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Poland and Haack: <i>Tomicus Piniperda</i> (Coleoptera: Scolytidae): Is Shoot Feedi

TOMICUS PINIPERDA (COLEOPTERA: SCOLYTIDAE): IS SHOOT-FEEDING REQUIRED FOR REPRODUCTIVE MATURATION?

Therese M. Poland and Robert A. Haack[1]

ABSTRACT

The pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae), is a univoltine pest of pine in its native range of Europe and Asia. *Tomicus piniperda* is now widely established in the Great Lakes region and poses a potentially significant threat to other pine-producing areas in North America. An unusual aspect of the life history of *T. piniperda* is the extended period of maturation-feeding that takes place in the shoots of living pine trees and subsequent overwintering before adults reproduce the following year. We investigated the extent to which shoot-feeding is required by newly-emerged *T. piniperda* before introduction into Scotch pine (*Pinus sylvestris*) logs and before any overwintering, in order for successful reproduction to occur. *Tomicus piniperda* F_1 adults successfully reproduced in pine logs in the laboratory after either no shoot-feeding or after 2 to 10 weeks of shoot-feeding. Thus, it is theoretically possible for *T. piniperda* to be multivoltine, yet it remains univoltine.

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), is a pest of pine, *Pinus* spp., in Europe, Asia, and parts of northern Africa (Långström and Hellqvist 1991, Ye 1997). Established populations of *T. piniperda* in North America were first discovered in Ohio in 1992 (Haack et al. 1997). As of January 2000, 271 counties in 11 U.S. states have been declared infested and quarantined, as well as 25 counties in Ontario, and 8 counties in Quebec, Canada (Figure 1). To date, *T. piniperda* has caused little physical or aesthetic damage to Scotch pine trees growing in managed plantations or to pines in native stands in infested areas of North America although some Christmas tree plantations require intensive management to keep the pest under control. Severe damage has been found in some unmanaged Scotch pine fields in New York State (Czokajlo et al. 1997) and in southwestern Ontario (Czerwinski 1998). Because several species of North American pines are suitable hosts for *T. piniperda* (Långström et al. 1995, Lawrence and Haack 1995), it may pose a significant threat as it spreads throughout North America.

Tomicus piniperda is univoltine throughout its native and North American range (Långström 1983). Overwintering adult beetles become active in early spring when they fly in search of suitable brood material such as severely stressed or weakened pines, freshly killed pines, or recently cut trees, stumps and slash. Host volatiles, including α-pinene, terpinolene, and (+)-3-

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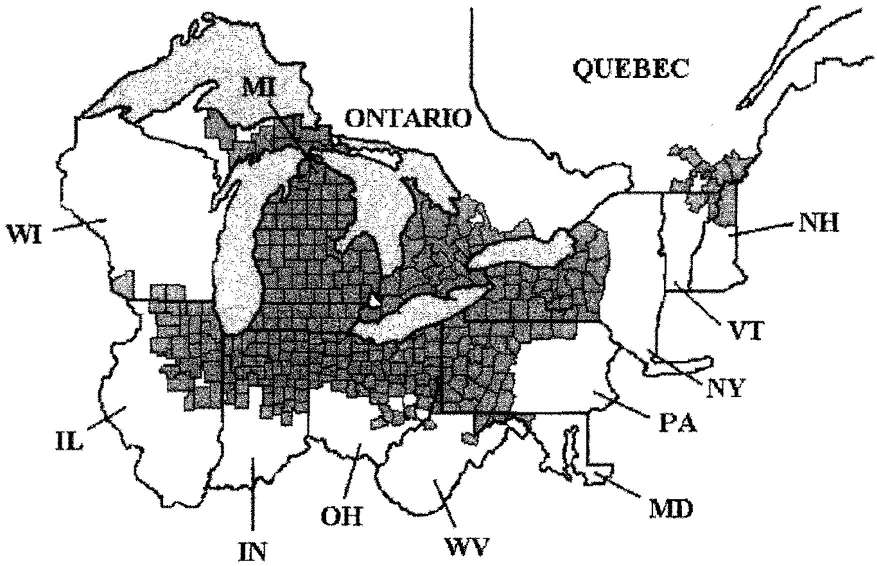

Figure 1. Known range of *Tomicus piniperda* in North American as of January 2000. (Sources: United States Department of Agriculture Animal and Plant Health Inspection Service and Canadian Food Inspection Agency.) State abbreviations are: IL = Illinois, IN = Indiana, MD = Maryland, MI = Michigan, NH = New Hampshire, NY = New York, OH = Ohio, PA = Pennsylvania, VT = Vermont, WI = Wisconsin, and WV = West Virginia.

carene are important in mediating attraction to suitable breeding material (Schroeder and Eidmann 1987). Recent studies suggest that pheromones may also be involved in locating brood material (Czokajlo 1998). Brood adults emerge in early summer and feed in the shoots of healthy pine trees throughout the summer to complete sexual maturation. In colder areas of *T. piniperda*'s range, when temperatures cool in autumn, beetles move down the trunk into the bark at the base of trees in which they have shoot-fed to overwinter.

Ecologically, *T. piniperda* differs from most other scolytids because of its unique behavior of post-emergence maturation-feeding inside live shoots of healthy pine trees after the beetles emerge from the brood host and before they enter future breeding material (Långström 1983). Although some scolytid species may fly from the brood host to complete maturation-feeding as adults on a living host [e.g., *Scolytus multistriatus* (Marsham) (Solomon 1995)], most bark beetles are able to breed immediately upon emergence as adults or else they complete maturation-feeding within the brood host after pupating but before they emerge. Some scolytid species may feed on a living host following emergence only when suitable brood material is not immediately available (Wood 1982).

The development time of *T. piniperda* is relatively short and callow adults (F_1 adults) emerge in early summer, however adults do not breed until the following spring. Thus this species remains univoltine even though there seems to be adequate time to complete a second generation. This raises the question as to whether *T. piniperda* has the potential to become multivoltine, especially in warmer climates. When *T. piniperda* F_1 adults emerge, their reproductive organs are rudimentary, but then mature through the summer as adults undergo maturation-feeding (Långström 1983). Salonen (1973) demonstrated that newly-emerged *T. piniperda* F_1 adults were able to breed successfully after feeding on pine shoots in a jar for 3–4 weeks (i.e., without undergoing winter diapause). The amount of maturation feeding on shoots that is required, if any, for successful reproduction to occur is unknown. Therefore, we investigated if shoot-feeding was required by *T. piniperda* before introduction of the beetles into fresh brood material in order for viable egg production to occur.

MATERIALS AND METHODS

Rearing bolts were made from a healthy Scotch pine tree that was felled on 25 June 1997 at the Michigan State University Kellogg Forest, Kalamazoo County, Michigan. The tree trunk was cut into bolts approximately 60 cm long and 15 to 25 cm in diameter. The cut ends of the bolts were sealed with melted paraffin wax to prevent desiccation, and the bolts were stored in the laboratory until used. To determine initiation of natural emergence of F_1 adults, infested Scotch pine logs, which had been naturally attacked by *T. piniperda* in early spring of 1997, were held outdoors in emergence cages at ambient temperatures at the Kellogg Forest and checked daily beginning on 9 June. Newly emerged F_1 adults, which had no opportunity to shoot-feed, were collected from the emergence cages. Every two weeks after the initiation of F_1 adult emergence until 4 September, 50 freshly colonized Scotch pine shoots were collected from a Christmas tree plantation in Ingham County, Michigan. *T. piniperda* adults were excised from these shoots and sexed according to Bakke (1968). Males and females collected from the outdoor emergence cages and from the four biweekly shoot collections were held separately in glass jars with moist tissue paper for up to 48 hours at room temperature before being introduced into the Scotch pine bolts in the laboratory. For each collection period, 20 females were introduced individually into pre-formed holes (4mm deep, 10 mm in diameter) spaced 15 cm apart on two bolts and confined with gelatin capsules. After 24 hours, one male was added to each gallery with an actively boring female and then the gelatin capsules were repositioned. Infested bolts were held separately in cardboard emergence tubes in the laboratory. The temperature in the laboratory varied between 24°C and 30°C throughout the duration of the experiment. At weekly intervals following inoculation, two galleries from each collection period were dissected, one from each bolt. Galleries were sampled until the presence of progeny was noted, after which remaining galleries were left undisturbed so larvae could complete development. When callow F_2 adults began to emerge, all remaining galleries were dissected.

RESULTS AND DISCUSSION

Successful reproduction occurred in all experimental treatments, even for callow F_1 adults that had not shoot-fed (Table 1). Overall, the time required

Table 1. Number of successful *Tomicus piniperda* galleries with progeny in Scotch pine logs that were artificially infested in the laboratory with F_1 adults that had completed 0 to 10 weeks of shoot-feeding in 1997 and then dissected at 2-week intervals.

Date of female introduction in 1997	Number of weeks of shoot feeding	Percent of galleries producing brood*	1997 Dissection date (Number of galleries with progeny / Number of galleries dissected)									
			July 7	July 22	Aug 8	Aug 25	Aug 30	Sept 5	Sept 12	Sept 20	Oct 3	Oct 28
June 27	0**	36%	0 / 2	0 / 2	1 / 2	1 / 1	1 / 1	1 / 3				
July 10	2	62%	—	0 / 2	1 / 2	2 / 2	—	1 / 1	1 / 1	5 / 8		
July 24	4	36%	—	—	0 / 2	2 / 4	—	—	—	2 / 5		
Aug 22	8	33%	—	—	—	—	0 / 2	0 / 2	—	1 / 2	—	4 / 9
Sept 4	10	35%	—	—	—	—	—	—	—	0 / 2	2 / 2	3 / 10

*The number represents the percent of all galleries with brood from the periodic dissections and from the final log dissections at the end of the experiment. N=20 galleries per date of female introduction.

**These F_1 adults were reared from field-collected pine logs and then placed on rearing logs without any shoot-feeding for complete development of F_2 callow adults was similar (8–9 weeks) regardless of the amount of shoot-feeding before introduction of F_1 adults into the Scotch pine bolts. Larvae were first observed six weeks after introduction of the F_1 adults that had not shoot-fed compared with only four weeks for the F_1 adults that had shoot-feeding experience. F_1 adults that had not shoot-fed may have required a longer period of time to tunnel and complete some maturation feeding in the logs before becoming sexually mature. On the other hand, this apparent two-week delay may have been an artifact of the sampling procedure given that only two galleries per treatment were sampled each week, and that development times to the F_2 callow adult stage were similar regardless of the amount of shoot-feeding by the F_1 adults (Table 1).

It is possible that some of the adults collected from shoots in the field could have been parent adults and not F_1 adults. After shoot-feeding for 2 or more weeks, newly emerged adults change from light to dark brown making it impossible to distinguish them morphologically from parent adults. In Scandinavia, Långström (1983) and Salonen (1973) reported that some *T. piniperda* parent adults shoot-feed immediately after overwintering and then look for breeding sites, while others first breed and then shoot-feed before starting their next egg gallery. Moreover, Långström (1983) found *T. piniperda* parent adults, especially females, shoot-feeding during the summer and fall. Nevertheless, we believe that the majority of *T. piniperda* adults that we collected from shoots during the summer were F_1 adults, given that abundant brood material was available for parent adults to colonize. Moreover, the percent of F_1 adults that had not shoot-fed yet produced viable brood (36%, Table 1) was similar to the percent of adults that produced brood after 2–10 weeks of shoot-feeding (33–56%).

Therefore, since we are certain that only light-brown F_1 callow adults were used in the first introductions in June, we are confident in reporting that *T. piniperda* can reproduce without shoot-feeding. Furthermore, we were able to repeat this observation in 1998 (Poland and Haack, unpubl. data). Thus, *T. piniperda* is capable of producing viable eggs soon after they begin to feed in suitable brood material without completing any post-emergence shoot-feeding and without overwintering. Therefore, it is theoretically possible that *T. piniperda* could develop a multivoltine life history. Similarly, Salonen (1973) concluded that it was theoretically possible for *T. piniperda* to complete two generations per year given three weeks of shoot-feeding for sexual maturation between generations. However, the occurrence of a second generation in nature has not been recorded even in the warmer areas of *T. piniperda*'s range (e.g., the Mediterranean area and southern China). Rather, as the growing season lengthens, *T. piniperda* extends the period of shoot-feeding.

Post-emergence maturation-feeding in living hosts has been observed in only a few scolytid species but not studied in detail, including the elm bark beetles, *Hylurgopinus rufipes* Eichhoff and *Scolytus multistriatus*, (Solomon 1995), the peach bark beetle, *Phloeotribus liminaris* (Harris) (Bright 1976), the European oak bark beetle, *Scolytus intricatus* (Ratzeburg) (Yates 1984), and several *Phloeosinus* spp. which attack many species of conifers (Bright 1976, Wood 1982).

The amount of intermediate-feeding required for reproductive maturation by these scolytids has not been studied in detail. However, Norris (1961) was able to rear *S. multistriatus* continuously in the laboratory without any twig-feeding or diapausing. Similarly, newly emerged *S. intricatus* adults were able to reproduce when placed directly on freshly cut logs (Doganlar and Schopf 1984, Habermann and Schopf 1987). Therefore, there is evidence that successful reproduction is possible immediately after emergence of new adults for other scolytids that ordinarily undergo some post-emergence maturation-feeding.

The post-emergence maturation-feeding in living hosts is responsible for the pest status of *T. piniperda* as a forest pest, as the original brood host is often dead by the time the brood adults mature. For instance, it is the shoot-feeding damage by *T. piniperda* that has resulted in growth loss to Scotch pine trees in Europe and in New York (Långström and Hellqvist 1991, Czokajlo et al. 1997). In southwestern China, extensive shoot-feeding weakened Yunnan pine trees, *Pinus yunnanensis*, so severely that they were subsequently used as brood material by *T. piniperda* (Ye 1997). In addition, extensive shoot-feeding damage by *T. piniperda* can lower the aesthetic quality of Christmas trees and nursery stock and thereby decrease sales.

There may be several adaptive advantages to conducting maturation-feeding in an intermediate host rather than in the original brood host. First, extensive shoot-feeding can weaken trees and thereby provide additional future breeding material. Second, by shoot-feeding, *T. piniperda* avoids extended pre-emergence maturation-feeding under the bark and thus could minimize intra- and interspecific competition for limited brood material. Third, extended maturation feeding may be required to accumulate the storage reserves necessary to successfully overwinter. Finally, extensive maturation feeding may result in higher fecundity such that the fitness benefit of maturation feeding would exceed the fitness cost of remaining univoltine. Further research is required to investigate these and other possible hypotheses concerning the adaptive advantages of extensive maturation feeding.

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