# *Tomicus piniperda* (Coleoptera: Scolytidae) Initial Flight and Shoot Departure Along a North-South Gradient

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J. Econ. Entomol. 95(6): 1195–1204 (2002)

**ABSTRACT** The exotic pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), established in the north central and northeastern United States (U.S.) and adjacent regions in Canada, is regulated by a federal quarantine that restricts movement of pine material during specific times of the year based on the beetle's life history. Although climatic variation occurs across *T. piniperda*'s range, a single set of dates is used for timing the movement of pine logs. We monitored *T. piniperda* spring flight, fall shoot departure, and air and internal tree temperatures at three sites along a 300-km north-south gradient in Michigan and Indiana. We also estimated dates for initial spring flight (12°C threshold) and fall shoot departure (0°C threshold) across an 850-km gradient using historical temperature records (1901 to 1999). Average daily temperatures in fall 1997 (8 October to 12 December) and spring 1998 (20 February to 21 April) were 1.8 to 2.4°C colder, respectively, at the northern field site than at the southern field site. Fall shoot departure began at approximately the same time (day 289 to 290) at all three field sites, but complete shoot departure was extended by 3 wk at the southern site (day 336) compared with the northern site (day 317). *T. piniperda* adults were first captured in funnel traps on calendar day 86 at the northern site and on day 59 at the central and southern field sites. Peak flight occurred at approximately the same time (day 86) at all three sites. Within-shoot temperatures were very similar to air temperatures in the fall and aboveground inside-bark temperatures were similar to air temperatures in the spring. Average predicted dates based on historical temperature records varied by 31 d for initial shoot departure and 84 d for initial spring flight between northern Michigan and southern Indiana. Because considerable variation can occur in *T. piniperda* behavior across a broad geographic range, dates specified in the U.S. Federal quarantine should be adjusted according to local temperatures.

**KEY WORDS** *Tomicus piniperda*, Scolytidae, shoot departure, flight initiation, north-south gradient

THE PINE SHOOT BEETLE, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), was first detected in North America in Ohio in 1992 (Haack et al. 1997, Haack and Poland 2001). As of May 2002, *T. piniperda* was established in 12 states in the north central and northeastern United States (U.S.) (NAPIS 2002) and in the adjacent Canadian provinces of Ontario and Quebec (CFIA 2002) (Fig. 1). *Tomicus piniperda* is an important pest of pine, *Pinus* spp., in Europe, Asia, and northern Africa (Schroeder and Eidmann 1987, Långström and Hellqvist 1991, Ye 1991, Hui and Lieutier 1997).

Overwintering *T. piniperda* adults emerge in early spring, typically from late February to early April in the Great Lakes region, and attack freshly cut or fallen pine trees or stumps (Haack and Lawrence 1997). In Europe, initial spring flight begins when daily maximum temperatures reach 10 to 12°C (Bakke 1968). In the Great Lakes region, initial spring flight typically occurs when temperatures reach or exceed 12°C (Haack and Lawrence 1995, 1997). Adult females bore into the bark of suitable host material and are joined by one male each. After mating, females construct egg galleries in the phloem (inner bark) and outer sapwood. Larvae feed primarily in the phloem, forming individual galleries that radiate out from the maternal egg gallery. Larvae construct pupal chambers at the ends of their feeding galleries. After pupation, the new brood adults emerge through exit holes by chewing through the outer bark. Brood adults generally begin to emerge in June in the Great Lakes region (Haack and Lawrence 1997). Newly emerged adults fly to healthy living pine trees where they bore into the shoots and feed throughout the summer. Each adult may tunnel into 1 to 6 shoots. During the shoot-feeding period, the new adults become sexually mature. In autumn, in response to freezing temperatures, the adults leave the shoots and move down the trunk to overwinter inside the outer bark at the base of the tree (Bakke 1968, Långström 1983, Haack et al. 2001, Pet-

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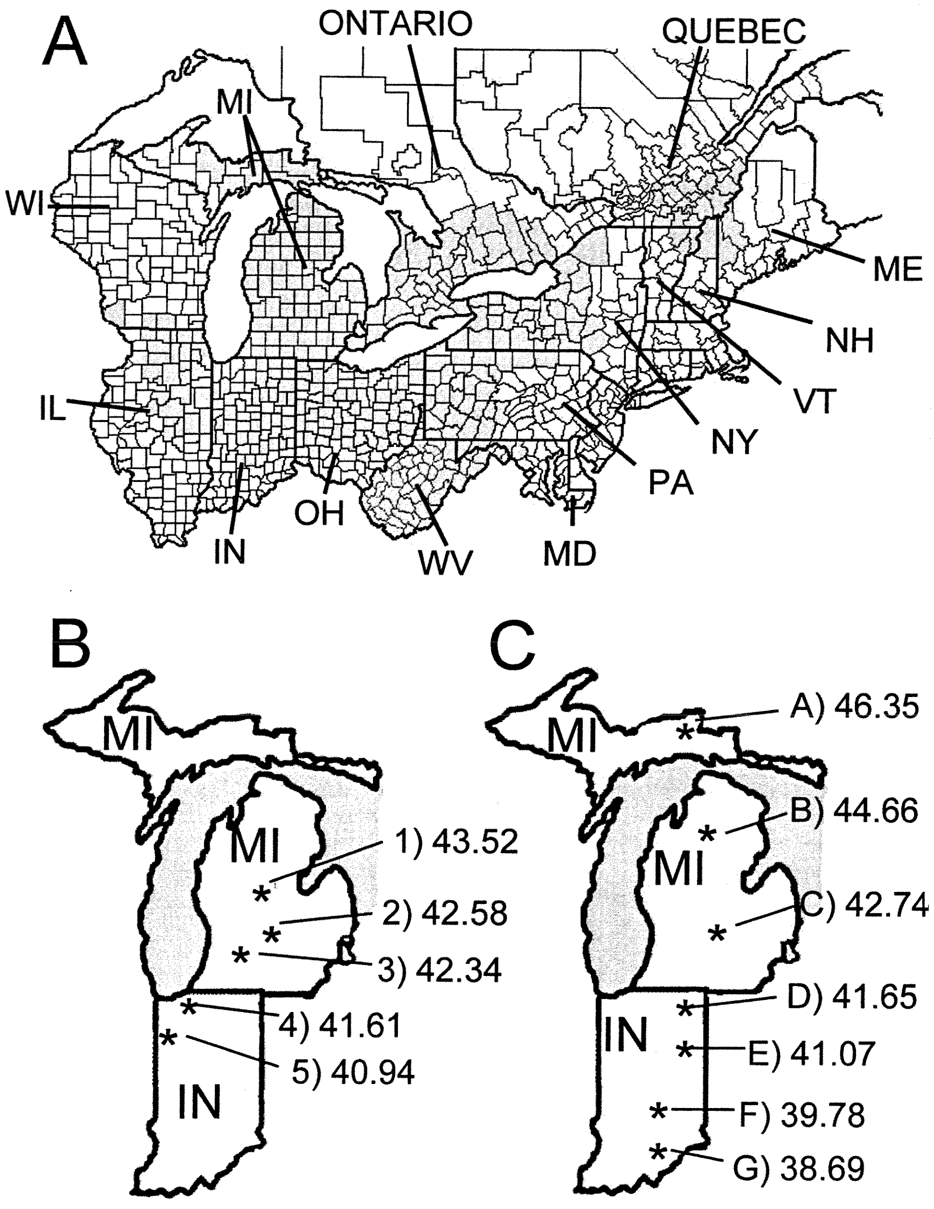


Fig. 1. A. Distribution of *Tomicus piniperda* in North America as of January 2001 (shaded counties). B. Field site locations were near (1) Shepherd, MI; (2) Mason, MI; (3) Augusta, MI; (4) LaPorte, IN; and (5) Rensselaer, IN. Field sites 1, 2, and 5 were used in fall 1997 and field sites 1, 3, and 4 were used in spring 1998. C. Weather recording stations for historical temperature data analysis were near: (A) Newberry, MI; (B) Grayling, MI; (C) East Lansing, MI; (D) Angola, IN; (E) Fort Wayne, IN; (F) Indianapolis, IN; and (G) Scottsburg, IN,

rice et al. 2002). Initiation of shoot departure in fall can be variable from year to year at a given location. Therefore, temperature rather than photoperiod appears to be the primary cue for shoot departure.

Soon after the initial discovery of *T. piniperda* in the U.S., the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) established a federal quarantine (USDA APHIS 1992). As of 28 May 2002, 366 counties in the U.S. were included in the U.S. federal quarantine (Fig. 1, NAPIS 2002). As of 10 April 2002, 60 counties in Ontario and Quebec were included in the Canadian federal quarantine (Fig 1, CFIA 2002). The U.S. federal quarantine regulates movement of pine articles that could be infested with *T. piniperda*, particularly pine Christmas trees, nursery stock, logs, bark chips, and raw materials for wreaths and garlands. Currently, the movement of pine logs from regulated areas to unregulated areas is restricted from November through June unless the logs are debarked or fumigated before being transported to unregulated areas. During late fall and winter, *T. piniperda* could be overwintering at the base of pine trees, while during spring, *T. piniperda* could be reproducing in the cut pine logs. Free movement of pine logs (with no attached foliage) is allowed from regulated to unregulated areas if the logs come from trees felled during July through October when *T. piniperda* adults are shoot feeding (Haack and Poland 2001).

A single set of dates has been used by USDA APHIS to regulate timing of log movement in the *T. piniperda* federal quarantine (Haack and Poland 2001). However, climatic variation occurs within the infested region, and considerably more variation will occur in the future as *T. piniperda* spreads to other parts of the U.S.

Our overall objective was to investigate the life history of the pine shoot beetle in relation to geographic location and local temperature conditions. Our specific objectives were to (1) determine when spring flight and fall shoot departure would begin at three geographic locations within *T. piniperda*'s current range; (2) monitor air and internal tree temperatures to determine temperature thresholds related to observed beetle activities; (3) use historical temperature records and temperature threshold criteria to estimate when initial spring flight and fall shoot departure would occur across a broad geographic range; and (4) develop recommendations based on local temperatures and historical records for adjusting the dates for *T. piniperda* quarantine regulations in different geographic regions.

## Materials and Methods

**Fall Temperature and *T. piniperda* Shoot Departure.** We determined the timing of *T. piniperda* shoot departure in relation to local temperature conditions at three field sites along a 300-km north-south gradient in Indiana and Michigan in 1997. Because populations of *T. piniperda* were low in northern Michigan and southern Indiana at the time of this study, we selected field sites in the central portion of the infested area. The most northerly field site was located near Shepherd, Isabella County MI; the central site was located near Mason, Ingham County, MI,; and the most southerly site was near Rensselaer, Jasper County, IN, (Fig. 1). All three field sites were active Christmas tree plantations but included fields of trees that were no longer being managed for sale. At each site, air temperature was measured on the north and south sides of an open-grown 4-m-tall Scotch pine, *Pinus sylvestris* L., tree, using two temperature probes enclosed in radiation shields (Campbell Scientific Inc., Logan, UT) and mounted ≈1.3 m above the ground in an open area within two m of the sample tree. In addition, upper- and lower-canopy inside-shoot temperatures were measured on the north and south sides of each sample tree. Small holes (1-mm diameter, 1-cm long) were drilled at an angle into the central pith of the current-year growth of each test shoot. A hypodermic thermocouple probe (1-mm diameter, Omega Scientific, Stamford, CT) was inserted into each hole such that the recording tip of the probe was in contact with the central pith of the shoot. The temperature probes were secured to the shoots with plastic-coated wire. Temperatures were sampled once per minute and the hourly averages, and daily maximum, minimum, and average temperatures were recorded for each probe from 8 October until 2 December 1997.

Timing of fall shoot departure was determined by collecting 50 current-year *T. piniperda*-attacked shoots at eight different sampling times between 27 August and 2 December 1997 at each site. Only shoots that had mostly green foliage were collected to ensure that they had been recently attacked and thus could potentially contain *T. piniperda* adults (Haack et al. 2001). All shoots were cut below the innermost (most basal) entrance hole if multiple tunnels occurred. The shoots were sealed individually in plastic bags, refrigerated at ≈4°C, and then dissected within 1 to 3 d. During dissection, the presence of live and dead adults was recorded. In addition, the number of feeding tunnels, the length of each tunnel, and the distance of each tunnel from the shoot tip was recorded.

**Spring Temperature and *T. piniperda* Initial Flight.** Temperature conditions and initiation of spring flight were monitored in three heavily infested Scotch pine plantations along a 215-km north-south gradient in Michigan and Indiana in 1998. The most northerly field site at Shepherd, MI, was the same site as was used in the 1997 fall shoot departure study. However, we selected alternative central and southern field sites where local field personnel could monitor insect traps daily. The central field site was located at Michigan State University's Kellogg Experimental Forest near Augusta, Kalamazoo County, MI, and the southern site was located near LaPorte, LaPorte County, IN, (Fig. 1B). The southern site was a Christmas tree plantation with areas of abandoned Scotch pine. The Kellogg Experimental Forest site consisted of a stand of 6-m-tall Scotch pine trees.

At each site, two 12-unit multiple funnel traps (PheroTech, Inc., Delta, BC, Canada) were set up and checked daily from 20 February until the first *T. piniperda* adults were captured and then were checked at ≈2 wk intervals. Each trap was baited with two low-density polyethylene bottles releasing α-pinene [96.1% purity, 76% (-) enantiomer] at a total combined release rate of 300 mg/d (Phero Tech, Inc.). Air temperature was measured in an open area on the north and south sides of a single 4-m-tall Scotch pine tree at each site as described above. Inside-bark temperatures along the trunk were measured 15 cm aboveground and 10 cm belowground on the north and south sides of each test tree. Holes (1-mm diameter and 1-cm long) were drilled into the bark at an upward angle along the phloem-sapwood interface. A hypodermic thermocouple probe (Omega Scientific, Stanford, CT) was inserted into each hole so that the tip of the probe, where temperature is measured, was in contact with the phloem-sapwood interface. The probes were secured to the trunk with plastic-coated wire. Hourly average temperatures, and daily maximum, minimum, and average temperatures for all six probes at each site were recorded from 20 February until 21 April 1998.

**Predicted *T. piniperda* Behavior Based on Historical Temperature Records.** Historical temperature and weather records for 1901 to 1999 were obtained for seven reporting stations located along an 850-km north-south gradient in Michigan and Indiana (Fig. 1C; NCDC 1901–1999). For each year and station, we estimated the initial day of *T. piniperda* spring flight by selecting the first day with a maximum temperature of 12°C or greater and with no recorded rainfall. The calendar day for peak *T. piniperda* emergence flight was estimated as the second of two consecutive days with no recorded rainfall and maximum temperatures of at least 12°C. Similarly, timing of initial shoot departure was estimated as the second day after 1 August when the minimum daily temperature fell to 0°C or lower. These temperature criteria were selected as conservative thresholds for *T. piniperda* behavior based on the field results from this study and data from the literature (Salonen 1973, Långström 1983, Saarenmaa 1989). To analyze differences in timing of *T. piniperda* behavior between the reporting stations, the calendar days estimated for each year were then averaged to determine the mean estimated calendar day for initial spring flight, peak spring flight, and initial fall shoot departure by *T. piniperda* at each of the seven stations. The earliest and latest (minimum and maximum) estimated calendar day over the 99 yr period for initial spring flight, peak spring flight, and initial fall shoot departure by *T. piniperda* were also calculated for each of the seven reporting stations to provide estimates of extreme conditions.

**Data Analysis.** To test the hypothesis that temperatures differed along the north-south gradient, temperatures were compared between the three field sites for both the fall and spring field studies. Average daily temperatures were compared among the three field locations in each study using two-way analysis of variance (ANOVA) with main effects for location and week. Daily temperatures were blocked by week to control for variation in temperatures at each site over time. Differences in average daily temperatures between the three sites were further compared using the Ryan–Einot–Gabriel–Welch (REGW) multiple comparison procedure (SAS Institute 1989).

For each field site, the mean number of live adults and entrance holes per shoot, the mean distance of entrance holes from the shoot tip, and the mean tunnel length were transformed by $\log(x + 1)$ and then analyzed by shoot sample collection date using one-way ANOVA followed by the REGW multiple comparison test (SAS Institute 1989).

For each field site, the cumulative proportion of empty shoots (i.e., from which beetles had exited) was plotted versus calendar day to determine if there were differences in the duration of the shoot departure period between sites. For all three field sites combined, internal shoot and inside-bark temperatures on the north and south sides of the sample trees were compared with air temperatures on the north and south sides, respectively, using linear regression (SAS Institute 1989). Air temperatures were compared with internal tree temperatures to determine whether air temperatures could serve as an indicator of temperatures to which *T. piniperda* are exposed for setting the threshold temperature criteria for *T. piniperda* behavior.

The mean estimated calendar days on which *T. piniperda* initial spring flight, peak spring flight, and initial fall shoot departure would occur based on historical weather records were analyzed by station using a one-way ANOVA followed by the REGW multiple comparison test (SAS Institute 1989). An $\alpha$ level of 0.05 was used in all analyses.

**Table 1. Mean (± SEM) average daily air temperature at three field sites along a 300 km north-south gradient in Michigan and Indiana during fall 1997 (day 282 to 336) and spring 1998 (day 55 to 92)**

| Field site | Average daily temperature (°C)[a] |
|---|---|
| 1997 Fall study[b] | |
| North | 1.9 ± 0.5b |
| Central | 2.2 ± 0.5b |
| South | 4.3 ± 0.6a |
| 1998 Spring study[c] | |
| North | 4.2 ± 0.9b |
| Central | 5.0 ± 0.91ab |
| South | 6.0 ± 0.89a |

[a] Means within each seasonal study followed by the same letter were not significantly different, REGW multiple comparison test, $P < 0.05$.

[b] Field sites compared in fall 1997 included North: Shepherd, MI; Central: Mason, MI; and South: Rensselaer, IN. See Fig. 1.

[c] Field sites compared in spring 1998 included North: Shepherd, MI; Central: Augusta, MI; and South: LaPorte, IN. See Fig. 1.

## Results

**Fall Temperature and *T. piniperda* Shoot Departure.** The average daily temperature during the 1997 fall shoot departure period (day 282 to 336) was significantly different between the three field sites ($F = 9.47$, df = 2, $P < 0.0001$). On average, temperatures were 2.4°C colder at the northern compared with the southern field site during the study period. The average daily temperature at the central field site was intermediate but not significantly different from the northern site (Table 1).

As minimum daily air temperatures decreased in fall, the percentage of shoots containing live *T. piniperda* adults declined (Fig. 2). Minimum air temperatures first dropped below 0°C on calendar day 284 at the northern site and on day 287 at both the central and the southern sites. The second day with below freezing temperatures occurred on days 288, 289, and 290 at the northern, central, and southern field sites, respectively. The majority of *T. piniperda* adults had left the shoots by day 302 at the northern site and by day 310 at the central and southern sites. All sampled shoots were empty by day 317 at the northern site and by day 336 at the central and southern sites (Fig. 2). The southern site trailed the northern site by ≈12 to

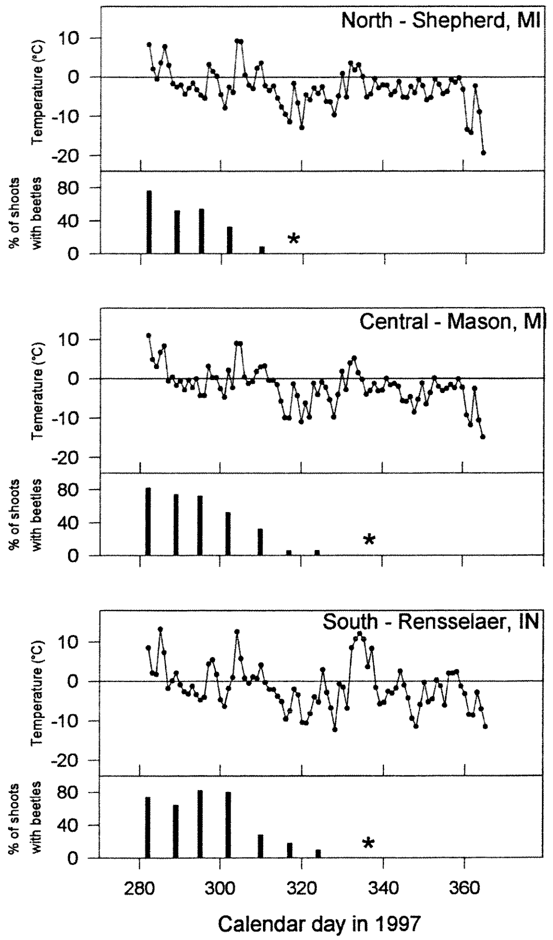


**Fig. 2.** Minimum daily air temperature and percent of current-year Scotch pine shoots recently attacked by *Tomicus piniperda* and still containing at least one live *T. piniperda* adult at three field sites along a north-south gradient in Michigan and Indiana. The first sample collection date on which no shoots contained adults is indicated by the * symbol along the x-axis.

20% in cumulative proportion of empty shoots during sampling dates 282 to 310 (Fig. 3).

Of the four measured shoot characteristics, only the mean number of live adults per shoot decreased significantly with time from 8 October to 2 December 1997 at all three sites (north, $F = 51.2$, $df = 7$, $P < 0.0001$; central, $F = 38.42$, $df = 7$, $P < 0.0001$; south $F = 44.11$, $df = 7$, $P < 0.0001$, Table 2). There were no consistent trends with time in the case of mean number of entrance holes per shoot (1.4 ± 0.02), mean distance from the entrance hole to the shoot tip (2.4 ± 0.03 cm), and mean tunnel length (7.5 ± 0.12 cm).

Figure 4 presents the results of linear regression of internal shoot and air temperatures on the north sides of the sample trees. Results for temperatures on the south sides of the trees were very similar (data not shown). Internal shoot temperatures in both the upper and lower crown were very similar to air temperatures and were significantly correlated (Fig. 4).

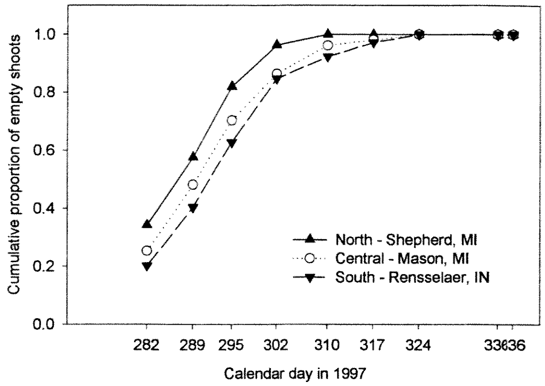


**Fig. 3.** Cumulative proportion of shoots from which beetles had emerged by calendar day for three field sites along a north south gradient in Michigan and Indiana.

**Spring Temperature and *T. piniperda* Initial Flight.** The average daily temperature during the 1998 spring flight period of *T. piniperda* (day 55 to 92) was significantly different between the three field sites ($F = 3.48$, $df = 2$, $P < 0.03$). The average daily temperature at the most northern field site was 1.8°C colder than at the most southern field site during days 55 to 92. The average daily temperature at the central field site was intermediate (Table 1).

The maximum daily temperature exceeded 13°C on days 58 and 59 at the central and southern sites but did not exceed 13°C until days 85 and 86 at the northern site. *Tomicus piniperda* adults were first captured in funnel traps on day 59 at the central and southern field sites and on day 86 at the northern site. Peak flight occurred at about the same time (approximately day 86) at all three sites (Fig. 5).

Figure 6 presents the results for linear regression of above and below ground inside-bark temperatures versus air temperatures on the north sides of the sample trees. Results for temperatures on the south sides of the trees were very similar (data not shown). Both

**Table 2. Mean (± SEM) number of live *T. piniperda* per shoot for 50 recently attacked shoots collected at approximately weekly intervals at three field sites along a 300-km north-south gradient in Michigan and Indiana**

| Calendar day | Mean number of live adults per shoot by site | | |
|---|---|---|---|
| | North Shepherd, MI | Central Mason, MI | South Rensselaer, IN |
| 282 | 1.02 ± 0.11a | 0.80 ± 0.09a | 0.64 ± 0.08b |
| 289 | 0.70 ± 0.12b | 0.88 ± 0.09a | 0.65 ± 0.07b |
| 295 | 0.60 ± 0.08bc | 0.88 ± 0.08a | 0.92 ± 0.07a |
| 302 | 0.35 ± 0.08cd | 0.54 ± 0.07b | 0.80 ± 0.05ab |
| 310 | 0.08 ± 0.04de | 0.33 ± 0.07bc | 0.27 ± 0.06c |
| 317 | 0 ± 0e | 0.06 ± 0.03cd | 0.18 ± 0.05cd |
| 324 | 0 ± 0e | 0.06 ± 0.03cd | 0.10 ± 0.04cd |
| 336 | 0 ± 0e | 0 ± 0d | 0 ± 0d |

Means within a column followed by the same letter were not significantly different, REGW multiple comparison test, $P < 0.05$.

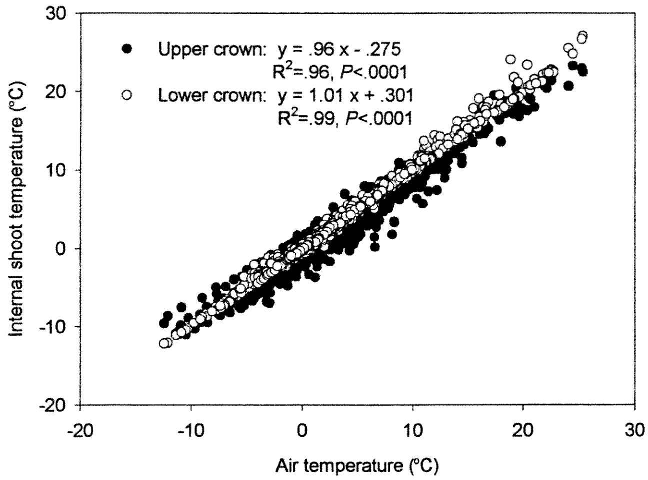


**Fig. 4.** Internal shoot temperatures measured during fall 1997 (day 282 to 336) in the north-side upper and lower crowns of Scotch pine sample trees versus air temperatures measured on the north sides of the sample trees at three field sites along a North South gradient in Michigan and Indiana.

above and below ground temperatures were significantly correlated with air temperature; however, when temperatures were below freezing, belowground inside-bark temperatures were much more stable than aboveground inside-bark or air temperatures (Fig. 6).

**Predicted *T. piniperda* Behavior Based on Historical Temperature Records.** Table 3 presents the mean, minimum and maximum predicted calendar dates for *T. piniperda* initial and peak spring flight and initial fall shoot departure based on historical temperature records from seven reporting stations along a 750 km north-south gradient in Michigan and Indiana. There were significant differences in the predicted calendar day of *T. piniperda* initial spring flight ($F = 211.9$, df = 6, $P < 0.001$), peak flight ($F = 207.8$, df = 6, $P < 0.0001$), and initial fall shoot departure ($F = 77.4$, df = 6, $P < 0.0001$) between the seven cities (Table 3).

## Discussion

**Fall Temperature and *T. piniperda* Shoot Departure.** The slower accumulation of days with freezing temperatures at the southern site compared with the northern site in fall 1997 was reflected in a prolonged period of shoot departure for adults at the southern site (Figs. 2 and 3). The majority of *T. piniperda* adults had left the shoots 1 wk later and all adults completed shoot departure 3 wk later at the southern site compared with the northern site (Fig. 2).

The second day in fall with temperatures below 0°C occurred within 2 d (day 288–290) among the three field sites (Fig. 2) suggesting that a cooling front had crossed the region. At that time there was a slight decrease in the percentage of shoots occupied by adults (Fig. 2), indicating that shoot departure had just begun. These results support the observation that *T. piniperda* adults first begin to exit shoots after only a few days with freezing temperatures (Haack and Lawrence 1997, Salonen 1973, Långström 1983, Kauffman et al. 1998, Haack et al. 2001, Petrice et al. 2002). A significant reduction in the number of beetles per shoot did not occur until days 289, 302, and 310 at the northern, central, and southern sites, respectively (Table 2). Several weeks were required to obtain complete shoot departure (Figs. 2 and 3, Table 2) indicating that individual *T. piniperda* adults display wide variation in response to freezing temperatures as they move to their overwintering sites. These results agree with those of other studies on *T. piniperda* shoot departure in southern Michigan and northern Indiana in which adults were found to initiate shoot departure in mid-October and to complete shoot departure usually by mid- to late-November (Kauffman et al. 1998, Haack et al. 2001, Petrice et al. 2002).

While some adults initiate shoot departure after the first few days with freezing temperatures, complete shoot departure is considerably delayed with some adults remaining in shoots during many days with temperatures as low as −10 to −15°C (Fig. 2). It is not known why adult *T. piniperda* vary so widely in shoot departure response to freezing temperatures. Extended shoot feeding could enhance fat reserves and this could increase overwintering survival and spring reproductive success. However, extended shoot feeding could increase the risk of being subjected to lethal freezing temperatures while in the shoots. The variability in the timing of shoot departure may reflect staggered development among sister broods of progeny adults. A sister brood is produced when a parent female reemerges from brood material and produces a subsequent gallery in fresh brood material. In general, progeny adults from the first brood would have initiated shoot feeding earlier in the summer than progeny adults from a subsequent sister brood and therefore the former may complete shoot-feeding earlier. While *T. piniperda* adults are able to reproduce when artificially introduced into pine logs with little or

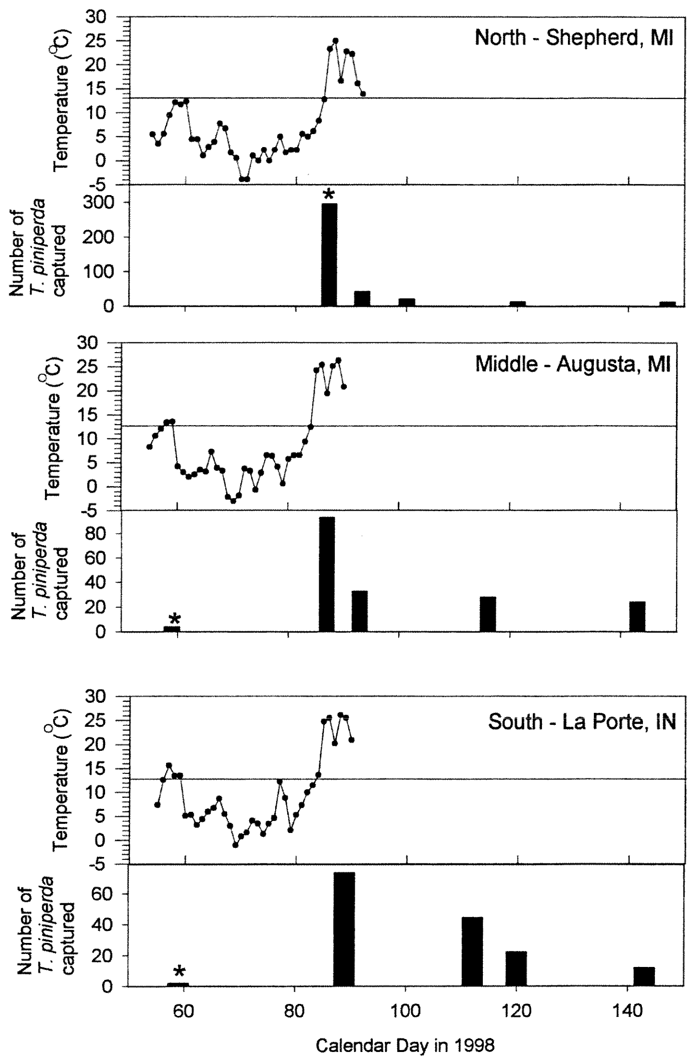


Fig. 5. Maximum daily air temperature during spring 1998 and mean number of *T. piniperda* captured in 12-unit multiple funnel traps baited with α-pinene at three field sites along a north-south gradient in Michigan and Indiana. The day of flight initiation by *Tomicus piniperda* is indicated for each site by the * symbol.

no shoot feeding (Poland and Haack 2000), they still shoot feed for the entire summer in nature. Similarly, Långström (1983) found that *T. piniperda* progeny adults were sexually mature after only a few weeks of shoot-feeding, yet they continued to shoot-feed for up to 5 mo before overwintering. In southern Europe and southern China, where winter temperatures seldom drop below freezing, *T. piniperda* adults overwinter in the shoots (Långström 1980, Ye 1991). In Europe and the U.S., some *T. piniperda* adults continue to shoot-feed in early spring before initiating egg galleries, even though they are sexually mature (Långström 1983, Haack et al. 2000).

Bakke (1968) and Saarenmaa (1985) found the supercooling point of *T. piniperda* larvae to be −12.5°C and that of adults to be −18°C. Shoot feeding by progeny adults in summer, rather than initiating subsequent generations that may not complete development to the adult stage before freezing temperatures, would ensure that the entire population overwinters as adults, which is the life stage with the greatest potential to survive low winter temperatures in the northern part of *T. piniperda*'s range.

Inside-shoot temperatures were very similar to air temperatures (Fig. 4), likely reflecting the limited insulation provided by the small diameter shoots (3 to 5 mm). Inside-shoot temperatures in the upper crown were slightly cooler on average than in the lower crown, possibly due to increased wind, transpiration, and evaporative cooling in the upper crown. Because inside-shoot temperatures were highly correlated with air temperatures, air temperatures would be suf-

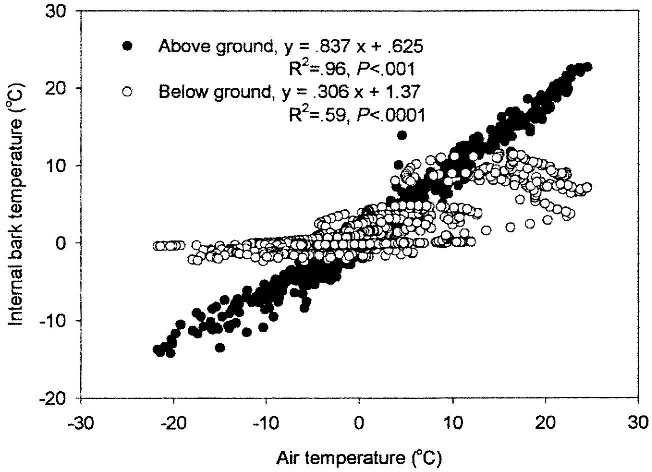


**Fig. 6.** Inside bark temperatures measured during spring 1998 (day 55 to 92) in the north-side 15 cm above and 10 cm below ground in the main trunk of sample Scotch pine trees versus air temperatures measured on the north sides of the sample trees at three field sites along a North South gradient in Michigan and Indiana.

ficient for predicting the timing of *T. piniperda* fall shoot departure.

The mean number of live adults per shoot decreased over time as adult *T. piniperda* left the shoots to overwinter (Table 2). The mean tunnel length of 2.4 cm found in this study agrees with the average of 2.3 cm found by Haack et al. (2001) and may correspond to the maximum length of tunneling before the distal end of the shoot begins to dry and the beetle must exit the tunnel and reenter in fresh living tissue, either further down on the same shoot or on a new shoot. The mean number of tunnels per shoot and the mean distance of

**Table 3. Mean (± SEM) and range (minimum–maximum) estimated calendar day based on historical weather records (1901 to 1999) for *T. piniperda* initial spring flight, peak flight, and initial fall shoot departure for seven cities located along a 850-km north-south gradient in Michigan and Indiana**

| Location | Estimated calendar day for spring flight or shoot departure | | |
|---|---|---|---|
| | Initial spring flight[a] | Peak spring flight[b] | Initial fall shoot departure[c] |
| Newberry, MI | 102 ± 1a | 110 ± 1a | 278 ± 1d |
| | 69–125 | 83–134 | 258–308 |
| Grayling, MI | 96 ± 8a | 99 ± 1b | 267 ± 2c |
| | 54–119 | 18–141 | 234–294 |
| East Lansing, MI | 59 ± 2b | 81 ± 1c | 286 ± 2b |
| | 1–99 | 11–109 | 266–312 |
| Angola, IN | 57 ± 3b | 79 ± 2c | 294 ± 1a |
| | 1–98 | 25–103 | 269–313 |
| Fort Wayne, IN | 45 ± 3b | 67 ± 2d | 294 ± 1a |
| | 1–97 | 5–99 | 272–313 |
| Indianapolis, IN | 25 ± 2c | 49 ± 2e | 299 ± 1a |
| | 1–79 | 8–88 | 280–314 |
| Scottsburg, IN | 18 ± 2c | 35 ± 2f | 297 ± 1a |
| | 1–79 | 2–85 | 271–332 |

Means within a column followed by the same letter were not significantly different, REGW test, $P < 0.05$.

[a] First day with maximum temperature ≥12°C and no rain.

[b] Two consecutive days with temperatures ≥12°C and no rain.

[c] Second day after August 1 with minimum temperature ≤0°C.

the tunnel entrance to the tip of the shoot are also similar to values reported in other studies (McCullough and Smitley 1995, Kauffman et al. 1998, Haack et al. 2001).

**Spring Temperature and *T. piniperda* Initial Flight.** Although the difference in average daily temperature during the 37-d study period was only 1.8°C between the southern and northern sites in spring 1998 (Table 1), there was a 1-mo delay in initial flight between the two sites (Fig. 5). The delay in initial flight at the northern site resulted from the prolonged period of cold that occurred across the entire region in March 1998, after initial flight had already occurred at the southern and central sites. At both the southern and central sites, the maximum daily air temperatures were just above 13°C for two consecutive days at the end of February 1998 when the adults were first captured in traps (average of two adults per trap). However, at the northern site, temperatures were 1 to 2°C cooler, just below 13°C, and no adults were captured. These results suggest that the threshold flight temperature for *T. piniperda* populations in Michigan and Indiana is ≈13°C. The flight threshold of 13°C generally agrees with flight thresholds reported in Europe of 10 to 14°C (Saarenmaa 1989), 10 to 12°C (Långström 1983), and 10 to 13°C (Salonen 1973). Långström (1983) and Saarenmaa (1989) found that the higher the temperature on the first warm day above the flight threshold, the greater the proportion of adults that flew on the first day of flight.

Adults overwintering aboveground at the base of the tree would most likely emerge earlier in spring than adults overwintering belowground because air and aboveground temperatures begin to increase while belowground temperatures remain cooler and more stable. In a study by Petrice et al. (2002) in LaPorte, IN, ≈97% of adults overwintered along the trunk within 10 cm of the duffline, with 32% below the duff, 48% within 5 cm above the duffline, and 17% between 5 and 10 cm above the duffline. The first adults to leave the shoots and arrive at the base of the tree selected overwintering sites within a few centimeters of the duffline (Petrice et al. 2002). Overwintering belowground may protect adults better from extreme cold temperatures in winter and would also insulate adults from warm temperatures in spring. Snow depth and the dates for the first and last snowfalls would influence temperature conditions and timing of adult emergence at different heights along the trunk of the tree. Therefore, a fairly wide window of spring flight initiation may exist at a given location, reflecting in part temperature differences among overwintering sites.

**Predicted *T. piniperda* Behavior Based on Historical Temperature Records.** The predicted dates for *T. piniperda* initial spring flight and fall shoot departure agreed with actual dates observed in the field studies. Temperatures fell below 0°C for the second time in Mason, MI on day 289 and day 290 in Rensselaer, IN (Fig. 2), similar to the predicted average dates for initial fall shoot departure at the nearby recording stations in East Lansing, MI (day 286) and Angola, IN (day 294, Table 3). Initial spring flight was observed at the central and southern field sites in 1998 on day 59, similar to the predicted average dates of initial spring flight for the nearby recording stations in East Lansing, MI (day 59) and Angola, IN (day 57, Table 3). These results validate the use of historical temperature data for estimating the timing of *T. piniperda* behavior. Analysis of historical weather data predicts that initiation of fall shoot departure could vary on average by 31 d from Indianapolis, IN (day 299) to Grayling, MI (day 268, Table 3) and that initial spring flight could vary by 84 d on average from Scottsberg, IN (day 18) to Newberry, MI (day 102, Table 3).

**Implications.** While fall shoot departure by *T. piniperda* in 1997 began at approximately the same time at the three field sites along a 300-km north-south gradient, the duration for complete shoot departure varied by three weeks between the northern and southern field sites (Fig. 2). The timing of initial shoot departure is important for setting the ending date for safe shipping of pine logs from infested areas because once beetles begin to leave the shoots they may be present under the bark at the base of trees. The date for complete shoot departure is important for determining when it is safe to ship Christmas trees. There could be considerably more variation in the timing of initial shoot departure across a broad geographic range. The predicted average date for initial fall shoot departure based on historical temperature records varied by about 19 d from northern Michigan to southern Indiana (Table 3). Regional maps based on historical temperature data and selected temperature thresholds could be developed for initiation of *T. piniperda* fall shoot departure. Examples of such maps for the Northeastern U.S. are presented in Haack et al. (1998) using thresholds of 0°C and −2°C based on data in the European literature. Our field results indicate that a conservative threshold of 0°C should be used for predicting initial fall shoot departure.

Similarly in spring, there can be considerable variation in timing of initial emergence flight across a broad geographic range. There was a difference of 27 d in the timing of initial flight between the three field sites located along a 300-km north-south gradient while peak flight was similar at all three field sites (Fig. 5). Estimates based on historical temperature records predict that initial flight could vary by 84 d on average along a 850-km gradient in Michigan and Indiana (Table 3). Again, regional maps based on historical temperature data can be developed to predict initial spring flight of *T. piniperda.* Haack et al. (1998) presents examples of such maps developed using thresholds based on average temperatures of 13°C and 15°C reported in European literature (Salonen 1973, Långström 1983, Saarenmaa 1989). The field results of the current study provide evidence that the dates predicted based on historical temperature data correspond with the actual observed dates for *T. piniperda* initial spring flight and fall shoot departure at different geographic locations. Further, the results of the field studies suggest that a more conservative threshold of 12°C for initial spring flight should be used.

To minimize the chance of accidental movement of material infested with *T. piniperda,* the cut off dates for shipping logs and Christmas trees should be adjusted for different geographic regions based on local temperature conditions. In atypical years, the actual dates of initial spring flight and initial fall shoot departure could differ significantly from long-term averages and there could be more or less variation among sites. Regulatory dates could be set locally each year using air temperatures from local reporting stations because they are very similar to the internal tree temperatures to which beetles are exposed. Alternatively, historical temperature records could be used; however, regulatory dates for each geographic region should be based on the extreme years rather than long-term averages (i.e., the earliest possible dates for spring flight and fall shoot departure). In both cases conservative threshold criteria should be used in setting the regulatory dates. Based on the field results of the studies reported here, we recommend using the first day with a maximum temperature at or above 12°C to predict initial spring flight and the second day with a minimum temperature at or below 0°C to predict initial fall shoot departure of *T. piniperda.*

## Acknowledgments

We thank Jeff Andressen for assistance with temperature monitoring equipment, Denise Daly for assistance with shoot dissections; Oleg Makhnin and Jan Hannig for assistance with data analyses; Ruth Ann Berry and Jim Curtis for assistance with field experiments; Warren Heilman for assistance with analysis of historical weather data; Deborah McCullough, Brian Potter and two anonymous reviewers for helpful comments on an earlier version of this manuscript; and Bert Crowley, Wayne Dudeck, Vern Matthews, and Ron Sheele, Jr. for providing use of their Christmas tree plantations.

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*Received for publication 19 December 2001; accepted 1 August 2002.*