REPRODUCTIVE SUCCESS OF THE INTRODUCED PINE SHOOT BEETLE, *TOMICUS PINIPERDA* (L.) (COLEOPTERA, SCOLYTIDAE) ON SELECTED NORTH AMERICAN AND EUROPEAN CONIFERS

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Abstract *Proc. ent. Soc. Ont.* 131: 113–121

The introduced pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera, Scolytidae), constitutes a potential threat to commercially important native conifer species. Reproductive success of the beetle was compared between its primary host, Scots pine (*Pinus sylvestris* L.), three native pines, specifically jack (*P. banksiana* Lamb.), red (*P. resinosa* Ait.), and white pine (*P. strobus* L.), and two larch species, eastern larch (*Larix laricina* (Du Roi) K. Koch) and European larch (*L. decidua* Mill.) using naturally infested trap logs during 1997 and 1998. No female beetles initiated galleries on either larch species. In contrast, red and jack pine were readily colonized by the parental generation and produced large numbers of offspring. Greater numbers of beetles were produced per m^2 (mean ± S.E.) on red pine (733.2 ± 29.1 and 1410.9 ± 49.8 offspring per m^2) than on Scots pine (240.1 ± 56.8 and 597.8 ± 570.7 offspring per m^2) in 1997 and 1998, respectively. White pine was colonized by significantly fewer female beetles (110.5 ± 28.6 galleries per m^2) than was Scots pine (276.3 ± 16.2 galleries per m^2), and low numbers of offspring were produced per m^2 on white pine (139.0 ± 41.6 offspring per m^2), suggesting that this pine is less well suited for reproduction. Beetle emergence per gallery was high on red pine (4.4 ± 1.2 and 19.2 ± 1.9 emergence holes/gallery in 1997 and 1998, respectively) and jack pine (1.9 ± 0.3 and 19.9 ± 6.5 in 1997 and 1998, respectively). Parasitism by native hymenopterans and predation by native dipterans differed significantly between the four pine species, with high parasitism levels on jack pine in both years (25.3 and 14.9% in 1997 and 1998, respectively) and very low levels on red pine (less than 2% in both years). Our work shows that *T. piniperda* readily colonizes at least two native pine species and that these hosts can support the production of a large number of offspring beetles, thus confirming previous North American and European research. These results highlight the potential impact of this exotic beetle on the future management of red and jack pine stands.

Introduction

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera, Scolytidae), was discovered in North America during 1992 (Haack and Kucera 1993). It has since been found in 11 north-central and north-eastern states of the United States (National Agricultural Pest Information Service (NAPIS) 2000), in 32 counties in the Great Lakes region of Ontario and in Quebec (Canadian

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Food Inspection Agency (CFIA) 2000). Across its widespread range, this beetle is often considered a pest of major economic importance. In both China (Ye 1991) and Sweden (Långström and Hellqvist 1990), *T. piniperda* has been associated with serious economic damage. Considerable tree mortality has been attributed to *T. piniperda* in central France (Levieux et al. 1985), Portugal (Ferreira and Ferreira 1986), and Italy (Triggiani 1984). While the primary host of this species in Europe is Scots pine (*Pinus sylvestris* L.), the beetle also attacks numerous other pine species over its range (Ferreira and Ferreira 1986; Ye 1991; Långström et al. 1995; Haack and Lawrence 1997).

The new range of the pine shoot beetle in southern Ontario contains its primary host (Scots pine), as well as a number of native species of *Pinus*. A study in Indiana near the Lake Michigan shoreline found *T. piniperda* adults to be feeding on shoots of red (*P. resinosa* Ait.), white (*P. strobus* L.), and jack pine (*P. banksiana* Lamb.), although a preference for red and Scots pine was apparent (Sadof et al. 1995). In addition, successful reproduction by this species has been observed on numerous pine species in the United States, including red, white, and jack pine (Lawrence and Haack 1995; Haack and Lawrence 1997). In France, Långström et al. (1995) found that *T. piniperda* would readily infest jack pine but not red or white pine. In Ontario, all three pines (red, white, and jack) are considered to be economically important timber species. The susceptibility of and threat to these valuable species is thus of concern. One objective of our paper, therefore, was to assess the ability of this exotic species to reproduce on red, jack, and white pine in Ontario. Colonization by female beetles (gallery density) and production of offspring, both per m^2 (brood production) and per gallery (gallery production), were quantified and compared between the various host species. In addition, other conifers, such as larch (*Larix*), spruce (*Picea*) and fir (*Abies*) are reported as occasional hosts for this beetle in Britain and Europe (Speight 1980; Lutyk 1984). In North America, the ability of the pine shoot beetle to reproduce on non-pine hosts is poorly understood; hence, we also tested two species of larch, eastern larch (*Larix laricina* (Du Roi) K. Koch) and European larch (*L. decidua* Mill.) to determine if they were acceptable hosts.

The rate of increase in the size of *T. piniperda* populations will be, in part, determined by the ability of the beetle to utilize new host species. Population dynamics of this beetle will also be impacted by changes in the level of mortality caused by natural enemies associated with these different host trees. Little is known about how natural enemies native to North America will respond to this introduced pest. Tree species have been cited as important influences of parasitoid abundance (Berisford et al. 1970; Berisford and Franklin 1972; Ball and Dahlsten 1973; Lawson et al. 1996), with observations that beetle broods developing on one host can be heavily attacked by a number of parasitoids, while broods on another host species escape or suffer only minor parasitism (i.e., by a few species). Hence, the second objective of our study was to evaluate the influence of the host pine species on the level of parasitism and predation in *T. piniperda* to improve our understanding about the potential mortality on and ultimate impact of this introduced pest on native pines.

Materials and Methods

Study site: Field research was conducted between March and July 1997 in a 40-year-old Scots pine stand south of Guelph, Ontario (43° N, 80.2° W) and between March and July 1998 in a red pine stand located near Elora, Ontario (43.5° N, 80.6° W). Both stands had established populations of *T. piniperda* based on evidence of shoot-feeding and breeding in standing trees. Trees of each of the four species (red, jack, white and Scots pine) in 1997 and five species (red, jack, and Scots pine, eastern and European larch) in 1998 were cut from a nearby 30 to 40-year-old stand that contained all species growing in close proximity to minimize variability in the conditions the trees were growing in.

Reproduction and Natural Enemies: In mid-March 1997 before the main spring flight of this species (early April in southern Ontario (Ryall and Smith 2000)), trees were felled and cut to obtain five sections, approximately 0.75 m in length, of each of four pines; jack, red, Scots and white. Again in mid-March 1998, three logs each of jack, red, and Scots pine and of eastern and European larch were cut. Only logs with rough bark from the lower section of the bole were selected, as it is known that *T. piniperda* prefers these regions for reproduction (Långström 1984). Log diameter ranged from 18 to 22 cm. Five plots of four logs (one log of each pine species) were placed on the ground in the infested site at least 20 m apart from each other, with only the first plot less than 10 m from a forest edge (a side road) in 1997. In 1998, three plots of five logs (one log of each conifer species) were placed in the stand. Within each plot, logs were arranged randomly (different species beside each other) in an "X" or "star" pattern with approximately 50 cm between each log.

Immediately after the first exit holes were visible in both years (early July (Ryall and Smith 2000)), all logs were brought back to the laboratory. The logs were placed in rearing cages covered with a fine mesh lid (0.5 × 0.5 mm) and all emergent adults as well as natural enemies were collected at 2- to 3-day intervals. Once the majority of adult emergence had occurred for each individual log, a 20-cm band (approximately one-third of the log surface area) was dissected down the length of the log (corresponding to the top of the log) and the following measurements were recorded: log length, log diameter, number of exit holes, number of galleries, number of *T. piniperda* larvae, pupae, and teneral adults, and number of natural enemy larvae and pupae, if any. All adult natural enemies were identified to species and sex by experts at the Royal Ontario Museum. Very small numbers of *Ips pini*, *Hylastes* sp., and *Hylurgops* sp. were also observed in the logs, but these were not considered further here.

Gallery density was calculated for each log as the number of *T. piniperda* galleries per square metre of bark surface area. Brood production for each log was calculated as the number of exit holes produced per square metre of bark surface area plus the number of pupae or teneral adults still remaining under the bark per square metre at the time of log dissection, which was typically very low. Few late instar larvae were typically observed under the bark at the time of log dissection and most larvae present could be attributed to galleries of other bark beetle species; hence, these were not included in the total *T. piniperda* production calculation. Measuring exit holes, and not adult offspring directly, tends to underestimate the population by approximately 10% because some holes are not visible and because a small number of beetles emerge through previously-cut holes (Salonen 1973). Gallery production (no. new beetles/gallery) was approximated by dividing brood production by gallery density for each log sample. Finally, percentage parasitism or predation was calculated by dividing the number of natural enemies produced by the sum of the number of new beetles plus the number of natural enemies for each log sample.

Statistical analyses: Differences in mean gallery density, mean brood production, and mean gallery production were compared between the different pine species using a one-way ANOVA for each year, followed by a Tukey's test for means separation (Zar 1984). Values for percentage parasitism or predation were arcsine transformed to normalize the data (Zar 1984), and then differences in these transformed percentage values were compared using a one-way ANOVA by year, followed by a Tukey's test for means separation (Zar 1984). All analyses were done using SYSTAT Version 5.05 (SYSTAT Inc., Evanston, IL).

Results

The pine shoot beetle preferentially selected red, jack, and Scots pine over white pine as hosts for gallery construction in 1997 ($F_{3,16} = 4.94$, $p = 0.01$) (Table I). White pine had significantly

TABLE I. Mean gallery density, offspring production (exit holes), and percentage parasitism and predation of *Tomicus piniperda* in naturally-infested trap logs of various conifer species during 1997 and 1998 (n = 5 logs/species in 1997 and 3 logs in 1998).

Year	Conifer	Mean gallery density ± SE (no./m^2)	Mean production (no. exit holes) ± SE /m^2	Mean production (no. exit holes) ± SE /gallery	Mean % parasitism and predation ± SE
1997	Jack pine	198.4 ± 24.9 ab[1]	329.5 ± 32.3 b	1.9 ± 0.3 ab	25.3 ± 10.1 a
	Red pine	204.8 ± 40.1 ab	733.2 ± 29.1 a	4.4 ± 1.2 a	0.9 ± 0.6 b
	Scots pine	276.3 ± 16.2 a	240.1 ± 56.8 bc	0.9 ± 0.3 b	4.6 ± 2.8 ab
	White pine	110.5 ± 28.6 b	139.0 ± 41.6 c	1.2 ± 0.2 b	6.3 ± 3.9 ab
1998	Jack pine	78.2 ± 24.1 a	1317.7 ± 355.4 a	19.9 ± 6.5 a	15.0 ± 10.5 a
	Red pine	75.3 ± 9.4 a	1410.9 ± 49.8 a	19.2 ± 1.9 a	1.5 ± 0.6 a
	Scots pine	71.9 ± 42.0 a	597.8 ± 570.7 a	9.1 ± 4.4 a	5.7 ± 2.7 a
	Eastern larch	0	-	-	-
	European larch	0	-	-	-

[1]Means followed by the same letter within each column and year are not significantly different at $p<0.05$ (Tukey's test for means separation).

fewer galleries per m^2 than Scots pine ($p = 0.008$). Again in 1998, red and jack pine had a similar number of galleries per m^2 as Scots pine ($F_{2,6} = 0.012$, $p = 0.988$). There was no evidence that female *T. piniperda* used either larch species for gallery construction in 1998; hence these two conifers were excluded from further analysis.

The reproductive success of *T. piniperda* varied among the different host tree species. Production (no. exit holes by offspring beetle/m^2), although highly variable (Table I), differed significantly between the four species in 1997 ($F_{3,16} = 39.2$, $p = 0.0001$). Significantly more beetles were produced on red pine than on jack pine ($p = 0.0001$), Scots pine ($p = 0.001$) or white pine ($p = 0.001$) in 1997. In addition, jack pine produced more beetles than white pine ($p = 0.03$). However, production did not differ significantly between the three pine species in 1998 ($F_{2,6} = 1.3$, $p = 0.34$), likely a function of the small sample size in that year.

The production of new beetles per gallery (no. exit holes/m^2 divided by no. galleries/m^2), as an indication of increasing or decreasing population size, was highly variable but differed between the four species in 1997 ($F_{3,16} = 5.3$, $p = 0.01$) (Table I). Red pine was the source of more new beetles per gallery than Scots pine ($p = 0.012$) or white pine ($p = 0.02$) in 1997. However, production per gallery did not differ significantly between the three pine species in 1998 ($F_{2,6} = 1.2$, $p = 0.36$).

Three species of hymenopteran parasitoids were reared from logs infested by *T. piniperda* in 1997. The most common parasitoid was a pteromalid, *Rhopalicus tutela* Foerster, found on all four species of pine. This was the only parasitoid species found in association with white pine. The second most common species was another pteromalid, *Dinotiscus dendroctoni* (Ashmead), which was found only in association with jack pine. Small numbers of a braconid, *Spathius* sp., were also reared from jack and red pine. In 1998, small numbers of one additional parasitoid and two predators were reared from the logs infested with *T. piniperda*. The first was a second species of *Rhopalicus*, namely, *R. pulchripennis* (Crawford), represented by only two specimens. The other two natural enemies were dipteran predators, the dolicopodid, *Medetera* spp., and the lonchaeid, *Lonchaea* spp. Overall parasitism and predation levels of *T. piniperda* were highly variable but differed significantly between the pine species in 1997 ($F_{3,16} = 3.95$, $p = 0.030$) (Table I). Significantly higher percentage parasitism and predation was observed on jack pine than on red pine ($p = 0.023$). In 1998, overall parasitism and predation levels followed the same trend, but were not significantly different between the three pine species ($F_{2,6} = 3.885$, $p = 0.083$).

Discussion

Female *T. piniperda* readily colonized trap logs of native jack and red pine, confirming that these species are hosts for the beetle. Indeed, the pine shoot beetle has been reported feeding naturally on the shoots of both red and jack pine in Michigan (Sadof et al. 1995). We corroborated the findings of Långström et al. (1996) that white pine was colonized by fewer female *T. piniperda* than Scots pine. Previous reports have shown that the density of female *T. piniperda* galleries on various pine hosts can be highly variable, ranging from 25–300 (1986), to 83–220 galleries/m^2 (Ryall and Smith 1997), to 262 galleries/m^2 (Haack and Lawrence 1995), to a maximum of 497 galleries/m^2 (Långström and Hellqvist 1993). Thus, actual gallery density is probably less informative, in terms of potential host species, as is the presence or absence of successful brood production. Based on these results, all three of these native North American pine species are acceptable for infestation, as the female beetles readily colonized the logs. Thus, our results confirm those of previous North American and European research into the acceptability of these North American pine species as hosts from *T. piniperda* (Lawrence and Haack 1995; Haack and Lawrence 1997), except that red pine was not infested by *T. piniperda* in a French study (Långström et al. 1995). The two larch species appear to be not acceptable to the colonizing female *T. piniperda* in this study, even though European larch has been reported as a host of *T. piniperda* in Britain (Speight 1980). The authors caution that the intent of this study was not to look specifically at host preference by this beetle; instead our research was more focused on examining the reproductive success of the beetle on different conifer hosts. Future research should continue to study the preference and ability of this beetle to reproduce on native conifers, including species belonging to the genera *Picea* and *Abies*.

Relatively few beetles emerged from galleries initiated on Scots pine in 1997, given that Scots pine is the primary host of this species and that previous reports and data from 1998 show production numbers ranging from 600–1200 beetles/m^2 (Långström 1984; Heliovaara and Vaisanen 1991;Sauvard 1993; Ryall and Smith 1997). The reason for this is unknown, but may possibly be due to the quality of the tree that was utilized for trap logs. Successful brood development did occur on white pine, although with very low numbers of offspring beetles produced. However, both red and jack pine were the source of large numbers of emerging offspring beetles (particularly in 1998), again confirming that they are highly acceptable as hosts for brood production by *T. piniperda*. Hence, it would seem likely that the beetle's population size and range will continue to expand, based on the relative abundance of these two pine species in Ontario.

Annila and Heikkila (1991) reported that *T. piniperda* produced between 3–6 new adults per gallery on Scots pine. Similarly, Heliovaara and Vaisanen (1991) found an average of 6.4 new adults per gallery while Ryall and Smith (1997) reported between 5–11 new adults per gallery, depending on gallery density. Salonen (1973) found that approximately 10 beetles/gallery were produced at a density of 200–300 galleries per m^2. Based on these reports, our work suggests that red and jack pine are both particularly suitable for colonization and production by the pine shoot beetle. In fact, we found an unusually high number of beetles emerging from each gallery on both red and jack pine (close to 20 beetles/gallery) during 1998. This is likely due to the low gallery density in this year, which would have reduced intraspecific competition for food resources among the developing larvae (Salonen 1973; Långström 1984; Sauvard 1993; Ryall and Smith 1997).

It is important to note the variation in mean gallery density and production of offspring (per m^2) between the two years studied. The number of *T. piniperda* galleries per m^2 was lower in 1998 than 1997, but there was higher production of offspring per m^2 in 1998 than in 1997. This could potentially be attributed to lower suitability of the logs in the first year studied or reduced competition among the larvae for food due to the lower attack density in 1998. In addition, trap logs were placed in different stands in the two years of the study, thus variation could represent differences between sites rather than year-to-year variation. Future research should continue to examine differences between sites and changes over time in the reproductive pattern by this exotic beetle on the various host pine species.

Most of the parasitoid and predator species reared in our study have been documented previously in association with *T. piniperda* and other scolytid species. Studies from Scots pine in Europe (Schroeder and Weslien 1994; Herard and Mercadier 1996) have reported *R. tutela* as one of the main parasitoids attacking *T. piniperda*, along with the braconid, *Spathius* spp. and the two dipteran predators. Similarly, in Bright's (1996) survey of a single *T. piniperda*-attacked Scots pine tree in the Niagara region of southwestern Ontario, he found all of the above species, as well as a number of other species. The main difference between our study and previous research is the lower numbers of parasitoid and predator species in our study. This may be due to the different orientation of the host pine (standing infested tree vs. horizontal trap logs on the ground), geographic location, or timing of log collection. It will be interesting to see whether this relatively low natural enemy diversity will increase over time as the beetle continues to establish in Canada. Future research will also examine the influence of the orientation of the brood material on the enemy complex abundance and diversity.

Parasitism of the developing bark beetle brood in our study was significantly influenced by the host pine species, and this is supported by other work with bark beetles. Both Ball and Dahlsten (1973) and Berisford et al. (1970) reported higher levels of parasitism and higher numbers of parasitoid species on *Ips* spp. in sugar pine (*Pinus lambertiana* Dougl.) than in other pine species. Unlike our study, where high numbers of parasitoids were observed on jack pine, Schenk and Benjamin (1969) reported no parasitoids from *I. pini* on jack pine in central Wisconsin. Similarly, Berisford et al. (1970) observed that *R. tutela* was one of the most common parasitoids on white pine infested with *I. pini* but was rarely recovered from loblolly pine. Finally, the parasitoid complex utilizing *I. typographus* Niijima in Japan was also significantly influenced by host conifer species (Lawson et al. 1996).

The proportionately higher numbers of parasitoids attacking *T. piniperda* on jack pine may help reduce or limit the damage caused by this pest to this economically important pine species. While the colonizing density of beetles was approximately equal on jack and red pine in 1997, the production of new beetles was approximately 50% lower on jack than on red pine. This may be due, in part, to the higher level of natural enemy-caused mortality on jack pine as opposed to the other species, however this trend was not apparent in the second year of study. The low levels of parasitism on red pine that we observed, combined with the very high production of new beetles, is cause for concern over the impact of this new pest on red pine stands. Our results highlight the importance of the plant host in terms of either detection or success of reproduction by the parasitoid complex. This may have important implications for the success of future biocontrol programs, whereby pest populations may escape control if they are colonizing hosts unsuitable to the natural enemy complex.

Our study has demonstrated the ability of this exotic beetle to successfully complete brood development on these new host pine species. Hence, populations could build up to very high levels if large volumes of non-resistant brood material are created in pine plantations through logging or thinning operations at inappropriate times. Forestry practices should be timed to ensure that large volumes of recently felled material are not present in red or jack pine stands in the early spring through to the early summer during the period of brood production by *T. piniperda*. However, infestation by this exotic beetle may still occur in weakened or stressed trees. Further research is necessary to determine the susceptibility of standing trees of the various pine species to infestation by this beetle and the subsequent action of natural enemies.

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References

Annila, E. and R. Heikkila. 1991. Breeding efficiency in *Tomicus piniperda* and shoot damage after late autumn thinning of young *Pinus sylvestris* stands. Scandinavian Journal of Forest Research, 6: 197–208.

Ball, J.C. and D.L. Dahlsten. 1973. Hymenopterous parasites of *Ips paraconfusus* (Coleoptera: Scolytidae) larvae and their contribution to mortality. I. Influence of host tree and tree diameter on parasitization. The Canadian Entomologist, 105: 1453–1464.

Berisford, C.W. and R.T. Franklin. 1972. Tree host influence on some parasites of *Ips* spp. bark beetles (Coleoptera: Scolytidae) on four species of southern pines. Journal of the Georgia Entomological Society, 7: 110–115.

Berisford, C.W., H.M. Kulman and R.L. Pienkowski. 1970. Notes on the biologies of hymenopterous parasites of *Ips* spp. bark beetles in Virginia. The Canadian Entomologist, 102: 484–490.

Bright, D.E. 1996. Notes on native parasitoids and predators of the larger pine shoot beetle, *Tomicus piniperda* (Linnaeus) in the Niagara region of Canada (Coleoptera: Scolytidae). Proceedings of the Entomological Society of Ontario, 127: 57–62.

Canadian Food Inspection Agency (CFIA). 2000. Plant protection requirements on pine plants and pine materials to prevent the entry and spread of pine shoot beetle. http://www.cfia~acia.agr.ca/english/plaveg/protect/dir/d-94-22e.shtml.

Ferriera, M.C. and G.W.S. Ferriera. 1986. Pest of maritime pine in Portugal – scolytids. Boletim-Agricola, 36: 4 pages.

Haack, R.A. and D. Kucera. 1993. New introduction – Common Pine Shoot Beetle, *Tomicus piniperda* (L.). USDA Forest Service, Northeastern Area. Pest Alert NA-TP-05-93. 2 pp.

Haack, R.A. and R.K. Lawrence. 1995. Attack densities of *Tomicus piniperda* and *Ips pini* (Coleoptera: Scolytidae) on Scotch pine logs in Michigan in relation to felling date. Journal of Entomological Science, 30: 18–28.

Haack, R.A. and R.K. Lawrence. 1997. Highlights of Forest Service research on *Tomicus piniperda*: 1992-1996. pp. 115–122 *In* Japanese beetle and pine shoot beetle regulatory review: Proceedings, Louisville, Kentucky, 24–26 February 1997. USDA APHIS, Riverdale, Maryland. 212 pp.

Heliovaara, K. and R. Vaisanen. 1991. Bark beetles and associated species with heavy metal tolerance. Journal of Applied Entomology, 111: 397–405.

Herard, F. and G. Mercadier. 1996. Natural enemies of *Tomicus piniperda* and *Ips acuminatus* (Col., Scolytidae) on *Pinus sylvestris* near Orleans, France: Temporal occurrence and relative abundance, and notes on eight predatory species. Entomophaga, 41: 183–210.

Långström, B. 1984. Windthrown pines as brood material for *Tomicus piniperda* and *Tomicus minor*. Silva Fennica, 18: 187–198.

Långström, B. and C. Hellqvist. 1990. Spatial distribution of crown damage and growth losses caused by recurrent attacks of pine shoot beetles in pine stands surrounding a pulp mill in southern Sweden. Journal of Applied Entomology, 110: 261–269.

Långström, B. and C. Hellqvist. 1993. Induced and spontaneous attacks by pine shoot beetles on young Scots pine trees: tree mortality and beetle performance. Journal of Applied Entomology, 115: 25–36.

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. 537–557 *In* F.P. Hain, S.M. Salom, W.F. Ravlin, T.L. Paine and K.F. Raffa (eds.) Behavior, population dynamics and control of forest insects, Proceedings of the joint IUFRO conference for Working Parties S2.07-05 and S2.07-06, Maui, Hawaii, 6–11 February 1994. Ohio State University, Wooster, Ohio. 644 pp.

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. Paine and K.F. Raffa (eds.) Behavior, population dynamics and control of forest insects, Proceedings of the joint IUFRO conference for Working Parties S2.07-05 and S2.07-06, Maui, Hawaii, 6–11 February 1994. Ohio State University, Wooster, Ohio. 644 pp.

Lawson, S.A., K. Furuta and K. Katagiri. 1996. The effect of host tree on the natural enemy complex of *Ips typographus japonicus* Niijima (Col., Scolytidae) in Hokkaido, Japan. Journal of Applied Entomology, 120: 77–86.

Levieux, J., F. Lieutier, and A. Delplanque. 1985. Scolytid pests of Scots pine. Revue Forestiere Francaise, 37: 431–440.

Lutyk, P. 1984. Feeding of *Tomicus piniperda* on shoots of Norway spruce and silver fir. Sylwan, 128: 65–68.

National Agricultural Pest Information System (NAPIS). 2000. Co-operative agricultural pest survey and NAPIS's page on pine shoot beetle, *Tomicus piniperda*. http://www.ceris.perdue.edu/napis/pests/psb/

Ryall, K.L. and S.M. Smith. 1997. Intraspecific larval competition and brood production in *Tomicus piniperda* (L.) (Col., Curculionidae, Scolytinae). Proceedings of the Entomological Society of Ontario, 128: 19–26.

Ryall, K.L. and S.M. Smith. 2000. Brood production and shoot-feeding by *Tomicus piniperda* (Coleoptera, Scolytidae). The Canadian Entomologist, 132: 939–949.

Sadof, C.S., R.D. Waltz and C.D. Kellam. 1995. Differential shoot feeding by adult *Tomicus piniperda* (Coleoptera: Scolytidae) in mixed stands of native and introduced pines in Indiana. Great Lakes Entomologist, 27: 223–228.

Salonen, K. 1973. On the life cycle, especially on the reproduction biology, of *Blastophagus piniperda* (Col., Scolytidae). Acta Forestalia Fennica, 127: 1–71.

Sauvard, D. 1993. Reproductive capacity of *Tomicus piniperda* L. (Col., Scolytidae). Journal of Applied Entomology, 116: 25–38.

Schenk, J.A. and D.M. Benjamin. 1969. Notes on the biology of *Ips pini* in central Wisconsin jack pine forests. Annals of the Entomological Society of America, 62: 480–485.

Schroeder, L.M. and J. Weslien. 1994. Reduced offspring production in bark beetle *Tomicus piniperda* in pine bolts baited with ethanol and α-pinene, which attract antagonistic insects. Journal of Chemical Ecology, 20: 1429–1444.

Speight, M.R. 1980. Tree Pests. 2. Sycamore aphid, *Drepanosiphum platanoides* Koch. 3. Common pine shoot beetle, *Tomicus piniperda* Linnaeus. Arboricultural Journal, 4: 32–33, 157–160.

Triggiani, O. 1984. *Tomicus piniperda* L. (Coleoptera, Scolytidae, Hylesininae): Biology, damage, and control in the Ionic coast (Italy). Entomologica (Bari), 19: 5–22.

Ye, H. 1991. On the bionomy of *Tomicus piniperda* (L.) (Coleoptera, Scolytidae) in the Kunming region of China. Journal of Applied Entomology, 112: 366–369.

Zar, J.H. 1984. Biostatistical Analysis. Second Edition. Prentice-Hall Canada, Inc. Toronto. 718 pp.

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