Selection of Overwintering Sites by *Tomicus piniperda* (Coleoptera: Scolytidae) during Fall Shoot Departure[1]

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J. Entomol. Sci. 37(1): 48-59 (January 2002)

Abstract Selection of overwintering sites at the base of Scotch pine, *Pinus sylvestris* L., trees by *Tomicus piniperda* (L.) adults was monitored in northwestern IN. We monitored adult movement five times during the period of 22 October 1998 to 31 January 1999 by dissecting shoots and trunks of four trees per sample date. For all adults collected, 100% were found in shoots on 22 October, 81% on 4 November, 10% on 18 November, 2% on 3 December, and <1% on 31 January. No overwintering adults were found on the lower trunks of trees sampled on 22 October. Some adults (N = 16) were found on 4 November, 1 day after the first subfreezing air temperatures were recorded. For all adults (N = 448) collected from lower trunks during the three sample periods in November and December, the mean height along the trunk where adults overwintered was 2.6 cm above the duff line. Mean overwintering height did not differ significantly among sample dates ($P > 0.21$). When distance along the trunk was divided into 5-cm intervals relative to the duff line, most adults were found either 0 to 5 cm above the duff line (48%) or below the duff line (32%). Overall, 98% of the overwintering adults were found at or below the 10-cm height level from the duff line and 99% were at or below the 25-cm height level. A significantly lower percentage of adults was found below the duff line on 4 November as compared to 18 November and 3 December. However, percentages of adults found in each 5-cm interval above the duff line did not differ significantly among sample dates. Overwintering adults were found above 20 cm from the duff line on 18 November and 3 December, but no adults were found above 8 cm on 4 November. Results suggest that the first adults to arrive at the tree base prefer to overwinter within the first 10 cm of the duff line but do not necessarily prefer the area closest to or below the duff line.

Key Words *Tomicus piniperda,* Coleoptera, Scolytidae, exotic pest, overwintering behavior, shoot departure, Scotch pine, *Pinus sylvestris,* Indiana, North America, quarantine

Tomicus piniperda (L.) (Coleoptera: Scolytidae) was first discovered in the United States near Cleveland, OH, in July 1992. By September 1992, *T. piniperda* had been found in five additional states, suggesting that it had been in the U.S. for several years before its initial discovery (Haack 1997). As of January 2001, *T. piniperda* has been detected in 303 counties in 12 U.S. states and 43 counties in 2 Canadian provinces (Haack and Poland 2002).

Tomicus piniperda is a serious pest of pines, *Pinus* spp., in Europe and Asia where it naturally occurs (Långström and Hellqvist 1991, Ye 1991). USDA APHIS (U.S.

[1]Received 22 December 2000; accepted for publication 23 May 2001.

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Department of Agriculture, Animal and Plant Health Inspection Service) imposed a federal quarantine on the shipment of pine logs with intact bark, pine Christmas trees, and pine nursery stock from infested to uninfested areas within the U.S. in November 1992 because of the destructive nature of this insect in its native range (USDA APHIS 1992). Since its discovery in North America, *T. piniperda* has been found to successfully shoot-feed and reproduce in many species of North American pines (Lawrence and Haack 1995, Långström et al. 1995). Little *T. piniperda*-related damage has been reported so far in North America; however, there have been two cases of reported growth loss and mortality to pines, especially Scotch pine, *Pinus sylvestris* L., in New York State (Czokajlo et al. 1997) and Ontario (Scarr et al. 1999) in which *T. piniperda* was involved.

The biology of *T. piniperda* is described in detail by Bakke (1968), Långström (1983), Haack et al. (2000, 2001), Salonen (1973), and Ye (1991). Briefly, adults become active in early spring when temperatures exceed 10 to 12°C and create one or more brood galleries in recently dead or dying pines. Progeny adults emerge several weeks later, usually starting in June in the Great Lakes region, and then tunnel in shoots of live pine trees throughout the summer and early fall. In fall, after daily low temperatures drop below freezing, adults begin to exit the shoots and typically walk along the branches and trunk to the base of the pine tree where they overwinter inside the bark of the lower trunk. In Michigan and Indiana, shoot departure usually spans a period of 4 to 6 wks (Haack and Lawrence 1997a, Haack et al. 2001, Kauffman et al. 1998).

Tomicus piniperda adults are often found overwintering along the trunk near or below the duff line (Haack and Lawrence 1997a, 1997b, Haack et al. 2001, Kauffman et al. 1998). However, a few overwintering adults can be found in the trunk more than 30 cm above the duff line. It is possible that *T. piniperda* adults prefer to overwinter along the trunk region that is closest to the duff line, and that adults found overwintering higher above the duff line do so only if most of the overwintering sites near the duff have already been filled by other adults. On the other hand, a large portion of the lower trunk may offer acceptable overwintering sites and adults may freely locate themselves anywhere in that area. Knowing how adults position themselves at the base of trees is useful when setting guidelines for proper timing of fall tree harvesting and proper stump height to reduce the chances of inadvertently moving *T. piniperda* adults with cut Christmas trees and logs (McCullough and Sadof 1996, Haack and Poland 2002). Moreover, coupling this knowledge with the timing of adult fall shoot departure could even further reduce the risk of accidental movement of *T. piniperda.*

The principal objective of this study was to investigate where and when overwintering *T. piniperda* adults position themselves along the lower trunks of trees. A secondary objective was to correlate the timing of *T. piniperda* fall shoot departure with local temperature conditions.

Materials and Methods

We conducted this study at an abandoned Christmas tree plantation in LaPorte Co. in northwestern IN. On 22 October 1998, we selected 20 Scotch pine trees to be cut that were 3 to 4 m tall and had no evidence of shearing for several years. Trees selected had heavy current-year *T. piniperda* shoot-feeding damage with >40 attacked shoots per tree. We selected trees with heavy shoot feeding to insure there would be large numbers of adults migrating to overwintering sites on each tree.

We placed temperature monitoring equipment on a single Scotch pine tree that was growing near the trees selected to be cut. We drilled three small holes (<2 mm diam) in the outer bark of the tree at an upward angle. Holes were drilled on the north side of the tree at the soil-duff interface, at 15 cm above the duff line, and at 45 cm above the duff line. We inserted a hypodermic thermocouple temperature probe (Omega Engineering, Stanford, CT) into each hole such that the tip of the probe was positioned at a depth of about 1 cm, but still within the outer bark. Bark thickness at the positions where probes were inserted varied from 0.25 to 0.5 cm. We used two air temperature probes (Campbell Scientific, Logan, UT): one on the east side and one on the west side of the tree at 1.5 m above the ground. Temperature data were recorded at 30-min intervals from 22 October 1998 through 31 January 1999 with a datalogger (Campbell Scientific). We obtained daily snow depth data from the NOAA reporting station at LaPorte, IN, which is about 16 km southwest of the study site.

We randomly chose and cut four of the 20 selected trees at 2-wk intervals from 22 October to 3 December 1998. The remaining four trees were cut on 31 January 1999. Before cutting, we marked the location of the duff line and soil line on the trunk of each tree using a wax crayon. We removed soil from around the base of each tree, and cut the trunk at about 5 to 7 cm below the soil line and at 60 cm above the soil line. Our previous studies indicated that cutting trees at 60 cm above the soil line would be high enough to collect nearly all overwintering adults (Haack and Lawrence 1997a, 1997b, Haack et al. 2001). We placed all shoots and the lower trunk section of each tree into separate plastic bags and stored them in the laboratory at 4°C until processing.

In the laboratory, we counted current-year shoots ≥3 mm thick and inspected them for *T. piniperda* feeding tunnels; *T. piniperda* seldom tunnel in shoots that are <3 mm thick (Haack et al. 2001, McCullough and Smitley 1995). We recorded the number of tunnels and number of live adults in each shoot. Only tunneled shoots with one or more green needles surrounding the entrance to the innermost tunnel were counted. In early fall, needle color near the entrance of the innermost tunnel is a good indicator of beetle presence in the shoot. For example, in early fall it is common to find a *T. piniperda* adult in a tunnel if the needles surrounding the tunnel are still green, but rare if needles are yellow to brown (Haack et al. 2001, Kauffman et al. 1998).

For each tree, we estimated duff layer depth by dividing the tree into four quadrants, measuring the distance between the soil and duff line for each quadrant, and averaging the four values. We also recorded tree diameter just below the soil line. We then removed all bark from each trunk section with a knife and recorded the vertical distance of each overwintering beetle from the duff line.

We compared daily minimum inside-bark temperature data at different heights above the duff line and air temperature in a one-way analysis of variance (ANOVA) using GLM (SAS 1988). Tree diameter, duff depth, percent *T. piniperda* adults in shoots, percent of adults at tree base, percent of adults in each 5-cm trunk-interval, and mean overwintering height were tested for differences among sample dates in a one-way ANOVA using GLM. We conducted a separate one-way ANOVA using GLM for each sampling date to determine if percent of adults varied among 5-cm trunk-intervals. We also tested for differences among sampling dates for the mean height of the one beetle per tree that was found at the height farthest above the duff line in a one-way ANOVA using GLM. To normalize the data, we performed arcsin square-root transformation on all percentage data before analysis. Means that were significantly different at the $P \leq 0.05$ level were separated using the Student-Newman-Keuls multiple range test (SAS 1988).

Results and Discussion

Shoot and tree data. Overall, we counted 8,386 current-year shoots ≥3 mm thick on the 20 test trees. Of these, 1,075 shoots possessed one or more *T. piniperda* feeding tunnels. On average, there were 419 current-year shoots per tree of which 15% had one or more *T. piniperda* feeding tunnels (Table 1). The percentage of tunneled shoots for this study site is somewhat higher than those of previous *T. piniperda* studies conducted in the U.S., ranging from 0.1% to 7.4% tunneled current-year shoots per tree (Haack et al. 2001, Haack and Lawrence 1997b, Kauffman et al. 1998).

Considering only *T. piniperda* tunneled shoots that were intact, i.e., not broken along their length (N = 778 shoots), the mean (±SE) number of tunnels per shoot was 1.45 ± 0.03, and the maximum number of tunnels per shoot was 7. On 22 October 1998, before adults were found at the base of the sampled trees, 35% of the tunneled current-year shoots contained no adults, 53% contained one adult, 9% contained two adults, 1% contained three adults, and 1% contained four adults.

Trunk diameter measured at the soil line averaged 11.9 ± 0.5 cm and there was no significant difference in mean diameter among trees cut on different sample dates (F = 1.80, df = 4, 15, P > 0.18). Duff depth averaged 3.1 ± 0.2 cm and did not vary significantly among sample dates (F = 1.90, df = 4, 15, P > 0.16). These results indicate that trees cut for each sampling period were similar in respect to trunk diameter and depth of the duff layer.

Movement to overwintering sites. In 1998, most of the movement to overwintering sites by *T. piniperda* occurred from 22 October to 18 November (Fig. 1). No adults were found at the base of the four trees sampled on 22 October, whereas 19 ± 4% of the adults present on the sampled trees on 4 November 1998 were in their overwintering sites (Fig. 1). Because adult shoot departure is typically preceded by subfreezing temperatures (Långström 1983, Kauffman et al. 1998, Salonen 1973), the presence of overwintering adults on 4 November may have been in response to the freezing temperatures that occurred for the first time during the morning hours of 3 November (Fig. 1). During the afternoon of 3 November, air temperatures increased

Table 1. Mean (±SE) number of current-year shoots per tree (≥3 mm diam.), and mean number and percent of these shoots with *Tomicus piniperda* feeding tunnels for Scotch pine trees sampled from October 1998 through January 1999 in LaPorte Co., IN

	Sampling date (N = 4 trees per sampling date)					
Parameter	22 Oct 98	4 Nov 98	18 Nov 98	3 Dec 98	31 Jan 99	Overall
Shoots per tree (mean ± SE)						
Number	470 ± 110	388 ± 134	490 ± 167	484 ± 151	265 ± 57	419 ± 55
Attacked shoots per tree (mean ± SE)						
Number	66 ± 13	46 ± 11	56 ± 18	64 ± 12	49 ± 8	57 ± 5
Percent	15 ± 1	11 ± 2	12 ± 2	16 ± 4	19 ± 2	15 ± 1

to 8°C, which were warm enough for adults to walk (Salonen 1973). On 4 November, trees were cut and sampled in late morning before air temperatures exceeded 4°C, so temperatures were probably too cool for any adults to have walked to the base of the trees that morning.

The percentage of all adults in overwintering sites increased significantly from October through November, while the percentage of current-year shoots containing live adults decreased significantly (Fig. 1). The percentage of tunneled shoots containing live adults decreased from 64% on 22 October, to 7% on 18 November, and to 2% on 3 December. Only one live adult (0.4%) was found in shoots collected on 31 January 1999.

Location of overwintering adults. We recovered 448 adults from the lower trunks of the 12 trees sampled from 4 November to 3 December 1998. Overall, the mean height of overwintering adults was 2.6 ± 0.5 cm above the duff line and did not differ significantly from 4 November to 3 December ($F = 1.82$; df = 2, 9; $P > 0.21$) (Table 2). The mean height of the one beetle per tree found farthest above the duff line was significantly higher on 3 December 1998 as compared to 4 November and 18 November ($F = 8.50$; df = 2, 9; $P = 0.0084$) (Table 2). We were not able to accurately determine where all adults were overwintering for the trees collected on 31 January 1999 because some adults became active and moved from their overwintering locations while awaiting dissection in the laboratory.

Most overwintering adults were found in the 0-5-cm interval above the duff line (Table 3, last column). Moreover, almost all (99.3%) adults were found at or below the 25-cm height level measured from the duff line. Only slightly fewer (97.8%) were found at or below the 10-cm height level (Table 3). These results are consistent with two similar studies conducted in Indiana and Michigan (Haack et al. 2001, Haack and Lawrence 1997b).

The percentage of adults found below the duff line was lower on 4 November as compared with 18 November and 3 December ($F = 20.46$; df = 2, 9; $P = 0.0004$). This, along with a corresponding mean overwintering height of 3.8 cm on 4 November, indicates that the first adults to arrive at the base of a tree prefer to overwinter near the duff line, but do not necessarily select the area closest to or below the duff line. Moreover, while 69% of the overwintering adults were at or below the 5-cm height level from the duff line on 4 November, the rest were found 5 to 10 cm above the duff line, even though there were several, apparently adequate, overwintering sites closer

Fig. 1. Data presented for (A) daily minimum air temperature, (B) mean percent (+ 1 SE) of current-year shoots with some green needles and one or more *Tomicus piniperda* feeding tunnels that still contained at least one live *T. piniperda* adult, and (C) mean percent (+ 1 SE) of all *T. piniperda* adults collected per tree that were found in overwintering sites in the lower trunk of Scotch pine trees sampled in LaPorte Co., IN, by sampling date in 1998 and 1999. *NOAA daily minimum air temperatures for LaPorte, IN, which is approximately 16 km southwest of the study site, were substituted for missing on-site temperature data for 12 November through 2 December 1998. **Mean values (within panels B and C) with the same letter are not significantly different at the $P = 0.05$ level (Student-Newman-Keuls multiple range test). ‡Data not available (NA) for 31 January 1999 (see text).

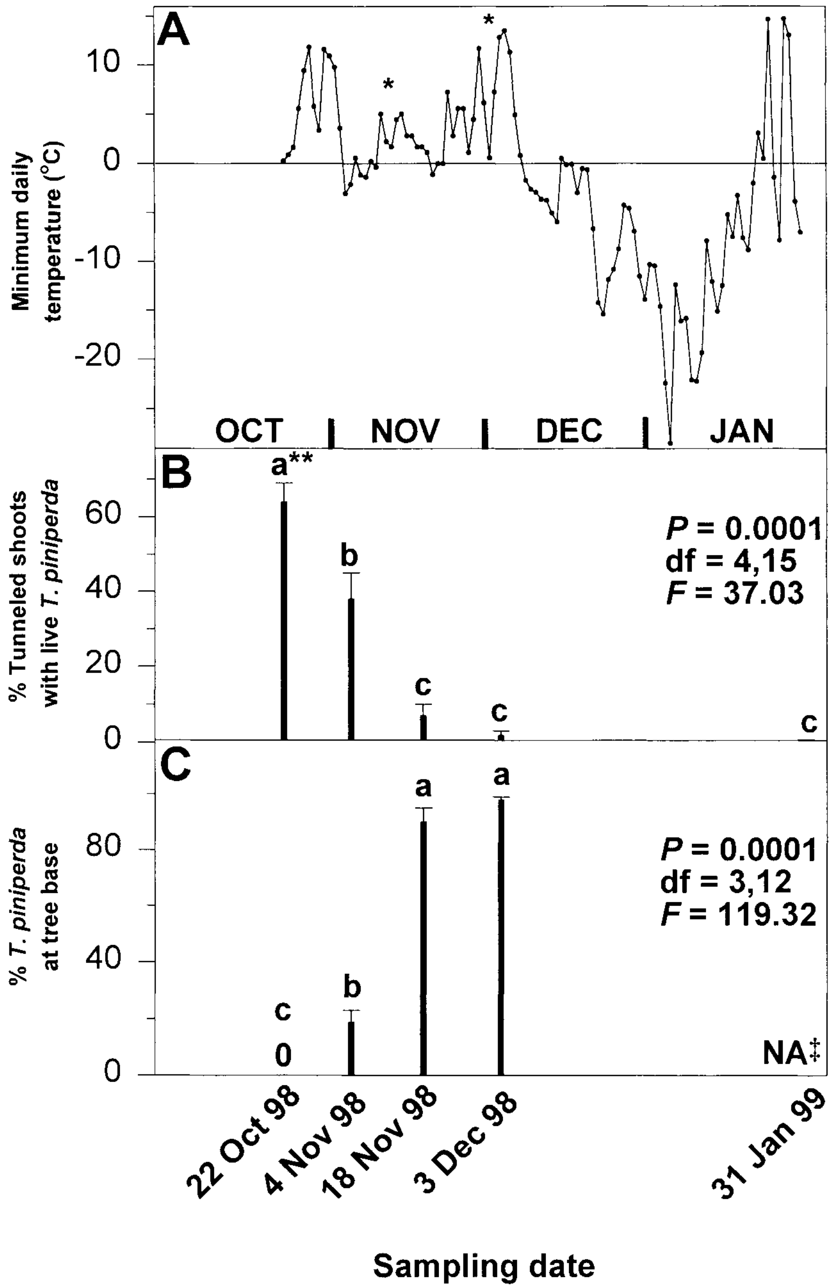
A
Minimum daily temperature (°C)
10
0
-10
-20
OCT
NOV
DEC
JAN
B
% Tunneled shoots with live T. piniperda
60
40
20
0
a**
b
c
c
c
P = 0.0001
df = 4,15
F = 37.03
C
% T. piniperda at tree base
80
40
0
c
0
b
a
a
NA‡
P = 0.0001
df = 3,12
F = 119.32
22 Oct 98
4 Nov 98
18 Nov 98
3 Dec 98
31 Jan 99
Sampling date

Table 2. Mean (±SE) number of adults found per tree base, and mean distance and maximum distance above the duff line where overwintering *Tomicus piniperda* adults were found along the lower trunk of Scotch pine trees (N = 4 trees per sampling date) during November and December 1998 in LaPorte Co., IN*

	Mean ± SE (range)		
Parameter	4 Nov 98	18 Nov 98	3 Dec 98
No. adults per tree base	4.0 ± 1.0 b (2-7)	34.5 ± 10.3 b (15-63)	73.5 ± 13.3 a (37-95)
Average distance above duff line (cm)	3.8 ± 1.0 a (2.3-7.5)	1.7 ± 0.6 a (0.2-3.4)	2.4 ± 0.2 a (1.8-2.9)
Maximum distance above duff line (cm)**	6.0 ± 0.9 b (4-8)	13.0 ± 5.8 b (8-30)	41.3 ± 9.4 a (20-59)

* Means within rows followed by the same letter are not significantly different at $P = 0.05$ level (Student-Newman-Keuls multiple range test).

** Average values were based on the location data for the one beetle per tree that was farthest above the duff line.

to the duff line. Percentages of adults found in the other 5-cm height intervals were not significantly different among sample dates ($P > 0.05$).

The fact that the mean height of the one beetle per tree that was found farthest above the duff line was significantly higher for 3 December as compared to 4 and 18 November, does suggest that when tree bases become overcrowded with overwintering adults, some adults will decide to overwinter at considerable distances above the duff line. If this is true, however, it is unclear at what density threshold such behavior is induced and how adults determine the tree base is overcrowded. Also, the number of adults that responded to overcrowding was low, given that the percentage of adults found above the 25-cm height level on 3 December was not significantly different from the other sample dates ($F = 1.61$; df = 2, 9; $P > 0.25$), even though the number of adults per tree base was significantly higher on 3 December ($F = 12.83$; df = 2, 9; $P = 0.0023$) (Table 2).

The advantages to overwintering near the duff line may be related to temperature (Fig. 2). Daily minimum inside-bark temperatures at the soil-duff interface were considerably warmer and more stable than those at 15 cm and 45 cm above the duff line (Fig. 2). In addition, daily minimum inside-bark temperature at the soil-duff interface averaged 5.7°C warmer than air temperature during the period of 22 October through 11 November 1998, and 7.3°C warmer during 3 December 1998 through 31 January 1999. On-site temperature data were not available during 12 November through 2 December 1998 because the datalogger battery malfunctioned.

Snow can further insulate adults that are overwintering near the ground. Table 4 compares air and inside-bark temperatures during three time periods in the present study that varied in snow depth and temperature: (1) 22 October-2 November 1998, daily minimum air temperatures were above freezing and there was no snow on the ground, (2) 17-28 December 1998, daily minimum air temperatures fell below freezing each day and there was no snow, and (3) 2-13 January 1999, daily minimum air

Table 3. Mean (±SE) percent of overwintering *Tomicus piniperda* adults located along the lower trunk of Scotch pine trees by 5-cm intervals starting at the duff line and sampling date during November and December 1998 in LaPorte Co., IN*

	Sampling date (N = 4 trees per sampling date)			
Parameter	4 Nov 98	18 Nov 98	3 Dec 98	Overall
Distance (cm)	%	%	%	%
≤0	3.6 ± 3.6 b	51.8 ± 7.3 a	40.8 ± 7.7 a	32.1 ± 7.1 b
0 ≥ 5	65.2 ± 22.3 a	32.4 ± 2.1 b	47.6 ± 08.0 a	48.4 ± 8.2 a
5 ≥ 10	31.3 ± 23.7 ab	13.0 ± 8.0 c	7.6 ± 1.6 b	17.3 ± 8.1 b
10 ≥ 15	0 ± 0 b	2.0 ± 2.0 d	1.3 ± 1.3 c	1.1 ± 0.8 c
15 ≥ 20	0 ± 0 b	0.4 ± 0.4 d	0.7 ± 0.7 c	0.4 ± 0.3 c
20 ≥ 25	0 ± 0 b	0 ± 0 d	0.3 ± 0.3 c	0.1 ± 0.1 c
>25	0 ± 0 b	0.4 ± 0.4 d	1.7 ± 1.1 c	0.7 ± 0.4 c
ANOVA results				
F	3.76	23.30	31.31	16.17
df	6, 21	6, 21	6, 21	6, 77
P<	0.0107	0.0001	0.0001	0.0001
N (adults)	16	138	294	448

* Means within columns followed by the same letter were not significantly different at $P = 0.05$ level (Student-Newman-Keuls multiple range test).

temperatures were below freezing each day and snow depth was 25 cm or deeper. Overall, mean daily minimum inside-bark temperatures at the soil-duff interface were significantly warmer than air temperatures during each time period, whether snow was present or not (Table 4). Mean inside-bark temperature at 15 cm above the duff line was significantly warmer than the air temperature only when snow was present and likely covered the temperature probe (Table 4). Mean inside-bark temperature at 45 cm above the duff line never differed significantly from mean air temperature during any of the three time periods (Table 4), suggesting that snow never covered the trunk to that height. It is likely, therefore, that overwintering adults are most protected from temperature extremes when near the duff line, or at least beneath the snow.

Management implications. The USDA Pine Shoot Beetle Compliance Management Program currently recommends that Christmas trees be cut so that the resulting stumps are 10 cm in height or less (McCullough and Sadof 1996). In wholesale Christmas tree operations, an additional 10 to 15 cm of the lower trunk is often removed to improve marketability and allow for easier handling during shipping (Haack and Lawrence 1997b). In the present study, in 1998, the percentages of overwintering adults found above 10 and 25 cm from the duff line were less than 3 and 1%, respectively, and did not differ significantly among sample dates ($F = 1.99$; df =

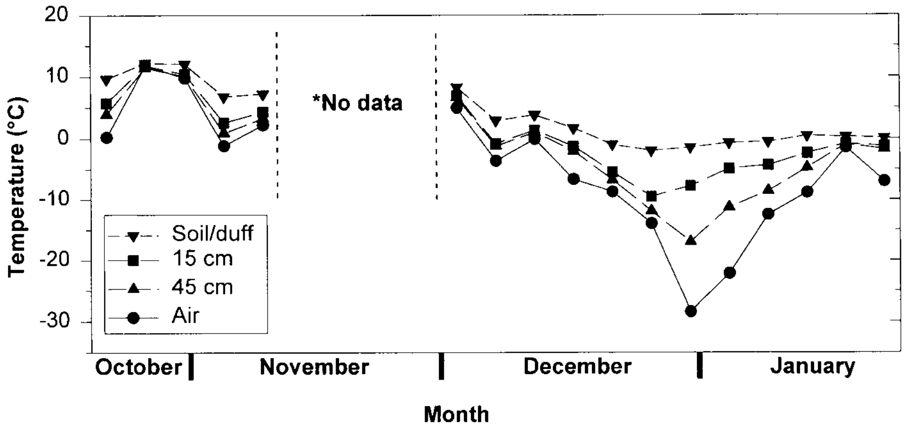

Fig. 2. Daily minimum air temperature at 1.5 m above the duff line and inside-bark temperatures at three locations (soil-duff interface, 15 cm above the duff line, and 45 cm above the duff line) along the lower trunk of a Scotch pine tree during 22 October 1998 through 31 January 1999 in LaPorte County, IN. Data shown at 5-day intervals for ease of display. *Data not available for 12 November through 2 December 1998 (see text).

2, 9; $P > 0.19$ for $\geq$10 cm; $F = 1.61$; df = 2, 9; $P > 0.25$ for >25 cm). Given that Christmas trees are typically harvested starting in mid-October, the above data suggest that harvesting date would have little effect on the number of adults that could potentially be moved at the base of cut trees. This is especially true if an additional 10 to 25 cm of the lower trunk is removed before shipping. The *T. piniperda* population in the present study was much higher than would typically be found in well-managed Christmas tree plantations. For example, in well-managed Christmas tree plantations in Indiana, there were seldom more that five *T. piniperda* adults present per 1000 trees (McCullough and Sadof 1998). At such low densities, almost all *T. piniperda* adults would likely overwinter no higher than 10 cm above the duff line, and therefore, never be in a position to be shipped with cut Christmas trees.

Harvesting date, however, could affect the likelihood of adults being present in shoots at the time of harvest. That is, if trees are cut and shipped before adults exit the shoots, the likelihood of moving *T. piniperda* adults with cut trees would increase. For example, in the present study, 100% of all adults were in the shoots on 22 October. This decreased to 81% on 4 November, 10% on 18 November, and 2% on 3 December. These percentages may vary from year to year and location to location, depending on the first occurrence of subfreezing temperatures (Haack et al. 1998, 2001). Considering that the current U.S. range of *T. piniperda* spans from northern MI to southern OH, adult shoot departure would likely begin as early as mid-September in northern MI and as late as early November in southern OH (Haack et al. 1998). Given that harvesting of Christmas trees usually begins in October and November, the risk of *T. piniperda* adults still being present in the shoots at the time of harvest would increase from the northern to the southern part of its U.S. range. Therefore, when possible, delaying harvesting in fields where *T. piniperda* might occur would

Table 4. Mean (±SE) daily minimum air temperatures (°C) at 1.5 m above the duff line and inside-bark temperatures recorded along the trunk of a Scotch pine tree at three heights (soil-duff interface, 15 cm above the duff line, and 45 cm above the duff line) during three periods: (1) daily minimum air temperatures >0°C and no snow on the ground, (2) daily minimum air temperatures ≤0°C and no snow, and (3) daily minimum air temperatures ≤0°C and snow depth ≥25 cm)*

	Mean (±SE) daily minimum temperature (°C)		
	>0°C, no snow** (22 Oct-2 Nov)	≤0°C, no snow (17 Dec-28 Dec)	≤0°C, with snow (2 Jan-13 Jan)
Position and height of temperature probe			
Air; 1.5 m above duff	6.2 ± 1.3 b	−6.7 ± 1.6 b	−17.0 ± 1.7 c
In bark; 45 cm above duff	7.2 ± 1.1 b	−5.7 ± 1.6 b	−15.0 ± 1.2 c
In bark; 15 cm above duff	8.5 ± 0.8 ab	−3.8 ± 1.2 b	−5.1 ± 0.5 b
In bark; duff-soil interface	11.0 ± 0.4 a	0.8 ± 0.6 a	−1.0 ± 0.1 a
ANOVA results			
F	4.75	6.65	49.83
df	3, 44	3, 44	3, 44
P<	0.0059	0.0008	0.0001

* Means (within columns) followed by the same letter were not significantly different at the $P = 0.05$ level (Student-Newman-Keuls multiple range test).

** Snow depth data taken from 1998-1999 NOAA records for LaPorte, IN, which is approximately 16 km southwest of the study site.

allow a greater percentage of adults to exit the shoots and reach the base of the tree, and these adults would most likely remain in the stump after harvest.

Acknowledgments

We thank Carolyn Aloo, George Heaton and Eric Schuette for field and lab assistance; Wayne Dudeck for use of his Christmas tree farm; and Deborah McCullough, Clifford Sadof and Robert Waltz for comments on an earlier draft of this manuscript.

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