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INTRASPECIFIC LARVAL COMPETITION AND BROOD PRODUCTION IN *TOMICUS PINIPERDA* (L.) (COL., CURCULIONIDAE, SCOLYTINAE)

K.L. RYALL¹ and S.M. SMITH²

University of Toronto, Toronto, ON M5S 3B3 Canada

Abstract

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The pine shoot beetle, *Tomicus piniperda* (L.) (Col., Curculionidae, Scolytinae), is a pest recently introduced into Ontario, for which we have little information. The present study used naturally-infested trees (1995) and trap logs (1996) near Guelph, Ontario to examine larval competition and the establishment of successful galleries for this species. Gallery density (number of egg galleries per m² bark surface area) was highly variable but differed significantly between years. Mortality in the galleries was generally high, 50.6% in 1995 and 86.3% in 1996, suggestive of intense intraspecific competition. Significantly more new adults (11.6 vs. 5.1 beetles per gallery) were produced from each gallery at lower (83.3 galleries per m²) than at higher (220.9 galleries per m²) gallery densities. The number of beetles produced per gallery was inversely related to the density of galleries only at high gallery densities (1996). The number of beetles produced per square metre of bark was similar in both years, around 900 new beetles per m², despite variation in gallery density. Comparison of these results to those from its native range in Europe suggest that *T. piniperda* is reproducing successfully here and should continue to increase in size and range.

Introduction

The pine shoot beetle, *Tomicus piniperda* (L.) (Col., Curculionidae), 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 attacking several native pines, as well as its primary host, Scots pine (*Pinus sylvestris* (L.)) (Haack 1996). *T. piniperda* is a major pest of Scots pine in Europe, establishing galleries in weakened trees or freshly cut logs early in the spring (Långström and Hellqvist 1993). Appropriate brood material releases allelochemicals that attract the parental beetles that are emerging from overwintering (Tunset *et al.* 1993). Females construct the main gallery chambers, the larvae feed on the inner bark layer and then pupate in the bark. Infested brood material can produce large numbers of beetles that then feed on shoots in the tree crowns for about three months (Fagerström *et al.* 1977; Långström 1983). Unlike tree-killing bark beetle species, the majority of the damage and growth loss is caused by this maturation shoot feeding, and not by the reproductive phase of the beetle's life cycle.

Brood material is often limited and widely spaced, causing competition among the parental generation and, especially, among the developing larvae (Huffaker *et al.* 1984). The present paper

¹ Department of Zoology, University of Toronto, Toronto, ON Canada M5S 3B3. Telephone 416-978-0879; krista.ryall@utoronto.ca

² Faculty of Forestry, University of Toronto, Toronto, ON Canada M5S 3B3. Telephone 416-978-5482; fax 416-978-3834; smith@larva.forestry.utoronto.ca

examines the relationship between gallery density and beetle production per gallery and per unit area (brood production) to assess the level of intraspecific larval competition in *T. piniperda*. In addition, because such recently introduced species can reach high levels in the absence of mortality factors (Speight and Wainhouse 1989), the reproductive potential of these beetles was compared to that in Europe to predict how successful they may become in southern Ontario.

Materials and Methods

Study Sites. Reproduction of *T. piniperda* was studied during 1995 and 1996 in a 40-year-old Scots pine stand 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. This stand was originally planted for erosion control with variable spacing.

Gallery Measurements. In December 1995, six naturally-infested Scots pine trees were felled and cut into approximately 1-m logs. All logs (n=15) with rough corky bark from the lower portion of the tree were brought to the laboratory. The number of exit holes and number of galleries in a 20-cm band on each log was recorded. Gallery length and number of egg grooves per gallery were measured for a representative sub-sample of 91 galleries from the 15 logs.

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 3-4 logs each and left in the field for natural infestation by *T. piniperda*. In August 1996, after the beetles had completed development, six of these logs were brought to the laboratory and the number of exit holes and number of galleries in a 20-cm band on each log was recorded. Gallery length and number of egg grooves per gallery were then measured for a representative sub-sample of 25 galleries from the six logs.

Gallery density for both years was calculated as the number of galleries per square metre of bark surface area. Production of new adults per gallery, approximated as the number of exit holes per gallery, was calculated by dividing brood production (number of exit holes per square metre) by gallery density for each log sample. 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 the same holes (Salonen 1973). Total mortality from 1995 data could be approximated using the initial mean number of egg grooves per gallery (based on the representative sample of 91 galleries from the 15 logs) and the 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 the sub-sample of 25 galleries from the six logs. Total mortality for 1996 was calculated using the initial mean number of egg grooves per gallery (using the sub-sample) and the number of exit holes per gallery calculated for each of the six logs.

Statistical Analyses. Mean gallery length, gallery density, production per gallery and brood production were compared between the two years using a non-parametric Mann-Whitney test (Zar 1984). The relationship between production of new adults per gallery and gallery density, and between brood production and gallery density, were both examined using a Spearman rank order correlation coefficient (SAS: PROC RANK, Spearman) (Zar 1984).

Results and Discussion

Mean gallery length was not significantly different between the two years; 79.5 ± 2.4 mm (mean \pm s.d.) in 1995 and 74.1 ± 0.9 mm in 1996 (Table I). The final gallery length of ca. 7 cm which we

TABLE I. Comparison between 1995 and 1996 of the mean gallery length, mean number of eggs per gallery, mean gallery density, mean number of new adults per gallery and mean number of new adults per m² for *Tomicus piniperda*.

	1995	1996		
	Mean ± s.d. (n)	Mean ± s.d. (n)	U	p
Gallery length (mm)	79.5 ± 2.4 (91)	74.1 ± 0.9 (25)	1020.5	0.4342
No. egg grooves (/gallery)	22.8 ± 11.7 (91)	24.5 ± 8.7 (25)	783.2	0.5348
No. galleries (/m ²)	83.3 ± 31.1 (15)	220.9 ± 131.9 (6)	3.0	0.0006
No. exit holes (/gallery)	11.6 ± 6.4 (15)	5.1 ± 2.7 (6)	13.0	0.0144
No. exit holes (/m ²)	917.1 ± 460.1 (15)	905.0 ± 204.3 (6)	45.0	0.9690

observed corresponds well with previous European studies of *T. piniperda* reproducing on Scots pine where lengths ranged from 3-5 cm (Gibbs and Inman 1991), 7-8 cm (Långström 1983), 8-9 cm (Salonen 1973; Sauvard 1989), to 10.5 cm (Långström and Hellqvist 1985).

The number of eggs laid per gallery by *T. piniperda* was similar in both years; 22.8 ± 11.7 in 1995 and 24.5 ± 8.7 in 1996 (Table I). These means are considerably lower than previous European work where both Långström (1983) and Sauvard (1993) found an average of 40-50 eggs per gallery. Our data may have underestimated the actual value because the egg notches were difficult to ascertain, especially in 1995 when the brood material was 6-8 months old. Alternatively, there may be a true reduction in fecundity for females because of a possible loss of adaptedness associated with the beetle's recent immigration into North America.

The mean density of galleries produced by *T. piniperda* per square metre of log surface was significantly lower in 1995 (83.3 ± 31.1) than in 1996 (220.9 ± 131.9) (Table I). Previous work in Europe has shown the density of *T. piniperda* galleries per square metre to vary, from 25 to 300 (Långström 1983), 200-300 (Salonen 1973), to 496.8 (Långström and Hellqvist 1993). Both densities we obtained, therefore, fall well within the expected range for this species on its native host.

More new adults were produced per gallery at the lower gallery densities in 1995 (11.6 ± 6.4 exit holes/gallery) than at the higher densities in 1996 (5.1 ± 2.7) (Table I). The number of adults produced from individual galleries in Europe has also ranged, depending on the density of beetle attacks. Långström and Hellqvist (1993) found an extremely low number of holes per gallery (0.4) at very high beetle densities (496.8 galleries/m²), as did Salonen (1973) (ca. 3 beetles/gallery at 301-400 galleries/m²), while at low densities, 27-32 holes/gallery were recorded by Långström and Hellqvist (1985) and 30-35 holes/gallery were recorded by Salonen (1973) (at densities of 1-100 galleries/m²). Saarenmaa (1985) found 2.5-7 holes/gallery at gallery densities ranging from 24-179 galleries/m². Other European values range from 3-6 adults/gallery (Annala and Heikkila 1991) to 6.4 adults/gallery (Heliovaara and Vaisanen 1991), at intermediate gallery densities. Both years of data in our study fall within this range, demonstrating successful gallery production of ca. 2-6 new adults per parental beetle. This suggests that the beetle is establishing itself in Ontario, and doing as well as in its native European habitat.

Total mortality in the egg, larval, and pupal stage of *T. piniperda* was 49.1 ± 26.2% in 1995 (low gallery density) and 79.2 ± 11.0% in 1996 (high gallery density). In 1996, mortality of the egg stage

alone averaged $16.5 \pm 9.4\%$, meaning that mortality of the other stages (larvae, pupae and new adults) was *ca.* 62.7%. Intraspecific larval competition is considered to be the largest source of egg-to-adult mortality in bark beetles (Kirkendall 1989). Saarenmaa (1985) found the survival rates of the early larval instars to be very low. Hui and Zhimo (1995) found total mortality of *T. piniperda* from the egg to new adult stage to be 78%. Of this, only 3% and 2% occurred in the pupae and new adult stage, respectively. Most of the 78% mortality was attributed to the larval stage, with approximately half caused directly by intraspecific larval competition (Hui and Zhimo 1995). Low levels of pupal and new adult mortality are assumed to be constant at differing densities (Salonen 1973) because there is no shortage of space in which to pupate. Therefore, it is reasonable to assume that most of the 62.7% mortality in our study was larval mortality and that the additional mortality (30.1%) in 1996 over that in 1995 may have resulted from increased larval competition at the higher gallery densities. Indeed, Salonen (1973) found that larval mortality ranged from 12 to 91% as the densities increased from 63 to 325 galleries/m². Clearly, the larval stage is highly sensitive to the effects of gallery density and intense levels of intraspecific competition can occur.

Gallery production and density were not found to be significantly correlated at low gallery densities (35 to 135 galleries/m²) in 1995 (Fig. 1a), however, at the higher densities (120 to 430 galleries/m²) in 1996, density and gallery production were negatively correlated (Fig. 1b). At the lower densities, resource limitations were probably not being experienced and additional galleries could be initiated without influencing the success rate of surrounding galleries. In contrast, at the higher densities, production per gallery was reduced correspondingly with a large percentage of the variation in production levels (82.9%) explained by gallery density. This suggests that high gallery densities have a serious impact on larval survival, possibly through increased competition. Indeed, Salonen (1973) and Sauvard (1993) both found that increasing densities of *T. piniperda* galleries caused a serious decline in larval survival and production per gallery, when density exceeded a critical level. Saarenmaa (1985) also reported that the effects of important mortality agents of *T. piniperda* are positively density-dependent. This effect has been commonly found for other bark beetles, such as *Ips typographus* L. (Weslien 1994; Anderbrant *et al.* 1985) and *Dendroctonus ponderosae* Hopkins (Raffa and Berryman 1983).

In our study, total brood production was found to be the same in both years, with 917.1 ± 460.1 exit holes/m² in 1995 and 905.0 ± 204.3 holes/m² in 1996 (Table I), despite the highly variable gallery density and production per gallery. This suggests that the beetle is operating at or near its carrying capacity on Scots pine in southern Ontario. Previous European studies have reported average values of around 1000 beetles/m² for *T. piniperda* on Scots pine (Långström 1984; Heliovaara and Vaisanen 1991; Sauvard 1993 and 1989). This is further indication of the beetle's successful establishment, as it is doing as well here as in its native European range.

At the lower densities in 1995, brood production was positively correlated with gallery density (Fig. 2a), suggesting that mortality is density-independent over this lower range. However, brood production in 1996 was not found to be significantly influenced by gallery density (Fig. 2b), indicative that density-dependant mortality may be occurring at these higher densities. European studies have also shown that density-dependent effects limit the brood production of *T. piniperda*, primarily due to increased intraspecific larval competition for food and space (Salonen 1973; Beaver 1974; Långström 1984; Långström and Hellqvist 1985; Sauvard 1989; Heliovaara and Vaisanen 1991).

Our results indicate that *T. piniperda* is successfully reproducing on the brood material in southern Ontario, making effective use of the available resource of Scots pine. They also suggest that this species will continue to increase in numbers and expand its range. A variety of factors may be contributing to the successful establishment of this pest in Ontario. First, newly invading species can often be found operating at very high numbers because there are few constraints on their growth as natural enemies and appropriate host plant defenses are often lacking (Speight and Wainhouse 1989). Indeed, *T. piniperda* has only been in Ontario for 4-5 years (Haack 1996), so it is unlikely that many

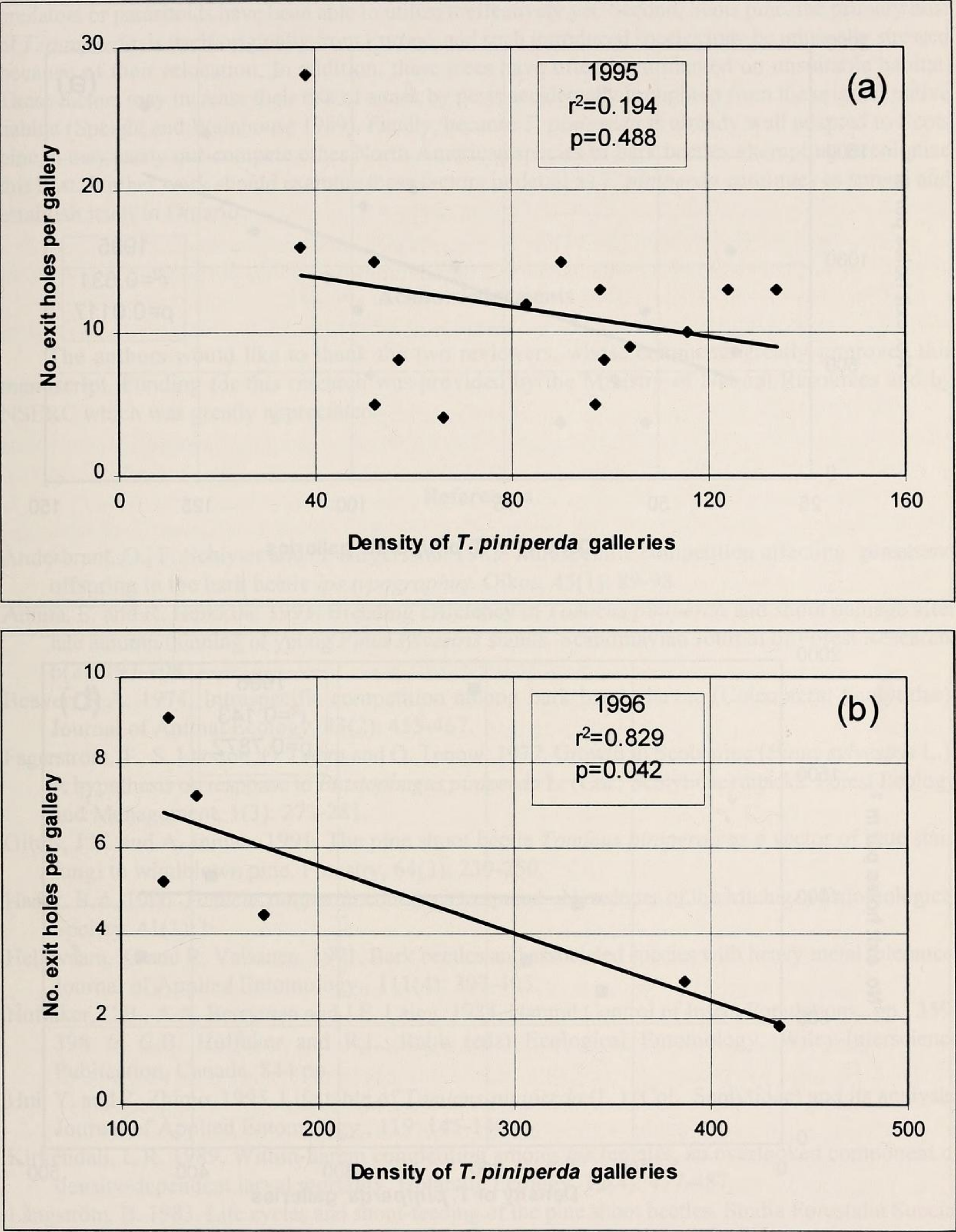


FIGURE 1. Relationship between the number of new *Tomicus piniperda* adults emerging per gallery and increasing gallery density on sections from (a) naturally infested standing Scots pine (*Pinus sylvestris*) trees (1995) and (b) cut Scots pine logs (1996) in a 40-year-old stand near Guelph, Ontario. Note difference in scale of x and y axis.

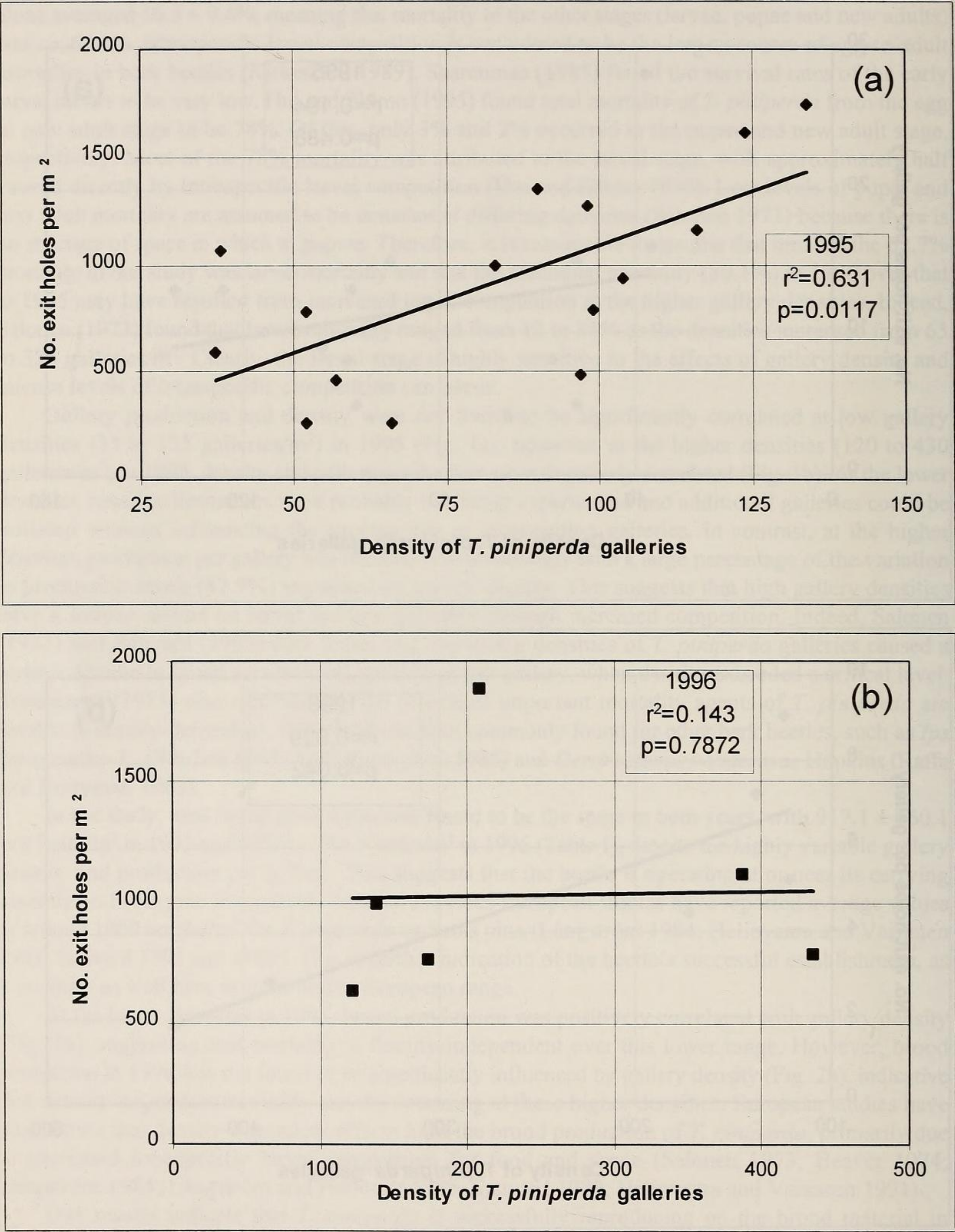


FIGURE 2. Relationship between the number of new *Tomicus piniperda* beetles emerging per square metre and gallery density on (a) naturally infested standing Scots pine (*Pinus sylvestris*) trees (1995) and (b) cut Scots pine trap logs (1996) in a 40-year-old stand near Guelph, Ontario. Note difference in scale of x axis.

predators or parasitoids have been able to utilize it effectively yet. Second, Scots pine, the primary host of *T. piniperda*, is itself originally from Europe, and such introduced species may be unusually stressed because of their relocation. In addition, these trees have often been planted on unsuitable habitat. These factors may increase their risk of attack by pests accidentally brought in from the original native habitat (Speight and Wainhouse 1989). Finally, because *T. piniperda* is already well adapted to Scots pine, it may easily out-compete other North American species of bark beetles attempting to colonize this host. Further work should examine these factors in detail as *T. piniperda* continues to spread and establish itself in Ontario.

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