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Life cycles and shoot-feeding of the pine shoot beetles

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Abstract

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The life cycle and shoot-feeding of *Tomicus piniperda* (L.) and *T. minor* (Hart.) (Col., Scolytidae) was studied in Simonstorp in southern Sweden (N. 58° 47′, E. 16° 10′) during the period 1972–1976. Special attention was given to the seasonal feeding activity in the shoots of Scots pine (*Pinus sylvestris* L.). This shoot-feeding was related to certain events in life cycle: flight period, departure of parent beetles from brood logs, length of oviposition period and emergence of the new generation. The spatial distribution of beetles within the pine crown was also studied. The influence of environmental conditions and some population factors upon the shoot-feeding was discussed.

Key words: Scolytidae, *Tomicus piniperda, T. minor, Pinus sylvestris,* life cycle, shoot-feeding.
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Introduction

The pine shoot beetles (*Tomicus* sp., Coleoptera, Scolytidae) have been recognized as major forest pests ever since the days of Ratzeburg (1839). Since that time hundreds of studies have been carried out on various aspects concerning the life cycle, ecology and economic importance of these beetles (cf. Holmgren, 1867; Altum, 1881; Boas, 1923; Escherich, 1923; Trägårdh, 1939; Saalas, 1949; Postner, 1974).

The pine shoot beetles belong to the genus *Tomicus* Latr. (synon. *Blastophagus* Eichh., synon. *Myelophilus* Eichh.). This is a worldwide genus with 14 species (Rühm, 1976), two of which occurring in Scandinavia: *T. piniperda* (L.) and *T. minor* (Hart.). The former is called "the common pine shoot beetle" and the latter "the lesser pine shoot beetle" (Bevan, 1962). Both species are widely distributed in the palearctic region from Europe throughout Siberia to Japan (Browne, 1968; Lekander et al., 1977). In Europe, a third species *(T. destruens* (Woll). occurs in the Mediterranean low lands (Lekander, 1971; Carle, 1973). In Fennoscandia, *T. piniperda* is widely distributed, whereas *T. minor* is common in southern Norway, central Sweden and southern Finland (Lekander et al., 1977).

Ecologically the pine shoot beetles are well separated from their allies in the subfamily *Hylesininae* because of their unique feeding behaviour. The adult beetles burrow into the pith of pine shoots and feed there to become sexually mature. Hence the common name "pine shoot beetles".

In Northern Europe the principal host tree of *T. piniperda* and *T. minor* is Scots pine, *Pinus sylvestris* L. Attacks on other pines and occasionally on other conifers have been observed both in Scandinavia (see e.g. Bakke, 1968; Butovitsch, 1972; Salonen, 1973) and elsewhere (Browne, 1968; Park & Lee, 1972; Postner, 1974).

Major contributions to the understanding of the life cycle and ecology of *T. piniperda* have been made by e.g. Šrot, 1966, 1968; Bakke, 1968; Eidmann & Nuorteva, 1968; Perttunen & Häyrinen, 1970; Kangas et al., 1971; Salonen, 1973; Beaver, 1974. Less work has been done on *T. minor* as regards its biology and ecology, but some important papers have been published (Ritchie, 1917; Greese, 1926; Bakke, 1968).

The present study describes the shoot-feeding of *T. piniperda* and *T. minor* under varying environmental conditions in relation to other important phases in their life cycles. The following events in the life cycle were considered relevant for the understanding of the seasonal shoot-feeding: the flight period, the length of the oviposition period, the departure from breeding material, the number of broods and the emergence of the new generation.

This paper is a shortened version of a thesis (Långström, 1980 *a*), and is focusing on the shoot-feeding of the pine shoot beetles, whereas much of the results and discussions concerning different life cycle events has been omitted. The thesis also contains a detailed description of material and methods as well as a review of the related literature.

Material and methods

Study areas

The major part of the field work was carried out in pine forests surrounding the village of Simonstorp in Östergötland in southern Sweden (N.58°47′, E.16°10′, 65 m above sea level). The study areas were chosen to represent different silvicultural treatments and logging situations.

In 1972–73 field studies were made in a 15-year old pine stand at Ålgöl (4 km south of Simonstorp). This stand was damaged by pine shoot beetles after pulp wood storage in 1971. An early thinning (= cleaning) was made in the winter 1971/1972, and in May 1972 high numbers of *T. piniperda* were observed in the waste wood.

In 1972–1976, field work was done at Tegnetorp, situated 6 km north-east of Simonstorp. Different age classes (10, 20, 40 and 100 years) of pine stands grew close to each other in this area. In 1974 part of the mature stand (2 hectares) was clear-felled, and thinnings were made over large areas in the vicinity. Thus plenty of logging waste including a pine wood stack was available to the pine shoot beetles in 1974, but not in other years.

In 1973, studies were also made at Klinta 6 km north of Simonstorp. A final felling had been made in the previous winter and seed trees were left. This area, about 10 hectares in size, was surrounded by young pine stands as well as mature mixed stands of pine and spruce.

Weather conditions

During the study period, 1972–1976, weather conditions were extremely variable from year to year. Daily temperatures are shown in Figure 1. In 1972 the early summer was warmer than normal. The following winter was extremely mild and there was no snow cover at all. The spring of 1973 was cold but June and July were warm. The summer was followed by another winter without snow. The summer of 1974 was cold and very rainy, but the winter again was mild. The snow fell late and covered the ground for only a short period. The spring and early summer of 1975 were rather normal, the late summer was very hot and the autumn slightly warmer than the average. In the winter of 1976 the depth of snow was normal, as was the growth period with the exception of September which was rather cold.

Field methods

Life cycle studies

Flight traps. The flight period of the pine shoot beetles was studied in 1973–1976 by means of "window-traps" (cf. Bakke, 1968; Southwood, 1978). The window-trap used in the present study was a transparent piece of plexi-glass (50×60 cm) on a wooden frame over a trough containing water and liquid soap as wetting agent. Below each trap (8 in 1975 and 4 in other years) fresh pine logs were placed to attract the beetles. In 1973, the traps were emptied at irregular intervals, but from 1974 collection took place every second day or at least 2–3 times a week. All beetles were stored in 70% ethanol.

Emergence bag traps. In 1973–1976, the course of departure of parent beetles and callow adults from the brood logs was studied by means of "emergence bag traps". Naturally infested pine logs were enclosed in bags of cotton sheeting, and the emerging beetles were collected in bottles which were attached by large funnels to the bags (cf. Annila, 1969). In 1973, four bag traps were used, two containing *T. piniperda* and two with *T. minor.* In other years one of each species was used.

Brood logs. In 1973 and 1974, naturally infested brood logs were destructively examined at 2–3 weeks' interval in order to evaluate in which phase of brood development the parent beetles left the egg galleries (cf. Bakke, 1968; Salonen, 1973). At each inspection two billets, one containing *T. piniperda* and the other *T. minor,* were barked and examined. The billets were approximately 10 cm in diameter and 50–100 cm in length. The presence of parent beetles in egg galleries, state of brood development, density of attack, bark thickness etc. was noticed. In 1973 two series of logs were inspected, one containing beetle attacks from the whole flight period and the other from the later part of the flight period. The former logs were felled before the flight period and are referred to as "early attacks" and the latter ones were felled on April 6 th and are called "late attacks". In 1974, only logs felled before the flight period were studied.

The length of the oviposition period was studied in 1973–1975 on brood logs which were felled before, during and after the main flight period. In the autumn at least two log sections (covering 0.5–1 m^2), one thick- and one thin-barked, of approximately 1 metre in length were carefully examined. The remaining trees were also inspected for pine shoot beetles, if the log samples contained none.

Stem traps. In 1974, funnels were attached to three pines at Tegnetorp in order to find out whether the pine shoot beetles left the pine crowns by walking down along the stem. Two funnels of soft plastic were attached to each stem at opposite sides, covering approximately 40% of the girth. Collecting bottles containing water were fitted to the funnels, and were emptied regularly from August to December in 1974.

Sampling of attacked shoots

Sample trees. In 1972–1976, sample trees (5–14 m in height) were felled at 1–4 weeks' interval from early spring to late autumn. Normally one tree was felled each time. Basic tree data are listed in appendices 2 and 3 in Långström (1980 *a*). All attacked shoots were collected whorl by whorl, and the shoots were stored in plastic bags and normally frozen within 24 hours. Shoot samples were collected by this method at Ålgöl 1972–73 and at Tegnetorp 1974–75.

Shoot samples. Samples of damaged shoots were collected at random in the young pine stands at Tegnetorp in 1972–1975 and at Klinta in 1973. Approximately 50 attacked shoots were taken one to three times a month from spring to autumn. The shoot samples were stored as was described above.

Labelling of attacks. Pine shoot beetle attacks were also counted on preselected trees throughout the growing seasons 1972–1975. Two techniques were

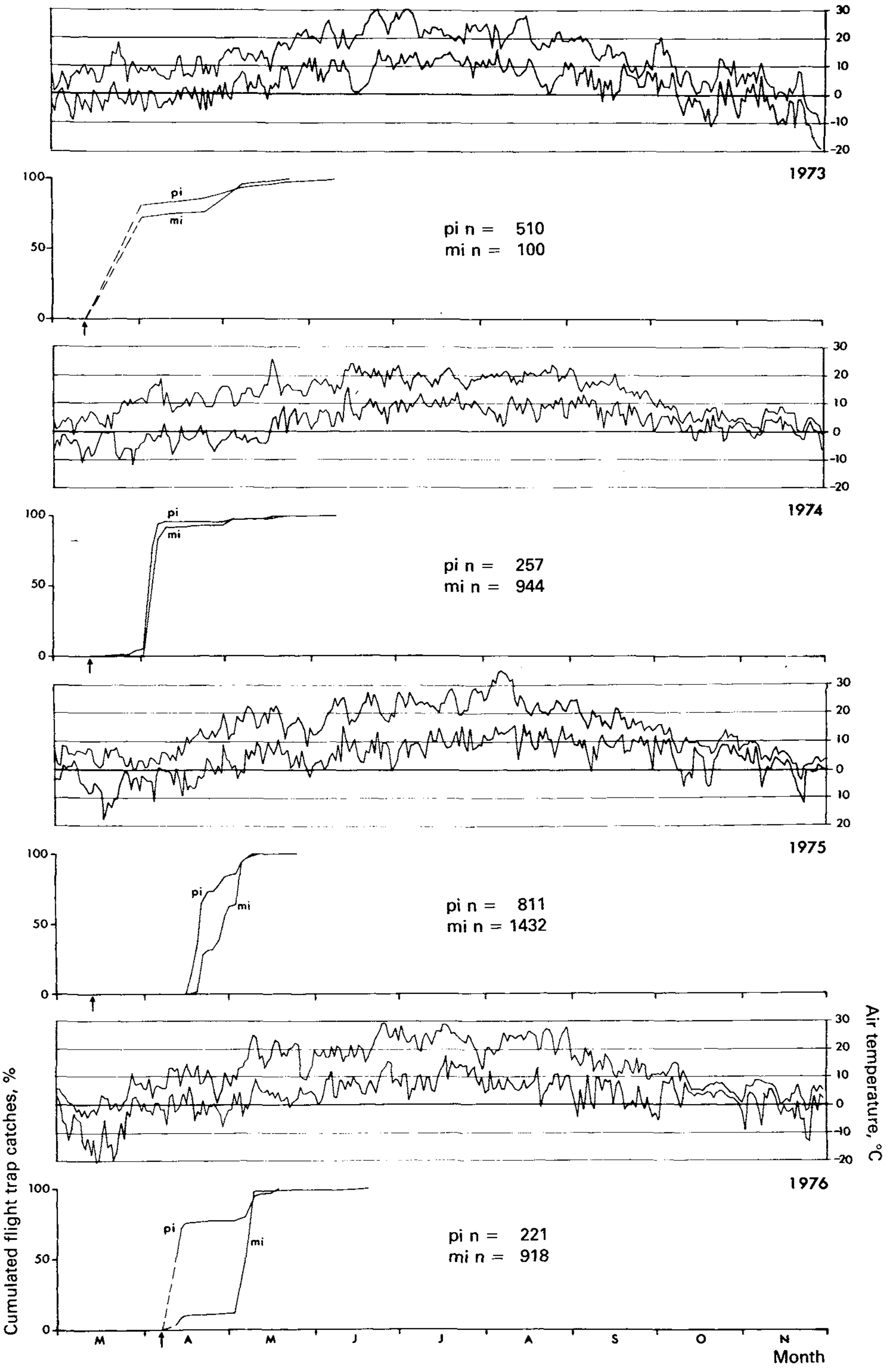

Fig. 1. The flight period of *T. piniperda* (pi) and *T. minor* (mi) in 1973–1976 according to window trap catches. The curves show cumulative percentages. Trapping started on dates which are indicated with arrows. The upper temperatures indicate daily maximum and the lower curves daily minimum air temperatures at Simonstorp station. Data were obtained from the Swedish Meteorological and Hydrological Institute (SMHI).

used: (1) labelling of all new attacks with plastic tape at the date of detection, (2) removal of all attacks at every inspection. Details are given together with the results.

Cage experiments

Experiments with caged beetles were used in order to obtain quantitative information about the feeding activity of the pine shoot beetles. Similar studies have been made by several authors, but their approach has mainly been to study the voltinism and number of broods of the pine shoot beetles (Sylvén, 1916; Ritchie, 1917; Hanson, 1937, 1940; Šrot, 1966, 1968). Cage studies were carried out at Tegnetorp in 1972–1974. Details are given together with the results.

Laboratory procedure

Shoot samples

Each shoot was classified according to its age as "current shoot" (C), "one-year-old shoots" (C+1) and "older shoot" (C>1). In 1972, the shoot diameter at the entrance hole to the feeding tunnel was measured to the nearest mm. From 1973 many more details were noted: the distance from the entrance hole to a distal node or bud in mm, the frequency of multiple attacks (i.e. more than one attack in the same internode), the direction of tunnelling, the length of the feeding tunnel and the degree of wilting as well as phenological status of each attacked shoot. In all years, the presence of pine shoot beetles (species and sex) in the feeding tunnels was noticed.

Beetles

The identification of the beetles to species and sex was done according to the well known characters which have been repeatedly described in the literature (see, eg. Bakke, 1968). The colour of the elytra was also classified as "light-brown", "intermediate" and "dark-brown". This was an auxiliary characteristic in the age classification of the beetles. The beetles were then dissected and classified according to Figure 2 (cf. Knoche, 1904; Ritchie, 1917; Greese, 1926).

Senile males (i.e. post-reproductive beetles in the state of regeneration feeding) were impossible to separate from developing ones. Some females had ovaries that were close to the senile type, but there was definitively no *corpora lutea* indicating that eggs had been laid. On the other hand females were found in early summer with ovaries containing large oocytes but again no *corpora lutea* were present. It was suspected that these females had not laid eggs and that the oocytes may have been resorbed while fertility was declining.

Life cycle

Flight period

The course of the flight period of *T. piniperda* and *T. minor* in 1973–1976 at Simonstorp is shown in Figure 1. The flight periods varied greatly during these four years. Differences were observed both in time and in specific patterns. The majority of beetles flew during a few days and this main flight varied from late March to early May (cf. Table 3). In 1973 and 1974, the flight of both species almost coincided, whereas in 1975 and 1976 the flight of *T. minor* was clearly delayed in relation to *T. piniperda*.

Flight activity started when maximum air temperature exceeded 10–12°C (Fig. 1). During these years 11.6°C was the lowest reading releasing flight in both species (Fig. 3). The flight culmination was also related to air temperature. The higher the temperature was at the beginning of the main flight, the larger was the proportion of beetles flying on that day. However, *T. minor* seems to require higher temperatures for its main flight than does *T. piniperda*.

In 1973 and 1974, there was no continuous snow cover in the study areas during the winter, whereas 1975 and 1976 were more normal in that respect. Since *T. piniperda* hibernates in the bark at the base of standing pines, and *T. minor* in the litter on the forest floor, the presence or absence of snow may explain the observed differences in flight patterns between the species.

The termination of the flight periods is difficult to assess. All curves of cumulated percentages in Figure 1 have a "tail" extending throughout May into June. The last catches most likely contained beetles which were departing from the brood logs after oviposition. No callow adults of the new generation were captured although plenty of exit holes were seen on the bait logs.

The relative frequencies of *T. piniperda* and *T. minor* differed between locations and years (Table 1).

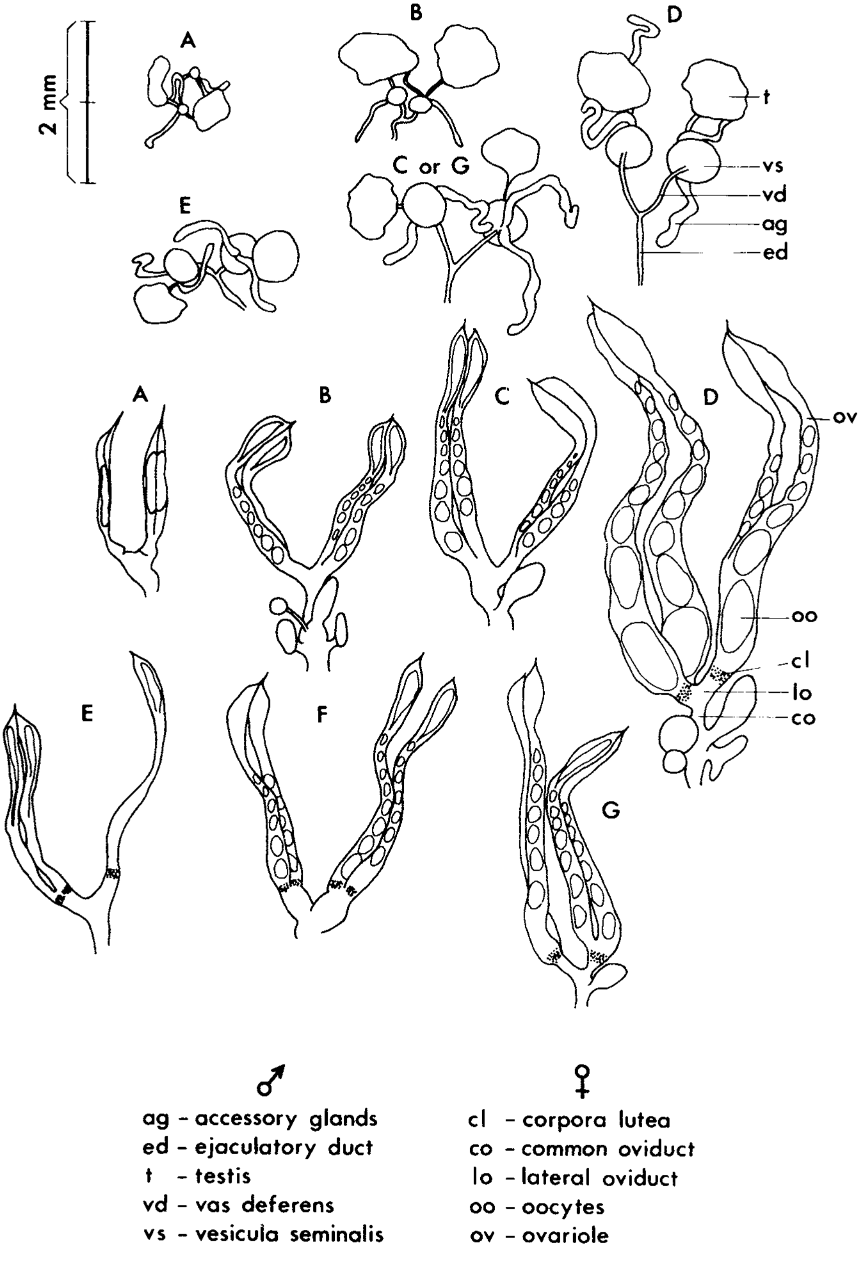

Fig. 2. Sexual organs of males and females of *T. piniperda* in different stages of sexual maturation. A/ Juvenile beetle after emergence. B/ Developing beetle excavated from a pine shoot. C/ Young beetle at hibernation site in late autumn. D/ Fertile beetle in egg gallery at the beginning of oviposition. E/ Senile beetle after oviposition. F/ Redeveloping beetle excavated from a pine shoot in early summer. G/ Redeveloping beetle at hibernation site in late autumn.

Heterogeneity analysis revealed that the samples were not homogeneous. Obviously, *T. piniperda* had bred successfully in the thinned stems at Ålgöl, whereas *T. minor* was more abundant in the clear-felled areas (Klinta and Tegnetorp).

All pine shoot beetles in the flight traps were sexed, and in both species the sex ratio was close to 1:1 (Table 1 in Långström, 1980 *a*).

Table 1. *The frequency of T. piniperda and T. minor in flight trap catches 1973–1976*

Locality and year	*T. piniperda*, %	*T. minor*, %	Total number of beetles	Remarks
Ålgöl 1973	83.6	16.4	610	Storage of pulp wood 1971. Thinning of pine stands in the winter of 1972
Klinta 1974	15.8	84.2	936	Clear felling in the winter of 1973
Tegnetorp 1974	41.1	58.9	265	Clear felling, thinning and storing of pulp wood in stacks 1974
Tegnetorp 1975	36.2	63.8	2 243	No new breeding material available
Tegnetorp 1976	19.4	80.6	1 139	As above
Heterogeneity χ^2 for all years				916.54*** (*d.f.*=4)
Heterogeneity χ^2 for Tegnetorp 1974–76				111.52*** (*d.f.*=2)

*p <0.05, *p <0.01, ***p <0.001.

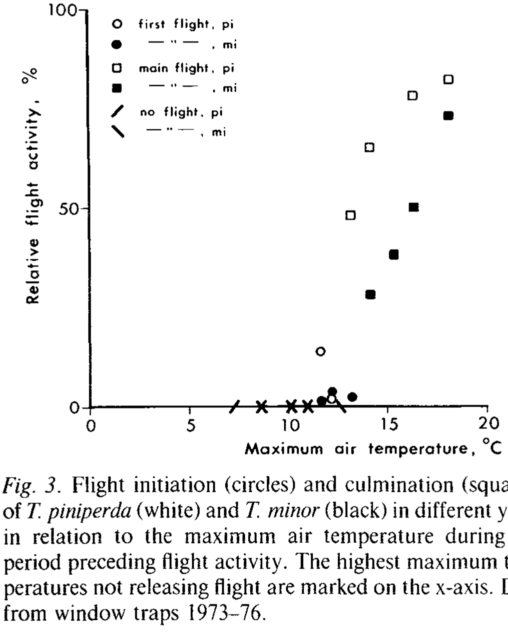

Fig. 3. Flight initiation (circles) and culmination (squares) of *T. piniperda* (white) and *T. minor* (black) in different years in relation to the maximum air temperature during the period preceding flight activity. The highest maximum temperatures not releasing flight are marked on the x-axis. Data from window traps 1973–76.

Re-emergence of parent beetles from brood logs

Males of both *T. piniperda* and *T. minor* generally left the brood logs earlier than the females did (Fig. 4). However, there were great variations from year to year both in time and departure course of the parent beetles. In 1973, the pattern was very similar for the two species, both in the case of "early attack" and "late attack", although these varied much from each other. However, the results may have been influenced by the density of attack which in both species was roughly twice as high in the case of early attack, as compared with the late attack.

The following year, some of the first re-emerging beetles may have been surplus beetles, which were not breeding in the logs. The departure in both sexes and species extended over several weeks, and the length of time between the median departure dates (when 50% had left) of the sexes for *T. piniperda* was as 28 and 16 days, respectively.

In 1975, the majority of *T. piniperda* males had already left the logs at the time of enclosure in bag traps. Thus only the curve showing the females of this species is included in Figure 4. For this year the pattern of departure resembled that of the "early attack" in 1973.

The presence of parent beetles in egg galleries, inspected at 1–3 weeks intervals in 1973 and 1974, is shown in Figures 5 and 6 for *T. piniperda* and *T. minor*, respectively.

Both parents of *T. piniperda* were found in the majority of egg galleries until early May and even later in the trees from the later felling date (Fig. 5). However, egg galleries with only one parent beetle were found from the first date of inspection. On the 26 May, egg galleries containing one parent beetle dominated in the early felling, whereas the corresponding situation was observed a month later in the later felling. In the former case the average egg gallery length had reached its maximum in late May, whereas in the latter case, gallery excavation was far from finished. In July 1975, nearly all galleries were empty, and no parent beetles were found dead in egg galleries.

The same pattern applies to *T. minor* although the results are not as clear in this species as in the former one (Fig. 6). Already at the first inspection on early felled trees, a large portion of the egg galleries contained only one parent beetle. A few abandoned egg galleries were also observed on 7th April. Another difference was that dead parent beetles were found

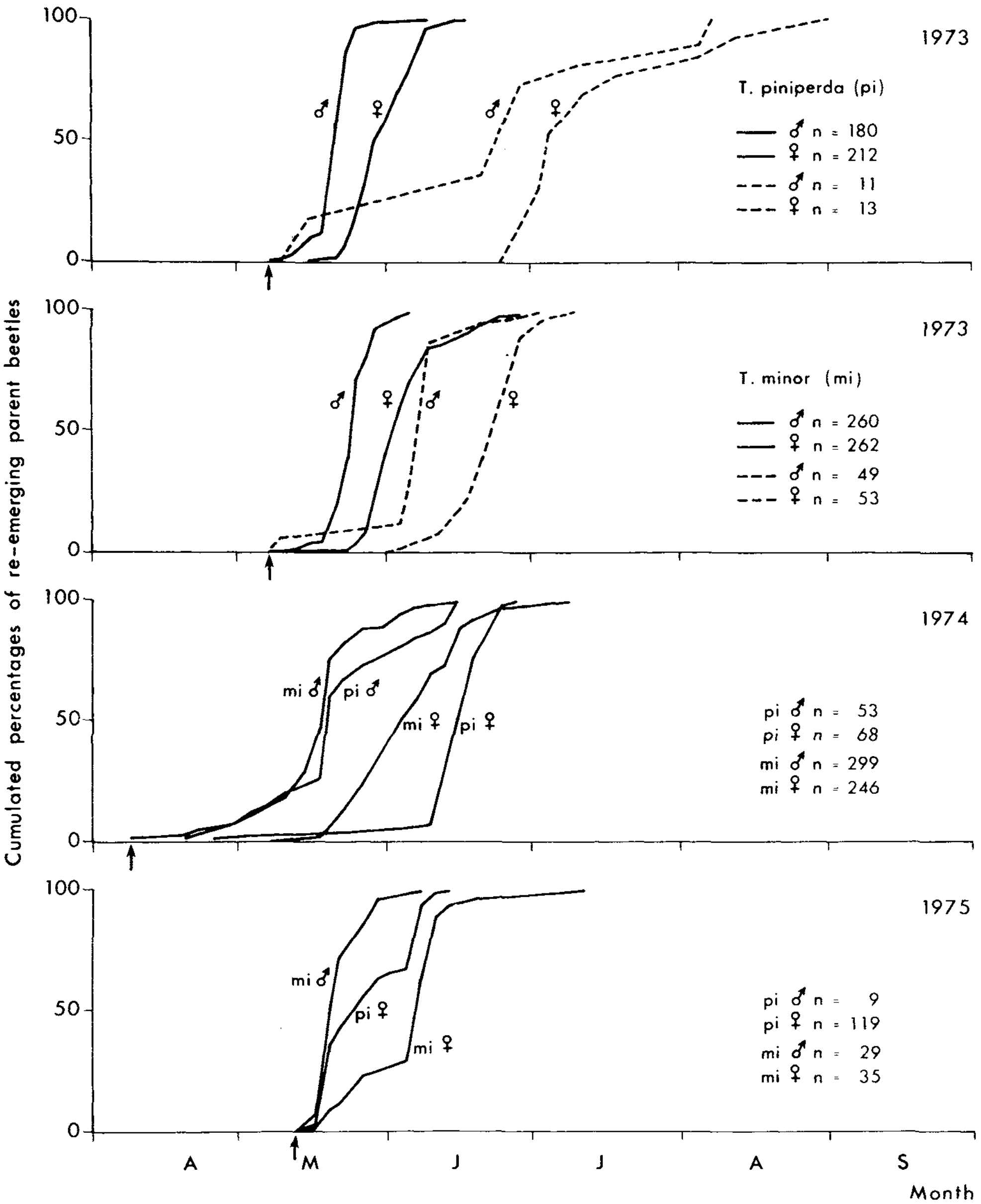

Fig. 4. The departure course of parent beetles from brood logs which were enclosed in emergence bag traps. In 1973, solid lines refer to "early attacks" and broken lines to "late attacks". Each curve shows the cumulative percentage of the species and sex in question. Arrows indicate dates of enclosure in bag traps.

regularly in the late inspections which may indicate a higher mortality of parent beetles of *T. minor* during the phase of brood establishment, than of *T. piniperda*. Despite these differences the general pattern is the same in both species.

The beetles were sexed after removal from the galleries. Table 2 shows that the males leave the egg galleries before the females. Only in a few cases were males found alone in the egg galleries. If both parent beetles were present in the egg galleries, the male was behind the female in both species.

The egg gallery lengths in Figures 5 and 6 were average figures for each inspection. However, the gallery lengths varied considerably within the same sample. At any inspection, the galleries containing both parent beetles were always longer than those

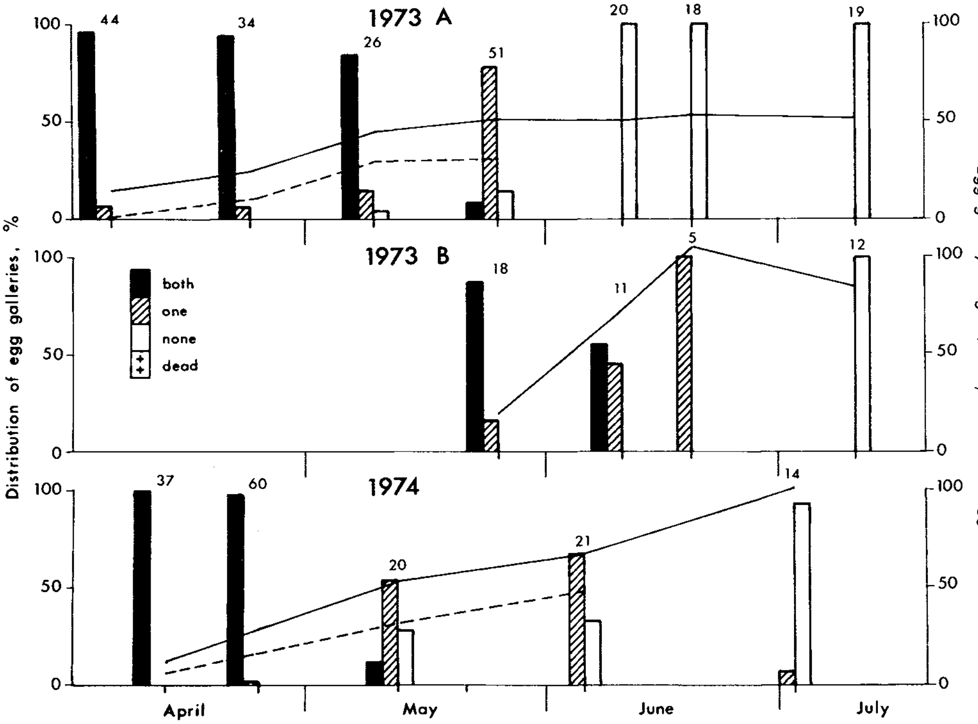

Fig. 5. Presence of parent beetles of *T. piniperda* in egg galleries during oviposition and brood development. Letters A and B refer to "early" and "late attacks", respectively. Columns indicate percentages of egg galleries containing both, one or none of the parent beetles at different inspections. Numbers above columns indicate sample sizes. Solid lines show average egg gallery lengths (mm) and broken lines the number of eggs at each inspection.

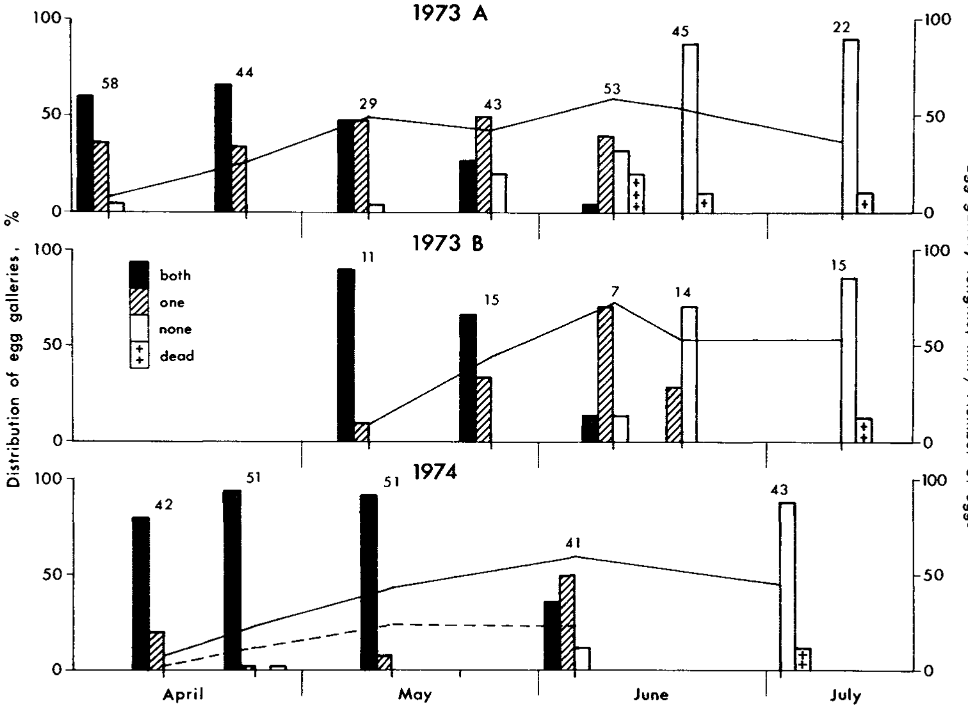

Fig. 6. Presence of parent beetles of *T. minor* in egg galleries during brood development. Same legend as in Figure 5.

with only one parent present, which in turn were longer than the empty galleries (Tables 6 and 7 in Långström, 1980 *a*).

The sex ratio amongst the re-emerging parent beetles was found to be very close to a 1:1 ratio in both species (Table 8 in Långström, 1980 *a*).

Length of oviposition period

Figure 7 shows that the majority of attacks in both species took place in the trees felled before the flight period. In 1973, some oviposition occurred until mid-May, whereas in other years only occasional attacks were recorded on later fellings, especially in *T. minor*. In 1974, attacks were noticed for *T. piniperda* on trees which were felled in early June. When the logs were inspected on 18th September, larvae were still dominating in the galleries from this felling date, whereas the earlier two had produced 11 and 19 exit holes per egg gallery, respectively. In *T. minor* normal development had only taken place in logs from the first felling, and the few larvae in the galleries of the second felling date had failed to enter the wood. No blueing could be seen on the latter logs either.

On 21st July 1973, 22 males and 28 females of *T. piniperda* were released in cages containing young pines and brood logs (for details, see Långström, 1980 *a*). The beetles had been collected the previous day from pine shoots which were attacked early in the season. The beetles were therefore apparently parent beetles in the phase of regeneration feeding. When the cages were removed on the 20th September, 50% of the beetles were found alive in the shoots. One egg gallery was found on the brood log and it contained 7 larval tunnels. All larvae were alive and ready to pupate. Thus only one of the 28 females had resumed oviposition.

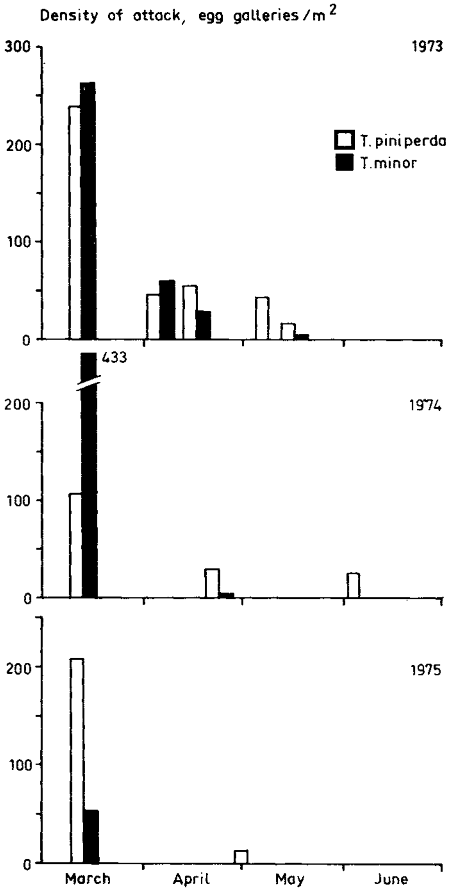

Fig. 7. The attack density of pine shoot beetles (number of egg galleries/m² bark area) on trees felled in spring and early summer in 1973–1975.

Emergence of new generation

In all years, the seasonal course of emergence followed a similar pattern, *T. piniperda* emerging several weeks before *T. minor* (Fig. 8). Emergence occurred

Table 2. *The frequency of males and females in egg galleries containing one or both parent beetles. Log samples from Simonstorp 1973*

	One parent beetle in egg gallery			Both parent beetles in egg gallery				
				Anterior		*Posterior*		
Species	♂	♀	Total	♂	♀	♂	♀	Total
T. piniperda	2	45	47	–	97	97	–	97
T. minor	12	81	93	3	83	83	3	86

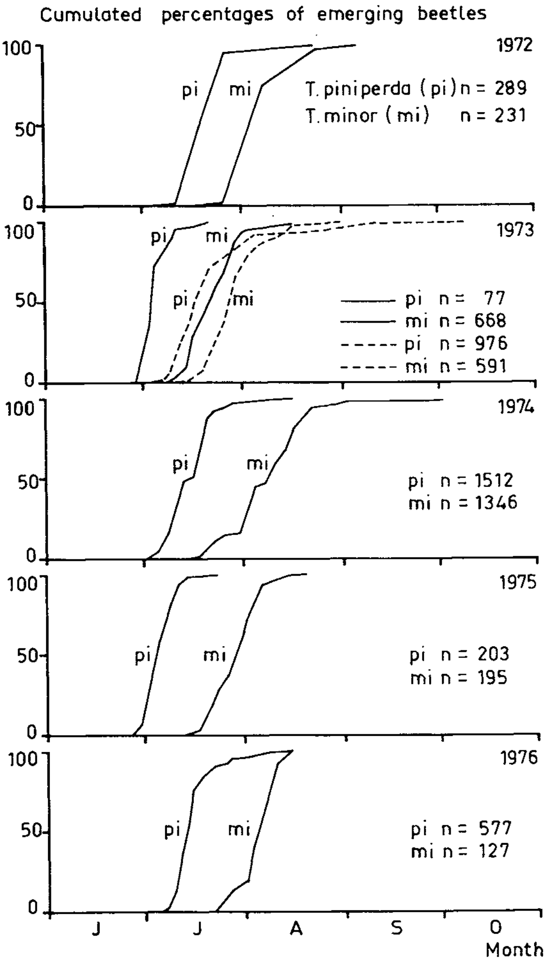

Fig. 8. The course of emergence of young pine shoot beetles from brood logs. The curves show cumulative percentages. Data from 1972 derive from counting of exit holes, in other years from emergence bag traps. In 1973, solid lines refer to "early" and broken lines to "late attacks".

already in June, although most of the young *T. piniperda* left the brood logs during the first half of July. Emergence of *T. minor* normally started during the second half of July with the culmination around the turn of the month. In both species emergence may continue throughout September.

The speed of brood development was estimated from the flight and emergence data. By comparing the median flight date with the median date of emergence, a rough estimate on the rate of development under field conditions was obtained. It was assumed that the start of oviposition was closely linked to the flight period (cf. Bakke, 1968; Eidmann, 1974). Thermal sums were calculated (day-degrees above 0 and 8°C) for the period between median flight and median emergence dates (cf. Knoche, 1904; Salonen, 1973).

The average period of development was 92 days in *T. piniperda,* and 105 for *T. minor* (Table 3). The thermal sums were found to be roughly 1 000 dd (day degrees) in *T. piniperda,* and 1 300 dd in *T. minor* with 0°C as zero point. The corresponding figures with 8°C as threshold value were 361 ± 29 and 547 ± 38, respectively. Student's *t*-tests revealed significant differences between the average thermal sums ($t_o = 7.56^{***}$ *d.f.* = 6, $t_8 = 9.03^{***}$ *d.f.* = 6), whereas this was not the case for the number of days ($t = 1.39$ *d.f.* = 6). Thus is can be concluded that the temperature requirements were higher for *T. minor* than for *T. piniperda.*

According to the pooled frequencies of males and females emerging from the bag traps, the sex ratio was 1:1 in both species, (Table 10 in Långström, 1980 *a*).

Table 3. *Development periods of T. piniperda and T. minor estimated (in days and day degrees) from the median date of flight (50% of the beetles swarming) to the median date of emergence (50% of new generation emerging from brood logs)*

	T. piniperda				*T. minor*			
Year	Median date of swarming	Median date of emerging	Difference in days	Day degrees, >0°C	Median date of swarming	Median date of emerging	Difference in days	Day degrees, >0°C
1972	?	-07-20	–	–	?	-08-01	–	–
1973	-04-01[a]	-07-04	95	989.6	-04-01[a]	-07-21	112	1 304.0
1974	-04-04	-07-17	104	1 091.2	-04-05	-08-09	127	1 419.7
1975	-04-21	-07-05	75	916.4	-04-29	-07-30	92	1 296.9
1976	-04-12	-07-14	93	1 066.1	-05-07	-08-05	90	1 321.2
Mean ±S.D.			92 ±12	1 016 ±79			105 ±18	1 335 ±57

[a] Estimated median date of swarming, cf. Figure 1.

Discussion

The observed flight data agree well with other observations in Fennoscandia regarding the course and weather dependence of the flight periods of *T. piniperda* and *T. minor* (for references, see e.g. Bakke, 1968; Salonen, 1973; Eidmann, 1974). The results also confirm that the flight of *T. minor* is affected by the thickness of the snow cover (cf. Bakke, 1968; Kangas et al., 1971). The different frequencies of *T. piniperda* and *T. minor* in the window-traps indicate that the population structure is affected by the silvicultural measures taken in an area. However, *T. minor* is probably over-represented in the trap catches due to the fact that this species is likely to have aggregating pheromones, whereas *T. piniperda* seems to lack that kind of chemical communication (Bakke, pers. comm.; cf. Schönherr, 1972).

The re-emergence of parent beetles from brood logs follows the pattern observed by e.g. Sylvén (1916) and Salonen (1973), i.e. that males leave the egg galleries before females. Depending on the progress of egg laying, which in turn is related to the time of attack and the weather conditions, the males of both species may leave the egg galleries already in early May, or may stay there until late into the summer. A similar situation was seen to occur in the females, although these always left the galleries a few weeks after the males.

It is noteworthy that mortality occurred regularly among parent beetles of *T. minor* during the phase of brood establishment, whereas dead specimens of *T. piniperda* were never found in the egg galleries. It can be assumed that the latter species is protected better against heat and desiccation under the thick bark than the former on its breeding sites under the thin bark.

Judging from the few attacks which were seen on logs felled after the main flight period, oviposition seems to be rare after flight has ceased, especially in *T. minor*. However, the results from 1974 showed that attacks by *T. piniperda* may occur in the month of June. These results compare well with earlier observations, at least those from northern Europe. Trägårdh (1921) demonstrated that the oviposition of *T. piniperda* ceased in May or early June. According to Eidmann (1965, 1974) 90% of all attacks made by *T. piniperda* and *T. minor* were recorded before the end of May, but occasional new egg galleries were started as late as the beginning of July. He also observed a tendency towards a shorter oviposition period in the latter species than in the former.

The first detailed presentation of the course of emergence is found in Eidmann (1974), but he did not separate the exit holes of *T. piniperda* and *T. minor,* although there is a note that the latter species started to emerge in early August, almost a month after the first exit holes of the former.

According to Bakke (1968), the first exit holes of *T. piniperda* were found in mid-July. In northern Norway emergence took place a month later, whereas emergence of *T. minor* took place in late August and September in the southern locality. However, in another year exit holes of *T. minor* were found in the middle of July in the same locality (Bakke, 1968). In general, these figures compare well with those obtained in the present study. However, it is important to observe that the emergence course may differ considerably from year to year even in the same locality.

The field data of Bakke (1968) indicate a period from first egg to first exit hole of approximately 80 days in 1964, and 100 days in 1965 for *T. piniperda,* whereas the development period was more than 120 days in *T. minor*. These figures compare well with those found in the present study. According to Eidmann (1965, 1974) the time from attack to first emergence was approximately 70 days for *T. piniperda,* whereas the period from the peak flight to peak emergence was 94 days in 1964. The first exit holes of *T. minor* occurred about three months after the attack. Salonen (1973) calculated the thermal sum required for the development of *T. piniperda* under field and laboratory conditions. The values found in the present study are in the range of his and Knoche's (1904) results. A detailed presentation of the brood development of *T. piniperda* and *T. minor* is given by Bakke (1968).

In Scotland Ritchie (1917) found the development period of *T. minor* to be 95 and 102 days in its narrower (egg to adult) and wider meaning (first flight to first exit hole), respectively. In Czechoslovakia, the development period (*sensu stricto*) of *T. piniperda* was much shorter than in Scandinavia, ranging from 40–80 days depending on the altitude (Šrot, 1968). Similar figures are given for *T. destruens* (Carle, 1973).

Much research has been devoted to the voltinism and occurrence of sister broods in *T. piniperda* and *T. minor* (for references, see Knoche, 1904; Trägårdh, 1921; Bakke, 1968; Salonen, 1973). Today, both species are considered to be strictly univoltine at least within their European range. No evidence of a true second generation (i.e. offspring of the new generation in the same year) has been demonstrated, although Salonen (1973) has shown that the thermal sum in certain years would allow *T. piniperda* to produce a second generation i southern Finland. In more southerly areas there exists every year this theoretical possibility. On the other hand the species may in most northerly areas be unable to complete its development (Kangas, 1963). In such a case the brood will succumb because the immature stages do not tolerate the low winter temperatures (Ehnström, 1963; Bakke, 1968). Regarding to *T. minor,* Bakke (1968) concluded that the summer season in northern Scandinavia normally is too short to allow the species to complete its brood development and subsequent maturation feeding, thus limiting the northern distribution of the species.

Although cage studies have shown that both *T. piniperda* and *T. minor* may produce a successful sister brood under field conditions (Sylvén, 1916; Ritchie, 1917; Šrot, 1966, 1968), observations on felled trees indicate that this is a rare phenomenon in Scandinavia (Trägårdh, 1921; Butovitsch, 1954; Eidmann, 1965). In Scotland Ritchie (1917) came to the same conclusion in his cage studies regarding *T. minor.* Using a similar technique, Šrot (1968) demonstrated that sister broods of *T. piniperda* are frequent in Czechoslovakia. He also found that the propensity for sister broods was more pronounced in lowland females as compared with those from higher altitudes. In the former case, 80% of the females established a sister brood, whereas, in the latter case, the corresponding figure was 65%. These sister broods were started 7–10 weeks after the first ones.

It is therefore possible that the observed late broods in the Scandinavian studies were not genuine sister broods, but a continuation of an interrupted oviposition. Thus it may be useful in the further discussion to distinguish between "interrupted oviposition" and "true sister brood". The former situation would be caused by external factors, and the change to new breeding material will not necessarily include a period of shoot feeding before oviposition is resumed, whereas the latter situation would be caused by primarily internal factors and always preceded by a normal first oviposition and a period of regeneration feeding. With such a definition, there is no evidence for true sister broods, neither in *T. piniperda* nor in *T. minor* from northern Europe whereas, in southern Europe, sister broods are frequent in *T. piniperda* as well as in *T. destruens* (Šrot, 1968; Masutti, 1969; Carle, 1973).

Seasonal feeding activity

Seasonal occurrence of pine shoot beetles in pine shoots

The seasonal occurrence of pine shoot beetles in attacked pine shoots is shown in Figure 9. *T. piniperda* was the dominant species in all the study areas. Few specimens of *T. minor* were found in each locality except at Tegnetorp 1974, where the species occurred in almost every sample, although in much less numbers than *T. piniperda.* Since sampling started at different times in different years and localities, it is impossible to tell when shoot-feeding started in each case. The first attacks were, however, observed at Ålgöl and Tegnetorp already in early April of 1973.

A direct observation on the mortality rate of pine shoot beetles during shoot-feeding was not possible, since most samples were frozen before they were studied. Of the 2 287 specimens found in the shoots, only 17 were apparently dead. Of these, 2 were *T. minor* and the remaining 15 specimens *T. piniperda,* and both callow and dark specimens were among the dead ones. Most of them had drowned in the resin flow, but a few were covered by fungi. Apart from this apparent mortality, it can be assumed that at least part of the desiccated specimens (which were seen in some samples) had died naturally in the feeding tunnels. The total mortality did, however, not exceed 10%. Nematodes were frequently found—sometimes in enormous quantities—in beetles, but the influence of these nematodes upon fecundity and mortality rate of the beetles, was not assessed.

In all study areas, empty feeding tunnels were found in nearly all shoot samples. The percentage of empty tunnels varied considerably, but in all years, the number of empty tunnels increased rapidly in late October, and in the month of November practically all pine shoot beetles had left the shoots.

Length and direction of feeding tunnels

All feeding tunnels were measured to the nearest millimetre, and the orientation of the tunnels was noted as being apical or basal. Under natural conditions, all feeding tunnels were orientated apically. Not a single case of clear basal orientation of the feeding tunnel was seen among the thousands of shoots which were dissected during this study. Under crowded conditions, e.g. in cages and in laboratory experiments, a few exceptions from this rule were observed.

The tunnelling lengths varied from a few milli-

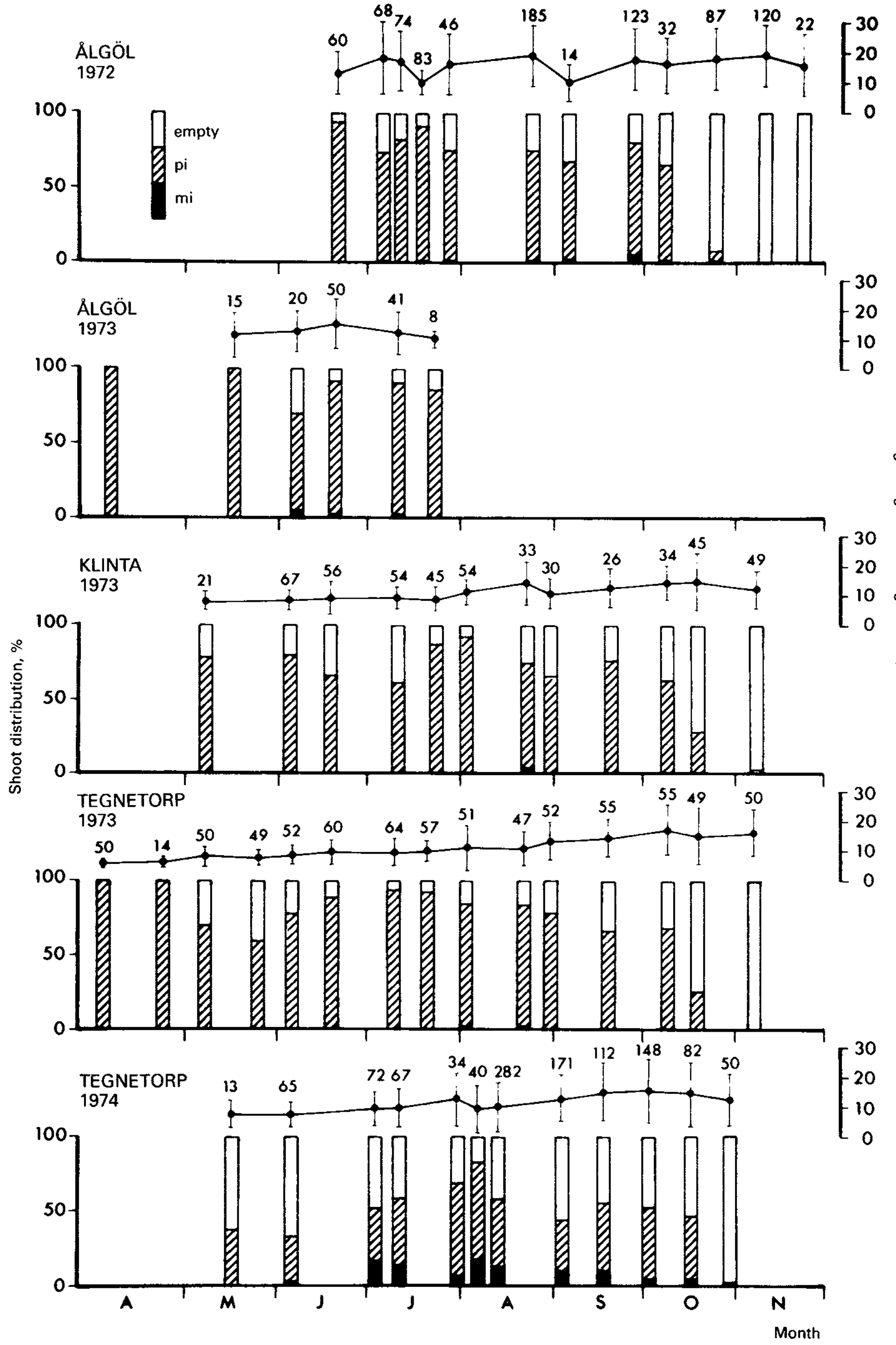

Fig. 9. Seasonal occurrence of pine shoot beetles in attacked pine shoots. The relative frequency (%) of empty feeding tunnels and tunnels containing *T. piniperda* or *T. minor* is shown for each date of sampling. The numbers above columns indicate sample size. The average length of feeding tunnels is indicated by dots above columns, and vertical lines express standard deviation of means.

metres to more than 50 mm. The recorded maximum length was 70 mm. This wide range in tunnelling lengths was observed in all sample series regardless of the inspection date, with the exception of the very first samples taken in April and May. Figure 9 shows the average tunnel length with calculated standard deviations. There was a slight tendency towards increasing mean lengths with time in several sample series. However, this trend was also accompanied by increasing dispersion of the values.

Sex ratio and generation structure

The large pine shoot beetle

All beetles were sexed and dissected in order to find out their state of sexual maturation and age, i.e. whether they belonged to the parent or offspring generation. Owing to difficulties in separating young beetles from old ones (especially males in certain phases of the sexual cycle), a number of the specimens could not be assigned to either group. Accidental desiccation during storage made it impossible to dissect some samples. In these cases, only callow adults could be sorted out with certainty.

Figure 10 shows the sex ratio and population structure of *T. piniperda* in shoot samples in the study areas. The sex ratio was fluctuating around a 1:1 ratio, with the exception of a significant excess of females in early summer. Altogether, the total frequencies of the sexes in the sample series varied around a 1:1 ratio (Table 11 in Långström, 1980 *a*).

As can be seen in Figure 10, the first young beetles were occurring in the shoots in early July. The relative number of young beetles was, however, varying from place to place. Since young males could only be separated from old ones in an early stage of sexual maturation, most of the conclusions had to be drawn from the investigation of females. In 1972, the percentage of young females increased with the proceeding of the summer. In the autumn, the major number of females in the shoots belonged to the new generation. However, old females were still found in the last samples. In 1974, the high percentage of unclassified specimens in July, August and early September was due to desiccated samples.

In the other study areas, very few young beetles were found in the shoots. This result was surprising, especially at Klinta, where the stumps and logging waste from the nearby final-felling were expected to produce large numbers of pine shoot beetles of both species. This was not the case at Tegnetorp, where in 1973, no breeding material was seen in the near vicinity of the study stand.

In Table 4 an attempt has been made to summarize the generation structure of *T. piniperda,* as it appeared in Figure 10. Although this compilation suffers from the fact that a large portion of the specimens could not be classified as old or young, it is evident that at least in these study areas, the feeding of the parent beetles in the shoots was common and may even have been of the same magnitude as that of the young generation.

The lesser pine shoot beetle

Since the total catch of *T. minor* was only 131 specimens, very little can be said about the sex ratio and population structure of this species during the phase of shoot feeding. The sex of each specimen of *T. minor,* as well as its relative age is shown in Figure 11. In many respects, the results resemble those of *T. piniperda.* Young beetles were only to be found at Ålgöl in 1972 and at Tegnetorp in 1974, the first ones occurring in early August. Old females were still recorded in late autumn. For most males it was impossible to decide whether sexual maturation had commenced and whether the elytra were fully darkened. Thus, the above results do not indicate any differences between the two species, in regard to the population structure during the period of maturation feeding.

The course of attacks on marked trees

In 1972, ten young pines were selected at Tegnetorp, and all new attacks were labelled with plastic tape from early July to late September. Simultaneously all new attacks were clipped off in a nearby cage containing young pines and brood logs. In 1973, labelling of attacks was carried out at Klinta on 20 young pines from early June to early October. In 1974, the pine shoot beetle attacks were followed from April to October on young pines at Tegnetorp. Attacks were labelled on 30 trees, and in the same stand all new attacks were clipped from 15 trees. In 1975, attacks were again marked on 15 trees at Tegnetorp. In all these years, maximum tree height was approximately 2.5 m.

The seasonal course of attacks differred considerably from year to year (Fig. 12). In 1972, only a few attacks were found on the marked trees, whereas frequent attacks occurred simultaneously in the large cage. In both cases, inspections started too late to catch the parent beetles. Thus, these curves show the

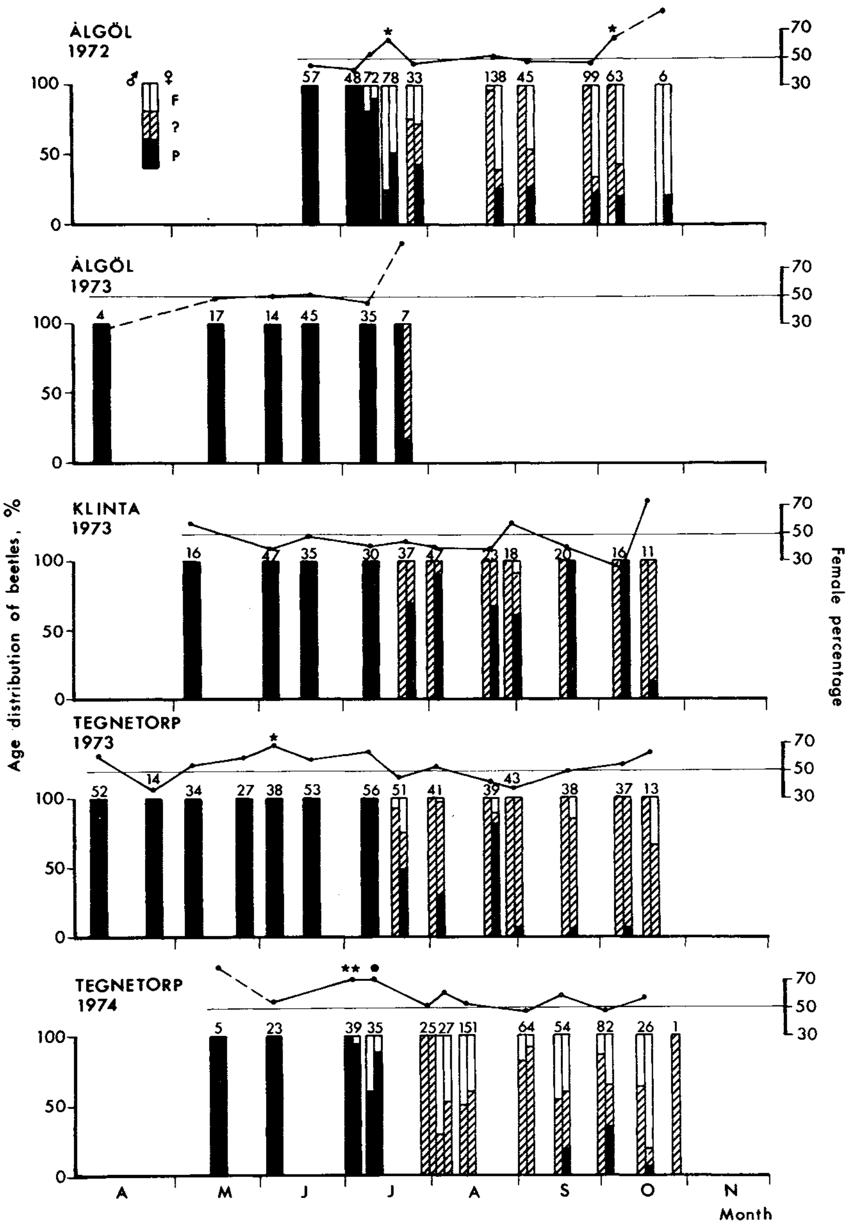

Fig. 10. Sex ratio and generation structure of *T. piniperda* during the period of feeding in pine shoots. In each pair of columns the left one refers to males and the right one to females. The percentage of parent beetles (P) is indicated in black, that of young beetles (F) in white, and the frequency of unclassified specimens is hatched. Figures above columns indicate number of beetles in each sample. The sex ratio is expressed as female percentage (solid line with dots). Significant deviations from a 1:1 sex ratio are marked with one or two asterisks according to level of significance (see, Table 1).

accumulated attacks of the new generation inside and outside the cage. In both cases the damaged shoots were collected. Thus these beetles were prevented from further feeding which, especially in the cage, must have affected the later course of feeding activity.

The following year, many of attacks were found during the first inspection at Klinta. New damaged shoots were observed and labelled to early October, but the increase in attacks was very slow after early July. A similar pattern was seen in 1975 (Tegnetorp) but in this case nearly all attacks were recorded in April and May. In 1974, attacks occurred throughout the growth period.

Table 4. *Percentages of parent (P), unclassified (?) and young (F) beetles amongst the males and females of T. piniperda in the shoot samples which were collected during the study period 1972–1975. Total numbers are given in brackets. Further information obtainable in the text*

Study area and year		Males				Females			
		P	?	F	Total	P	?	F	Total
Ålgöl	1972	30.8	57.9	11.3	100.0 (302)	47.0	11.0	42.0	100.0 (336)
Ålgöl	1973	100.0	0.0	0.0	100.0 (61)	91.8	8.2	0.0	100.0 (61)
Klinta	1973	42.0	58.0	0.0	100.0 (169)	84.0	15.3	0.7	100.0 (131)
Tegnetorp	1973	44.6	54.6	0.8	100.0 (251)	68.4	26.3	5.3	100.0 (285)
Tegnetorp	1974	12.1	57.3	30.6	100.0 (232)	29.0	41.7	29.3	100.0 (300)
Tegnetorp	1975	93.3	6.7	0.0	100.0 (15)	91.7	8.3	0.0	100.0 (12)

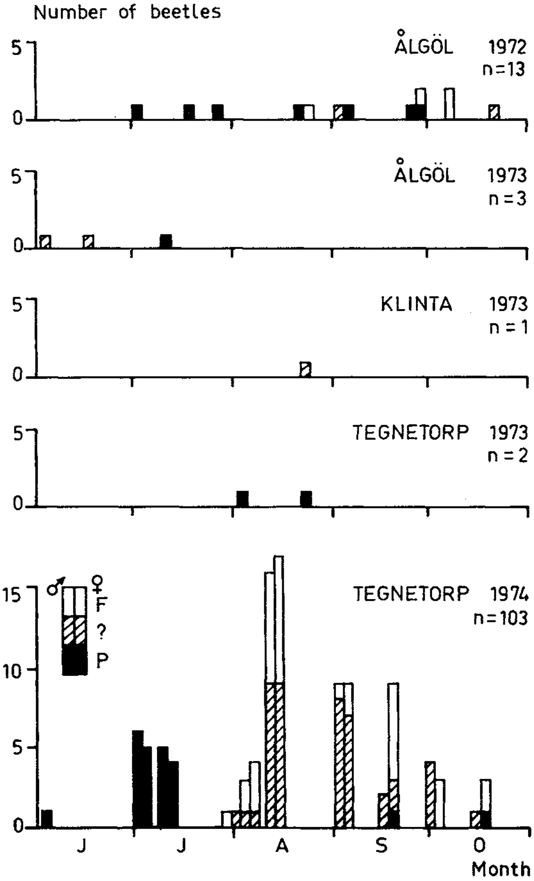

Fig. 11. Population structure of *T. minor* during the phase of shoot-feeding. Sex and relative age of each individual beetle in given according to the legend in the previous figure.

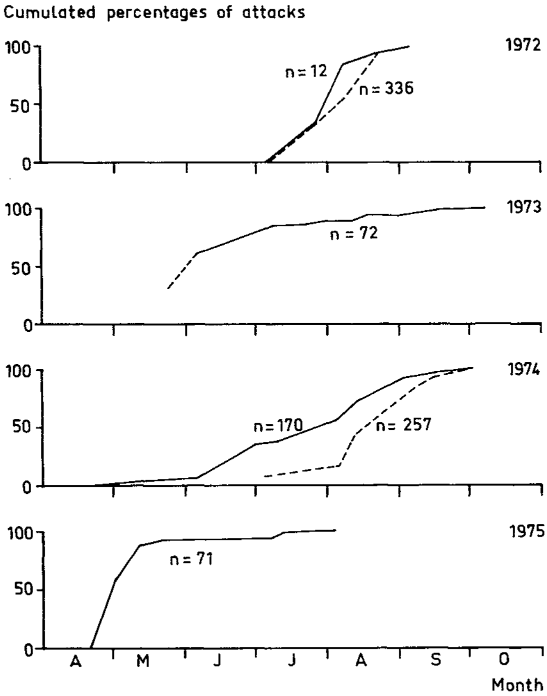

Fig. 12. The course of pine shoot beetle attacks on regularly inspected young pines in 1972–1975. In 1972, new attacks were also counted on pines in a cage (broken line). New attacks were clipped off in experiments in 1972 and 1974 (broken lines), whereas they were marked with plastic labels in all others (solid lines).

Thus, the present material indicates two different attack patterns. At Klinta (1973) and Tegnetorp (1975) most shoot feeding took place early in the season, whereas in the other cases, attacks were gradually accumulating over a long period of time.

If these results are seen against the background of the population structure which was described in the previous section, it becomes obvious that the observed attack patterns reflect differences in the local beetle populations. A steep increase of shoot feeding early in the season was connected to a population structure, where parent beetles were dominant (Klinta 1973, Tegnetorp 1975). At Tegnetorp 1974, the majority of the population was young beetles, and consequently a large portion of shoot-feeding took place late in the season.

Termination of shoot-feeding

Figure 9 showed the sudden increase of empty feeding tunnels in late October, indicating the termination of the beetles' feeding activity. In 1974, this came under direct study and the results are shown in Figure 13. Altogether, the stem funnels on three pines caught a total of 31 pine shoot beetles, all being *T. piniperda* (11 males, 20 females). During the same period of time, shoots were collected on two circle plots, each being 4 m^2 in size, under the canopy. These shoots contained a total of 30 pine shoot beetles, two thirds being *T. minor* and one third *T. piniperda.* After 28th October, no pine shoot beetles were left in the shoots on the ground.

As can be seen in Figure 13 (and Fig. 1), the departure from the pine shoots was preceded by a period of cold weather. In all years these first periods of night frost occurred in late October, except in 1976, when this happened already in September, but unfortunately no shoot samples were taken that year.

Discussion

The destructive feeding behaviour of the pine shoot beetles was familiar already to Linnaeus, who gave the specific name "piniperda" and characterized the species as "hortulanus naturae famulus" (see Ratzeburg, 1839). The existence of two different feeding periods, one in early summer and another in the autumn, was noted by several authors in the 19th century (see e.g. Ratzeburg, 1839; Holmgren, 1867; Altum, 1881) but the full explanation to this phenomenon was provided by Knoche (1904). He demonstrated the importance of the maturation and regeneration feeding for the sexual maturation of the young and parent beetles, respectively.

The regeneration feeding of parent beetles after oviposition has thereafter been observed to occur regularly in both species (see e.g. Trägårdh, 1921; Greese, 1926). However, shoot-feeding has also been found to occur very early in the season, before or during the flight period (Ritchie, 1917; Salonen, 1973).

The present results show that shoot-feeding of pine shoot beetles occurred from early spring to late autumn. However, the seasonal course of attacks varied from year to year and from place to place. *T. piniperda* was the dominant species in all study areas, while *T. minor* was occurring in numbers only at Tegnetorp in 1974. The first specimens of the latter species were not to be found in the shoots until early June, but the material is too small to allow any conclusions regarding possible differences in the seasonal feeding patterns between the species.

The termination of the shoot-feeding in the autumn, seems to coincide with periods of low temperatures. However, the termination of the feeding activity may be initiated by other factors, such as photo-

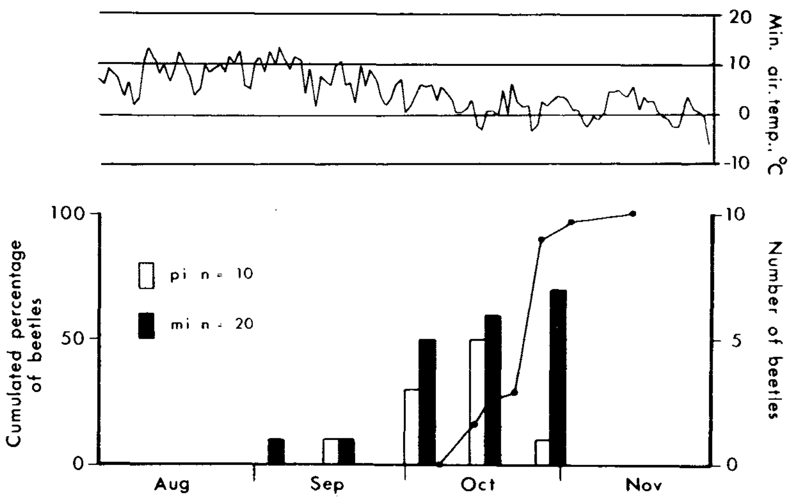

Fig. 13. The termination of shoot-feeding at Tegnetorp 1974. Solid line with dots shows cumulative percentages of pine shoot beetles (*T. piniperda* only, $n=31$) which were caught in stem funnels. Columns show the number of *T. piniperda* (white) and *T. minor* (black) in shoots on the ground under the canopy. Temperature curve shows daily minima at Simonstorp according to data from SMHI.

period or internal physiological stimuli. The different frequencies of *T. piniperda* and *T. minor* in stem funnels and shoot samples from the same trees may indicate behavioural differences between the species. Since active flight is not likely under the prevailing temperatures, the beetles may either drop themselves to the ground, or walk down along the branches and the trunk. The observations indicated, that at least some specimens of *T. piniperda* actively walked down along the trunk towards the hibernation sites at the base of the stem.

The pine shoot beetles cannot hibernate in the shoots in the pine crowns. They would not survive the Scandinavian winter temperatures in the shoots (cf. Annila & Perttunen, 1964; Bakke, 1968). The results of Greese (1926) indicate that in the Ukraine *T. minor* does not hibernate in the shoots. Similar results are given by Šrot (1968) regarding *T. piniperda* in Czechoslovakia. However, according to Ritchie (1917) the beetles may in Scotland spend the winter in the shoots. In southern Europe, hibernation in the shoots seems to occur regularly. According to Masutti (1969) *T. piniperda* may in Italy hibernate either in the shoots or at the stem base. In southern France this species as well as *T. destruens* have been observed to hibernate in the shoots (Carle, 1973).

Quantitative aspects on shoot-feeding

Cage studies

In 1972, pine billets containing developing broods of *T. piniperda* and *T. minor* were put into a large cage of nylon netting which had been raised over young pines. The pines were inspected several times and all attacks were removed. In both species more than 400 exit holes were found on the billets, whereas the total recapture of beetles in the shoots was only 18% in *T. piniperda* and 57% in *T. minor*. The average length of feeding tunnels was less than one centimetre. Competition for suitable shoots had apparently been very strong, and obviously a shortage of shoots had developed in the cage.

In 1973, two smaller cages were used. The regeneration feeding of *T. piniperda* was studied as well as the propensity of the females to resume oviposition. After about two months, approximately half of the released beetles were found to be alive in the shoots (Table 5). No dead beetles were seen in the shoots. It is not known whether the missing beetles had died or made their way out of the cages. The rate of recapture and the feeding activity was of the same magnitude in both sexes. Approximately 50% more feeding tunnels were found than the number of released beetles.

In 1974, the upper whorls of young pines were enclosed in bags of synthetic curtain netting with a smaller mesh size (approximately 0.5 mm) than had been used in the previous years. Males and females of both species were released in the bags at three occasions: (1) swarming beetles in April (2) parent beetles in June (3) young beetles in July. In October the pines were cut and all twelve bags were carefully examined.

The survival of the beetles in the bags varied very much (Tables 6 and 7). After two months, about 60% of the young beetles of both species were found alive whereas the remaining ones had disappeared. For *T. minor* survival rates decreased according to the time the beetles had been enclosed in the bags, whereas for *T. piniperda,* approximately the same percentages were recaptured from the first and second date of enclosure.

Table 5. *Regeneration feeding of T. piniperda on two caged young pines. Tegnetorp 1973. Further information obtainable in the text*

Number of beetles released on 21st July	Number (and percent) of beetles recaptured on 20th Sept.	Number of feeding tunnels	Average length of feeding tunnels	Average number of tunnels per beetle
22 males	10 (46%)	33	14.7 ±8.3	1.5
28 females	14 (50%)	44	12.7 ±8.6	1.6
$\chi^2=0.04$ (*d.f.*=1)			$t=1.56$ (*d.f.*=75)	

Table 6. *Shoot-feeding and survival of T. piniperda in bag cages at Simonstorp 1974. Average tunnel lengths are given as means ± standard deviations (ranges in brackets). Further information obtainable in the text*

Number of beetles and period of enclosure	Number of surviving beetles (%)	Total number of feeding tunnels	Average tunnel length, mm, (range)	Tunnel length/ enclosed beetle, mm	Entrance hole/ enclosed beetle
14♂♂ 12.4–2.10	6 (42.9)	25	14.1 ± 9.1 (4–30)	25.1	1.7
14♀♀ 12.4–2.10	3 (21.4)	22	10.9 ± 8.5 (3–32)	17.1	1.6
14♂♂ 7.6–23.9	7 (50.0)	12	16.7 ±12.4 (2–36)	14.3	0.9
12♀♀ 7.6–23.9	2 (16.7)	14	11.7 ±10.3 (3–35)	13.7	1.2
30♂♂ 12.7–23.9	19 (63.3)	49	21.7 ±16.1 (5–75)	35.5	1.6
30♀♀ 12.7–23.9	20 (66.7)	61	19.5 ±15.7 (3–70)	39.6	2.0

The results generally indicated a lower rate of female recapture. However, Chi-square tests (2×2 contingency tables) did not reveal any significant differences in recapture between sexes (in those three cases where no values were <5).

Again, the number of feeding tunnels in most of the bags was higher than the number of released beetles. The length of feeding tunnels varied from a few millimetres to several centimetres, the maximum length being 7 cm. The feeding tunnels were generally shorter in *T. minor* than in *T. piniperda* and in three cases the difference was significant ($t_{(\text{swarming males})} = 2.62^*$, *d.f.* = 50, $t_{(\text{re-emerging males})} = 2.08^*$, *d,f,* = 60, $t_{(\text{re-emerging females})} = 2.97^{**}$, *d.f.* = 76). No significant differences were found between the sexes regarding mean tunnel lengths. All the beetles were dissected and their sexual maturity was inspected. Both males and females were in an advanced state of sexual maturation, and it was concluded that the recaptured beetles had undergone a normal sexual development.

Field observations

In april 1973, many fresh attacks of pine shoot beetles were found at Tegnetorp, On 4 th April, a total of 63 attacks were labelled on 10 trees. These shoots were cut and inspected on the 30th August 1973, and the results are shown in Table 8.

Five months after the attacks were labelled, 40% of the tunnels still contained living beetles. Since there is little reason to believe that the beetles may have left the tunnels and returned to them later, the most likely conclusion is that the beetles had stayed in the shoots for 5 months. The percentage of empty tunnels corre-

Table 7. *Shoot-feeding and survival of T. minor in bag cages at Simonstorp 1974. For further information, see legend to Table 6*

Number of beetles and period of enclosure	Number of surviving beetles (%)	Total number of feeding tunnels	Average tunnel length, mm, (range)	Tunnel length/ enclosed beetle, mm	Entrance hole/ enclosed beetle
30♂♂ 13.4–3.10	5 (16.7)	27	8.6 ± 6.2 (2–30)	7.8	0.9
30♀♀ 13.4–3.10	3 (10.0)	25	7.7 ± 4.8 (3–23)	6.4	0.8
31♂♂ 7.6–3.10	15 (48.4)	50	11.4 ± 6.8 (3–31)	18.5	1.6
23♀♀ 7.6–20.9	8 (34.8)	29	8.9 ± 7.3 (2–30)	11.1	1.3
23♂♂ 12.7–2.10	15 (65.2)	34	12.7 ± 9.3 (3–45)	18.7	1.5
23♀♀ 12.7–3.10	13 (56.5)	47	14.4 ±10.3 (4–35)	29.3	2.0

Table 8. *Presence of pine shoot beetles in a shoot sample on the 30th August, 5 months after the attacks were observed and labelled. Tegnetorp 1973*

Attack description	Number	Per cent
Tunnels with living beetles	26	41.3
Tunnels with dead beetles	2	3.1
Empty tunnels	24	38.1
Occluded tunnels	11	17.5
Total	63	100.0

sponds well with other results in this study. Nearly a fifth of the tunnels were occluded by callus tissue less than six months after the attack.

If these attacked shoots are regrouped according to the presence of beetles in relation to shoot vitality, it becomes clear that the beetles leave the tunnels when the damaged shoots start wilting (Table 9).

It is, however, obvious that the vigour of the shoot depends on its size. The shoot diameter at the entrance hole was measured in April to the nearest 0.5 mm. The mean diameter of all shoots was 4.5 ±1.0 mm, but the thickness of those shoots that would eventually die in the course of the summer was 4.2 ±1.1 mm. The corresponding figure for the shoots that would heal over the feeding tunnels was 5.1 ±1.8 mm. However, these means did not differ significantly from each other (*t*-test). A larger difference would have been expected between the victims and survivors among the shoots, since the total range in shoot diameter was from 3 to 7 mm. The most vigorous shoots reacted strongly with abnormal growth, and in August the shoots had swelled to more than 2 cm in thickness over a length of a few centimetres. The feeding tunnels had healed over, and therefore no beetles were present in these shoots.

Table 9. *Presence of pine shoot beetles in feeding tunnels in relation to shoot vitality. Same sample as in Table 8, but occluded tunnels and those containing dead beetles have been omitted*

Shoot vitality	Beetles in tunnel	Empty tunnel	Total
Shoot alive, green cambium at entrance hole	26	3	29
Apical part of shoot dead, no green cambium at entrance hole	0	21	21
Total	26	24	50

Discussion

The average length of feeding tunnels in both naturally infested shoots and caged shoots was found to be less than 2 centimetres. These results agree quite well with the few existing observations in literature. According to Sylvén (1916) the corresponding figure was only 8 mm, whereas Šrot (1968) gives 1.6–2.3 cm as the average tunnelling length of parent beetles during regeneration feeding.

Although many of the caged beetles could not be recollected, this study has shown that many beetles may survive from spring to autumn, and that shoot feeding may extend over such a long period of time. Butovitsch (pers. comm.) came to similar results in his cage studies in northern Sweden. His studies (as well as the present one) failed to give a definite answer regarding the time and amount of food which the beetles required to reach sexual maturity. According to him, a young pine shoot beetle on average excavates 1–3 shoots during its maturation feeding. Population estimates in pine stands gave a rough average of 1–2 beetles per fallen shoot (Långström, 1979). However, these estimates tell nothing about the actual consumption of shoot tissue in different phases of the beetles' life cycle.

The shoot-feeding has been studied under laboratory conditions at constant temperatures by Larroche (1971, see Carle, 1973) and Carle (1973). *T. destruens* became sexually mature in 46–49 days at a temperature of 15°C, whereas *T. piniperda* needed only 27–35 days. In this respect *T. minor* was intermediate between the other two species. According to Salonen (1973) *T. piniperda* finished its maturation feeding in a period of 3–4 weeks at room temperature (22–24°C). However, no information is provided regarding the amount of shoot tissue consumed.

Distribution of pine shoot beetles within pine crown

Distribution in relation to shoot age and size

In 1974, more than 1500 pine shoot beetle attacks were counted on felled trees at Tegnetorp. Approximately one third of these contained pine shoot beetles, 83% being *T. piniperda,* and 17% being *T. minor.* The distribution of these beetles in shoots of different age can be seen in Table 10. The criterion used for grouping the data was the age of the internode where the entrance hole was situated.

The frequency distribution according to the shoot age was quite similar in both species. About 40% of the attacks occurred in the current year's shoots, 50% in one-year-old and the remaining attacks in older shoots.

The shoot diameter was measured at the entrance hole for all shoots containing *T. minor* and a sample of shoots containing *T. piniperda* (sample tree of 14th August). The shoots were grouped in diameter classes of 0.5 mm class width. The diameter ranged from 2.0 to 6.0 mm (Fig. 14). The means were compared by Student's *t*-test. No significant differences were found between *T. piniperda* and *T. minor* when pairs of means were tested within the same shoot age. Neither did the means differ significantly when all shoots containing *T. piniperda* were tested against those containing *T. minor.*

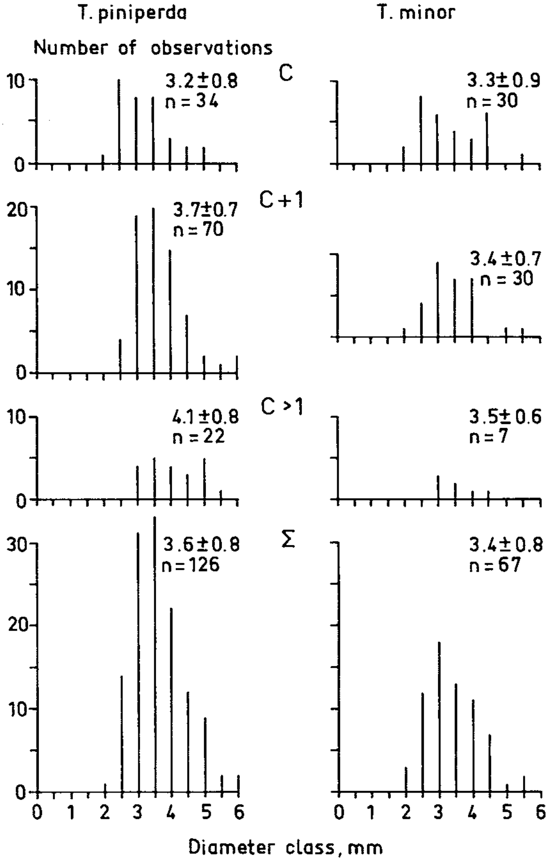

Fig. 14. Distribution of shoots damaged by *T. piniperda* and *T. minor* according to shoot age and diameter at entrance hole of feeding tunnel. The shoot sample contains all measurable shoots with. *T. minor* from 1974 and all *piniperda*-shoots from one sample tree, which was felled on 14th August. Letter C refers to current shoots, C+1 to one year old shoots and C >1 to older shoots.

Location of entrance hole

The location of the entrance hole on the shoot axis was studied in the shoot samples just mentioned. The position of the entrance hole was described as the distance in mm to the apical node or bud. As can be seen from Figure 15, most entrance holes were situated within the first centimetre from the bud or node. Since many of the distant entrance holes occurred in shoots with multiple attacks, it is obvious that the beetles have a preference for the outermost part of the shoots regardless of their age. This pattern was similar in both species, and all shoot ages.

Table 10. *Per cent distribution of T. piniperda and T. minor in attacked shoots of different age. Tegnetorp 1974*

	Entrance hole in				
Species	current shoot, C	1-year-old shoot, C+1	older shoots, C >1	Total	Number of beetles
T. piniperda	37.3	51.8	10.9	100.0	461
T. minor	37.6	46.3	16.1	100.0	93

Chi-square analysis of 2×3 contingency table $\chi^2=2.32$, *d.f.* =2

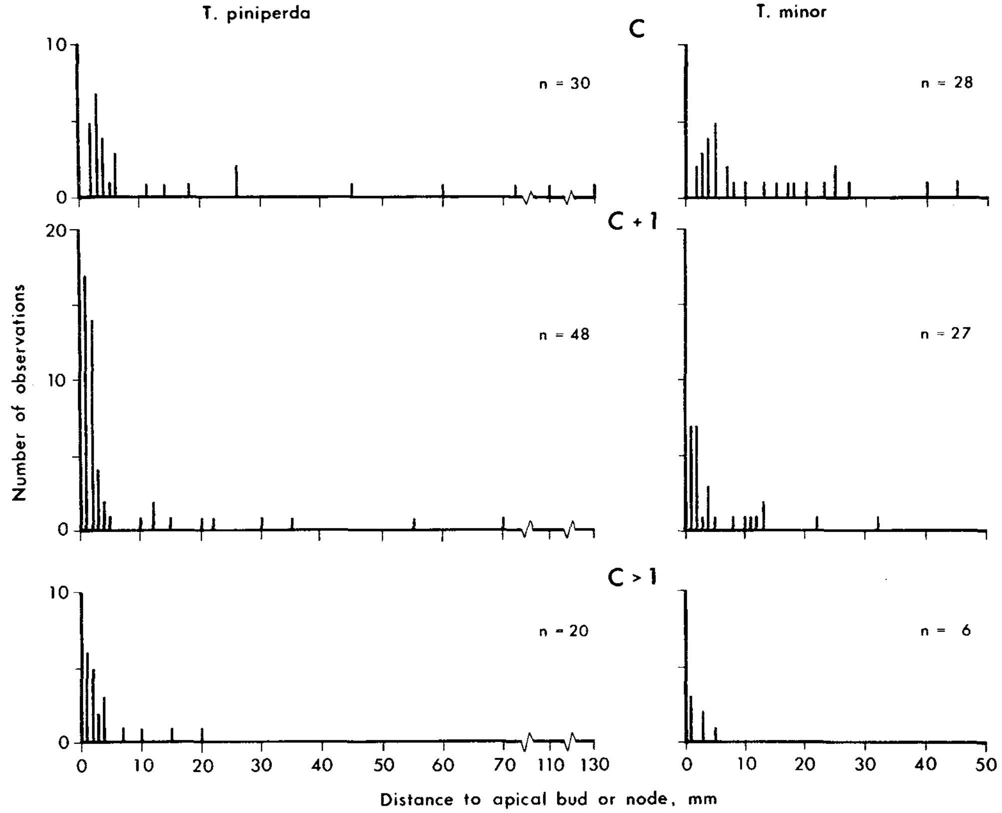

Fig. 15. Location of entrance hole to feeding tunnel on attacked shoots according to beetle species, shoot age and distance to apical bud or node. Same shoot sample as in previous figure, but broken shoots were omitted. For further explanations, see legend to Figure 14 and the text.

Vertical distribution

Table 11 shows that both species were distributed all over the pine crown. However, there was a tendency towards a higher concentration of *T. piniperda* in the upper whorls compared with *T. minor,* which reached e.g. 30% and 60% levels (of cumulated percentages), two whorls below *T. piniperda.* According to a median test (see Zar, 1974), the medians differred significantly ($p < 0.001$) from each other (Table 12), indicating a real difference in vertical distribution between the species.

Discussion

The results indicate a similar attack pattern for *T. piniperda* and *T. minor.* Whether the observed difference in vertical distribution between the species was occasional or real cannot be stated without further studies. However, Sylvén (1916) observed that *T. piniperda* preferred vigorous shoots of "1st and 2nd order" whereas *T. minor* mostly was found in shoots of "higher orders". Unfortunately, he made no measurements of the shoots and gave no explanation for the order classification.

Since this study was confined to young pines, it

Table 11. *Per cent distribution of T. piniperda and T. minor in whorls of sample trees at Tegnetorp 1974*

Whorl number	*T. piniperda*, %	*T. minor*, %
1 (1974)	3.7	
2 (1973)	7.3	2.3
3 (1972)	19.3	12.8
4 (1971)	7.9	2.3
5 (1970)	6.0	7.0
6 (1969)	17.0	11.6
7 (1968)	11.6	9.3
8 (1967)	9.7	17.5
9 (1966)	7.3	22.1
10 (1965)	5.1	7.0
11 (1964)	3.0	8.1
12 (1963)	1.9	
13 (1962)	0.2	
Total	100.00	100.0
Number of beetles	466	86

Table 12. *Median test of the data in Table 11. Frequencies of median whorl (number 6) have been omitted*

	T. piniperda	*T. minor*	Total
Above median	206	21	227
Below median	181	55	236
Total	387	76	463
Chi-square analysis	$\chi^2 = 15.64^{***}$	($d.f. = 1$)	

does not tell anything about the distribution of the species in mature or over-aged pines. Sylvén (1916) has suggested that. *T. minor* may prefer older pines than *T. piniperda* for its maturation feeding. He found that *T. piniperda* was the dominant species in 20-year-old pines, wereas *T. minor* was more frequent in one 80-year-old pine. This idea gets some indirect support from the findings at Klinta 1973, where *T. minor* was the dominant species in the flight traps, but no specimens were found in the young stand, where trees were felled and studied. Unfortunately it was not possible to fell mature pines in the nearby stand.

In September 1977, the crowns of a few windthrown pines were examined in a stand of seed trees close to the Klinta area. Of the 42 beetles which were found in the crowns of the felled trees, 29% were *T. minor*. In broken shoots on the ground below the seed trees, 33 beetles were found, and of these 67% were *T. minor*. In a similar stand at Garpenberg, one wind–thrown pine was examined in September 1977. In the crown of this tree only 7 beetles were found, 3 of them being *T. minor*.

Altogether, these figures give some evidence for the hypothesis that *T. minor* may prefer old trees for its shoot-feeding. As a matter of fact this could be understood as a natural adaptation to conditions prevailing at most breeding sites of *T. minor*, which are windthrown trees and logging waste after clear fellings and late thinnings.

Conclusions

Shoot-feeding in relation to life cycle

The life cycle and the seasonal course of shoot-feeding are summarized in Figure 16. The course of the shoot-feeding and the three feeding periods are shown schematically. As will be seen below the course of attacks is probably largely influenced by size and structure of the beetle population.

Naturally, the seasonal course of shoot-feeding is linked to the re-emergence of parent beetles and emergence of the young generation. Since the time of parent departure from brood logs may vary considerably (from early May to late summer), depending on weather conditions, and probably also on competition and substrate quality, the time of commencement of the regeneration feeding may vary from place to place and year to year. Similarly, the start of maturation feeding is affected by the course of emergence of the young beetles. In 1973 and 1975, shoot-feeding was observed already during the flight period, and this early feeding may have occurred in other years as well. Salonen (1973) has suggested that this early feeding is done by individuals which had not finished their maturation feeding in the previous autumn. However, dissections of beetles in the present material did not support this hypothesis. Not a single clearly immature or developing specimen could be found in the samples which were collected during April or May.

Abnormal feeding activity may be caused eg. by endoparasites (cf. Greese, 1926; Gurando & Tsarichkova, 1974). Although nematodes were frequently found in the abdomen of pine shoot beetles, sexual maturation of these infested beetles was not—at least not at a visual judgement—much affected by the nematodes. However, there were exceptions where the sexual organs were undeveloped and clearly misshaped, and in these cases enormous amounts of nematodes were present in the beetles.

There was something strange with the beetles from the study areas where this early feeding was seen. Later in the season many females were found which were difficult to classify according to their sexual maturity. These females were suspected of not having laid eggs at all. These ovaries were typically senile in their general appearance, but *corpora lutea* were lacking. If these females really were in a state of declining fertility, they must have been prevented from breeding for some reason.

The availability of suitable breeding material is a major factor in the population dynamics of the pine shoot beetles. What happens if the beetles fail to find suitable breeding material? In 1974 there were large amounts of fresh logging waste at Tegnetorp and practically none the next year. The course of shoot

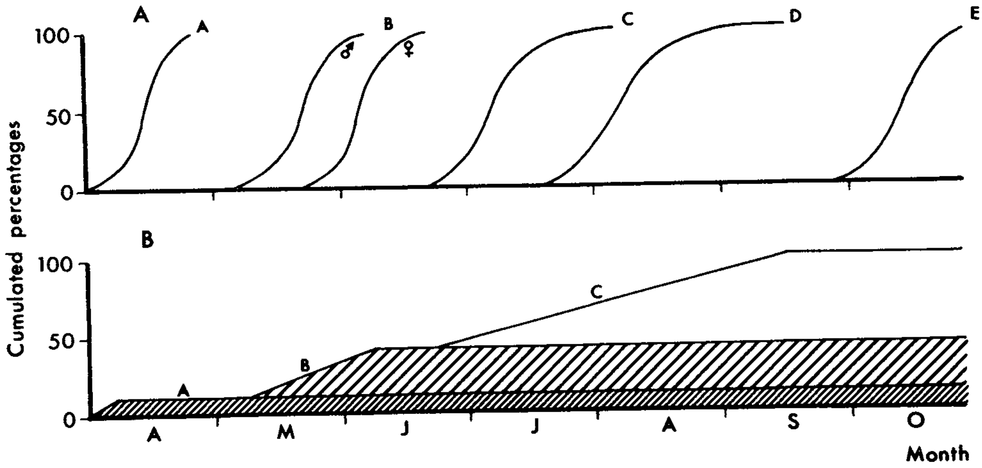

Fig. 16. Schematical representation of the life cycle (A) and the maturation feeding (B) of the pine shoot beetles according to field data from Simonstorp 1972–1976. The upper curves show (a) the flight period, (b) reemergence of parent beetles, (c) (d) emergence of *T. piniperda* and *T. minor* respectively and (e) termination of shoot-feeding. The lower figure shows the seasonal course of the maturation feeding divided in three hypothetical feeding periods: (a) early shoot-feeding of nonbreeding (?) beetles, (b) regeneration feeding of parent beetles and (c) maturation feeding of young beetles.

attacks on marked trees differed radically between these two years (cf. Fig. 12).

Although vague, these results may indicate that the occurrence of the early shoot feeding may be related to a shortage of suitable breeding material. Thus, the early shoot-feeding could be a way to avoid starvation when the beetles have exhausted their food resources during the search for breeding material.

The early shoot-feeding is interesting from another point of view, too. As was seen above, parent beetles were found in the shoots throughout the summer season. It was also found that there is no propensity for sister broods. Thus, the surprising fact seems to be that part of the population may spend the whole summer season (aestivating or diapausing?) in the shoots apparently awaiting a second hibernation and a new flight period. The mechanism preventing the beetles from a second flight period is probably behavioural (cf. Perttunen & Häyrinen, 1970). From an evolutionary point of view it can be understood that such behaviour may be an adaptation for survival under the harsh climatic conditions prevailing in the most northerly part of the dispersal area, where the brood in some years may not develop successfully (see eg. Kangas 1963, Juutinen 1978). But it is more difficult to accept this phenomenon in southern Scandinavia, where the climate in most years would allow the development of another brood (cf. Salonen, 1973).

The seasonal course and intensity of shoot-feeding depends on the structure of the local pine shoot beetle population, i.e. the proportions of nonbreeding beetles, re-emerging parent beetles and emerging young beetles in the population. If breeding material is absent or very scarce, the first group will dominate and the shoot-feeding will culminate very early in the season. If breeding success is low, there will be comparatively few young beetles. In such a case regeneration feeding of parent beetles will dominate, and consequently the shoot-feeding will culminate in early summer. If again, the population increase in large, the young beetles will be responsible for most of the shoot-feeding which in such a case will reach its maximum in late summer.

Elements pertaining to these feeding types can be traced in the present material (cf. Fig. 12). Tegnetorp 1974 represents the situation in the year of felling when plenty of breeding material is available and the population increase is large. Consequently, the young beetles dominate in the local population, and most attacks in pine shoots occur late in the season. Tegnetorp 1975 shows the situation with a high local beetle population, and a relative shortage of breeding material. Population increase will then be low and perhaps part of the beetles do not breed at all. Thus, shoot damage mainly occurs early in the season.

Before far-reaching conclusions can be drawn from these results, more quantitative information is needed about the beetle populations and the shoot-feeding. If significant shoot-feeding occurs only at very high population levels, then the regeneration feeding of parent beetles is probably not attaining such critical levels very often. Unfortunately, there is very little information on the relation between population size and subsequent shoot damage. However, it has been demonstrated that high population levels do not necessarily imply a high breeding success, although this often seems to be the case (Långström, 1979). For example, it can be mentioned that the population at Ålgöl 1972 was estimated to be about 200 000 pine shoot beetles, 38% of these being parent beetles.

The general impression was that the intensity of attacks was lower in those study areas where the regeneration feeding of the parent beetles was predominant (Ålgöl 1973, Klinta 1973, Tegnetorp 1973, 1975) as compared with those cases where the young beetles dominated (Ålgöl 1972, Tegnetorp 1974).

Practical implications

The general opinion has been that the young pine shoot beetles are responsible for most of the shoot feeding in the pine crowns. Consequently, most control measures aim at preventing the emergence of the new generation (see eg. Anon., 1978). However, the present study shows that considerable shoot-feeding may take place before the young beetles emerge. Furthermore, there is some evidence for the fact that the population increase may be moderate or low in areas with high population densities owing to severe intraspecific competition (Dehlen & Långström, 1977; Långström, 1979). In such a case the parent beetles will constitute a large proportion of the local population.

Thus, some shoot-feeding will take place early in the season in one-year-old or even older shoots, and not always predominantly in the current shoots as generally has been assumed. Since each attack in an older shoot eventually may cause the death of several current shoots, while an attack in a current shoot only affects that particular shoot, it becomes obvious that the shoot-feeding early in the season may exert a greater impact upon pine growth than has been anticipated.

On the other hand, artificial defoliations have shown that the pines reacted differently, when needles were removed early or late in the season; the late defoliation having a more severe growth impact than the early one (Ericsson et al., 1980 *b*). This difference in response may be linked to the seasonal changes in the carbohydrate reserves, which have been discussed by Ericsson et al. (1980 *a*). It has also been shown that the net photosynthesis of an early attacked shoot was dramatically reduced a month after the attack, whereas the reaction on a late pine shoot beetle attack was immediate but more moderate (Troeng et al., 1979).

Thus, with the present state of knowledge, it it not possible to compare quantitatively the significance of the early shoot feeding with that of the late one. Further research is needed on the population dynamics of the pine shoot beetles as well as on the physiological interaction between the pest and the host. It may, however, become necessary to reconsider the present schemes of forest protection. At least in certain situations with very high population levels, it may be necessary to time the control measures in such a way as to prevent the re-emergence of the parent beetles. In practical terms this would mean that control measures in such extraordinary cases should be carried out within a few weeks after the flight period. Technically this could be achieved by quick hauling, barking or spraying with insecticides, but the main problem for an adequate operational planning is probably the recognition of such high hazard areas.

The present study has confirmed the generally accepted rule that very few attacks take place after the main flight period. Thus, pine wood felled after the flight period can be stored in the forest during the remainder of the year without being infested with pine shoot beetles. The schemes for early thinning (= cleaning) of young pine stands are also based upon this fact.

The present study has also shown that the shoot-feeding behaviour of *T. minor* is as destructive as that of *T. piniperda* although the former species generally occurs in smaller numbers than the latter one. However, if the hypothesis that *T. minor* prefers old pines for its maturation feeding can be confirmed, this implies that the most valuable increment may be affected particularly by this species. Besides the impact on growth, it is obvious that the shoot feeding may negatively affect the cone production of seed trees. Thus, there is no reason to consider the shoot-feeding of *T. minor* to be less important than that of *T. piniperda*.

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