BROOD PRODUCTION AND SHOOT FEEDING BY *TOMICUS PINIPERDA* (COLEOPTERA: SCOLYTIDAE)

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Abstract

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Brood production and shoot feeding by the pine shoot beetle, *Tomicus piniperda* (L.), were studied over 3 years in naturally infested plantations of Scots pine, *Pinus sylvestris* L. (Pinaceae), near Guelph and Waterloo, Ontario, using trap-logs. Adult beetles produced a single brood in 1996 and 1997 and two broods in 1999. Galleries for the first brood were all initiated under the bark over a 2- to 3-week period from mid-April to early May. The lone second brood occurred in early June. In all years, eggs were present by late April, larvae by mid-May, pupae by late June, and new adults by mid-July. Complete development (egg–pupa) required 12–13 weeks for the first brood and 8 weeks for the second brood. First-brood adults emerged over a 2- to 3-week period from early to mid-July in all years, with second-brood adults emerging in late July. The effective heat sums (degree-days (°d) > developmental-threshold temperature) were 77–79°d for eggs, 267–293°d for the larval stage, 139–152°d for the pupal stage, and 43.2°d for the pre-emergence stage, depending on the developmental-threshold temperature used. The total heat sums for the first brood (1249.8 ± 73.3°d > 0°C) were larger that those required for the second brood (856.4 ± 124°d > 0°C). Overall, values for first-brood development were similar to those calculated for European and Asian populations. Pine shoots in the upper tree crowns were used by adult beetles for maturation feeding between late July and late September in both 1995 and 1996. The re-emerging parental adults fed upon 1-year-old shoots, whereas newly emerging adults fed primarily upon current-year shoots. The beetles appeared to move to overwintering sites in late October to November, and no adults were found overwintering in shoots on the trees or the ground. Our results parallel those obtained by others under similar climatic conditions in Europe, and can be used to improve the management and regulation of this species as it becomes established in our native pine forests.

Ryall KL, Smith SM. 2000. Ponte et consommation des pousses de pin chez le scolyte *Tomicus piniperda* (Coleoptera : Scolytidae). *The Canadian Entomologist* **132** : 939–949.

Résumé

La ponte et l'alimentation à même les pousses ont été étudiées pendant 3 ans chez le scolyte *Tomicus piniperda* L., un parasite du pin, au moyen de troncs-pièges dans des plantations de pins sylvestres, *Pinus sylvestris* L. (Pinaceae), où il y a des infestations naturelles de l'insecte, près de Guelph et de Waterloo, en Ontario. Les adultes ont pondu une seule fois en 1996 et 1997, mais deux fois en 1999. L'initiation du creusage des galeries sous l'écorce par les individus de première portée s'est faite sur une période de 2 à 3 semaines, de la mi-avril au début de mai. Les individus de deuxième portée sont apparus au début de juin. Les oeufs étaient présents à la fin d'avril, les larves au milieu de mai, les nymphes à la fin de juin et les nouveaux adultes, à la mi-juillet tous les ans. Le développement complet (oeuf à la nymphe) des premières portées a duré 12–13 semaines, celui des deuxièmes, 8 semaines. L'émergence des adultes de première portée a duré 2–3 semaines, du début au milieu de juillet tous les ans et l'émergence des adultes de seconde portée, à la fin de juillet. Le nombre de degrés-jours nécessaire au développement (> le seuil thermique de développement) a été évalué à 77–79 pour les oeufs, à 267–293 pour

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le stade larvaire, à 139–152 pour le stade nymphal et à 43,2 pour le stade précédant l'émergence, selon le seuil de température de développement utilisé. La somme totale de chaleur nécessaire à l'obtention de la première portée (1249,8 ± 73,3 degrés-jours > 0°C) était supérieure à la somme nécessaire au développement de la seconde (856,4 ± 124 degrés-jours > 0°C). De façon générale, les valeurs de base du développement d'une première portée étaient semblables à celles calculées en Europe et en Asie. Les pousses de pin dans la couronne supérieure des arbres étaient consommées par les adultes pour leur maturation, de la fin de juillet à la fin de septembre en 1995 et 1996. Les adultes parents réapparaissant l'année suivante se nourrissaient de pousses de 1 an; les adultes nouvellement émergés consommaient des pousses de l'année. Les adultes semblent gagner les sites d'hiver de la fin d'octobre à novembre et aucun adulte n'a été retrouvé sur les pousses des arbres ou dans le sol en hiver. Nos résultats confirment ceux d'autres travaux de recherche faits dans des conditions climatiques semblables en Europe et peuvent être utilisés pour améliorer la gestion et le contrôle de cette espèce qui s'établit graduellement dans nos pinèdes indigènes.

[Traduit par la Rédaction]

Introduction

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), a pest widely distributed across Europe and Asia, was recently introduced into Ontario. An established population was first found in Ohio in July 1992, and the species has since been found in 11 north-central and northeastern states of the United States, 32 counties in the Great Lakes region of Ontario, and Quebec [National Agricultural Pest Inspection Service (NAPIS) 2000; Canadian Food Inspection Agency (CFIA) 2000]. In Europe, *T. piniperda* is a major pest of Scots pine, *Pinus sylvestris* L. (Pinaceae), often causing considerable growth loss. Långström and Hellqvist (1990) found growth losses of 20–40% that lasted over several years in mature stands after only 1 year of beetle attack. The non-native status of this species, combined with its potential to cause damage to the Christmas tree and timber industries, resulted in the imposition of a federal quarantine by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service (USDA APHIS), and by the Plant Protection Division, Agriculture and Agri-Food Canada. There are numerous European studies on various aspects of this species' life cycle, ecology, and impact (*e.g.*, Bakke 1968; Salonen 1973; Långström 1983, 1984, 1986), but little is known about its biology in North America.

From European studies, the pine shoot beetle is typically univoltine (Fagerstrom *et al.* 1977; Långström 1980; Schlyter and Lofqvist 1990), with adults emerging from overwintering sites in early spring when the maximum air temperature reaches 10–13°C (Långström 1986). Female beetles normally produce only one brood under field conditions, but have been shown to establish up to five broods in the laboratory (Sauvard 1993). Additional broods of decreasing size over a season have also been reported in warm regions of southern France and China (Schroeder 1990; Ye 1991). Galleries are initiated by the female in rough-barked sections of weakened trees or freshly cut logs. The emergence of the new generation occurs approximately 3 months later (Fagerstrom *et al.* 1977), after which shoot feeding begins.

The requisite period of maturation shoot feeding is the primary source of damage by this pest and is unique to this genus. Shoot feeding typically occurs in current or 1-year-old growth (Långström 1980), and is concentrated in the exterior and upper third of the tree crown (Långström 1980). Wilted shoots often fall to the ground at the end of the season and are identifiable as pine shoot beetle damage by their hollow interior (Salonen 1973). The beetles typically leave the shoots in midautumn, and overwinter under the bark at the base of the tree (Salonen 1973).

Management of this pest will depend upon accurate knowledge of its seasonal phenology, in particular: infestation of brood material, emergence of the new generation, and onset of shoot feeding. Our objectives were to (*i*) determine the timing of spring reproduction, (*ii*) assess the occurrence of successful multiple broods in the summer, and (*iii*) measure the timing and extent of summer shoot feeding by *T. piniperda* in southern Ontario. Also, heat sums [degree-days (°d) > 0°C] and effective heat sums (°d > developmental-threshold temperature) were calculated to predict occurrence of the various life stages for management purposes, particularly the emergence of adults of new generations. Heat sums (°d > 0°C) were calculated in addition to effective heat sums, because they are often easier for managers to compute in the field when timing regulatory or control interventions. Finally, results were compared with those of previous research, to assess the similarity of the beetle's life cycle between North America and its native ranges in Europe and Asia.

Materials and Methods

Timing of Brood Production. The timing of spring reproduction was studied in the field during 1996–1997 in a 40-year-old *P. sylvestris* stand, 15 km south of Guelph, Ontario (43°N, 80.2°W). Tree height ranged from 13 to 17 m and diameter at a height of 1.3 m (DBH) was 14–18 cm. This stand was selected because adult beetles prefer wood >7–10 cm in diameter with rough corky bark for reproduction (Salonen 1973).

In spring (March) 1996, trap-logs were created by cutting six trees into logs, each measuring about 0.75 m long. A total of 28 trap-logs were placed in eight piles of three to four logs each, with at least 20 m between piles. In spring (early April) 1997, five Scots pine trap-logs of the same size were cut and left in the field in five locations at least 20 m apart. In 1996, each trap-log was inspected at 4- to 6-d intervals for evidence of colonization and subsequent development by *T. piniperda*. In 1997, only colonization and emergence were monitored. The timing of gallery initiation was assessed by counting the number of entrance holes visible in the bark on each date.

In 1996, once evidence of colonization (entrance holes and boring debris) was apparent, one trap-log was selected on each sampling date and brought back to the laboratory for debarking. In the laboratory, the bark was removed, to assess the stage of development of the galleries. On each sampling date, a minimum of 10 galleries was examined. The following data were recorded for each gallery: its length (to the nearest 0.1 cm), and the numbers of adults, eggs, and larvae present. After 21 June, it could no longer be determined to which gallery the individual larvae or pupae belonged and, therefore, the ratio of larvae to pupae and of pupae to new adults was recorded for the entire log instead of per gallery. The timing of emergence of the new generation was monitored in July by counting the number of exit holes visible in the bark of the log on each sampling date. Counting exit holes and not adult offspring directly tends to underestimate the population by approximately 10%, because some holes are not visible and because a small number of beetles emerge through the same holes (Salonen 1973). Counts were expressed as the percentage of the total, either per gallery or (after 21 June) per log, for each stage (egg, larvae, pupae, callow adult, emerged adult). The duration of each stage was estimated from graphical representation of these data.

The timing of later broods was studied during 1999 in a 25- to 35-year-old mixed stand of Scots pine (65%) and jack pine (*Pinus banksiana* Lamb.) (35%), 35 km north of Waterloo, Ontario (43.5°N, 80.6°W). This stand was selected because of its large population of and damage from *T. piniperda*. Tree height ranged from 10 to 14 m, with a DBH of 11–15 cm. In early June, six Scots pine trees were selected: three with galleries of mid- to late-instar larvae (first brood) and three with galleries of recently laid eggs (second brood). Five galleries were exposed on each tree and the insect stages present were recorded (eggs, early, mid- or late-instar larvae, pupae, teneral adults, or exit holes). In early, and again in late July, an additional five galleries were exposed on each tree and the same variables measured. In addition, a 2-m-wide transect, 200 m in length, was placed in this stand during early July, to determine the proportions of trees with broods. All Scots pine trees (n = 31) in the transect were examined for evidence and stage of infestation (eggs, early, mid- or late-instar larvae, pupae, teneral adults, or exit holes). In addition, during mid-July, one Scots pine tree from outside the transect was cut into sections of about 1 m (n = 7) and these trap-logs were placed in the same stand to detect any additional gallery establishment by *T. piniperda*.

Degree-day Predictions. From 10 April to 2 June 1996, environmental conditions were monitored at the first site locally, using a Campbell Scientific CR-10 digital data logger. Hourly air temperatures were collected using a probe attached to a tree, at a height of 1.5 m, and averaged to provide mean daily temperature. Because the mean daily temperatures over this period were the same as those obtained from the Waterloo–Wellington Airport (Environment Canada) about 25 km from the site (Wilcoxon's z = –0.147, n = 31, 31, P = 0.8831), temperatures recorded at the airport between April and July 1996 were used for all data analyses.

Mean daily air temperatures were calculated from the time of gallery initiation until the first eggs and the first larvae were observed. The duration of each developmental stage derived from the trap-logs above was then used to calculate both the heat sums (°d > 0°C) and the effective heat sums (°d > developmental-threshold temperature) for each stage. Threshold temperatures for the effective heat sums were derived from Salonen (1973) and Ye (1994). To calculate the heat sums required for emergence of the second brood in 1999, another temperature data recorder measuring air temperature was established within the stand on 15 June on the north side of one tree at a height of 1.5 m. Mean daily air temperatures were summed from this date until the period of median emergence for the new generation.

Timing of Summer Shoot Feeding. The timing of summer maturation feeding was studied during 1995 and 1996 in a young (12–15 years old) Scots pine stand, 20 km south of Guelph, Ontario (43.3°N, 80.2°W). Tree height ranged from 2.5 to 3.5 m, with a DBH of 3–7 cm, providing easy access to a large number of shoots. The stand consisted of several hundred trees, originally planted (in a 2 × 2 m spacing) for Christmas tree production, that had been left untended for 2 years prior to the study. Every 2 weeks from late July until mid-September in 1995, 50 randomly selected trees in this stand were examined for shoot feeding. In 1996, 35 of these 50 tree were examined similarly at biweekly intervals from mid-July to late August.

To determine whether *T. piniperda* overwintered in shoots, 43, 55, and 56 visibly attacked shoots were randomly collected from trees in the young stand on 21 July, 16 October, and 9 November 1995 and examined for the presence of beetles. In addition, on 9 November 1995, 65 attacked shoots were collected from the ground and examined for the presence of adult beetles.

Results and Discussion

Timing of Brood Production. Adults of *T. piniperda* initiated galleries over a 2- to 3-week period in April during 1996 and 1997 (Fig. 1*a*). In 1996, the first attacks were observed on a day when the air temperature reached 14°C (17 April); prior to that, the mean temperature was 9°C or less. This pattern is similar to that seen previously in the

northern United States and Europe (Saarenmaa 1985), where flight initiation occurs when temperatures are at least 10–12°C over a full day (Bakke 1968). Adult beetles initiated their spring flight from February to March in China (Ye 1991), from February to late March in Michigan (Haack and Lawrence 1995) and southern Scandinavia and Sweden (Långström 1983; Schlyter and Lofqvist 1990), and from February to mid-April or mid-May in Finland (Salonen 1973).

The new generation completed development and emerged about 12–13 weeks (88 ± 5 d from median egg laying to median emergence) after gallery initiation (Fig. 1*a*). Emergence occurred over a 2-week period during July in both years (Fig. 1*a*). These results are similar to those under analogous temperature conditions. For example, Långström (1983) found that *T. piniperda* took 92 d to develop in southern Sweden and that most new beetles left their brood logs during the first half of July. In warmer areas, such as Kunming, China, Ye (1991) found that development from egg to adult took 45–60 d. At constant temperatures in the laboratory, median emergence has varied: 99 d at 14.5°C (Saarenmaa 1985), 80 d (Långström and Hellqvist 1985) and 85 d (Salonen 1973) at 15°C, 66 d at 17.6°C (Saarenmaa 1985), and only 30 d at 25°C (Salonen 1973).

In 1999, two broods were established by the parental generation, as evidenced by the co-occurrence of both eggs and late-instar larvae in midsummer. On 15 June, 50% of the six colonized Scots pine trees being examined contained late instars, whereas the other 50% contained eggs or early instars (Table 1). By 7 July, two thirds of the first brood had completed development and emerged, whereas about two thirds of the second brood had developed into late instars and pupae (Table 1). This suggests that two broods were produced, one in early spring (April) and one sometime in early to mid-June. Two broods of decreasing size were found both in China (Ye 1991) and Poland (Lutyk 1988). In France, Sauvard (1993) reported three brood phases of decreasing size between late June and late August.

Data from the transect survey conducted in early July showed that one tree had viable eggs or early instars under the bark, five had late instars or pupae, and four had unsuccessful egg-laying attempts (possibly owing to the large amounts of pitch produced by the tree). The remaining 21 trees had no evidence of infestation. Both broods had completed emergence by 27 July (Table 1), although one third (one of three trees) of the second brood had been pitched out, suggesting that, overall, second broods were successful in only a small proportion of trees. Ye (1991) also reported that many second-brood galleries were unsuccessful, owing to resin production by the tree. Similarly, Schroeder (1990) found that *T. piniperda* was successful at reproducing in only a small proportion of unhealthy standing trees.

In our study, no galleries were observed in trap-logs placed in the field during July. Similarly, Haack and Lawrence (1995) found that the number of galleries declined in trap-logs cut from February through May in Michigan, with no galleries being established later in the season. Långström (1986) also found that there were no attacks on trees felled after early June in northern Sweden, although small numbers of beetles occasionally continued to attack until late June and early July in southern Sweden.

The duration of each life stage for *T. piniperda* in the field varied but was generally similar to previous reports (Fig. 1*b*). Our study found that the first eggs were laid about 12 d after adults began colonizing the brood material [at a mean daily air temperature (MDAT) of 7.5°C], slightly longer than the 7 d at 10°C and only 4 d at 15°C observed by Salonen (1973) (Table 2). Eggs were present in the field over a 3.5-week period from early to late May in 1996 (MDAT = 10.6°C) (Table 2), a shorter period than previously reported for constant temperatures in the laboratory (Salonen 1973). First larvae were also observed earlier [35 d after the initiation of galleries (MDAT = 9.6°C); Table 2] than reported by Salonen (1973) (51 d at a constant 10°C). In this

TABLE 1. Proportion of galleries (n = 5 galleries per tree) with life stages of *Tomicus piniperda* in standing *Pinus sylvestris* near Waterloo, Ontario, during 1999.

Tree	15 June				7 July				27 July			
	Eggs and early instars	Late instars and pupae	Exit holes	Pitched	Eggs and early instars	Late instars and pupae	Exit holes	Pitched	Eggs and early instars	Late instars and pupae	Exit holes	Pitched
1	0.8	0.0	0.0	0.2	0.4	0.0	0.0	0.6	0.0	0.0	0.0	1.0
2	1.0	0.0	0.0	0.0	0.0	0.8	0.0	0.2	0.0	0.0	1.0	0.0
3	1.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0
4	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	1.0	0.0
5	0.0	1.0	0.0	0.0	0.0	0.8	0.2	0.0	0.0	0.0	1.0	0.0
6	0.0	1.0	0.0	0.0	0.0	0.6	0.4	0.0	0.0	0.0	1.0	0.0
% total	0.47	0.5	0.0	0.03	0.07	0.7	0.1	0.13	0.0	0.0	0.83	0.17

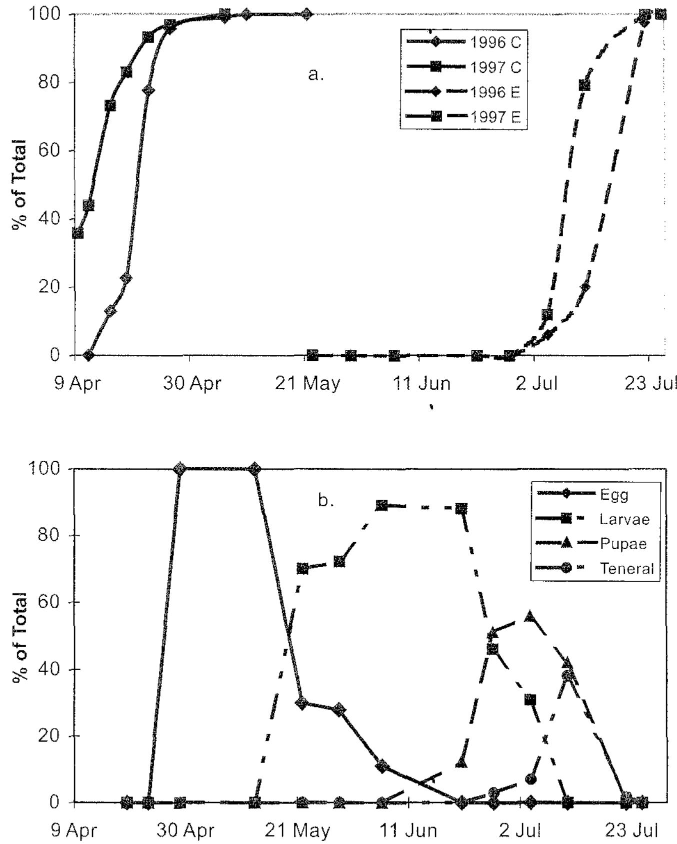

FIGURE 1. Phenology of *Tomicus piniperda* infesting *Pinus sylvestris* trap-logs during 1996 and 1997 in a 40-year-old plantation near Guelph, Ontario. (*a*) Pattern of colonization (C) by the parental generation and emergence (E) of the offspring (1996, n = 598 galleries and 589 exit holes; 1997, n = 168 galleries and 1449 exit holes). (*b*) Occurrence of the different life stages in the galleries (based on 10 galleries per log before 21 June and on all galleries in a log after 21 June).

study, the duration of both larval (32 d at MDAT = 16.6°C) (Table 1) and pupal (15 d at MDAT = 18.7°C) stages was similar to values reported in laboratory and field studies by Salonen (1973) and Ye (1994). We found that adults remained under the bark in a pre-emergence stage for about 10 d (MDAT = 18.4°C), a period similar to the 11 d at 15°C found by Salonen (1973) (Table 2).

The effective heat sums observed for both egg (79.6°d) and larval (267.3°d) stages of *T. piniperda* corresponded well with those of Salonen (1973), but were lower than those found by Ye (1994) (Table 3). In contrast, effective heat sums for the pupal and pre-emergence stages were higher than previously reported (Table 3). This suggests that overall brood production is similar for populations of *T. piniperda* in southern Ontario and Europe, but that slight variations in the timing of the different stages exist.

The egg heat sum value (°d > 0°C) we calculated was about 25% lower than that previously shown; however, values for both the larval and pre-emergence stages corresponded well with those reported by Knoche (1904) and Salonen (1973) (Table 3). Differences in methodology may account for the discrepancies observed between these

TABLE 2. Mean ± SE number of days until the first eggs and larvae were observed (from mean gallery initiation) and the duration of each developmental stage for *Tomicus piniperda* in *Pinus sylvestris* trap-logs placed in the field (southern Ontario) during 1996 compared with Salonen's (1973) study in

	Current study				Salonen (1973)	
		Air temperature (°C)*				
	Days ± SE	Mean	Minimum	Maximum	Days	Air temperature (°C)†
First egg	12±2	7.5	3.7	14.4	7	10
Egg	24±3	10.6	4.3	22.2	30–40	11
First larvae	35±3	9.6	3.7	22.2	51	10
Larvae	32±2	16.6	10.6	21.3	36	15
Pupae	15±2	18.7	15.3	24.3	17	15
Pre-emergent stage	10±1	18.4	14.8	23.1	11	15

*Daily temperatures derived from the Waterloo–Wellington Airport (Environment Canada), about 25 km from the field site, and confirmed with those from an on-site data logger.
†Based on constant temperatures in the laboratory.

TABLE 3. Comparative effective heat sums (°d > developmental-threshold temperature) and heat sums (°d > 0°C) required by different life stages of *Tomicus piniperda* developing in *Pinus sylvestris* trap-logs during 1996.

	Effective heat sums (°d > threshold)				Heat sums (°d > 0°C)		
		Current study					
	Salonen (1973)*	First*	Second†	Ye (1994)†	Current study	Knoche (1904)	Salonen (1973)
Egg‡	82	79.6±7.5	77±6.1	95.8	310.2±25.5	409	408
Larva	255	267.3±16.4	292.9±27.9	358.1	523.3±35.4	513	541
Pupa	107	139.1±24.7	152.3±38.2	115.9	245.1±42.3	154	257
Pre-emergent stage‡	24	43.2±12.3	—	—	171.2±38.4	142	167
Total	—	—	—	—	1249.8±73.3	1218	1375

*Developmental thresholds from Salonen (1973) used: egg, 8°C; larvae, 8°C; pupae, 8.8°C; pre-emergence adults, 13°C.
†Developmental thresholds from Ye (1994) used: egg, 8.2°C; larvae, 7.2°C; pupae, 7.9°C.
‡Sums calculated from median (50%) gallery initiation for the egg stage and to median (50%) adult emergence for the pre-emergence stage.

studies, as well as for the difficulty in determining the exact start and end dates of the stage (see footnote for egg and pre-emergence stages in Table 3).

Our total heat sum value for development of the first brood corresponds closely with other studies (Knoche 1904; Salonen 1973; Långström 1983), suggesting that about 1100–1300°d (> 0°C) are required by first-brood *T. piniperda* to develop from median spring swarming to median summer emergence. The mean ± SE heat sum value for the second brood observed in 1999 was 856.4 ± 124°d, a value less than those reported in the literature for either first or second broods (Knoche 1904; Salonen 1973). Our heat-sum values can be used to predict emergence for both generations of *T. piniperda*, thus helping managers and regulators to identify when infested material must be removed from the field to prevent future population buildup and damage.

Timing of Summer Shoot Feeding. Our study found that adult *T. piniperda* spent about 25% of the year feeding in shoots of the host trees (July through to September in

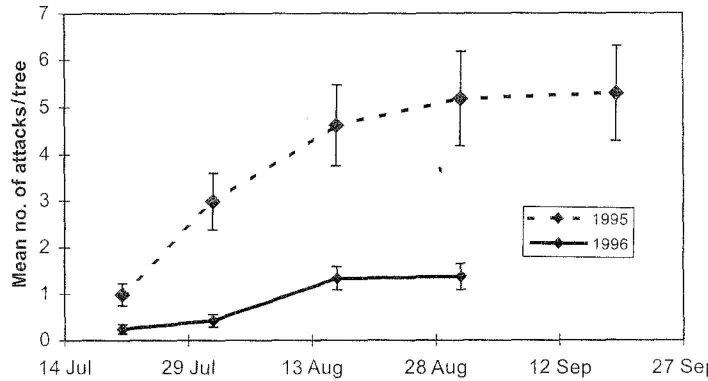

FIGURE 2. Mean ± SE number of shoots attacked per tree by adult *Tomicus piniperda* over the summer of 1995 and 1996 in a 10- to 12-year-old stand of *Pinus sylvestris* near Guelph, Ontario (n = 50 trees in 1995 and 35 trees in 1996).

1995) in southern Ontario (Fig. 2). The mean ± SD number of shoots attacked per tree increased over the summer of 1995 until late August—up to 5.28 ± 7.12 shoots per tree (Fig. 2). In 1996, overall populations in the stand were smaller, and little feeding was observed (mean ± SD number of shoots attacked per tree = 1.25 ± 0.71). Elsewhere, the onset and duration of shoot feeding by *T. piniperda* was found to vary with geographic location. In Kunming, for example, where the climate is warmer than in Ontario, adults spend two thirds of the year feeding on pine shoots (Ye 1991). Långström (1980) found that shoot feeding by the new generation of beetles began in July, and results from our study suggest that, during 1995, beetles were present in the shoots as early as mid-July. Thus, it appears that shoot feeding by *T. piniperda* in southern Ontario is similar to that in its native range, with feeding duration being dependent on local climatic conditions.

In 1995, almost 40% of the shoots attacked early in the summer were 1 year old, with the remainder being shoots of the current year (Fig. 3). In 1996, the majority of attacks were located in 1-year-old growth early in the season. Ryall (1997) provides details on the pattern of tree attack in a stand, although specific preferences were not ascertained at tree level. Långström (1980) found that 1-year-old shoots were attacked by the parental generation early in the summer after oviposition. Thus, the attacks observed in 1-year-old shoots early in 1995 and 1996 were likely due to the parental generation rather than to their offspring. Over the course of the summer, all subsequent attacks occurred on current-year growth (Fig. 3). Because we did not measure the availability of the two types of shoots, it is difficult to determine whether beetles displayed a preference for current-year shoots or whether they were simply more available. Långström (1980, 1983) found a large variation between study sites in the age of shoots attacked, with current-year shoots accounting for 1.5–67.3% and 1-year-old shoots for 31.5–98.5% of all attacks. Overall, we observed a lower proportion of attacks on 1-year-old shoots than did Långström (1980). It is possible that the older shoots in our study had hardened and were difficult to feed on; however, it is more likely that the intensive pruning associated with past Christmas tree production in our stand may have artificially increased the proportion of current-year shoots.

The percentage of shoots attacked that contained an adult beetle declined gradually over the summer of 1995. In the first sample (21 July), 75% of the shoots contained a feeding beetle and in the second (16 October), 45%; in the final sample (9 November), 25% of the shoots still contained a beetle. By this same date (9 November), 65 shoots

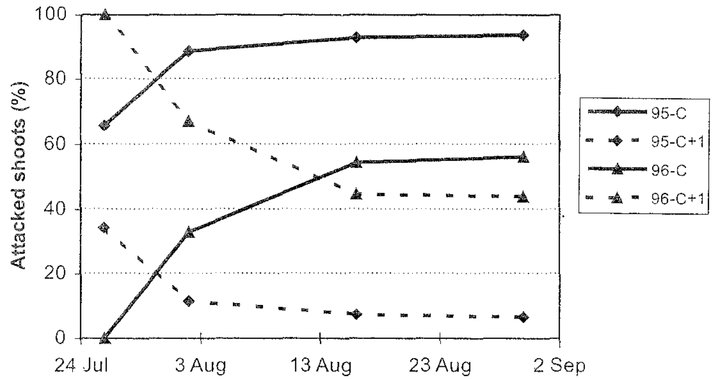

Figure 3. Percentage of *Pinus sylvestris* shoots of different ages (C = current year *versus* C + 1 = 1 year old) fed upon by adult *Tomicus piniperda* during 1995 and 1996 in a 10- to 12-year-old stand of *P. sylvestris* near Guelph, Ontario.

collected from the ground contained no feeding beetles. No further samples were taken. Previous results from Fennoscandia also found increasing numbers of empty attacks in October and November, until practically all the beetles had left the shoots (Långström 1983). It is likely that beetles overwinter under the bark at the tree base, as has been found in previous studies in similar climates (Salonen 1973), but this was not confirmed in our study.

Our study provides important parameters for the effective management of this introduced species. First, we have outlined the phenology of the pine shoot beetle and have provided heat sums and effective heat sums for its general life cycle, to help with the timing of control interventions in southern Ontario. Second, we have shown that, in southern Ontario, a second brood can be produced during long warm summers. Managers must be especially vigilant in making their assessments under such conditions, to prevent rapid population expansion and resulting damage. The occurrence of a second brood during warm summers is also important for regulators, because it means that beetles will be emerging from brood material up to and including the end of July or early August, rather than up to early July, with the result that quarantine restrictions must be extended to cover this period, to limit the spread and impact of the beetle.

Finally, shoot feeding by *T. piniperda* in tree crowns from early July through to the fall can be substantial and may have an impact on crown vigour. We observed adults feeding on shoots in the tree crown throughout this period: the parental generation feeds in 1-year-old shoots (from early to mid-July), whereas the emerging offspring feed on current-year shoots (August to September). Owing to the relative size of the parental and emerging populations, current-year foliage suffers the most damage. Thus, high levels of shoot feeding may have impact on the growth rate and long-term health of infested pine stands. Future research should focus on techniques to be used by forest managers to either prevent or reduce losses associated with this feeding activity, and should also examine the susceptibility of various pine stands to infestation by this exotic species.

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