dispersal, which at first appeared random, may, however, have been influenced by the logging activities that took place in 1998 and spring of 1999. When examining the daily catches (Fig. 3), it can be seen that a relatively large proportion of the released *I. typographus* were caught close to, or within, the felling sites: the north-east and eastern areas of the experimental plot in 1998 and its south-eastern area in spring 1999.

These observations were supported by the data on unmarked beetles. In 1998 and in spring 1999, catches were made predominantly on the outskirts of the study plot where timber harvesting was underway. Spatial analyses showed autocorrelation between sample points, confirming that aggregation took place in the felling areas. This was expressed by a linear increase in catches from the south-west towards the north-east for 1998, and by high correlations between trapping values separated by less than 265 m in spring 1999. During summer 1999, when no activities took place, the distribution of catches was more uniform (Fig. 1B). Spatial analyses yielded weaker autocorrelations, suggesting some aggregative pattern up to distances of 250 m.

Attraction was maximal on days of active work, such as when debranching took place less than 5 m from a trap tree (replicate 99–5, Fig. 4). This attraction was short-lived however, as it decreased the next day, after the processing machine had moved to another area. No bark beetle attacks were detected on standing trees in the thinned stands, whether before or after felling had taken place.

A common theory is that aggressive, tree-killing bark beetles such as *I. typographus* find their host by random landing without the help of long-range host volatiles (Raffa & Berryman, 1980; Moeck *et al*., 1981; Byers, 1996). Our study suggests that the movement of the endemic beetle population may be influenced by such host volatiles. The source of attraction probably came from odours released by tree felling and debranching, mostly spruces (1998, 1999), but also larches and Douglas firs (1998). Although unusual, attraction to these latter species has been observed previously, as *I. typographus* occasionally colonizes other conifers such as pine and larch (Abgrall & Soutrenon, 1991) or Douglas fir (personal observations).

Two sets of field experiments on *I. typographus* support our data. Work by Lindelöw *et al*. (1992) showed that beetle attraction was maximal for stored Norway spruce wood when comparing controls (empty cylinders), freshly cut wood and stored wood, but that some attraction existed for fresh wood. When Austara *et al*. (1986) placed traps close to heaps of spruce branches and to controls (bare ground), they caught significantly more beetles around the branches. The higher catches could well have been caused by host tree odours, as it has been shown by electrophysiological experiments that *I. typographus* possesses receptors for α-pinene, a major component of the host tree volatiles (Dickens, 1981).

In another bark beetle study, Mason (1969) observed that summer thinning in a pine plantation was responsible for a massive concentration of two *Ips* species (*I. avulsus* and *I. grandicollis*) in the area of the operation. Prior to thinning, no beetle flight was recorded in the plantation, whereas after thinning, significant numbers of beetles were trapped in the area. During the same period, almost no flight took place in adjacent unthinned plots. The attracted beetles only colonized felled trees. *Ips avulsus* in particular showed a behaviour similar to the one observed for *I. typographus* in this experiment: during later cuttings, fresh slash attracted a large proportion of the local emerging population, whereas, in the absence of local attractive material, most emerging beetles dispersed quickly from the experimental area.

Our results do not imply that deliberate landing is made on trees or cut-off material emitting high quantities of volatiles, but rather that the beetles are able to modify their general dispersal direction when encountering such host odours. Final host selection could then be made by random landing, as we observed previously with pheromone-free trap-trees (Franklin & Grégoire, 1999), or be influenced by other factors such as gustatory cues.

Sex ratio

The sex ratios observed during this study were nearly always female-biased, a feature commonly found with *Ips* species, whether emerging insects or flying beetles attracted by host material or pheromones (Cameron & Borden, 1967; Bakke, 1968; Annila, 1971; Lindelöw & Weslien, 1986).

The sex ratio of both marked and unmarked beetles decreased between flight seasons. Equal number of males and females were caught at the beginning of the first flight then gradually more females were trapped, with the percentage females rising over 70% during the second flight. Zumr (1982) and Lindelöw & Weslien (1986) also reported a larger number of *I. typographus* males emerging at the beginning of the flight period, whereas the proportion of females was significantly higher later in the season.

No variation in the sex ratio was found as a function of distance, therefore showing no differences in behaviour or dispersal capacity between males and females at our scale of study. As they are the host finding and colonizing sex, the males are likely to have a higher mortality rate than the females. For catches of unmarked beetles, the shift in sex ratio between the flight seasons could then be caused by the re-emergence of a greater number of females, which would fly in search of new hosts to found sisterbroods (Zumr, 1982).

Population management implications

Better understanding of the patterns and rate of dispersal is fundamental to the improvement of management of bark beetle infestations. Our study indicates that if the direction of initial dispersal is mostly a random phenomenon, probably influenced by wind parameters when the wind speed is greater than 2 m/s (Byers, 1996), further orientation can be influenced by forest management practices.

Bark beetles such as *I. typographus* are highly mobile and are able to disperse far from their emergence site (Nilssen, 1984). Either flying actively or being carried downwind, they are susceptible to encounter zones where felling activities are under way. Although pheromonal attraction is likely to be much more potent than primary attraction, the presence of host odours seems to induce a response from the beetles. Therefore, if susceptible trees are found among or in the vicinity of harvested material, an infestation could be generated.

In areas of intensive forest management, such as Belgium, felled conifers should be removed quickly from the forest, not only from the stand where they were harvested but also from their storage places along forest roads. Residual material, such as cut-off tree tops and branches, may also present a risk of beetle attraction and, ideally, should be processed in stands at risk from attacks. Indeed, preliminary results from a study on *I. typographus* development in logging residues (Thiel, 1999) indicate that fresh residual material such as tree tops and butt

ends can be highly attractive to the beetle if felling takes place during its flight season.

Results from this study suggest that more research is needed on the interaction between *I. typographus* dispersal and host attraction. In particular, future research should focus on the effect of harvesting on bark beetle population movements and on its implication in the generation of new infestations.

Acknowledgements

References

Abgrall, J.-F. & Soutrenon, A. (1991) *La Forêt et ses Ennemis.* Cemagref-Dicova, Grenoble.

Anderbrant, O. (1985) Dispersal of reemerged spruce bark beetles, *Ips typographus* (Coleoptera, Scolytidae): a mark-recapture experiment. *Journal of Applied Entomology*, **99** (1), 21–25.

Annila, E. (1969) Influence of temperature upon the development and voltinism of *Ips typographus* L (Coleoptera: Scolytidae). *Annales Zoologici Fennici*, **6**, 161–207.

Annila, E. (1971) Sex ratio in *Ips typographus* L (Col, Scolytidae). *Annales Entomologici Fennici*, **37**, 7–14.

Austara, O., Bakke, A. & Midtgaard, F. (1986) Response in *Ips typographus* to logging waste odours and synthetic pheromones. *Zeitschrift für Angewandte Entomologie*, **101**, 172–177.

Bakke, A. (1968) Field and laboratory studies on sex ratio in *Ips acuminatus* (Coleoptera: Scolytidae) in Norway. *Canadian Entomologist*, **100**, 640–648.

Bakke, A., Froyen, P. & Skattebol, L. (1977) Field response to a new pheromonal compound isolated from *Ips typographus Naturwissenschaften*, **64**, 98.

Botterweg, P.F. (1982) Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Zeitschrift für Angewandte Entomologie*, **94**, 466–489.

Byers, J.A. (1996) An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecological Modelling*, **91**, 57–66.

Byers, J.A. (1999) Effects of attraction radius and flight paths on catch of scolytid beetles dispersing outward through rings of pheromone traps. *Journal of Chemical Ecology*, **25**, 985–1005.

Cameron, E.A. & Borden, J.H. (1967) Emergence patterns of Ips confusus (Coleoptera: Scolytidae) from Ponderosa pine. *Canandian Entomologist*, **99**, 236–244.

Dickens, J.C. (1981) Behavioural and electrophysiological responses of the bark beetle, *Ips typographus*, to potential pheromone components. *Physiological Entomology*, **6**, 251–261.

Dubois, G. (1992) *Migration de* Ips typographus *L (Coleoptera: Scolytidae) en Forêt d'Épicéa Commun (Picea Abies Karst). Mémoire de Fin d'Études.* Université Libre de Bruxelles, Brussels.

Duelli, P., Zahradnik, P., Knizek, M. & Kalinova, B. (1997) Migration in spruce bark beetles (*Ips typographus*) and the efficiency of pheromone traps. *Journal of Applied Entomology*, **121**, 297–304.

Fisher, N.I. (1993) *Statistical Analysis of Circular Data.* Cambridge University Press, Cambridge.

Franklin, A. & Grégoire, J.-C. (1999) Flight behaviour of *Ips typographus* L. (Col., Scolytidae) in an environment without pheromones. *Annals of Forest Science*, **56** (7), 591–598.

Gries, G., Nolte, R. & Sanders, W. (1989) Computer simulated host selection in *Ips typographus. Entomologia Experimentalis et Applicata*, **53**, 211–217.

Jactel, H. (1991) Dispersal and flight behaviour of *Ips sexdentatus* (Coleoptera: Scolytidae) in pine forest. *Annales des Sciences Forestières*, **48**, 417–428.

Kareiva, P.M. (1983) Local movement in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. *Oecologia*, **57**, 322–327.

Liebhold, A.M., Rossi, R.E. & Kemp, W.P. (1993) Geostatistics and geographic information systems in applied insect ecology. *Annual Review of Entomology*, **38**, 303–327.

Lindelöw, W.A., Risberg, B. & Sjodin, K. (1992) Attraction during flight of scolytids and other bark- and wood- dwelling beetles to volatiles from fresh and stored spruce wood. *Canadian Journal of Forest Research*, **22**, 224–228.

Lindelöw, W.A. & Weslien, J. (1986) Sex-specific emergence of *Ips typographus* L. (Coleoptera: Scolytidae) and flight behaviour in response to pheromone sources following hibernation. *Canadian Entomologist*, **118**, 59–67.

Mason, R.R. (1969) Behavior of *Ips* populations after summer thinning in a loblolly pine plantation. *Forest Science*, **15**, 390–398.

Moeck, H.A., Wood, D.L. & Lindahl, K.Q. (1981) Host selection behavior of bark beetles attacking *Pinus ponderosa*, with special emphasis on the Western pine beetle, *Dendroctonus brevicomis. Journal of Chemical Ecology*, **7**, 49–83.

Nilssen, A.C. (1984) Long-range aerial dispersal of bark beetles and bark weevils (Coleoptera, Scolytidae and Curculionidae) in Northern Finland. *Annales Entomologici Fennici*, **50**, 37–42.

Pannatier, Y. (1996) *Variowin. Software for Spatial Data Analysis in 2D.* Springer-Verlag, New York.

Perry, J.N. (1986) Multiple-comparison procedures: a dissenting view. *Journal of Economic Entomology*, **79**, 1149–1155.

Raffa, K.F. & Berryman, A.A. (1980) Flight responses and host selection by bark beetles. *Proceedings of the Second IUFRO Conference on Dispersal of Forest Insects: Evaluation, Theory and Management Implications* (ed. by A. A. Berryman and L. Safranyik), pp. 213–233. Canadian Forestry Service, USDA Forest Service and Canusa-West Washington State University.

Raty, L., Drumont, A., De Windt, N. & Grégoire, J.-C. (1995) Mass trapping of the spruce bark beetle *Ips typographus* L: trap or trap trees ? *Forest Ecology and Management*, **78**, 191–205.

Rossi, R.E., Mulla, D.J., Journel, A.G. & Eldon, H.F. (1992) Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs*, **62**, 277–314.

Safranyik, L., Linton, D.A., Silversides, R. & McMullen, L.H. (1992) Dispersal of released mountain pine beetles under canopy of a mature lodgepole pine stand. *Journal of Applied Entomology*, **113**, 441–450.

Safranyik, L., Silversides, R., McMullen, L.H. & Linton, D.A. (1989) Dispersal of the mountain pine beetle in relation to sources of attraction, wind direction and speed. *Journal of Applied Entomology*, **108**, 498–511.

Salom, S.M. & McLean, J.A. (1989) Influence of wind on the spring flight of *Trypodendron lineatum* (Olivier) (Coleoptera: Scolytidae) in a second-growth coniferous forest. *Canadian Entomologist*, **121**, 109–119.

Salom, S.M. & McLean, J.A. (1991) Environmental influences on

dispersal of *Trypodendron lineatum* (Coleoptera: Scolytidae). *Environmental Entomology*, **20**, 565–576.

Schlyter, F., Birgersson, G., Byers, J.A., Löfqvist, J. & Bergström, G. (1987a) Field response of spruce bark beetle, *Ips typographus*, to aggregation pheromone candidates. *Journal of Chemical Ecology*, **13**, 701–716.

Schlyter, F., Byers, J.A. & Löfqvist, J. (1987c) Attraction to pheromone sources of different quantity, quality, and spacing: density-regulation mechanisms in bark beetle *Ips typographus*. *Journal of Chemical Ecology*, **13**, 1503–1523.

Schlyter, F. & Cederholm, I. (1981) Separation of the sexes of living spruce bark beetles, *Ips typographus* L., (Coleoptera: Scolytidae). *Zeitschrift für Angewandte Entomologie*, **92**, 42–47.

Schlyter, F., Löfqvist, J. & Byers, J.A. (1987b) Behavioural sequence in the attraction of the bark beetle *Ips typographus* to pheromone sources. *Physiological Entomology*, **12**, 185–196.

Taylor, R.A.J. (1978) The relationship between density and distance of dispersing insects. *Ecological Entomology*, **3**, 63–70.

Thiel, J. (1999) The development of bark beetles in logging residues in spruce stands. Methodology of forest insect and disease survey in Central Europe. *Proceedings of the Second Workshop of the IUFRO WP 7.03.10, April 20–23 1999, Sion, Switzerland* (ed. by B. Forster, M. Knižek and W. Grodzki), pp. 236–237. Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf.

Turchin, P. (1998) Quantitative analysis of movement. *Measuring and Modeling Population Redistribution in Animals and Plants.* Sinauer Associates Inc, Sunderland MA.

Turchin, P. & Thoeny, W.T. (1993) Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecological Applications*, **3**, 187–198.

Weslien, J. & Lindelöw, W.A. (1990) Recapture of marked spruce bark beetles (*Ips typographus*) in pheromone traps using area-wide mass trapping. *Canadian Journal of Forest Research*, **20**, 1786–1790.

Wollerman, E.H. (1979) Attraction of European elm bark beetles, *Scolytus multistriatus*, to pheromone-baited traps. *Journal of Chemical Ecology*, **5**, 781–793.

Zar, J.H. (1996) *Biostatistical Analysis*. 3rd edn. Prentice Hall, London.

Zolubas, P. & Byers, J.A. (1995) Recapture of dispersing bark beetle *Ips typographus* in pheromone baited traps: regression models. *Journal of Applied Entomology*, **119**, 285–289.

Zumr, V. (1982) Studies on the relation of sexes in beetles of *Ips typographus* (Coleoptera: Scolytidae) found in pheromone traps. *Anzeiger für Schädlingskunde, Pflanzenschutz, Umweltschutz*, **55**, 68–71.

Zumr, V. (1992) Dispersal of the spruce bark beetle *Ips typographus* (L) (Col, Scolytidae) in spruce woods. *Journal of Applied Entomology*, **114**, 348–352.