Tomicus piniperda (Coleoptera: Scolytidae) Shoot-Feeding Characteristics and Overwintering Behavior in Scotch Pine Christmas Trees

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ABSTRACT Overwintering behavior of *Tomicus piniperda* (L.) was studied in a Scotch pine (*Pinus sylvestris* L.) Christmas tree plantation in Indiana (1992–1994) and a plantation in Michigan (1994). In general, adults feed inside shoots during summer, then move to overwintering sites at the base of trees in autumn. In early autumn, adults were most often found in shoot-feeding tunnels that were still surrounded by green needles, whereas few were in tunnels surrounded by yellow or brown needles. For all years and sites combined, the range in the percentage of recently tunneled shoots that contained live *T. piniperda* adults decreased from 89 to 96% in mid-October, to 15–66% in early November, to 2–10% in mid-November, and to 0–2% by late November to early December. In each year, the first subfreezing temperatures in autumn occurred in October, before most adults left the shoots. Of 1,285 *T. piniperda*-tunneled shoots, one to seven tunnels (mean = 1.6) and zero to three adults were found per infested shoot. Of these 1,285 attacked shoots, 55% of the shoots had one tunnel, 33% had two, 9% had three, 3% had four, and <1% had five to seven tunnels each. When two or more tunnels occurred in a single shoot, adults were most commonly found in the innermost (most basal) tunnel. For the 2,070 tunnels found in the 1,285 shoots, average shoot thickness at the tunnel entrance was 6.0 mm, average distance from the tunnel entrance to the shoot tip was 6.3 cm, and average tunnel length was 2.3 cm. Four Scotch pine Christmas trees were dissected in January 1993. Eighty percent of the tunneled shoots were in the upper quarter of the tree crown and 98% were in the upper half. For the four trees inspected in January, one live adult was found in a shoot and 85 adults were found in the outer bark along the lower trunk from 1 cm below the soil line to 19 cm above the soil line. No overwintering adults were found outside the trunk in the duff or soil near the base of each test tree. Implications of these results are discussed in terms of surveying, timing the cutting of Christmas trees, and cutting height for Christmas trees.

KEY WORDS *Tomicus piniperda*, Scolytidae, bark beetle, exotic pest

ESTABLISHED POPULATIONS OF the pine shoot beetle *Tomicus piniperda* (L.), an Eurasian bark beetle, were first discovered in Ohio in July 1992; as of November 2000, *T. piniperda* was known to occur in 303 counties in 12 U.S. states and 43 counties in two Canadian provinces (Fig. 1). This Eurasian scolytid was considered a potential threat to North American pines by the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS), and therefore a federal quarantine was imposed on the movement of pine from infested counties to uninfested counties in the United States in November 1992 (USDA APHIS 1992, Haack et al. 1997).

The general biology of *T. piniperda* is well documented (Bakke 1968; Salonen 1973; Långström 1983; Ye 1991; Haack and Lawrence 1995a, 1995b, 1997a; Lawrence and Haack 1995; McCullough and Smitley 1995; Haack et al. 1997, 2000a; Kauffman et al. 1998). Briefly, *T. piniperda* is a univoltine bark beetle. In colder parts of its range, adults overwinter in the outer bark at the base of live pine trees. In the Great Lakes region, adults first become active between February and April, when temperatures begin to exceed 12°C. To reproduce, adults typically fly to recently cut pine stumps, logs, and slash, using host monoterpenes such as alpha-pinene for orientation. Adults are monogamous and construct egg galleries in the inner bark (phloem) that run parallel to the wood grain. The first progeny adults usually appear in early June in the Great Lakes region. After emerging, progeny adults fly to the crowns of live pine trees and feed inside one or more shoots during the remaining months of summer and early autumn. In autumn, adults exit the shoots and usually walk back along the branches to the trunk, and then down the trunk to the base of the tree, where they tunnel into outer bark and spend the winter.

Although the general life history of *T. piniperda* is well known in Eurasia, specific information about within-tree distribution of shoot attacks and overwintering sites, and timing of shoot departure, was unknown in the Great Lakes region at the time of this

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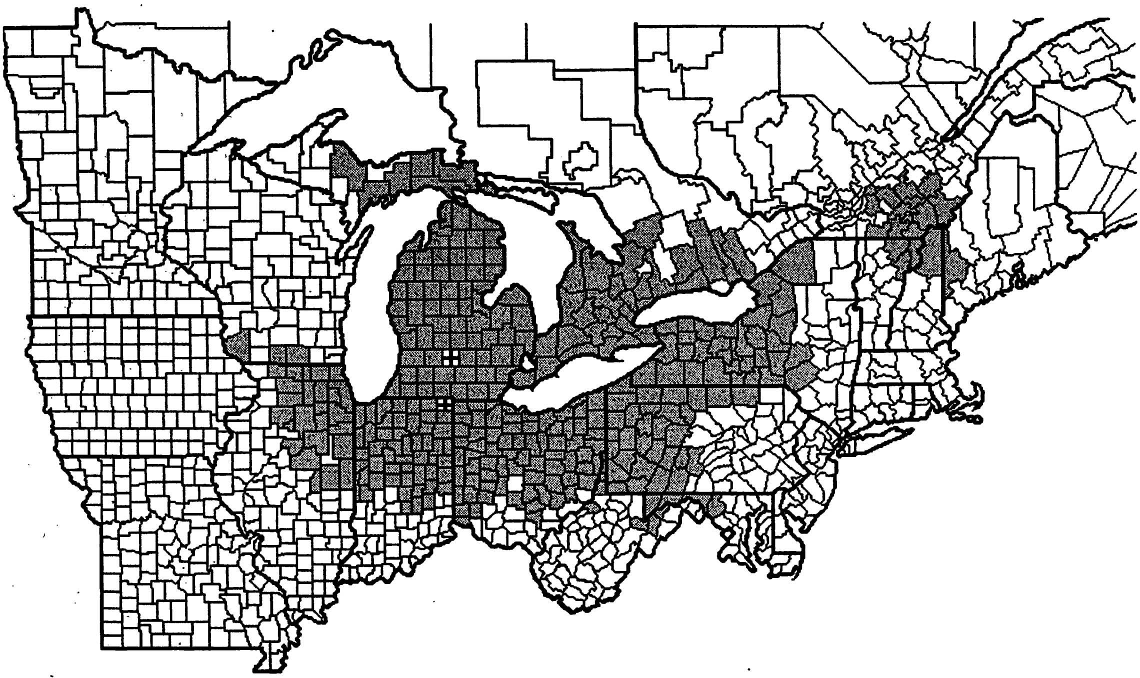

Fig. 1. Known distribution of *T. piniperda*-infested counties in North America as of January 2000 (Source: USDA APHIS and Canadian Food Inspection Agency). The two counties marked with a "+" indicate where the plantations in the current study were located (Steuben County, IN, and Eaton County, MI).

study. Such information was important to help formulate and modify quarantine regulations and develop management programs for this new exotic pest. The two major objectives of the current study were to describe characteristics of *T. piniperda*-infested shoots and their within-tree distribution and to determine when adults exit from pine shoots for overwintering sites at the base of the tree. A secondary objective was to determine the location of overwintering *T. piniperda* adults.

Materials and Methods

Study Sites and Temperature Records. The studies were conducted in two Scotch pine (*Pinus sylvestris* L.) Christmas tree plantations where nearly every pine tree had at least one current-year shoot that was infested with *T. piniperda*. One site was in northeastern Indiana ≈5 km south of Orland, Steuben County (41° 45′ N, 85° 10′ W). The Indiana plantation was ≈15 ha in size with pine trees ranging from 2 to 4 m tall. The second site was ≈13 km south of Lansing, MI, in Eaton County (42° 33′ N, 84° 36′ W), and was ≈116 km north of the Indiana plantation (Fig. 1). The Michigan plantation was ≈10 ha in size with pine trees ranging from 1 to 4 m tall. We obtained daily minimum air temperature data from the weather recording stations nearest the two field sites: the Prairie Heights station (41° 38′ N, 85° 12′ W), ≈8 km from our Indiana field site, and the East Lansing station (42° 40′ N, 84° 29′ W), ≈9 km from our Michigan site.

Characteristics of Attacked Shoots. We collected 50–70 *T. piniperda*-tunneled shoots at 2-wk intervals from September to December in 1992, 1993, and 1994 in the Indiana plantation. The Michigan site was sampled similarly but only in 1994. We collected attacked shoots with mostly green foliage to increase the probability that they still contained *T. piniperda* adults. All shoots were cut below the innermost (most basal from the shoot tip) entrance hole when multiple tunnels occurred. Shoots were bagged and refrigerated until dissected over the next 2 d. For each shoot, we recorded needle color near the entrance hole (i.e., green to fading green, yellow to brown), number of tunnels, diameter of the twig at the tunnel entrance (i.e., the entrance hole into the twig), distance from each entrance hole to the shoot tip, tunnel length, presence or absence of an adult, and whether each adult was alive or dead. In cases where the shoot was swollen at the entrance hole, twig diameter was measured in the nearest adjacent unswollen area of the twig.

Timing of Shoot Departure. For each collection date, we calculated the percentage of attacked shoots that had one or more live adults present. To make these calculations, we used only shoots with one or two feeding tunnels and where at least one tunnel was surrounded by green or fading-green needles (see below).

Within-Tree Distribution of Overwintering Adults. On 21 October 1992, we selected four Scotch pine Christmas trees at the Indiana field site that each had evidence of *T. piniperda* current-year shoot feeding.

These four trees had not been pruned during the 1992 growing season. The trees averaged (mean ± SEM) 2.3 ± 0.4 m tall and 12 ± 1 cm in diameter at ground level. From additional Scotch pine trees, we collected 80 shoots with current-year *T. piniperda* tunnels and mostly green foliage, and therefore likely still contained *T. piniperda* adults. Twenty infested shoots were tied to branches in the upper crown of each test tree. Each cut shoot was tied to a live shoot of a test tree so that the two twigs touched for most of their common length. This was done to facilitate adults walking between branches as they moved toward overwintering sites at the base of each tree.

On 2 December 1992, we removed the 80 shoots, bagged them separately, and refrigerated them until dissected over the next 2 wk. We recorded all tunnel data for each shoot as described above.

In January 1993, the four test trees were completely dissected to locate and count all overwintering adults. We removed all shoots, whorl by whorl, in the field and inspected them for *T. piniperda* tunnels and adults. As each branch was inspected, we counted all current-year shoots that were ≥3 mm in diameter to estimate the total number of shoots that could potentially have been attacked by *T. piniperda* (Långström 1983, McCullough and Smitley 1995). We collected separately the duff layer and the upper 3–4 cm of soil within a 30-cm radius of each test tree to determine whether any adults were overwintering in the duff or soil near the base of each tree. The duff and soil were bagged separately, and refrigerated in the laboratory until inspected over the next few weeks. The duff was inspected by hand for *T. piniperda* adults, and the soil was inspected after sifting. The original soil line was marked on the bark surface of each tree, and then the trunk was cut 3–6 cm below the original soil line. The entire trunk was returned to the laboratory and kept frozen until debarked with a knife over the next few weeks. The location of each overwintering *T. piniperda* adult was recorded with respect to distance above or below the soil line.

Statistical Analyses. For most analyses the shoot data were pooled among years and sites. A one-way analysis of variance (ANOVA) (GLM procedure, SAS Institute 1988) was used to test for differences in total tunnel length per shoot for shoots with different numbers of tunnels, attack rate of the available shoots at different canopy levels, and the location of overwintering adults along the lower trunk. Percentage data were analyzed using arcsine square-root transformation. Mean separation was conducted with Tukey's multiple comparison test when the ANOVA was significant at the $P = 0.05$ level. Linear regression (GLM procedure) was used to analyze the relationship between the number of infested shoots per tree and the number of overwintering adults found per tree. Differences in categorical variables, such as *T. piniperda* presence in tunnels relative to foliage color, were analyzed using chi-square analysis and the z-test (SigmaStat 1994).

Results and Discussion

Characteristics of Attacked Shoots. Of the 1,285 *T. piniperda*-tunneled shoots collected at all sites and years from 20 September to 2 December, we found from one to seven tunnels per attacked shoot and from zero to three adults per attacked shoot. The average (mean ± SEM) number of tunnels per attacked shoot was 1.6 ± 0.02 ($n = 1{,}285$). Overall, 55% of the shoots had one tunnel, 33% had two, 9% had three, 3% had four, and <1% had five to seven tunnels. For the 2,070 *T. piniperda* tunnels found in these 1,285 shoots, average shoot thickness at the tunnel entrance was 6.0 ± 0.04 mm (range, 3–17 mm), average distance from the tunnel entrance to the shoot tip was 6.3 ± 0.1 cm (range, 0.3–25.7 cm), and average tunnel length was 2.3 ± 0.03 cm (range, 0.1–9.1 cm). Considering only the most apical tunnel on each shoot, when more than one tunnel per shoot occurred, the average distance from the tunnel entrance to the shoot tip was 4.8 + 0.1 cm (range, 0.3–24.8 cm). The mean total tunnel length per shoot increased with increasing numbers of tunnels per shoot ($F = 249$; df = 6, 1,247; $P < 0.0001$; Table 1); however, because of some shoot breakage, complete measurements were made on only 1,254 of the original 1,285 shoots. On average, total tunnel length per shoot increased by ≈2 cm for each additional tunnel present (Table 1).

When only a single adult was found in a shoot with multiple tunnels, for the entire September to December collection period, the adult was most commonly found in the innermost (most basal) tunnel (95% of 239 shoots). More specifically, 97% of the adults found in the 183 shoots with one adult and two tunnels were found in the innermost tunnel. Similarly 86% of the adults in the 44 shoots with three tunnels, 89% of the adults in the nine shoots with four tunnels, and 100% of the adults in the two shoots with five tunnels and one shoot with seven tunnels were in the most basal tunnel. Also, for the 180 shoots with one adult and multiple tunnels that were collected from 20 September to 21 October, before most shoot departure occurred, 97% of the adults were located in the innermost tunnel (Table 2). Such patterns suggest that when *T. piniperda* adults construct multiple tunnels on the same shoot, each succeeding tunnel is constructed below the previous tunnel. This behavior ensures that each new tunnel is constructed in living tissue.

In other studies, mean shoot diameter at the tunnel entrance varied from 4.5 to 5.8 mm on Scotch pine (Långström 1980, McCullough and Smitley 1995, Kauffman et al. 1998) and from 7 to 8.5 mm on Yunnan pine, *Pinus yunnanensis* Franchet (Ye 1996). Moreover, the tunnel entrance hole was typically within 4 cm of the shoot tip on Scotch pine (McCullough and Smitley 1995) and within 3–4 cm of the shoot tip on Yunnan pine (Ye 1996). On Scotch pine trees in Sweden, *T. piniperda* tunnel length averaged 2 cm with a maximum of 7 cm (Långström 1983), and an average of 1.4 tunnels per attacked shoot was recorded with a maximum of seven tunnels (Långström 1980). In an insecticide study where *T. piniperda* adults were caged

Table 1. Total tunnel length per *T. piniperda*-attacked shoot, within-crown location of infested shoots, and overwintering location along the lower trunk of Scotch pine Christmas trees in Indiana

Parameter	Mean ± SEM	Range	*n*
Total tunnel length per shoot (cm)			
1 tunnel per shoot	2.4 ± 0.05d	0.1–9.1	689 shoots
2 tunnels per shoot	4.3 ± 0.08cd	1.3–11.3	419
3 tunnels per shoot	6.6 ± 0.2bc	2.6–13.1	107
4 tunnels per shoot	8.1 ± 0.3b	5.4–13.1	32
5 tunnels per shoot	11.9 ± 1.7a	7.2–15.0	4
6 tunnels per shoot	13.2 ± 1.0a	12.2–14.2	2
7 tunnels per shoot	14.3a	14.3	1
Within-crown location of shoots that were naturally tunneled by *T. piniperda* (%)			
1st (upper) quarter	79.8 ± 17.7a	27–100	4 trees
2nd quarter	18.3 ± 18.3b	0–73	4
3rd quarter	2.0 ± 2b	0–8	4
4th (lower) quarter	0.0 ± 0b	0	4
Overwintering location along trunk relative to soil line (%)			
15 ≥ 20 cm	1.9 ± 1.1b	0–4.3	4 trees
10 ≥ 15 cm	11.1 ± 6.6b	0–30.4	4
5 ≤ 10 cm	18.7 ± 7.6b	0–34.8	4
0–≥ 5 cm	61.6 ± 11.5a	30.4–85.7	4
−2.5–≥ 0 cm	6.6 ± 2.8b	0–13.8	4

Means (within a given parameter) followed by the same letter are not significantly different at the $P = 0.05$ level (Tukey's multiple range test).

on Scotch pine branches, mean tunnel length varied from 1.2 to 2.6 cm on untreated control trees (McCullough and Smitley 1995).

Timing of Shoot Departure. To estimate timing of shoot departure, we first needed to know if *T. piniperda* adults were evenly distributed among autumn-collected shoots that differed in foliage color. In late summer and early autumn (August–October), needle color near *T. piniperda* tunnels varies from green to brown. For *T. piniperda*-attacked shoots of similar thickness and age, it is logical to assume that current-year tunnels surrounded by brown (dead) needles were constructed earlier in summer than tunnels surrounded by green (live) needles. For shoots collected in late summer or autumn that have multiple *T. piniperda* tunnels, foliage near the outermost (most apical) tunnel is usually yellow to brown, whereas foliage near the innermost (most basal) tunnel is often green or pale green (Table 2). For shoots collected from 20 September through 21 October, at least one *T. piniperda* adult was present in 85% of the 466 shoots that had at least one tunnel surrounded by green to pale-green foliage (Table 3), however, only 11% of 47 shoots that had yellow to brown foliage near all tunnels contained a live *T. piniperda* adult.

Because the presence (yes or no) of *T. piniperda* in shoots versus foliage color (green to pale-green or yellow to brown) varied significantly ($\chi^2 = 134$, df = 1, $P < 0.0001$), we used only shoots that had at least one tunnel surrounded by green or pale-green foliage to estimate timing of *T. piniperda* fall shoot departure. Our logic was that shoots where all tunnels were surrounded by yellow or brown needles would almost invariably be empty at the time of sampling and, therefore, including them in the calculations would overestimate the true rate of shoot departure. As further support for this procedure, ≈90% of the *T. piniperda*-attacked Scotch pine shoots collected in August in Sweden (Långström 1983) or in October in Indiana (Kauffman et al. 1998) contained live adults when the shoots had green foliage or green cambium at the tunnel entrance, whereas no adults were found in shoots with brown foliage or brown cambium at the tunnel entrance.

When calculating the timing of fall shoot departure it is also important to know how many adults are typically found in a single attacked shoot, especially when multiple tunnels occur. This is important because it would be best to use shoots that never contained more than one *T. piniperda* adult in such cal-

Table 2. Location of live *T. piniperda* adults and associated needle color for 180 Scotch pine shoots that had two to five tunnels each but only one adult when collected between 20 September and 21 October 1992–1994 in Christmas tree plantations in Indiana and Michigan

No. of tunnels per shoot	No. of shoots with one adult	Tunnel in which adult was found: apical (#1) to basal					Needle color at tunnel with adult[a]		% of tunnels with green or pale-green needles: apical (#1) to basal				
		1	2	3	4	5	G-PG	Y-B	1	2	3	4	5
2	147	2	145	—	—	—	147	0	7	100	—	—	—
3	26	0	3	23	—	—	26	0	0	12	100	—	—
4	5	0	0	0	5	—	5	0	0	0	0	100	—
5	2	0	0	0	0	2	2	0	0	0	0	0	100

[a] Foliage color: G-PG, green to pale-green; Y-B, yellow to brown.

Table 3. Number of live *T. piniperda* adults found in Scotch pine shoots with one to six tunnels per shoot and green or pale-green foliage surrounding at least one tunnel when collected from 20 September through 21 October 1992–1994 in Christmas tree plantations in Indiana and Michigan

No. *T. piniperda* tunnels per shoot	Total no. of		No. of shoots with 0–2 adults each		
	Shoots	Tunnels	0 adults	1 adult	2 adults
1	230	230	43	187	0
2	179	358	21	147	11
3	46	138	5	26	15
4	8	32	1	5	2
5	2	10	0	2	0
6	1	6	0	0	1

culations. For example, if there is only one adult per shoot, and no adult is found, then it is obvious that the adult had exited the shoot. However, if two adults were present in a shoot and one exited before inspection, then the inspector would have no knowledge that one adult had already left the shoot and thus would classify the shoot as occupied when in fact it is only 50% occupied. For the 466 *T. piniperda*-attacked shoots that had green or pale-green foliage surrounding at least one tunnel and were collected from 20 September through 21 October, we found one to six tunnels per shoot and zero to two adults per shoot (Table 3). Overall, 15% of the 466 shoots had no *T. piniperda* adults present, 79% had one adult, and 6% had two adults (Table 3). Of the 236 shoots that had two or more tunnels per shoot (Table 3), 11.4% of the shoots had no adults present, 76.3% had one adult, and 12.3% had two adults per shoot. Likewise, there were two adults in none of the 230 shoots with one tunnel, 6% of the 179 shoots with two tunnels, and 32% of the 57 shoots with three or more tunnels (Table 3). Therefore, to better estimate timing of fall shoot departure, we analyzed shoots that probably contained only one adult by restricting the data set to only those shoots with one or two tunnels and foliage that was green or pale-green near at least one tunnel.

Using the above criteria, *T. piniperda* adults tended to initiate shoot departure in the second half of October and complete shoot departure by mid-November at both the Indiana and Michigan study sites (Fig. 2). Overall, for the four graphs in Fig. 2, the percentage of recently tunneled shoots that contained at least one live adult ranged from 89 to 96% during 18–21 October, 15 to 66% during 1–4 November, 2 to 10% during 16–18 November, and 0 to 2% during 30 November to 2 December (Fig. 2). The first subfreezing temperatures (<0°C) in autumn occurred on 19 October 1992, 5 October 1993, and 11 October 1994 at the Indiana site, and on 10 October at the Michigan site (Fig. 2). In 1994, adults at the more northerly site in Michigan departed earlier than did adults at the Indiana site during the second half of October (39% of 49 shoots were occupied in Michigan versus 66% of 32 shoots in Indiana, $z = 2.13$, $P = 0.033$; Fig. 2).

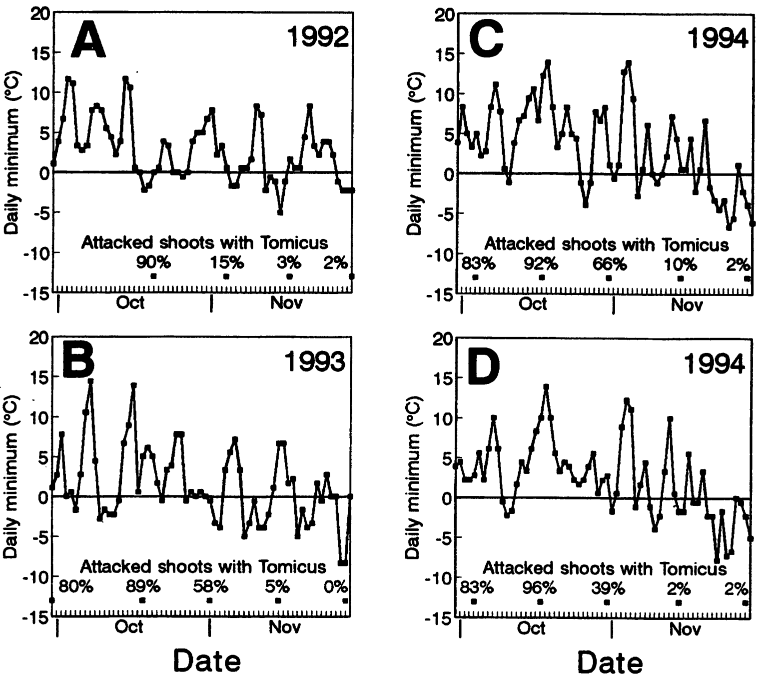

Fig. 2. Daily minimum temperatures for October and November at Prairie Heights, Steuben County, IN (≈8 km from the Indiana study site) during (A) 1992, (B) 1993, and (C) 1994; and for East Lansing, Ingham County, MI, (≈9 km from the Michigan study site) during (D) 1994. Values within each figure indicate the percent of *T. piniperda*-infested shoots with one or two feeding tunnels and green foliage surrounding at least one tunnel that still contained a live *T. piniperda* adult.

Table 4. Summary data for four Scotch pine Christmas trees that had 20 *T. piniperda*-infested shoots added to the upper crown of each tree in September 1992 and were later dissected and examined during December 1992 or January 1993 in Indiana

Parameter	Tree				Mean ± SEM
	1	2	3	4	
Tree characteristics					
No. naturally tunneled shoots	13	2	11	1	6.8 ± 3.1
No. shoots ≥3 mm in diam	745	702	835	733	754 ± 29
% shoots that were tunneled	1.7	0.3	1.3	0.1	0.9 ± 0.4
No. *T. piniperda* shoots added to tree	19[a]	20	20	20	19.8 ± 0.3
No. natural + added *T. piniperda* shoots	33	22	31	21	26.8 ± 3.1
No. adults in January in shoots	1	0	0	0	0.3 ± 0.3
No. adults in January along trunk	23	19	29	14	21.3 ± 3.2
No. adults/No. potential adults (%)[b]	73	86	94	67	79.8 ± 6.2

[a] Only 19 of the original 20 shoots added to this tree were successfuly attackd by *T. piniperda*.
[b] Number of adults found along the trunk divided by the sum of the number of naturally attacked shoots plus the number of *T. piniperda*-attacked shoots that were added to each tree.

In other studies that were conducted in northern temperate climates, initiation of *T. piniperda* shoot departure was usually preceded by one to a few nights of sub-freezing temperatures (Salonen 1973, Långström 1983, Haack and Lawrence 1997b, Kauffman et al. 1998). Haack et al. (1998) developed regional maps of the northeastern quadrant of the United States that depicted likely initiation dates for *T. piniperda* shoot departure based on historical temperature records. For the two plantations in the current study, the maps in Haack et al. (1998) indicated that shoot departure would typically start in the second half of October, which is consistent with the results of this study. In addition to freezing temperatures, other factors such as daylength could serve as stimuli for shoot departure. Nevertheless, in southern Europe and southern China, where winter temperatures seldom drop below freezing, *T. piniperda* adults overwinter in the shoots (Långström 1980, Ye 1991).

Within-Tree Distribution of Overwintering Adults. Dissection of 62 extra attacked shoots collected on 21 October 1992 at the Indiana site indicated that 94% of the shoots contained live *T. piniperda* adults. Therefore, when we tied 20 shoots on each of the four test trees, we were likely adding an average of 19 adults per tree. In December, when we collected and dissected the 80 shoots that had been tied to the test trees, we found 79 empty shoots that had been tunneled successfully by *T. piniperda* and one shoot that had been tunneled by a lepidopteran species, likely the tortricid *Eucosma gloriola* Heinrich (Table 4).

When examining the actual shoots of the four test trees in January 1993, we found 1–13 shoots per tree that had been attacked in 1992 by *T. piniperda*, representing 0.1–1.7% of all current-year shoots ≥3 mm thick per tree (Table 4). These values are similar to results of a 1993 study conducted on 12 Scotch pine Christmas trees at the same Indiana site in which the attack rate ranged from 0.2 to 4.8% of current-year shoots per tree (Haack and Lawrence 1997b). At another Indiana site, Kauffman et al. (1998) reported that 7.4% of the lateral shoots on Scotch pine Christmas trees were attacked by *T. piniperda*. Overall, 80% of the attacked shoots in our study occurred in the upper quarter of the crown ($F = 10.3$; df = 3, 12; $P < 0.002$; Table 1), which is similar to other reports (Långström 1983, Ye and Li 1994, McCullough and Smitley 1995, Kauffman et al. 1998).

If we consider the number of attacked shoots per tree, including the additional 20 shoots that we tied to each tree, and assume one adult per infested shoot, then there were potentially 21–33 *T. piniperda* adults on each of the four test trees (Table 4). The number of overwintering adults found on each test tree thus represented 67–94% of the estimated total number of tunneled shoots on those same trees (Table 4). In fall, most *T. piniperda* adults are thought to walk along the branches and trunk to reach overwintering sites along the lower trunk. In fact, Långström (1983) trapped *T. piniperda* adults as they migrated down the trunks of pine trees in autumn. Considering one adult per attacked shoot, there was no significant linear relation ($P > 0.13$) for the four test trees in the current study between the number of infested shoots per tree and the number of overwintering adults per tree. However, after including data for four similarly treated trees from the same plantation (trees 1–4 in Haack and Lawrence 1997b), a significant linear relation was found between the number of infested shoots and the number of overwintering adults per tree ($F = 10.0$; df = 1, 6; $P < 0.02$; $r^2 = 0.63$; $n = 8$ trees), suggesting that adults tend to overwinter on the same tree on which they last shoot-fed. Two reasons, among several, for <100% agreement between the number of infested shoots and the number of overwintering adults per tree include (1) a single adult can attack multiple shoots on the same tree or different trees, and (2) more than one adult can be found in the same shoot.

Of the 86 overwintering *T. piniperda* adults recorded on the four test trees in January 1993, 85 were found along the trunks and one was still inside a shoot (Table 4). All 86 adults were still alive, including the adult in the shoot. The 85 adults from the trunks were located in short tunnels in the outer bark from 1 cm below the original soil line to 19 cm above the soil line, averaging 4.6 ± 0.5 cm above the soil line. When the overwintering location along the trunk was divided into 5-cm intervals, most adults were found along the first 5 cm of the trunk above the soil line ($F = 8.5$; df =

4, 15; $P < 0.001$; Table 1). Overall, 7% of the 85 overwintering adults were found below the soil line, 68% were below the 5 cm mark on the trunk measured from the soil line, 87% were below 10 cm, and 98% were below 15 cm (Table 1). Similarly, in an earlier study where 12 Scotch pine trees were examined (Haack and Lawrence 1997b), 34% of the overwintering sites were below 5 cm, 80% were below 10 cm, and 95% were below 20 cm.

Regulatory and Management Implications. Several aspects of this study relate to *T. piniperda* inspection and management practices. First, when actual *T. piniperda* adults must be collected during summer and autumn, inspectors should look for attacked shoots that still have green foliage near the most basal entrance hole. Moreover, care must be taken to ensure that each attacked shoot is cut below the most basal tunnel because that is where the adult will most likely be found. Although adults are rarely found in shoots with primarily yellow to brown foliage, such shoots can help inspectors locate trees that are potentially infested. Second, inspectors should look for *T. piniperda* infested shoots primarily in the upper crowns of pine trees. Third, inspections aimed at locating adults in shoots would be most successful if conducted from late summer to early autumn, which is after shoot discoloration begins but before all adults have exited the shoots. Once nighttime freezing temperatures begin in autumn, inspectors can continue shoot examinations for at least 2–3 wk and still have a high likelihood of finding adults inside some of the attacked shoots. Fourth, given that live adults can still be found in shoots in mid-November, harvesting of Christmas trees should be delayed as long as practical so that more adults will depart from shoots for overwintering sites in the lower trunks. And fifth, given that most adults overwinter within the lower 20 cm of the trunk, Christmas trees should be cut as high above the soil as practical. Alternatively, before shipping, a second cut that removes an additional portion of the lower trunk of each tree would further reduce the risk of moving overwintering adults with cut trees. However, growers should treat high stumps and recently cut trunk sections appropriately because such host material can serve as breeding material for *T. piniperda* the following spring (McCullough and Sadof 1998, McCullough et al. 1998, Haack et al. 2000b).

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