

Susceptibility of Defoliated Scots Pine to Spontaneous and Induced Attack by *Tomicus piniperda* and *Tomicus minor*

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In 1990–1991, *Diprion pini* extensively defoliated Scots pine (*Pinus sylvestris* L.) trees in Lauhanvuori National Park in southwestern Finland. Many trees lost all their foliage, while others had ca. 10 % foliage left after the second year of defoliation. Outside the national park, many nearby stands were also heavily defoliated in 1990, but were sprayed with diflubenzuron (Dimilin®) in 1991. This protected the current year needles, corresponding to ca 30 % of full foliage.

In spring 1992, pine trees with 0, 10, 30 and 100 % foliage remaining (10 small and 10 large trees in each category) were baited with pine bolts to induce stem attacks by pine shoot beetles. All baited trees were attacked by *Tomicus piniperda* and some by *T. minor*. The attacks failed in all these trees except those that were totally defoliated and some of the small trees with 10 % foliage left. Many unbaited trees escaped attack entirely, but only totally defoliated trees were successfully colonized (i. e. produced brood). Attack densities and brood production figures peaked in baited, large and totally defoliated trees. None of the measures (cambial electrical resistance, resin flow, induced lesion length by fungal inoculation, amount of hydrocarbons or phenolic compounds) used to describe tree vigour at the time of attack gave better information than the estimated remaining foliage.

We conclude that the risk for beetle-induced mortality following defoliation is a function of remaining needle biomass and beetle pressure. Even at high beetle densities (as was simulated by baiting of trees), trees with 10 % of the foliage remaining were able to defend themselves against attacking pine shoot beetles.

Keywords Scolytidae, Diprionidae, induced attack, Scots pine, *Tomicus piniperda*, *Tomicus minor*, *Diprion pini*, defoliation

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1 Introduction

In Scandinavia, outbreaks of defoliating insects in forests of Scots pine (*Pinus sylvestris* L.) have occurred during almost every decade of the last two centuries (Lekander 1950). Among these defoliators, the European pine sawfly, *Neodiprion sertifer* (Geoffr.) (Hymenoptera: Diprionidae), is the most common species causing severe defoliation on vast areas from time to time (Lekander 1950, Christiansen 1970, Ehnström et al. 1974, Austarå et al. 1983, Juutinen and Varama 1986, Virtanen et al. 1996). Outbreaks of *Diprion pini* (L.) (Hymenoptera: Diprionidae) are less frequent and more local than those of the former sawfly species (Lekander 1950, Kangas 1963, Ehnström et al. 1974, Austarå et al. 1983), but *D. pini* is more harmful. This is because *D. pini* larvae eat all age classes of needles in late season, whereas *N. sertifer* larvae feed only on old foliage in early season, leaving the developing foliage of the current year untouched (for details on the biology of the two species, see Juutinen 1967 and Geri 1988). Defoliation in late season has been found to be more detrimental than in early season (Ericsson et al. 1980, Larsson et al. 1993). Elsewhere in Europe, these sawflies are well-known defoliators, causing substantial growth losses from time to time (Schwenke 1978, 1982, Speight and Wainhouse 1989).

Normally, pine stands survive one or two years of severe defoliation by *N. sertifer*, and the main impact is growth loss (Austarå et al. 1987). Defoliation by *Diprion pini* in two consecutive years may, however, render these trees susceptible to secondary attacks by stem-attacking insects, i.e. pine shoot beetles, *Tomicus piniperda* (L.) and *Tomicus minor* (Hart.) (Coleoptera: Scolytidae), or other stem-borers like pine weevils (mainly *Pissodes pini* L.) (Coleoptera: Curculionidae). Vulnerability to stem-attacking insects occurs after one year of total defoliation, whereas two consecutive years of defoliation may be fatal even without subsequent stem-attacks (Butovitsch 1946, Lekander 1953, Croke 1959). Altogether, the risk for beetle-induced tree mortality following late-season defoliation is often considered a more important justification for control operations to prevent further defoliation than the growth losses saved through the operation (Speight and

Wainhouse 1989).

In 1990 and 1991, an outbreak of *D. pini* caused widespread defoliation in pine forests of 1700 hectares in Kauhajoki in the southern part of the province Etelä-Pohjanmaa, including parts of the Lauhanvuori National Park. Most trees were totally defoliated in 1990. Because cocoon counts in spring 1991 revealed high sawfly densities, commercial pine stands surrounding the national park were sprayed with diflubenzuron (Dimilin®) to prevent further defoliation. Sprays are prohibited in the park. Thus, trees within the national park that became severely defoliated during two years were growing next to trees outside the park border that were protected from the second year of defoliation by the spraying. As stands were otherwise fairly similar, this situation offered an opportunity to study: i) the effect of different defoliation levels on pine recovery, and ii) the susceptibility of trees with different defoliation levels to secondary pests like pine shoot beetles.

In this study, we compared the susceptibility of trees that experienced different defoliation level to spontaneous and induced attacks by pine shoot beetles. We also tried to assess the tree susceptibility to beetle attack by different physiological measures. Some preliminary results have previously been reported in Finnish (Annala et al. 1993).

2 Material and Methods

2.1 Study Area

The study was conducted in Kauhajoki (62°8'N lat.; 22°12'E long.), in Lauhanvuori National Park (established in 1982) and surrounding pine forests (Fig. 1). Lauhanvuori rises to 231 m above sea level, and ca 100 m above the surrounding flatlands. The study area was selected on the southern slope of Lauhanvuori at both sides of the border of the national park. Site conditions were homogeneous and poor of *Calluna*-type with patches of *Cladonia*-type sites (Lehto and Leikola 1987). Mature stands of Scots pine totally dominated the area and stand conditions were fairly similar on all study sites inside and outside the park. In these pine stands, there were solitary large silver birches

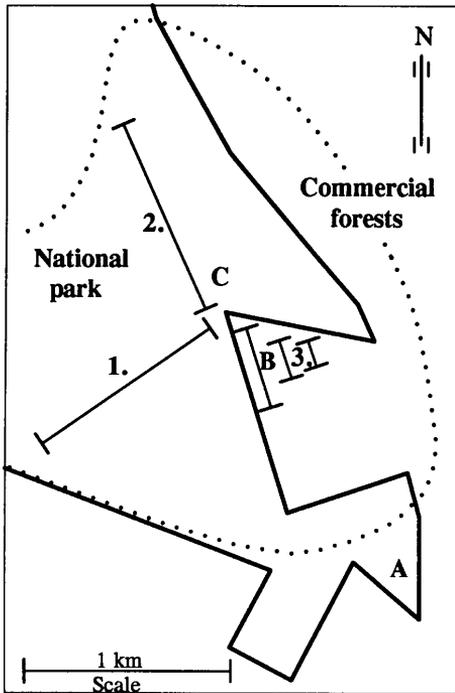


Fig. 1. A sketch-map of the study area. Solid line = boundary between national park and commercial forests; broken line = boundary of defoliation area; lines with a number = survey lines with stand plots; letters = study sites with different percentages of remaining foliage in spring 1992: A = 100 %, B = 30 %, C = 10 and 0 %).

(*Betula pendula* Roth) and Norway spruces (*Picea abies* Karst.) (0.9 and 0.4 % of the total stem number, respectively). There was no understory vegetation in the study stands.

The following stand data were derived from 20 circular sample plots ($r = 12.6$ m) situated at intervals of 100 metres along each of two survey lines in the national park and one in the adjoining commercial forest (cf. Fig. 1). Site index was 15.7 (dominant height of 100 thickest trees/ha at the age of 100 years). Mean diameter of the dominant trees was 25.9 cm, age at breast height from 50 to 100 years, stand density from 240 to 840 trees /ha. Open patches and dead trees killed by blister rust (*Cronartium* sp.) or snow damage were more abundant inside the park than in surrounding commercial forests.

Meteorological information was taken from

Table 1. Diameter (mean and standard error) of the experimental trees of different vigour in spring 1992. Large trees were dominant or co-dominant; small trees were suppressed ($n = 10$).

Remaining foliage, %	Trees baited	Diameter of large trees		Diameter of small trees	
		mean	SE	mean	SE
100	Yes	24.6	0.7	12.8	0.4
30	Yes	23.2	1.4	11.5	0.7
10	Yes	25.3	1.1	12.8	0.8
10	No	27.0	0.8	12.8	0.4
0	Yes	23.8	0.8	12.6	0.7
0	No	27.1	1.3	14.3	0.6

the nearest weather station (Karvia), 20 kilometers east of the study area. Mean air temperature in May and June in 1992 was higher (1.8° and 1.3° C, respectively) than the long term average while July and August were cooler than normal. Rainfall in May and June was lower (27 and 83 % of the norm in 1961–90) but in July and August higher than normal.

2.2 Field Procedures

In late April 1992, study trees representing different defoliation levels and size classes were selected on both sides of the southern border of the national park. Trees were sampled from the following defoliation classes: 100 = all (100 %) foliage intact (site A, 3–4 age classes of needles, Fig. 1), 30 = 30 % of needles intact (site B, trees totally defoliated in 1990, sprayed with diflubenzuron in 1991, 1 needle age class present), 10 = 10 % intact (site C, totally defoliated in 1990 having small amounts of the 1991 needle age class left), and 0 = 0 %, no needles left (site C, totally defoliated in 1990 and 1991). Ten timber-sized and ten pole-sized trees were included in the defoliation classes 100 and 30, 20 trees of both sizes were included in defoliation classes 10 and 0. The average diameter of the experimental trees can be seen in Table 1, showing that the unbaited trees were somewhat larger than the baited ones in both size classes.

On 28 April 1992, before *Tomicus* flight began, 10 experimental trees of both size classes

within each foliage class were baited with two split Scots pine logs (ca 50 cm in length; cut from a few trees felled on the same day) to increase the attractiveness of the trees to the pine shoot beetles. In defoliation classes 10 and 0, 10 trees were left unbaited.

On the next day, baited trees were inoculated with growing mycelia on malt agar of *Ophiostoma minus* (Hedge), a blue-stain fungus associated with *T. piniperda*. This inoculation provided us with a bioassay of resistance to stem borers. We used a standard technique with a 5 mm cork borer in four points evenly distributed along the perimeter at breast height (for details and references, see Solheim and Långström 1991).

We also measured the cambial electrical resistance (CER) of the inner bark with a Shigometer (for a technical description and references, see Piene et al. 1984, Lindberg and Johansson 1989). This technique has also been used in bark beetle studies to describe tree vitality, but results have sometimes been contradictory (Långström and Hellqvist 1993a, and references therein). CER-readings were taken from the experimental trees on two occasions: on 28 April (ambient temperature ranging between 5 and 7 °C) and on 17 June (ambient temperature ca 15 °C). Readings were taken in early afternoon, and the ambient temperature was recorded every 30 min. Two readings were taken from each tree with the probes inserted vertically into the bark at opposite sides of the stem at breast height (1.3 m). Uncorrected readings were used since ambient temperature was stable during the procedure.

In addition, resin flow was measured in test trees during 24 hours on 16–17 June when *Tomicus* beetles had already attacked the trees. At that moment the differences between trees were expected to be at the highest level (cf. Schroeder 1990, Lieutier et al. 1995). A 25 mm cork borer was used to cut two holes to the sapwood on opposite sides of the stem at breast height (Lorio et al. 1990). The running oleoresin was collected in vials attached below the holes after 24 hours, and weighed.

In late August, the trees were inspected and the remaining needle biomass present on surviving trees was estimated as none, less than one age class of needles (i.e., ca. 10 % of full crown foliage), one age class (ca. 30 %), two age classes (ca.

50 %), and 3–4 age classes (full crown foliage). Occurrence of bark beetle attacks was determined on bark samples (25 cm high and 10 cm wide) that were taken at 0.50–0.75, 1.50–1.75, 2.50–2.75, and 3.50–3.75 m stem heights. On dead or dying trees, the samples were carefully removed and inspected for beetle galleries and exit holes. On surviving trees, the outer bark was superficially removed to allow inspection of gallery development. If entrance holes to beetle galleries were found, galleries were fully exposed and measured. *Tomicus*-attacks were classified as failed if the gallery was shorter than 1 cm; otherwise successful. Presence of exit holes indicated successful brood production (and that the tree was dead). The two upper samples were taken only if beetles were present on either of the two lower ones. If no *Tomicus*-attack was found in any of the bark samples, the whole lower stem (rough bark area) was inspected for presence or absence of *Tomicus*-attack. Thus, an attacked tree may have had zero attacks on the bark samples.

2.3 Chemical Analyses

The bark samples that were removed with the cork borer for the resin flow studies in June were collected and frozen for later analyses of carbohydrates and phenolics in the stem phloem. No *Tomicus* or other insect attacks were found on sample points. In addition, samples of the current and previous year foliage were collected on 13 August 1992 from the large experimental trees representing 100, 30 and 10 % foliage left (ca 10 trees per category). Samples were stored at a temperature of –18 °C and each tree was analyzed separately.

The needle samples and part of the phloem samples were split into two parts for chemical analyses. Water-soluble carbohydrates (“sugars”) were analysed with gas chromatography-mass spectrometry (GC-MS) after silylation (Mason and Slover 1971, Mahmud and Catterall 1986). Starch content of the samples was determined enzymatically (Karkalas 1985). The Folin-Ciocalteu method was used for determination of total phenolic content (Julkunen-Tiitto 1985).

2.4 Statistics

Data were analysed using the SAS statistical program package (SAS 1987). Treatment means were compared within each test group (large or small, baited or unbaited trees) by one-way analysis of variance followed by Tukey's test for multiple comparisons (Zar 1984). We used $P = 0.05$ as the critical significance level, and all tests were done with untransformed data.

3 Results

3.1 Measures of Tree Vigour

CER-readings taken in April, before beetle flight differed between some of the defoliation classes (Table 2), but the pattern was not consistent for both size classes of trees. In June, Shigometer-readings were lower than in April (due to a higher temperature). The totally defoliated trees had lower readings than the other three groups of trees, but this difference was significant only for larger trees.

Rate of resin flow was significantly lower in the totally defoliated trees than in the undefoliated and least defoliated trees; trees with 10 % remaining foliage were intermediate (Table 2).

Lesion length formed in response to the fungal inoculation did not differ among trees and different defoliation levels, but the trend was similar for large and small trees, i. e., lesion size increased with increasing defoliation level (except for the totally defoliated trees where only one large and one small trees survived and could be measured, cf. Table 2).

In 1992, all surviving trees had developed some new shoots. The weakest trees that were seriously defoliated in 1990 and 1991 (class 0), were estimated to carry approximately 10 % needles (or one third of one age class) in 1992. The next group (class 10) had increased from ca. 10 % to at least 20 %. The trees sprayed with diflubenzuron (class 30) that suffered no additional defoliation in 1991 were estimated to carry about two full age classes of needles (or roughly 50 % of the normal). The undefoliated trees (class 100) had the usual 3–4 age classes of foliage.

Table 2. Resin flow, cambial electrical resistance (CER) and lesion formation after fungal inoculation of the baited experimental trees ($n = 10$, except for lesion length where n is given) at Lauhanvuori in 1992.

Tree group	Remaining foliage, %	Resin weight in June		April		CER		Lesion length		
		mean	SE	mean	SE	mean	SE	mean	SE	n
Large	100	4.4 <i>a</i>	2.3	26.7 <i>a</i>	1.2	16.0 <i>a</i>	1.2	12.4 <i>a</i>	1.2	10
	30	5.6 <i>a</i>	3.8	20.4 <i>b</i>	0.7	16.8 <i>a</i>	0.5	14.7 <i>a</i>	1.1	10
	10	3.1 <i>ab</i>	1.7	22.9 <i>ab</i>	1.0	17.3 <i>a</i>	0.7	16.2 <i>a</i>	1.0	10
	0	1.1 <i>b</i>	1.1	19.7 <i>b</i>	1.2	11.1 <i>b</i>	0.9	14.9 <i>a</i>	–	1
F-value		6.18		9.61		10.81		2.07		
df		3.36		3.36		3.36		3.30		
P-value		0.0017		0.0001		0.0001		0.1272		
Small	100	–	–	23.9 <i>ab</i>	0.9	17.7 <i>a</i>	1.7	7.8 <i>a</i>	0.6	10
	30	–	–	21.2 <i>b</i>	0.6	19.6 <i>a</i>	1.0	8.7 <i>a</i>	0.8	9
	10	–	–	26.0 <i>a</i>	1.4	19.9 <i>a</i>	1.6	10.0 <i>a</i>	1.6	6
	0	–	–	22.5 <i>ab</i>	0.8	15.7 <i>a</i>	2.6	8.8 <i>a</i>	–	1
F-value			4.65		1.13		0.93			
df			3.36		3.36		3.22			
P-value			0.0076		0.3487		0.4443			

Means in columns followed by the same letter were not significantly different according to Tukey's test for multiple comparisons.

3.2 Tree Mortality

During 1992, 9 out of 10 of the large, totally defoliated trees died, but none of the trees with at least 10 % needles left died. Among the small trees, the survival of the undefoliated and totally defoliated trees was the same as for the large trees, but some small trees in the intermediate class also died (4 trees with 10 % and 1 with 30 % foliage left).

3.3 Chemistry of Stem Phloem and Needles

Starch levels were generally low in the stem phloem (sampled in mid-June) as well as in the needle samples taken in mid-August (Table 3). As expected, undefoliated trees had, however, higher starch concentrations in the stem and in needles than the diflubenzuron-trees (30 % foliage left), and even more so when comparing with trees suffering 90 % defoliation. The totally defoliated trees displayed the lowest level of starch in the stem. Small trees showed a similar pattern as did the large trees.

The total amounts of sugars in stem phloem showed a similar pattern to starch, i.e., severe defoliation resulted in lower totals compared with

the less defoliated trees. No such pattern in sugar levels was seen in the needles, but the 1992-needles invariably had somewhat more sugars than the 1991-needles. Fructose, glucose (a- and b-glucose) and pinitol were the main constituents in the stem phloem whereas saccharose, sorbitol and inositol were rare (Table 4). There was clearly more pinitol and inositol in the needles than in the stem, otherwise the pattern was similar for the needles.

There was slightly higher phenolic levels in the stem phloem of severely defoliated pine trees (the total phenolic fraction being 113 vs 104 mg/g), but the difference was not significant ($P = 0.2178$). As phenolic compounds were not analysed in more detail, nothing can be said about possible qualitative differences between the two groups.

3.4 Occurrence of Stem-feeding Insect Species on the Trees

The trees were attacked by a number of stem-feeding insect species, but the pine shoot beetles, especially *T. piniperda*, were most abundant. None of the 120 trees were attacked only by *T. minor*, while 71 trees were attacked only by *T. piniperda*, 23 by both species, and the

Table 3. Starch and sugar content of stem phloem sampled in mid-June, and of needles sampled in mid-August 1992.

Size class	Remaining foliage	phloem	Starch content, %		Total sugar content, mg/mg		
			1991 needles	1992 needles	phloem	1991 needles	1992 needles
Large	100	3.6 <i>a</i>	5.1 <i>a</i>	3.0 <i>a</i>	235.9 <i>a</i>	158.2 <i>a</i>	198.5 <i>ab</i>
	30	2.6 <i>ab</i>	2.7 <i>b</i>	1.7 <i>b</i>	259.4 <i>a</i>	193.3 <i>a</i>	240.8 <i>a</i>
	10	2.4 <i>ab</i>	1.3 <i>c</i>	0.9 <i>c</i>	143.1 <i>b</i>	144.4 <i>a</i>	158.1 <i>b</i>
	0	1.2 <i>b</i>			130.7 <i>b</i>		
	F-value		7.44	38.28	23.89	8.33	2.25
df		3.36	2.29	2.29	3.36	2.29	2.29
P-value		0.0005	0.0001	0.0001	0.0002	0.1238	0.0061
Small	100	3.3 <i>ab</i>			252.2 <i>a</i>		
	30	3.5 <i>a</i>			212.1 <i>ab</i>		
	10	1.9 <i>b</i>			129.0 <i>b</i>		
F-value		3.68			7.25		
df		2.23			2.23		
P-value		0.0411			0.0036		

Means in columns followed by the same letter were not significantly different according to Tukey's test for multiple comparisons.

Table 4. The sugar fraction ($\mu\text{g}/\text{mg}$; %) from stem phloem and needles (cf. Table 3) as individual sugars (large trees only; totally defoliated trees excluded).

Remaining foliage, %	Sugar content							Total
	fru	pin	alf	sor	bet	ino	sac	
Phloem								
100	106.8	26.0	61.3	1.7	32.1	1.8	6.2	235.9
100	45.3	11.0	26.0	0.7	13.6	0.7	2.6	100.0
30	120.2	31.0	66.2	2.1	34.7	2.3	2.7	259.4
30	46.4	11.9	25.5	0.8	13.4	0.9	1.1	100.0
10	59.7	18.5	36.3	1.8	24.3	1.4	1.2	143.1
10	41.7	12.9	25.4	1.2	17.0	1.0	0.8	100.0
1991 yrs needles								
100	47.0	48.4	32.5	0.7	22.7	6.2	0.7	158.2
100	29.7	30.6	20.5	0.5	14.3	3.9	0.4	100.0
30	57.3	59.0	39.4	1.1	27.1	8.5	0.8	193.3
30	29.7	30.5	20.4	0.6	14.0	4.4	0.4	100.0
10	37.3	43.6	32.4	1.1	23.0	6.6	0.4	144.4
10	25.9	30.2	22.5	0.7	15.9	4.6	0.3	100.0
1992 yrs needles								
100	56.4	62.1	48.5	1.4	22.3	7.1	0.6	198.5
100	28.4	31.3	24.4	0.7	11.2	3.6	0.3	100.0
30	75.1	69.7	55.3	2.7	27.7	9.2	1.2	240.8
30	31.2	28.9	23.0	1.1	11.5	3.8	0.5	100.0
10	37.2	57.0	34.8	1.5	19.3	7.5	0.8	158.1
10	23.5	36.1	22.0	1.0	12.2	4.7	0.5	100.0

fru = fructose; pin = pinitol; alf = a-glucose; sor = sorbitol; bet = b-glucose; ino = inositol; sac = saccharose (Total = same as total in Table 3)

remaining 26 trees escaped attack. No galleries were recorded within the bark samples from 12 of the attacked trees.

Larval galleries of *Pissodes pini* and of two long horned beetles (*Rhagium inquisitor* L. and *Acanthocinus aedilis* L., Cerambycidae) occurred on some of the trees, but always together with *T. piniperda*. No other bark beetles, except occasional attacks by *Trypandendron lineatum* were recorded on the studied part of the stem. Thus, it is obvious that the common pine shoot beetle is the main colonizer of these trees, and probably the only one influencing the fate of the trees under attack.

3.5 Distribution of *T. piniperda* and *T. minor* at Different Stem Heights

The distribution of two *Tomicus*-species along the stems followed the expected pattern: *T.*

piniperda dominating at the base and *T. minor* dominating at higher part of the stem (Table 5, see also Fig. 2). The latter was never in fact recorded at the bottom parts of large trees, and the former was rare on the higher sections of the small trees. Quite often, the two species occurred together, especially in sections from 1.5 to 2.75 m high on tree stems.

The different preferences of the *Tomicus*-species is clearly seen in the attack densities at different stem heights (Fig. 2A). Especially on the small trees, the attack density of *T. piniperda* declined with increasing stem height, while *T. minor* displayed the opposite pattern.

The brood production followed a similar pattern (Fig. 2B), but it is worth noticing that both species did equally well on the second section of the small trees.

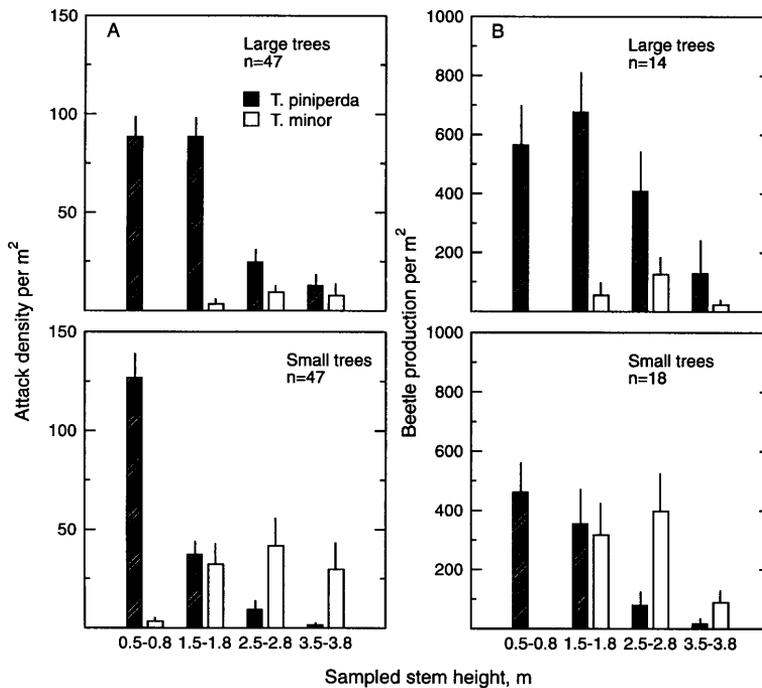


Fig. 2. Vertical patterns of A) attack density (egg galleries per m²) and B) brood production (exit holes per m²) of *T. piniperda* and *T. minor* at ca 0.5, 1.5, 2.5 and 3.5 m stem height, respectively (stem sections 1–4). The inspected areas were 10 cm wide and 25 cm high. Only attacked and successfully attacked trees (i. e. trees having at least one gallery or one exit hole of either beetle species) were included; trees of different defoliation classes were pooled; vertical bars show standard errors of means.

3.6 Beetle Attack Related to Tree Vigour and Baiting

Baiting of trees resulted in attack attempts on all baited trees, large as well as small, and even in the most healthy trees with intact foliage (Fig. 3). For the large trees, all attacks failed in the trees having 10 % or more needles left. The proportion of galleries longer than 1 cm increased with increasing defoliation level. In the totally defoliated large trees, baiting induced successful beetle attack (produced brood) in 9 of 10 trees, which all died in summer 1992.

The same pattern can be seen for the small, baited trees. These were, however, more sensitive, as 7 out of 10 of the trees having 10 % needles left were successfully attacked and killed; as was one of the diflubenzuron-trees with 30 % needles left.

Table 5. Occurrence of *Tomicus piniperda* and *T. minor* on sample sections (n = 60).

Sample section	Occurrence of <i>Tomicus</i> , %				Total
	<i>T. piniperda</i> only	<i>T. minor</i> only	Both species	Not attacked	
Large trees					
1	60.0	0.0	0.0	40.0	100
2	58.3	0.0	3.3	38.3	100
3	15.0	1.7	11.7	71.7	100
4	8.3	1.7	1.7	88.3	100
Small trees					
1	63.3	0.0	5.0	31.7	100
2	25.0	5.0	13.3	56.7	100
3	1.7	10.0	8.3	80.0	100
4	0.0	8.3	3.3	88.3	100

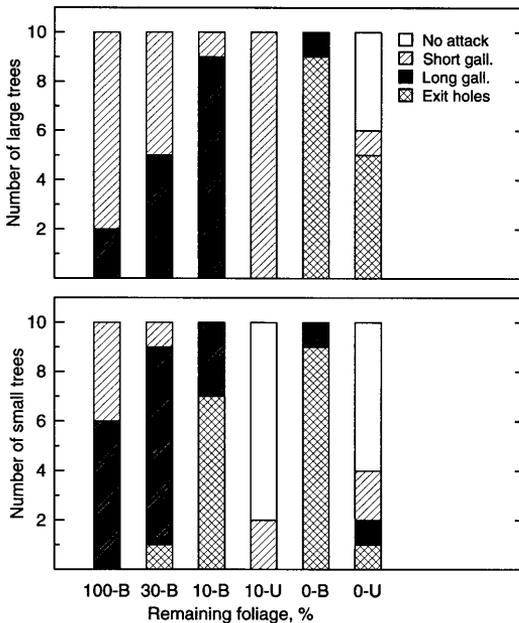


Fig. 3. Distribution of the experimental trees ($n = 10$) as related to attack by *Tomicus*. B = baited, U = unbaited.

In contrast, most of the unbaited trees with 10 % needles left totally escaped beetle attack, and those attacked displayed only short beetle galleries. Some of the totally defoliated trees that were unbaited also escaped attack, but most of the large ones and one of the small ones attacked were colonized (Fig. 3).

3.7 Performance of Pine Shoot Beetles

The average attack density of *T. piniperda* (calculated by pooling the sections; cf. Fig. 2) on baited trees increased with decreasing needle biomass, both for large and small trees (Fig. 4A). *T. minor* displayed a similar pattern on small trees, but was almost lacking on large trees, except for the severely defoliated ones.

Egg galleries of both beetle species were short in the large trees, except, in the totally defoliated ones (Fig. 4B). In the small trees, gallery lengths of both species increased with increasing defoliation level. The galleries were also longer in baited than in unbaited trees.

Successful brood production in large trees oc-

curred only in the totally defoliated trees (Fig. 4C). For the small trees, however, some of the less defoliated individuals also succumbed to the beetles and produced brood of both *Tomicus* species.

4 Discussion and Conclusions

The beetle attacks were successful only in the trees that were totally defoliated in two consecutive years. Thus, tree resistance was high despite the fact that weather conditions were favourable for beetle attack, as temperature in May and June was distinctly higher but precipitation lower than normal. All large trees, having 10 % or more foliage left, resisted the attacks. This was true for the small trees as well, except for the baited ones with ca 10 % foliage left, many of which succumbed to beetle attacks. This finding agrees with earlier observations that only small or totally defoliated trees were killed by pine shoot beetles during an outbreak of *B. piniarius* in southern Sweden (Butovitsch 1946, Lekander 1953), and eastern Finland (Annala and Varama 1985, and unpubl. data). Thus, defoliated Scots pine trees display a remarkable resistance to stem-attacks by pine shoot beetles, and a relatively small amount of intact foliage may be the difference between life and death.

All baited trees, regardless of size and defoliation class, were attacked by *T. piniperda*, whereas some of the unbaited trees escaped attack. The *Tomicus* beetle's clear preference for baited trees has previously been observed by Schroeder and Eidmann (1987), Långström and Hellqvist (1988, 1993b) and Schroeder (1990). It has also been demonstrated that alpha-pinene and ethanol, emanating from wounds or newly cut host material play an important role in guiding the pine shoot beetles to potential host trees (Klimetzek et al. 1986, Vité et al. 1986, Lanne et al. 1987, Schroeder 1988).

In contrast to *T. piniperda*, *T. minor* never occurred alone on a tree, and both species were found together on every fourth attacked tree. Thus, the latter species was not capable of colonizing trees alone (see also Långström and Hellqvist 1993b). *T. minor* beetle normally attacks after *T. piniperda* (Långström 1983, and refer-

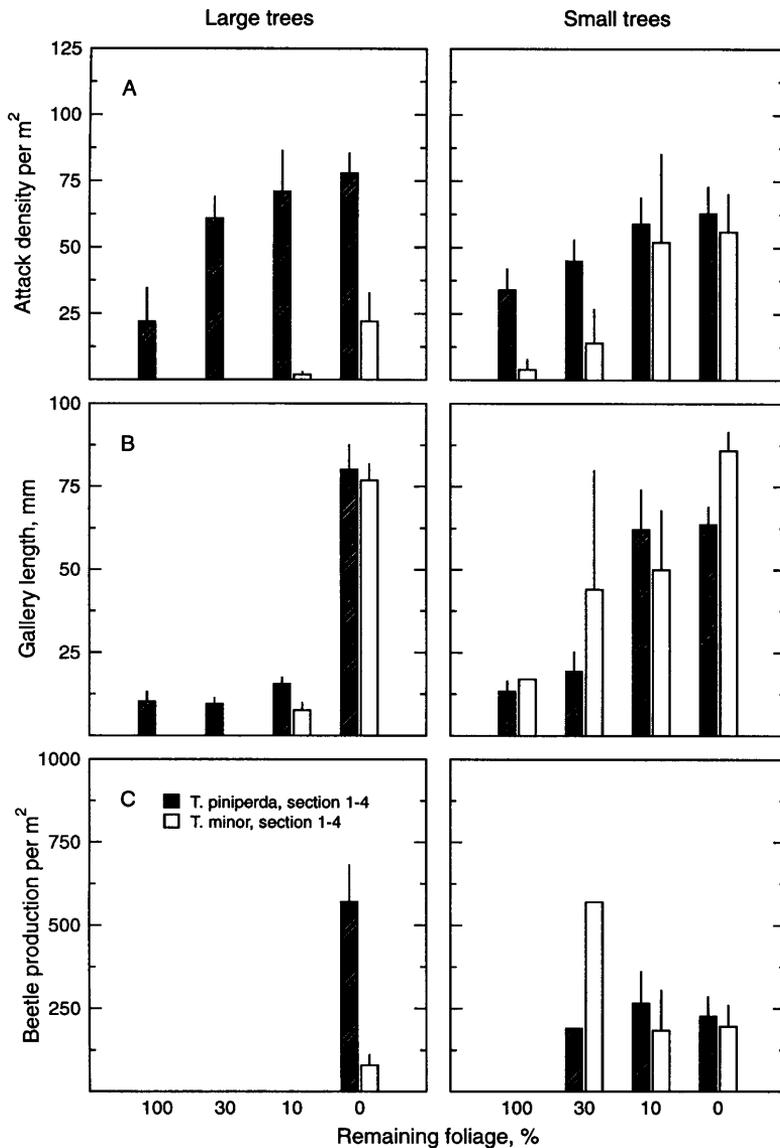


Fig. 4. A. Attack densities (egg galleries per m²; 10 trees), B. gallery lengths (10 trees), and C. brood production (expressed as the number of exit holes per m²; for 9 large, totally defoliated trees, 1, 7 and 9 for small trees having 30, 10 and 0 % foliage left, respectively) of *T. piniperda* (black) and *T. minor* (white) in attacked trees of different defoliation classes; only baited trees included; vertical bars indicate standard errors of means.

ences therein), flying beetles of the former species may be attracted to trees under attack by the latter. Although the species have different preferences in terms of bark thickness (Långström 1984, and references therein), some overlapping

attacks occurred on those sample sections having intermediate bark thickness. Considering that the mean attack densities at Lauhanvuori were far below the levels considered to be needed to overwhelm the resistance of the tree (Långström

and Hellqvist 1993b), the concomitant occurrence of the two species may in some cases have been necessary to successfully colonize the trees.

Although the physiological mechanisms underlying host resistance to bark beetles are poorly understood, it is generally believed that conifers counteract attacking bark beetles and their associated blue-stain fungi by a dual defence system. This system is based on primary resin which is exuded when resin ducts are severed, and by an induced secondary resinosis that contains the aggressor (beetle or fungus) in resin soaked lesions (for an overview, see Christiansen et al. 1987). Furthermore, the intensity of the defense reactions seems to depend on the tree's vigour, i.e. its capacity to allocate carbohydrates to support the energetically expensive defense chemistry (Christiansen and Ericsson 1986, Miller and Berryman 1986, Långström et al. 1992). The underlying assumption is that vital trees quickly confine the intruder in a small lesion whereas weak trees need to spend proportionally more energy to stop the intruder, and consequently lesions get larger (see e.g. Långström et al. 1992, and references therein). Hence, defoliated trees should be far less capable of defending themselves than undefoliated trees.

The resin flow results of this study indicate that the constitutive defense in the severely defoliated trees was weaker than in the less defoliated ones, but the difference was not striking. Lorio et al. (1990) stated that intensity of resin flow is highly dependent on temperature and moisture. Temperature can be relatively low during the attack time of *Tomicus piniperda* since the threshold temperature for beetle flight is 11 °C (Långström 1983). Later on when beetles are excavating tunnels air temperature may rise over 20 °C. It happens rather often that beetles do not lay eggs because of heavy resin flow, for instance in windthrown trees (Annala and Petäistö 1978). This has also been found experimentally by Lieutier et al. (1995). Because there are great differences in resin flow even between healthy trees (e.g. Schroeder 1990, Kytö et al. 1998) it is difficult to evaluate the exact role of resin flow in tree resistance. Schroeder (1990) reported that resin flow has only minor importance during the attack of *T. piniperda* while Lieutier et al. (1995) considered its role high during gallery construction.

Similarly to resin flow, the fungal inoculation pointed in the same direction: larger lesions were produced in weaker trees than in more vital trees (see e.g. Långström et al. 1992 for a discussion of the underlying physiological assumptions). On the other hand, lesion formation may also have been biased by the ongoing and different beetle attacks in these trees. Altogether, measuring resin flow and induced defense reaction did not separate tree groups better than the visual defoliation classification with respect to resistance properties.

Sawfly defoliation does not seem to have any great effect on the amount of phenolics in phloem. Kytö et al. (1998) found that treatment with different fertilizers did not affect on the phenolic concentration of the phloem in Scots pine. It appears that phenolic synthesis is accelerated only when bark and phloem are wounded, and that the resulting changes are qualitative rather than quantitative (Lieutier et al. 1991, Bois and Lieutier 1997).

Earlier findings that defoliation can affect the carbohydrate content of foliage and phloem in Scots pine, are in accordance with our results. Ericsson et al. (1980, 1985) found that the loss of new shoots resulted in lowered starch content in remaining needles. Webb (1980) demonstrated that starch content in needles, twigs and phloem of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) declined with increased needle loss by Douglas-fir tussock moth or artificial defoliation. Furthermore, the rate of starch decline in defoliated trees during the growing season was faster than in undefoliated trees. He also stated that tree recovery was strongly related to starch reserves.

Little information is available about possible changes in the sugar composition following defoliation. According to Lyytikäinen (1993) light defoliation increased the saccharose content of Scots pine but severe needle loss had a reverse effect.

The finding of this and other studies that even severely defoliated pine trees are capable of defending themselves against pine shoot beetles, implies that the defense reactions, at least in pine, are less dependent on carbon availability than previously believed (Christiansen and Ericsson 1986, Miller and Berryman 1986, Långström et al. 1992). The starch levels observed in this

study, were (regardless of defoliation level) much lower than reported from pine needles and stem phloem in some Swedish studies. In mid-June, starch levels should be building up towards a seasonal peak around 20 % (d.w.) both in needles (Ericsson et al. 1980, 1985, Långström et al. 1990) and in stem phloem (Långström et al. 1992). The latter results were, however, obtained for much younger pine trees than the presently studied ones. Despite this discrepancy in starch levels that we cannot explain, undefoliated vital trees had clearly more starch both in stem phloem and in needles than less vital trees.

Another possible explanation for the observed high resistance of severely defoliated trees to *Tomicus*-attacks, is that beetle population levels may have been low compared to the sudden increase of suitable host material. This is impossible to know, as no systematic surveys were conducted before to the experiment. The fact that all baited trees were attacked, however, indicates a substantial beetle population. The average attack density was, on the other hand, well below the critical attack density for successful colonization of live trees, ca 200–300 egg galleries per m² bark surface (Schroeder and Eidmann 1987, Långström et al. 1992). The attack density on the most heavily attacked trees was sometimes twice as high as the corresponding mean value for all attacked trees (cf. Fig. 4A). Hence, some of the large trees that had suffered 90 % defoliation sustained substantial attack levels which became fatal to the totally defoliated ones.

The role of the pine shoot beetles in causing tree mortality gets even more complex when we consider that some of the totally defoliated trees died without being attacked by *Tomicus*. The reason for this mortality is not clear, but we suspect that bud mortality, possibly due to incomplete winter hardiness or desiccation due to the bark-feeding of the sawfly larvae, played an important role here. Thus, totally defoliated trees may die from the defoliation itself, and 90 % or less defoliation may not render trees suitable for beetle attack, unless the population density of *Tomicus* is high.

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