DISPERSAL OF *TOMICUS PINIPERDA* (COLEOPTERA: SCOLYTIDAE) FROM OPERATIONAL AND SIMULATED MILL YARDS

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Abstract

The Canadian Entomologist **132**: 853 – 866 (2000)

The pine shoot beetle, *Tomicus piniperda* (L.), is an exotic pest that is regulated by federal quarantines in the United States and Canada. Mark–release–recapture experiments were performed with infested logs coated with fluorescent powder to determine if overwintering beetles in logs would leave a mill yard if infested logs were transported to sawmills in uninfested areas. Overwintering *T. piniperda* adults were marked with powder as they emerged in spring. Dispersal studies were conducted in four simulated mill yards and five operational sawmills to determine whether *T. piniperda* would colonize only the log pile in which they overwintered, fly to nearby log piles, or disperse beyond the mill yard. Each simulated mill yard was composed of 36 uninfested red pine logs, *Pinus resinosa* Ait. (Pinaceae), and 12 α-pinene-baited funnel traps set up to 100 m from a central release pile of six uninfested red pine and nine infested logs of Scotch pine, *Pinus sylvestris* L. At the five operational sawmills, baited funnel traps were set up to 400 m outside of each mill yard. Overall, 482 *T. piniperda* galleries were found on the experimental logs recovered from the four simulated mill yards combined. *Tomicus piniperda* adults dispersed and attacked the most distant logs at 100 m from the release point in the simulated mill yards. Likewise, adults were captured in baited funnel traps at distances up to 230 m in simulated mill yards and 250 m around operational sawmills. Although numbers of recaptured *T. piniperda* were generally low, in all cases some adults dispersed outside the mill yards despite the presence of abundant suitable breeding material. Therefore, logs containing overwintering adults pose a risk of spreading *T. piniperda* if not processed prior to initiation of spring flight.

Poland TM, Haack RA, Petrice TR, Sadof CS, Onstad DW. 2000. Dispersion de *Tomicus piniperda* (Coleoptera : Scolytidae) depuis des cours à bois simulées et réelles. *The Canadian Entomologist* **132** : 853–866.

Résumé

Le scolyte *Tomicus piniperda* (L.) est un parasite exotique dont les dommages sont limités grâce à des programmes fédéraux de quarantaine aux États-Unis et au Canada. Des expériences de marquage–recapture au moyen de troncs infestés recouverts d'une poudre fluorescente ont été mises au point pour déterminer si les scolytes qui passent normalement l'hiver dans les troncs quitteraient la cour à bois si les troncs infestés étaient transportés à des moulins à scie dans des zones non

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infestées. Des *T. piniperda* ont été marqués de poudre fluorescente au moment de leur émergence au printemps. Des études de dispersion ont été entreprises dans quatre cours à bois simulées et dans cinq moulins à scie actifs pour déterminer si les scolytes coloniseraient seulement la pile de troncs où ils ont passé l'hiver, envahiraient des piles avoisinantes ou quitteraient la cour à bois. Chaque cour à bois simulée comptait 36 troncs sains de pin rouge, *Pinus resinosa* Ait. (Pinaceae), et 12 pièges à entonnoir garnis d'α-pinène disposés à 100 m d'une pile centrale de 6 troncs sains de pins rouges et de 9 troncs infestés de pins sylvestres, *Pinus sylvestris* L. Près des cinq moulins à scie actifs, les pièges à entonnoirs garnis ont été installés jusqu'à 400 m au-delà des limites des cours à bois. Au total, 482 galeries de *T. piniperda* ont été dénombrés dans les troncs expérimentaux récupérés dans les quatre cours à bois simulées combinées. Les scolytes adultes ont quitté leurs troncs d'origine et ont attaqué d'autres troncs situés à 100 m de leur point de libération dans les cours à bois simulées. De même, des adultes ont été capturés dans les pièges à entonnoirs garnis jusqu'à 230 m de distance dans les cours à bois et jusqu'à 250 m des moulins à scie actifs. Bien que le nombre de scolytes recapturés ait été plutôt faible, dans tous les cas, des adultes se sont dispersés au-delà des cours à bois, en dépit de l'abondance de sites de reproduction adéquats à l'intérieur de ces cours. Il faut conclure que les troncs contenant des adultes pendant l'hiver constituent un risque d'infestation de scolytes s'ils ne sont pas traités avant le début de l'envol de printemps.

[Traduit par la Rédaction]

Introduction

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), is a pest of pine, *Pinus* spp. (Pinaceae), in Europe, Asia, and parts of northern Africa (Schroeder and Eidmann 1987; Långström and Hellqvist 1991; Ye 1991; Hui and Lieutier 1997). *Tomicus piniperda* has severely damaged more than 0.5 million ha of Yunnan pine, *Pinus yunnananensis* (Franch.), in southwestern China over the past 15 years (Hui and Lieutier 1997; Ye 1997). In Europe and Asia, high populations of *T. piniperda* have been reported after periods of severe drought or when brood material such as pine logging slash has been abundant (Ye 1991; Eidmann 1992; Långström and Hellqvist 1993). Growth losses of 20–45% and reduced vigor of attacked Scotch pine trees, *Pinus sylvestris* L., have been reported after severe shoot-feeding in Europe (Långström 1980).

Established populations of *T. piniperda* in North America were first detected in Ohio in 1992 (Haack *et al.* 1997). As of January 2000, the beetle was established in 271 counties in 11 states in the north-central and northeastern region of the United States, 25 counties in Ontario and eight counties in Quebec, Canada. Severe damage, including tree mortality, has been found only in some unmanaged Scotch pine stands in New York (Czokajlo *et al.* 1997) and southwestern Ontario (Czerwinski 1998).

Tomicus piniperda can successfully shoot-feed and breed in several species of North American pines (Långström and Hellqvist 1985; Sadof *et al.* 1994; Långström *et al.* 1995; Lawrence and Haack 1995; Haack and Lawrence 1997). Therefore, *T. piniperda* may represent a significant threat to pines as it spreads throughout North America.

Tomicus piniperda is univoltine throughout its range. In spring, overwintering adult beetles emerge from under the bark at the base of trees in which they have shoot-fed and fly in search of suitable brood material such as recently cut or killed pine trees, stumps, slash, or severely stressed or weakened pines. Adult beetles use host volatiles to locate suitable breeding sites (Byers *et al.* 1985; Schroeder 1988; Byers 1991; Tunset *et al.* 1993). Recent studies demonstrate that aggregation pheromones may also be involved in locating breeding sites (Czokajlo 1998). Parent adults excavate galleries in the inner bark of brood material, lay up to 65 eggs per gallery, and then reemerge and move to new breeding sites to form a subsequent sister brood (Salonen 1973). Adult progeny emerge in early summer and fly to the crowns of live pine trees where they feed in the shoots throughout the summer to complete sexual maturation. During autumn, in the colder parts of the range of *T. piniperda*, adults generally move down the trunk to overwinter (Bakke 1968; Långström 1980).

Soon after the initial discovery of *T. piniperda* in North America, a federal quarantine was established for infested counties in the United States (US Department of Agriculture Animal and Plant Health Inspection Service 1992) which restricts the movement of articles that may be infested by *T. piniperda*, particularly pine Christmas trees, nursery stock, logs, bark chips, wreaths, and garlands. Currently, free movement of pine logs (with no attached foliage) is allowed if the logs come from trees felled and moved during July through October when *T. piniperda* adults are shoot-feeding. The quarantine has affected pine sawmills in unregulated areas that rely on pine logs from counties infested with *T. piniperda* for a large portion of their wood supply. Therefore, modifications of the federal quarantine have been proposed that would allow movement of logs from regulated to unregulated areas during the months of November to June. The proposal to relax regulations was made under the assumption that if overwintering *T. piniperda* were inadvertently moved to mill yards in pine logs, all beetles would likely stay and reproduce in logs within the mill yard when temperatures warmed in spring. If true, then transporting infested pine logs to mills in areas free of *T. piniperda* would pose little risk of spreading *T. piniperda* as long as all pine logs were processed before progeny adults completed development and dispersed to shoot-feed.

Relatively little is known about the dispersal behavior of *T. piniperda*. Studies on the dispersal and distribution of *T. piniperda* in Europe and Asia have focused primarily on the timing of the spring dispersal flight (Bakke 1968; Långström 1980; Saarenmaa 1989), on the effective attraction radius of traps for parent adults (Byers *et al.* 1989; Schlyter 1992), or on movement of progeny adults during the shoot-feeding period (Sauvard *et al.* 1987; Ye and Li 1994). No previous dispersal studies have been conducted in mill yard situations where abundant sources of brood material are present. In North America, Barak *et al.* (2000) examined the spring dispersal of overwintered *T. piniperda* parent adults in a mark–recapture experiment. Beetles were recaptured up to 2035 m away from the release site. Sauvard *et al.* (1987) estimated dispersal of *T. piniperda* adults in Scotch pine stands near Orléans, France, by comparing the spatial distribution of beetles and damage at different times of the year. Their results suggest that in spring, the beetles were distributed in dense aggregations on brood material. They estimated that overwintering *T. piniperda* were attracted to operational log decks within an area of several tens of hectares. Sauvard *et al.* found that during the time of shoot-feeding some progeny adults may disperse relatively long distances, averaging approximately 1 km, whereas others remain close to their reproductive sites. In China, Ye and Li (1994) found that during the period of shoot-feeding, *T. piniperda* dispersed progressively from their reproductive sites to a distance of about 30 m.

Our overall goal was to evaluate the assumption that overwintering *T. piniperda* adults will remain in a mill yard when temperatures warm sufficiently in spring to support flight. Our specific objectives were to determine if *T. piniperda* parent adults that overwinter in decked pine logs (*i*) reproduce within the same log deck where they overwintered, (*ii*) fly to other pine logs within the mill yard and then reproduce, or (*iii*) disperse beyond the mill yard in search of suitable host breeding material.

Methods

Simulated Mill Yard Study in 1998. A simulated mill yard study was conducted in spring 1998 to determine pine shoot beetle dispersal and reproductive behavior in an artificial mill yard environment. Four simulated mill yards (200 × 200 m) were separated by at least 25 m and laid out in an open agricultural field near Walkerville, Oceana County, Michigan (43.7°N, 86.1°W). Each simulated mill yard consisted of nine Scotch pine logs infested with *T. piniperda* and 42 uninfested red pine, *Pinus resinosa* Ait., logs. No pine stands were within 5 km of the study site. The uninfested red pine logs (13.1 ± 0.1 cm, mean ± SE, diameter at base) were obtained from a 50-year-old red pine plantation near Newaygo, Newaygo County, Michigan. Trees were felled, delimbed, and cut to an average length of 180 ± 0.6 cm. Infested Scotch pine logs (11.9 ± 0.2 cm, mean ± SE, diameter at base) were obtained from an abandoned Christmas tree plantation near Rolling Prairie, LaPorte County, Indiana (41.6°N, 86.7°W), which was heavily infested with *T. piniperda*. Trees displaying heavy 1997 shoot-feeding damage were delimbed and cut approximately 15 cm below the soil line in January 1998 to obtain logs with overwintering adults. The tree trunks were cut to an average (± SE) length of 185 ± 0.3 cm. To estimate the total number of beetles potentially dispersing from the experimental logs, six of the Scotch pine logs were randomly selected and dissected to determine the average number per tree. The remaining 36 experimental Scotch pine logs were held outdoors from January until early February in a shaded forest stand near Newaygo, Newaygo County, Michigan (43.4°N, 85.8°W). During the first week of February 1998, the logs were transported to the test site and the basal 60-cm portion of each log was sprayed with a solution containing 100 g fluorescent pigment/L of water (Day-Glo Color Corp., Cleveland, Ohio). Only the lower 60 cm was sprayed because nearly all overwintering *T. piniperda* adults are found within 25 cm of the soil line (Haack and Lawrence 1997). A different color of fluorescent pigment was used to spray the logs in each simulated mill yard so that the origin of each marked beetle could be determined. Dusting infested logs with fluorescent powders has been shown to be an effective method to ensure self-marking of emerging adults for several species of scolytids. McMullen *et al.* (1988) found that for the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), 99.1% of beetles emerging from treated logs were marked. Fluorescent pigments appear to have no negative effect on emergence, flight initiation, or semiochemical perception of bark beetle species that have been tested (Cook and Hain 1992). McMullen *et al.* found no difference in survival between self-marked and unmarked *D. ponderosae* in the laboratory; however, Cook and Hain (1992) found that marking decreased longevity of both the southern pine beetle, *Dendroctonus frontalis* Zimmermann, and the southern pine engraver, *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae). Because the majority of bark beetles are recaptured soon after emergence (Linton *et al.* 1987; Salom and McLean 1990; Turchin and Thoeny 1993), any effect on long-term survival should not influence field experiments on dispersal.

Each simulated mill yard was composed of a central log deck containing six uninfested red pine logs and nine infested Scotch pine logs. The central log decks were composed of a mix of both uninfested logs and logs infested with *T. piniperda* to create a situation that would be similar to log decks in an actual mill yard. Cutting infested logs to a length of approximately 2 m and including uninfested logs in the central log decks ensured that ample brood material was present for emerging *T. piniperda* adults, as would be available in an operational mill yard. The triangular log piles were constructed with five uninfested red pine logs on the bottom, followed by three rows of infested Scotch pine logs containing four, three, and two logs, respectively, and one red pine log on the top. Additional satellite log decks, each composed of three uninfested red pine logs, were set out 25, 50, and 100 m from the central log deck along north, south, east, and west transects. Therefore, each simulated mill yard consisted of 51 logs (42 red pine and nine Scotch pine). All log decks were propped approximately 3 cm above ground on softwood lumber to prevent water-logging and debarking by small mammals inhabiting the field site. In addition, one 12-unit multiple funnel trap baited with the attractant host volatile α-pinene released at 350 mg/24 h (Phero Tech, Inc., Delta, British Columbia) was set out at each of the three distances (25, 50, and 100 m) along northeast, southeast, southwest, and northwest transects from the central log deck ($n = 48$ funnel traps, 12 traps per simulated mill yard). Traps were hung from L-shaped rebar poles with the bottom of the trap located approximately 1 m above ground. A small piece of insecticidal strip impregnated with dichlorvos was placed in the collection cup of each trap to kill all captured insects. Logs and traps were set out during the first week of February 1998, before initiation of *T. piniperda* spring flight.

At 3-week intervals, captured *T. piniperda* adults were collected from the traps and all logs were inspected for frass. All traps and logs were collected on 4 and 5 May 1998, after *T. piniperda* peak flight had occurred. All *T. piniperda* adults captured in the traps were counted and examined under ultraviolet light to determine the presence and color of any fluorescent pigment. Within 10 days after final collection, all logs were measured and debarked and the number of *T. piniperda* egg galleries greater than 1 cm in length were tallied. Galleries less than 1 cm in length were not counted because some beetles could have moved between logs while waiting for final debarking. In addition, the number of dead overwintering *T. piniperda* adults on the Scotch pine logs was recorded. For each gallery, the length, position (top or bottom of log), and presence of eggs or larvae were recorded. Gallery density and total gallery length per square metre of bark surface area were calculated by dividing the number of galleries and the total gallery length for each log by the surface area of the log.

Data for gallery density, total gallery length per square metre, and average gallery length were transformed by $\log(x + 1)$ prior to analysis. Data for percentage of galleries with eggs or larvae were transformed by $\arcsin(x + 0.5)^{0.5}$ to satisfy assumptions of normality and homoscedasticity. Transformed data were analyzed by an analysis of variance (ANOVA, GLM procedure, SAS Institute Inc. 1990) to test for differences among directions and distances, treating replicate as a blocking factor. When ANOVA results were significant, differences among directions and distances were compared using the Student–Newman–Keuls multiple comparison test. The α level was set at 0.05 for all statistical tests, and means presented are always followed by standard error (SE).

We also fit the following two-dimensional function for diffusion of marked–released–captured insects described by Turchin (1998) to our data points for the four trapping distances in the simulated mill yard study:

$$C(r) = Ar^{-0.5} \exp\left(-\frac{r}{B}\right) \quad [1]$$

where C is the number of beetles captured (or in our case the number of galleries on a log pile), r is the radius or distance from the release point, and A and B are model parameters. The parameters have a biological interpretation. Parameter A is a scale parameter that is proportional to the product of the total number of marked beetles released at the origin and the trap-recapture efficiency. Parameter B measures the spatial scale of dispersal and is proportional to the rates of diffusion and disappearance. We used a radius of 1 m to represent the average distance from the release point for galleries at the central log pile, since the logs were 2 m long and galleries were distributed along the entire length of the log. We used procedure PROC REG for linear regression using natural logarithms of both sides of the function and PROC NLIN to fit the function using a nonlinear algorithm (SAS Institute Inc. 1990).

After fitting the model and solving for values of A and B, we then evaluated the probability distribution for the galleries found around the central release point. We used Mathematica (Wolfram Research 1999) and the values for B estimated by both the linear and nonlinear models to numerically solve the following function described by Turchin and Thoeny (1993) for finding the radius (r) that encircles a given proportion (P) of the galleries created after diffusion:

$$\frac{\int_0^{rp} r^{\frac{1}{2}} \exp\left(-\frac{r}{B}\right) \mathrm{d}r}{\int_0^{\infty} r^{\frac{1}{2}} \exp\left(-\frac{r}{B}\right) \mathrm{d}r} = P \qquad [2]$$

We evaluated the function for P = 0.50, 0.90, and 0.99.

Operational Sawmill Study in 1998. A field study investigating *T. piniperda* dispersal in five operational sawmills was conducted in counties infested with *T. piniperda* in the northern part of Michigan's Lower Peninsula in the spring of 1998. Thirty infested Scotch pine logs, each representing the lower trunk of an individual tree, were obtained from Indiana in January 1998 as described earlier. The logs were cut to a length of 1 m and held outdoors in a shaded woodlot in Dansville, Ingham County, Michigan (42.6°N, 84.3°W) until March. The logs were then set out at the five sawmills and the basal 60 cm of each trunk section was sprayed with fluorescent pigment. Near the center of each mill yard, six of the sprayed Scotch pine logs infested with *T. piniperda* were placed in or near a deck of pine logs. Twelve-unit multiple funnel traps baited with α-pinene were employed to capture *T. piniperda* adults within and outside each mill yard. Nine traps were placed within 20 m of the central release area in each mill yard. In addition, up to 16 more funnel traps were placed around each mill yard, with one trap each at 50, 100, 200, and 400 m from the edge of the mill yard along north, south, east, and west transects. In some cases, depending on land ownership patterns, traps were placed at intermediate distances within 50 m of the target distance (6 traps) or were omitted (13 traps). Logs and traps were set out at each sawmill during the first week of March 1998, which was before *T. piniperda* spring flight occurred. Captured *T. piniperda* parent adults were collected from the traps at 2-week intervals during April and May 1998.

All captured *T. piniperda* adults were examined under the microscope with ultraviolet light to determine the presence and color of fluorescent pigment. Logs were dissected in May 1998 following completion of the experiment to determine the number of dead overwintering *T. piniperda* adults and the number of *T. piniperda* galleries. The numbers of *T. piniperda* adults captured in each funnel trap were tallied and summarized by direction and distance. Although marked *T. piniperda* adults were recaptured at each of the five sawmills, numbers captured were low and therefore data for the five sawmills were combined.

Results

Simulated Mill Yard Study in 1998. Overall, 482 *T. piniperda* galleries were found on the 202 experimental logs recovered from the four simulated mill yards (Table 1). Of the 482 galleries, 426 galleries (88%) were found on logs in the four central decks. Within the central log decks, 199 (53%) of the 426 galleries were found on the Scotch pine logs, which had been infested with the overwintering beetles, and 227 (47%) were found on the previously uninfested red pine logs. Only 56 (12%) of the 482 *T. piniperda* galleries were established on the surrounding log decks: 26 (5.4%) of the 482 galleries were found at 25 m, 21 (4.3%) at 50 m, and 9 (1.9%) at 100 m. Considering the four cardinal directions, 29 (6.1%) of the 482 galleries were found on logs along the north

TABLE 1. Mean (± SE) number of *Tomicus piniperda* galleries per log, gallery density, total gallery length per square metre of log surface area on pine logs at various distances and directions from a central release point in four simulated mill yards in Michigan.

	No. of logs	Galleries: Total number	Galleries: Percent of total	No of galleries/m^2	Total gallery length (cm)/m^2
Central logs	60	426	88.4	6.7±0.8*a*	51.9±6*a*
Distance from central log pile					
25 m	46	26	5.4	0.5±0.1*b*	4.8±1*b*
50 m	48	21	4.3	0.4±0.1*b*	3.7±0.9*b*
100 m	48	9	1.9	0.2±0.05*b*	1.6±0.5*b*
Subtotal	142	56	11.6		
Direction from central log pile					
North	35	29	6.1	0.8±0.1*b*	6.9±1*b*
West	35	16	3.3	0.4±0.1*b*	4.1±1*b*
South	36	5	1.0	0.13±0.05*b*	1.3±0.6*b*
East	36	6	1.2	0.15±0.07*b*	1.2±0.8*b*
Subtotal	142	56	11.6		
Total	202	482	100.0		

NOTE: In each simulated mill yard, the central log piles consisted of six uninfested *Pinus resinosa* logs and nine *Pinus sylvestris* logs infested with *Tomicus piniperda*. Satellite log piles consisted of three uninfested red pine logs set out at 25, 50, and 100 m along north, south, east, and west transects from the central log pile. Logs were placed in the field in February 1998 and collected in May 1998. Data for the four simulated mill yards were pooled. Means for each distance or direction from the central log pile within a column followed by the same letter are not significantly different [Student–Newman–Keuls test on density and length data transformed by log(x + 1), $P > 0.05$].

transect, 16 (3.3%) along the west transect, 5 (1%) along the south transect, and 6 (1.2%) along the east transect.

Gallery density ($F_{3,194}$ = 104.6, $P < 0.0001$) and total gallery length per square metre ($F_{3,194}$ = 74.8, $P < 0.0001$) were higher on logs in the central log pile than on logs set out at 25, 50, or 100 m (Table 1). There was no difference in average gallery length (8.3 ± 0.2 cm, overall mean ± SE) ($F_{3,91}$ = 1.3, P =.27) or percentage of galleries containing eggs (95 ± 2%) ($F_{3,91}$ = 2.4, P = 0.07) and larvae (82 ± 3%) ($F_{3,91}$ = 0.4, P = 0.72) among log piles at the various distances.

Similarly, gallery density ($F_{4,193}$ = 83.9, $P < 0.0001$) and total gallery length per square metre ($F_{4,193}$ = 67.7, $P < 0.0001$) were higher on logs in the central log pile than on logs set out along north, south, east, or west transects (Table 1). There was no difference in average gallery length ($F_{4,90}$ = 2.5, P = 0.06) or percentage of galleries containing eggs ($F_{4,90}$ = 1.3, P = 0.27) or larvae ($F_{4,90}$ = 1.6, P = 0.18) between log piles in the central pile or along transects in any direction.

The six extra infested Scotch pine logs from the Indiana plantation contained an average (± SE) of 115 ± 40 overwintering *T. piniperda* adults when dissected in March 1998. Overwintering beetles were found in the outer bark from 10.5 cm below the duff line to 85 cm above the duff line on these six trees. Overall, 96% of the beetles (110 ± 36 beetles, for reference in later analyses) were found overwintering within the basal 60 cm of the logs, and 91% (105 ± 34 beetles) were within the basal 30 cm. Based on the average of 115 ± 40 beetles per log, the potential number of beetles present in all 36 infested Scotch pine logs set out at the four simulated mill yards was estimated to be 4140 ± 1440. A total of 1517 dead overwintering *T. piniperda* adults were found during debarking of the experimental logs following completion of the experiment. Therefore, adjusting for this mortality, we estimated that 2623 ± 1440 *T. piniperda* adults could

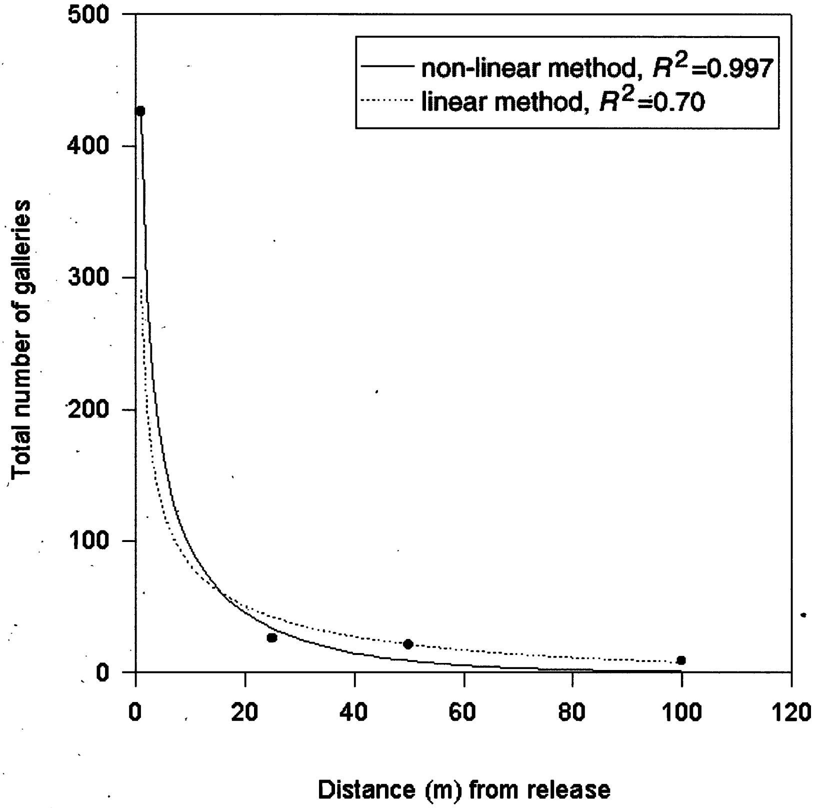

FIGURE 1. Total number of *Tomicus piniperda* galleries on log piles at 0, 25, 50, and 100 m from a central release point for four simulated mill yards (data pooled). The curves represent the fitted model $C(r) = Ar^{-0.5}\exp(-r/B)$ (Turchin and Thoeny 1993), with parameters *A* and *B* estimated by nonlinear regression (solid line) or linear regression after log transformation (broken line).

have potentially emerged from the 36 logs. The 482 galleries found on the red pine and Scotch pine logs (assuming two beetles per gallery, no sister broods, and no wild beetles) represent 962 beetles or a recapture rate of 37 ± 13%.

Linear regression (R^2 = 0.70) produced values of A = 294 and B = 76, whereas nonlinear regression (R^2 = 0.997) produced values of A = 442 and B = 26 (Fig. 1). Clearly, the change in gallery distribution is more gradual when the slope ($1/B$) is estimated with B = 76 than with B = 26. In neither case did the statistics indicate that the slopes ($1/B$) were significantly different from 0. Nevertheless, we believe that the two slope values represent the range of ecologically realistic dynamics possible in this particular beetle–environment system.

Using eq. 2 to evaluate the probability distribution for galleries found around the central release site with B = 26 as estimated from the nonlinear regression, the radii encircling 50, 90, and 99% of the galleries measured from a central release point in a mill yard would be 31, 81, and 147 m, respectively. With B = 76 as estimated from the linear regression, the same percentages are encircled at radii of 90, 238, and 431 m, respectively.

Only four *T. piniperda* adults were captured in the 48 funnel traps in the four simulated mill yards. Based on the color of the fluorescent pigment present on the captured beetles, we determined that one beetle was collected at 25 m along a southwest transect, one beetle at 25 m along a southeast transect, one beetle at 50 m along a northeast

TABLE 2. Number of *Tomicus piniperda* adults captured in α-pinene-baited funnel traps set out at 50, 100, 200, and 400 m along north, south, east, and west transects from the perimeter of five sawmills located in counties infested with *Tomicus piniperda* in the northern Lower Peninsula of Michigan.

Direction from release site	Distance from release site (m)	No. of traps deployed	No. of marked *T. piniperda* captured*	No. of marked *T. piniperda*/ trap	No. of unmarked *T. piniperda* captured	No. of unmarked *T. piniperda*/ trap
Center	0	45	8	0.18	3	0.07
North	50	5	0	0	1	0.20
	100	5	0	0	0	0
	150[†]	1	1	1	0	0
	200	4	0	0	5	1.25
	250	2	3	0.66	0	0
	400	3	0	0	1	0.33
East	50	4	0	0	1	0.25
	100	3	1	0.33	1	0.33
	150	1	0	0	0	0
	200	2	0	0	0	0
	400	2	0	0	0	0
South	50	4	1	0.25	10	2.50
	100	5	0	0	7	1.40
	150	2	3	1.5	0	0
	200	4	0	0	9	2.25
	400	2	0	0	3	1.50
West	50	5	1	0.20	3	0.60
	100	5	0	0	5	1.00
	200	5	1	0.20	5	1.00
	400	3	0	0	0	0

* Self-marked *Tomicus piniperda* adults emerged from six infested Scotch pine logs coated with fluorescent pigment. Data from the five sawmills were combined.

† Funnel traps were at times placed at intermediate positions due to land ownership patterns.

transect, and one beetle at 230 m along a north transect. These four beetles represent 0.2% of the estimated 1661 (2623 – 962 = 1661) beetles that could have potentially dispersed from the logs.

Operational Sawmill Study in 1998. Overall, 19 marked *T. piniperda* adults were captured at the five Michigan sawmills (Table 2). At least two beetles were captured at each of the sawmills. Of the 19 recovered beetles, eight were collected in traps surrounding the pine log decks adjacent to where the infested Scotch pine logs had been placed. Two beetles were collected at 50 m, one at 100 m, four at 150 m, one at 200 m, and three at 250 m from the property boundaries of the sawmills.

At the end of the experiment, 490 *T. piniperda* galleries were found on the 30 infested Scotch pine logs set out at the five sawmills. In addition, 303 dead overwintering *T. piniperda* adults were found in the logs. Based on the 110 ± 36 beetles found on average in the basal 60 cm of the six extra logs, 3300 ± 1080 *T. piniperda* adults were potentially overwintering in the 30 infested logs, of which an estimated 2997 could have survived (3300 – 303 = 2997). The 490 *T. piniperda* galleries represent 980 beetles, or 33% of 2997. Using the same assumptions as those given earlier, the 19 beetles captured in the traps represent a 0.8% recapture rate of the estimated 2117 emergent beetles that could have dispersed from the logs (2997 – 980 = 2117).

Discussion

Tomicus piniperda adults dispersed and attacked the most distant logs at 100 m from a release point in simulated mill yards (Table 1) and were captured in α-pinene-baited funnel traps at distances up to 230 m in simulated mill yards and 250 m around operational sawmills (Table 2). Although the numbers of *T. piniperda* adults recaptured in funnel traps at the operational mill yards were very low (<1%), in all cases some beetles dispersed and were captured in traps outside of the mill yards and thus are clearly capable of long-distance flight, even when in the presence of large quantities of suitable host material. Therefore, the hypothesis that *T. piniperda* parent adults will always remain in a mill yard to breed and thereby not disperse to surrounding forest stands must be rejected. Even a small percentage of dispersing beetles could pose a risk of establishment.

Both the linear and nonlinear modeling approaches support the conclusion that a certain proportion of the beetle population will disperse beyond 100 m. This is particularly the case using the linear regression model with a slope parameter of $B = 76$. Nevertheless, even with a smaller rate of diffusion and a slope parameter (B) between 26 and 76, we predict that at least 10% of the population will fly farther than 100 m. In fact, in the present studies at least one *T. piniperda* adult was captured at 230 and 250 m from the release points of the simulated and operational mill yards. Moreover, in a 1999 study (TM Poland *et al.*, unpublished data), where baited funnel traps were deployed at 400-m intervals out to 2000 m from a central release point, marked *T. piniperda* adults were recaptured out to 800 m. Similarly, Barak *et al.* (2000) recaptured *T. piniperda* adults up to 2035 m from a release point.

Of the estimated 37% of *T. piniperda* adults that were recovered from logs in the simulated mill yard study, the majority remained in the central log deck where they had overwintered (Table 1). Both the originally uninfested red pine logs and the Scotch pine logs infested with *T. piniperda* in the central log decks were about equally attacked by the end of the experiment (Table 1). Therefore, emergent beetles moved about readily within the central log piles in search of reproductive sites or mates.

The significantly higher density of *T. piniperda* galleries and total gallery length per square metre on the central log piles compared with the surrounding log decks (Table 1) was due simply to more *T. piniperda* attacks on the central log piles because average gallery length did not differ between logs in the central piles compared with log piles at any distance or in any direction. The fact that average gallery length and percentage of galleries with eggs or larvae did not differ between the central and surrounding log piles suggests that all attacks occurred at approximately the same time (*i.e.*, soon after the *T. piniperda* adults emerged from their overwintering sites).

Although it was estimated that less than 1% of released beetles were recaptured in funnel traps outside of the simulated and operational mill yards, the actual number of overwintering *T. piniperda* adults that likely dispersed out of the study areas was likely considerably higher, since trapping efficiency of funnel traps is probably very low. The effective attraction radius of sticky cylindrical mesh traps baited with host volatiles for *T. piniperda* was estimated to be between 0.2 and 1.1 m (Byers *et al.* 1989; Schlyter 1992). In comparison, the effective attraction radius of similar traps baited with pheromones for *Ips typographus* L. (Coleoptera: Scolytidae) was estimated to be as high as 2.7 m (Schlyter 1992). The effective attraction radius is a ratio of the relative trapping power of baited versus blank traps and is correlated with the strength of the attractant and the distance of attraction. Another measure of the area of action of an attractant source is the "range of attraction," which is defined as the maximum distance over which insects can be shown to direct their movement to a source (Schlyter 1992). Estimates of the range of attraction for *I. typographus* are between 16.7 and 67.0 m

(Schlyter 1992). Using a conceptually different measure, Turchin and Odendaal (1996) estimated the effective sampling area of pheromone-baited traps for *D. frontalis* to be 0.1 ha, or an area with a radius of approximately 18 m. Although the range of attraction has not been estimated for *T. piniperda*, it is likely considerably less than that for *I. typographus* because the effective attraction radius of the pheromone-baited traps for *I. typographus* was greater than that of the host-volatile-baited traps for *T. piniperda*. The traps and lures used to determine the effective attraction radius for *T. piniperda* in Europe (Byers *et al.* 1989; Schlyter 1992) were very different from the baited traps and log piles used in our study. Nevertheless, it is likely that the range of attraction of the host-volatile-baited funnel traps or host logs would be much less than estimated ranges of attraction for other species using pheromone-baited traps. The area sampled by the funnel traps would have been a relatively small proportion of the total study area, especially for the operational sawmill study. The minimum distance between attractant sources in our simulated mill yard study was 24 m (between any satellite log deck at 25 m from the release point and an adjacent funnel trap at 25 m from the release point). Therefore, minimal interference may have occurred between the central release piles and the nearest attractant sources at 25 m from the release point.

The estimated recapture rate of 0.2% found in the baited funnel traps in the simulated mill yard study was likely low for a number of reasons, including low trapping efficiency. Traps were set out in an open field with no shelter from strong and gusty winds. Salom and McLean (1991) found that more than three times as many beetles were recaptured in forested settings than in open settings due mostly to the calmer wind conditions under the forest canopy. Such conditions appear to facilitate oriented flight and response to olfactory stimuli. In studies with higher recapture rates, the majority of beetles recaptured were in traps that were 1.5 m away or closer to the release site (*e.g.*, Wollerman 1979; Schmitz *et al.* 1980; Zolubus and Byers 1995). Low recapture efficiency is desirable in studies of dispersal patterns so that traps situated nearest the release point do not deplete the population of marked insects, preventing them from reaching more distant traps and thus underestimating the true dispersal potential (Turchin and Thoeny 1993). With a limited number of traps in the vicinity of the release point (two traps at 50 m), Turchin and Thoeny (1993) recaptured 0.4–6.6% of marked and released *D. frontalis*. Probably the most important factor limiting the recapture rate in the funnel traps in the simulated mill yard study was the large number of experimental pine logs in the same fields. An estimated 7% of the marked released beetles attacked logs set out in the simulated mill yards. Thus the log piles had a higher trapping efficiency than the funnel traps. Trap logs and other suitable brood material appear to be more attractive to *T. piniperda* than traps baited with synthetic lures (Haack and Lawrence 1997). The overall trapping efficiency of funnel traps and log piles was similar to those from other studies of dispersal behavior.

There was considerable mortality of the *T. piniperda* adults overwintering in the infested Scotch pine logs used in the simulated mill yard and operational sawmill studies in 1998. In both studies, logs were set out at the field sites during cold winter conditions. Minimum daily temperatures ranged from –14°C to –8°C in Hesperia, Michigan (within 10 km of the simulated mill yard site) during the week of 7 February 1998 when logs were placed at the simulated mill yard field site (NOAA 1998*a*). Similarly, minimum daily temperatures ranged from –23°C to –8°C in Baldwin, Grayling, Mio, and Alpena, Michigan (within 10 km of each of the Lower Peninsula operational sawmills) during the week of 10 March 1998 when logs were placed at the operational sawmills (NOAA 1998*b*). Because the logs were sprayed with a water solution containing the fluorescent pigment and then positioned horizontally when placed in the field, liquid may have entered the *T. piniperda* overwintering sites and subsequently frozen. In addition, the logs were propped up above ground level and therefore were not insulated by the duff layer and snow, as would occur commonly under natural overwintering conditions at the base of a standing tree. Therefore, exposure to cold temperatures and ice may have resulted in the higher adult mortality rates. Such conditions could have also negatively influenced the vigor of the surviving beetles and thereby reduced their flight capacity to some degree. Therefore, our results may underestimate the actual dispersal capacity of more vigorous beetles.

Conclusions

The results of our studies demonstrate that many overwintering *T. piniperda* adults colonized the pine logs and log decks where they had overwintered; however, some *T. piniperda* adults dispersed to other log decks in simulated mill yards. A very small percentage (less than 1%) were recaptured in traps outside of the simulated and operational mill yards. Given that marked *T. piniperda* adults were captured outside of the mill yards, it is apparent that some *T. piniperda* adults will leave a mill yard regardless of how much host material is present. Such results suggest that transporting logs infested with *T. piniperda* from infested counties to mills in uninfested counties poses a risk of spreading *T. piniperda* if the logs are not processed by the time the overwintering adults initiate spring flight.

Acknowledgments

We thank A Barak, B Birr, C Cheatham, R Felpausch, S Hanson, G Heaton, A Lang, J McCallion, D McGrevy, and R Snyder for assistance with field experiments; J Kelly for assistance in locating field sites; JJ Weinkam, T Ellsworth, and G Gertner for assistance with modeling and statistical analyses; and A Barak, D McCullough, L Safranyik, and two anonymous reviewers for helpful suggestions on an earlier version of the manuscript. We also thank W Dudeck for use of his Christmas tree plantation, and Biewers Sawmill, GYMs Sawmill, Hoeberling Wood Products, Northwood Lumber, and Weyerhauser for permission to conduct experiments at their sawmills.

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(Date received: 27 April 2000; date accepted: 23 June 2000)