

# Susceptibility of pine plantations to attack by the pine shoot beetle (*Tomicus piniperda*) in southern Ontario

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**Abstract:** The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), was first discovered in North America in 1992, and by the late 1990s it was associated with tree mortality and stand decline throughout southern Ontario. To assess whether this beetle was capable of killing vigorous trees (a primary pest) or would kill only trees already stressed (a secondary pest), we surveyed 43 sites of varying Scots pine (*Pinus sylvestris* L.), red pine (*Pinus resinosa* Ait.), and jack pine (*Pinus banksiana* Lamb.) composition. Specifically, our objective was to determine the relationship between tree and site characteristics and the number of stem and shoot attacks by *T. piniperda* in southern Ontario. An abundance of recently dead and low-vigour pine trees increased susceptibility of sites to stem and shoot attacks by *T. piniperda*. Significant negative linear relationships were detected between the number of beetle attacks and the mean height, age, diameter at breast height, basal area, canopy cover, duff depth, and radial growth increments. Pure red pine sites had significantly fewer attacks than sites of pure Scots pine and mixed jack pine, which was attributed to differences in tree vigour and forest management. *Tomicus piniperda* appears to be a secondary bark beetle in southern Ontario, successfully colonizing only recently dead pine trees or trees suffering from stress.

**Résumé :** L'hylésine des pins, *Tomicus piniperda* (L.) (Coléoptère : Scolytidae), a été observé pour la première fois en Amérique du Nord en 1992. Vers la fin des années 1990, cet insecte a été associé à la mortalité des arbres et au dépérissement des peuplements partout dans le sud de l'Ontario. Pour déterminer si cet insecte est capable de tuer des arbres vigoureux (ravageur primaire) ou seulement des arbres déjà affaiblis (ravageur secondaire), les auteurs ont inventorié 43 sites caractérisés par diverses compositions de pin sylvestre (*Pinus sylvestris* L.), de pin rouge (*Pinus resinosa* Ait.) et de pin gris (*Pinus banksiana* Lamb.). Plus spécifiquement, leur objectif consistait à cerner les relations entre les caractéristiques des arbres et du site et le nombre de tiges et de pousses attaquées par *T. piniperda* dans le sud de l'Ontario. Un grand nombre d'arbres morts récemment ou moribonds ont augmenté la vulnérabilité des sites aux attaques de la tige et des pousses par *T. piniperda*. Il y avait des relations linéaires négatives significatives entre le nombre d'attaques par les insectes et la hauteur moyenne, l'âge, le diamètre à hauteur de poitrine, la surface terrière, la fermeture du couvert, la profondeur de la litière et la croissance radiale. Les sites de pin rouge pur ont subi significativement moins d'attaques que les sites de pin sylvestre pur et de pin gris mélangé, vraisemblablement à cause des différences dans la vigueur des arbres et de l'aménagement forestier. Dans le sud de l'Ontario, *T. piniperda* semble être un insecte secondaire qui réussit à coloniser seulement les pins morts récemment ou les arbres qui subissent un stress.

[Traduit par la Rédaction]

## Introduction

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), is recognised as a serious pest in pine forests throughout its native range of Europe, North Africa, and Asia (Långström and Hellqvist 1991; Eidmann 1992). It was first discovered in Ohio in 1992, and it has subsequently been found in 45 municipalities of Ontario, 28 municipalities of Quebec, and more than 350 counties across 13 states

in the north-central and northeastern United States (Canadian Food Inspection Agency 2003). It was likely transported to North America during the 1980s aboard cargo ships carrying infested wooden packing material (Humphreys and Allen 1998; Haack and Poland 2001).

*Tomicus piniperda* feeds on both the shoots and the inner bark (phloem) of pine trees. Scots pine, *Pinus sylvestris* L., is the principal host of the beetle in its native range; however, the beetle will breed and shoot feed in most species of North American pines (Schroeder 1987; Sadof et al. 1994; Lawrence and Haack 1995). *Tomicus piniperda* breeds and lays eggs under the bark of dying or recently killed pine trees (Schroeder 1987; Långström and Hellqvist 1993). Soon after development, the progeny adults emerge and feed by mining the shoots of healthy or weakened pines, causing the shoots to break and fall to the ground. Shoot feeding results in a loss of foliage and has been demonstrated to significantly reduce tree growth (Långström and Hellqvist 1990, 1991; Czokajlo et al. 1997). In addition to impairing photosynthetic ability and stunting growth, intensive shoot feeding

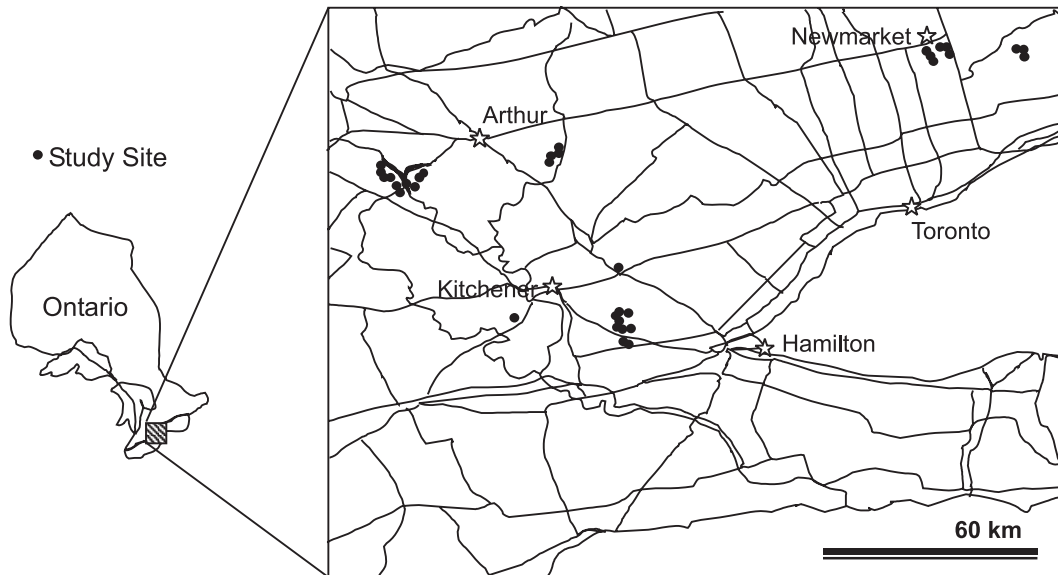
Received 12 March 2004. Accepted 30 July 2004. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 8 January 2005.

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**Fig. 1.** Locations of study sites in southern Ontario sampled for stem and shoot attacks by *Tomicus piniperda* in 2001.



reduces tree vigour and may predispose the trees to stem attacks (Ye 1991; Annala et al. 1999; Långström et al. 2002).

Information on the susceptibility of North American pine forests to shoot and stem attacks by *T. piniperda* is limited. The beetle has been extensively studied in its native range; however, most of the studies have focussed on its breeding biology and on individual tree susceptibility and vulnerability to stem attack. Few studies have considered the forest characteristics that affect the susceptibility of sites to shoot and stem attacks by *T. piniperda*. Haack and Lawrence (1995) found that when breeding material was plentiful, attack densities of *T. piniperda* were high on Scots pine trap logs in Michigan, Indiana, and Ohio. Långström and Hellqvist (1990, 1991) demonstrated that shoot damage increased significantly the closer the trees were to a timber storage yard in Sweden, and Annala and Heikkilä (1991) found that shoot damage by *T. piniperda* in Finland was greater in stands that contained large-diameter felled trees than on sites in which the largest felled trees had been removed. Only one known study has directly linked forest characteristics to the rate of shoot pruning by *T. piniperda*. Amezaga (1997) observed that altitude, incidence of fires and thinning, forest sanitation, and the presence of other insect defoliators affected the susceptibility of trees and sites to shoot pruning by *T. piniperda* in northern Spain.

In southern Ontario, there are numerous stands and plantations of Scots pine, red pine (*Pinus resinosa* Ait.), and jack pine (*Pinus banksiana* Lamb.). By the late 1990s, many of these plantations were heavily infested with *T. piniperda* and suffered from considerable tree mortality and stand decline. It appeared that populations of the beetle were growing rapidly in size and distribution, and there was concern that the beetle would begin to kill healthy and vigorous trees. Because the ability to rate the susceptibility of forests to attack by *T. piniperda* would be of importance in reducing attacks or in slowing the further spread of this beetle in North America, we initiated a study to determine the relationship between tree and site characteristics and the number of stem and shoot attacks by *T. piniperda* in southern Ontario. Data

derived from this work also provided insight into whether *T. piniperda* was a primary beetle (able to colonize and successfully produce offspring in healthy, vigorous pine trees) or a secondary beetle (able to colonize only recently killed or severely stressed trees) in southern Ontario.

## Materials and methods

### Study sites

The study was conducted between June and December 2001 in southern Ontario, Canada. Forty-three sites were selected within the municipalities of Wellington County, Hamilton–Wentworth Region, and York Region (Fig. 1). These three municipalities contained large numbers of pine plantations of various species compositions, were within the beetle's known distribution for 3 years or longer, and were close to each other, thus reducing any intersite differences in climate and arrival date of the beetles. The sites surveyed in this study were located within pine plantations of varying compositions of Scots, red, and jack pine. Plantations were established as forested stands on government-owned land and were maintained by the Ontario Ministry of Natural Resources or the appropriate conservation authorities. On the basis of availability, 16 pure Scots pine sites, 9 pure red pine sites, 2 pure jack pine sites, and 16 mixed pine sites were surveyed. Study sites were a minimum of 70 m × 70 m in size and ranged in plantation ages from 27 to 70 years (mean = 42.23; SE = 1.63). Sites were chosen only on the basis of their size, characteristics, and availability, independent of the levels of beetle attack.

### Sampling and data collection

A randomly located starting point was selected within each site at a minimum distance of 35 m from any edge. From this selected starting point, four 30 m × 5 m transects were positioned at right angles to each other; data collection started at the 5-m mark of each transect, to prevent overlap. The first transect was positioned at a random compass direc-

tion, and the remaining three transects were offset by 90°, 180°, and 270°.

Diameters at breast height (DBHs) of all trees having >5 cm DBH were collected along each transect. A cut-off point of 5 cm was used, because diameters less than this are not frequently selected as brood material by *T. piniperda* (Annala and Heikkilä 1991). Sample measurements on each pine tree (>5 cm DBH) included DBH, species, crown position, and crown density (<25%, 25%–50%, or >50% relative foliage). These crown density scores indicated the amount of foliage relative to that of a completely dense tree of the same species and did not necessarily mean that a tree had lost foliage (Innes 1990). The typical crown density score for a vigorous plantation-grown pine tree in our study was >50% relative foliage, which did not change among species.

The volume of downed woody debris (>5 cm diameter) was measured along each transect with the line intercept method developed by Van Wagner (1968). The density and DBH of all standing dead pine trees (snags) (>5 cm DBH) along each transect were recorded. The species and stage of decay of all measured coarse woody debris were recorded with a five-stage decay classification system adapted from Thomas et al. (1979). Only snags in decay classes 1–3 were used in the analysis. Class 1 snags represented trees that had recently died and were characterized by intact bark, with twigs and often some dead needles still attached. Class 2 snags represented trees that had been dead for a year or two and were showing signs of decay, such as loose bark. Class 3 snags represented trees that had been dead for several years and were beginning to show more advanced signs of decay, such as sloughing of the bark and the absence of all twigs and most branches. Snags in these three decay classes represented recent-past, present, and future sources of breeding material for the beetles. Snags in decay classes 4 and 5 were left out of the analysis, because these snags were in advanced stages of decay and probably would not have been used by *T. piniperda* for reproduction.

The total heights of two dominant or codominant pine trees per transect were measured with a clinometer and used to estimate stand height. Canopy cover was estimated at four points along each transect with a spherical densiometer. The canopy cover was measured in February 2002 to avoid the influence of deciduous understory.

Four dominant or codominant pine trees were selected along each transect at random and cored at breast height. A bark gauge was used to measure the bark thickness of each cored tree at breast height. Individual cores were air dried, glued into slotted mounting boards, and sanded. Ring widths of increment cores were measured to the nearest 0.01 mm with a dissecting microscope equipped with a sliding stage interfaced with a computer. The age, periodic growth ratio (current 5-year radial growth increment divided by the previous adjacent 5-year radial growth increment), and 2000, 1999–2000, and 1996–2000 radial growth increments were determined for each core. When obvious false rings (drought or frost rings) were identified in the cores, these rings were excluded from the measurement. No attempt was made to identify missing growth rings.

Feel test methods for describing soils (Ontario Institute of Pedology 1985) were used to determine soil texture at 15-cm depth at the 10-m mark of the first and third transects, and

duff depth was measured as described by McRae et al. (1979). More detailed information regarding the soil characteristics of the sites was obtained from regional soil survey maps (Hoffman and Richards 1955; Hoffman et al. 1963; Presant et al. 1965).

Sites were categorized as having been previously thinned or not, on the basis of the presence or absence of stumps and (or) cut trees. Thinning occurred many years before the study (ca. 1950s–1996), making it difficult to determine exact harvest dates. Thus, except for a few sites where this information was known, logging dates were estimated on the basis of the stage of decay observed in the stumps and slash. The frequency of thinning and the amount of wood removed varied considerably between sites, as they were thinned to remove trees of low vigour and to reduce competition for the remaining trees. Although proximity of the sites to areas that had been recently logged was not known, no heavily logged stands or timber piles were observed near the sites, nor was there any evidence of recent storm damage.

### Intensity of the beetle infestation

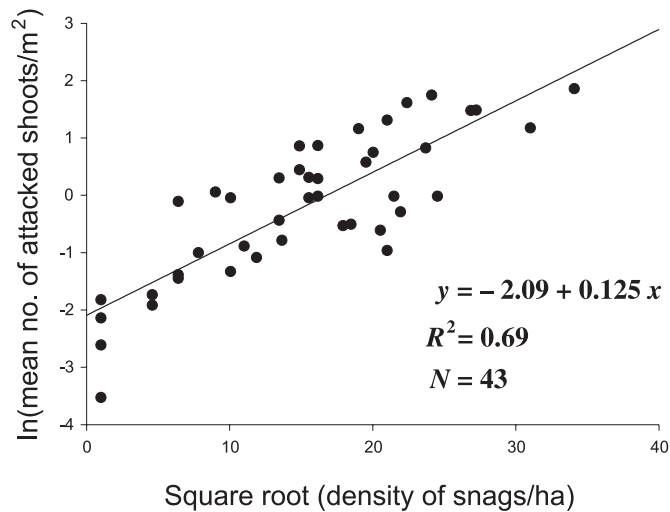
Shoots attacked by the pine shoot beetle were counted on the forest floor from 10 November to 22 December 2001 after shoot feeding by the beetles was completed (Haack and Lawrence 1997; Ryall and Smith 2000). Attacked shoots were identified as having a frass-free tunnel bored from the base of the shoot toward the tip. Attacked shoots were counted and assigned to the current year's or previous year's attack, depending on the condition of the shoot. Only shoots attacked by *T. piniperda* in the current year (2001) were used in the statistical analysis. Attacked shoots were counted in a total of sixty-eight 1 m × 1 m quadrats per site. Quadrats were positioned every 3 m along each transect and in all four compass directions around the base of two pine trees per transect with ≥25% crown density values. Shoots hollowed out by *T. piniperda* may not break off equally among species (Sadof et al. 1994); therefore, shoots were counted as late in the season as possible to allow for shoots to break off and drop. Sites were sampled in random order to reduce any effect of sampling date.

The number of living pine trees attacked by *T. piniperda* was determined along each transect and converted to the number of pine trees attacked per hectare. Beetle attacks on living trees were easily identified by the presence of resin exuding from the point of entry. Each potential attack was excavated with a knife to reveal the gallery shape and size. Only attacks that could be positively identified as pine shoot beetle attacks were recorded; attacks were identified by the distinctive shape and size of the gallery and entrance hole or by the presence of adult beetles in the galleries. Brood success or failure was noted for all attacks by observing the presence or absence of brood galleries and exit holes. The species, DBH, crown position, and crown density of all attacked trees were recorded.

### Statistical analysis

The dependent variables used in the analyses were the mean number of shoots attacked by *T. piniperda* per square metre and number of attacked pine trees per hectare. Using the technique of all possible regressions, both simple and multiple linear regression analyses (PROC REG, SAS Insti-

**Fig. 2.** Relationship between the mean numbers of shoots per square metre attacked by *Tomicus piniperda* in 2001 and the density of recently dead pine snags per hectare for study sites located in southern Ontario.



tute Inc. 1985a) were used to identify relationships between the dependent variables and the tree and site variables. To correct for departures from normality, we transformed the mean number of shoots attacked by *T. piniperda* per square metre by using a natural logarithmic transformation; and we transformed both the number of attacked trees per hectare and the density of snags per hectare by using square-root transformations. Variables were tested at the  $p = 0.05$  level of significance. Errors were tested for normality and constant variance by using normal probability plots (PROC UNIVARIATE, SAS Institute Inc. 1985b) and plots of residual values versus predicted values. A Pearson's correlation matrix (PROC CORR, SAS Institute Inc. 1985b) was used to identify correlations between the independent variables.

Because of sampling design and tree availability, the number of cored trees for each pine species (Scots, red, and jack) differed between sites. To identify relationships among the dependent variables and tree growth, a weighted simple linear regression analysis was performed (PROC REG, SAS Institute Inc. 1985a). Mean radial growth increments per site were weighted by the square root of the number of cores that the means were calculated from. This analysis was done separately for each species. Growth data from 375 Scots pine cores across 29 sites, 209 red pine cores across 16 sites, and 104 jack pine cores across 14 sites were used for the analysis. Site-specific radial growth means were calculated for 2–16 cores per site.

Sites were grouped according to species (Scots, red, jack, Scots mix, red mix, or jack mix), thinning category, soil type, soil texture, and soil parent material. The placement of sites into species categories was determined by the percentage of each pine species within the site. In pure species sites, >90% of the total pine density was that of the pine species listed; and mixed species sites contained >60% of the pine species listed. A one-way analysis of variance (ANOVA) (PROC GLM, SAS Institute Inc. 1985a) was used to compare dependent variable means between treatments. When the ANOVA results were significant ( $p = 0.05$ ), a

Tukey's multiple comparisons test was used to determine which treatments differed significantly. Homogeneity of variance was tested with Levene's test.

The probability of stem attack by *T. piniperda* on an individual living pine tree was a binary dependent variable; thus, logistic regression (PROC LOGIST, SAS Institute Inc. 1985a) was used to examine the relationships between the probability of *T. piniperda* stem attack and species, DBH, crown position, and crown density. Logistic regression analysis was done on each species individually.

## Results

### Relationship between site and tree characteristics and *T. piniperda* shoot attacks

The number of shoots attacked by *T. piniperda* per square metre per site ranged from 0.03 to 6.43 (mean = 1.54; SE = 0.25;  $n = 43$ ). The single variable that explained the greatest amount of variation in the number of attacked shoots among study sites was the density of recently dead pine snags per hectare ( $P < 0.0001$ ;  $R^2 = 0.69$ ) (Fig. 2). Significant negative relationships were found between the number of shoots attacked and six of the site variables measured, with relationships with the mean height of pine ( $P < 0.0001$ ;  $R^2 = 0.59$ ) and the mean pine canopy cover ( $P < 0.0001$ ;  $R^2 = 0.58$ ) being the most significant (Table 1). Significant negative linear relationships also were found between the number of attacked shoots and the mean DBH of pine ( $P < 0.0001$ ;  $R^2 = 0.48$ ), the basal area of pine ( $P < 0.0001$ ;  $R^2 = 0.35$ ), the mean duff depth ( $P = 0.001$ ;  $R^2 = 0.24$ ), and the mean age at breast height ( $P = 0.002$ ;  $R^2 = 0.22$ ) (Table 1). There were no significant linear relationships found between the number of attacked shoots and the volume of downed wood ( $P = 0.69$ ), the mean bark thickness ( $P = 0.64$ ), the basal area of deciduous trees ( $P = 0.06$ ), and the total density of trees ( $P = 0.37$ ). Several significant multivariate models were also found that explained 70%–79% of the variation in the number of attacked shoots (Table 1).

From a Pearson's correlation matrix (Table 2), the height, canopy cover, DBH, basal area of pine, duff depth, and age all showed significant positive correlations, whereas the density of snags was negatively correlated with these variables. Significant correlations were also found between the total density (>5 cm DBH) of living trees and the mean DBH, bark thickness, and basal area of deciduous trees.

Weighted regression analysis detected many significant relationships between the number of attacked shoots and the mean radial growth increments of Scots, jack, and red pine (Table 3). The number of attacked shoots decreased with increasing mean radial growth increments in Scots pine for 2000 and 1999–2000 (Table 3), and the number of attacked shoots was also negatively related to the mean radial growth increments of jack pine for 2000, 1999–2000, and 1996–2000 (Table 3). Similarly, a negative linear relationship was found between the number of attacked shoots and the mean periodic growth ratio (1996–2000 growth:1991–1995 growth) for red pine (Table 3).

Significantly fewer attacked shoots were found in sites that had been previously thinned than in unthinned sites ( $F_{[1,41]} = 19.21$ ;  $P < 0.0001$ ;  $R^2 = 0.32$ ) (Table 4). The density of snags per hectare also was found to be significantly

**Table 1.** Other significant regression models from the regressions of site and tree variables with the number of shoots per square metre (natural-log transformed) attacked by *Tomicus piniperda* in southern Ontario in 2001 ( $n = 43$ ).

Variable(s) used in model	Regression model	$R^2$
Mean height of pine (m)	Shoots = 4.75 – 0.293 (height)	0.59
Mean pine canopy cover (%)	Shoots = 2.25 – 0.050 (cover)	0.58
Mean DBH (cm)	Shoots = 3.54 – 0.184 (DBH)	0.48
Basal area of pine (m <sup>2</sup> /ha)	Shoots = 1.72 – 0.080 (bapine)	0.35
Mean duff depth (cm)	Shoots = 0.82 – 0.434 (duff)	0.24
Mean age of pine at breast height (years)	Shoots = 2.11 – 0.055 (age)	0.22
Density of pine snags (n/ha); mean height of pine (m)	Shoots = 0.94 + 0.085 (snags) – 0.145 (height)	0.76
Density of pine snags (n/ha); mean pine canopy cover (%)	Shoots = –0.42 + 0.087 (snags) – 0.024 (cover)	0.74
Density of pine snags (n/ha); basal area of pine (m <sup>2</sup> /ha)	Shoots = –1.15 + 0.108 (snags) – 0.029 (bapine)	0.72
Mean pine canopy cover (%); mean height of pine (m)	Shoots = 4.29 – 0.032 (cover) – 0.179 (height)	0.71
Mean pine canopy cover (%); mean DBH (cm)	Shoots = 3.77 – 0.039 (cover) – 0.108 (DBH)	0.70
Density of pine snags (n/ha); mean pine canopy cover (%); mean height of pine (m)	Shoots = 1.54 + 0.067 (snags) – 0.017 (cover) – 0.117 (height)	0.79

**Note:** All variables used in the models were significant at  $\alpha = 0.05$ . Bapine, basal area of pine; DBH, diameter of pine at breast height; shoots, number of shoots per square metre attacked by *T. piniperda*. Density of pine snags was square-root transformed before analysis.

**Table 2.** Pearson correlation matrix of site and tree characteristics of study sites sampled for *Tomicus piniperda* in southern Ontario in 2001 ( $n = 43$ ).

	Snags	Height	Cover	DBH	Bapine	Duff	Age	Density	Bark	Badec
Snags	1.00 <sup>a</sup>									
Height	–0.69	1.00								
Cover	–0.73	0.65	1.00							
DBH	–0.70	0.86	0.51	1.00						
Bapine	–0.52	0.74	0.67	0.61	1.00					
Duff	–0.50	0.41	0.63	0.21	0.52	1.00				
Age	–0.48	0.63	0.42	0.50	0.43	0.40	1.00			
Density	0.06	–0.16	0.20	–0.31	0.23	0.18	–0.15	1.00		
Bark	–0.04	0.06	0.03	0.19	–0.04	–0.17	0.10	–0.32	1.00	
Badec	0.02	–0.15	–0.27	–0.06	–0.16	–0.05	–0.07	0.32	–0.13	1.00

**Note:** Badec, basal area of deciduous trees; bapine, basal area of pine; bark, mean bark thickness of pine; DBH, mean diameter of pine at breast height; density, total density of living trees (>5 cm DBH); snags, density of pine snags per hectare (square-root transformed); duff, mean duff depth.

<sup>a</sup> $r_{0.05} = 10.311$ ;  $r_{0.01} = 10.321$ .

different among sites that had been thinned and those that had not received thinning ( $F_{[1,41]} = 11.66$ ;  $P = 0.002$ ;  $R^2 = 0.22$ ) (Table 4).

The number of attacked shoots differed significantly between species ( $F_{[5,37]} = 5.87$ ;  $P = 0.0004$ ;  $R^2 = 0.44$ ); pure red pine sites had 87%, 85%, and 79% fewer attacked shoots than sites composed of Scots pine mix, pure Scots pine, and jack pine mix, respectively. Pure sites of jack pine and mixed red pine sites had intermediate numbers of attacked shoots and did not differ significantly from the other site types (Table 5). The number of snags per hectare on pure red pine sites were significantly different from those on sites consisting of pure Scots pine ( $F_{[5,37]} = 2.55$ ;  $P = 0.04$ ;  $R^2 = 0.26$ ) (Table 5). Also, significant differences in the mean height ( $F_{[5,37]} = 8.54$ ;  $P < 0.0001$ ;  $R^2 = 0.54$ ) and DBH ( $F_{[5,37]} = 8.59$ ;  $P < 0.0001$ ;  $R^2 = 0.54$ ) were found between species categories, whereas the mean age of trees was not significantly different between species ( $F_{[5,37]} = 0.79$ ;  $P = 0.56$ ;  $R^2 = 0.10$ ) (Table 5). Management practices in the form of thinning also differed between species categories (Table 5). Pure red pine sites and mixed red pine sites had been thinned prior to this

study at a rate of 56% and 75%, respectively, whereas only 29% of the mixed Scots pine sites, 25% of the pure Scots pine sites, and none of the pure or mixed jack pine sites had been previously thinned (Table 5). The density of Scots pine in the mixed pine sites had no effect on the number of native pine shoots attacked by *T. piniperda* ( $P = 0.64$ ;  $n = 14$ ).

The number of attacked shoots differed between soil types ( $F_{[2,40]} = 6.41$ ;  $P = 0.004$ ;  $R^2 = 0.24$ ), with sites on loamy soils having significantly more attacked shoots than sites on sandy soils and sandy loam soils (Table 6). The density of snags per hectare did not differ significantly between soil types ( $F_{[2,40]} = 2.65$ ;  $P = 0.08$ ;  $R^2 = 0.12$ ) (Table 6).

The number of attacked shoots also differed between soil parent material classes ( $F_{[4,38]} = 5.54$ ;  $P = 0.001$ ;  $R^2 = 0.37$ ), with sites of calcareous sandy outwash or medium-grained to fine sand parent material having significantly fewer attacked shoots than sites of clay loam till parent material (Table 6). Other differences in the number of attacked shoots between parent material classes were not significant. Significant differences in the density of snags per hectare were detected among sites with parent materials consisting of medium-

**Table 3.** Regression parameters from the weighted regression analyses modelling the mean radial growth increments of pine per site with the number of shoots per square metre (natural-log transformed) and pine trees per hectare (square-root transformed) attacked by *Tomicus piniperda* in southern Ontario in 2001.

Growth interval	No. attacked shoots/m <sup>2</sup>				No. attacked trees/ha			
	$\beta_0$	$\beta_1$	<i>P</i>	<i>R</i> <sup>2</sup>	$\beta_0$	$\beta_1$	<i>P</i>	<i>R</i> <sup>2</sup>
<b>Scots pine (sites = 29, cores = 375)</b>								
2000	1.49	-15.2	0.002	0.30*	8.95	-37.3	0.03	0.16*
1999-2000	1.71	-8.23	0.002	0.30*	9.12	-17.9	0.06	0.13
1996-2000	0.83	-1.22	0.41	0.03	7.18	-2.64	0.60	0.01
1996-2000/1991-1995	1.02	-0.91	0.09	0.11	8.56	-3.15	0.07	0.11
<b>Jack pine (sites = 14, cores = 104)</b>								
2000	1.33	-14.5	0.04	0.30*	11.40	-60.1	0.13	0.18
1999-2000	1.43	-7.43	0.03	0.33*	11.20	-25.8	0.19	0.14
1996-2000	1.66	-3.15	0.04	0.31*	12.70	-12.6	0.14	0.17
1996-2000/1991-1995	1.68	-1.71	0.08	0.24	15.30	-10.2	0.05	0.29*
<b>Red pine (sites = 16, cores = 209)</b>								
2000	-0.10	-12.2	0.07	0.21	4.99	-17.9	0.35	0.06
1999-2000	-0.30	-4.94	0.17	0.13	4.59	-6.71	0.51	0.03
1996-2000	-0.31	-1.83	0.23	0.09	4.24	-1.83	0.67	0.01
1996-2000/1991-1995	1.83	-3.78	0.01	0.37*	12.40	-11.1	0.005	0.44*

**Note:** Mean radial growth increments per site were weighted by the square root of the number of cores that the means were calculated from. \*, *P* < 0.05.

**Table 4.** Comparison of the numbers of shoots per square metre (natural log transformed) and pine trees per hectare (square-root transformed) attacked by *Tomicus piniperda* in southern Ontario in 2001 and the total density of pine snags per hectare of thinned and unthinned sites.

	Mean no. of attacked shoots/m <sup>2</sup>	Mean no. of attacked trees/ha	Mean no. of snags/ha	No. of sites
Thinned	0.69 (0.34)a	20.0 (5.9)a	120.0 (42.8)a	14
Not thinned	1.95 (0.31)b	49.7 (11.5)b	384.8 (49.6)b	29

**Note:** Standard errors in parentheses. Means within a column followed by the same letter were not significantly different at  $\alpha = 0.05$  (Tukey's multiple comparisons test).

grained to fine sand and clay loam till ( $F_{[4,38]} = 3.45$ ;  $P = 0.02$ ;  $R^2 = 0.27$ ) (Table 6).

Sites with sandy clay loam soil textures had significantly fewer attacked shoots than sites with silty clay and silty clay loam soil textures ( $F_{[6,36]} = 3.39$ ;  $P = 0.01$ ;  $R^2 = 0.36$ ) (Table 6). Other differences in the number of attacked shoots between soil texture classes were not significant. Similarly, differences in the density of snags per hectare were not significant between soil texture classes ( $F_{[6,36]} = 0.78$ ;  $P = 0.59$ ;  $R^2 = 0.11$ ) (Table 6).

#### Relationship between site and tree characteristics and *T. piniperda* stem attacks

The total number of pine trees attacked by *T. piniperda* per site ranged from 0 to 15 (mean = 2.00; SE = 0.41;  $n = 43$ ). Of the 1455 living jack, red, and Scots pine trees examined, 91 were attacked by *T. piniperda*, and only 8 of the attacks were successful (offspring produced).

Linear regression analysis on the number of pine trees attacked by *T. piniperda* per hectare as the dependent variable showed results similar to those of the regression analysis on the number of attacked shoots per square metre as the dependent variable (Table 7). In fact, the number of pine trees

attacked was significantly related to the number of shoots attacked by *T. piniperda* ( $P < 0.0001$ ;  $R^2 = 0.43$ ). As with shoot attacks, the four variables that explained the greatest amount of variation in the number of pine trees attacked by *T. piniperda* among sites were canopy cover, height, DBH, and density of snags per hectare (Table 7). Several significant multivariate models were found that explained 50%–51% of the variation in the number of trees attacked (Table 7).

Weighted linear regression analysis showed that the number of pine trees attacked by *T. piniperda* increased with decreasing mean radial growth increments of Scots pine for 2000 and with periodic growth ratios of jack pine and red pine (Table 3). Significantly fewer pine trees were attacked on thinned sites than on unthinned ones ( $F_{[1,41]} = 4.54$ ;  $P = 0.04$ ;  $R^2 = 0.10$ ) (Table 4).

As with the number of attacked shoots, the one-way ANOVA and Tukey's multiple comparisons test showed that the number of attacked pine trees differed significantly between species ( $F_{[5,37]} = 6.22$ ;  $P = 0.0003$ ;  $R^2 = 0.46$ ) (Table 5). Mixed jack pine sites had significantly more attacked trees than sites with compositions of pure red pine and Scots pine mix (Table 5). Sites of pure red pine also had significantly

**Table 5.** Differences in the number of shoots per square metre and pine trees per hectare attacked by *Tomicus piniperda* in southern Ontario in 2001 and the total density of snags per hectare, total height, DBH, age, and percentage of sites thinned among study sites of different pine species compositions.

Pine species	Mean no. of attacked shoots/m <sup>2</sup>	Mean no. of attacked trees/ha	Mean no. of snags/ha	Mean height (m)	Mean DBH (cm)	Mean age (years)	% of sites thinned	No. of sites
Pure red	0.30 (0.11)a	6.7 (4.7)a	57.8 (36.40)a	20.9 (0.80)a	26.3 (1.4)a	47.3 (3.6)a	55.6	9
Red mix	1.33 (1.02)ab	30.0 (17.3)abc	250.0 (158.90)ab	19.2 (2.26)ab	21.5 (1.8)ab	44.8 (8.9)a	75.0	4
Pure Scots	1.99 (0.43)b	45.0 (7.4)bc	403.8 (73.90)b	15.5 (0.49)b	19.1 (0.8)b	41.2 (2.8)a	25.0	16
Scots mix	2.36 (0.85)b	20.0 (6.2)ab	328.6 (98.70)ab	15.7 (0.70)b	18.4 (1.4)b	40.3 (3.2)a	28.6	7
Pure jack	1.21 (0.57)ab	40.0 (20.0)abc	280.0 (100.00)ab	15.4 (2.40)ab	17.5 (1.1)b	43.5 (4.5)a	0.0	2
Jack mix	1.44 (0.33)b	120.0 (52.5)c	400.0 (65.42)ab	14.4 (0.68)b	15.9 (0.8)b	36.6 (2.9)a	0.0	5

**Note:** Standard errors in parentheses. Means within a column followed by the same letter were not significantly different at  $\alpha = 0.05$  (Tukey's multiple comparisons test). DBH, diameter at breast height; height, mean total height of pine.

fewer attacked trees than sites of pure Scots pine (Table 5). Other differences in the number of pine trees attacked among species composition classes were not significant (Table 5).

More trees were attacked by the pine shoot beetle on sites with loamy soils than on sites with sandy soils ( $F_{[5,37]} = 3.94$ ;  $P = 0.03$ ;  $R^2 = 0.16$ ), whereas the number of attacked trees on sites with sandy loam soils were not significantly different from those on sites with the other soil types (Table 6).

Similarly, sites with calcareous sandy outwash, medium-grained to fine sand, or <30 cm of loam till over bedrock parent soil material had fewer attacked trees than sites with clay loam till parent material ( $F_{[4,38]} = 7.27$ ;  $P = 0.0002$ ;  $R^2 = 0.43$ ), whereas the number of attacked trees on sites with loam till parent material were not significantly different from those on sites with the other parent materials (Table 6). The number of attacked trees did not differ significantly between soil texture classes ( $F_{[6,36]} = 1.80$ ;  $P = 0.13$ ;  $R^2 = 0.23$ ) (Table 6).

The probability of *T. piniperda* attacking stems was significantly greater for jack pine than for Scots pine and red pine and significantly greater for Scots pine than for red pine ( $N = 1455$ ; Wald  $\chi^2 = 34.98$ ;  $P < 0.0001$ ) (Table 8). A total of 13.3% of the jack pine trees were attacked (44 attacks on 332 trees), and 9.1% (4 attacks) of these attacks were successful. Scots pine trees were attacked at a rate of 5.5% (38 attacks on 694 trees), with 10.5% (4 attacks) of the attacks being successful. Red pine was attacked at a rate of 2.1% (9 attacks on 429 trees), and there were no successful attacks.

Crown density appeared to have influenced the susceptibility of trees to stem attack: for all species grouped together, 53.8% of the attacks were on trees carrying <25% relative foliage, 23.1% of the attacks were on trees with 25%–50% foliage, and 23.1% of the attacks were on trees carrying >50% foliage. The probability of attack differed significantly between Scots pine trees of various crown density scores (Wald  $\chi^2 = 24.56$ ;  $P < 0.0001$ ) (Table 9). Trees with <25% foliage were more likely to be attacked than those with crown densities of 25%–50% and trees with >50% foliage (Table 9). There was no significant difference in the probability of stem attack between trees with crown densities of 25%–50% and trees with >50% foliage (Table 9) or between Scots pine trees of varying crown positions (Wald  $\chi^2 = 5.06$ ;  $P = 0.28$ ) and DBH (Wald  $\chi^2 = 2.99$ ;  $P = 0.08$ ).

Jack pine with 25%–50% foliage had a significantly greater probability of being attacked than trees with >50% foliage (Wald  $\chi^2 = 18.51$ ;  $P < 0.0001$ ) (Table 9). There were no significant differences in the probability of attack between jack pine with <25% foliage and jack pine with crown densities of 25%–50% and >50% (Table 9). Similarly, the probability of stem attack did not differ between jack pine trees on the basis of crown position (Wald  $\chi^2 = 2.96$ ;  $P = 0.56$ ) or DBH (Wald  $\chi^2 = 0.33$ ;  $P = 0.57$ ).

As was found for Scots pine and jack pine, the probability of attack differed significantly between red pine trees of differing crown density scores (Wald  $\chi^2 = 19.81$ ;  $P < 0.0001$ ) (Table 9). Red pine trees with <25% foliage were significantly more likely to be attacked than red pine trees with >50% foliage (Table 9). There were no significant differences in the probability of attack found between red pine trees with 25%–50% foliage and red pine with <25% and

**Table 6.** Comparison of the number of shoots per square metre and pine trees per hectare attacked by *Tomicus piniperda* in southern Ontario in 2001 and the total density of snags per hectare among study sites of various soil types, parent materials, and soil textures.

	Mean no. of attacked shoots/m <sup>2</sup>	Mean no. of attacked trees/ha	Mean no. of snags/ha	No. of sites
<b>Soil type</b>				
Loam	2.18 (0.37)a	56.0 (13.0)a	359.2 (57.5)a	25
Sand	0.71 (0.17)b	17.1 (4.6)b	260.0 (59.8)a	14
Sandy loam	0.42 (0.17)b	20.0 (8.2)ab	55.0 (17.1)a	4
<b>Parent material</b>				
Calcareous sandy outwash	0.71 (0.17)a	17.1 (4.6)a	260.0 (59.8)ab	14
Medium-grained to fine sand	0.42 (0.17)a	20.0 (8.2)a	55.0 (17.1)a	4
Loam till	1.71 (0.88)ab	33.3 (17.6)ab	226.0 (41.3)ab	3
Loam till over bedrock	1.08 (0.33)ab	20.0 (5.2)a	246.7 (123.5)ab	10
Clay loam till	3.21 (0.57)b	91.7 (22.6)b	498.3 (99.0)b	12
<b>Soil texture</b>				
Sandy clay loam	0.05 (0.02)a	0.0 (0.0)a	0.0 (0.0)a	2
Silty sand	0.82 (0.24)ab	16.0 (7.5)a	192.0 (73.1)a	5
Loamy sand	0.89 (0.30)ab	26.7 (6.7)a	373.3 (96.0)a	6
Sandy loam	0.88 (0.49)ab	10.0 (10.0)a	340.0 (100.0)a	2
Clay loam	0.38 (0.22)ab	10.0 (10.0)a	170.0 (170.0)a	2
Silty clay	1.57 (0.85)b	60.0 (30.6)a	386.7 (286.9)a	3
Silty clay loam	2.14 (0.40)b	54.8 (13.8)a	324.3 (57.8)a	23

**Note:** Standard errors in parentheses. Means within a column followed by the same letter were not significantly different at  $\alpha = 0.05$  (Tukey's multiple comparisons test).

**Table 7.** Significant regression models from the regression of site and tree variables with the number of pine trees per hectare attacked by *Tomicus piniperda* in southern Ontario in 2001.

Variable(s) used in model	Regression model	R <sup>2</sup>
Mean pine canopy cover (%)	Stems = 11.22 – 0.129 (cover)	0.42
Mean height of pine (m)	Stems = 17.08 – 0.695 (height)	0.41
Mean DBH (cm)	Stems = 14.18 – 0.435 (DBH)	0.33
Density of pine snags (n/ha)	Stems = 1.65 + 0.243 (snags/ha)	0.32
Mean age of pine at breast height (years)	Stems = 12.75 – 0.175 (age)	0.28
Basal area of pine (m <sup>2</sup> /ha)	Stems = 9.75 – 0.185 (bapine)	0.23
Basal area of deciduous trees (m <sup>2</sup> /ha)	Stems = 4.20 + 0.590 (badec)	0.15
Mean duff depth (cm)	Stems = 7.63 – 0.979 (duff)	0.15
Mean bark thickness of pine (cm)	Stems = 8.76 – 2.842 (bark)	0.11
Total density (stems/ha)	Stems = 2.05 + 0.003 (stems/ha)	0.10
Mean pine canopy cover (%); mean bark thickness of pine (cm)	Stems = 14.33 – 0.128 (cover) – 2.678 (bark)	0.51
Mean pine canopy cover (%); mean height of pine (m)	Stems = 15.93 – 0.079 (cover) – 0.414 (height)	0.50
Mean height of pine (m); basal area of deciduous trees (m <sup>2</sup> /ha)	Stems = 15.39 – 0.648 (height) + 0.457 (badec)	0.50
Mean pine canopy cover (%); mean age of pine at breast height (years)	Stems = 14.42 – 0.103 (cover) – 0.104 (age)	0.50
Mean pine canopy cover (%); DBH (cm)	Stems = 14.75 – 0.096 (cover) – 0.250 (DBH)	0.50

**Note:** All variables used in the models were significant at  $\alpha = 0.05$ . Badec, basal area of deciduous trees; bapine, basal area of pine; DBH, diameter of pine at breast height; snags, density of pine snags per hectare (square-root transformed); stems, number of pine trees per hectare attacked by *T. piniperda* (square-root transformed).

**Table 8.** Relationship between stem attacks by *Tomicus piniperda* in southern Ontario in 2001 and the species of pine, based on logistic regression analysis ( $n = 1455$  pine trees).

Pine species	Estimate	$\chi^2$	$P > \chi^2$
Jack vs. Scots	0.98	34.97	<0.0001
Red vs. Scots	-0.99	17.23	<0.0001
Jack vs. red	0.98	27.62	<0.0001

>50% foliage (Table 9). The probability of stem attack also differed significantly between red pine trees of varying crown positions (Wald  $\chi^2 = 24.24$ ;  $P < 0.0001$ ) (Table 9): dominant and codominant red pine were significantly less likely to be attacked than intermediate and suppressed red pine (Table 9). Intermediate trees had a significantly greater probability of being attacked than suppressed trees (Table 9). The probability of attack was not significantly different for dominant and codominant trees (Wald  $\chi^2 = 0.48$ ;  $P = 0.49$ ). The significant negative coefficient associated with the DBH of red pine indicated that red pine trees with small DBHs were



**Table 9.** Characteristics of the living pine trees and their significance in explaining the probability of stem attack by *Tomicus piniperda* in southern Ontario in 2001, based on logistic regression.

Variable	Estimate	$\chi^2$	$P > \chi^2$
<b>Scots pine (n = 694)</b>			
Crown density (%)			
<25 vs. >50	1.48	23.60	<0.0001
<25 vs. 25–50	0.50	4.45	0.0300
25–50 vs. >50	0.50	1.78	0.1800
<b>Jack pine (n = 332)</b>			
Crown density (%)			
<25 vs. >50	0.30	1.43	0.2300
<25 vs. 25–50	-0.18	0.59	0.4400
25–50 vs. >50	0.65	6.39	0.0100
<b>Red pine (n = 429)</b>			
Crown density (%)			
<25 vs. >50	2.07	15.80	<0.0001
<25 vs. 25–50	0.65	2.22	0.1400
25–50 vs. >50	0.76	1.53	0.2200
Crown position			
Dom. vs. sup.	-1.55	5.77	0.0200
Codom. vs. sup.	-2.41	8.68	0.0030
Inter. vs. sup.	1.40	6.23	0.0100
Dom. vs. inter.	-1.48	10.80	0.0010
Codom. vs. inter.	-1.91	11.10	0.0009
Diameter (1.38 m)	-0.39	19.50	<0.0001

**Note:** Codom., codominant; dom., dominant; inter., intermediate; sup., suppressed.

more likely to be attacked by *T. piniperda* than those trees with large diameters (Table 9).

Very few *T. piniperda* attacks on living trees were successful. Successful attacks were primarily on trees carrying <25% foliage: seven of the successful attacks (87.5%) were found on these trees. Only one successful attack (12.5%) was found on trees with 25%–50% foliage, and no successful attacks were found on trees carrying >50% relative foliage.

## Discussion

### Susceptibility of sites to shoot attack by *T. piniperda*

*Tomicus piniperda* depends primarily on recently dead trees for successful reproduction, and brood production correlates positively with the number of attacked shoots that fall to the forest floor (Schroeder 1987; Annala and Heikkilä 1991; Långström and Hellqvist 1993). It has also been reported that the progeny of *T. piniperda* attack primarily the shoots of trees close to their emergence site (Eidmann 1974, cited in Eidmann 1992). Therefore, it was not surprising that the density of standing dead trees was the variable that explained the greatest amount of variation in the number of shoots attacked by *T. piniperda* in our study. The number of attacked shoots increased with increasing quantities of recently dead pine trees (Fig. 2). This result agrees with those found by Långström and Hellqvist (1990, 1991) and Amezcaga (1997), who both reported that the greatest number of shoots at-

tacked by *T. piniperda* were in pine forests that contained, or were close to, large quantities of suitable breeding material.

The effect of thinning on the level of shoot attacks (Table 4) further illustrates the strong relationship between the abundance of brood material and the number of attacked shoots. Sites that had been thinned had fewer shoots attacked and fewer snags than sites that had not been thinned (Table 4). Thinning has been shown to have a negative effect on the number of shoot attacks by *T. piniperda* in pine plantations of Finland and northern Spain (Annala and Heikkilä 1991; Amezcaga 1997). Amezcaga (1997) found that plantations of *Pinus radiata* D. Don thinned three or four times prior to the study had significantly fewer shoot attacks than unthinned plantations or ones that had been thinned one or two times. Removing the least vigorous trees reduces the amount of future breeding material for bark beetles. Also, thinning has been demonstrated to reduce the susceptibility of forests to bark beetle attack by increasing the availability of light, thus improving the photosynthetic capacity of the trees, which improves overall tree vigour (Mitchell et al. 1983; Waring and Pitman 1985). Of the 43 sites investigated in our study, 14 had been thinned in the past. All logging had been performed many years prior to our study, and according to our observations, only the least vigorous pine trees had been removed. Three of these 14 thinned sites had small quantities of cut wood left on site, and one of these had only the tops of the trees left behind. It is worth noting that *T. piniperda* galleries were not observed in any of the cut wood left after logging; thus, this material did not serve as breeding sites for the beetles.

The volume of downed woody debris on the forest floor was not correlated with the number of attacked shoots, probably because the volume of downed wood detected in our study was low, and most was from trees that had died many years before our study (indicated by the advanced stages of decay observed in the downed wood).

Canopy cover is a measure of canopy closure or the amount of light passing through the canopy, and basal area is a measure of the cross-sectional area of the living pine trees (>5 cm DBH). The number of attacked shoots increased with decreasing values of canopy cover and basal area (Table 1), and canopy cover and basal area were negatively correlated with the density of snags (Table 2). In other words, canopy cover and basal area were inverse measures of the number of snags. As discussed earlier, snags were important sources of brood material for *T. piniperda* and thus strongly influenced the intensity of shoot feeding.

Significant negative correlations were detected between the number of attacked shoots and the mean height, DBH, and age of the sites (Table 1). Results from the linear regression analysis indicated that of these three significantly inter-correlated variables (Table 2), the variable that explained the greatest amount of variation in the number of attacked shoots was the mean height of the pine (Table 1). Height and diameter may have been indicators of tree vigour, with increases in the mean height and DBH of the sites reflecting increases in the vigour of the trees. In fact, mean height and DBH had a strong negative correlation with the density of snags. Therefore, sites with vigorous trees (expressed as larger values of

mean height and DBH) had less available brood material for the beetles than did sites with low-vigour trees, which in turn led to lower populations of the pine shoot beetle and subsequently fewer attacked shoots. Since height and DBH are intercorrelated with age (Table 2), age may have been contributing to this relationship between height, DBH, and shoot attacks. However, when models were developed that used age with height and age with DBH, the variable age was no longer significant in either of the models.

Mean height and DBH were found to be significantly different among the species of pine in this study (Table 5). Sites consisting of pure red pine had significantly larger values of mean height and DBH and had significantly fewer attacked shoots than sites of pure Scots pine, Scots pine mix, and jack pine mix (Table 5). Mixed Scots pine sites had the greatest numbers of attacked shoots, followed by sites of pure Scots pine and sites of mixed jack pine. The mean age of the sites was not found to be significantly different between species (Table 5); thus, it can be assumed that age was not responsible for the observed differences in the mean height and DBH found among pine species.

Species composition explained approximately 44% of the variation in the number of shoots attacked by *T. piniperda*. It could be argued that the effect of species on the level of shoot attack was more an artefact of tree vigour and management than of species itself. Based on its relative size, red pine appeared to be the most vigorous of the three pine species examined in this study. This high vigour of red pine resulted in less breeding material for the beetles and reduced the susceptibility of the red pine sites to shoot attack. In fact, pure sites of red pine were found to have significantly fewer snags than sites of pure Scots pine (Table 5). Red pine is native to North America and naturally occurs in the Great Lakes – St. Lawrence forest region of south-central Ontario, jack pine naturally occurs in the boreal forest region of northern Ontario, and Scots pine is an introduced pine species native to Europe and Asia (Farrar 1995). Presumably, red pine is better suited to growing in southern Ontario than jack pine and Scots pine, leading to the higher vigour of red pine trees and thus a lower susceptibility of red pine sites to pests and pathogens, including *T. piniperda*. Proper forest management, such as thinning, also appears to be influencing the vigour of the trees growing in southern Ontario. Thinning practices were most often applied to sites dominated by red pine; Scots pine sites were thinned less frequently, and jack pine sites received no thinning (Table 5). As was discussed earlier, thinning reduces future sources of breeding material for the beetles and can often improve the vigour of the remaining trees on the site (Mitchell et al. 1983; Waring and Pitman 1985).

Soil parent material and soil texture profoundly influence the characteristics of a soil, such as aeration, drainage, its capacity to absorb and retain moisture and nutrients, and its chemical and mineralogical composition (Brady 1974). Sandy soils tend to be relatively loose, with better aeration and drainage than clay soils (Brady 1974). Because red, jack, and Scots pine prefer well-drained, sandy soils (Farrar 1995; Kershaw 2001), it is likely that the soil parent materials and the textures and types of soils in this study influenced the growth and survival of the pine trees, which in turn affected

the susceptibility of the sites to shoot attacks by the pine shoot beetle. Excessive moisture on sites without sand or on sites with higher clay content may have negatively affected the trees growing on these sites. In fact, the mean density of snags on sites with clay loam till parent material was significantly greater than that on sites with parent materials derived from medium-grained to fine sands. Sites with medium-grained to fine sand parent material had the lowest mean number of attacked shoots.

Duff is defined as the matted, partly decomposed organic layer on the surface of forested soils (Brady 1974). The significant negative linear relationship found between the depth of the duff layer and the number of attacked shoots may reflect the influence of the duff on the soil characteristics and in turn on tree vigour. Sites with thicker layers of duff might have been less prone to drought, erosion, and nutrient losses, and the organic matter in the duff layer may have provided the trees and important microorganisms with nutrients. The depth of the duff layer may have also influenced soil temperatures. Therefore, a thicker duff layer may have improved soil conditions, which increased tree vigour and reduced the susceptibility of sites to shoot attacks. However, this relationship might have also reflected differences in the amount of inputs of biomass (needles, shoots, and branches) from the living pine trees, as indicated by the correlations found between duff depth, canopy cover, basal area, and the density of snags (Table 2). Sites with greater numbers of attacked shoots were also sites with higher snag densities and fewer surviving pine trees. Therefore, the litter inputs on these sites would have been lower, and this in turn would have affected the thickness of the duff layer.

Radial growth is considered an indicator of tree vigour and reflects the many biotic and abiotic stressors affecting trees (Hicks 1980). Studies conducted on the southern pine beetle (*Dendroctonus frontalis* Zimm.) and the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopk.) have demonstrated that an increased susceptibility to beetle attacks on stems was associated with reduced radial growth of the trees (Coulson et al. 1974; Negron 1998; Shore et al. 1999). Similarly, findings from our study (Table 3) indicated that sites containing dominant and codominant pine trees with low increments of growth over the 1–5 years prior to our study were the sites that had the most shoot attacks. It was evident that the number of shoots attacked by *T. piniperda* was greatest in sites that contained the least vigorous trees, and the low vigour of these trees might have been reflected in their radial growth increments. Presumably, either *T. piniperda* was attracted to sites containing trees with reduced radial growth or shoot feeding by *T. piniperda* was responsible for the reductions in radial growth.

Studies conducted in Sweden and the United States have reported that the shoot-feeding activity of *T. piniperda* was responsible for significant reductions in tree growth (Långström and Hellqvist 1990, 1991; Czokajlo et al. 1997). *Tomicus piniperda* has been in Ontario since at least 1993; therefore, it is possible that shoot feeding by *T. piniperda* is at least partially responsible for the lower values of radial growth observed in the pine trees growing on sites with severely attacked shoots. The pine shoot beetle seems to prefer sites that have numerous dead and dying pine trees that can be ex-

exploited for reproduction. These low-vigour sites support large populations of the beetles, which subsequently attack the living shoots of trees, leading to additional stress on the trees and an increased potential for growth reductions. Långström and Hellqvist (1991) reported that growth reductions in Scots pine in southern Sweden became evident when >100 shoots per tree had been attacked (corresponding to approx. 10 fallen shoots/m<sup>2</sup>) over 3 years by *T. piniperda*. The greatest number of shoots per square metre detected on the forest floor in our study was 6.43; however, this value represented shoot attacks from 2001 only. Therefore, damage to the trees over many years of recurrent shoot attacks may have far exceeded 100 attacked shoots per tree, making it quite possible that the beetles were at least partially responsible for reductions in growth. Unlike deciduous trees, which can easily replace their foliage soon after defoliation, conifers are not able to replace their foliage as readily. This is especially true for the type of damage caused to coniferous trees by shoot-feeding insects like *T. piniperda*, which can permanently destroy the shoots and severely hinder the future development of new foliage.

Although we found several multivariate models that were significantly related to the intensity of shoot attacks (Table 1), these models failed to explain much more of the variation in the number of attacked shoots than the single-variable model that used the density of recently dead pine snags as the predictor variable (Fig. 2).

#### Susceptibility of sites to stem attacks by *T. piniperda*

As previously discussed, *T. piniperda* depends on non-resistant breeding material for successful reproduction; however, it has been found to attack living pine trees when beetle populations were high and when host trees were severely weakened by other stress factors (Schroeder 1987; Ye 1991; Långström and Hellqvist 1993; Annala et al. 1999; Långström et al. 1999). It appears that characteristics of the sites that were correlated with the intensity of shoot attacks by *T. piniperda* were the same as those correlated with the level of stem attacks. In fact, shoot attacks were significantly correlated with the number of stem attacks by *T. piniperda*. Variables that were indicators of the amount of potential breeding material for the beetles, such as the density of snags, canopy cover, and the basal area of pine, were all significantly correlated with the number of living pine trees attacked (Table 7). Likewise, characteristics of the sites that were indicators of tree vigour or might have influenced tree vigour, such as DBH, height, radial growth, soil type, soil parent material, history of thinning, and species, were also found to be significantly correlated with the number of trees attacked by *T. piniperda* (Tables 3–7). Although the correlations found between the site and tree characteristics and the numbers of trees attacked by *T. piniperda* were not as strong as those found for the level of shoot attacks, the same trends were evident.

Sites with an abundance of low-vigour pine trees had increased susceptibility to stem attacks, presumably because these sites contained large quantities of brood material or because the beetles were attracted to volatiles released by the low-vigour pine trees (Schroeder 1987). Sites with an abundance of brood material had large pine shoot beetle populations, and large populations may have increased the susceptibility

of the sites to stem attack because competition for suitable breeding material was high, which would have forced some of the beetles to attempt reproduction on the living trees. This would likely have happened in situations where the abundance of suitable brood material was lower than in previous years.

#### Susceptibility of trees to stem attack by *T. piniperda*

Differences in the probability of stem attack by the pine shoot beetle were found between the species of pine (Table 8). Jack pine had a higher probability of stem attack than Scots pine or red pine, and Scots pine was found to have a higher probability of attack than red pine (Table 8). Few attacks were attempted on red pine, and all attempted attacks on red pine were unsuccessful. Siegert and McCullough (2001) reported that *T. piniperda* preferentially attacked cut logs of Scots pine over cut logs of red pine and jack pine in laboratory choice experiments, which may have been attributed to differences in the host volatiles released by the logs. *Tomicus piniperda* and other species of scolytids use host volatiles such as  $\alpha$ -pinene and ethanol to locate suitable breeding material (Schroeder and Lindelöw 1989). Tree vigour may alter the quantity or quality of volatiles released by the trees, which in turn may alter the trees' attractiveness to *T. piniperda* (Schroeder 1987). Schroeder (1987) reported that *T. piniperda* attacked Scots pine trees of low vigour more frequently than trees of higher vigour (vigour was expressed as differences in crown appearance). Waring and Pitman (1985) found that as the vigour of lodgepole pine trees increased (expressed as increases in tree growth efficiency), the susceptibility of the trees to stem attacks by the mountain pine beetle decreased, and the trees' resistance to attack improved. As previously discussed, red pine appears to be more vigorous than the other two species of pine examined in our study, either because red pine was better managed or because red pine is better suited to the growing conditions of southern Ontario. Therefore, it is likely that the differences in the probability of stem attack between species were due to differences in the relative vigour of the trees.

Crown density was used as a measure of tree vigour in our study. We assumed that pine trees with more foliage (denser crowns) were more vigorous than trees of the same species with less foliage. Crown density had a significant effect on the probability of stem attack by *T. piniperda* for all three species of pine examined (Table 9). Jack pine trees carrying 25%–50% of their foliage had a higher probability of stem attack than jack pine trees carrying >50% of their foliage. Similarly, both red pine and Scots pine trees carrying <25% of their foliage were more likely to be attacked by *T. piniperda* than were trees carrying >50% of their foliage. Scots pine trees with <25% of their foliage also had a higher probability of stem attack than Scots pine trees with 25%–50% of their foliage intact. Thus, *T. piniperda* appears to have selected the least vigorous pine trees as breeding material. This result was similar to that found by Långström et al. (1999), who reported that *T. piniperda* attacks on fire-damaged Scots pine trees in Sweden were avoided by all trees carrying at least 50% of their foliage. Another study, conducted in southwestern Finland, found that stem attacks by *T. piniperda* were often avoided on Scots pine trees that retained 10% of

their needles after defoliation by *Diprion pini* (L.) (Annala et al. 1999).

The influence of tree vigour on the probability of stem attack by *T. piniperda* was further supported by the effect of red pine crown position on the likelihood of stem attack (Table 9). Intermediate and suppressed red pine trees had higher probabilities of stem attack than codominant and dominant red pine (Table 9). These findings show that intraspecific competition had an effect on the susceptibility of red pine to stem attack by *T. piniperda*. Dominant and codominant red pine had a competitive advantage over the intermediate and suppressed trees in their ability to acquire available sunlight. Because of this advantage, dominant and codominant red pine trees likely had greater photosynthetic surface areas than the intermediate and suppressed trees, which improved their ability to compete for other resources like water and nutrients. The advantages associated with increased light availability would have led to increased tree vigour and a reduced susceptibility to stem attack (Mitchell et al. 1983; Waring and Pitman 1985).

The probability of stem attack also increased as the DBH of red pine trees decreased (Table 9). Again, this relationship may have reflected the influence of tree vigour on the probability of attack, with smaller red pine trees being less vigorous than larger red pine trees.

Although *T. piniperda* occasionally attacked living pine trees in southern Ontario, the attacks were on low-vigour trees, and most of the attacks (91%) were unsuccessful. Seven of the eight successful attacks were on trees that were carrying <25% of their foliage, and no successful attacks were found on trees carrying >50% of their foliage. The majority of attacks were unsuccessful because the beetles were either repelled or encrusted by resin exuding from the trees. This result, as well as those found for other studies in Scandinavia (Annala et al. 1999; Långström et al. 1999), suggests that *T. piniperda* is a secondary bark beetle species, able to successfully colonize only pine trees that are severely weakened by other predisposing factors. Annala et al. (1999) found that defoliated Scots pine trees carrying 10% or more of their foliage were able to resist *T. piniperda* stem attacks, and Långström et al. (1999) reported that all *T. piniperda* attacks were unsuccessful on fire-damaged Scots pine trees with at least 40% of their foliage intact.

## Conclusions and recommendations

Shoot-feeding activity by *T. piniperda* in southern Ontario was predominantly related to the amount of breeding material made available to the beetles. Sites that were most susceptible to shoot attack had a large abundance of recently dead pine trees as well as many living pine trees of poor vigour. The relationships between forest characteristics and the level of shoot attacks paralleled those found for the level of stem attacks. In fact, a significant correlation was found between the number of attacked shoots and the number of pine trees attacked by *T. piniperda*. The susceptibility of sites to stem attacks by *T. piniperda* was strongly dependent on the vigour of the pine trees growing on the sites. High beetle populations and an abundance of stressed pine trees led to an increased susceptibility of the sites to stem attacks. Overall, the number of living pine trees attacked by *T. piniperda* in

southern Ontario was low, and most attacks on the living pine trees were unsuccessful. Attempted attacks by *T. piniperda* on the trunks of living pine trees were primarily concentrated on trees with severely reduced crown densities, and of these attempted attacks, very few were successful (brood produced). Also, of the eight successful attacks observed on the 1455 living pine trees examined, seven were on trees with <25% relative foliage. Under low population levels of *T. piniperda* the beetles primarily attack only the severely stressed, dying, or recently killed trees; however, in situations where the population level is elevated, the beetles may start attacking trees of higher vigour, but most often with little success. Thus, *T. piniperda* appears to be a secondary bark beetle species in southern Ontario, colonizing only recently dead pine trees or trees suffering from severe forms of stress. It is possible that during periods of intensive shoot feeding, *T. piniperda* may predispose the trees to stem attacks; however, this scenario would only occur in forested areas that contain large quantities of suitable breeding material.

*Tomicus piniperda* populations could be kept at low levels if proper silvicultural practices, such as thinning and the removal of recently dead pine trees, were applied and also if “offsite” plantings of pine were avoided. Many of the pine plantations in southern Ontario that had large *T. piniperda* populations were on less than ideal soils. These sites had many dead and dying pine trees that served as sources of breeding material for the beetles. Prioritizing highly susceptible pine forests for management initiatives might help to slow the spread of this beetle across North America.

## Acknowledgements

We would like to acknowledge the assistance provided by the staff and students at the University of Toronto’s Faculty of Forestry; and the help with site selection provided by Bill Tilt of the Ontario Ministry of Natural Resources (MNR). We are also grateful to Taylor Scarr of MNR for financial support.

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