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**BIOLOGY OF THE RECENTLY INTRODUCED PINE SHOOT BEETLE
TOMICUS PINIPERDA (L.) (COLEOPTERA: SCOLYTIDAE)
IN SOUTHERN ONTARIO**

BY

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A thesis submitted in conformity with the requirements
for the degree of Master's of Science in Zoology
Graduate Department of Zoology
University of Toronto

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ABSTRACT

Biology of the recently introduced pine shoot beetle *Tomicus piniperda* (L.)
(Coleoptera: Scolytidae) in southern Ontario.

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This study examined the biology of an introduced species, the pine shoot beetle, *Tomicus piniperda*, in southern Ontario. Timing of spring emergence and colonization occurred in mid- to late-April or early-May, following a similar pattern as found previously in Europe. Emergence of the new generation occurred in late-July (heat sum of 1249.8 degree-days $>0^{\circ}\text{C}$) and the adults fed in the shoots until mid-October. Production per gallery was negatively influenced only at high gallery densities (1996). Brood production was approximately 900-1000 beetles per m^2 . Mortality of the juvenile stages was high (79.% in 1996). Gallery density declined with increasing height on a given tree and with increasing tree diameter. Shoots with longer needles and larger diameters were preferred by adult beetles for feeding. The majority of the shoot-feeding by the new generation of beetles occurred in current-year shoots. Results indicate that European information may be used with confidence when creating management protocols.

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Chapter One : INTRODUCTION

Problem Definition

In 1993, a new insect species was found in southern Ontario (Sajan *et al.* 1994). The species is the pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera, Scolytidae), a damaging and often economically important forest insect pest native to Europe and Asia (Haack *et al.* 1993). A breeding population was found in a Christmas tree plantation near Cleveland, Ohio, in July 1992 and it has since been found in eight US states and in 13 counties in southern Ontario (Kucera 1992, Haack and Lawrence 1994, Haack 1996). Using DNA fingerprinting, Carter *et al.* (1996) discovered that *T. piniperda* populations in the United States were the result of at least two separate introductions, one in Illinois near Lake Michigan and the second in Ohio along Lake Erie. It is generally believed that *Tomicus* arrived on a cargo ship at a Great Lakes port, but the number of entries and country of origin are unknown (Haack and Lawrence 1994).

Tomicus piniperda typically completes one generation per year (see Appendix 1). Early in the spring, colonization of weakened or stressed trees and cut pine stumps and logs is initiated by the emerging parent generation. Developing larvae feed upon the inner bark or phloem layer. The new generation of beetles, upon emergence from the brood material, spends the summer and autumn feeding inside the shoots of living pine trees. This period of shoot feeding, unique to this bark beetle genera, is the primary cause of damage by this species in Europe, resulting in its major pest status (Haack and Kucera 1993, Haack and Lawrence 1994, Sajan *et al.* 1994).

The pine shoot beetle is often considered to be a pest of economic importance over its widespread range. *Tomicus piniperda* has caused serious economic losses in the Chinese forest industry, damaging over 20 million acres of Yunnan pine forest in the 1970's alone (Ye 1991). In Sweden, several million cubic metres of growth were lost annually during the 1970's (Langstrom and Hellqvist 1990). It has caused considerable tree mortality in Central France (Levieux *et al.* 1985), Portugal (Ferreira and Ferreira 1986), and Italy (Langstrom and Hellqvist 1993). Indeed, this species is considered to be

one of the most serious pests on pine woods on Southern Italy's Ionic coast (Triggiani 1984). Growth losses of 20-40% lasting over several years after only one year of beetle attack have also been found in older European stands (Langstrom and Hellqvist 1990). In addition to causing growth reductions, the blue-stain fungi, associated with *T. piniperda*, actually stains the wood, thus reducing its commercial value. This is especially important in Europe where Scots pine (*Pinus sylvestris* L.) is used for lumber (Gibbs and Inman 1991).

The new range of southern Ontario into which the pine shoot beetle (*Tomicus piniperda*) has just expanded contains its primary host, Scots pine (*P. sylvestris*) as well as a number of other pine species. Ontario partially consists of eastern boreal forest: composed of Jack pine (*P. banksiana* Lamb.), white (*P. strobus* L.), red pine (*P. resinosa* Ait.), and Scots pine, as well as spruce, fir, birch, and poplar (Bright 1976). Other common conifer species in the transition forest of the Lake States region are: tamarack (*Larix laricina* (DuRoi) K.Koch); Austrian pine (*Pinus nigra* Arnold); Ponderosa pine (*Pinus ponderosa* Laws.); Norway spruce (*Picea abies*); blue spruce (*Picea pungens* Engelm.); white spruce (*Picea glauca* (Moench) Voss); black spruce (*Picea mariana* (Mill.) B.S.P.); balsam fir (*Abies balsamea* (L.) Mill.); douglas fir, (*Pseudotsuga menziesii* (Mirb.) Franco.); eastern hemlock (*Tsuga canadensis* (L.) Carr.); Canadian yew (*Taxus canadensis* Marsh.); northern white cedar (*Thuja occidentalis* L.); eastern red cedar (*Juniperus virginiana* L.); and common juniper (*Juniperus communis* L.) (Wilson 1977). Hence, there are a number of conifer species, in particular, pines, that are present in *Tomicus piniperda*'s new range that may turn out to be susceptible to attack by this pest. Indeed, this species already attacks a variety of pine species over its wide-spread distribution (Ye 1991 and 1994, Ferreira and Ferreira 1986, Speight 1980).

In Ontario, all three of red, white, and jack pine are considered to be economically important timber tree species. As of 1991, softwood species, like these, accounted for more than 90% of the estimated 138 million m³ harvest in Canada's timber industry (Forestry Canada 1993). Softwood lumber is Canada's principal export commodity, accounting for 46% of its total world trade and equaling \$11 billion in 1994 (Canadian Forest Service 1996). Red pine was originally planted around the turn of the century to

strong growth and disease, insect and drought resistance, this species is now an important source of poles and sawlogs and, secondarily, pulpwood, pallet material, posts and fuel. The commercial area for this pine species ranges throughout the Great Lakes-St. Lawrence region of southern and central Ontario (Kerrio and Mogford 1986a). White pine is also a very important timber species, producing sawlogs and other high quality products. It has been adopted as Ontario's official tree (Forestry Canada 1993) and has a commercial range throughout the Great Lakes-St. Lawrence region, as well as extending northward into the southern boreal forests of Ontario (Bernier and Macnee 1973). Jack pine is not as highly valued as red and white pine for lumber, however, it is a major softwood species for pulpwood production (Smith and Brown 1983). The use of this species has more than doubled since the mid-1960's with 50% being used for pulpwood and the other 50% being used for sawlogs as a result of the increased acceptance for construction purposes (Kerrio and Mogford 1986b). In 1990, jack pine constituted 34.3% of the total conifer harvest in Ontario (Morris and Parker 1991). Jack pine is a northerly species, ranging broadly across northern Ontario and is the most widely distributed pine species in Canada (Smith and Brown 1983). A recent study near the Lake Michigan shoreline found *Tomicus* adults to be feeding naturally on all three of these pine species, although a preference for red and Scots pine was apparent (Sadof *et al.* 1994). The susceptibility of and threat to these valuable pine species in Ontario is of extreme concern.

In Ontario, Scots pine (*Pinus sylvestris*) is not used for timber due to the poor stock quality that was imported here approximately 40 years ago. However, many small stands of Scots pine were planted around south-western Ontario primarily for erosion control. These stands provide a perfect refuge for the invading beetle and that may increase the success of its establishment and spread. More importantly, Scots pine has played a significant economic role as one of the most popular and widely-grown tree species in the Ontario Christmas tree industry (Bell and White 1966). Christmas trees are graded, based on the presence of visible defects, and are priced accordingly. Grading ranges from premium, choice, standard, or cull depending on shape, taper and presence of

damage from any cause (Bell and White 1966). Feeding by this new beetle in the shoots of Christmas tree crowns may result in costly aesthetic damage (Bright 1996). Hence, this species is also of major concern to Christmas tree growers (Sajan *et al.* 1994). The pine shoot beetle joins a group of insect pests and plant diseases that make producing high-quality salable trees complicated and expensive.

The non-native status of this species, combined with its potential to cause damage to the timber and Christmas tree industry, has resulted in the imposition of a federal quarantine by the USDA APHIS (Animal and Plant Health Inspection Service) on all areas known to be infested with *Tomicus* (Haack and Lawrence 1994). In Canada, infested areas, which now includes most of southern Ontario (Hall 1996), are also quarantined and movement of potentially infested pine material out of these regions is prohibited by the Plant Protection Division of Agriculture and Agri-Food Canada (Hollebone 1996). Regulated material includes: pine Christmas trees; pine nursery stock; pine forest products with bark attached; and pine bark. This regulation is an attempt to reduce the spread and potential damage by this species, however, more detailed information on this species' biology is needed to accurately assess and control its impact.

Objectives

Quarantine restrictions, industrial concern over the potential for this species to cause damage, combined with the complete lack of information on this species' life cycle, behaviour, and impact in the newly infested region of southern Ontario were the impetus behind the present work. This thesis was initiated to develop our knowledge on the biology of *Tomicus piniperda* in southern Ontario. The background information (Chapter Two) provides a summary of previous research findings on this species from Europe, Asia and America. Selected detail is given on topics that will be discussed in the chapters to follow. Chapter Three provides important fundamental information about the bionomics of this species in southern Ontario and discusses it in a management context. Chapter Four examines the influence of temperature on the development of the various juvenile stages while Chapter Five discusses the effect of gallery density on the production of new beetles per gallery and per unit area (brood production). Chapter Six provides some information on reproductive and shoot feeding preferences by the adult beetles, which may be of relevance to the timber and Christmas tree industry. A summary of these findings, along with a discussion of management implications, completes the thesis. One overall bibliography for the entire thesis can be found at the end. Chapters Four through Six follow the format of journal articles, as the intention is to eventually submit them for publication. Because of this, there exists some replication in introducing this species and in describing some of the methods and study sites, however, the results and discussions are distinct.

Chapter Two : BACKGROUND INFORMATION

General Bark Beetle Biology

Bark beetles belong to the family Scolytidae and are widely recognized as one of the most damaging groups of forest insects. The earliest scolytid fossils date back to the Eocene epoch and the early evolution of most scolytids has been closely correlated with the evolution of conifers. In North America, 73 genera with 625 species, including 23 species of *Dendroctonus*, the 'tree killer' are recognized. In general, the adults are small, compact, cylindrical insects ranging in size from 1-18 mm long. Their antennae are elbowed and the terminal segments are enlarged and clublike. Most species are brown or black with strong jaws (mandibles) for boring through wood (Mitton and Sturgeon 1982).

Bark beetles will attack all parts of the plant on a wide variety of host tree species, from hardwoods to conifers. Reproduction occurs in the cambium region of the trees. The adult beetle (either male or female) bores a hole through the bark into the cambium region and then tunnels away from the entrance hole along the surface of the wood, laying eggs along the gallery (Bright 1976). Mating can occur on the bark surface, underneath the bark or prior to colonization. The characteristics of the egg gallery, position and arrangement of egg niches and grooves, and the character and position of the larval mines provide features for field recognition of the various species. Polygamy is common in many species, although others are strictly monogamous. Species are often separated vertically on a tree, each preferring specific portions of the bole. In addition, some galleries are kept clean of frass whereas other species pack their galleries with it. The apodous larvae create tunnels at about right angles to the parent gallery and their tunnels can be either straight and regular, or irregular and meandering. In general, larval tunnels do not cross unless there exists crowded conditions. The larvae may feed individually or gregariously, depending on the species (Mitton and Sturgeon 1982). Pupation then occurs in enlarged pupal chambers in the inner or outer bark, or in the cambium region. Most emerging beetles create their own exit hole out through the bark, leaving the outer bark covered with holes (Bright 1976).

aggressive, or primary, bark beetles aggregate on, attack and then kill living trees (Borden 1992). Much research has been conducted describing the complicated species-specific aggregation pheromones required by these species to overcome host-tree defenses (e.g. Borden 1992). In contrast, secondary beetles locate, aggregate on, and infest stressed or moribund hosts, only rarely attacking healthy living trees. Bark beetles which must breed in dead/weakened trees must use sensitive and specific host orientation stimuli to find this scarce and unevenly distributed resource (Sjodin *et al.* 1989, Lindelow *et al.* 1992). These secondary bark beetles actually help initiate and stimulate the process of nutrient turnover, even though they are typically considered pests (Huffaker *et al.* 1984). By removing stressed trees, these bark beetles can actually increase the species diversity of a forest and decrease fire hazards (Schowalter and Filip 1993b).

A large number of bark beetle species attacking conifers are recognized in Canada. In particular, there are many native bark beetle species attacking pine trees in Ontario. (Table 2-1, adapted from Bright 1976). At least 12 different genera are found on pines located within Ontario, with *Ips* and *Dendroctonus* being most common. While some of these species are able to kill otherwise apparently healthy trees, the majority of them also require weakened or recently felled tree boles for reproduction. Hence, the pine shoot beetle, which is known to require such stressed material (Salonen 1973), will encounter a number of potential new insect competitors, possibly trying to utilize the same brood material.

Table 2-1. Summary of better known bark beetle species attacking conifer trees in Ontario (from Bright 1976).

Species/(size)	Hosts/Range	Brood type	Galleries
<i>Ips grandicollis</i> (2.8-4.7 mm)	<i>Pinus</i> spp./ eastern Canada	logging slash but can kill healthy trees	3-5 egg galleries radiate from central chamber
<i>Ips calligraphus</i> (3.5-6.5 mm)	<i>Pinus</i> spp./ south eastern Canada	stumps, and trunks of felled trees, can kill healthy trees	several generations per year, 4-6 egg galleries radiating from central chamber up to 100 eggs per female
<i>Ips perturbatus</i> (4.2-4.8 mm)	<i>Picea</i> spp. <i>Pinus</i> <i>banksiana</i> , <i>P.</i> <i>contorta</i> /Canada	biology similar to <i>I. pini</i>	
<i>Ips perroti</i> (2.8-3.8 mm)	<i>Pinus</i> <i>banksiana</i> , <i>contorta</i> , & <i>resinosa</i> /across Canada	slash or thin barked portions of dying trees	galleries similar to <i>I. pini</i> , one generation per year
<i>Ips pini</i> (3.5-4.2 mm)	<i>Pinus</i> spp./ across Canada	thin barked sections or dead/dying trees	3-4 egg galleries radiating from central chamber, 2 generations per year
<i>Ips latidens</i> (2.7-3.5 mm)	<i>Pinus</i> spp. / eastern and western Canada	attack slash or dying trees mostly	large central chamber with radiating egg galleries, each containing 16-23 eggs, number of generations unknown
<i>Orthotomicus caelatus</i> (2.4-3.2 mm)	all species of conifer across Canada	breed in boles of recently dead trees or stumps	polygamous, radiate gallery system with 2-6 eggs per gallery
<i>Pityogenes plagiatus</i> (1.7-2.4 mm)	<i>Pinus banksiana</i> & <i>resinosa</i> <i>Picea</i> spp. across Canada	biology not known	
<i>Pityogenes hopkinsi</i> (1.8-2.3 mm)	<i>Pinus strobus</i> , <i>resinosa</i> , <i>banksiana</i> , <i>Picea</i> spp. / eastern Canada	thin barked tops and limbs of dead or dying white pines	3-5 females join male and form radiating egg galleries with up to 60 eggs, generation takes 28-43 days, emerge in April - May
<i>Dryocoetes affaber</i> (2.5-3.3 mm)	<i>Picea</i> and <i>Pinus</i> spp. / across Canada		central nuptial chamber with 3 egg galleries
<i>Dryocoetes autographus</i> (3.4-5 mm)	attacks all conifers / across Canada	base of injured trees or in bole of felled trees	biology not known

Table 2.1 (Cont.)

<i>Trypodendron lineatum</i> (2.7-3.5 mm)	attacks all conifers / across Canada	adults fly from late March through August in B.C., mainly logs and slash	galleries with 2-3 branches, new adults emerge from July through September, one generation per year, hibernate for 7-11 months
<i>Crypturgus borealis</i> (1.1-1.3 mm)	conifers in its range / across Canada		galleries start from main galleries of other bark beetles 1.5-4 cm long
<i>Polygraphus rufipennis</i> (2.1-3.1 mm)	attacks all conifers in its range / across Canada	in Ontario, adults start flight in late April; one generation / year	several egg galleries from same initial chamber, eggs laid in niches along gallery walls, larvae burrow at right angles
<i>Phloeosinus pini</i> (2.1-2.5 mm)	<i>Pinus</i> and <i>Picea</i> spp. / across Canada	biology not known	
<i>Dendroctonus murrayanae</i> (5-7.3 mm)	<i>Pinus</i> spp. / Great Lakes area to B.C.	stumps, windfalls, overmature or weakened trees	egg galleries average 12 cm groups of 20-50 eggs laid larvae feed communally one generation per year
<i>Dendroctonus punctatus</i> (5.4-6.8 mm)	sometimes on <i>Pinus</i> spp. / across Canada	attacks standing or fallen trees; flight from late May/early June until late August	vertical egg galleries up to 20 cm long with 20-50 eggs; larvae feed communally, overlapping generations;
<i>Dendroctonus valens</i> (5.4-9.0 mm)	attacks <i>Pinus</i> spp. mostly / across Canada	mostly freshly cut tree stumps and injured or dying trees; also apparently healthy trees	flight occurs throughout warm season; larvae feed gregariously, larval stage lasts months to over a year depending on climate; 2 years probably required in Canada per generation; overlapping generations typical
<i>Hylastes tenuis</i> (2.4-2.9 mm)	<i>Pinus</i> spp. / southern Ontario	biology not known	
<i>Hylurgops pinifex</i> (4-5 mm)	<i>Pinus</i> and <i>Picea</i> spp. / eastern Canada west to Alberta	secondary species found in thick bark portion of trees	monogamous; vertical egg galleries 2.5-9 cm long; 2-6 eggs in grooves; larvae feed communally; pupate in bark, cambium, or wood; one generation per year
<i>Pityophthorus</i> spp.	<i>Pinus</i> spp. / Canada	dead/dying twigs	

Biology of Tomicus piniperda

A great deal of research specifically pertaining to the biology of *Tomicus piniperda* has been done. This section provides an overview of that research with selected details on topics that will be covered in the later chapters.

Identification

Taxonomy

Class Insecta

Order Coleoptera

Family Scolytidae

Subfamily Hylesininae

Tribe Tomicini: 14 genera including *Dendroctonus*

(Bright 1993)

Recent revisions now place the Scolytids within the family Curculionidae as a subfamily, Scolytinae, however the older taxonomic convention will be followed here.

Body Features

Egg: small, approximately 1 mm, oval, smooth and shining white, located in individual grooves along either sides of the main galleries

Larvae: Length up to 5 mm, whitish with a yellow head, curled, creates lateral feeding tunnels away from the main gallery chamber

Pupae: Length about 4 mm, at ends of larval tunnels in pupal cells in bark

Adult: Length 3.5-5.2 mm, cylindrical, dull brown or black with a glossy black thorax.

The elytra have rows of punctures alternating with rows of tubercles. The whole body has a covering of hair. Antennae are clubbed. May be found in the shoots of the host pine, which will show yellowing and wilting. (Anonymous 1972)

Damage Description

Reproduction in tree bole

Reproduction typically occurs in thick-barked sections of stressed or moribund pine trees. Adults create small piles of reddish and white sawdust as they bore through the bark. The main maternal gallery tends to be vertical, with the eggs laid singly in individual grooves along either sides of the gallery. Larvae create tunnels out from the main gallery that typically do not cross except under high gallery densities. Larvae construct enlarged pupal cells in the outer bark and then bore their own hole out through the bark upon emergence. This causes the bark surface to become riddled with round exit holes (Anonymous 1972).

Shoot feeding

Shoot feeding attacks typically occur in current or one-year-old growth. Sometimes attacks are located at the very end of the growth, hollowing out the buds. The adults create a circular entrance hole and proceed to hollow out the inside of the shoot. The entrance hole often becomes encrusted with resin and the shoot ends up wilting and turning pale-green then reddish-brown. Shoot attacks occur in the exterior of the crown, with the majority in the upper one-third of the tree crown. The wilted shoots often fall to the ground at the end of the season and are identifiable as pine shoot beetle damage by the hollowed-out interior (Salonen 1973).

Distribution

The pine shoot beetle is widely distributed throughout Europe. *Tomicus piniperda* is considered an economically important forest insect on Scots pine (*Pinus sylvestris*) in northern Europe because of the damage it causes (Langstrom 1980, Ericsson *et al.* 1985). It is considered a major pest on pines in the Palearctic region, but rarely causes tree mortality in the Nordic countries (Langstrom and Hellqvist 1993). In contrast, it has caused considerable tree mortality in Central France, Portugal, and Italy (Langstrom and Hellqvist 1993, Triggiani 1983). In Sweden, there are 86 bark beetle species, of which six are of major importance. *Tomicus piniperda* and *Ips typographus* L. are two of the

1992). *Tomicus piniperda* has been found to be more abundant and damaging in polluted than in non-polluted areas in Europe (Heliövaara and Vaisanen 1991). In Portugal, this species is one of the most injurious pests on Maritime pine (*Pinus pinaster*), killing many trees during periodic outbreaks (Ferreira and Ferreira 1986). Spruce and fir trees, to a limited extent, as well as the often heavily damaged Scots pine, are used for reproduction and feeding by this species in Poland (Lutyk 1984). *Tomicus piniperda* is considered the most important bark beetle attacking windblown pine in Britain (Gibbs and Inman 1991). In Britain, it commonly attacks Scots and Corsican pine, and occasionally larch and spruce, especially after a period of stress through drought, fire, windblow or attacks by other species (Speight 1980).

Tomicus piniperda is also distributed all over the provinces and regions of China, causing damage to virtually all species of pine in this area, including *P. sylvestris* (Ye 1994). This species is also a major pest of the Yunnan pine (*Pinus yunnanensis* L.), an important silvicultural tree species in the Kunming region of China (Ye 1991).

Finally, *Tomicus piniperda* has recently become established in North America. The initial breeding population of this species was found in Cleveland, Ohio in 1992 (Haack and Lawrence 1994). The most recent survey indicates that the beetle is located in 147 counties in eight U.S. states (Haack 1996). Infested states include: Illinois, Indiana, Maryland, Michigan, New York, Ohio, Pennsylvania, and West Virginia (Hollebone 1996). In Canada, it has been found in a number of counties in south-western Ontario, including: Brant, Dufferin, Grey, Lambton, Middlesex, Oxford, Simcoe, and Wellington, as well as the following Ontario regional municipalities: Durham, Haldimand-Norfolk, Halton, Hamilton-Wentworth, Metropolitan Toronto, Niagara, Peel, Waterloo, and York (Hollebone 1996).

Spring Emergence

Emergence of the parental generation occurs quite early in the spring season. The adults, upon emerging, begin a period of flight searching for suitable substrate for gallery initiation. Emergence occurs when the ambient air temperature reaches 10-13°C. In Europe, the flight period typically lasts for only a few days to weeks depending on weather conditions (Salonen 1973).

Reproduction

The pine shoot beetle is monogamous and it is the female that initiates the gallery attack (Schroeder 1990, Salonen 1973). Janin and Lieutier (1988) found that up to 50% of females had already mated during feeding and overwintering before swarming the following spring. Salonen (1973) found that the beetles were capable of establishing galleries in the same stump as they overwintered in. In Kunming, China, egg galleries can be successfully established on standing living trees (Ye 1991). One possible reason for this is the yearly drought in the Kunming region which is known to reduce the amount of resin that the beetles encounter while boring through the bark (Ye 1991). In contrast, in Fennoscandia, *T. piniperda* does not establish egg galleries in the trees in which they fed in the shoots the previous year. Instead, the species requires dying, windbroken or otherwise weakened trees for reproductive success (Salonen 1973). In a previous study, trees with few living branches were assumed to be suitable as breeding material for *T. piniperda* and were classified as low vigour trees (Schroeder 1990). Such damaged trees, however, are believed to have shoots which are low in nutritive value, making the tree unsuitable for subsequent feeding (Ye 1991).

Egg galleries were found to be 3-5 cm long by Gibbs and Inman (1991) and 2.5 cm on average by Salonen (1973), however, Langstrom (1983) and Langstrom and Hellqvist (1985) found an average gallery length of 7-8 cm. Sauvard (1993) found that, after fertilization, *T. piniperda* females were able to produce several successive broods in the absence of males and concluded that females were able to keep viable spermatozoa for several months. *Tomicus piniperda* females are able to produce up to five sister

broods (Sauvard 1993), given the limits of their longevity and fecundity. Assuming that 40 to 50 eggs are laid per fertile gallery, the mean potential fecundity of *T. piniperda* females was estimated by Sauvard (1993) at about 200 eggs. No correlation between *T. piniperda* female size and fecundity has been found (Sauvard 1993). High levels of larval mortality have been reported for this species (Langstrom 1983). Once finished feeding, the larvae burrow into the bark for pupation (Salonen *et al.* 1968). In *T. piniperda*, re-emerging parent beetles are easily discerned from new generation adults on the basis of colour differences. Parental beetles are black or dark-brown, whereas newly-emerged adults are light brown in colour (Schroeder and Risberg 1989).

Further detailed information on the timing of reproduction and on the influence of temperature on the development of the galleries can be found in Chapters 3 and 4, respectively. A discussion of intraspecific larval competition and the effects of gallery density can be found in Chapter 5. Finally, more information on the preferences for brood material by this species can be found in Chapter 6.

Shoot Feeding

In Europe, shoot feeding by *T. piniperda* typically begins shortly after emergence of the new generation although some feeding may occur by the parental generation prior to this. A number of shoots are consumed by each individual beetle over the course of the feeding period. Timing of shoot feeding will be discussed in detail in Chapter 3 and shoot feeding preferences are examined in Chapter 6.

Overwintering

Tomicus beetles tend to move to overwintering locations in the autumn as the temperature drops below or close to the freezing point. Snow cover has been found to provide protection against the cold for adult beetles overwintering in the litter layer and at the bases of trees (Salonen 1973). In Fennoscandia, *T. piniperda* hibernates as adults at ground level in the bark of living pines (Salonen 1973). Gibbs and Inman (1991) reported the overwintering site to be at the junction between the outer and inner bark at or just above ground level. In southern France, it was found that they overwinter in the bark

overwinter in the shoots still on the tree. In Kunming, China, where it is much warmer, the majority of the beetles remain in the shoots over the winter (Ye 1991). In a study by Schroeder and Risberg (1989), adult *T. piniperda* were able to survive two hibernations and successfully establish new broods in the second year. Mortality rates for parental beetles were found to be no higher than the offspring beetles for the shoot feeding and hibernation period.

Timing/Chronology

Temperature is believed to be one of the limiting factors affecting the growth of a pine shoot beetle population (Ye 1994). Colder temperatures restrict the timing of flight and the success of reproductive attacks. In northern Fennoscandia, larval development and survival are negatively affected by the onset of the winter season (Schroeder and Risberg 1989). In addition, the production of a sister brood in the same year is a very rare event in many European areas (Langstrom 1980). In Sweden, *T. piniperda* has one generation per year, swarming in early spring to initiate galleries (Fagerstrom *et al.* 1977). In southern Scandinavia, flight and colonization occurs in late March to mid-April on sunny days when the temperature reaches 12°C or greater (Schlyter and Lofqvist 1990). In contrast, the beetle has two main flight periods in Kunming, China where the temperature is generally significantly warmer (Ye 1991). The first occurs in February to March when the temperature exceeds 13°C and the second occurs in April to May, consisting of parent beetles which have re-emerged after a period of shoot feeding (Ye 1991). In France, three brood phases of decreasing size were found in February-March, June-July, and July-August, with three emergence waves between late-June and late-August (Sauvard 1993). This species can also have a successful sister generation on Scots pine in Poland (Lutyk 1988).

In Kunming, the beetles spend about eight months in the pine crowns, remaining in each shoot for about one to two months (Ye 1991). Thus, each beetle consumes about four or five shoots during the feeding period. However, in Fennoscandia, adults consume only one to two shoots per year, mainly because the feeding period is much shorter

Langstrom 1990). New generation adults emerge in July and feed in the canopy. Each beetle hollows out one or two shoots, which dry out and fall to the ground. In October, the beetles then leave the shoots and bore under the bark at the base of the trees for hibernation (Fagerstrom *et al.* 1977).

Further information on the timing of this beetle's life cycle, and on the influence of temperature, can be found in Chapters 3 and 4 in relation to its newly expanded range into south-western Ontario.

Spatial Distribution

A previous study (Ye 1991) found the spatial distribution of feeding *Tomicus* beetles to be relatively homogeneous but with higher densities in living trees adjacent to local spots where several trees had provided breeding material. Shoot feeding by *Tomicus* adults tended to occur close to the emergence site of the beetles, especially for newly-emerged individuals (Eidmann 1992). A study by Langstrom and Hellqvist (1990) found decreasing shoot damage with increasing distance from the source of adult beetles, a saw-mill. After the first year of attack, however, they found the number of damaged shoots decreased close to the timber yard and increased at greater distances from the saw mill. This spatial change in shoot attack pattern over time was attributed to an increased dispersal of beetles, which was possibly due to a shortage of suitably sized shoots in the original area.

Orientation

The initial or primary attraction hypothesis of host tree colonization states that selection is based on chemical and/or visual cues from the host (Tunset *et al.* 1993). Studies have found that *T. piniperda* does not have a long-range attractant pheromone (Loyttyniemi *et al.* 1988, Kangas *et al.* 1967, Schroeder 1987), but recognizes its host by odour. It has been found that *T. piniperda* can recognize suitable hosts (both preferred species and susceptibility) while still in flight by using olfactory stimuli involving three plant monoterpenes (Tunset *et al.* 1993). A previous study has found that a majority of trees yielded duct resin at the time of the main *T. piniperda* flight period (Schroeder 1990). This resin flow may help beetles to locate suitable host material, as it flows from

wounds on windthrown or otherwise weakened trees. *Tomicus piniperda* orients preferentially towards fresh wood, which releases alpha-pinene and alpha-terpinol in high quantities compared to stored wood (Lindelow *et al.* 1992, Kangas *et al.* 1965). Certain terpene alcohols (trans- and cis- carveol) have been demonstrated to increase the attractant effect of alpha-terpinol (Kangas *et al.* 1970). These chemicals have also been shown to be present in the phloem in high quantities during the spring, especially in felled trees (Oksanen *et al.* 1968). Schroeder (1988) found that alpha-pinene alone was more attractive to this species than when mixed with increasing amounts of ethanol, however, Schroeder and Lindelow (1989) found that a combination of the two resulted in synergistically increased attraction. Volz (1988) found this species to prefer flight barrier traps baited with ethanol and oleoresin collected from its preferred host (*Pinus sylvestris*) over traps baited with ethanol or various monoterpenes. Vite *et al.* (1986) concluded that colonization of pine stumps and logs is in part due to the synergistic attractant effect of monoterpenes (especially the host-specific terpinolene) and ethanol secondarily formed in the damaged wood tissue of appropriate brood material. Finally, verbenone has been illustrated to have an effective anti-aggregation effect on *T. piniperda* (Baader and Vite 1990).

Impact

Tomicus piniperda is a serious pest of Scots pine stands, causing damage to a tree by developing in the phloem and by feeding on yearling shoots which then fall off (Zumr 1989). This herbivory decreases forest productivity by consuming or destroying needles, shoots, and buds, resulting in differing levels of growth loss (Langstrom *et al.* 1990, Fagerstrom *et al.* 1977). At high population levels, this feeding in the shoots, necessary for maturation of the beetles, causes reduced needle biomass and subsequent growth losses (Langstrom and Hellqvist 1990, Langstrom *et al.* 1990). The beetle primarily attacks the upper whorls which are the most photosynthetically productive shoots (Ericsson *et al.* 1985). Because *T. piniperda* also destroys the next year's buds, it can cause even worse damage than other defoliating pests (Langstrom *et al.* 1990).

diameter, and volume (Eidmann 1992, Langstrom 1991). Some reports have suggested that intensive shoot feeding in the pine crowns by *T. piniperda* predisposes the trees to successful stem attacks (Ye 1991) but other studies found that this was not the case (Langstrom and Hellqvist 1993). The extent of the feeding damage caused by the adult beetles has been shown to depend directly on the number of feeding adults (Eidmann 1992). Langstrom and Hellqvist (1990) found that the spatial pattern of growth reduction, measured as the basal area growth, followed that of the shoot feeding pattern. Different magnitudes of growth loss have been demonstrated in several studies. Growth loss has sometimes been found to be modest in young stands, even at high attack densities, where several hundred shoots must be lost to result in severe growth loss (Ericsson *et al.* 1985, Langstrom *et al.* 1990). Langstrom *et al.* (1990) demonstrated a low reduction in growth in young stands, but longer and more severe reductions in older tree stands after pruning to simulate shoot feeding by adult beetles. Growth losses of 20-40%, lasting over several years, after only one year of beetle attack have also been found in older stands (Langstrom and Hellqvist 1990).

Langstrom and Hellqvist (1993) concluded that Scots pine trees seemed to have a powerful defence system against bark beetle attack and their associated blue-stain fungi. Fungi associated with the attacking beetles and mechanical stress caused by boring of adult *T. piniperda* elicits an energy-costly hypersensitive defense reaction creating a necrotic area surrounding the egg gallery (Schroeder 1990). The area is the result of resin impregnation of the tissues located directly ahead of the attack front (Lieutier *et al.* 1991 and 1995).

Control Methods

Chemical

Typically, insecticides have been used in pest management strategies to prevent bark and ambrosia beetles from attacking host logs and/or to keep emerging beetles from spreading (Kohnle *et al.* 1992). Spraying stems with Xylamon ® and lindane has been shown to be effective both in preventing attacks and in suppressing existing attacks

repelling adults away from brood material (Parkk and Lee 1972). McCullough and Smitley (1995) found that survival of feeding beetles caged on trees treated with acephate, a mixture of acephate and bifenthrin, and imidacloprid was significantly reduced in comparison to beetles caged on untreated trees. However, in their subsequent field trial, none of the tested insecticide products were successful in reducing the number of shoots fed upon by *T. piniperda*. Glowacka *et al.* (1988) found that spraying stocks of unbarked Scots pine logs by hand with 1% Decis 2.5 EC ® (deltamethrin) up to three weeks before the first days of flight was successful at reducing *T. piniperda* populations.

Silvicultural

Alternatives to pesticide use include careful timing of cutting, rapid logging, and wet/dry storage of logs (Kohnle *et al.* 1992). Annila and Heikkila (1991) reported that young pines should be thinned at 3-4 m in height before rough bark develops on the trees. If rough bark was already present, they recommended thinning in June or July so that the trees would dry during the summer and be unsuitable for breeding the following spring. Altering the routines used to harvest, transport, and store timber can significantly reduce the availability of suitable breeding substrate (Eidmann 1992). Historically, large amounts of felled conifer stem were left in the forests and stored at the sides of forest roads. In addition, thinnings were performed during unsuitable periods (e.g. during colonization or in the previous winter), leading to further beetle damage (Eidmann 1992). The Swedish National Board of Forestry now have regulations limiting the amount of conifer material (damaged stems, thinning, or logging waste) that may be left in a forest, defining the periods during which thinning and cleaning can occur, and defining periods during which bark beetle breeding substrate may not be stored in the forest (Eidmann 1992). At present in Europe, growth losses mainly occur around timber yards, pulp mills and any other place where large amounts of unbarked pine timber are stored (Langstrom and Hellqvist 1990, Annila and Heikkila 1991). In Korea, thinning to improve the condition of the stand and to remove infested trees proved to be the most successful control method (Parkk and Lee 1972). In Italy, Triggiani (1984) found that the use of

“bait trunks” in open areas in September was an efficient way of controlling *T. piniperda* populations.

Natural Enemies

Populations of *T. piniperda* can be controlled to a certain extent by: specialized or generalized predators and parasitoids; nematodes; competition with other species; fungi; and viral and bacterial diseases. The larvae, pupae and adults are susceptible to infection by the dauerlarvae of the steinernematid and heterorhabditid nematodes (Triggiani 1983). Triggiani (1984) found the following natural enemies and symbiont nematodes in Italy: Coleoptera Histeridae: *Plegaderus otti* (Fabr.), and *Cylister elongatus* (Oliv.); Cleridae: *Thanasimus formicarius* (L.); Tenebrionidae: *Hypoploeus fraxini* (Kug.); Hymenoptera Braconidae: *Androsoter middendorffii* (Rat.); Pteromalidae: *Metacolus* (?) sp.; Neuroptera Raphidiidae: *Raphidia* sp.; Rhabditidae: *Parasitorhabditis piniperda* (Ruhm); Nematoda Aphelendroididae: *Parasitaphelenchus* sp. (Fuchs); and the fungus: *Beauveria bassiana* (Vuill.). Schroeder and Weslien (1994a and 1994b) found that the number of offspring produced per m² by *T. piniperda* could be reduced 92% when it was reared together with the predator, *Thanasimus formicarius* (Col., Cleridae).

In a recent Ontario study, Bright (1996) found a number of species of parasitoids and predators to be associated with *T. piniperda* in an infested Scots pine (*Pinus sylvestris*): Hymenoptera Braconidae: *Coeloides pissodis* (Ashmead), *Spathius* sp.; Pteromalidae: *Dinotiscus dendroctoni* (Ashmead), *Rhopalicus tutela* (Walker), *Roptrecerus xylophagorum* (Ratzeburg); Eupelmidae: *Eupelmus* sp.; Eurytomidae: *Eurytoma* sp.; Coleoptera: Histeridae: *Cylistix gracilis* (LeConte); Tenebrionidae: *Corticeus praetermissus* (Fall); Diptera: Dolichopodidae: *Medetera signaticornis* Loew, *M. pinicola* Kowarz. Most of the species listed were described as habitat-specific, not host-specific, and are commonly found associated with different Scolytidae on a variety of conifers.

Chapter Three : The Bionomics of a Recently Introduced Pest, *Tomicus piniperda* (L.)(Col., Scolytidae) in Southern Ontario

ABSTRACT

The bionomics of the exotic pine shoot beetle, *Tomicus piniperda* (L.) (Col., Scolytidae) were studied near Guelph, Ontario from 1995 to 1997. A large increase in the mean number of shoot feeding attacks per tree occurred from late-July to mid-September in 1995. The decline in the percentage of attacked shoots containing an adult beetle indicated that the beetles moved to overwintering sites in mid to late-October in 1995. In 1996, the number of new galleries initiated under the bark of Scots pine (*Pinus sylvestris*) logs by the emerging parental generation peaked sharply in the last two weeks of April, earlier than most bark beetle species. Colonization in 1997 occurred from mid-April to early-May. Complete development of the galleries required a 12- to 13-week period in 1996. Emergence of the new generation in 1996 occurred over a two-week period at the end of July. The very low levels of shoot feeding observed in 1996 suggest that successful reproduction did not occur near enough for immigration into the young stand being studied. Shoot feeding activity was evident in the older stand in 1996, where reproduction is known to have occurred. Timing of critical life cycle events is similar to European reports under similar climatic conditions. Knowledge of this timing will be important in designing management protocols.

INTRODUCTION

The pine shoot beetle, *Tomicus piniperda* (L.) (Col., Scolytidae), is a widely distributed pest that has only recently been introduced into Ontario. An established population was first found in Ohio in July 1992 and it has since been found in eight U.S. states and in 13 counties in the Great Lakes region of Ontario (Haack 1996). *Tomicus piniperda* is a major pest of Scots pine, *Pinus sylvestris* (L.), in Europe, often causing considerable growth loss (Langstrom and Hellqvist 1990). While there are numerous European studies on various aspects of the species' life cycle, ecology and impact (e.g. Bakke 1968; Salonen 1973; Langstrom 1983, 1984, 1986), information on how the beetle is affected by Canadian conditions is non-existent.

From European studies, the pine shoot beetle is known to typically emerge from overwintering early in the spring, when the maximum air temperature reaches 13°C (Langstrom 1986). Galleries are initiated by the female in rough-barked sections of weakened trees or freshly cut logs. Emergence of the new generation occurs approximately three months later (Fagerstrom *et al.* 1977), after which shoot feeding can be expected to begin. This requisite maturation shoot feeding period is unique to this genus and is the primary source of damage by this pest. The beetles typically leave the shoots in mid-autumn and overwinter under the bark at the base of the tree (Salonen 1973).

Accurate knowledge of the timing of critical events in this species' life cycle, in particular: infestation of brood material; emergence of the new generation; and onset of shoot feeding will play an important role in developing effective management protocols. Thus, this paper examined the timing of spring reproduction and summer shoot feeding of *T. piniperda* in southern Ontario over a two-year period in order to make comparisons with that known from its native range in Europe.

Study Sites

Timing of spring emergence and reproduction were studied in the field during 1996-7 in a 40-year-old Scots pine stand, 15 km south of Guelph, Ontario (43°30'latitude, 80°20'longitude). The height of the trees ranged from 13-17 m and their DBH (diameter at 1.3 m height) from 14-18 cm. A mature stand was selected because it was known that adult beetles require wood >7-10 cm in diameter with rough corky bark in order to reproduce (Salonen 1973).

Timing of summer maturation feeding was studied in the field during 1995-96 in a young (12-15 year old) Scots pine stand, 20 km south of Guelph, Ontario (43°27'latitude, 80°21'longitude). Trees ranged from 2.5-3.5 m in height and 3-7 cm DBH. The stand consisted of several hundred trees, which were planted in rows at a 2 by 2 m spacing. A young stand was selected here because, in addition to providing a large number of shoots appropriate for feeding by the beetles, the tree's small height allowed for quick, easy, and accurate sampling. The trees in this stand had been maintained previously as Christmas trees but had been abandoned two years previously.

Timing of Spring Reproduction

In the spring of 1996 (March), six trees in the older stand which had been damaged by a storm the previous week were felled and cut into logs approximately 0.75 m long. A total of 28 logs were placed into eight separate piles of three to four logs each. In the spring of 1997 (early April), five Scots pine logs of the same size were again cut and left in the field in five separate locations. In both years, each log was inspected at four to six-day intervals for evidence of colonization by *T. piniperda* and timing of gallery initiation was assessed by counting the number of entrance holes bored into the bark. Timing of emergence of the new generation was monitored by counting the number of exit holes visible in the bark of the logs remaining in the field after the galleries were complete.

Summer Shoot Feeding

In the summer of 1995 (July), 50 trees in the young Scots pine stand were used to follow shoot feeding. The trees were selected randomly by placing several non-overlapping 50-m transect lines through the stand and picking every second apparently healthy tree that was closest to the transect line. Once a tree was selected, it was numbered and all damaged shoots were counted and flagged. The trees were examined for new attacks every two weeks from late-July until mid-October. In 1996, 35 of the 50 trees from the previous year were examined similarly at bi-weekly intervals from mid-July to mid-September. In mid-August 1996, due to the low numbers of damaged shoots observed, a survey of similar appropriate sites was made of the surrounding region in an attempt to find additional evidence of shoot feeding activity by the beetle. In mid-November 1996, to examine for evidence of shoot feeding activity in the older stand, the ground of 25 randomly selected plots (1.5 m by 1.5 m) were examined for fallen shoots attacked by *T. piniperda*.

On 21 July, 16 October and 09 November 1995, 43, 55 and 56 visibly attacked shoots, respectively, were randomly collected from trees in the young stand and the presence or absence of a feeding beetle within each attacked shoot was noted. In addition, on 09 November 1995, 65 attacked shoots which had fallen to the ground was dissected to examine for the presence of active feeding adult beetles.

RESULTS

Timing of Spring Reproduction

The colonization period of *Tomicus piniperda* in southern Ontario began in mid-April during 1996. The majority of the galleries were initiated over a 2-week period (Figure 3-1). In 1997, colonization began in mid-April and continued over a 3-week period (Figure 3-1). The parental generation was assumed to have emerged at the same time or shortly before this period of colonization. In 1996, the first attacks were observed on a day when the air temperature reached 14°C (see Figure 4.2). The new generation completed development and emerged approximately 12-13 weeks later over a 2-week period at the end of July in 1996 (Figure 3-2).

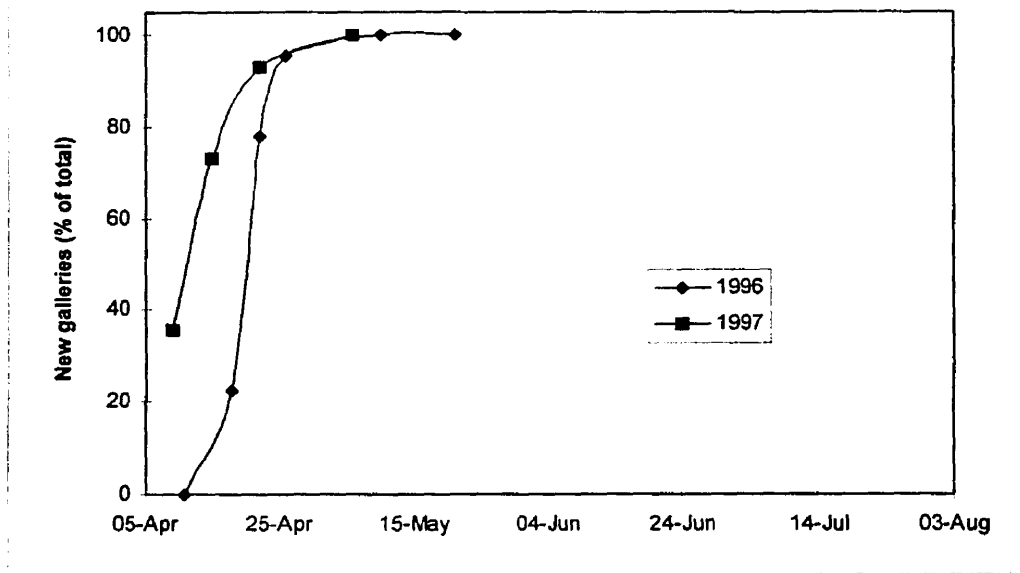


Figure 3-1. Colonization pattern of Scots pine (*Pinus sylvestris*) trap logs by the parent generation of the pine shoot beetle (*Tomicus piniperda*) during the spring of 1996 in a 40-year-old stand near Guelph, Ontario. (n=598 galleries in 1995 and 168 in 1996 in total)

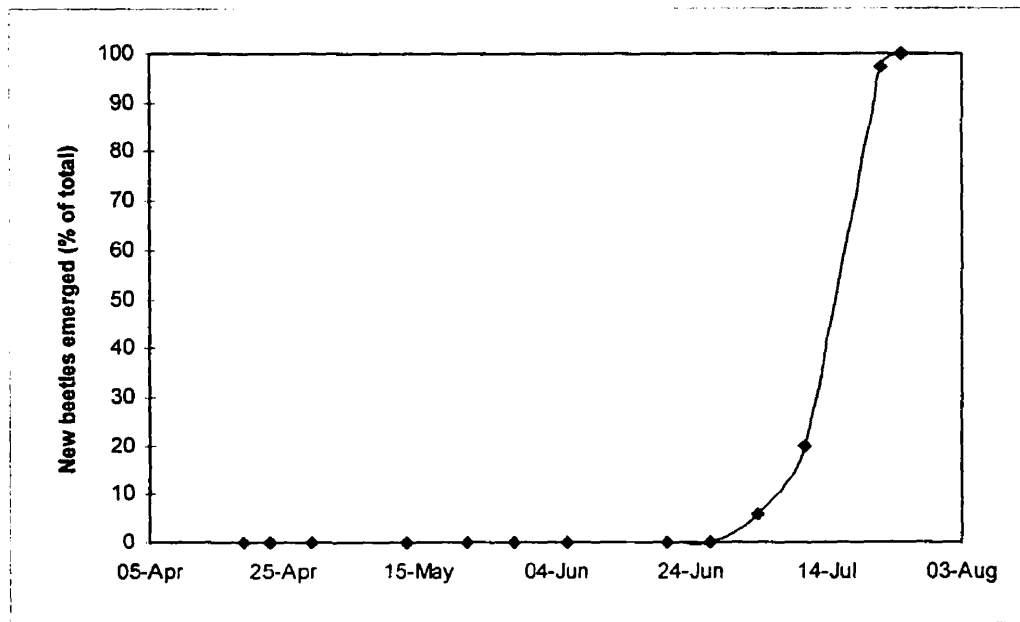


Figure 3-2. Emergence pattern from Scots pine (*Pinus sylvestris*) trap logs of the new generation of the pine shoot beetle (*Tomicus piniperda*) during the summer of 1996 in a 40-year-old stand near Guelph, Ontario. (n=5429 new beetles in total)

The mean number of shoots attacked on each tree (up to 5.28 attacked shoots per tree, s.d. = 7.12) increased over the summer of 1995 (Figure 3-3). By late August, the majority of the shoot attacks had occurred and very little increase was seen after this date. In contrast, very low numbers (mean 1.33 attacked shoots per tree, s.d. = 1.53) were observed over the entire summer of 1996 (Figure 3-3). The percentage of trees being attacked by *T. piniperda* also increased over the summer of 1995 and 1996 (Figure 3-4). This was particularly apparent in 1996 where most new shoot attacks occurred on new trees. Twelve other young sites were examined intensively for evidence of shoot feeding in early August 1996, however, only two individual beetles were found at one of these locations. Shoot feeding did occur in the older stand in November during 1996 (mean 3.4 fallen shoots per plot sample, s.d.=4.6, n=25).

The percentage of attacked shoots containing an adult beetle declined gradually over the summer of 1995. In the first sample (21 July), 75% of the shoots contained a feeding beetle, in the second sample (16 October), 45%, and in the final sample (09 November), only 25% of the shoots still contained a beetle. By this same date (09 November), 65 shoots collected from the ground contained no feeding beetles. No further samples were taken.

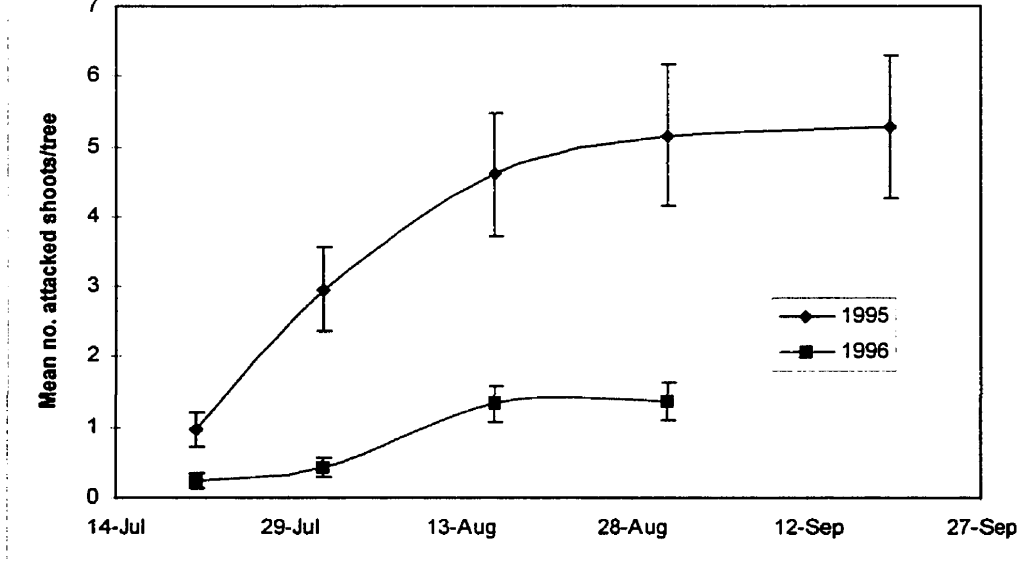


Figure 3-3. Mean number of shoots attacked per tree by adult *Tomiscus piniperda* over the summer of 1995 and 1996 in a young (10-12 year old) Scots pine (*Pinus sylvestris*) stand near Guelph, Ontario. (Vertical bars indicate standard error) (n=50 trees in 1995 and 35 trees in 1996)

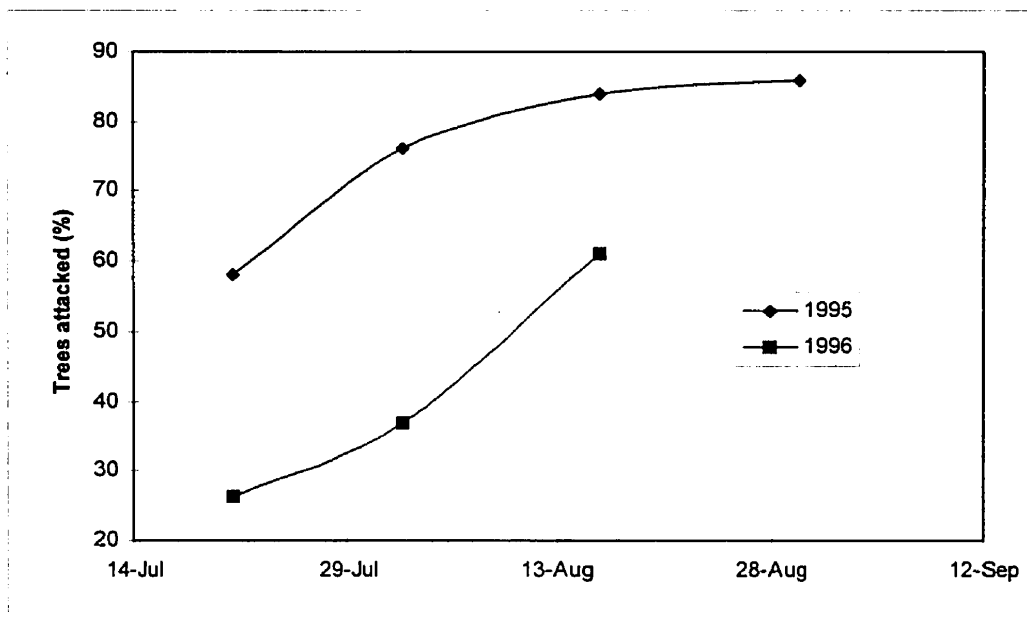


Figure 3-4. Percentage of trees attacked by adult pine shoot beetles (*Tomiscus piniperda*) in 1995 and 1996 in a young (10-12 year old) Scots pine (*Pinus sylvestris*) stand near Guelph, Ontario. (n=50 trees in 1995 and 35 trees in 1996)

Timing of Spring Reproduction

New galleries are initiated by the emerging *Tomicus piniperda* in early spring (mid- to late-April or early-May) in southern Ontario. The pattern is very similar to that seen previously in other regions of the continent (northern U.S.A.) and Europe. In Michigan, the adults initiated spring flight in late-March and the density of attacks on logs cut after this point was very low (Haack and Lawrence 1995). In southern Scandinavia, the main flight and host colonization period of *T. piniperda* begins in late-March to mid-April, on sunny days when the temperature rises above 12°C (Schlyter and Lofqvist 1990). In southern Sweden, flight activity starts when the peak air temperature exceeds 10-12°C and this varies annually from late-March to early-May (Langstrom 1983). Bakke (1968) also found that emergence depended on a minimum temperature of 10-12°C over the course of a day. Finally, in Finland, adult swarming occurs from mid-April in the southern Helsinki region to mid-May in the northern Rovaniemi region, again when the temperature reaches a threshold of 10-12°C (Salonen 1973). The majority of the emerging parental generation typically fly over a period of only a few days (Langstrom 1983, Schlyter and Lofqvist 1990). In general, studies have found that the flight and colonization period of *Tomicus piniperda* tends to occur over a brief period of time, early in the season once the threshold temperature of approximately 10-12°C has been reached. The results from the current study correspond well with these previous findings. Indeed, during 1996, in the weeks prior to the onset of colonization, the mean temperature was 9°C or less. The first major evidence of colonization was on the first day when the mean air temperature reached 14°C (Figure 4-2).

The close synchrony and early initiation of galleries by *T. piniperda* may be related to the limited brood material available. Typically, stressed or moribund trees, or cut logs, are required by this species for reproduction (Langstrom 1983). Larvae developing in galleries established later are subject to intense intraspecific and/or interspecific competition from older, larger larvae who arrived earlier (Beaver 1974). Early gallery initiation by *T. piniperda* helps to prevent or reduce the effects of

inter-specific competition. Indeed, different bark beetle species have specific swarming temperatures. The required temperature for swarming of *T. piniperda* (10-12°C) is lower than that required for many other species (Salonen 1973). For example, *Tomicus minor* Hart., a European species, swarms only after the daily air temperature reaches 12-14°C and *Ips acuminatus* Gyll. begins to swarm at temperatures of 14-16°C (Bakke 1968). Haack and Lawrence (1995) found that in Michigan, the native species, *I. pini* (Say), initiated spring flight and colonization approximately one month after *T. piniperda*. They concluded that the earlier spring flight allowed *T. piniperda* to colonize most of the available brood material, and possibly reduce populations of *I. pini*. Finally, European *I. typographus* beetles require temperatures of at least 18-20°C before flight can occur (Annala 1969). Hence, the lower temperature requirements for *T. piniperda* will enable this species to be among the first to find and colonize appropriate brood material, which can be a limited resource.

Knowing that the colonization period of *T. piniperda* is early and brief is important for management. If appropriate brood material is present in a stand during this time, then it may be highly attacked and become the source of a large number of emergent beetles later in the season. Brood material includes any weakened or storm-damaged trees, bolts or logs with rough bark, and sizable stumps from trees cut the previous winter. Alternatively, populations of the beetle may be able to be 'trapped out' by intentionally placing trap logs in the field before the initiation period. This method has been efficient at controlling Italian populations of *T. piniperda* (Triggiani 1984). The logs, and the developing galleries within them, could then be destroyed before the new generation emerges. This brief period of gallery initiation by *T. piniperda* suggests that it is unlikely that further galleries will be established later in the summer. Indeed, Langstrom (1983) found that new galleries were rarely established after the main flight period had ended.

After the colonization period, the galleries of *T. piniperda* seem to require a considerable length of time to complete development. In southern Ontario during 1996, I found development to take approximately 12-13 weeks or 88 days; this is very similar to reports from overseas. For example, in a European study, the average period of

development was 72 days in the field (Langstrom 1985). In southern Sweden, Langstrom (1983) found that most new *T. piniperda* left their brood logs during the first half of July. In my study, emergence of the new generation occurred over a relatively brief two week period at the very end of July in southern Ontario in 1996. It is possible that this was delayed by up to two weeks because of cool seasonal temperatures in southern Ontario during the spring of 1996 (see Chapter 4). Saarenmaa (1985) found that emergence of adults occurred from the first week of July to the middle of August and that the emergence times varied greatly between years. He concluded that the new adults emerged over a long period of time because of differing developmental rates, sequential gallery establishment, and sequential egg-laying during gallery excavation. In my field study, the galleries were established over a fairly brief period and this may be why emergence of the new generation was relatively synchronous.

The timing of new *T. piniperda* adult emergence from the brood logs is also extremely important for management. If susceptible brood material is present in a stand, intentionally or not, it should be removed and destroyed before the new generation emerges in mid- to late-July. Because complete gallery development requires a fairly lengthy period of time, there should be no problem in finding an opportunity to destroy the brood material. However, care must be taken not to leave this procedure until too late, as the entire new generation will quickly emerge from the material. Shortly after the emergence period, feeding in the shoots of susceptible trees can be expected to begin. Hence, prevention of the emergence of the new generation would help to reduce damage from subsequent shoot feeding.

Timing of Summer Shoot Feeding

The long period of shoot feeding required by *T. piniperda* to mature is unique, and can cause considerable damage. My study found that, in southern Ontario, adults of *T. piniperda* spent about 25% of the year feeding in the shoots of the host trees (August through to October). The onset and duration of shoot feeding by *T. piniperda* has been found to vary depending on its location. For example, adults spend two-thirds of the year feeding in the pine crowns of Kunming, China (Ye 1991). Feeding in tree crowns is

begin shortly after the emerging adults leave the brood material. In one study by Langstrom (1980), shoot feeding by the new generation of beetles did not begin until July. Results from my study suggest that the beetles were present in the shoots as early as mid-July during 1995. Ye (1991) found the main flight period of *T. piniperda* was in February and March with shoot feeding beginning shortly thereafter. In China, however, temperature has a major effect on the timing of these events. This suggests that the climate there is much warmer than in southern Ontario.

Population structure of *T. piniperda* is known to affect the pattern of shoot feeding. If breeding success is high, there will be a large increase in the number of shoots attacked over the summer. However, if breeding success is low, shoot feeding attacks will only occur early in the summer by the reemerging parent generation (Langstrom 1983). Hence, the rapid increase in shoot feeding at my site in 1995 suggests that there was a high level of successful gallery establishment and development. This stand had many weakened trees available as potential breeding sites due to damage caused in the previous winter. An influx of new generation beetles, distinguishable by their light brown color, was noticed during the 1995 field work but was not recorded. In contrast, during 1996, there was very little increase in the number of shoots attacked, suggesting that only the reemerging parental generation was feeding. Shoot feeding was observed in the older stand, where successful reproduction was known to have occurred. Therefore, it is possible that there were no new suitable breeding sites near to or within the young stand in that year. That my survey of other seemingly appropriate sites in that same year found few beetles suggests that there may be a seasonal, rather than a site, problem in these younger stands.

The decline in the percentage of attacked shoots which contained a feeding beetle, combined with the increasing number of attacks per tree, is indicative that each feeding adult beetle consumes more than one shoot over the course of the summer. Langstrom (1980) found that the adults consumed at least one to two shoots over the feeding period in Fennoscandia. Ye (1991) estimated that each adult consumed four to five shoots over the feeding period, but concluded that this was directly related to the longer period of

the summer, as evidenced by the increase in the percentage of trees attacked.

The beetles left the shoots for overwintering sites during October in 1995. This suggests that the beetles do not overwinter in the shoots on the trees in southern Ontario, unlike in areas with warmer climates (Ye 1991). Previous results from Fennoscandia have also found increasing numbers of empty attacks in October and November until practically all of the beetles had left the shoots (Langstrom 1983). In addition, I never found beetles overwintering in the fallen shoots on the ground. It is likely that the beetles overwinter under the bark at the tree base, as has been found in previous studies with similar climates (Salonen 1973), but further studies would be necessary to confirm this.

In summary, the pine shoot beetle was observed to complete one generation per year in southern Ontario. In 1996 and 1997, the flight and colonization period of the parental generation occurred from mid- to late-April or early-May. Emergence of the new generation occurred approximately three months later, during late-July in 1996. In 1995, levels of shoot feeding rose until late-summer while, in 1996, very few shoots were attacked in the young stands. Movement to overwintering sites by adult beetles began around mid-October with no beetles overwintering in the shoots. Overall, the timing of the life cycle of *T. piniperda* closely followed that of the European literature. This is important in that European studies can now be used to manage this potentially damaging pest, as long as the different temperature conditions in southern Ontario are taken into consideration.

Chapter Four : Influence of Mean Daily Air Temperature on the Development of *Tomicus piniperda* (L.) (Col., Scolytidae) Galleries in Southern Ontario

ABSTRACT

The effect of mean daily air temperature on the development of the various juvenile stages of the recently introduced pine shoot beetle, *Tomicus piniperda* (L.), was studied in the field in southern Ontario during 1996. Colonization of brood material by the emerging parental generation peaked in late-April and gallery development was completed approximately 88 days later (from median swarming to median emergence). Emergence of the new generation occurred during the last two weeks of July. The duration of the juvenile stages corresponded well with European findings. Both heat sums (d.d.>0°C) and effective degree days (d.d.>developmental threshold temperature) corresponded well with previous European and Asian studies. This work suggests that temperature data can be used to accurately predict the emergence of the new *T. piniperda* generation which is responsible for the damaging shoot feeding.

INTRODUCTION

Bark beetles, as with all insects, are exothermic and, as such, are highly influenced by the effect of temperature. Developmental rates of juveniles and activity rates of adults typically increase sigmoidally with increasing ambient air temperature (Salonen 1973). Knowledge of this close relationship can be helpful when attempting to model and predict insect development and activity periods (Saarenmaa 1989). Simple temperature data can be used to model insect biology independent of calendar date. Physiological models of insect development have commonly been created with the calculation of accumulated heat units in degree-days (Higley *et al.* 1986, Ring and Harris 1983). Summation of the mean daily air temperature, above a predetermined developmental threshold temperature, provides a measure of the required heat accumulation by the various developmental stages (Hochberg *et al.* 1986, Petite *et al.* 1991).

Timing of life cycle events and the success of reproduction by *T. piniperda* is highly affected by cold temperatures in northern regions (Saarenmaa 1989). Emergence of the new generation of *Tomicus piniperda* (L.) (Col., Scolytidae) beetles leads to a subsequent damaging period of shoot feeding in its host pine trees, often Scots pine (*Pinus sylvestris* L.). Information about the effect of temperature on the development of *T. piniperda* juvenile stages could help to predict when emergence will occur and possibly prevent or reduce it. While numerous studies have been conducted in Europe and elsewhere (for example: Langstrom 1983, Ye 1994, Salonen 1973), information about the influence of temperature on the timing of critical life cycle events is lacking in the beetle's newly expanded range of southern Ontario.

This paper examined the development of naturally established galleries in the field in southern Ontario during 1996. Heat sums (degree-days above 0°C) and effective degree days (degree-days above the developmental threshold temperature) were calculated and compared with previous studies.

Study Sites

Timing of spring emergence and reproduction was studied in the field during 1996 in a 40-year-old Scots pine stand located south of Guelph, Ontario (43°30'latitude, 80°20'longitude). In the fall of 1995, the height of the trees ranged from 13-17 m and their DBH (diameter at 1.5 m height) ranged from 14-18 cm.

Weather Data

Environmental conditions were monitored using a Campbell Scientific CR-10 digital data logger which was established at the site from 10 April to 2 June 1996. Four thermocouples recorded temperatures: two in the air in a Stevenson screen and two under the bark crevices of a tree (one facing south and the other facing north).

Mean hourly temperature were recorded and averaged to provide a mean daily temperature. Mean daily air temperature from the time of gallery initiation until the first egg and the first larvae were calculated. Mean hourly air temperature was compared between the sites (air and bark) and also between the north- and south-facing probes located under the bark.

Temperature data were then obtained for the months of April through July from the Waterloo-Wellington Airport (Environment Canada). Mean daily air temperatures were compared between the airport and the CR-10 data with a Wilcoxon signed-ranks test (SYSTAT: Wilcoxon). The heat sum (degree-days above 0°C) for the various developmental stages and then the effective degree-days (above the developmental threshold temperature) were calculated. The threshold temperatures used were those determined by Salonen (1973) and Ye (1994). Mean temperatures for the duration of the various stages were determined and compared with the CR-10 data.

Gallery Development

On 28 March 1996, six trees were felled and cut into logs approximately 0.75m long. A total of 28 logs were placed into eight separate piles of three to four logs each. Each of the logs was inspected weekly for evidence of colonization by *T. piniperda*.

Timing of colonization was monitored by counting the number of entrance holes bored into the outside bark of the logs. Once evidence of colonization (entrance holes and sawdust) was apparent, one log was randomly selected on each sample date and brought back to the laboratory for dissection. In the laboratory, the bark was removed to assess the stage of development of the galleries. On each sample date, a minimum of ten galleries were examined. The following measurements were recorded for each gallery: length (to the nearest 0.1 cm), number of adults present, and number of eggs and larvae. As of 21 June, it could no longer be determined to which gallery the individual larvae or pupae belonged. After this point, the ratio of larvae to pupae was recorded for one entire log, instead of on a per-gallery basis. Timing of emergence of the new generation was monitored beginning in mid-July by counting the number of exit holes visible on the bark of the log on each sample date.

RESULTS

Development of the Galleries and the Influence of Mean Daily Air Temperature

Approximately 12-13 weeks were required after initiation of the galleries before the new generation of *T. piniperda* beetles emerged (Fig. 4-1a and b). The egg stage lasted approximately 24 days and the larval stage, 32 days (Fig. 4-1a). The pupal stage lasted an additional 15 days and the new adults remained under the bark in a pre-emergence stage for a final 10 days. Curves for the pupae and new adults are skewed right, indicating that the occurrence of these stages were slow to start but ended up fairly synchronous (Fig. 4-1b). Emergence of the new generation occurred over a 2-week period at the very end of July (Fig. 4-1b).

The mean daily air temperature rose gradually over the 4-month period from April through July 1995 (Fig. 4-2). Mean daily air temperature as recorded by the CR-10 datalogger corresponds closely with the values recorded at the Waterloo-Wellington airport, indicating that the airport data is representative of the conditions within the stand (Wilcoxon, $z=-0.147$, $n=31,31$, two-tailed $p=0.8831$) (Fig. 4-2).

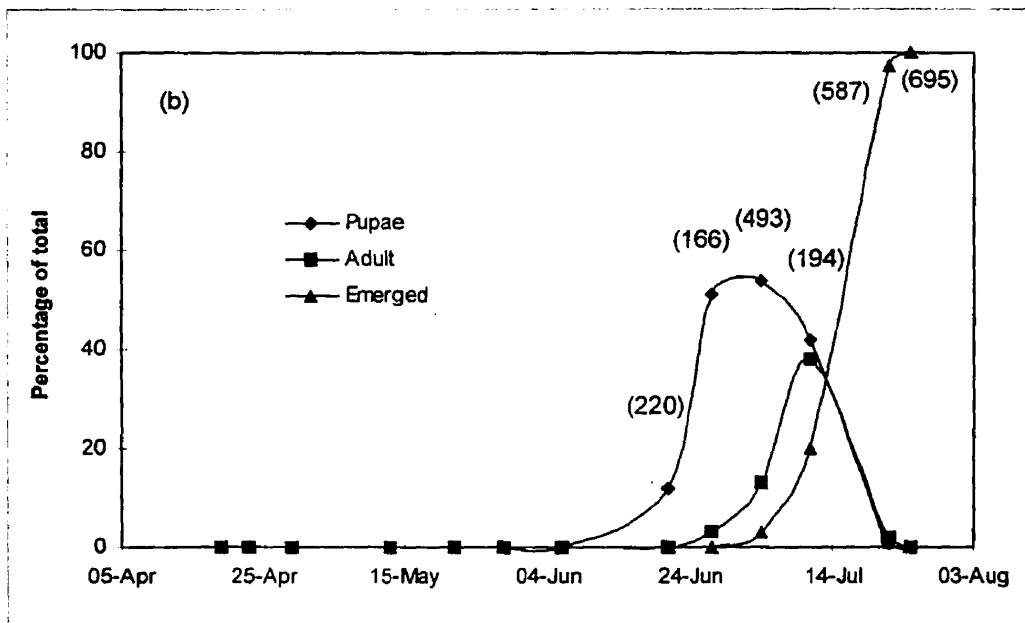
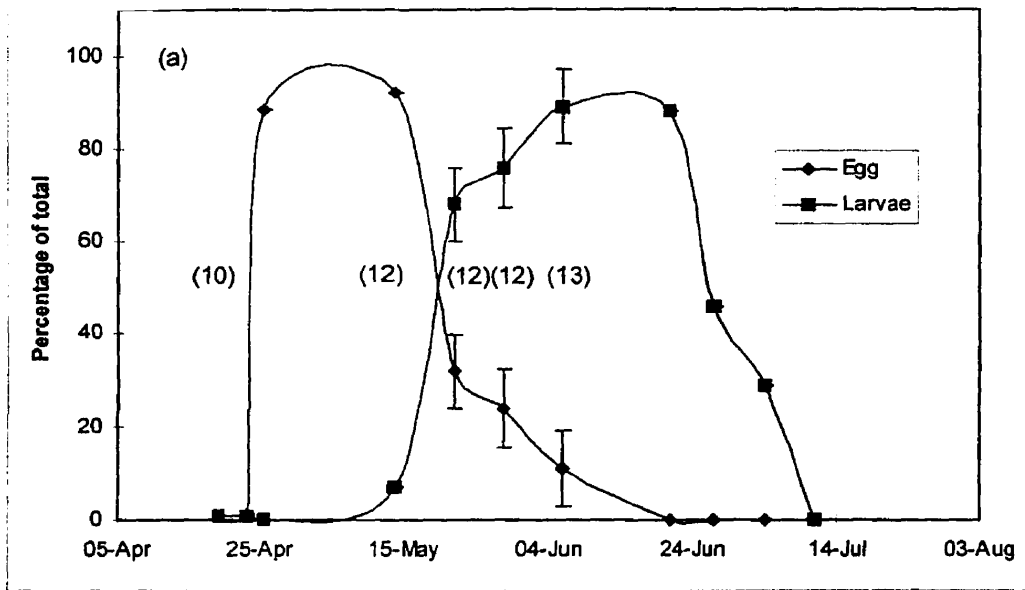


Figure 4-1a and b. Development of pine shoot beetle (*Tomicus piniperda*) galleries in Scots pine (*Pinus sylvestris*) trap logs during the spring of 1996 in a 40-year-old stand near Guelph, Ontario. (Fig. 4-1a. Numbers in brackets indicate number of galleries examined on each sample date.) (Data points after 21 June are based on 1 entire log per sample date) (Fig. 4-1b. Numbers in brackets indicate total number of individuals counted). (Vertical bars indicate the standard error).

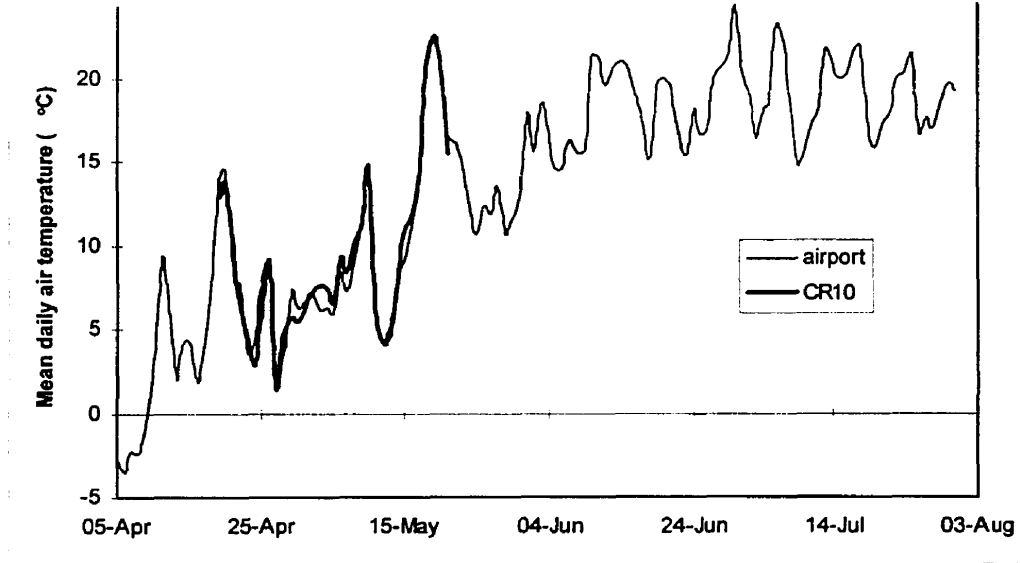


Figure 4-2. Mean daily air temperatures recorded at the Waterloo-Wellington airport from April to July 1996 and by the CR-10 data logger from April to June 1996 in a 40-year-old Scots pine (*Pinus sylvestris*) stand infested with pine shoot beetle (*Tomicus piniperda*) near Guelph, Ontario.

For 3 specific periods (time until first egg, duration of egg stage, and time until first larva), the airport data closely represents the temperature experienced within the stand as recorded by a CR-10 datalogger (Table 4-1). Over the course of any given stage, the mean daily air temperature ranged in value, as illustrated by the minimum and maximum temperatures (Table 4-1). This is in contrast to the constant laboratory conditions used in Salonen (1973). The time until the first egg was seen was longer in this current study than in Salonen (1973) but the mean temperature in the current study during this time period was 2.5°C colder (Table 4-1). The egg stage lasted a shorter amount of time than in Salonen (1973), even though the mean temperatures were similar. However, there were warmer days in the field, as indicated by the maximum temperature of 22.2°C (Table 4-1). Similarly, the time until the first larva was shorter than in Salonen (1973) with a similar mean temperature, however, in the current study, warmer days (maximum of 22.2°C) were experienced (Table 4-1). Durations and mean temperatures during the larva, pupa, and preemergence (the period that the new adults remain under the

Salonen (1973) (Table 4-1).

The egg heat sum value ($d-d>0^{\circ}\text{C}$) is seen to be approximately 25% lower than values found previously by both Salonen (1973) and Knoche (1904) (Table 4-2). The larval stage alone accounted for approximately 40% of the total heat sum required (Table 4-2). The larval heat sum value corresponds very closely with the values from both previous studies. The pupal heat sum value corresponds well with Salonen (1973) but is much larger than that found by Knoche (1904). The value obtained for the preemergence stage corresponds well with both of these previous studies (Table 4-2). The total heat sum also corresponds well with Knoche (1904) and Salonen (1973) but is approximately 25% higher than that reported by Langstrom (1983). All of the values presented for this current study indicate a possible range, because of the difficulty in determining precisely on which days each stage began and ended.

The effective heat sum for the egg stage (degree days above the developmental threshold temperature) corresponds well with Salonen (1973), but is much lower than that found by Ye (1994) (Table 4-3). Threshold temperatures for zero development used for the various stages were from both Salonen (1973) and Ye (1994). The larval stage required a much larger effective heat sum to complete development compared to the other juvenile stages (Table 4-3). Again, the current value corresponded well with Salonen (1973) but was lower than that reported by Ye (1994). The effective heat sum calculated for the pupal stage was higher than either previous result (Table 4-3). Finally, the value for the preemergence stage was also much higher than that found by Salonen (1973) (Table 4-3). The possible range in the values presented for the current study are again the result of the difficulty in determining the exact day upon which each stage began and ended.

Mean monthly temperatures for April through July of 1996 were $1-2^{\circ}\text{C}$ lower than the thirty year normals, except for June which was 1.3°C warmer than the 30-year normal value (Table 4-4). The maximum monthly temperatures for April to July of 1996 were $0.2-2.5^{\circ}\text{C}$ less than the thirty year normal temperatures and the minimum monthly

temperatures for April, May and July were 0.5-0.9°C lower than the 30-year normal temperatures. The minimum temperature for June of 1996 was 3°C higher than the 30-year normal minimum temperature (Table 4-4).

Table 4-1. Duration of various developmental stages of *Tomicus piniperda* and mean daily air temperatures from the Waterloo-Wellington airport and the CR-10 datalogger and from Salonen (1973).

Stage	Current Study				Salonen (1973)	
	Days	Air Temp. (°C)			Days	Air Temp. (°C) ¹
		Airport		CR-10		
		mean	min./max.	mean		
First egg	12+/-2	7.5	3.7/14.4	7.7	7	10
Egg	24+/-3	10.6	4.3/22.2	10.4	30-40	11
First larvae	35+/-3	9.6	3.7/22.2	9.5	51	10
Larvae	32+/-2	16.6	10.6/21.3	-	36	15
Pupae	15+/-2	18.7	15.3/24.3	-	17	15
Preemerge	10+/-1	18.4	14.8/23.1	-	11	15

¹) Results obtained from laboratory experiment with constant temperatures

Table 4-2. Heat sums (degree-days above 0°C) required by various developmental stages of *Tomicus piniperda* calculated in the current study during 1996, and reported in three other studies.

Stage	Current study		Knoche (1904)		Salonen (1973)		Langstrom 1983
	(dd>0°C)	mean temp. (°C)	(dd>0°C)	mean temp. (°C)	(dd>0°C)	mean temp. (°C)	
egg ¹	310.2+/-25.5	10.6	409	9.1	408	10.2	-
larvae	523.3+/-35.4	16.6	513	15.1	541	15	-
pupae	245.1+/-42.3	18.7	154	17	257	15.1	-
preemerge ²	171.2+/-38.4	18.4	142	15.9	167	15.4	-
total	1249.8+/-73.3		1218		1375		1016

¹) Calculated from median colonization (50% of galleries initiated)

²) Calculated to median emergence (50% of new generation emerged)

temperature) required by various developmental stages of *Tomicus piniperda* calculated in the current study during 1996 using developmental threshold temperatures from two other studies

Stage	Current study ¹	Salonen 1973 ¹	Current study ²	Ye 1994 ²
Egg	79.6+/-7.5	82	77+/-6.1	95.8
Larva	267.3+/-16.4	255	292.9+/-27.9	358.1
Pupa	139.1+/-24.7	107	152.3+/-38.2	115.9
Preemerge	43.2+/-12.3	24	-	-

⁽¹⁾ Developmental threshold for egg=8 °C, larvae=8 °C, pupae=8.8 °C, and preemerge=13 °C (Salonen 1973)

⁽²⁾ Developmental threshold for egg=8.2°C, larvae=7.2 °C, and pupae=7.9 °C (Ye 1994)

Table 4-4. Comparison between 1996 and the 30-Year normal values of the mean, maximum, and minimum monthly temperatures for April through July from the Waterloo-Wellington airport.

Month	Mean (°C)		Max. (°C)		Min. (°C)	
	1996	30-Year	1996	30-Year	1996	30-Year
April	3.9	5.8	8.7	11.2	-0.8	0.4
May	11.2	12.5	17.0	18.6	5.4	6.3
June	18.3	17.0	23.0	23.2	13.7	10.7
July	18.9	19.9	24.5	26.1	13.1	13.6

The mean number of adult beetles present in the galleries gradually declined over the summer. An average of two adult beetles per gallery could be found until mid-May after which, only one adult was present until mid-June (Figure 4-3). A steady increase in the mean number of eggs laid per gallery, up to a mean of 32, occurred until early-June (Figure 4-4). The mean length of the gallery increased steadily, up to approximately 7 cm, at the beginning of June (Figure 4-5).

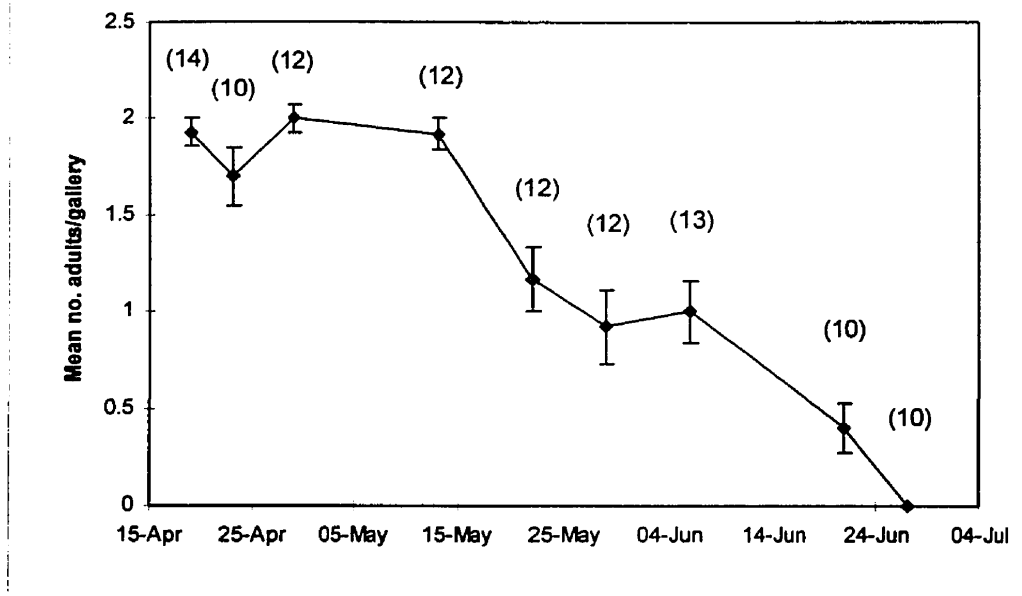


Figure 4-3. Mean number of *Tomicus piniperda* adults located within galleries on Scots pine (*Pinus sylvestris*) trap logs in a 40-year-old stand near Guelph, Ontario during 1996. (Numbers above each point indicates the number of galleries examined on each sample date) Vertical bars indicate the standard error.

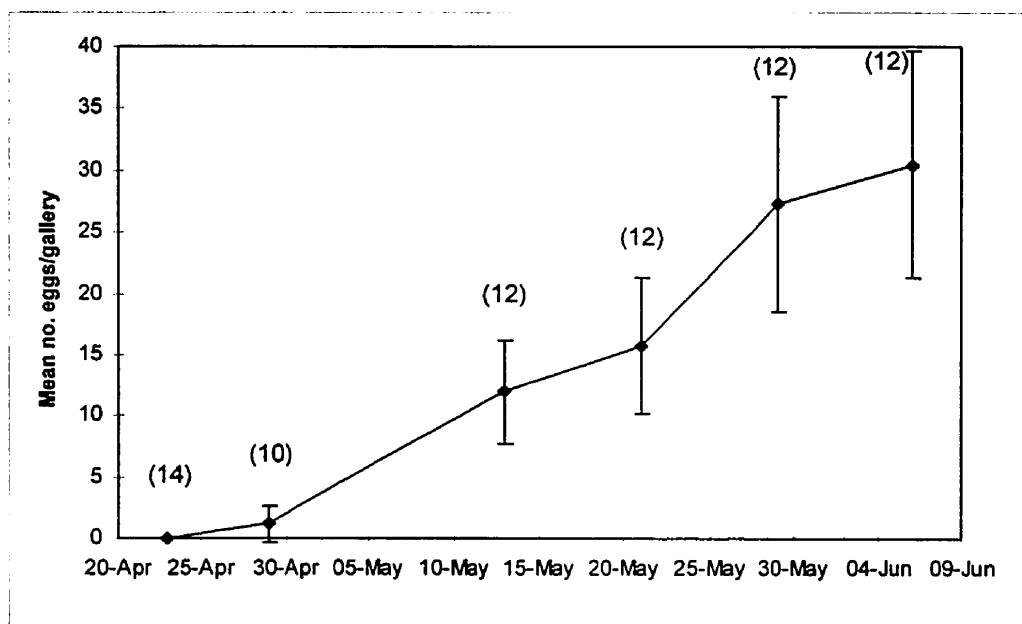


Figure 4-4. Mean number of eggs laid per gallery by female *Tomicus piniperda* on Scots pine (*Pinus sylvestris*) trap logs during 1996 in a 40-year-old stand near Guelph, Ontario. (Numbers above each point indicate the number of galleries examined on each sample date) Vertical bars indicate the standard error.

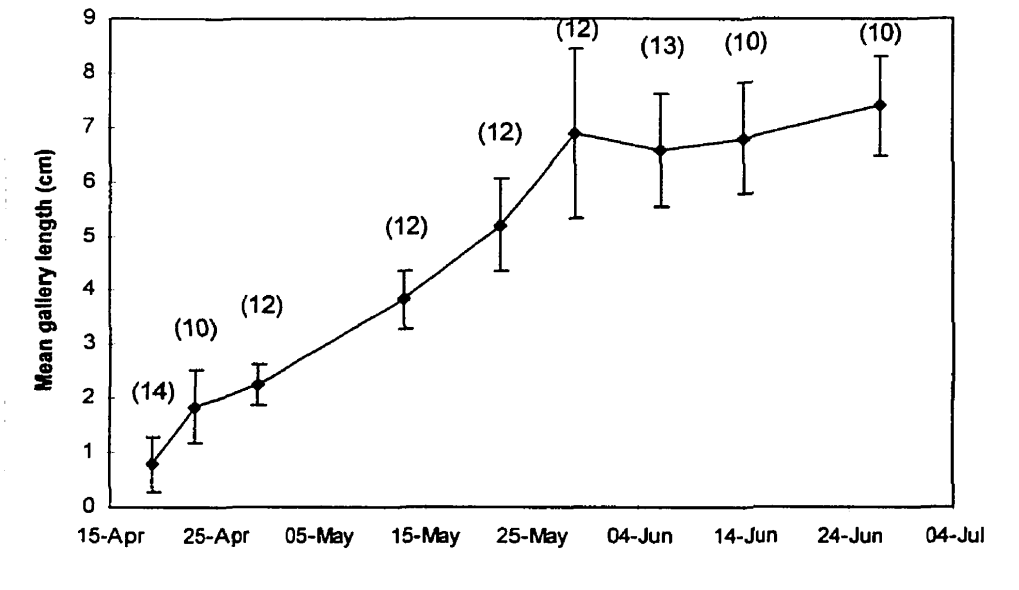


Figure 4-5. Mean gallery length excavated by adult female *Tomicus piniperda* on Scots pine (*Pinus sylvestris*) trap logs during 1996 in a 40-year-old stand near Guelph, Ontario. (Numbers above each point indicate the number of galleries examined on each sample date) Vertical bars indicate the standard error.

Comparative Temperature Readings between Ambient Air and Underneath Bark

When morning and evening hourly temperatures recorded under the bark were averaged, they varied from 0-2⁰C higher than the ambient air temperature recorded at the same time (Figure 4-6). The greatest difference was apparent during the night and dropped to its lowest point in mid-afternoon. On average, from mid-morning to mid-evening, the probe located on the more southerly face recorded mean hourly temperatures up to 2.5⁰C higher than the northerly facing probe at the same time (Figure 4-7). A diurnal pattern was also apparent here, where the greatest difference was in the afternoon and dropped off in the evening and early-morning.

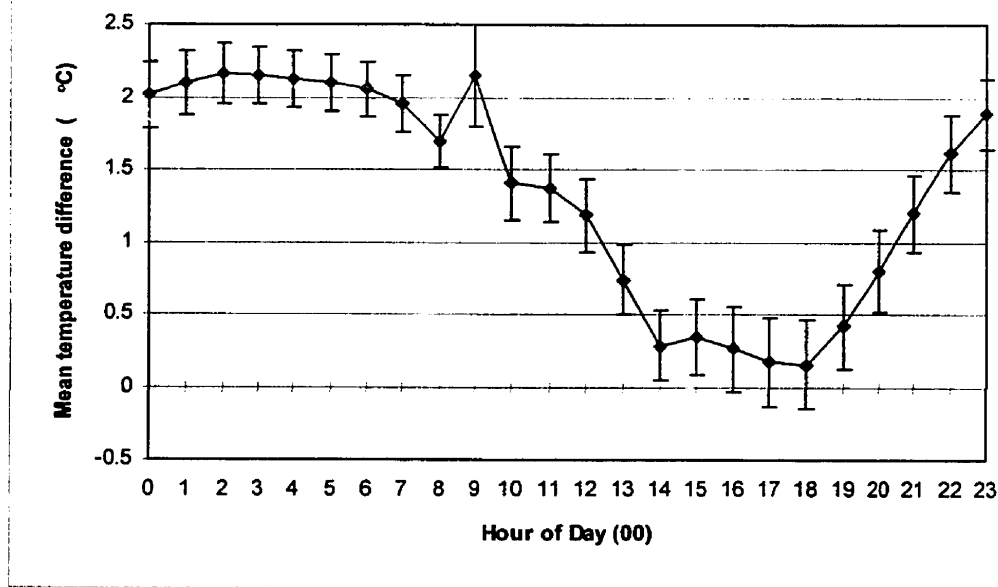


Figure 4-6. Difference in mean hourly temperatures underneath the bark of a mature Scots pine tree (*Pinus sylvestris*) and in the air as recorded by a CR-10 datalogger during April and May 1996 near Guelph, Ontario. Vertical bars indicate standard deviation (n=30days).

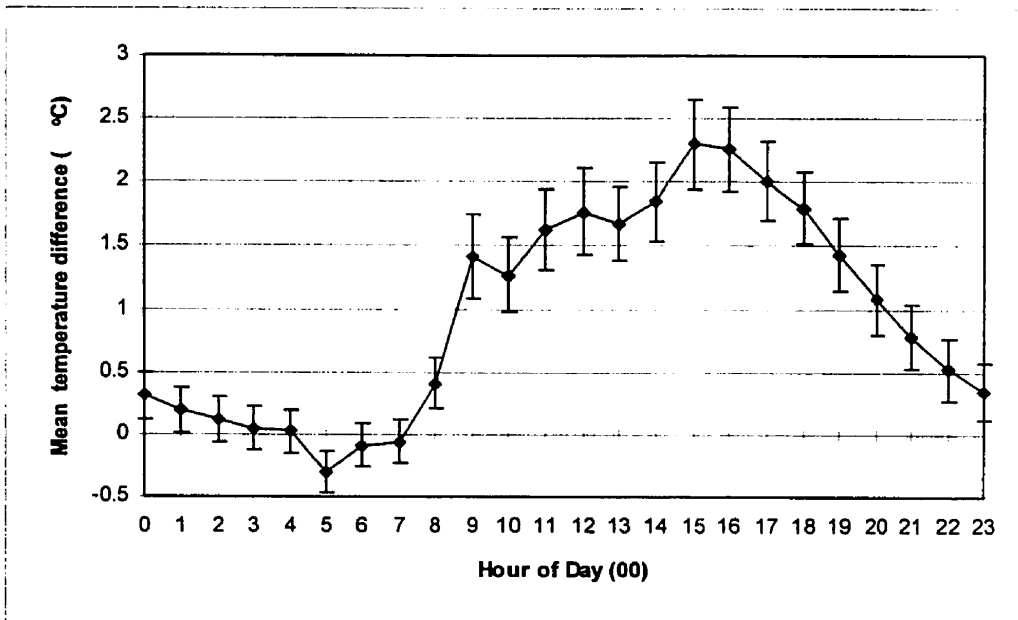


Figure 4-7. Difference in mean hourly temperatures underneath the bark of a standing mature Scots pine (*Pinus sylvestris*) tree between the north side and the south side of the tree, as recorded by a CR-10 datalogger during April and May 1996 near Guelph, Ontario. Vertical bars indicate standard deviation. (n=30 days).

DISCUSSION

Development of the Galleries and the Influence of Mean Daily Temperature

Complete gallery development from egg through to newly emerged adult for *Tomicus piniperda* required approximately 12-13 weeks (88 days) in southern Ontario in 1996. Initial colonization of logs began in mid-April and emergence of the new generation occurred at the very end of July. The average period of development was found previously to be 92 days in the field (Langstrom 1983). Langstrom and Hellqvist (1985) found that 80 days until median emergence were required at a constant temperature of 15 °C. At a constant temperature of 15°C, Salonen (1973) found that complete development required 85 days, but only 30 days at 25°C. Temperatures in the spring of 1996 were cooler than the 30-Year normals, which may have delayed emergence of the parent generation and development of the galleries. Indeed, three of the four mean monthly temperatures examined were approximately 1-2°C below the 30-year normal mean. Given this, it is possible that in warmer years, emergence of the new generation in southern Ontario could occur at least a week earlier than in the current year.

Durations of the various stages in the field were variable and difficult to determine exactly, causing some of the uncertainty in the values calculated. Initiation and rate of egg-laying are known to be affected by temperature (Salonen 1973). My study found that the first eggs were laid approximately 12 days after the adults began colonizing the brood material. Salonen (1973) found that, at 10°C, seven days elapsed before the first eggs were observed, compared to only four days at 15°C. A mean daily air temperature of 7.52°C was observed in my study and this was cooler than that observed by Salonen (1973). This difference would explain the comparative delay I observed for the appearance of the first eggs. Under laboratory conditions, the egg stage has been found to last about 30-40 days at 11°C, 7-8 days at 20°C, and only 4 days at 26°C (Ye 1994, Salonen 1973). An average daily temperature of 10.59°C during the 24 days of egg-laying in my study indicates that these eggs developed faster in the field than those under the constant laboratory conditions of Salonen's study. This is because high temperatures affect the developmental rate more than low temperatures (Salonen 1973,

Gordon 1984). Indeed, temperatures during the egg stage of my study ranged from a low of 4.3°C to a high of 22.2°C. I calculated an effective heat sum value for the egg stage (above 8°C) of 79.6 degree-days which corresponds well with previous findings, especially Salonen (1973). However, the heat sum value (>0°C) was about 25% lower than the values reported by earlier studies. Differences in methodology could have caused this difference, as well as difficulty in determining the start and end dates of the stage. Thus, initiation of egg laying and development of the eggs for *T. piniperda* seem to vary according to the ambient air temperature and are relatively consistent with previous studies.

Development of the larval stage was also highly affected by temperature. The first larva was seen 35 days after the initiation of the galleries when the mean daily air temperature was 9.6°C (range=3.7 to 22.2°C). Salonen (1973) found that, under a constant temperature of 10°C, the first larvae were observed after 51 days. The fact that this is longer than in my study suggests again that warm temperature fluctuations have a greater influence on development than cooler temperatures. The larval stage in my study lasted about 32 days at a mean temperature of 16.6°C. Under laboratory conditions, Salonen (1973) found the larval stage to last 36 days at a constant temperature of 15°C and approximately four weeks in the field (mean daily air temperature=11.7°C). The effective heat sum value that I calculated for the larval stage also corresponded well to Salonen's (1973) finding. When my current value is derived using Ye's (1994) developmental thresholds, these values are even closer. The heat sums (>0°C) in my study corresponded extremely closely with those from older studies (Salonen 1973, Knoche 1904).

Metamorphosis of larvae into pupae and new adults was also affected by temperature. The pupal stage lasted approximately 15 days in the current field study at an average temperature of 18.7°C. Under laboratory conditions, others found the pupal stage lasted 17 days at 15°C and 6 days at 26°C (Ye 1994, Salonen 1973). Again, my effective and absolute heat sum values corresponds relatively well with previous findings (Salonen 1973, Knoche 1904). After pupation, the beetles remain under the bark in a

In my study, adult beetles were found to remain under the bark in the field for approximately 10 days at a mean temperature of 18.4°C before they emerged. The heat sum (>0°C) for the preemergence stage calculated in the current study corresponded closely with that of Salonen (1973) and Knoche (1904), but the effective heat sum was more than 50% larger than the only previously published record (Salonen 1973). Again, this could be due to differences in methodology or because of difficulties in determining the exact start and end date. Overall, the duration of both of these stages corresponded well with previous reports.

The heat sum values calculated in my study corresponded quite closely with those in the literature suggesting that a heat sum value (>0°C) of approximately 1100-1300 degree-days (>0°C) is consistently required by *T. piniperda* to develop from median swarming to median emergence. Indeed, Coeln *et al.* (1996) found that three different spruce bark beetle species had significantly different species-specific zero developmental temperatures and required thermal sums that were consistent in both laboratory and field experiments. Hence, this value can be used to predict the emergence of each new generation of *T. piniperda* based on mean daily air temperatures, and help create management protocols capable of preventing or reducing emergence.

The parental generation of *T. piniperda* begins feeding again in the shoots before the emergence of their offspring (the new generation), even though they remain in their galleries for a long time after gallery initiation. It is known that, in this species, the female initiates the gallery and that the male follows her and remains for a lengthy period of time (several weeks) as is typical of other monogamous bark beetle species. Salonen (1973) describes the male's task as to push the frass cut by the female out of the gallery. Reid and Roitberg (1994) performed a male-removal experiment on the pine engraver beetle, *Ips pini*, and concluded that the males significantly contributed to the reproductive rate of their mates by removing frass and defending the egg galleries against predators. In addition, they concluded that the male undoubtedly guards the female to prevent her from mating with additional males. This is of extreme importance to the male because, as a

additional matings later in the reproductive season. Salonen (1973) found that the time of departure of the males corresponded approximately with the end of egg-laying. Indeed, I found that the increase in the mean number of eggs per gallery leveled off at about the same time as the male is thought to leave the galleries. Obviously, the male has a need to protect his investment in sperm as it is this success in finding and keeping mates that affects his contribution to the genetic makeup of the next generation (Price 1975).

Comparative Temperature Readings between Ambient Air and Underneath Bark

Temperature is known to have a great influence on the development and activity rates of juvenile and adult insects (Evans 1984). Degree-days for development of the juvenile stages can be determined in the laboratory and compared with field results. This has been done for *Tomicus piniperda* in previous studies as well as the current one. Calculations are commonly made using values recorded for ambient air temperature, however, galleries of *T. piniperda* are located underneath the rough bark of trees or logs and this protected location influences the actual temperature experienced by the developing stages. Indeed, I found that mean temperatures under crevices in the bark were greater than the ambient air temperature throughout the course of the day. This was expected, as dark-coloured bark is able to absorb and retain the energy from direct sunlight. A diurnal pattern of change was apparent. Very little difference in temperatures was observed in mid-afternoon, however, from late-evening and until mid-morning, the temperatures were up to 2°C warmer under the bark than the ambient air. Overall mean daily temperature under the bark was approximately 1°C greater than the mean ambient air temperature. These findings have relevance to the developing *T. piniperda* galleries beneath the bark as this will speed up the development of the juvenile insects relative to the ambient air temperature. Emergence of the overwintering parental generation from under the bark near the base of the trees would also be affected by this temperature differential. Hence, it is important to consider and understand exactly what conditions the insect population is experiencing locally before describing any biological relationships.

south had higher mean daily temperatures than northern aspects. A diurnal pattern of change is again apparent. The greatest differential was observed from mid- to late-afternoon and falls off to negligible levels from late-evening until early-morning. Temperature differences of up to 2.5°C were observed beneath the bark crevices from mid-morning to mid-evening on the south when compared to north-facing sections. Thus, galleries established on these southern faces of the standing trees would have faster overall rates of development than those on the north, even though the ambient temperature was the same. This is, again, an indication of the importance of the actual microhabitat conditions experienced by the developing *T. piniperda* larvae. While ambient air temperature certainly provides useful information about the developmental rates, it is important to examine and consider the actual conditions that are being experienced by the developing insects. Further studies could attempt to determine if there is faster gallery development and if any preference exists for gallery establishment on southerly facing sections of the tree bole.

Chapter Five : Brood Production of *Tomicus piniperda* (L.) (Col., Scolytidae): Indications of Intraspecific Larval Competition

ABSTRACT

The density of galleries and its effect on beetle production per gallery and per unit area for the exotic bark beetle, *Tomicus piniperda*, (L.) (Col., Scolytidae) was studied near Guelph, Ontario using naturally infested standing trees in 1995 and trap logs in 1996. Gallery density (number of egg galleries per m² bark surface area) was highly variable but significantly different between the two years studied. Significantly more new adults (11.62 vs. 5.09 beetles per gallery) were produced from each gallery at a lower (83.3 galleries per m²) than at a higher (220.9 galleries per m²) gallery density. The number of beetles produced per gallery was negatively related with to the density of galleries only at high gallery densities (1996). The number of beetles produced per m² of bark, however, was similar in both years, ranging around 900 new beetles per m², despite the highly variable gallery density. High levels of larval mortality were observed in both years, suggesting that there was intense intraspecific competition for a limited food resource.

INTRODUCTION

The pine shoot beetle, *Tomicus piniperda* (L.) (Col., Scolytidae) is a widely distributed pest that can cause considerable growth loss in pine stands. The beetle's primary host is Scots pine, *Pinus sylvestris* (L.) (Langstrom 1980). Unlike many other bark beetle species, the majority of the damage is caused by the maturation shoot feeding, and not by the reproductive phase of the beetle's life cycle. Indeed, *T. piniperda* tends to establish galleries only in weakened trees or freshly cut logs (Langstrom and Hellqvist 1993). Appropriate brood material releases allelochemicals that attract the emerging parent beetles (Tunset *et al.* 1993). The females construct the main gallery chambers and lay a number of eggs along either side. The larvae then form feeding tunnels out from this main maternal gallery and pupate in the bark. Infested brood material can be the source of a very large number of emergent beetles that then begin feeding on shoots in the tree crowns.

Brood material appropriate for this species often exists as a limited and widely spaced resource, causing competition for space and food among the parent generation and, especially, among the developing larvae (Huffaker *et al.* 1984). This paper examined the relationship between gallery density and beetle production per gallery and per unit area (brood production) to assess the level of intraspecific larval competition by *Tomicus piniperda*.

MATERIALS AND METHODS

Study Sites

Reproduction of *T. piniperda* in the field was studied during 1995 and 1996 in a 40-year-old Scots pine stand located south of Guelph, Ontario (43°30'latitude, 80°20'longitude). The height of the trees ranged from 13-17 m and their DBH (diameter at 1.3 m height) ranged from 14-18 cm. This stand was originally planted for erosion control.

Characteristics of Galleries

In December 1995, six naturally-infested Scots pine trees were selected, felled, and cut into approximately 1m logs. All logs (n=15) with rough corky bark from the lower portion of the tree were brought to the laboratory. In the laboratory, a 20-cm band from the top end of each log was selected and the following measurements were recorded: number of exit holes, number of galleries, gallery length, and (for a sub-sample of 91 galleries) the number of eggs per gallery.

In March 1996, six trees which had been damaged by a storm the previous week were felled and cut into logs approximately 0.75 m long. A total of 28 logs were placed into eight separate piles of three to four logs each and left in the field for natural infestation by *T. piniperda*. Twenty-two of these logs were destructively sampled to follow gallery development for another study (see Chapter 4). In August 1996, the six logs from which the beetles had completed development were brought to the laboratory and the same measurements were recorded for the galleries as in 1995.

Gallery density was calculated for both years as the number of galleries per square metre of bark surface area. Production of new adults per gallery was calculated by dividing brood production (number of exit holes per square metre) by gallery density for each log sample. These values (gallery density, production per gallery, and brood production) were each compared between the two years using non-parametric Mann-Whitney tests (Zar 1984). The relationship between production of new adults per gallery and gallery density was examined for both 1995 and 1996 using Spearman rank order correlation coefficients (SAS: PROC RANK, Spearman). Finally, the relationship between brood production and gallery density was examined, also using Spearman rank order correlation coefficients (Zar 1984).

From the 1995 data, total mortality could be approximated using the initial mean number of egg grooves per gallery (using the representative sample of 91 galleries from the 15 logs) and the final mean number of exit holes per gallery calculated for each of the 15 logs. In 1996, egg mortality was determined directly by counting the total number of egg grooves and the maximum number of larval tunnels visible for a sub-sample of 20

galleries. Total mortality for 1996 was calculated using the initial mean number of egg grooves per gallery (using the sample of 20 galleries from the six logs) and the final mean number of exit holes per gallery calculated for each of the six logs.

RESULTS

Characteristics of Galleries

Mean gallery length was not significantly different between the two years, 79.5 mm (s.d.=2.42, n=91) in 1995 and 74.1 mm (s.d.=0.92, n=25) in 1996 ($U=1020.5$, $n=91, 25$, $p=0.43$). A Mann-Whitney U test was used because the standard deviations were significantly different ($F=4.61$, $p<0.0001$). The number of eggs laid per gallery was also similar, 22.78 (s.d.=11.74, n=91) in 1995 and 24.5 (s.d.=8.74, n=25) in 1996. Gallery density of *T. piniperda* varied considerably between the two years. A mean gallery density of 83.3 (s.d. = 31.13) in 1995 was significantly lower than the 220.9 galleries per square metre (s.d. = 131.92) in 1996 ($U = 3.0$, $n=15, 7$, two-tailed $p = 0.0006$). Mean production of new adults per gallery was significantly higher in 1995 (11.62 exit holes per gallery, s.d. = 6.38) than in 1996 (5.09 exit holes per gallery, s.d. = 2.68) ($U = 13$, $n=15,6$, two-tailed $p = 0.01$). However, total brood production in both years was the same, with 917 exit holes per square metre in 1995 (s.d. = 460.1) and 905 (s.d. = 204.3) in 1996 ($U = 45$, $n=15,6$, two-tailed $p = 0.97$).

Gallery production and density were not correlated at the low densities (35 to 135 galleries per square metre) observed in 1995 ($r^2=-0.19$, $n=15$, $p=0.49$) (Figure 5-1). However, at the higher gallery densities (120 to 430 galleries per square metre) observed in 1996, density and gallery production were negatively correlated ($r^2=0.83$, $n=6$, $p=0.04$) (Figure 5-2). In 1995, a significant positive correlation was found between brood production and higher gallery density ($r^2=0.63$, $n=15$, $p=0.01$) (Fig. 5-3). However, at the densities in 1996, brood production was not influenced by gallery density ($r^2=0.14$, $n=6$, $p=0.79$) (Fig. 5-4). Total *T. piniperda* mortality (egg, larvae, and pupae) was 49.08% in 1995 ($n=15$, s.d.=26.17) and 79.20% in 1996 ($n=6$, s.d.=10.95). In 1996, mean egg mortality alone was 16.5% (s.d.=9.39, $n=20$ galleries). Mortality of the larvae, pupae and new adults was then approximated to be 62.7%.

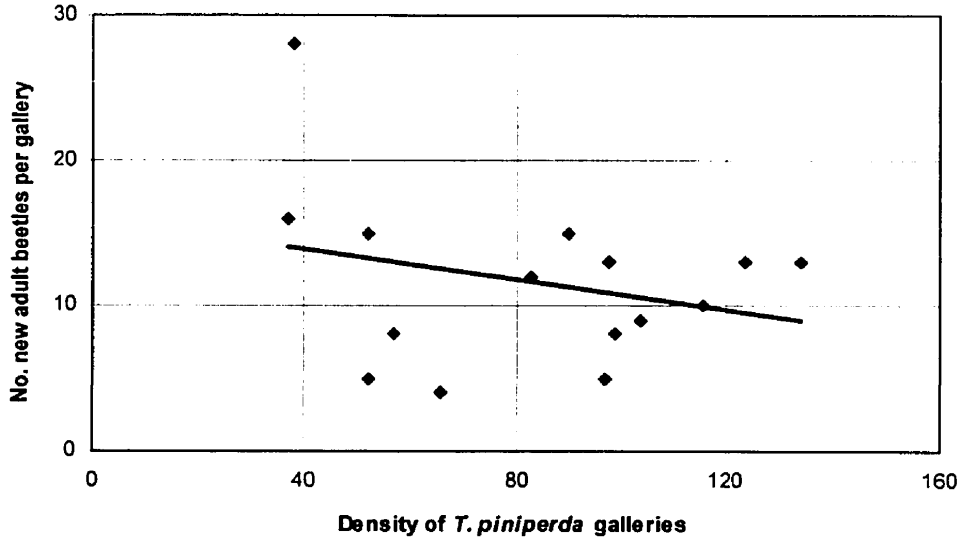


Figure 5-1. Relationship between the number of new *Tomicus piniperda* adults emerging per gallery and increasing gallery density on sections from naturally infested standing Scots pine (*Pinus sylvestris*) trees during 1995 in a 40-year-old stand near Guelph, Ontario. (Spearman's $r^2=0.19$, $n=15$ logs, $p=0.48$)

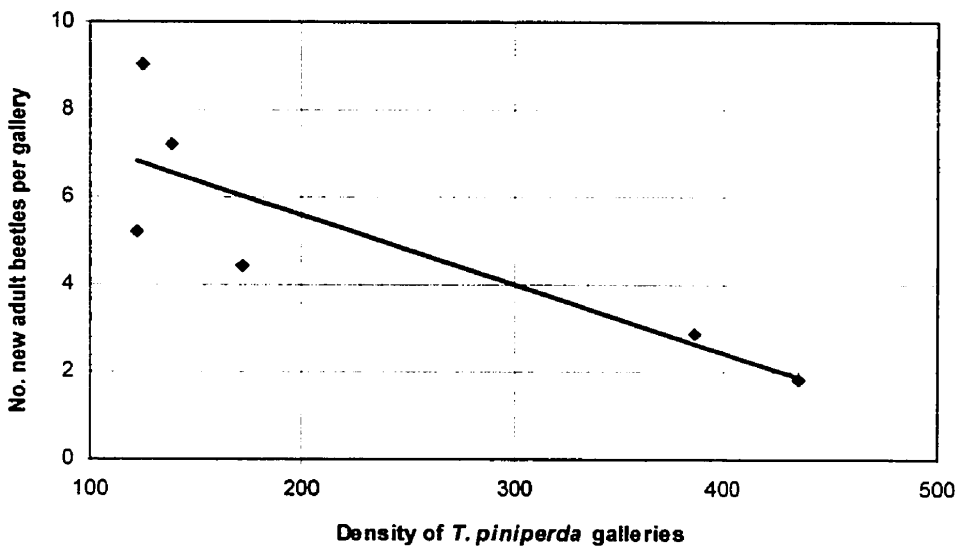


Figure 5-2. Relationship between the number of new *Tomicus piniperda* adults emerging per gallery and increasing gallery density on cut Scots pine (*Pinus sylvestris*) logs during 1996 located in a 40-year-old stand near Guelph, Ontario. (Spearman's $r^2=0.83$, $n=6$ logs, $p=0.04$)

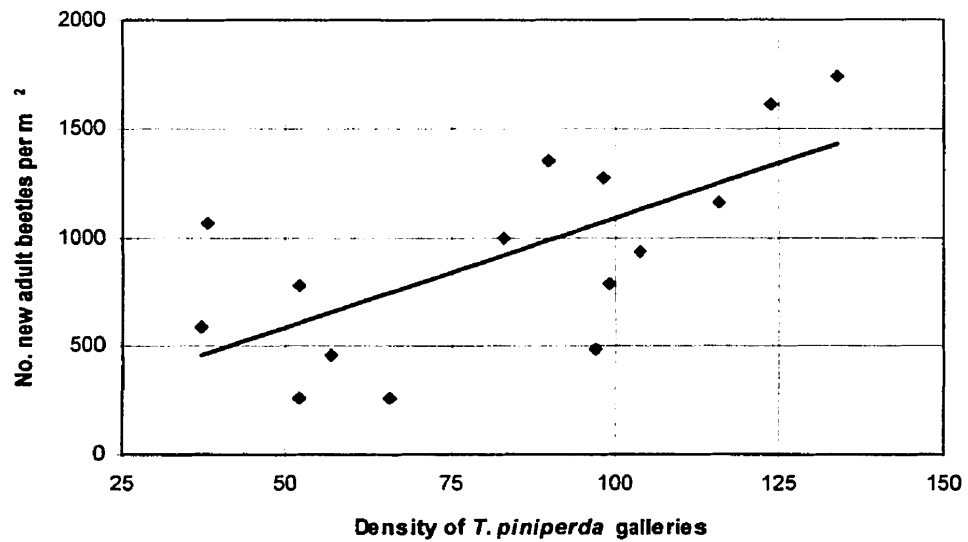


Figure 5-3. Relationship between the number of new *Tomicus piniperda* beetles emerging per square metre and gallery density on naturally infested standing Scots pine (*Pinus sylvestris*) trees during 1995 in a 40-year-old stand near Guelph, Ontario. (Spearman's $r^2=0.63$, $n=15$, $p=0.01$)

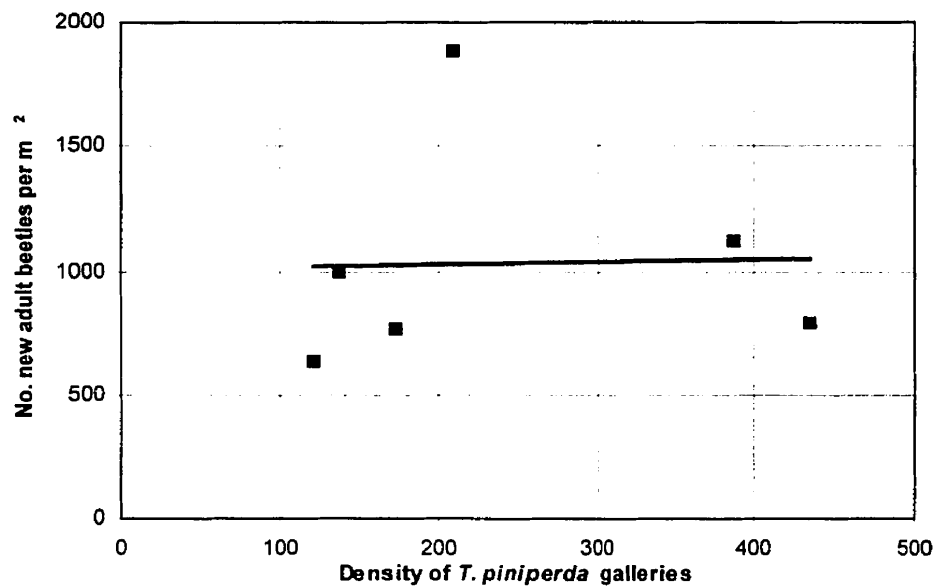


Figure 5-4. Relationship between the number of new *Tomicus piniperda* beetles emerging per square metre and gallery density on cut Scots pine (*Pinus sylvestris*) trap logs in 1996 in a 40-year-old stand near Guelph, Ontario. (Spearman's $r^2=0.14$, $n=6$, $p=0.79$)

Gallery Density and Production of New Adults

The final gallery length of approximately 7 cm which I observed corresponds well with that of Langstrom (1983) who found a mean gallery length of 7-8 cm, also on Scots pine (*Pinus sylvestris*). Langstrom and Hellqvist (1985) found a mean gallery length of 10.5 cm and Salonen (1973) found a mean gallery length of 8-9 cm while Gibbs and Inman (1991) found them to be only 3-5 cm on average. The length of the egg gallery (which is linearly related to egg number) is inversely correlated to the density of attack by *T. piniperda* (Langstrom 1984, Sauvard 1989, Salonen 1973), although Heliovaara and Vaisanen (1991) found that egg gallery length may remain constant even at high attack densities. This suggests that intraspecific competition among the adult beetles initiating galleries requires further study for the pine shoot beetle. Indeed, I found the mean length of the galleries to be the same in both years of my study, despite a large variation in the density of the galleries.

The mean number of eggs being laid per gallery that I found is somewhat lower than previous European findings. Both Langstrom (1983) and Sauvard (1993) found an average of 40-50 eggs are laid by female *T. piniperda* in each gallery. This could perhaps be due to counting errors, especially in 1995 when the brood material was 6-8 months old. Alternatively, the females may be experiencing some stress caused by their recent invasion of North America which is presently reducing their fecundity.

Langstrom (1986) found the density of *T. piniperda* galleries to be variable, from 25 to 300 galleries per square metre while Langstrom and Hellqvist (1993) found a maximum of 496.8 galleries per square metre and Haack and Lawrence (1995) found a density of 262 attacks per square metre. Hence, the densities I observed fall well within the range of previous findings. Several possibilities may explain the significant difference I observed in gallery density between the two years of my study. First, the size of the parent generation initiating the attacks may have differed. Successful reproduction in 1995 may have increased the size of the population emerging in the spring of 1996. The mean gallery density observed in 1996 was 250% greater than that observed in 1995,

gallery in 1995 corresponds to an almost 600% population increase (almost 6 new adults per parent beetle). In addition, successful feeding is known to have occurred in 1995 (see Chapter 3), suggesting that many beetles were likely able to survive through the winter to reproduce in 1996. A certain level of mortality would have occurred over the shoot-feeding and overwintering periods, thus reducing the new beetle population somewhat. However, the reproductive and feeding success of the *T. piniperda* population in 1995 likely would still have caused an overall increase in populations in 1996.

An second explanation for higher gallery densities in 1996 involves the different types of brood material used in the two years. Data in 1995 were collected from naturally-infested standing trees. In 1996, data were collected from trap logs which were felled in March and left to be infested in the field. The act of cutting the logs may have caused them to become more highly attractive to the emerging parent generation in 1996. A study by Schlyter and Lofqvist (1990) shows that logs and fallen trees were preferentially attacked over standing trees. Four major kairomone components have been isolated from logs ((R)- and (S)- α -pinene, Δ^3 -carene, and terpinolene) that are highly attractive to *T. piniperda* (Tunset *et al.* 1993). Schroeder and Eidmann (1987) found galleries were always initiated by *T. piniperda* when healthy trees were baited with any one of the following: 1.) a mixture of the four kairomones listed above; 2.) any one of the kairomones; 3.) ethanol alone; or 4.) chips from freshly cut trees. Gallery establishment on the healthy trees was typically not successful but the attractiveness of the kairomones is apparent. Finally, Loyttyneimi *et al.* (1988) concluded that *T. piniperda* is attracted to breeding sites by log odour alone. Hence, it is possible that the cut logs were more attractive than any of the individual standing trees from the previous year. As such, perhaps this caused the attacking generation to aggregate on the log piles at higher densities than on the trees.

Important information about the production of new adults per gallery can be gathered from both years, even though the difference in gallery density may, in fact, be partially due to the different methodology used. Annila and Heikkila (1991) found that,

On average, *T. piniperda* produces between 5-8 new adults per gallery. Henttonen and Vaisanen (1991) found an average of 6.4 new adults per gallery. Salonen (1973) found that, at a density of 200-300 galleries per m², approximately 10 beetles were produced per gallery. At a very low gallery density, Langstrom and Hellqvist (1985) found a high value of 27-32 exit holes per gallery, while at high gallery densities (496.8 galleries per m²) Langstrom and Hellqvist (1993) found an extremely low value of only 0.4 exit holes per gallery. Hence, the values from the two years studied fall within the range of previous findings, with more beetles being produced per gallery at the lower density. In both years, an increase in the population was occurring, with successful gallery establishment and the production of approximately 2-6 new adults per parent beetle. This suggests that the beetle has successfully established itself in its newest region, and is doing as well as in its native European habitat.

Two potential problems with the method of counting exit holes on the bark exist. First, holes that were not readily apparent on the bark surface may have been missed, thus reducing the average number of holes per gallery. Second, Schlyter *et al.* (1984) found that, for the spruce bark beetle (*Ips typographus*), higher gallery density led to increased beetle production per unit area which resulted in an increased number of beetles emerging from the same exit hole. Indeed, Salonen (1973) found that *T. piniperda* populations were underestimated by about 10% because not all holes were detectable and because two or more beetles sometimes emerged from the same hole. If this is the case, production per gallery and per unit area in my study may be underreported at the higher gallery densities (1996), and this would affect the relationships observed.

Production of new *T. piniperda* adults was influenced by the density of the developing galleries. At the lower densities of 35 to 135 galleries per m² (1995), resource limitations were probably not yet being experienced. Additional galleries could be initiated without influencing the success rate of surrounding galleries. In contrast, at the higher densities (1996), a significant negative correlation between gallery density and production per gallery was observed. The high r² value (0.829) indicates that a large percentage of the variation in production levels is explained by this simple relationship.

and suggest that intraspecific competition, occurring at the highest gallery densities, is having a serious impact on larval survival. The proportion of larvae able to obtain enough food resources and complete development is greatly reduced. At these higher densities, the developing galleries are interfering with each other at an ever-increasing level. Indeed, Salonen (1973) and Sauvard (1993) both found that increasing gallery density caused a serious decline in larval survival and production per gallery, when the density exceeded a critical level. This effect is commonly found for this type of insect, for example the bark beetle species, *Ips typographus*, productivity per gallery is also adversely affected by increasing gallery density (Weslien 1994, Anderbrant *et al.* 1985).

Mortality within the galleries supports the suggestion that increased larval competition reduces the number of new adults produced per gallery. In fact, intraspecific larval competition is commonly considered to be the largest source of egg-to-adult mortality in bark beetles (Kirkendall 1989). Egg mortality alone was found to be 16.5% in 1996, larval+pupal+new adult mortality can be determined to account for 62.7% of the total overall mortality in 1996. Pupal and new adult mortality has been found to be very low in a study by Hui and Zhimo (1995), only 3% and 2%, respectively. In their study, most of the total 78% mortality occurred in the larval stage. Indeed, Hui and Zhimo (1995) concluded that almost 40% of the total mortality was due to intraspecific larval competition alone. Low levels of pupal mortality can be assumed to be constant at differing densities (Salonen 1973) because there is no shortage of space in which to pupate. While increasing gallery density had a positive density-dependent effect on larval mortality, no effect was found on either egg or pupal mortality for the bark beetle species, *Phloeotribus scarabaeoides* (L.) (Lozano *et al.* 1996) or *Leperisinus varius* (Fabr.) (Lozano *et al.* 1993). Therefore, it is not unreasonable to assume that most of the 62.7% mortality in my study was larval mortality. The additional 30.12% overall mortality occurring in 1996 over 1995 may be a result of increased larval competition at the higher gallery densities. Indeed, Salonen (1973) found that larval mortality ranged from only 12% to a high of 91% with increasing gallery densities from 63 to 325 galleries per square metre. Clearly, the larval stage is highly sensitive to the effects of gallery density and intense levels of intraspecific competition can occur. Beaver (1974) found evidence

of density-dependent mortality for *T. piniperda*. Indeed, this has been found in a number of other studies on a variety of bark beetle species. Lozano *et al.* (1996) found that mortality of the bark beetle, *Phloeotribus scarabaeoides*, was greatest at the larval stage with only 25% of the original egg number surviving to adulthood. For another species, *Leperisinus varius*, only 10% of the original egg number survived to adulthood, with most of the mortality occurring in the larval stage (Lozano *et al.* 1993). Finally, for the larch bark beetle (*Ips cembrae* (Heer)), egg to adult mortality increased exponentially with increasing attack density, with most of the mortality attributable to competition among females for breeding space and between larvae for limited food resources (Zhang *et al.* 1992).

Insects which occur in limited, widely spaced habitats often exhibit this 'scramble' or exploitation competition at high densities, whereby the crowded larvae have to scramble for available space and food, with only a few surviving to maturity (Evans 1984, Caltagirone 1984). Scramble competition has been also been found for the bark beetle species, *Ips typographus* and *I. duplicatus*, based on the near complete consumption of phloem and the similar adult re-emergence times (indicating end of egg-laying) (Schlyter and Anderbrant 1993). *Tomicus piniperda* can only reproduce on severely stressed or weakened trees. In addition, the brood material is only suitable for use for a brief time before drying out (Speight and Wainhouse 1989). Hence, the entire emergent parental generation must utilize this limited brood resource simultaneously. Consequently, this causes competition among the developing pine shoot beetle larvae. At high densities, the larval tunnels cross, causing some larvae to die because of a food shortage (Hui and Zhimo 1995). Overt competition, such as the cannibalism of the younger smaller larvae by the older more developed larvae, often occurs under crowded conditions in species that are otherwise considered herbivores, such as *T. piniperda* (Price 1975). The food source that is being utilized by the developing larvae, the inner bark or phloem layer, can be considered to be limited and finite as the larvae have no ability or opportunity to move to a less densely populated area. In addition, it can be considered a two-dimensional layer because the feeding layer is approximately the same thickness as that of the developing larvae. Hence, the amount of food available to a individual

female, and the stage of development of the neighboring galleries and of neighboring siblings.

This situation presents an interesting dilemma for the attacking females when trying to select a gallery site. Brood material must be of an appropriate state of decay or the invading beetles can be easily 'pitched out' by healthier resistant trees (Schroeder 1990). In addition, even weakened standing trees will still be able to produce some measure of resistance to the invading beetles, so it is advantageous for the parent generation to congregate on certain trees to ensure that the tree succumbs to the invasion. However, at higher gallery densities, competition for food increases, thereby reducing larval survival and successful production of new adults per gallery. Clearly, a trade-off must exist between successfully invading and saturating a potential host so that the attacks do not fail and over-utilizing a specific host such that individual gallery production falls extremely low. Sauvard (1993) concluded that the tendency of *T. piniperda* to saturate its environment enables it to limit interspecific competition from other phloem-eating insects. Langstrom and Hellqvist (1995) found that the earlier flight of *T. piniperda* allowed it to outcompete, and decrease, the population of the native *Ips pini*. This saturation and preemption of other species, however, leads to high intraspecific competition and mortality as observed in previous studies as well as this current one.

Resource Saturation as Indicated by Production of New Adults per Area

In contrast to gallery density and beetle production per gallery, mean brood production remained relatively constant between the two years. The values found in my current study fell within the range of previous findings. Sauvard (1989) also found that, despite large differences in attack density, a fairly constant number of young *T. piniperda* adults were produced per unit of bark surface area. Interestingly, at the lower densities observed in 1995, the initiation of additional galleries is able to increase the overall brood production. This again suggests that food resources are not being fully utilized at these lower densities. In contrast, additional galleries do not influence brood production at the high densities experienced in 1996. Sauvard (1993) found that, in the laboratory, when

produced per square metre. In the same study, logs attacked naturally in the field, produced an average of 600-900 beetles per square metre. In addition, Heliovaara and Vaisanen (1991) found an average production of 1130 new adults per square metre and Langstrom (1984) noted that the brood production of *T. piniperda* seldom exceeded 1000 per m² with a typical maximum of 500 exit holes per m². In a later study, Langstrom (1986) found brood production to be highly variable, from a few to more than 900 beetles per m². The fact that the brood production was nearly the same in both years of my study, despite the significantly variable gallery density, suggests that the beetle population was operating at or near its carrying capacity for these host conditions and region.

As discussed above, the inner bark layer on which the larva feed represents a limited finite resource because the larvae are incapable of relocating to a new food source. In addition, each larva requires a certain minimal amount of food to complete its development and emerge as a new adult. Much of the available energy may simply be dissipated by individuals who do some feeding but are not able to obtain enough resources to survive through to pupation (Price 1975). Therefore, a given surface area of bark or wood will only be able to support a certain maximum number of larvae through to pupation, even though many more larvae may be present. Lozano *et al.* (1993, 1994) found that, for the bark beetle *Leperisinus varius*, its population was regulated by density-dependent larval mortality at an equilibrium of 1100 new beetles per m². Beaver (1974) also found that density dependent mortality caused the brood production of *T. piniperda* to level off at 925 beetles per m². That 900-1000 beetles per m² has been found previously suggests that this may represent a maximum production per unit area of wood. The attractive allelochemicals released by damaged or stressed wood probably helps this species to aggregate on appropriate brood material so as to fully utilize the resources available. Indeed, once development in the galleries is finished, the bark is easily peeled off and the inner surface of the wood can be seen to be completely covered with larval tunnels. However, reports of higher values of around 2300 new beetles per square metre have been found, given gallery densities of 200-300 galleries per square metre (Salonen 1973). Langstrom and Hellqvist (1985) also found high values of 1810-3031 beetles per

conditions. Perhaps a closer examination is needed of the relationship between the actual thickness of the phloem layer and the number of larvae that can be supported per unit area. Indeed, Amman (1972) clearly showed that phloem thickness was important for the production of the scolytid, *Dendroctonus ponderosae* Hopkins. Thicker phloem layers may produce greater numbers of new beetles per unit area as there is a larger food volume for the developing larvae.

In conclusion, the results from the current study indicate that *T. piniperda* is successfully reproducing on available brood material in its newly expanded range of southern Ontario. In addition, *T. piniperda* is using its resources at a highly effective and efficient level. Indeed, newly invading species are commonly found to be operating at very high population levels because there are few constraints on their growth (Speight and Wainhouse 1989). Natural enemies and appropriate host plant defenses are often lacking in the newly invaded region. *Tomicus piniperda* has only been in Ontario for four to five years (Haack 1996), so it is unlikely that many predators or parasitoids are able to utilize it effectively yet. In addition, Scots pine, the primary host of *T. piniperda*, is itself originally from Europe. Introduced species of trees, like Scots pine, may already be stressed due to their relocation and often run the additional risk of attack by pests accidentally introduced from the native habitat (Speight and Wainhouse 1989). *Tomicus piniperda* is already well adapted to completing its life cycle on this host species. It may experience little competition or interference from North American species also trying to use Scots pine. Finally, it is exhibiting a pattern of production and resource utilization that suggests that a large positive population growth trend may be occurring.

Chapter Six : Within- and Between-Tree Preferences for Reproduction and Shoot Feeding by the Pine Shoot Beetle, *Tomicus piniperda* (L.)(Col., Scolytidae)

ABSTRACT

Reproduction and shoot feeding preferences of the exotic pine shoot beetle, *Tomicus piniperda* (L.) (Col., Scolytidae) were studied in the field near Guelph, Ontario during 1995. To study reproduction, six naturally infested Scots pine trees were cut and examined. Gallery density declined slightly with increasing height. Beetles preferred an intermediate bark thickness of 5-9 mm for oviposition, with no successful galleries in thin bark over a height of 6-7 m. Feeding in the shoots was examined in a 10-12-year-old Scots pine stand. Early in the summer, many of the attacks were located in one-year-old shoots, however, attacks later in the season occurred only in current-year-growth. Non-attacked trees had significantly shorter current year needles than attacked trees. Likewise, the diameter of attacked shoots on attacked trees were significantly larger than those of non-attacked shoots on non-attacked trees, indicating a selection for the larger shoots. Tree height did not influence the number of attacks on a tree, but tree diameter and the branch radius both had a small but positive effect on the level of attack experienced by a tree. These results suggest that the bushiest, most vigorous young trees may actually be the most susceptible to shoot feeding attack by this exotic species.

INTRODUCTION

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera, Scolytidae) has only recently established itself in Ontario. The most recent survey has found it to be in eight U.S. states and 13 counties in southern Ontario (Haack 1996). This species is considered to be a serious pest over its widespread European and Asian distribution. Reproduction occurs during the spring in dying, damaged, or cut trees. Secondary bark beetle species, like *T. piniperda*, that must use weakened trees for reproduction have tended to become spatially segregated on the tree bole in order to minimize interspecific competition (Speight and Wainhouse 1989). European studies have found this species to prefer rough barked sections, corresponding to the lower sections of a tree bole (Schroeder 1990, Salonen 1973). Upon emerging from the brood tree, the new generation begins a period of maturation feeding on tree shoots. It is this feeding that results in the majority of the damage caused by this species (Langstrom 1980). *Tomicus piniperda* also has feeding preferences, which help separate the adults from other species, such as *T. minor*. Indeed, *T. piniperda* tends to attack the uppermost section of a crown, starting with the outermost shoots (Langstrom 1980).

The timber industry in Europe experiences regular losses in tree growth from shoot feeding by this species and by the transmittance of blue-stain fungus during reproduction (Langstrom and Hellqvist 1990). In Ontario, the primary host of this species, Scots pine (*Pinus sylvestris*), is typically not grown for timber but is one of the most popular and widely grown species in the Christmas tree industry. The requisite maturation feeding by *Tomicus piniperda* may result in costly aesthetic damage to these intensively managed trees (Bright 1996). In addition, other pine species (such as *P. resinosa*, *P. strobus*, and *P. banksiana*) are important timber trees and may eventually suffer attack by this newly introduced species. An understanding of reproductive and shoot feeding preferences of *T. piniperda* will help determine which trees will be at risk in Ontario. This paper examines some preferences in colonization by the parental generation and preferences in shoot feeding by the adult beetles.

Study Sites

Beetle reproduction was studied in the field during 1995 in a 40-year-old Scots pine stand located south of Guelph, Ontario (43°30'latitude, 80°20'longitude). The height of the trees ranged from 13-17 m and their diameter at breast height (DBH) ranged from 14-18 cm. This stand was originally planted for erosion control.

Summer maturation feeding was studied in the field during 1995 in a young (12-15 year old) Scots pine stand located south of Guelph, Ontario (43°27'latitude, 80°21'longitude). This stand was intended for use as Christmas trees but had been abandoned 2 years previously. In the summer of 1995, the trees ranged from 2.5-3.5 m in height and 3-7 cm DBH. This Scots pine stand consisted of several hundred trees, which were planted in rows with a 2 by 2 m spacing. Fifty trees were chosen at random from the stand.

Reproductive Preferences

In December 1995, six naturally infested Scots pine trees were selected, felled, and cut into approximately 1-metre logs. All logs with rough corky bark from the lower portion of the tree were labelled according to tree and position (height) and then brought to the laboratory. In the laboratory, the following log measurements were made: length, diameter, and bark thickness (at top end of the log). A 20 cm band from the top end of each log was then selected and the following measurements for *T. piniperda* were recorded: number of exit holes, number of galleries, gallery length, and number of larval tunnels per gallery. Differences in the mean gallery density between the trees were tested (SYSTAT: Kruskal-Wallis). Differences in log diameter between the trees were also tested (SYSTAT: Kruskal-Wallis).

Age and Position of Attacked Shoots

On each biweekly sample date from late July to early September in 1995 and 1996, the age of each attacked shoot on the 50 trees was recorded (either as C for current year, or C+1 for one-year-old growth).

The position of all shoot attacks on the 50 trees was observed on 23 August 1995 and recorded as: top one-third, middle one-third, or lower one-third of the tree crown.

Needle Length

On 26 July 1995, ten needles were taken from one shoot, five from the current year growth (C) and five from 1-year-old growth (C+1) on each of the fifty trees. In the laboratory, the length of each needle was measured and then the mean lengths for needles from attacked current year growth was compared to that of non-attacked current year growth needles using a nested general linear model, with subsamples of shoots nested within the category "attacked vs unattacked". The mean length of one-year-old (C+1) needles on attacked trees was then compared to the mean length of one-year-old (C+1) needles on non-attacked trees in the same manner (SYSTAT: GLM, Nested).

Shoot Diameter

On 26 July 1995, the diameter of the current year shoots was measured and recorded for 50 trees. Up to three attacked shoots were measured on each attacked tree and two non-attacked shoots on each non-attacked trees. On 02 August 1995, two non-attacked shoots were measured on each attacked tree. Shoot diameter was measured to the nearest 0.5 millimetre using fine dial calipers. The mean diameter of attacked shoots was compared to that of non-attacked shoots on non-attacked trees and to non-attacked shoots on otherwise attacked trees using a one-way ANOVA (SYSTAT: MGLH, ANOVA).

On 23 August 1995, the height, DBH, and "branch radius" were measured for each of the 50 trees. Height of the trees was measured to the nearest 0.1 m using a tree height pole while DBH was measured to the nearest 0.25 cm using large-scale calipers. Branch radius refers to the fullness or volume of a tree's branches and was measured to the nearest five centimetres using a metre-stick held perpendicularly to the tree trunk at breast height. The total number of shoot attacks visible on each of the trees on this date were counted and recorded. A stepwise multiple regression with the number of attacks per tree as the dependent variable examined whether tree height, DBH, or branch radius significantly influenced the level of attack (SYSTAT: REGRESSION, Stepwise).

RESULTS

Reproductive Preferences

The six naturally infested trees sampled in 1995 varied significantly in their mean gallery densities (K.W.=17.8, $p=0.003$, $df=5$). Gallery density, when expressed as the percent of the total attacks within each of the trees, declined slightly with increasing tree height within any given tree (Fig. 6-1). The majority of the attacks occurred in the lower 4-5 m of the tree. No galleries established above a height of approximately 6 m based on the presence of exit holes. An intermediate bark thickness of 5-9 mm had a higher mean gallery density than did thicker or thinner bark regions (Fig. 6-2). No galleries were successful on areas where the bark was < 2 mm thick. The six trees also varied significantly in their diameters (K.W.=16.65, $p=0.005$, $df=5$), with the density of galleries decreasing slightly with an increasing tree diameter at breast height (Fig. 6-3).

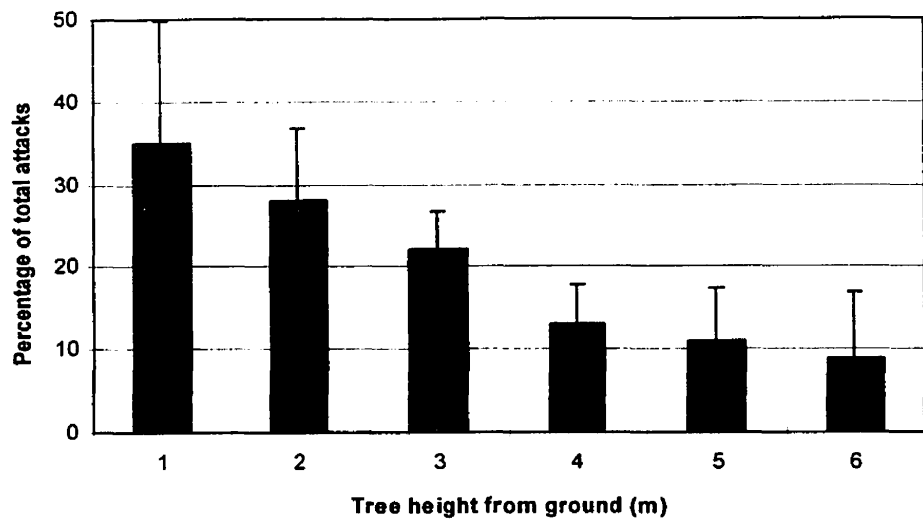


Figure 6-1. Relationship between mean percentage of total *Tomicus piniperda* attacks per tree and tree height (m) for six naturally infested standing Scots pine (*Pinus sylvestris*) trees during 1995 in a 40-year-old stand near Guelph, Ontario (Vertical bars indicate standard error).

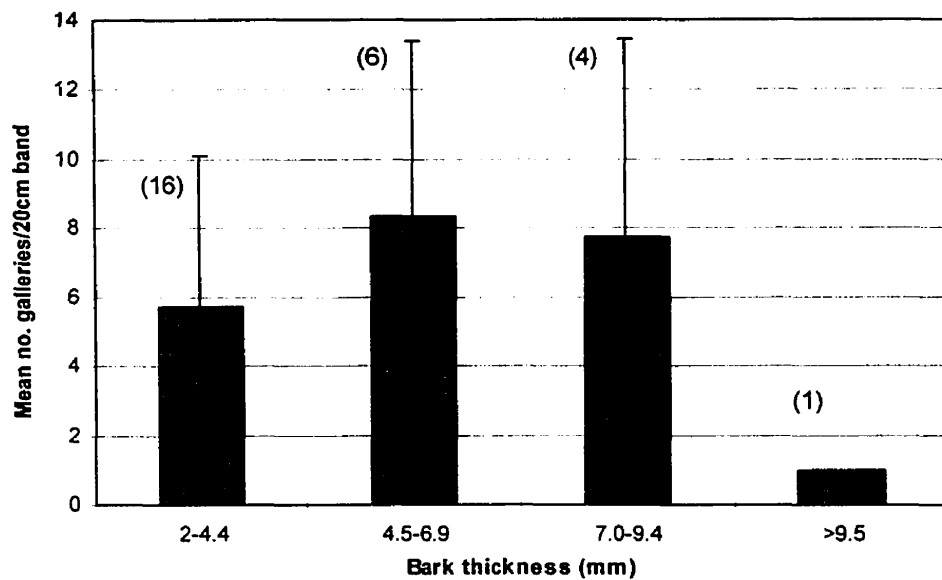


Figure 6-2. Relationship between mean number of *Tomicus piniperda* galleries per 20 cm band sample and bark thickness (mm) for 6 naturally infested Scots pine (*Pinus sylvestris*) trees during 1995 in a 40-year-old stand near Guelph, Ontario (No.'s above each point indicates the number of samples). Vertical bars indicate the standard error.

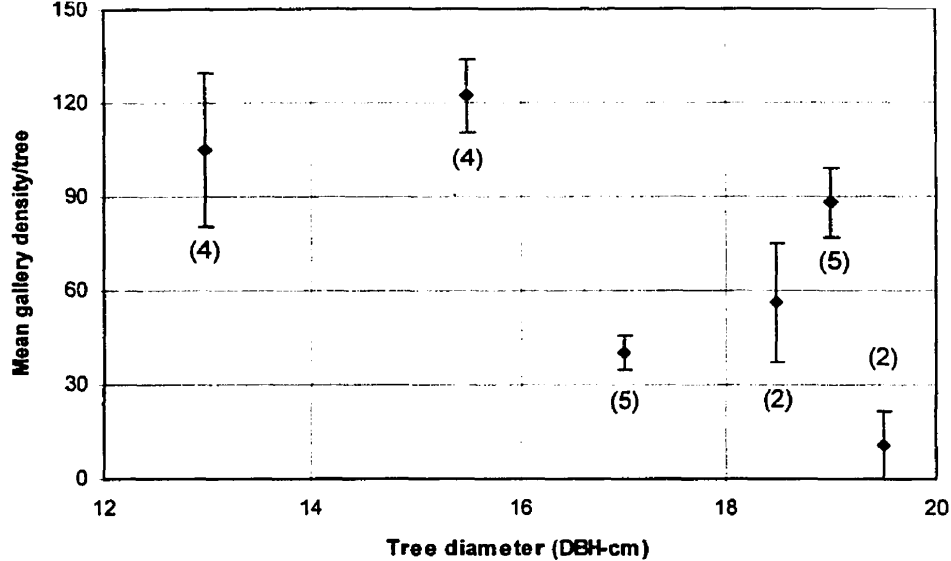


Figure 6-3. Relationship between mean *Tomicus piniperda* gallery density per tree and tree diameter at breast height (cm) for six naturally infested standing Scots pine (*Pinus sylvestris*) trees during 1995 in a 40-year-old stand near Guelph, Ontario (Numbers above each point indicates the number of samples/tree) Vertical bars indicate the standard error.

Shoot Feeding Preferences

Age of Attacked Shoots

In 1995, almost 40% of the attacks early in the summer were on one-year-old shoots (Fig. 6.4), however, over the course of the summer, all subsequent attacks occurred on the current-year-growth. In 1996, the majority of the attacks were located in one year old growth early in the season but by the end of the season, the attacks were equally distributed on both ages of shoots. This arose because the majority of subsequent feeding occurred on the current-year-growth (Figure 6-4).

The majority of the shoot attacks (79%) occurred in the upper third of the tree, 20% in the middle third, and the final 1% close to the ground in the bottom third of the tree crown (n=222).

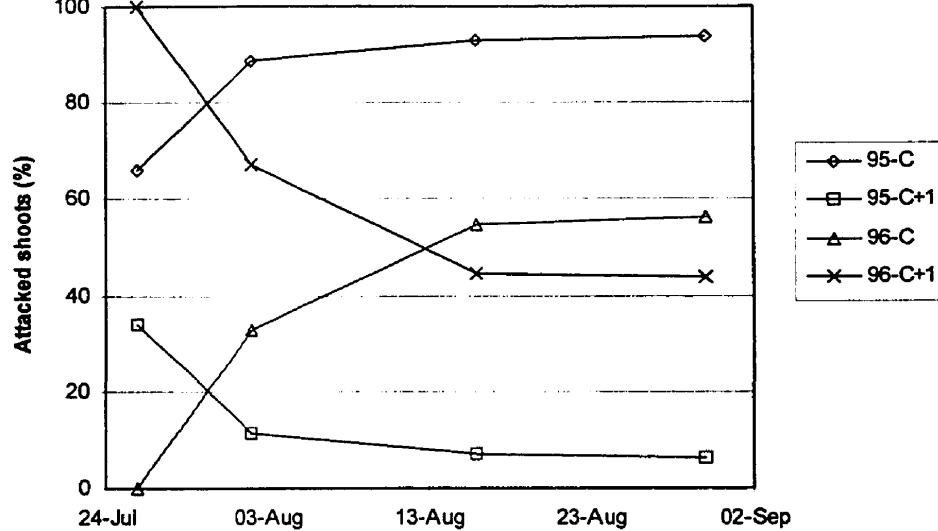


Figure 6-4. Percentage of different aged shoots (current, C vs one year old, C+1 shoots) fed upon by adult pine shoot beetles (*Tomicus piniperda*) during 1995 and 1996 in a young (10-12 year old) Scots pine (*Pinus sylvestris*) stand near Guelph, Ontario

Needle Length

The mean length of tip needles on attacked trees (53.93 mm) (n=23) was significantly greater than those needles (42.22 mm) (n=21) on non-attacked trees (F=401.4, p=0.001, df=1,42) (Figure 6-5a). However, the mean needle length was significantly different on shoots within each category (F=84.14, p<0.0001, df=42,176). The mean length of one-year-old needles on attacked shoots (61 mm) (n=26) was significantly greater than those needles on non-attacked trees (58.2 mm) (n=21) (F=38.28, p<0.0001, df=1,45) (Figure 6-5b). Again, the mean needle length was significantly different on shoots within each category (F=78.26, p=0.001, df=45,188).

Shoot Diameter

The mean diameters of current year non-attacked shoots on otherwise attacked trees (4.9 mm, n=40, s.d.=2.239) (p=0.012) and of attacked shoots (5.77 mm, n=24, s.d.=1.989) (p<0.001) was greater than the mean diameter of non-attacked shoots on non-attacked trees (3.86 mm, n=42, s.d.=1.01) (F=14.247, p=0.0002) (Fig. 6-6). In addition,

shoots on otherwise attacked trees ($p=0.018$).

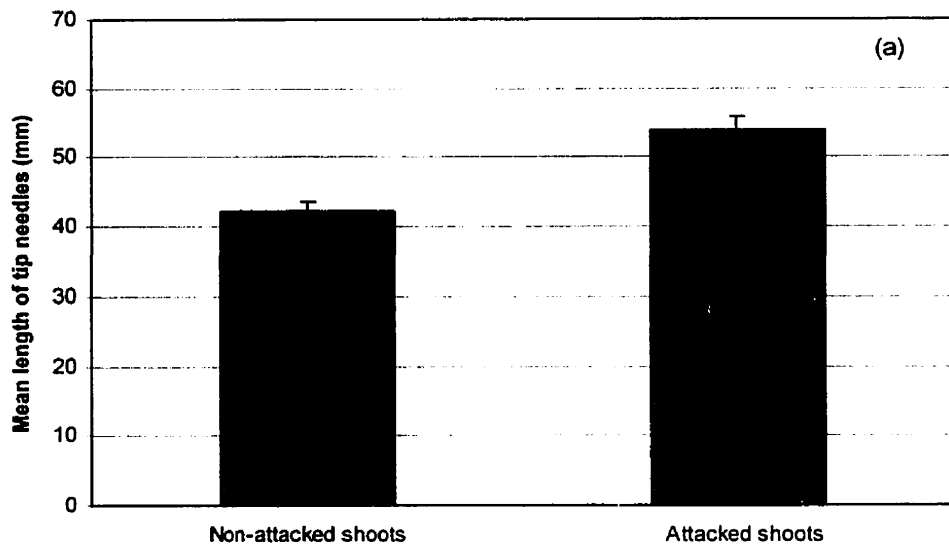


Figure 6-5. a and b. Mean length of tip (a) and one-year-old (b) needles on non-attacked shoots and shoots attacked by *Tomicus piniperda* shoots in a young (10-12 year old) Scots pine (*Pinus sylvestris*) stand during 1995 near Guelph, Ontario. (Vertical bars indicate standard error).

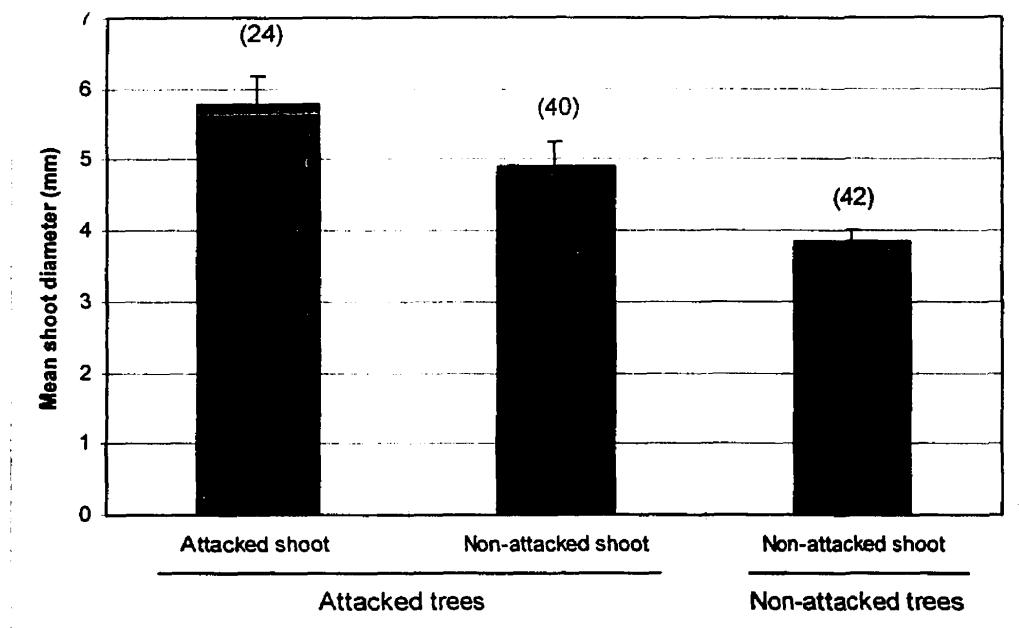


Figure 6-6. Mean diameter (mm) of current-year shoots attacked by *Tomicus piniperda*, non-attacked current-year shoots on otherwise attacked trees, and non-attacked current-year shoots on non-attacked trees in a young (10-12 year old) Scots pine (*Pinus sylvestris*) stand near Guelph, Ontario during 1995. ($F=14.247$, $p=0.0002$) (Numbers above each point indicates the number of shoots measured) Vertical bars indicate the standard error.

Tree Height, DBH, and Branch Radius

Stepwise multiple regression, with a minimum tolerance for entry of 0.01, showed that DBH (Fig. 6-7) and branch radius (Fig. 6-8) were both positively related to the number of attacks on a given tree (adjusted $r^2=0.262$, $F=8.166$, $p=0.001$, $n=49$), whereas height had no effect (Fig. 6-9). Step 1 included branch radius ($r^2=0.204$, $F=12.010$, $p=0.001$) and then step 2 included DBH ($r^2=0.262$, $F=3.646$, $p=0.062$). The branch radius had a slightly larger standardized coefficient (0.360, $p=0.013$) than did DBH (0.298, $p=0.062$), indicating that branch radius played a slightly larger role in predicting attack levels, although the r^2 value was low overall.

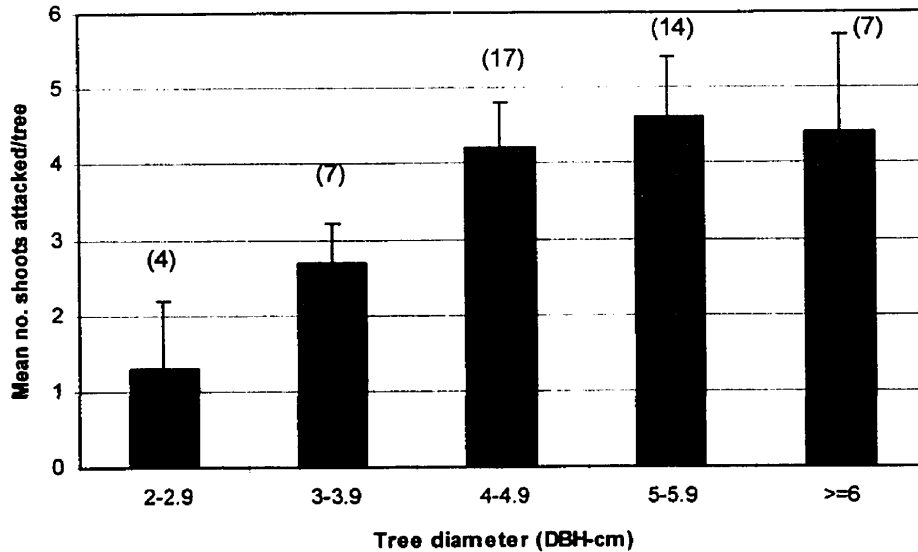


Figure 6-7. Relationship between tree diameter at breast height (cm) and mean number of shoot attacks by *Tomiscus piniperda* on young (10-12 year old) Scots pine (*Pinus sylvestris*) trees during 1995 in a stand near Guelph, Ontario (Numbers above each point indicates the number of trees per category) Vertical bars indicate the standard error.

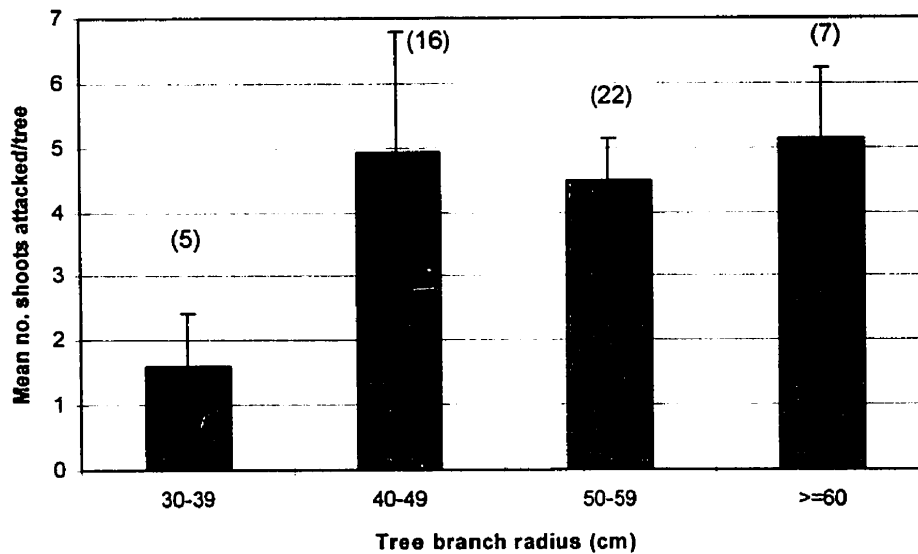


Figure 6-8. Relationship between tree branch radius (cm) and mean number of shoot attacks by *Tomiscus piniperda* on young (10-12 year old) Scots pine (*Pinus sylvestris*) trees during 1995 in a stand near Guelph, Ontario (Numbers above each point indicates the number of trees per category) Vertical bars indicate the standard error.

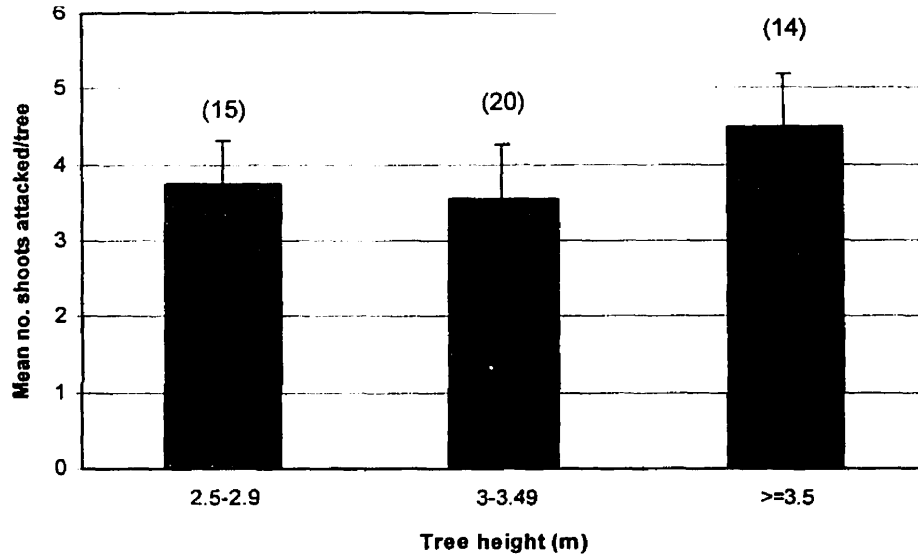


Figure 6-9. Relationship between tree height (m) and mean number of shoot attacks by *Tomicus piniperda* on young (10-12 year old) Scots pine (*Pinus sylvestris*) trees during 1995 in a stand near Guelph, Ontario (Numbers above each point indicates the number of trees per category) Vertical bars indicate the standard error.

Reproductive Preferences

Bark beetle species, such as *Tomicus piniperda*, are often separated from each other by the specific areas of the host plant that they use. Often, the largest species is found on the lower part of the bole while smaller species are found higher up on the tree under the thinner bark (Speight and Wainhouse 1989). This spatial segregation enables a number of species to share a common, often limited, resource. Schroeder (1990) found that the majority of attacks by *T. piniperda* occurred on the lower 3 m of Scots pine. In a study by Salonen (1973), 34 of 45 galleries were found in the lowest 1 m of the tree. Langstrom and Hellqvist (1993) also found density of attack by *T. piniperda* was higher on the bottom stem sections (0.3-0.6 m) than on the higher ones (2.3-2.6 m). Bouhot *et al.* (1988) found *T. piniperda* initiated attacks in the lower 10 m of the bole, with the largest numbers in the first 5 m. In my study, numerous attacks on standing trees during 1995 were observed up to a height of 5-6 m and the slightly negative relationship between gallery density and tree height supports previous findings. Because samples were taken only from the rough-barked regions of the bole, as suggested in the literature (Langstrom 1984), gallery density appeared to decline only slightly. If samples containing no galleries had been obtained from the higher bole sections, this trend would have been much more apparent.

A preference by *T. piniperda* for intermediate bark thickness has been often reported. Bouhot *et al.* (1988) found that the majority of *T. piniperda* attacks occurred on regions of the bole where the bark was 5-7 mm thick. Schlyter and Lofqvist (1990) found that attack density was positively related to bark thickness, although, extremely thick regions of bark were often not selected by the colonizing beetles, as too much energy was required to bore through to the phloem layer. While no direct samples were taken from the fine-barked regions of the upper bole in my study, no exit holes were seen while in the field, indicating that galleries were either not successful or not established above a height of 5-6 m. It has been suggested that the fine bark does not allow for the proper development of galleries, especially in a bark beetle the size of *T. piniperda* (Bouhot *et*

in 1966). Trees with a very small diameter and thin bark have been found to dry too fast to allow for successful development of *T. piniperda* galleries (Salonen 1973). This spatial preference allows smaller bark beetle species to colonize the higher, thin-barked regions of a tree, without experiencing interspecific competition from the pine shoot beetle. The lower, thicker regions of bark may have a correspondingly thicker inner bark or phloem layer on which larvae of *T. piniperda* feed. It is possible that a minimum thickness is required for proper feeding and development to occur for this species. Further studies could determine if the width of this feeding layer corresponds to the bark thickness preferences exhibited by *T. piniperda*.

The density of attacks by *T. piniperda* has also been found previously to decline with tree diameter (Langstrom and Hellqvist 1993). Schlyter and Lofqvist (1990) showed that attack rates depended on log diameter up to a point with beetles showing a preference for larger logs and rough bark. It is possible that large trees have expansive areas of extremely thick bark and this is not as preferred by *T. piniperda*. Larval survival is known to depend on the diameter of the attacked trunk, with few larvae successfully pupating in trees <3 cm diameter (Ye 1991). Annala and Heikkila (1991) found that all trees attacked by *T. piniperda* had a diameter at breast height (DBH) >9 cm.

The six infested trees examined in the current study were not all attacked at the same intensity. Bouhot *et al.* (1988) also found that some trees were over- and under-attacked throughout the whole colonization period. They concluded that *T. piniperda* does not shift attacks from one tree to another, unlike other species, such as *Ips sexdentatus*. This supports the idea that *Tomicus piniperda* does not have a species-specific aggregation pheromone helping it locate appropriate brood material, but instead responds to allelochemicals released by the dying or stressed trees. Indeed, Loyttyneimi *et al.* (1988) concluded from window flight traps baited with uncovered and covered pine bolts and infested covered bolts that *T. piniperda* is attracted to its breeding sites by log odours alone. All three of their treatments caught equal numbers of potential colonizing adults. In my study, it is possible that greater levels of chemicals were being released from the trees that ended up with the highest attack densities.

The age of shoots preferred for feeding has been seen to vary greatly between sites, between years, as well as over the course of a summer (Langstrom 1980). Overall, the majority of feeding during 1995 occurred in current-year shoots. In 1996, more one-year-old shoots were attacked. In both years, one-year-old shoots were attacked only at the very beginning of the season for about one week. Langstrom (1980) found that, in early summer, one-year-old shoots were attacked by the parental generation after oviposition. Thus, the attacks I observed in one-year-old shoots early in 1995 and 1996 were likely due to the parental generation. Overall, Langstrom (1980) found a large variation in the age of attacked shoots between study sites with current-year shoots accounting for 1.5-67.3% and one-year-old shoots for 31.5-98.5 % of all attacks. In another study, Langstrom (1983) found that in a 15-year-old pine stand in southern Sweden, 40% of feeding occurred in the current year's shoots, 50% in the one-year-old shoots, and the remaining in older shoots. In his 1983 study, older shoots made a significantly larger proportion of the shoots used for feeding by the adults than in my study. In my study, perhaps the older shoots had hardened off too much for feeding by *T. piniperda*. Alternatively, because this stand was originally managed as Christmas trees, intensive pruning may have artificially increased the number of current-year shoots.

A large amount of aesthetic damage can be caused by the shoot feeding of this species. Although there were fewer attacks located on the older shoot growth than on current-year growth, such attacks could reduce subsequent growth because they destroy all of the current-year growth. In so doing, a visible gap or hole in the crown of the tree would be created by the emerging parental generation early in the summer and this could reduce a tree's value at Christmas. Langstrom (1980) found that, in Europe, current-year shoots are not attacked in June during the phase of shoot elongation. Current-year shoots begin to be attacked as the new generation emerges from the brood material and enters a stand, searching for suitable material on which to feed. By this time, the new shoots have elongated enough to provide adequate nutrition for the young beetles. In fact, the new shoots may even be a superior food source because of all of the resources that would be allocated to the new growth regions, in an effort by the tree to grow vigorously. Attacks

destroying their growth for the following year. Hence, high populations of *T. piniperda* could lead to a large amount of aesthetic damage and may stress the tree, thereby utilizing significant amounts of resources that should have been allocated to growth. Indeed, studies have shown that trees with many shoots attacked by *T. piniperda* may sometimes become susceptible to colonization by the emerging parental generation, thus perpetuating their own population growth (Ye 1991).

In my study, the mean diameter of attacked shoots was 5.8 mm with the majority ranging from 4.5-8.5 mm. These results are very similar to those of Langstrom (1983) who found the mean diameter of attacked shoots to be 4.5 mm. Earlier, Langstrom (1980), found that attacked shoots had an average diameter of 4.5 mm, with large variation and without any consistent seasonal change. The same preference of 4.5 mm for attacked shoots was shown in Michigan by McCullough and Smitley (1995). In a study by Ye (1991), the shoot diameter preferred by *T. piniperda* was 6-10 mm; somewhat larger than that preferred in Sweden by *T. piniperda*. The much warmer temperatures in China cause smaller shoots to wilt if attacked, thus becoming unsuitable for feeding. Although the mean diameter of attacked shoots found in my study was smaller than that found by Ye (1991), the attacked shoot diameters were significantly larger than the non-attacked diameters, indicating that the beetles selected the largest shoots available in the stand for feeding.

In my study, attacked trees were found to have significantly longer tip and one-year-old needles than non-attacked trees. It is possible that longer needle length is correlated with larger shoot diameter and that faster growing, more vigorous trees are most suitable for shoot-feeding. If true, this would pose a problem for Christmas tree growers as they attempt to grow vigorous, healthy trees, thereby creating the best food source for emerging beetles.

Both tree diameter and branch radius significantly influenced the amount of shoot-feeding on a given tree. Bushier trees with larger diameters had higher levels of shoot-feeding in their crowns than did smaller diameter trees with a smaller crown of branches.

for attack, (which was not measured here), this type of bushy growth is exactly what is desired by Christmas tree growers. Hence, this aesthetic damage may have a significant negative influence on the selection and price of harvested trees. In conclusion, by being aware of these species-specific preferences for colonization and feeding, management protocols can be designed which help reduce or prevent losses caused to both the timber and Christmas tree industries.

Chapter Seven : Summary

Pine Shoot Beetle Biology in Southern Ontario

The pine shoot beetle, *Tomicus piniperda*, was introduced into Ontario approximately four to five years ago. This thesis represents the first research initiated on *T. piniperda* in Canada. My study found that its life cycle here follows a similar pattern as that in its native European range. Emergence of the parental generation occurs relatively early in the spring when the maximum daily air temperature reaches 11-12°C. Appropriate brood material in the stand at this time is extremely susceptible to colonization by the emerging adults. *Tomicus piniperda* requires weakened or stressed trees in which to reproduce and also readily colonizes logs that have been cut mid-winter or early-spring. In southern Ontario, emergence of the parental generation begins in mid-to late-April with the next generation emerging approximately three months later, in late-July. Both colonization of brood material and emergence of the new generation occur over a relatively brief period of time. This period of maturation feeding which follows emergence from the brood material is unique to this bark beetle genus and is the primary cause of damage. Each individual beetle feeds on several shoots over a period from late-July through to mid-October at which point the adult beetles begin moving to overwintering sites. It is known that, in Ontario, the beetles do not overwinter in the shoots, either on the tree or on the ground in the litter.

An examination of the temperature requirements for development of this species showed close correspondence to those of previous studies with a calculated heat sum value of approximately 1250 degree-days (>0°C). The effective degree-days (> developmental threshold) were also in close correspondence with previous findings. These values may be used to predict when emergence of the new generation will occur. The timing of the emergence of this new generation is critical because, shortly after emergence, the beetles will begin a requisite period of maturation feeding in the shoots of pine trees.

A positive growth trend was observed in some years (see Table 1), indicating that the beetle is reproducing successfully and may increase its damage levels and range of infestation. Gallery density was observed to be highly variable, possibly related to the size of the attacking parental generation and/or the type of brood material examined. Declining production per gallery with increasing gallery density is consistent with previous research findings. Brood production by *T. piniperda* on Scots pine was found to be relatively constant at around 900-1000 new beetles produced per square metre of bark surface area, even under highly variable gallery densities (ranging from 80 to over 220 galleries per square metre). This suggests that populations of *T. piniperda* may be operating very near to their carrying capacity, efficiently and fully utilizing the available resources. Indeed, similar values have been reported previously in the literature. Hence, appropriate brood material left in a stand may be readily colonized by this species and will be the source of a large number of emergent beetles later in the season. High mortality levels among the juvenile stages, especially at high gallery densities, indicates that intense intraspecific competition occurs for food and space resources, especially amongst the larvae.

Certain reproductive and feeding preferences were apparent and were consistent with prior European findings. Galleries were typically initiated only on the lower portion of the tree bole with an intermediate thickness of bark preferred for colonization. Large diameter trees tended to have a low density of galleries, possibly because of an abundant amount of thick bark. Feeding attacks tended to occur in shoots with the longest needles and largest diameters and in trees with the largest diameters and branch radii. At the beginning of the feeding period, a variable proportion of attacks were located in one-year-old growth while during the latter period, the majority of the feeding occurred in current-year shoots. This will be especially damaging in Christmas tree management because all of the current-year shoots will be destroyed and a large loss in growth will occur.

Information from the European literature on *Tomicus piniperda* can be incorporated into the design of management strategies because it is now known the biology in southern Ontario is very similar. Knowing when the parental generation establishes galleries and when the new generation of beetles is likely to emerge is critical in the design of protocols to prevent or reduce these events. A heat sum of approximately 1200 degree-days ($>0^{\circ}\text{C}$) can also be used to predict when the new generation will emerge. Knowledge of the beetle's reproductive and feeding preferences identify those trees most susceptible to attack by this species.

In Europe, shoot-feeding had a negative impact on the timber industry where large populations are present. Thus, a potential negative impact on the Canadian timber industry exists and needs to be assessed. In addition, this species may have a negative impact on the production of Christmas tree in this province where trees free of aesthetic damage are desired. Gaps or holes may be created in the tree's crown by shoot-feeding and this may reduce the profits realized by Christmas tree growers. Additional control measures, whether chemical or manual removal, will increase the costs of producing these trees. The negative impact on these industries is an area that needs to be addressed further to determine the pest status of this newly introduced species.

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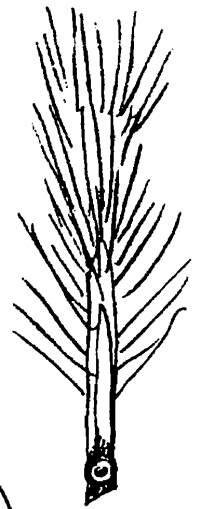
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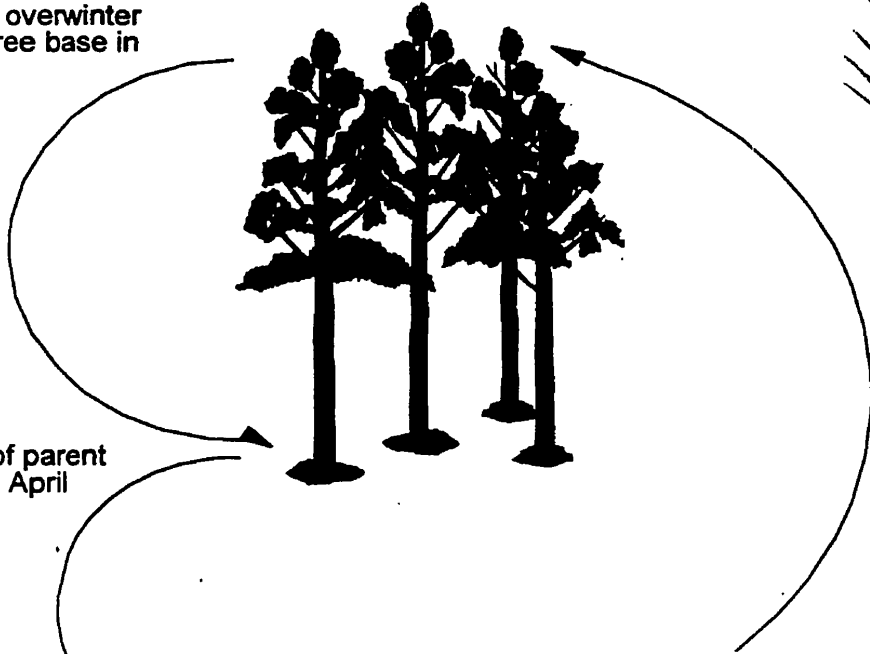


Adults fly to tree crowns to feed on shoots from July through October

Adults move to overwinter under bark at tree base in October



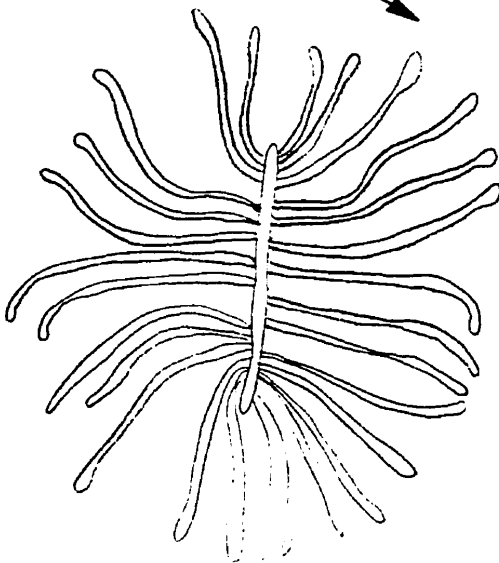
entrance hole into shoot made by a beetle



Emergence of parent generation in April

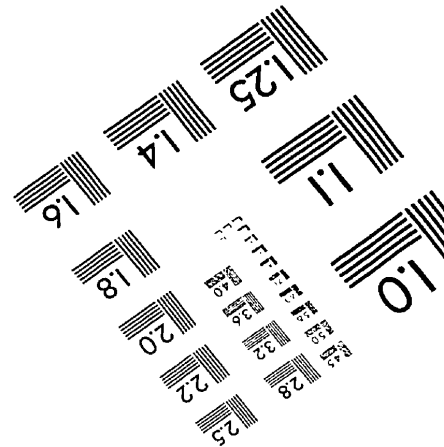
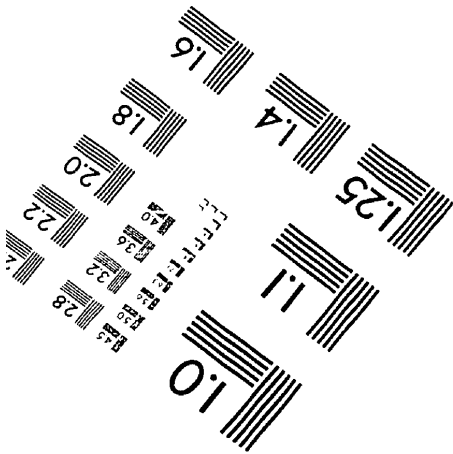
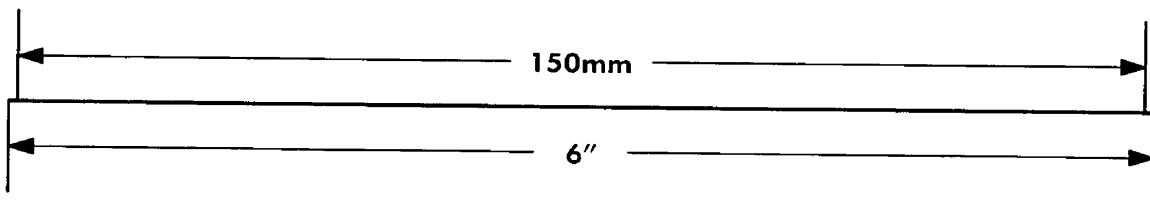
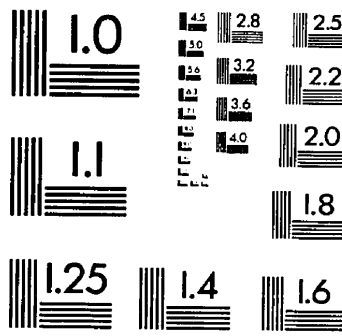
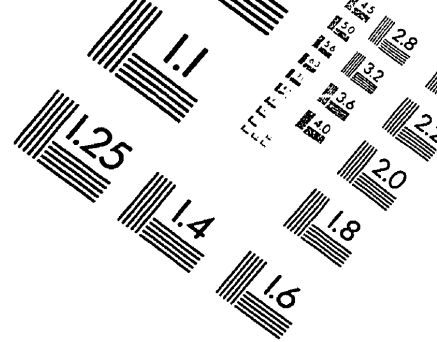
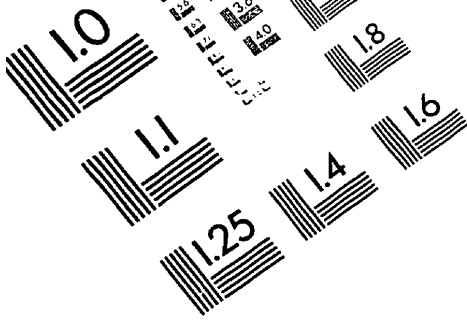


pine log or weakened tree



T. piniperda gallery

Colonization of weakened trees or freshly cut logs in April
Larvae feed on phloem layer
New generation emerges in July



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