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Wind-aided dispersal of simulated bark beetles flying through forests

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Abstract

Larger bark beetles such as *Ips typographus* (Coleoptera: Scolytidae) fly at about 2 m s^{-1} for up to several hours. Computer simulations in two dimensions showed that bark beetles are capable of dispersing from a brood tree over wide areas while drifting with the wind. For example, if beetles take an angle of maximum turn (AMT) at random up to 10° either left or right each second, about 90% of the beetles become distributed over a 31.9 km^2 area after 1 h of flight. Larger maximum turning angles by beetles decrease the area of dispersal in proportion to the reciprocal of the square of the AMT. An increase in the dispersal time causes a linear increase in dispersal area and downwind drift distance, while increases in wind speed have no affect on the ultimate dispersal area but do increase the drift distance. Dispersal of bark beetles in a 10×10 km forest of 5 million trees of 0.15 m trunk radius, corresponding to the natural density and trunk size of a 70-year-old Norway spruce forest (*Picea abies*), was simulated by spacing trees at appropriate density in a 50 m radial area centred on a beetle. A new area with trees was constructed similarly whenever the beetle left the former area. These simulations showed trees reduced the size of the dispersal area by 11% and downwind drift by 18% after 1 h of flight due to the effect of turning some beetles back toward the release point, similar to the effects of increasing the AMT. The average dispersal distance and downwind distance decreased as linear functions of trunk density. Given step size, number of steps, and AMT, the correlated random walk equation of Kareiva and Shigesada [1983, Oecologia 56, 234–238] predicts mean squared dispersal distance. This can be transformed to the more meaningful average dispersal distance by taking the square root and multiplying by a proportion obtained from a three dimensional surface equation fitted from simulation results. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Dispersal; Migration; Host selection; Populations; Correlated random walk

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1. Introduction

Bark beetles (Coleoptera: Scolytidae) are important predators of coniferous forests. For example, Norway spruce (*Picea abies*), predominating in many regions of Europe and Asia, is attacked

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by *Ips typographus*, the tree's most serious enemy (Austarå et al. 1984). The adults of 'aggressive' bark beetle species in the genera *Ips* and *Dendroctonus* must kill the host tree so that it does not continue to produce toxic resin that can also entrap the beetles and their larvae (Byers, 1995). Thus, newly emerged adults emerge from the brood tree or over-wintering sites and fly in search of the usually rare hosts that are more susceptible due to disease and abiotic factors such as drought and storm damage. A few beetles of the population are termed 'pioneers' since they presumably are first to locate and 'attack' a susceptible tree and begin the colonisation. If the tree is of low resistance, then insufficient resin is produced to repel the pioneer beetle so it has time to feed and produce pheromone. This causes a large part of the flying population in the vicinity to aggregate in response to the pheromone and exploit the food and mate resource (Byers, 1996a). The host-selection process by pioneers and the population dispersal flight are still not well understood.

Insects disperse when their habitat is becoming unsuitable. This can be from a lack of food resources, mating possibilities, territories and suitable domiciles or from the need to escape the local build-up of parasites and predators (c.f. Ricklefs, 1990). Apparently for the same reasons, bark beetles emerge from the dead brood tree, or litter near the brood tree, and begin a dispersal flight that probably can range from a few meters to several kilometres. Evidence from the laboratory has shown that bark beetles can fly remarkably far. For example, Jactel and Gaillard (1991) flew *I. sexdentatus* on rotary flight mills connected to computer and found that 50% of the beetles could fly more than 20 km based on about 50 interrupted flights (a total of at least 2.5 h of flight). In another study where *I. typographus* were placed on flight mills, the longest continuous fight was 6 h and 20 min (Forsse and Solbreck, 1985). This indicates that a few *I. typographus* flying at 2 m s^{-1} (Byers et al., 1989) could travel up to 45.6 km without the aid of wind. Strong individuals of the Douglas-fir beetle, *Dendroctonus pseudotsugae*, flew up to 8 h uninterrupted on flight mills (Atkins, 1961), and the southern pine beetle, *D. frontalis*, has flown up to 6 h on a flight mill (G. Birgersson, personal communication).

Knowledge of how far and where bark beetle populations disperse is mainly from (1) mark–release–recapture studies using pheromone traps and from (2) the geographical occurrence of new infestations relative to previous ones. Both lines of investigation are inconclusive since (1) only a few pheromone traps were used, usually some tens to hundreds of meters from the release site, so that a large proportion of released beetles escaped, or (2) the origins of attacking beetles were uncertain. Several studies have placed various sized rings of pheromone traps around a source of marked beetles. For example, the spruce bark beetle of Europe, *I. typographus*, was recaptured at various outer distances from 120 to 1000 m (Botterweg, 1982; Zumr, 1992; Zolubas and Byers, 1995; Duelli et al., 1997). In California, *I. paraconfusus* was recaptured in outer traps at 2 km (Gara, 1963). The ambrosia beetle, *Trypodendron lineatum*, was recaptured at 500 m (Salom and McLean, 1989). As expected, a small proportion of the released beetles were recaptured by the widely-spaced outer traps, and the large gaps between traps probably allowed many to slip through as they drifted with the wind (e.g. gaps of 785, 1257, and 393 m in Zumr, 1992; Gara, 1963; and Salom and McLean, 1989, respectively). An adverse effect of marking, although discounted, might also influence the dispersal.

Anecdotal evidence of long-range dispersal (Miller and Keen, 1960; Nilssen, 1978) is inconclusive since it is difficult to rule out all possible sources of beetles. The best evidence of this type is found in Miller and Keen (1960) who summarise results of studies by the US Forest Service in California on the western pine beetle, *Dendroctonus brevicomis*. This beetle infested 'islands' of ponderosa pine, initially free of beetles, that were separated from the main forest by open sagebrush areas. They concluded that significant numbers of bark beetles must have flown a minimum of 3.2 km in one study, and 9.6 km or even 20 km in another study, to reach the infested trees and kill them.

Little is known about the flight paths of bark beetles since they are small and dark, thus difficult to observe for any significant distance. *I. typographus* and some other *Ips* and *Dendroctonus* species have been caught primarily under 10 m in height or under the forest canopy (Gara and Vité, 1962; Forsse and Solbreck, 1985; Duelli et al., 1986; Byers et al., 1989). I once ran after several individual *I. typographus* that had taken flight from a brood log pile in a clearcut in a 3–4 m s^{-1} wind in which they flew or drifted generally downwind (none flew crosswind) at 2–3 m height in an approximately straight path for some 60 m. Bark beetles, including *I. typographus*, usually fly away from release sources in all directions unless winds are strong where they appear to drift with the wind (Meyer and Norris, 1973; Botterweg, 1982; Helland et al., 1984; Byers et al., 1989; Salom and McLean, 1989; Thoeny et al., 1992; Zolubas and Byers, 1995; Duelli et al., 1997).

The first objective was to simulate dispersal of bark beetles using various wind and flight parameters in order to visualise how natural dispersal distributions might appear that otherwise are nearly impossible to observe. A second objective was to simulate the occurrence of trees at the density of a Norway spruce forest to see what effects they might have on flight dispersal. The ability to construct theoretical distribution patterns based on realistic parameters may allow a better understanding of the dispersal ecology of bark beetles and the probability of them killing trees next to outbreak centres. Finally, simulations can be used to test results from previous studies proposing equations that predict dispersal distances of populations based on the distribution of turning angles, number of steps, and average step length (e.g. Kareiva and Shigesada, 1983). It might also be possible to modify or correct such equations if they are found to diverge from the simulated reality.

2. Methods

2.1. Wind-aided bark beetle dispersal in forests or clearcuts

The algorithms for simulating insect flight movement in two dimensions have been developed in earlier models (Patlak, 1953; Rohlf and Davenport, 1969; Kitching, 1971; Byers, 1991, 1993, 1996a,b). Briefly, modelled insects take steps in a forward direction with possible random deviations up to an angle of maximum turn (AMT), either right or left at random. The flight path of an insect, from x_0, y_0 to x, y is determined by calculating the insect vector using polar coordinates from the former position based on the step size (s), or distance travelled in 1 s, and former direction (α in radians) plus the random angle of turn ($-\mathrm{AMT} < \gamma < \mathrm{AMT}$). The wind vector, wind speed (w) and direction (θ), is then added to the polar coordinates of the insect vector to obtain the resulting path [i.e. $x = x_0 + \cos(\alpha + \gamma)s + \cos(\theta)w$ and $y = y_0 + \sin(\alpha + \gamma)s + \sin(\theta)w$]. The input parameters of the model are dispersal time, average insect speed and step size, coordinates of the brood tree, wind direction and speed, number of insects and the area length and width. Initial directions of insects are chosen randomly (0–360°).

In all simulations, flight speed was 2 m s^{-1} which is about what larger bark beetles such as *I. typographus* can maintain in still air (Byers 1996a). Most simulated dispersal periods were limited to 1 h, although these beetles on flight mills have flow up to 6 h (Forsse and Solbreck, 1985; Forsse, 1991). In one simulation, the dispersal times of the population were varied about a mean of 1 h according to a normal distribution with standard deviation of 15 min (Walker, 1985). The AMT was either 10 or 20° unless varied from quite straight (2°) to highly random and circuitous (90°). At the end of each simulation period the positions of all insects were recorded for plotting and analysis.

The dispersal patterns of distribution were visualised by constructing isolines that encircle approximately 90% of the points (N). This was done by using the coordinates of all points to calculate a centre of mass (averages of x and y). From this centre usually $N/20$ pie-shaped sectors, evenly dividing 360°, were calculated, and the angles to all points were found to determine which points were within each sector. The distances to enclosed points within each sector then were calculated and sorted based on increasing distance from the centre. For a 90% isoline, an average distance was calculated from the distances of the two points less than, and greater than, the 90th percentile of distances. This distance was then used as a radius from the centre along the middle of the sector to find an endpoint. These endpoints were used in a three-point rolling average to form a polygon whose area was found by summing the areas of the polygon's triangles about the centre.

The dispersal patterns were further analysed by centring the points just inside a rectangle and then constructing a grid of cells (30 × 30) in which points were counted. The grid cell counts were smoothed by a surrounding nine-cell rolling average and plotted as bars in three-dimensions without perspective. The possible effects of random wind directions and speeds were investigated with this analysis method. For example, the dispersal of 500 beetles was simulated in a 10 × 10 km area with a grid of 50 × 50 cells (200 × 200 m each) in which each cell had a random (0–360°), but consistent, wind direction. A variation of this model had cells with consistent wind vectors up to 90° left or right, at random, of an eastward direction. Finally, wind direction and speed were varied (0–360° and 0–2 m s^{-1}) for each beetle at each step, but with an average wind speed of 1 m s^{-1}.

Trees could affect the dispersal patterns of bark beetles. This is difficult to simulate because there are 50 000 Norway spruce trees (0.15 m radius, 70 year plantation) in a square km (Magnussen, 1986) or 5 million in a 10 × 10 km area needed for simulating dispersal for an hour. The array needed to hold and search these tree coordinates requires more memory and speed than possible with program software and personal computers. However, the task was accomplished by simulating one beetle at a time, many times, and placing a radial area of forest centred on the beetle at the start. The area's radius was 50 m and within this area 393 trees are expected (Magnussen, 1986). The trees were spaced apart at least 50% of the maximum hexagonal spacing possible, a distance equal to a minimum allowed distance (MAD) of 2.4 m between trees (Byers, 1984, 1992). Trees were also spaced this distance or more from the beetle at the centre, but otherwise the trees were placed at random within these constraints. The beetle was then allowed to move as above. However, if it would have struck a tree trunk (algorithm in Byers, 1991) according to the flight and wind vectors, then an algorithm picks an angle α (0.57°) either left or right at random from the former flight angle and tests this flight angle. If the beetle still would strike the tree, then the angle α is expanded incrementally (0.57°), but alternating left and right from the former flight angle, until the beetle misses the trunk. This means that beetles will pass by the tree either left or right in a realistic way usually according to which side of the tree they tended toward initially.

The beetle continues until eventually passing out of the circular area, whereupon a new set of 393 spaced trees is centred about the beetle (using the same memory array). This requires little memory and speeds the searches of tree coordinates by 12 723 times compared with searching 5 million pairs (requiring 80 MB memory). All simulations and graphical analyses were done using a combination of QuickBASIC 4.5 and PostScript 2.0 programming languages.

2.2. Equations predict mean dispersal distance

During the studies, I wondered whether it is possible to use an equation to predict the average distance of dispersal of a population of animals from a release point given: (1) the step size (or average step size); (2) the number of steps; and (3) the AMT. The average distance of dispersal and variance can be found by simulation to check the validity of any such equation. The equation of Kareiva and Shigesada (1983) uses move lengths, turning angles, and total moves to calculate dispersal distances. However, their formula gives the expected mean squared dispersal distance, $E(R_n^2)$

$$E(R_n^2) = nE(L^2) + 2E(L)^2 \frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right) \qquad (1)$$

where L is the step size (since L is constant then $E(L^2) = E(L)^2 = L^2$), n is the number of steps, and c is the average of the cosines of all possible turning angles (in radians) from a specified random distribution:

$$c = \int_{-\pi}^{\pi} \cos\theta\, g(\theta)\, \mathrm{d}\theta \tag{2}$$

The mean squared dispersal distance, unfortunately, is difficult to compare to the intuitively more meaningful mean dispersal distance. Assuming a uniform distribution of random angles between $-$AMT and AMT, I calculate a mean c from the AMT (converted to radians, AMT$*\pi/180$) by summing the cosines of θ in incremental steps of $2*\mathrm{AMT}/i$ (where $i = 20\,000$) from $-$AMT to AMT and dividing the sum by the number of iterations:

$$S = \sum_{-\mathrm{AMT}}^{\mathrm{AMT}} \cos\theta \quad \text{and} \quad c = \frac{S}{i} \tag{3}$$

The problem is now to use the mean square distance of Kareiva and Shigesada (1983) from Eq. (1) using c from Eq. (3) to find the mean dispersal distance. A first approximation is to take the square root, but this over-estimates the actual mean distance found by simulation by up to 12.4%.

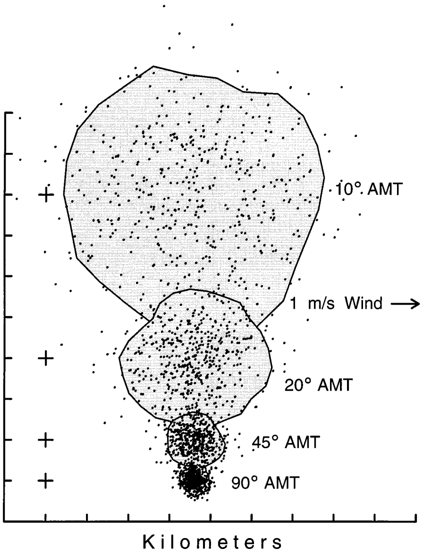

Fig. 1. Dispersal patterns of 500 simulated bark beetles flying from a source (pluses at left) in 1 m s^{-1} wind (from left) for 1 h with different flight angles of maximum turn (AMT). Beetles took steps of 2 m (2 m s^{-1} speed), and at each step they could turn either left or right up to a maximum of 10, 20, 45 or 90° at random. The largest polygon includes 90% of the beetles having an AMT of 10° in an area of 31.9 km^2. The beetles with flight AMT's of 20, 45 and 90° are enclosed in areas of 9.1, 1.4, and 0.4 km^2, respectively.

Simulations using various step sizes, and varying both the number of steps (X) and the AMT (Y, from 0 to 180°) stepwise, were used to calculate the mean distance of dispersal with the pythagorean formula (averages of four simulations of 1000 points at each X, Y). It is then possible to compare the resulting distances to square roots of expected mean square distances based on Eq. (1) and Eq. (3) using appropriate parameters. The comparisons were used to find correction factors (which vary with number of steps and AMT) based on the ratio of the simulated values and the calculated square root values.

3. Results

3.1. Wind-aided bark beetle dispersal in forests or clearcuts

An increase in the angle of maximum random turn (AMT) caused the area of distribution of simulated bark beetles enclosed by a 90% isoline to decrease proportional to the reciprocal of the AMT squared ($Y = 3609X^{-2.03}$, $R = 1.00$), but had no affect on the centre of the distribution relative to the brood tree source (Fig. 1).

The average distance beetles flew away from the centre of mass (or from the brood tree in still air) after 1 h is expressed as a reciprocal relation of the AMT ($Y = 21.377X^{-1.02}$, $R = 1.00$). The constant wind speed and direction affected all beetles similarly so the patterns were all symmetrical and drifted to the same position as shown by the equivalent positions of the centres of mass (Fig. 1). Simulations showed that the patterns were the same relative size and symmetry regardless of wind speed, which only caused the 'centres of mass' to drift more rapidly. The convex polygon area containing about 90% of the 500 simulated beetles ranged from 31.9 km^2 (or about 6.4 km diameter) for reasonably 'normal-flying' beetles (10° AMT) to only 0.4 km^2 (0.7 km diameter) for the highly circuitous-flying ones (90° AMT).

Given that beetles all had random turning angles less than 20° right or left, an increase in time of dispersal caused a linear increase in the area of distribution of simulated bark beetles (Fig. 2; $Y = -0.46 + 9.547X$, $R = 1.00$).

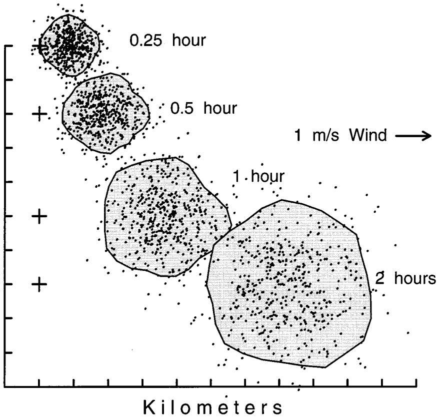

Fig. 2. Dispersal patterns of 500 simulated bark beetles flying from a source (pluses at left) in 1 m s^{-1} wind (from left) for different time periods. Beetles took steps of 2 m (2 m s^{-1} speed), and at each step they could turn either left or right up to a maximum of 20° at random. The largest polygon includes 90% of the beetles having flown for 2 h to cover an area of 18.3 km^2. The beetles flight periods of 0.25, 0.5, and 1 h are enclosed in areas of 2.2, 4.2, and 9.6 km^2, respectively.

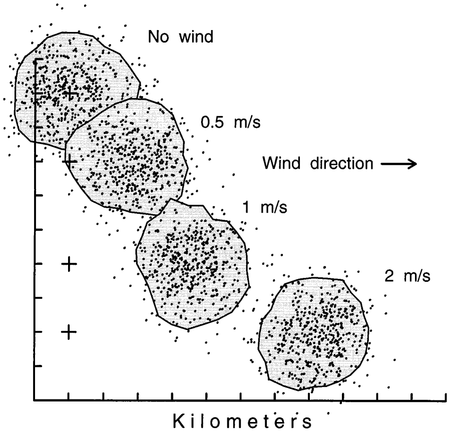

Fig. 3. Dispersal patterns of 500 simulated bark beetles flying from a source (pluses at left) for 1 h in different wind speeds, from left to right. Beetles took steps of 2 m (2 m s^{-1} speed), and at each step they could turn either left or right up to a maximum of 20° at random. The polygons include 90% of the beetles having flown in various wind speeds of 0, 0.5, 1, and 2 m s^{-1} to disperse over similar areas of 9.3, 9.2, 9.0, and 8.4 km^2, respectively.

As expected, the average distance travelled in 1 h by beetles away from the centre of mass, or brood tree in still air, is expressed in relation to the square root of time ($Y = 1.05X^{0.516}$, $R^2 = 1.00$; Gamov and Cleveland, 1969). The 90% isoline polygon at 0.25 h dispersal covered an area of 2.2 km^2 which increased to 18.3 km^2 after 2 h of dispersal. The centres of mass also drifted farther downwind with more time (about 7.2 km in 2 h, Fig. 2). If the AMT was held constant at 20° and the time at 1 h, then not surprisingly an increase in wind speed has no affect on the area of distribution, being about 9.0 ± 0.6 km^2 ($\pm$95% C.L.) at any wind speed (Fig. 3). However, the centres of the distributions drifted farther with higher wind speeds (Fig. 3).

Initially beetles dispersing from a point source would fly out in all directions. If the flight direction was nearly straight (AMT = 2°) then a concentric ring of points would flow outward as seen after 1 h in Fig. 4A. The density of points in the ring along a radial transect approximates a nor-

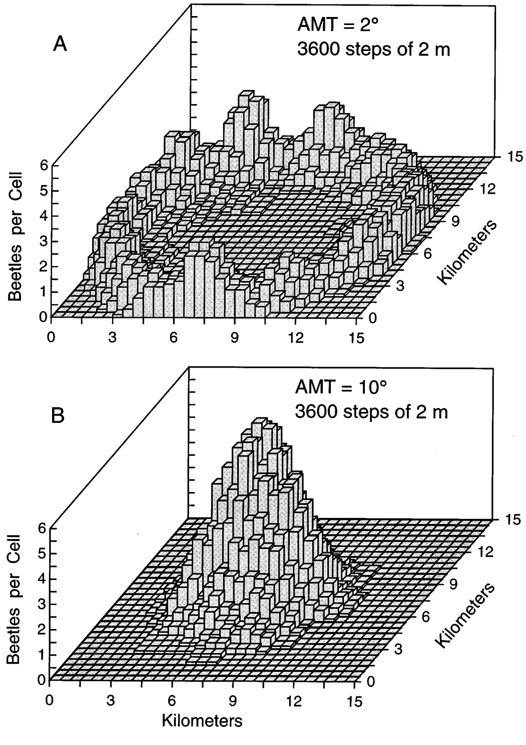

Fig. 4. (A) Cell counts (nine-cell rolling average) of 500 simulated bark beetles after dispersal from a point source for 1 h. Beetles flew at 2 m s^{-1} and at each step of 2 m they could turn either left or right at random up to a maximum of 2°. (B) The same conditions except that beetles took random turns with deviations up to 10° from straight ahead.

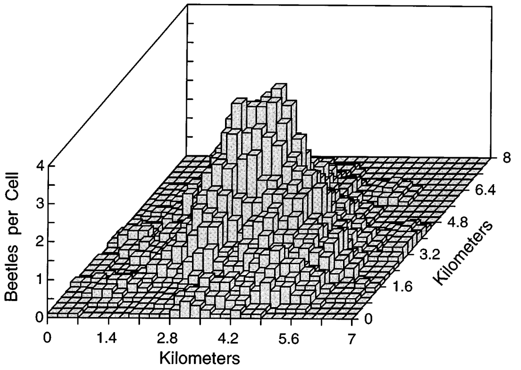

Fig. 5. Cell counts (9-cell rolling average) of 500 simulated bark beetles after dispersal from a point source for 1 h. Beetles flew from a source centred in a 10 × 10 km area with a 50 × 50 grid of 200 × 200 m cells each with a random, but consistent, wind direction of 1 m s^{-1} velocity. Beetles flew at 2 m s^{-1} and at each step of 2 m they could turn either left or right up to a maximum of 10° at random.

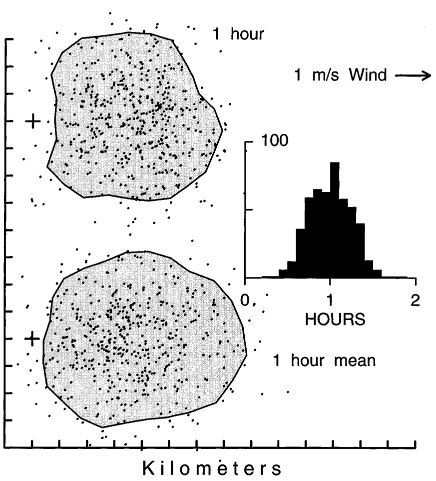

Fig. 6. Dispersal patterns of 500 simulated bark beetles flying from a source (pluses at left) in 1 m s wind (from left) for 1 h (top polygon) or for a mean of 1 h with normal variation (SD = 15 min, bottom polygon). Inset frequency histogram pertains to bottom polygon. Beetles took steps of 2 m with random turns at each step either left or right up to a maximum of 10°. The top and bottom polygons include 90% of the beetles and cover an area of 30.7 and 36.8 km^2, respectively.

mal curve. Eventually, beetles by random turns can fly back toward the source. This happens more often if the AMT is larger at 10° in which the density distribution becomes a three-dimensional bell-shaped curve (Fig. 4B). A constant wind direction and wind speed does not affect the dimensions of the density distributions.

An attempt to influence the density distributions by variable wind directions was done by placing a grid of 2500 cells (200 m square) in which each had a random wind direction that was constant during the period. The density distribution was virtually unaffected when wind speed was 1 m s^{-1} (compare Fig. 5 to Fig. 4B). If the wind speed is made more than the flight speed of 2 m s^{-1} then beetles can be forced along the narrow boundaries of the cells when two wind vectors oppose each other. This situation seems unnatural and so is not considered further. Finally, a highly random scenario was simulated in which wind direction varied at random for each beetle at each step, and also the wind speed was varied at random up to 2 m s^{-1} (average 1 m s^{-1}). Again, the density distribution or diameter of the area was not significantly affected.

Individuals of a population of bark beetles are expected to vary in fat content and flight range according to a normal distribution. Therefore, simulated insects were allowed to vary in flight duration about a mean of 1 h with a standard deviation of 15 min (Fig. 6). Compared to an exact flight duration of 1 h, the variable range insects became distributed over a slightly larger area (90% isoline of 36.8 km^2 versus 30.7 km^2; mean distance from centre of mass of 2.14 versus 2.01 km). Otherwise there were little differences in spatial distribution or downwind movement (Fig. 6).

The presence of 5 million Norway spruce trees (0.15 m radius, 70 years) in a 10 × 10 km area (Magnussen, 1986) had a subtle affect on the paths and reduced somewhat the dispersion area of the simulated beetles. After 1 h of dispersal in a 1 m s^{-1} wind, 100 bark beetles in the simulated forest had a 90% isoline area of 25.3 km^2 and moved downwind an average of 2.85 km (Fig. 7A). In comparison, the same beetles in an open field covered more area 30.8 km^2 and moved further downwind at 3.53 km (Fig. 7B). Using ten simulations of 500 beetles each for each type, the 'forest' beetles covered an average 90% isoline area of 30.94 ± 0.98 km^2 (±95% C.L.) and drifted on average 2.93 ± 0.05 km downwind compared to dispersal in an open area covering 34.81 ± 1.13 km^2 and moving 3.57 ± 0.06 km downwind (means significantly different $P < 0.001$, t-test). The average dispersal distance from the centre of mass was 1.98 ± 0.03 km in the forest and was significantly less than 2.08 ± 0.04 km in the open ($P < 0.001$). These results indicate that the trees reduced the dispersal area by about 11%, the downwind drift by 18%, and the average dispersion distance from the centre of mass by 5%.

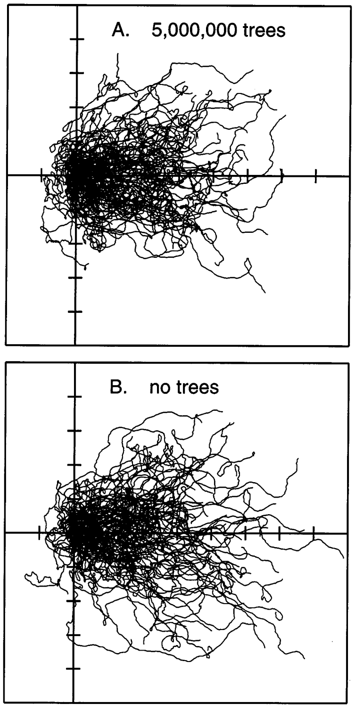

Fig. 7. (A) Dispersal paths of 100 simulated bark beetles flying from a source (at cross in lines) for 1 h in 1 m s^{-1} wind (left to right) in a 10 × 10 km forest of 5 million trees. Beetles took steps of 2 m (2 m s^{-1} speed), and at each step they could turn either left or right up to a maximum of 10° at random. The 90% isoline polygon of dispersion was 25.2 km^2, the centre of mass drifted 2.85 km downwind from the release, and the average distance beetles travelled from the centre of mass was 1.85 km. (B) Dispersal paths of 100 simulated bark beetles flying from a source (at cross in lines) for 1 h in 1 m s^{-1} wind (left to right) in a 10 × 10 km open area. Beetles took steps as in A. The 90% isoline polygon of dispersion was 30.8 km^2, the centre of mass drifted 3.53 km downwind from the release, and the average distance beetles travelled from the centre of mass was 2.00 km.

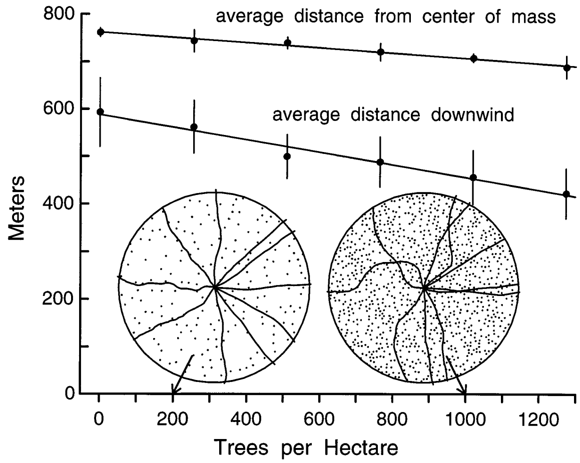

Fig. 8. Average dispersal distances either downwind from a source or from the calculated centre of mass of 200 simulated bark beetles flying in Norway spruce forests of different trunk densities. Bars represent 95% confidence limits for a mean of five simulations. Beetles flew at 2 m s^{-1} for 10 min, taking steps of 2 m with turns at each step either right or left up to a maximum of 10° at random. Beetles turned when encountering spruce tree trunks of 0.15 m radius, as shown in circular regions of 50 m radius. Initial paths of ten beetles, released uniformly, are shown in regions with 200 and 1000 trees.

Simulations of varying densities of Norway spruce trunks, from 0 to 1000 trees within the 50 m radius about a beetle, shows that the average dispersal distance downwind (m) decreases as a linear function of tree density ($Y = 588.2 - 0.1326X$, $R^2 = 0.97$, Fig. 8). Also, the average dispersal distance (m) from the centre of mass ($Y = 762.5 - 0.0549X$, $R^2 = 0.98$) and the 90% isoline area (km^2) ($Y = 3.0576 - 0.000232X$, $R^2 = 0.96$) decreases linearly with tree density (Fig. 8). The paths of beetles were more twisting at the higher trunk densities (Fig. 8) due to the need to more often avoid trees, the same effect as if the angle of maximum turn (AMT) had been made larger (as in Fig. 1).

3.2. Equations predict mean dispersal distance

The equations of Kareiva and Shigesada (1983) for mean square dispersal distances gave square root values very similar, but not always, to simulation results (actual mean dispersal distances). The comparisons show that for a large number of steps ($n > 5000$), the actual dispersal distance is actually about 0.89 of the square root of the expected mean square distance from the formula. Also, when the AMT is above 30° the correction factor stabilises at 0.89. Interestingly, there is a complex interplay between the AMT and number of steps which makes it necessary to describe the correction factor (about 0.89 above) as a three-dimensional surface at angles $< 30°$ and steps $<$ 5000 (Fig. 9).

The step size surprisingly has no affect on the correction factor. The surface equation of the correction factor (Z) can be described reasonably well by a multivariate least squares cubic polynomial:

$$Z = aX^3 + bX^2 + cX + dX^2Y + eXY + fXY^2 + gY + hY^2 + iY^3 + 1.021 \quad (4)$$

where $a = -1.123\text{E}-12$, $b = 9.27\text{E}-9$, $c = -2.663\text{E}-5$, $d = 1.464\text{E}-10$, $e = -2.38\text{E}-6$, $f = 6.449\text{E}-8$, $g = -5.695\text{E}-3$, $h = 1.677\text{E}-4$, and $i = -3.227\text{E}-6$ (MATHCAD, MathSoft Inc.). However, the fit is best over a limited range, therefore five constraints applied in order improve the fit: (1) if $Z < 0.89$ then $Z = 0.89$, (2) if $Z > 1$ then $Z = 1$, (3) if AMT $> 30°$ then $Z = 0.89$, (4) if number of steps > 5000 then $Z = 0.89$, and (5) if AMT > 20 AND steps > 2000 then $Z = 0.89$.

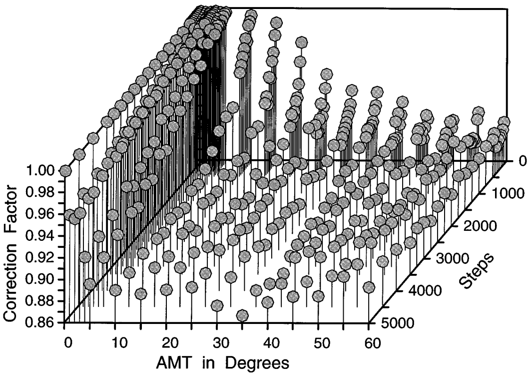

Fig. 9. Correction factor as a three dimensional surface function of the number of steps and the angle of maximum turn (AMT) at each step. The mean dispersal distance is obtained by multiplying the correction factor by the square root of the expected mean square dispersal distance. Points represent averages of four simulations of 1000 points each. See text for the best-fitting multivariate cubic polynomial equation.

Thus, the mean dispersal distance is found from Eqs. (1), (3) and (4). For example, if $L = 2$ m, $n = 1000$ steps, and AMT = 30° or 0.5236 radians, then $c = 0.9549$ from Eq. (3) and the mean square dispersal distance is 169 752 m from Eq. (1) and the mean dispersal distance (MDD) is:

$$\text{MDD} = Z\sqrt{E(R_n^2)} = 0.89 * \sqrt{169\,752} = 367 \text{ m} \quad (5)$$

where $Z = 0.89$ from Eq. (4) and constraints. Five simulations with the same parameters and 1000 insects each gave a mean dispersal distance of 364.0 ± 5.3 m (95% C.L.).

4. Discussion

The dispersal patterns shown in Figs. 1–6 are similar to expected point distributions based on earlier studies of correlated random walks and diffusion models (Okubo, 1980). The results of dispersion of bark beetles differ only because of the specific parameters for flight duration (number of steps), step size (or frequency of possible turn) and the angle of turn taken at random, either left or right, within an angle of maximum turn (AMT). Earlier simulations of animal movements have either used random turns of increments of 45 or 90° on a lattice (Rohlf and Davenport, 1969; Gries et al., 1989; Johnson et al., 1992), a uniform random distribution within a range of AMT (Byers, 1991, 1993, 1996a,b, 1999; Kindvall, 1999), or random turns using a normal distribution with a specified standard deviation (Cain, 1985; Weins et al., 1993). At least for the latter two methods, the resulting distributions after dispersal can be made nearly identical by adjusting the AMTs and standard deviations of turning angles appropriately (Byers, unpublished).

The turning angle and step size parameters are difficult to measure for flying bark beetles and may be complicated by the scale chosen for measurement due to habitat heterogeneity and periodic behavioural changes (Kaiser, 1983; Cain, 1985; Turchin, 1991; Johnson et al., 1992; Crist et al., 1992; Weins et al., 1993; With and Crist, 1996). However, if the movement is regular as might occur in a uniform habitat, then the scale chosen is not critical over large ranges since smaller divisions of the path give smaller angles of turn while larger division yield larger angular deviations. This can be easily seen in simulations where approximately the same paths can be constructed from larger steps and larger possible turning angles as from smaller steps and appropriately smaller turning angles.

The simulation of dispersal in a ‘natural’ forest of tree trunks shows that the trunks deflect beetles enough to reduce the dispersal area of the population about 11% compared with no trunks (Fig. 7A and B). This is similar in effect to increasing the AMT of beetles (Fig. 1). Interestingly, the dispersal distance downwind, the dispersal distance from the centre of mass, and the 90% isoline area (not shown) all decrease as linear functions of trunk density (Fig. 8). Part of the observed reduction in dispersal rates of populations and the encounter rates between predators and prey in heterogenous environments (Kaiser, 1983; Johnson et al. 1992; Crist et al., 1992; With and Crist, 1996) can be due to avoidance of obstacles as shown here, or due to attractive or arresting properties of the obstacles (e.g. food items).

The results of flight mill studies with larger bark beetles (Atkins, 1961; Forsse and Solbreck, 1985; Forsse 1991; Jactel and Gaillard, 1991) indicate that these beetles which fly at about 2 m s^{-1} could travel up to 45 km. The models here reveal the potential extent that bark beetles, and similar insects, can disperse in a relatively short time of 1 h. In regard to bark beetle epidemics, truly laminar wind of either consistent or variable direction (even highly random in patches) has no affect on the shape or extent of the dispersal area other than causing the point pattern to drift in unidirectional wind (Fig. 3). In nature, of course, wind-aided dispersal is probably more complicated. First of all, wind is usually not laminar but because of topography may flow in ways to separate and transport beetles into different regions. Beetles may settle after different flight durations which will tend to increase the dispersal area in wind (Fig. 6). There is some evidence from field traps that beetles avoid both clearcuts and deep forest, preferring the edges of forests — thus further disrupting the theoretical dispersal patterns (Botterweg, 1982; Byers, unpublished). Recently, the spruce bark beetles *I. typographus* and *Pityogenes chalcographus* have been shown to avoid volatiles of nonhost birch trees (both from bark and leaves) which suggests the possibility that beetles may not enter areas of primarily birch (Byers et al., 1998).

The dispersal flight of a bark beetle may vary from only a few meters (as observed during epidemics) to possibly several kilometers. Several factors interact to cause the dispersal flight distance to vary between individuals. The most obvious is that a beetle encounters a susceptible tree early in the dispersal flight. However, whether this tree is attacked may depend on the level of fat reserves that can be mobilised for flight (Atkins, 1966, 1969; Byers 1999). A beetle should have higher reproductive fitness if it flies rather far from the brood tree since it can both avoid inbreeding with siblings and, more importantly in my view, escape predators and parasites that are locally more dense near the brood tree. Thus, the dispersal distance has been optimised over evolutionary time to balance the probably logarithmically increasing benefits of flying farther against the probably exponentially increasing likelihood of exhaustion and failing to find a host. The fat level required for lengthy dispersal will depend on the conditions in the brood tree during larval development, for example, disease, insect, and climatic factors will affect the nutritional quality of the host. Severe competition among the larvae will reduce the size of adults as well as their fat content (Atkins, 1975; Anderbrant et al., 1985). Parasites would reduce the size and fat content of some adults while predators would lessen competition for those remaining locally, thereby increasing the variability of dispersal range in the population. The population density of bark beetles should be stabilised by a frequency-dependant competition for the susceptible trees that would produce increasingly stronger, longer-flying individuals with decreasing attack and larval density while giving weaker, shorter-flying ones with increasing competition.

Pioneer bark beetles find susceptible trees either by landing at random or by response to volatiles from damaged or weakened trees. Most species that have an aggregation pheromone appear not attracted, or only weakly, by host volatiles (Byers, 1995). For these species, it is not known if there are two types of beetles, one that behaves as a pioneer and tests trees for susceptibility, and another type that only searches for aggregation pheromone and trees undergoing colonisation. Most likely, all beetles have a strategy that depends on the level of their fat reserves (Byers, 1999). At higher fat reserves during the period immediately after emerging, the beetle disperses and ignores host trees and pheromone, but as the fat reserves are depleted both trees and pheromone become increasingly attractive (Atkins, 1966; Borden et al., 1986; Gries et al., 1989; Byers, 1999). Finally, if no pheromone is present the beetle may test any tree at random in the desperate hope of landing on a susceptible tree (Byers 1995, 1996a, 1999).

If the pioneer beetle is fortunate to land on a tree of low resistance that can not produce sufficient resin to repel the beetle, then it has time to feed and excrete pheromone components with the faecal pellets. This then functions as a beacon to the population in the surrounding area that a weakened host can be exploited as a food and mate resource (Byers, 1996a). Aggregation pheromone is an evolutionarily adaptive signal since only trees too weak to vigorously repel beetles with resin will allow beetles to produce pheromone and joining beetles will likely suffer little mortality. Some species, usually termed less aggressive ones, such as the European pine shoot beetle, *Tomicus piniperda*, are attracted to volatiles produced after injury to the host tree by biotic or abiotic factors that indicate susceptibility (Byers 1995, 1996a).

Whether larger bark beetles can disperse in the manner described in the models is not known since these beetles have not been observed in flight over any appreciable distance while seeking hosts. However, in addition to the accounts about *D. brevicomis* mentioned earlier (Miller and Keen, 1960), *I. typographus* appears to have migrated as in the models. An infestation of these beetles in several hectares on the side of a valley in the Harzt Mountains, Germany, was surrounded by uninfested spruce forest for several km until the following season when the beetles probably left en masse and flew about 1.5–2 km downwind to attack an area of some 20 ha killing hundreds of trees in several scattered groups on the other side of the valley (H. Niemeyer, personal communication).

Control strategies that attempt to contain epidemic populations of bark beetle by use of trap trees or pheromone-baited traps in border zones must consider the potentially wide dispersal areas, especially in mild winds, that can result. A border area of only 500–1000 m width, as proposed for containment of the *I. typographus* outbreak in the Bayerischer Wald National Park of Germany (Schröter, 1998), may likely be inadequate. However, the dispersing population from an epidemic area, where severe competition has reduced the fat content for extended flight, may respond to host and pheromone after a short flight so that narrower border zones of treatments would be effective in stopping the spread.

Earlier studies have investigated whether it is possible to use an equation to predict the average distance of dispersal of a population of animals from a release point given (1) the step size (or average step size), (2) the number of steps, and (3) the AMT. The well-known diffusion equation for two dimensions (Pielou 1977; Okubo 1980; Rudd and Gandour 1985) predicts the density of organisms at any distance from the release point after a certain time or number of steps, but only for random walks (AMT = 180°). Insects and many other organisms do not exhibit truly random or Brownian movement but rather show correlated random walks in which the previous direction influences the direction of the next step. Patlak (1953) reports a modification of the Fokker–Planck equation that can predict densities of points at any distance and time for correlated random walks where the average angle of turn is known. However, his equation (42) is exceeding complex in my view and thus has not been used in practice. Turchin (1991) took the Patlak equation for one dimension and ‘simplified’ it in his work on patch density transitions. His equation is still complex and difficult to use, and it is not as yet applicable in two dimensions.

The equation of Kareiva and Shigesada (1983) comes close to calculating the mean distance of dispersal when move lengths, turning angles, and total moves are known. However, their formula gives the expected mean squared dispersal distance which obviously is much larger than the intuitively meaningful, mean dispersal distance. By taking the square root of the mean squared dispersal distance, this value still overestimates the actual mean dispersal distance of a population (simulated population) by up to 12.4%. Only for animals with a straight path (AMT = 0°) do the formula square root and simulation values become identical, for all other turning angle distributions and numbers of steps, the square root of the formula values give incorrect results. However, correct mean dispersal distances can be found by multiplying correction factors from the three dimensional surface equation from simulated results (Eqs. (4) and (5)) by the square root of the formula values. This means that instead of using longer running simulations of many points, the mean dispersal distance can be predicted using equations with only the mean step size, number of steps, and AMT.

The dispersal program software is available from the author for IBM-compatible personal computers by downloading (BB-DISP.ZIP) from the Internet URL (http://www.vsv.slu.se/johnb/software.htm).

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