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TOMICUS PINIPERDA (COLEOPTERA: SCOLYTIDAE) REPRODUCTION AND DEVELOPMENT IN SCOTS, JACK, RED AND EASTERN WHITE PINE UNDER LABORATORY CONDITIONSHui Ye¹, Robert A. Haack², and Toby R. Petrice²**ABSTRACT**

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), is an exotic bark beetle in North America that was first found in the Great Lakes region in 1992. We evaluated *T. piniperda* reproduction and development in one Eurasian pine (Scots pine, *Pinus sylvestris* L.) and three North American pines (jack pine, *P. banksiana* Lamb.; red pine, *P. resinosa* Ait.; and eastern white pine, *P. strobus* L.) under laboratory conditions. We introduced one pair of adults into individual pine bolts, allowed development, collected brood, and later debarked all bolts and measured galleries. Reproduction and development occurred in all pine species tested. Mean phloem thickness varied significantly among the bolts used to represent the four pine species; it was thickest in red pine (1.3 mm) and thinnest in jack pine (0.6 mm). Linear regression analysis indicated that initial brood production (larval galleries per cm of egg gallery) increased significantly with increasing phloem thickness ($r^2 = 0.36$), using the pooled data set for all four pine species. Using phloem thickness as a covariate, mean initial brood density (larval galleries per cm of gallery) was significantly highest on red pine, intermediate on Scots pine and white pine, and lowest on jack pine. Overall brood survival was highest on Scots pine (86%) and lowest on jack (72%) and white pine (76%); phloem thickness was not a significant covariate in this analysis.

The pine shoot beetle [*Tomicus piniperda* (L.) (Coleoptera: Scolytidae)] is a serious pest of pines (*Pinus*) in Eurasia (Bakke 1968, Långström 1983, Ye 1991). This bark beetle is native to Eurasia and parts of North Africa where it can cause severe growth loss and occasional tree mortality (Kaplan and Mokrzycki 1988, Amezaga 1996, Hui and Lieutier 1997, Långström et al. 2001). In North America, *T. piniperda* was first discovered in 1992 in Ohio, and as of January 2006, it was found in 15 US states and 2 Canadian provinces (Haack and Poland 2001, Haack 2006).

Tomicus piniperda is univoltine throughout its range (Långström 1983). Adults fly from overwintering sites in early spring and breed in recently cut pine trees, stumps, and severely stressed pine trees (Bakke 1968, Salonen 1973, Ye 1991, Haack and Lawrence 1995a, 1995b). Adults utilize primarily host monoterpenes to locate suitable brood material (Byers et al. 1985, Brattli et al. 1998), but may also use pheromones (Poland et al. 2003). Larvae develop beneath the bark in the cambial region. Progeny adults emerge from brood material in early summer, fly to live pine trees, and complete their sexual maturation by tunneling and feeding inside shoots (Ye 1996, Haack and Lawrence 1997, Siegert and McCullough 2001a, 2001b, Poland et al. 2002). Shoot-feeding continues throughout summer and autumn (Haack et al. 2000, Ryall and Smith 2000). When freezing temperatures occur in autumn, adults move to overwintering sites along the lower trunk of live pine trees (Haack et al. 2001, Petrice et al. 2002, Ye et al. 2002). In regions where winters are mild, however, adults often overwinter in shoots (Ye 1991).

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In northern Eurasia, Scots pine (*Pinus sylvestris* L.) is the principal host of *T. piniperda*. Scots pine also is widely planted throughout the Great Lakes region of North America where the three native pines are jack pine (*P. banksiana* Lamb.), red pine (*P. resinosa* Ait), and eastern white pine (*P. strobus* L.; we will refer to this species simply as "white pine" in this paper). Several field and laboratory studies have been conducted in recent years to evaluate the relative attractiveness and suitability of Scots pine and various North American pines for *T. piniperda* reproduction and shoot-feeding (Sadof et al. 1994, Långström et al. 1995, Lawrence and Haack 1995, Haack and Lawrence 1997, Ryall and Smith 2000, Siegert and McCullough 2001a, 2001b, 2003, Eager et al. 2004, Morgan et al. 2004). In some field studies, for example, *T. piniperda* attack densities were significantly higher on Scots pine compared with various North American pines; however, subsequent brood production was at times significantly lower on Scots pine in these same studies (Långström et al. 1995, Ryall and Smith 2000). In these cases, lower brood production on Scots pine could have resulted from higher levels of intraspecific competition that resulted from the higher initial attack densities on Scots pine. Given the difficulties in controlling attack densities in field studies, we initiated a laboratory study in which we could control initial *T. piniperda* attack density on pine bolts. Our objective was to compare *T. piniperda* gallery construction, oviposition, and progeny production in jack, red, Scots, and white pine under controlled laboratory conditions.

As an introduction to bark beetle egg-galleries, there is typically an initial egg-free zone, followed by a zone of active oviposition that we will refer to as the egg zone, and then a terminal egg-free zone (Haack et al. 1987b). Eggs are laid sequentially as the female extends her gallery, i.e., the oldest eggs are those nearest the entrance (Schmitz 1972, Gouger et al. 1975). The initial egg-free gallery usually reflects the time period when flight muscles of parent females diminish in size, ovaries enlarge, and the first eggs mature. By contrast, the terminal egg-free zone typically represents the period when egg production stops, ovaries diminish in size, and flight muscles enlarge as parent females prepare to depart the current gallery and seek a new host (Reid 1958, Borden and Slater 1969). Egg laying typically is terminated when egg galleries reach the end of a log or approach other galleries, brood, or phloem already colonized by bluestain fungi (Franklin 1970, Yearian et al. 1972, Wagner et al. 1982, Ye and Dang 1986, Haack et al. 1987b). After completing their first gallery, many parent adults initiate a second gallery, or sister brood, on the same or a different host plant (Stark 1982). Production of sister broods is common in *T. piniperda* (Sauvard 1993).

MATERIALS AND METHODS

Bolt Collection. In late March 2002, we cut 30-35 bolts per tree species from trunks of apparently healthy jack, red, Scots, and white pine trees at the Michigan State University's W. K. Kellogg Experimental Forest near Augusta, Michigan (42°22'N, 85°21'W). Bolts were cut to 30-cm lengths and ranged from 13.5 to 14.1 cm in diameter (outside bark). We dipped the bolt ends in melted wax to slow moisture loss and stored them indoors. Each bolt was considered a separate experimental unit given that bolt diameter and phloem thickness often varied from bolt to bolt even within an individual tree.

Adult Collection. We collected *T. piniperda* adults with α -pinene-baited funnel traps placed in a Scots pine Christmas tree plantation near Mason, Michigan (42°34'N, 84°22'W), in early April 2002 when *T. piniperda* adults were emerging from their overwintering sites and seeking brood material. We placed bark and phloem strips of Scots pine in the collection cups to provide the beetles with food and a substrate to walk on. Adults were collected daily, taken to the laboratory, sexed, and refrigerated at 4-5°C until used, which was usually within 1-2 days. Only active, undamaged adults were used in the laboratory studies.

Introduction of Adults into Bolts. We punched a “starter hole” with a 2.5 mm diameter nail through the outer bark to the underlying phloem (inner bark) at an upward angle near the base of each bolt. One pair of *T. piniperda* adults was inserted into each bolt. First, a single female was inserted into each starter hole and covered with one-half of a gelatin capsule to prevent the female from exiting. We pierced the end of the gelatin capsule with a heated probe to allow ventilation. Bolts were stood upright so that the inserted beetle was near the bottom of each bolt. Given that *T. piniperda* adult females construct egg galleries along the wood grain, we assumed that most females would excavate their gallery in an upward direction. We checked the bolts daily for frass accumulation in the gelatin capsules, which would indicate that females had initiated egg gallery construction. In bolts where frass was accumulating in the gelatin capsules, we added a single male to each capsule 2-3 days after the female had been introduced. If no frass was present after 2 days, we replaced the female. We continued this procedure until there was active tunneling in all bolts. After about 1 week, we removed the gelatin capsules and placed each bolt inside an individual cardboard tube. Plastic lids with screening for ventilation were placed on the tube ends, and a clear collection cup was attached to each end to capture emerging progeny adults. Tubes were laid horizontally on shelves in the laboratory and checked daily for adult emergence. Bolts were positioned within the tubes so that the introduced adults were located on the upper surface of the bolt.

Data Collection. Adult *T. piniperda* were collected from each tube for 2 months and then counted, dried, and weighed. All bolts were dissected over the next few weeks. We measured phloem thickness at six or more locations along the length of each egg gallery where no feeding had occurred to estimate average phloem thickness. We identified the boundary between phloem and periderm (outer bark) based on color. Given that phloem thickness was not measured for 2-3 months after the trees were cut, some desiccation of the phloem likely occurred even though the bolt ends were waxed. Therefore, the phloem thickness values reported in our study are conservative. For each egg gallery, we recorded total gallery length, distance from the tunnel entrance to the first egg niche, length of gallery that contained eggs (egg zone), terminal egg-free gallery length, and number of associated larval galleries. Bark beetles deposit a single egg in each egg niche. The number of eggs laid per unit length of egg gallery is commonly called egg density (Haack et al. 1984a, 1984b, Popp et al. 1989). However, because not all egg niches were clearly visible due to feeding by larvae and brood adults, we calculated initial brood density based on the number of larval galleries in relation to (a) the total length of the first egg gallery constructed on each bolt (no sister broods included) and (b) the length of the egg zone.

Statistical Analyses. Data were analyzed by chi-square analysis and one-way analysis of variance (ANOVA) to test for significant differences among tree species (Statistix 2003). Because mean phloem thickness was found to vary significantly among pine species, we conducted one-way analysis of covariance (ANCOVA) on some brood parameters using phloem thickness as a covariate. Percentage data were analyzed after arcsine square-root transformation. Linear regression analysis was performed on the number of *T. piniperda* larval galleries per centimeter of total egg gallery vs. phloem thickness. When means varied significantly at $P = 0.05$, a means separation test was conducted with the LSD multiple range test.

RESULTS

Bolt Parameters. Mean bolt diameter and surface area did not vary significantly among pine species (diameter: $F = 1.3$; $df = 3,93$; $P > 0.27$; area: $F = 1.4$; $df = 3,93$; $P > 0.26$). However, mean phloem thickness did vary significantly among the four pine species ($F = 19.6$; $df = 3,93$; $P < 0.0001$); phloem was thickest

in red (1.3 mm; range 0.9-2.0 mm thick) and white pine (1.1 mm; 0.7-2.2), intermediate in Scots pine (0.9 mm; 0.4-1.5), and thinnest in jack pine (0.6 mm; 0.4-1.2; Table 1).

Gallery Construction. Overall, more than 80% of *T. piniperda* females in our study successfully excavated egg galleries and oviposited in bolts of Scots pine, red pine and white pine, whereas only 53% of females excavated egg galleries in jack pine (Table 1; chi square = 12.3; df = 3; $P < 0.007$). When females produced multiple broods, the second gallery was constructed on portions of the bolts that were previously not occupied and therefore there was minimal interference between multiple broods on individual bolts. Of the 97 bolts with at least one successful gallery, 39 had a second gallery (Table 1). Overall, 48% of Scots pine bolts with one gallery had a second gallery, and similarly, 48% on white pine, 32% on red pine, and 25% on jack pine. These proportions did not differ significantly (chi square = 3.7; df = 3; $P > 0.29$). Total length of the initial (first) egg gallery constructed in each bolt was longest in jack pine ($F = 4.8$; df = 3,93; $P < 0.004$; Table 1). This resulted from egg galleries in jack pine having significantly longer initial egg-free zones ($F = 10.8$; df = 3,93; $P < 0.0001$) and terminal egg-free zones ($F = 9.9$; df = 3,93; $P < 0.0001$), considering that no significant differences were noted among pine species in average egg-zone length ($F = 1.3$; df = 3,93; $P > 0.28$; Table 1).

Brood Characteristics. Mean brood density (No. larval galleries per cm egg gallery) based on total gallery length varied significantly among pine species when calculated using either ANCOVA ($F = 8.7$; df = 3,92; $P < 0.0001$) or ANOVA ($F = 23.5$; df = 3,93; $P < 0.0001$); phloem thickness was a significant covariate ($F = 12.6$; df = 1,92; $P < 0.0006$). In both analyses, mean brood density was highest in red pine and lowest in jack pine (Table 1).

Phloem thickness was not a significant covariate when mean brood density within the egg zone was compared among tree species ($F = 0.7$; df = 1,92; $P > 0.406$); therefore, only ANOVA was performed. The ANOVA results indicated that mean initial brood density within the egg zone varied significantly among pine species ($F = 23.5$; df = 3,93; $P < 0.0001$), being highest in red pine and lowest in jack pine (Table 1).

Linear regression analysis, for all host species combined, indicated that initial brood density based on total egg-gallery length and not adjusted for phloem thickness increased significantly and positively with increasing phloem thickness (Fig. 1). When the linear relationship between initial brood density and phloem thickness was evaluated separately for each pine species, significant relationships were found for jack ($F = 11.6$; df = 1,14; $P < 0.005$), Scots ($F = 5.43$; df = 1,22; $P < 0.03$), and white pine ($F = 5.47$; df = 1,29; $P < 0.027$), but not red pine ($F = 0.5$; df = 1,23; $P > 0.48$).

Mean number of larval galleries present in the initial egg gallery varied significantly among pine species when calculated using either ANCOVA ($F = 3.3$; df = 3,92; $P < 0.025$) or ANOVA ($F = 23.5$; df = 3,93; $P < 0.0001$); phloem thickness was a significant covariate ($F = 18.4$; df = 1,92; $P < 0.0001$). Mean separation tests following both analyses indicated that the mean number of larval galleries per egg gallery was significantly highest in red pine (Table 1). The maximum number of larval galleries recorded for a single egg gallery was 95 in red pine, 92 in Scots pine, 93 in white pine, and 45 in jack pine.

Progeny Adults. Mean survivorship of progeny from larvae to adults was significantly highest on Scots pine (86%), intermediate on red pine (80%) and lowest on white pine (76%) and jack pine (72%) (ANOVA, $F = 3.9$; df = 3, 93; $P < 0.012$; Table 1). Mean body size (dry weight) of progeny adults did not vary significantly among host species (ANOVA; $F = 1.87$; df = 3,93; $P > 0.15$; Table 1). Phloem thickness was not a significant covariate with respect to either brood survival ($F = 0.08$; df = 1,92; $P > 0.77$) or body size ($F = 0.42$; df = 1,92; $P > 0.51$); therefore, only ANOVA was performed.

Table 1. Summary data for bolts and *T. piniperda* gallery construction, reproduction, and brood production in jack, red, Scots and white pine bolts under laboratory conditions.

Parameter	Total or mean (± SE)					Test**
	Jack pine	Red pine	Scots pine	White pine		
Bolt diameter (cm)	14.1 ± 0.2 a*	13.4 ± 0.2 a	13.5 ± 0.3 a	13.8 ± 0.2 a		ANOVA
Bolt area (dm ²)	13.3 ± 0.2 a	12.6 ± 0.2 a	12.7 ± 0.3 a	13.0 ± 0.2 a		ANOVA
Phloem thickness (mm)	0.6 ± 0.1 c	1.3 ± 0.1 a	0.9 ± 0.1 b	1.1 ± 0.1 a		ANOVA
Initial No. females	30	31	31	35		
No. successful first galleries	16	25	25	31		
No. bolts with multiple broods	4	8	12	15		
Total egg gallery length (cm)	11.1 ± 0.6 a	9.0 ± 0.6 b	8.2 ± 0.5 b	8.3 ± 0.5 b		ANOVA
Initial egg-free gallery (cm)	3.7 ± 0.4 a	1.7 ± 0.3 b	1.6 ± 0.3 b	1.8 ± 0.2 b		ANOVA
Length of egg zone (cm)	4.6 ± 0.7 a	6.1 ± 0.5 a	5.4 ± 0.5 a	5.0 ± 0.4 a		ANOVA
Terminal egg-free gallery (cm)	2.8 ± 0.3 a	1.2 ± 0.1 b	1.2 ± 0.3 b	1.5 ± 0.1 b		ANOVA
Larval galleries per cm of egg gallery	2.6 ± 0.5 c	5.7 ± 0.3 a	4.3 ± 0.3 b	4.4 ± 0.3 b		ANCOVA
Larval galleries per cm of egg gallery	1.8 ± 0.3 c	6.2 ± 0.3 a	4.0 ± 0.4 b	4.7 ± 0.3 b		ANOVA
Larval galleries per cm of egg zone	4.8 ± 0.6 c	9.8 ± 0.7 a	6.9 ± 0.7 b	8.4 ± 0.6 ab		ANOVA
No. larvae in 1st egg gallery	31.3 ± 4.9 b	48.6 ± 3.8 a	37.2 ± 3.6 b	35.2 ± 3.24 b		ANCOVA
No. larvae in 1st egg gallery	20.9 ± 3.1 c	55.2 ± 4.3 a	33.4 ± 3.9 b	38.3 ± 3.4 b		ANOVA
Survival from larva to adult (%)	72.2 ± 4.1 b	80.1 ± 2.2 ab	85.6 ± 1.8 a	75.9 ± 2.2 b		ANOVA
Progeny adult dry wgt (mg)	1.7 ± 0.04 a	1.6 ± 0.04 a	1.7 ± 0.05 a	1.6 ± 0.04 a		ANOVA

* Means (within rows) followed by the same letter are not significantly different at the *P* = 0.05 level (LSD multiple range test).
** Analyses for the brood parameter data (lower 7 lines) were first performed with a one-way analysis of covariance (ANCOVA), using phloem thickness as a covariate. If the covariate was significant (< 0.05), then the test was listed as ANCOVA and the adjusted means are given. If the covariate was not significant, then a one-way ANOVA was performed and the unadjusted means are presented in the table.

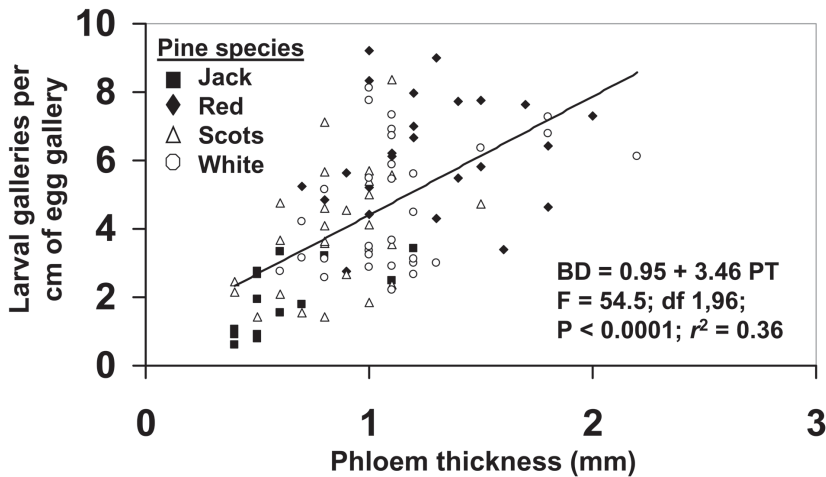


Figure 1. Linear regression analysis for *Tomicus piniperda* brood density (BD; larval galleries per centimeter of total egg gallery for the first egg gallery constructed on each bolt) vs. phloem thickness (PT in mm) for all four pines species combined.

DISCUSSION

As adult bark beetles construct their galleries, they tunnel primarily in phloem, which is softer and more nutrient rich compared with either xylem or outer bark (Stark 1982, Haack and Slansky 1987). Phloem thickness is known to strongly influence many life-history attributes of bark beetles, and insect performance generally increases with increasing phloem thickness (Amman 1972, Amman and Pace 1976, Haack et al. 1984a, 1984b, Slansky and Haack 1986, Haack et al. 1987a, 1987b). The diameter of an egg gallery is only slightly larger than the diameter of the parent female and therefore adult pronotal width is a good indicator of gallery diameter (Haack et al. 1984b). Based on our earlier studies where more than 600 *T. piniperda* adults from Michigan were measured (R. A. Haack et al., unpublished data), average adult pronotal width was 1.4 mm (range: 1.0-1.6 mm). Considering the phloem thickness of the bolts we used in our study (see results) and assuming that adult females averaged 1.4 mm wide, then females introduced into red and white pine bolts would have tunneled primarily in phloem, whereas females in jack and Scots pine bolts would have etched deeper into xylem when tunneling. When phloem is thinner than adult body width, females typically construct their galleries deeper into xylem rather than outer bark (Amman 1972, Haack et al. 1984b). For a given length of egg gallery, females would likely obtain fewer nutrients and expend more energy when tunneling in thin vs. thick phloem. Egg density can be considered as a measure of reproductive efficiency, demonstrating how much energy is extracted from host tissues and converted to eggs for each length of gallery constructed. For example, Haack et al. (1984a) noted that egg density increased in thick phloem and decreased in thin phloem for individual adult females when switched between thick and thin phloem at 3-day intervals. Similarly, Popp et al. (1989) noted that egg density decreased with increasing adult size when adults tunneled only in thin phloem. Adjusting egg density to local conditions of food quality or quantity should allow for relatively high brood survival over a range of food resource conditions. Such relationships have been reported for bark beetles (Amman 1972, Haack et al. 1987a).

Lower reproductive success in jack pine, as well as longer initial and terminal egg-free zones in jack pine, provides evidence that the jack pine bolts in our study were of lower quality than the other three pine species tested. The poorer performance on jack pine was likely related to the relatively thin phloem of the bolts we used, considering that performance on jack pine in other studies was similar to that on red pine or Scots pine (Långström et al. 1995, Ryall and Smith 2000, Siegert and McCullough 2003). Even after adjusting for phloem thickness with ANCOVA, brood density in our study was still highest in red pine and lowest in jack pine, suggesting that red pine was superior over jack pine as a host for *T. piniperda*. However, given that the relationship between increasing phloem thickness and increasing bark beetle egg-density is curvilinear rather than linear (Haack et al 1984b), ANCOVA cannot be expected to equalize all the factors that influence brood density when phloem thickness varies from much thinner (0.4 mm) to much thicker (2.2 mm) than the width of the average adult (1.4 mm).

In retrospect, we should have selected trees with phloem that was very similar in thickness, or thicker than the width of the adult beetles to be tested. These observations indicate the importance of considering phloem thickness when conducting studies with bark beetles, especially studies that measure beetle performance among several host species. In field studies that have evaluated *T. piniperda* host suitability, as evidenced by variation in attack density (No. egg galleries per unit area of bark), Scots pine was typically the most preferred species, red and jack pine were intermediate, and white pine the least preferred (Långström et al. 1995, Haack and Lawrence 1997, Ryall and Smith 2000, Siegert and McCullough 2003). Phloem thickness was not reported in any of the above field studies, and therefore we do not know to what degree host selection and subsequent colonization were influenced by variation in phloem thickness. Others have reported that bark beetle attack-density increases with increasing phloem thickness (Amman and Pace 1976, Haack et al. 1987b, Reid and Glubish. 2001).

Nevertheless, one important finding from our study was that *T. piniperda* successfully reproduced and developed in all four pine species tested in this study. Given that *T. piniperda* has successfully colonized and reproduced in all North American pines tested so far in both North America and Europe (where many North American pines have been planted), it is highly likely that *T. piniperda* will establish itself successfully throughout North America as it continues to expand its geographic range.

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LITERATURE CITED

- Amezaga, I. 1996. Monterrey pine (*Pinus radiata* D. Don) suitability for the pine shoot beetle (*Tomicus piniperda* L.) (Coleoptera: Scolytidae). For. Ecol. Manag. 86: 73-79.
- Amman, G. D. 1972. Some factors affecting oviposition behavior of the mountain pine beetle. Environ. Entomol. 1: 691-695.
- Amman, G. D., and V. E. Pace. 1976. Optimum egg gallery densities for the mountain pine beetle in relation to lodgepole pine phloem thickness. USDA Forest Service, Intermountain For. Range Exp. Sta., Research Note INT-209.

- Bakke, A. 1968. Ecological studies on bark beetles (Coleoptera: Scolytidae) associated with Scots pine (*Pinus sylvestris*) in Norway with particular reference to the influence of temperature. Medd. Nor. Skogforsok. 21: 443-602.
- Borden, J. H., and C. E. Slater. 1969. Flight muscle volume change in *Ips confusus* (Coleoptera: Scolytidae). Can. J. Zool. 47: 29-32.
- Brattli, J. G., J. Andersen, and A. C. Nilssen. 1998. Primary attraction and host tree selection in deciduous and conifer living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. J. Appl. Entomol. 122: 345-352.
- Byers J. A., B. S. Lanne, J. Löfqvist, F. Schlyter, and G. Bergström. 1985. Olfactory recognition of host-tree susceptibility by pine shoot beetles. Naturwissenschaften 72: 324-326.
- Eager, T.A., C. W. Berisford, M. J. Dalusky, D. G. Nielson, J. W. Brewer, S. J. Hilty, and R. A. Haack. 2004. Suitability of some southern and western pines as hosts for the pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae). J. Econ. Entomol. 97: 460-467.
- Franklin, R. T. 1970. Observations on the blue stain-southern pine beetle relationship. J. Georgia Entomol. Soc. 5: 53-57.
- Gouger, R. J., W. C. Yearian, and R. C. Wilkinson. 1975. Feeding and reproduction behavior of *Ips avulsus*. Fla. Entomol. 58: 221-229.
- Haack, R.A. 2006. Exotic bark- and wood-boring Coleoptera in the United States: recent establishments and interceptions. Can. J. For. Res. 36: 269-288.
- Haack, R. A., and R. K. Lawrence. 1995a. Attack densities of *Tomicus piniperda* and *Ips pini* (Coleoptera: Scolytidae) on Scotch pine logs in Michigan in relation to felling date. J. Entomol. Sci. 30: 18-28.
- Haack, R. A., and R. K. Lawrence. 1995b. Spring flight of *Tomicus piniperda* in relation to native Michigan pine bark beetles and their associated predators, pp. 524-535. In F. P. Hain, S. M. Salom, W. F. Ravlin, T. L. Payne and K. F. Raffa (eds.), Behavior, population dynamics and control of forest insects, Proc. of the Joint IUFR Conf. For Working Parties S2.07-05 and S2.07-06, 6-11 February 1994, Maui, HI. Ohio State University, Wooster, OH.
- Haack, R. A., and R. K. Lawrence. 1997. Highlights of Forest Service research on *Tomicus piniperda*: 1992-1996, pp. 111-118. In 1997 Japanese beetle and the pine shoot beetle regulatory review: Proceedings, 24-26 February 1997, Louisville, KY. USDA APHIS, Riverdale, MD.
- Haack, R. A., and T. M. Poland. 2001. Evolving management strategies for a recently discovered exotic forest pest: the pine shoot beetle, *Tomicus piniperda* (Coleoptera). Biol. Invasions 3: 307-322.
- Haack, R. A., and F. Slansky. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera, and Hymenoptera, pp. 449-486. In F. Slansky and J. G. Rodriguez (eds.), Nutritional Ecology of Insects, Mites, and Spiders. John Wiley, New York, NY.
- Haack, R. A., J. L. Foltz, and R. C. Wilkinson. 1984a. Longevity and fecundity of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness. Ann. Entomol. Soc. Am. 77: 657-662.
- Haack, R. A., R. C. Wilkinson, J. L. Foltz, and J. A. Corneil. 1984b. Gallery construction and oviposition by *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness and temperature. Can. Entomol. 116: 625-632.
- Haack, R. A., R. C. Wilkinson, and J. L. Foltz. 1987a. Plasticity in life-history traits of the bark beetle *Ips calligraphus* as influenced by phloem thickness. Oecologia 72: 32-38.

- Haack, R. A., R. C. Wilkinson, J. L. Foltz, and J. A. Corneil. 1987b. Spatial attack pattern, reproduction, and brood development of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness: a field study. *Environ. Entomol.* 16: 428-436.
- Haack, R. A., R. K. Lawrence, and G. C. Heaton. 2000. Seasonal shoot-feeding by *Tomicus piniperda* (Coleoptera: Scolytidae) in Michigan. *Great Lakes Entomol.* 33: 1-8.
- Haack, R. A., R. K. Lawrence, and G. C. Heaton. 2001. *Tomicus piniperda* (Coleoptera: Scolytidae) shoot-feeding characteristics and overwintering behavior in Scotch pine Christmas trees. *J. Econ. Entomol.* 94: 422-429.
- Hui, Y., and F. Lieutier. 1997. Shoot aggregation by *Tomicus piniperda* L. (Col.: Scolytidae) in Yunnan, southwestern China. *Ann. Sci. For.* 54: 635-641.
- Kaplan, M., and T. Mokrzycki. 1988. A contribution to the knowledge of the occurrence of the pine shoot beetles *Tomicus minor* and *Tomicus piniperda* in Scots pine thickets in Niedzwiady forest district. *Sylvan* 132: 35-39.
- Långström, B. 1983. Life cycles and shoot-feeding of the pine shoot beetles. *Stud. For. Suec.* 163: 1-29.
- Långström, B., F. Lieutier, C. Hellqvist, and G. Vouland. 1995. North American pines as hosts for *Tomicus piniperda* (L.) (Col., Scolytidae) in France and Sweden, pp. 547-553. *In:* F. P. Hain, S. M. Salom, W. F. Ravlin, T. L. Payne and K. F. Raffa (eds.), Behavior, population dynamics and control of forest insects, Proc. of the Joint IUFRO Conf. For Working Parties S2.07-05 and S2.07-06, 6-11 February 1994, Maui, HI. Ohio State University, Wooster, OH.
- Långström, B., E. Annala, M. Varama, and P. Niemelä. 2001. Tree mortality, needle biomass recovery and growth losses in Scots pine following defoliation by *Diprion pini* and subsequent attack by *Tomicus piniperda*. *Scand. J. For. Res.* 16: 342-353.
- Lawrence R. K., and R. A. Haack. 1995. Susceptibility of selected species of North American pines to shoot-feeding by an Old World scolytid: *Tomicus piniperda*, pp. 536-546. *In* F. P. Hain, S. M. Salom, W. F. Ravlin, T. L. Payne and K. F. Raffa (eds.), Behavior, population dynamics and control of forest insects, Proc. of the Joint IUFRO Conf. For Working Parties S2.07-05 and S2.07-06, 6-11 February 1994, Maui, HI. Ohio State University, Wooster, OH.
- Morgan, R. E., P. de Groot, and S. M. Smith. 2004. Susceptibility of pine plantations to attack by the pine shoot beetle (*Tomicus piniperda*) in southern Ontario. *Can. J. For. Res.* 34: 2528-2540.
- Petrice, T. R., R. A. Haack, and T. M. Poland. 2002. Selection of overwintering sites by *Tomicus piniperda* (Coleoptera: Scolytidae) during fall shoot departure. *J. Entomol. Sci.* 37: 48-59.
- Poland, T. M., R. A. Haack, and T. R. Petrice. 2002. *Tomicus piniperda* (Coleoptera: Scolytidae) initial flight and shoot departure along a north-south gradient. *J. Econ. Entomol.* 95: 1195-1204.
- Poland, T. M., P. de Groot, S. Burke, D. Wakarshuk, R. A. Haack, R. Nott, and T. Scarr. 2003. Development of a new operational lure for the pine shoot beetle, *Tomicus piniperda* (Coleoptera: Scolytidae). *Agric. For. Entomol.* 5: 293-300.
- Popp, M. P., R. C. Wilkinson, E. J. Jokela, R. B. Harding, and T. W. Phillips. 1989. Effects of slash pine phloem nutrition on the reproductive performance of *Ips calligraphus* (Coleoptera: Scolytidae). *Environ. Entomol.* 18: 795-799.
- Reid, M. L., and S. S. Glubish. 2001. Tree size and growth history predict breeding densities of Douglas-fir beetles in fallen trees. *Can. Entomol.* 133: 697-704.

- Reid, R. W. 1958. Internal changes in the female mountain pine beetle, *Dendroctonus monticolae* Hopk., associated with egg laying and flight. Can. Entomol. 90: 464-468.
- Ryall, K. L., and S. M. Smith. 2000. Reproductive success of the introduced pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera, Scolytidae) on selected North American and European conifers. Proc. Entomol. Soc. Ontario. 131: 113-121.
- Sadof, C. S., R. D. Waltz, and C. D. Kellam. 1994. Differential shoot feeding by adult *Tomicus piniperda* (Coleoptera: Scolytidae) in mixed stands of native and introduced pines in Indiana. Great Lakes Entomol. 27: 223-228.
- Salonen, K. 1973. On the life cycle, especially on the reproductive biology of *Blastophagus piniperda* L. (Col., Scolytidae). Acta For. Fennica 127: 1-72.
- Sauvard, D. 1993. Reproductive capacity of *Tomicus piniperda*. 2. Analysis of the various sister broods. J. Appl. Entomol. 116: 25-38.
- Schmitz, R. F. 1972. Behavior of *Ips pini* during mating, oviposition, and larval development (Coleoptera: Scolytidae). Can. Entomol. 104: 1723-1728.
- Siebert, N. W., and D. G. McCullough. 2001a. Preference of *Tomicus piniperda* (Coleoptera: Scolytidae) parent adults and shoot-feeding progeny adults for three pine species. Can. Entomol. 133: 343-353.
- Siebert, N. W., and D. G. McCullough. 2001b. Survey of shoot damage caused by the exotic pine shoot beetle in Michigan pine stands. N. J. Appl. For. 18: 101-109.
- Siebert, N. W., and D. G. McCullough. 2003. Colonization of Scots, red and jack pine logs by *Tomicus piniperda* (L.) (Coleoptera: Scolytidae) in Michigan pine stands. Can. J. For. Res. 33: 2238-2244.
- Slansky, F., and R. A. Haack. 1986. Age-specific flight behavior in relation to body weight and lipid content of *Ips calligraphus* (Coleoptera: Scolytidae) reared in slash pine bolts with thick or thin phloem. Entomol. Exp. Appl. 40: 197-207.
- Stark, R. W. 1982. Generalized ecology and life cycles of bark beetles, Pp. 21-45. In J. B. Mitton and K. B. Sturgeon (eds.), Bark Beetles in North American Conifers. Univ. Texas Press, Austin, TX.
- Statistix. 2003. Statistix 8 User's Manual. Analytical Software, Tallahassee, FL.
- Wagner, T. L., W. S. Fargo, L. L. Keeley, R. N. Coulson, and J. D. Cover. 1982. Effect of sequential attack on gallery construction, oviposition, and reemergence by *Dendroctonus frontalis* (Coleoptera: Scolytidae). Can. Entomol. 114: 491-502.
- Ye, H. 1991. On the bionomy of *Tomicus piniperda* (L.) (Col., Scolytidae) in the Kunming region of China. J. Appl. Entomol. 112: 366-369.
- Ye, H. 1996. Studies on the biology of *Tomicus piniperda* (L.) (Col., Scolytidae) in the shoot feeding period. Acta Entomol. Sinica 39: 58-62.
- Ye, H., and C. L. Dang. 1986. Studies on damages of *Tomicus piniperda* (L.) (Col., Scolytidae) to Yunnan pine (*Pinus yunnanensis*) trees. J. Yunnan Univ. 8:218-222.
- Ye, H., R. A. Haack, and T. R. Petrice. 2002. *Tomicus piniperda* (Col., Scolytidae) within and between tree movement when migrating to overwintering sites. Great Lakes Entomol. 35: 183-192.
- Yearian, W. C., R. J. Gouger, and R. C. Wilkinson. 1972. Effects of the bluestain fungus, *Ceratocystis ips*, on development of *Ips* bark beetles in pine bolts. Ann. Entomol. Soc. Amer. 65: 481-487.