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Scots pine susceptibility to attack by *Tomicus piniperda* (L) as related to pruning date and attack density

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Summary — The susceptibility of young Scots pine to bark beetle attack was increased by pruning trees to a similar crown size ≈ 10, 7 and 1 month(s) prior to beetle flight. Beetle population in the study area was high, and spontaneous attacks were expected to occur on the pruned trees. Half of the trees were baited with split pine bolts in order to attract more beetles to attack these trees. Thus, experimental trees carrying ≈ one-third of their original foliage and with different vigour indices due to the pruning history were exposed to 2 levels of beetle attack. The pine shoot beetles preferentially attacked baited trees, whereas attack rates did not differ between pruning dates. Six wk after attack, beetle performance was better in trees pruned shortly before attack than in trees pruned earlier. Vigour indices differed between the 2 treatments, but phloem starch, secondary resinosis (expressed as lesion size and resin acid content) and tree survival did not. Trees that eventually survived were significantly less attacked than those that died, but the 2 groups did not differ in tree characteristics (except in cambial electrical resistance).

pine shoot beetles / *Pinus sylvestris* / beetle performance / defence reactions / host vitality

Résumé — Susceptibilité du pin sylvestre aux attaques de *Tomicus piniperda* L en fonction de la date d'élagage et de la densité d'attaque. *La susceptibilité de jeunes pins sylvestre aux attaques de scolytides a été accrue en élagant les arbres, de façon à ce que la taille de leur couronne soit comparable. Les élagages ont eu lieu environ 10, 7 et 1 mois avant le vol des insectes. Les niveaux de population dans la zone d'étude étaient élevés et des attaques spontanées étaient prévisibles sur les arbres élagués. Pour augmenter leur attractivité, la moitié des arbres ont été appâtés avec des rondins de pin. Ainsi, des arbres portant environ un tiers de leur feuillage d'origine, et ayant différents indices de vigueur à cause de l'élagage (tableau I) ont été soumis à 2 niveaux d'attaque. La moitié des arbres ont été coupés début juin, les autres fin août.* T piniperda *a attaqué de préférence les arbres appâtés (figs 1, 2) mais le taux d'attaque a été le même pour les différentes dates d'élagage (fig 1). Six semaines après les attaques, les arbres élagués le plus tardivement renfermaient plus d'insectes parents et plus de galeries contenant des larves que les arbres élagués précocement (tableau II). Les galeries maternelles étaient aussi significativement plus longues dans le premier cas (fig 1). Les arbres élagués environ 1 an avant l'attaque représentaient donc un matériel moins favorable pour les insectes. Les indices de vigueur différaient également entre les 2 traite-*

ments (tableau I), mais l'amidon présent dans le liber, la réaction secondaire (mesurée par la taille de la zone réactionnelle et son contenu en acides résiniques) et le taux de survie des arbres étaient semblables (fig 1, tableau III). La réaction de défense induite a avorté sur certains des arbres qui supportait une densité d'attaque supérieure à 200 galeries maternelles par m^2 *(fig 3). La longueur moyenne des galeries dépassait 40 mm (fig 4). Cependant, des arbres plus densément attaqués ont survécu. Chez les arbres résistants, les lésions occupaient au maximum 30% de la surface du phloème dans la partie basse du tronc (fig 5). Les arbres supposés survivants étaient significativement moins attaqués que les morts, mais leur taille, leur croissance et leur indice de vigueur étaient les mêmes (tableau IV). Cependant, la résistance électrique du cambium mesurée à la date de l'attaque était significativement différente dans les 2 groupes, ce qui paraît illogique (tableau IV). Une descendance a été observée uniquement sur les arbres tués, avec un taux de multiplication inférieur à l'unité (tableau IV). Un début d'occlusion de l'aubier a été remarqué sur quelques arbres (potentiellement mourants ?) après 6 sem. L'aubier des arbres morts était fortement bleui, mais pas celui des arbres survivants.*

Tomicus piniperda / Pinus sylvestris / *performance des insectes / réactions de défense / vitalité de l'hôte*

INTRODUCTION

In contrast to herbivores in general, most bark beetles attacking live trees need to kill their hosts in order to reproduce successfully. Consequently, host trees have evolved strong defence systems against bark beetles. Conifers counteract attacking bark beetles and their associated blue-stain fungi by a dual defence system based on primary resin which is exuded when resin ducts are severed, and by an induced secondary resinosis containing the aggressor in resin-soaked lesions (for an overview, see Christiansen *et al,* 1987). Successful colonisation by bark beetles occurs when the beetles can exhaust the defence system of the host trees by massive synchronized attacks (Berryman *et al,* 1989; and references therein). Possession of aggregation pheromones as well as association with pathogenic blue-stain fungi seem to be typical features of tree-killing bark beetles (Christiansen *et al,* 1987; and references therein). As the resistance varies with host vitality, more beetles are needed to overwhelm the resistance of vigourous and fast-growing trees than less vital ones (Christiansen *et al,* 1987; and references therein). Thus, trees or stands may become susceptible to bark beetles as a result of reduced vitality and/or increased beetle populations, as exemplified by the concept of epidemic threshold (Berryman, 1982).

In Europe, *Tomicus piniperda* (L) (Col Scolytidae) is the most important bark beetle attacking Scots pine (for references, see *eg* Escherich, 1923; Postner, 1974; Långström, 1983). In northern Europe, however, *T piniperda* is seldom capable of successfully mass attacking living pine trees, whereas in more southerly areas it has been reported to kill trees from time to time (for references, see Långström and Hellqvist, 1991). This difference in beetle aggressiveness or host susceptibility triggered our interest in studying this pest–host relation under our conditions.

So far, we have found that even low-vigour Scots pines that were additionally weakened by pruning have a remarkable resistance to induced attacks by *T piniperda* (Långström and Hellqvist, 1988). Trees responded with vigourous induced defence reactions, enclosing the beetles in resin-soaked lesions. Typically, trees that failed to resist attacks accumulated less resin acids in the lesions and depleted their starch reserves in the phloem (Långström *et al,* 1992). Two species of blue-stain fungi, *Leptographium wingfieldii* Morelet and *Ophiostoma minus* (Hedgc) H et P Syd, were frequently isolated from the sapwood of killed trees (Solheim and Långström, 1991). The same species have been found to be associated with *T piniperda* in France (Lieutier *et al,* 1989b). Thus, the interaction between the beetle, its fungi and Scots pine seems to be similar in Sweden and in France (Lieutier *et al,* 1988; 1989a; Lieutier, in press).

The physiological mechanisms underlying host resistance to bark beetles are poorly understood. Carbohydrates, being both an energy source and raw material for the defence chemistry, may be important (Christiansen *et al,* 1987; and references therein); especially the tree's capacity to translocate carbohydrates to the area under attack (Christiansen and Ericsson, 1986; Miller and Berryman, 1986; Långström *et al,* 1992). Hence, manipulation of needle biomass and tree vitality (defined as vigour index *sensu* Waring and Pitman, 1985) should affect the tree's defence capacity in a predictable way. Our previous studies also showed that pruned trees succumbed more frequently to beetle attack than unpruned trees, but as the former were also subject to more attacks, we could not separate the effect of attack density on the induced defence reaction from that of host tree vigour.

Thus, in the present study, we compared the susceptibility of weakened trees with a similar needle biomass but different vigour indices (*ie* a similar capacity to produce carbohydrates, but different growth efficiency) to induced attacks by pine shoot beetles. By relating beetle performance and defence reactions to tree characteristics, we attempted to identify factors typical for resistant trees, as well as critical attack levels for trees of different vitality.

MATERIAL AND METHODS

Field work

The experimental site was a ≈ 30-yr-old pure pine stand at Norrsundet in Gästrikland, Central Sweden (≈ 61 °N lat, 16 °C long). The pine trees displayed misshapen crowns due to intensive shoot-feeding by pine shoot beetles over many years, and were obviously not in good condition (see also Långström and Hellqvist, 1988; Långström *et al,* 1992).

In order to create a tree population with reduced but similar capacity for carbohydrate production despite different vigour indices, trees were pruned to similar needle biomass on 3 occasions prior to beetle attack. In June 1988, 60 similar-looking (diameter, height and crown size) pine trees were selected for this pruning experiment in the low-vigour stand described above. Twenty of these trees were pruned on 21 June (after beetle flight in 1988), 9 September 1988 and 9 March (prior to beetle flight in 1989), respectively, leaving the 7–8 uppermost whorls intact (table I).

As the beetle population was high in the area, beetle attacks were expected to occur on the pruned trees (*cf* Långström and Hellqvist, 1988). In order to induce a higher level of beetle attack, half of the trees (10 in each treatment) were furnished with split bolts of fresh pine wood to enhance host attraction to the beetles (Långström and Hellqvist, 1988). This baiting was carried out on 9 March 1989, but as beetle flight started later than expected, all bait-bolts were replaced with new bolts on 13 April, when flying beetles were observed in the stand. Judging from meteorological data, that day was probably the first day of *Tomicus* flight in the area.

In an attempt to measure tree vitality at the time of beetle attack, we measured the cambial electrical resistance (CER) of the inner bark with a Shigometer, especially developed for this purpose (for a technical description and references, see Lindberg and Johansson, 1989). This technique has been used in different contexts for describing tree vitality (see *eg* Piene *et al,* 1984a, 1984b; Matson *et al,* 1987), and also in bark beetle studies, but with contradictory results (Christiansen, 1981; Lieutier and Ferrell, 1988). CER readings were taken from experimental

Table I. Characteristics of experimental trees felled at Norrsundet in June 1989 ($n = 10$).

Variable	*Date of pruning*		
	21 June 1988	*9 September 1988*	*9 March 1989*
Diameter ub at 1.3 m in 1988 (mm)	59.9^{a}	60.7^{a}	55.7^{a}
Height in 1988 (m)	5.35^{a}	5.33^{a}	5.57^{a}
Total height growth 1983–1988 (m)	0.70^{b}	0.68^{b}	1.04^{a}
Crown length after pruning (m)	1.66^{b}	1.98^{ab}	2.01^{a}
No of whorls after pruning	8.8^{a}	9.2^{a}	8.1^{a}
Crown fresh weight (kg)	1.53^{a}	2.27^{a}	1.62^{a}
Radial growth in 1988 (mm)	0.56^{b}	0.64^{ab}	0.93^{a}
Basal area growth in 1988 (%)	3.71^{b}	4.27^{b}	6.59^{a}
Vigour index in 1988 (%)[1]	3.80^{b}	4.38^{ab}	6.79^{a}
Vigour index 1986–1988 (%)[c]	14.35^{ab}	13.30^{b}	20.28^{a}
Cambial electrical resistance (CER) (kΩ) 11 April	22.1^{a}	20.6^{a}	20.2^{a}

[a, b] Means in a row followed by the same letter were not significantly different at the 0.05 level according to Tukey's test for multiple comparisons; [c] calculated as the cross-sectional area of annual ring(s) in percent of sapwood area; see text for further explanations.

trees on 2 occasions: 11 April (all trees) and 13 April (baited trees only). Readings were taken in early afternoon, and the ambient temperature was recorded every 30 min. From each tree, 2 readings were taken with the probes inserted vertically into the bark at opposite sides of the stem at breast height. Uncorrected readings were used since ambient temperature was stable during the procedure and close to the standard 15 °C.

Half of the pruned trees were felled on 1 June (when beetle tunelling was still in progress and developed lesions were expected to be found; *cf* Långström *et al,* 1992), and the remaining pruned trees on 24 August 1989 (when the brood had emerged and trees had either died or survived). After felling, tree length, crown length, annual height growth back to 1983, crown fresh weight (*ie* all live branches), and the number of live whorls were recorded. The trees were classified as surviving, survival uncertain, dying or dead, according to the appearance of the foliage and the inner bark.

A stem disc was sawn at breast height, and the border between the translucent sapwood and opaque heartwood marked immediately. All stems (up to the first living whorl at ≈ 3 m height) were transported to the laboratory within 24 h, and cold-stored at +2 °C until the next day.

Laboratory procedures

On the day after felling, the stems were cut at 20 and 30 cm stem height. The lower sections were discarded, and the upper 10-cm pieces were placed in trays with a few cm of a water suspension of Fast Green (0.25 g per 1 l water; Parmeter *et al,* 1989) and were allowed to take up the dye for 24 h at room temperature. Then new surfaces were cut ≈ 5 cm above the lower end of the bolts and the presence of unstained non-conducting sapwood and heartwood was delineated.

After cutting the stem in sections, the bolts between 30–80 and 130–180 cm stem heights were immediately frozen, the 80–130-cm section taken for isolation of fungi from beetle galleries and sapwood (Solheim and Långström, 1991), and the remaining sections up to live crown were cold-stored until analysed.

Before removing the bark on the 30–80-cm stem section (and section 130–180 cm, if *T minor* (Hart) was present), all exit holes of the emerging new brood of pine shoot beetles were counted (not applicable for June-felled trees). If galleries of *T minor* were present under the bark, the exit holes of this species were counted on the wood surface, the difference between the 2 counts then being attributable to *T piniperda*. As the bark was relatively thin, no correction was made for the few beetles emerging through old exit holes (*cf* Salonen, 1973). The presence of blue-stain on the cut bolt ends was noted in 10% area classes.

For the first 20 galleries encountered of each beetle species after bark removal, the following were recorded: total gallery length, length of lesion tip ahead of the gallery tip, total lesion length, presence of parent beetle(s), eggs, larvae or pupae in the gallery; then the lesions surrounding the galleries were delineated on transparent film; finally, the lesions were cut out along the lesion periphery and refrozen for later chemical analyses (June-felled tree only). All additional galleries as well as those found on the other stem sections (including that taken for isolation of fungi) were counted, separating beetle species and attack attempts (< 1 cm in gallery length) from longer egg galleries (> 1 cm in length).

For trees felled in June, additional phloem samples were taken from an unaffected part of the stem (> 10 cm from the nearest lesion) for later analyses of resin acids and starch, and from phloem adjoining lesions for starch analyses; all samples were refrozen as the lesion samples mentioned above.

The discs taken at breast height were polished, and annual ring widths were measured with 0.01 mm accuracy along 2 opposite radii. Radial growth, basal area growth, vigour index (*ie* the cross-sectional area of a given annual ring (or rings) in percent of the total sapwood area; see Waring and Pitman, 1980; for a discussion of the underlying physiological assumptions, see Waring and Pitman, 1985), and sapwood percentage were calculated and used as expressions of tree vitality prior to beetle attack (table I).

Lesion areas were calculated as lesion length by mean lesion width (obtained from measurements of lesion widths for every cm in length from the drawings on transparent film). A net lesion area was obtained by subtracting the egg gallery area (calculated as gallery length x 2 mm average egg gallery width). Knowing the attack density and the mean lesion area, the total lesion area per m^2 inner bark could be calculated.

Chemical analyses

Inner bark samples were pooled within each pruning date into 3 attack density classes (see below) prior to analysing resin acids and starch as previously described by Långström *et al* (1992).

Statistics

Data were analysed using the SAS statistical program package (SAS, 1987). Treatment means were compared by analyses of variance followed by Tukey's test for multiple comparisons, or by 2-way ANOVAs (Zar, 1984). Pairs of means were tested with Student's *t*-test, correcting for unequal variances when appropriate (Zar, 1984). The resin acid composition in the samples was analysed by principal component analysis (PCA). Relationships between variables were analysed using correlation coefficients and stepwise linear regressions were computed in order to explain the variation.

RESULTS

Tree vigour

Tree diameter, height and number of remaining whorls after pruning were similar for experimental trees of the 3 pruning dates (table I; ANOVA followed by Tukey's test for multiple comparisons). Height growth, crown length, ring widths and several other expressions of tree vigour were significantly lower for the trees pruned in June 1988 than for trees pruned in April 1989, and intermediate for trees pruned in

August 1988 (table I). However, there was no difference in cambial electrical resistance.

Beetle performance

Beetle attack

All but one of the 60 trees included in the study were attacked by *T piniperda* and 13 trees were also attacked by *T minor.* The attack density of the latter species was negligible (maximum of 5 galleries on the tree attacked most); hence no further attention will be paid to *T minor* in this study. Since no other bark-living insects were found on the stem sections in any numbers, *T piniperda* (and its associated blue-stain fungi) was the major challenge of the tree's defensive capacity.

The attack density of *T piniperda* on the lower stem (0.3–0.8 m) did not differ significantly between pruning dates (fig 1; 2-way ANOVA; data for the 2 sampling dates were pooled, as they did not differ). As expected, the attack density was higher on baited trees than on unbaited ones (see also figure 2).

The attack density on the lower stem was well correlated with the total number of egg galleries on the whole trunk exploited by the beetles (fig 2). Although baited trees were clearly more attacked, there was a great overlap between the 2 groups.

Gallery construction

Egg galleries were significantly shorter in trees pruned in June 1988 than in those pruned in March 1989 (fig 1; ANOVA followed by Tukey's test for multiple comparisons), indicating more persistent oviposition attempts in the latter than the former trees. Correspondingly, the percentage of galleries < 1 cm, *ie* failed attack attempts rather than true galleries, differed clearly between tree groups (fig 1).

At attack densities < 200 egg galleries per m^2, mean egg gallery length remained short, indicating failure in establishing a brood (fig 3). This was true for both batches of trees, *ie* trees felled in June as well as in August. At higher attack densities, gallery lengths were also similar between the 2 groups of trees, indicating that full gallery length had been reached by 1 June. It is noteworthy that some of the surviving trees had gallery lengths similar to those that eventually died.

Beetle behaviour and brood development

Since attack densities on baited and unbaited trees were overlapping (*cf* fig 2), trees were regrouped in 3 attack density classes within each pruning date (< 150, 151–300, > 300 egg galleries per m^2, respectively) regardless of whether they had been baited or not, before further analyses of beetle behaviour and defence chemistry were made.

By 1 June, all trees with a low attack density were abandoned by the parent beetles and no larvae had hatched in the galleries (table II), regardless of pruning date. Presence of parent beetles as well as the percentage of galleries with developing brood was higher in severely than in intermediately attacked trees. For the trees attacked most, these percentages increased from the oldest to the latest pruning date. Thus, attack density had a large influence on the probability for successful colonisation, and the beetles seemed to do better on trees pruned shortly before than long before attack (successful brood development occurred only in trees that were eventually killed by the attacks; see below).

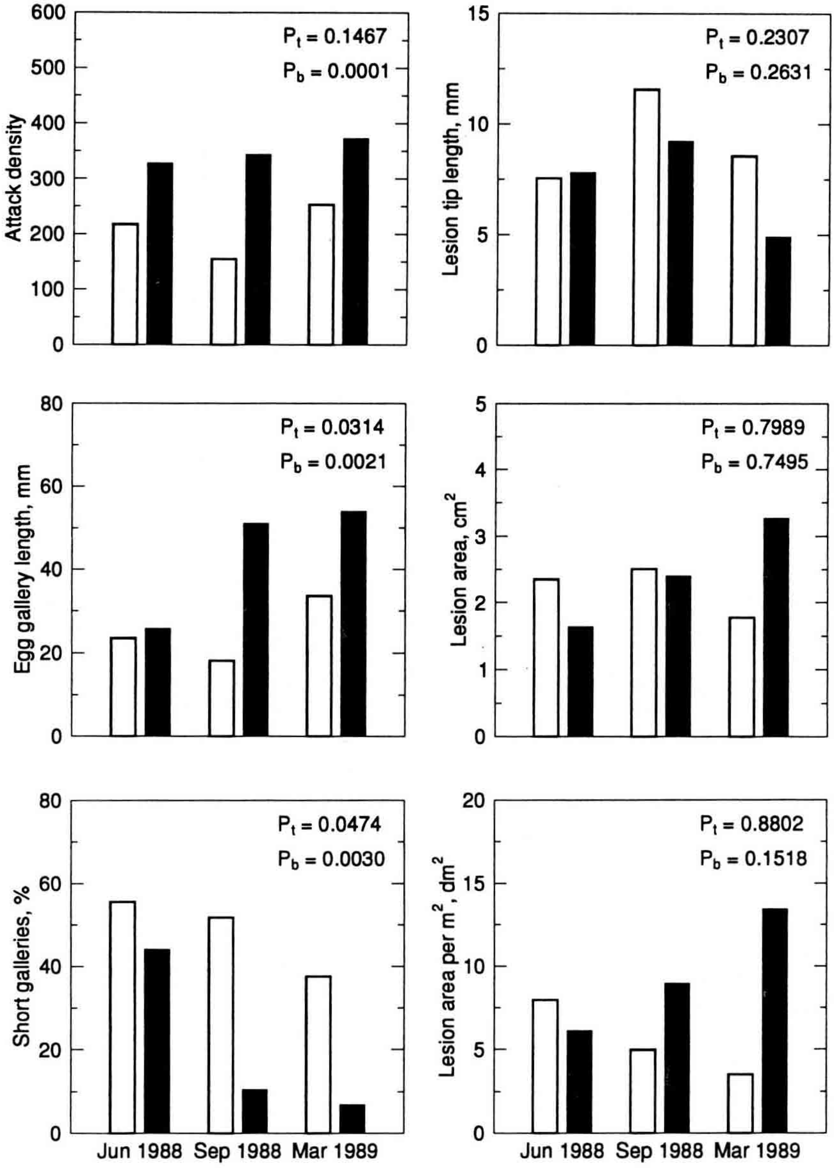

Fig 1. Left : Attack density (*ie* egg galleries/m^2), mean gallery length, percentage of failed attacks *ie* short galleries (< 1 cm) of *T piniperda* on lower stem of baited and unbaited trees (filled and open columns, respectively) pruned on 21 June 1988, 9 September 1988 and 9 March 1989, respectively (n = 20, both felling dates pooled); right : mean lesion tip length (in advance of the gallery tip), mean lesion area (excluding the gallery area), and total lesion area (including the gallery area) of trees felled on 1 June 1989 (n = 10). P values indicate probabilities of exceeding the observed F-statistic (2-way ANOVA); P_t and P_b refer to pruning dates and baiting, respectively.

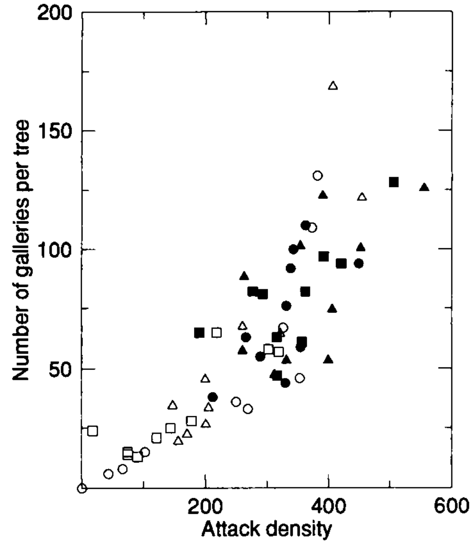

Fig 2. Attack density of *T piniperda* on lower stem of baited and unbaited trees (filled and open symbols, respectively) as related to the total number of egg galleries per tree at Norrsundet in 1989 (*N* = 60, pruning dates pooled).

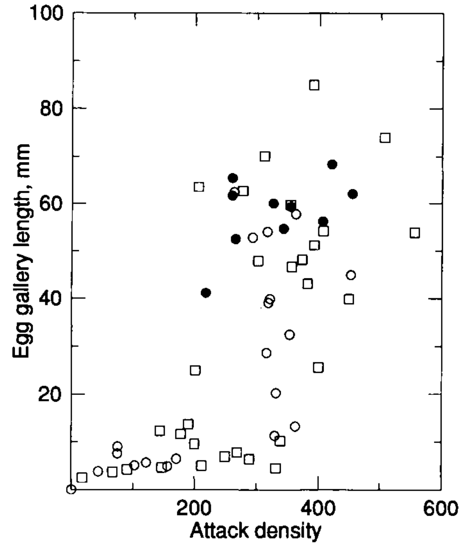

Fig 3. Attack density of *T piniperda* on lower stem as related to the corresponding mean gallery length of trees felled on 1 June (squares) and on 24 August 1989 (open and filled circles refer to surviving and killed trees, respectively); pruning dates pooled (*N* = 60).

Table II. Brood development (*ie* percentage of galleries containing larvae) and presence of parent beetles (percentage of galleries containing one or both parent beetles) in trees felled on 1 June 1989 and grouped in 3 attack density classes; number trees in brackets.

Pruning date	*Attack density class*			*No of galleries examined*
	< 150	*150–300*	*> 300*	
Percentage of galleries containing larvae				
23 June 1988	0 (1)	0 (4)	19 (5)	184
9 September 1988	0 (3)	25 (3)	46 (4)	168
9 March 1989	0 (1)	4 (3)	56 (6)	193
Percentage of galleries containing parent beetles				
23 June 1988	0	1	31	178
9 September 1988	0	25	51	168
9 March 1989	0	32	62	192

Defence reactions

Induced defence reaction

None of the several variables used to describe the size of the lesion developing around the egg gallery differed significantly between treatments (fig 1, right column). Plotting the lesion tip length against the mean gallery length revealed a strongly non-linear relationship (fig 4), indicating that the induced defence reaction culminated at ≈ 20 mm gallery length, and thereafter failed to contain an increasing proportion of the galleries within the lesions. This result was valid for both batches of trees, demonstrating that gallery expansion and lesion formation was, in fact, finished by 1 June.

In the surviving trees, the defensive lesions covered an increasing proportion of the inner bark with increasing attack density, occupying at the most ≈ 30% of the inner bark area on the lower stem (fig 5).

Defence chemistry

Starch

Starch levels did not differ systematically between pruning dates or attack density levels (table III). However, means (control phloem) for the attack density classes displayed decreasing levels: 13.0, 11.9 and 10.3% with increasing attack density. In 8 cases out of 9, starch levels of control samples were somewhat higher than for samples taken close to a lesion.

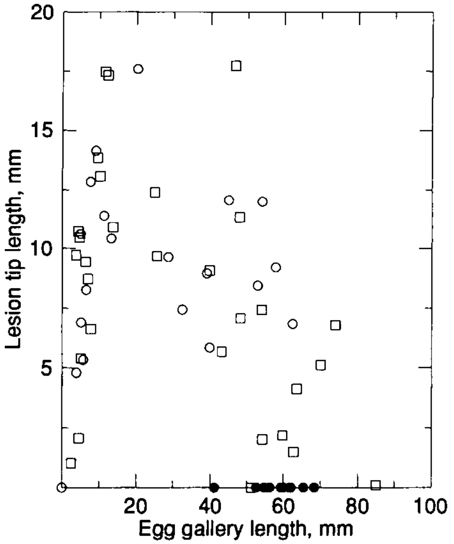

Fig 4. Mean gallery length of *T piniperda* on lower stem as related to the corresponding mean lesion tip length (*ie* defence reaction ahead of the gallery tip) of trees felled on 1 June (squares) and on 24 August 1989 (open and filled circles refer to surviving and killed trees, respectively); pruning dates pooled (*N* = 60).

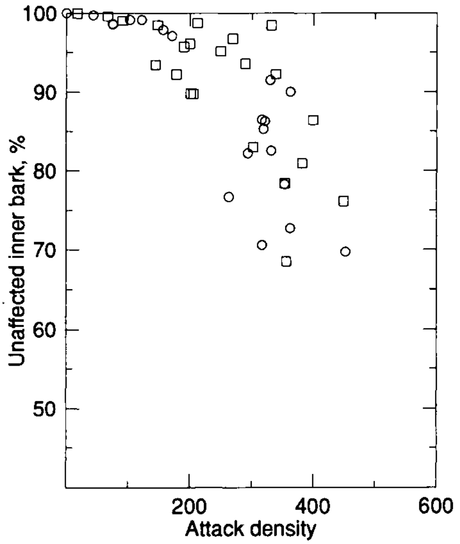

Fig 5. Percentage of inner bark on lower stem that was not affected by lesion formation in response to beetle attack as related to the attack density of *T piniperda* on the lower stem of trees felled on 1 June (squares) and on 24 August 1989 (circles); pruning dates pooled (*N* = 50; 10 dead trees with all inner bark destroyed were omitted).

Table III. Contents of resin acids and starch (% dw) in inner bark samples as related to pruning date and attack density class on experimental trees felled on 1 June 1989.

Resin acids or starch	*Pruning date and attack density class (egg galleries/m^2)*								
	23 June 1988			*9 September 1988*			*9 March 1989*		
	< 150	*151–300*	*> 300*	*< 150*	*151–300*	*> 300*	*< 150*	*151–300*	*> 300*
Resin acids in control bark [a]	1.0	0.9	1.3	1.3	0.9	1.2	0.8	1.9	1.0
Resin acids in lesion bark	20.6	21.2	14.4	17.9	19.0	13.4	17.7	19.2	21.4
Starch in control bark [a]	11.7	13.1	11.7	15.6	12.2	11.5	11.8	10.6	7.7
Starch in bark adjoining lesions	10.8	10.0	10.8	11.7	10.2	9.6	10.1	9.3	8.0

[a] Control bark samples taken from an unaffected part of the bolt; ie > 10 cm from the nearest lesion.

Resin acids

On 1 June, the content of resin acids were > 10-fold in the lesion phloem as compared to unaffected control bark samples (table III). No clear differences could be seen in the total amounts of resin acids either between pruning dates or attack density classes.

As the resin acid composition did not differ between trees of different pruning dates and attack density classes, data are not shown. The principal component analysis of lesion and control samples only confirmed the quantitative effects shown in table III, but did not reveal any consistent qualitative patterns between sample groups (data not shown). Thus, the defence reaction seems to be mainly quantitative.

Comparison between surviving and dead trees

Tree mortality and characteristics

Ten of the 30 trees felled in August 1989 were classified as dead, and of these 4, 2 and 4 trees had been pruned in June 1988, September 1988 and March 1989, respectively. As 6 of the dead trees had been baited and 4 not, tree mortality was not clearly linked to either baiting or pruning date. Six of the dead trees had been attacked by *T piniperda* alone, and 4 trees by both *Tomicus* species.

The surviving trees did not differ from the dead ones in tree size, radial growth, or in vigour index, but the CER readings were significantly different between the 2

Table IV. Comparison between surviving (n = 20) and dead trees (n = 10) at Norrsundet in August 1989. Trees from different pruning dates were pooled; all gallery data refer to *T piniperda*.

Variable	*Surviving trees*	*Dead trees*	*Probability* (t) [a]
Diameter ub at BH in 1988 (mm)	55.3	56.2	0.7188
Crown length (m)	1.85	1.62	0.0901
Radial growth 1988 (mm)	0.73	0.80	0.5692
Basal area growth 1988 (%)	5.2	5.6	0.6460
Vigour index 1988 (%)	5.4	5.7	0.7513
Vigour index 1986–1988 (%)	17.2	16.6	0.7739
Cambial electrical resistance (CER) (kΩ) on 11 April	23.1	20.0	0.0153
Cambial electrical resistance (CER) (kΩ) on 13 April [b]	25.5	21.9	0.0463
No galleries/tree	47.7	77.1	0.0164
No galleries/m^2	238.5	331.2	0.0508
Total gallery length (m)	8.2	19.5	0.0003
Mean gallery length (mm)	26.3	58.1	0.0001
Percent galleries < 1 cm	43.1	0.2	0.0001
No exit holes/m^2	0	328	0.0003
No exit holes/gallery	0	1.1	0.0017
Percent blue-stain, lower stem [c]	0.1	86.3	0.0001
Percent blue-stain, upper stem [c]	1.0	42.3	0.0007

[a] Level of significance according to Student's t-test; [b] n = 9 for surviving and n = 6 for dead trees; [c] Estimated in 10% classes at cut bolt ends.

groups (table IV). Furthermore, the 2 CER readings taken 2 d apart were highly interrelated ($r = 0.895$; $P = 0.0001$), and thus reproducible. CER readings also correlated with vigour indices, the best correlation being that between first CER measurement and the vigour index for the period 1986–1988 ($r = -0.63$; $P = 0.012$). However, this negative correlation is not consistent with the larger CER reading for surviving trees.

Beetle performance

The attack density of *T piniperda,* as well as the total number of attacks per tree were significantly higher on trees that eventually died than on surviving trees (table IV), whereas *T minor* occurred in low numbers on both groups of trees (< 1 gallery per tree on average). Thus, *T minor* obviously had a negligible influence on the outcome of the beetle attack as compared to *T piniperda.*

Mean and total gallery lengths were also significantly higher on the trees successfully attacked by *T piniperda* than on surviving trees (table IV). Furthermore, no successful brood development occurred on the surviving trees, while exit holes of *T piniperda* occurred in all dead trees on the lower stem covered with rough bark. However, the brood production per m^2 was low even in the successfully colonised trees, and the average rate of reproduction was less than unity, *ie* the number of emerging beetles was less than the ovipositing parent beetles (table IV).

Occlusion and blue-staining of sapwood

At felling on 1 June, the treatment with Fast Green disclosed wedge-shaped sections of non-functional sapwood on cut discs immediately below beetle galleries in some (potentially dying?) trees (fig 6B). In other (surviving?) trees, all sapwood was stained by the dye and was hence functional (fig 6A). In August, surviving trees still had all or most of the sapwood fully functional, albeit with deep occluded wedges in some cases (fig 6C), whereas irregular patches of stained sapwood were typical for dead trees (fig 6D). Whether the staining of the dead trees was a result of active transportation of dye in the dying sapwood, or a passive absorption by desiccated wood, remains unclear.

All dead trees displayed a high percentage of blue-stain in the sapwood of the cut ends at the lower and upper stem sections, whereas the blue-staining of the sapwood was negligible on both stem sections of surviving trees (table IV; see also Solheim and Långström, 1991).

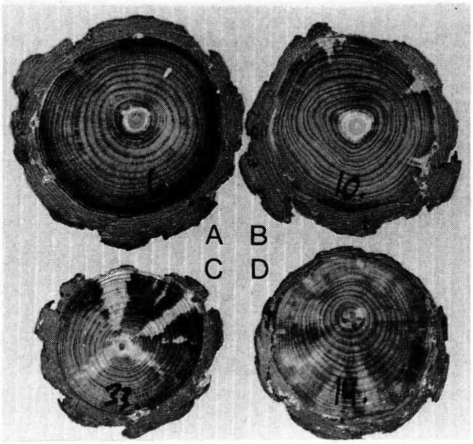

Fig 6. Cross-sectional view of stem discs cut from bolts taken at 20–30 cm stem height after allowing the bolts to absorb a suspension of Fast Green for 24 h. (A) Surviving and (B) possibly dying (note wedges of occluded sapwood below galleries; also note absence of wedges below other galleries) trees felled on 1 June; (C) probably surviving tree with partially occluded sapwood and (D) killed tree (note irregular staining of dessicated wood) felled on 24 August 1989.

DISCUSSION

According to Larsson (1989), phloem-feeders like bark beetles should be more favoured by changes in host vigour than other guilds of herbivores. In several studies, conifer susceptibility to bark beetles has been found to be correlate with tree vigour, expressed as the efficiency of the foliage to produce stemwood (Waring and Pitman, 1980, 1985; Larsson *et al,* 1983; Mulock and Christiansen, 1986). It has been postulated that stress factors like defoliation or drought mainly interfere with the tree's ability to allocate carbohydrates for defence and thus render them susceptible to beetle attack (Christiansen *et al,* 1987). Similarly, the concept of growth differentiation balance suggests that trees are prone to beetle attack during periods of intensive growth when less carbohydrates are available for defence (Lorio, 1988).

In the present study, we succeeded in creating a tree population with a similarly reduced needle biomass but different vigour indices, representing a similar photosynthetic capacity but different growth efficiencies (*sensu* Waring and Pitman, 1985). Furthermore, the vigour index at the time of attack should have been in the critical range for successful colonisation, which in several conifer species have been found to be < 10% in annual sapwood area growth (equalling 100 g stem wood per m^2 needle area/yr; *cf* Waring and Pitman, 1980, 1985; Larsson *et al,* 1983; Mulock and Christiansen, 1986). Needle biomass was also sufficiently reduced to render some of the trees susceptible to attack (Långström *et al,* 1992).

We also managed to get the trees with different pruning history attacked in a similar way. The attack density of *T piniperda* was comparable to that found in other studies in the same area (Långström and Hellqvist, 1988, (1993); Långström *et al,* 1992). Furthermore, the mean attack densities on baited and unbaited trees were, respectively, above and below 300 egg galleries per m^2, a level found to be critical for successful colonisation in the studies mentioned above. In these small trees, the critical attack density corresponded ≈ 50 egg galleries/tree.

Judging from trees felled on 1 June, the parent beetles stayed longer in galleries of densely attacked trees than on trees of low attack density. A similar pattern could be seen for the frequency of galleries containing developing brood. For the densely attacked trees, parent beetle presence as well as brood development was lower in trees pruned in June 1988 than in other trees. Correspondingly the frequencies of failed attacks (*ie* short galleries) tended to be higher and mean gallery lengths shorter in trees pruned in June 1988 than in trees pruned closer to the beetle attack, despite similar attack densities (both felling dates; *cf* fig 1). Thus, the trees pruned ≈ 1 yr prior to beetle attack were less suitable brood material than those pruned 1 month before beetle flight. Obviously, attacking beetles responded to some (chemical or physiological) cues, and abandoned the former trees sooner than the latter.

The observed differences in parent beetle behaviour and gallery development, could not, however, be related to any corresponding differences in the extent of the induced defence reaction, *ie* the size of the lesion formed in response to the attack. This lack of relationship can, however, be understood when considering the strong non-linear relation between lesion expansion and gallery length. Thus, the linear relationship between gallery expansion and lesion formation observed by Lieutier *et al* (1988), was valid only until the defence system started to collapse when an increasing number of beetles succeeded in breaking out from the lesions. In our data, this occurred when galleries, on average, were ≈ 25 mm long, and such galleries started to occur when attack density exceeded 200 egg galleries/m^2. In surviving trees, lesions covered a maximum of ≈ 30% of the phloem area on lower stem; thus at least two-thirds of the phloem was still fully functional.

As neither phloem starch nor lesion resin acid content displayed variation that could be linked to the above pattern in parent beetle behaviour and gallery development, other factors must have been involved. For example, primary resin flow (Schroeder, 1990), oleoresin pressure (Vité and Wood, 1961) or phloem thickness may have played a role (Amman, 1972; Lieutier and Ferrell, 1988). Other defence components such as phenolics may also be involved (Lieutier *et al,* 1991). The observed resin acid accumulation in the lesions was similar to that found by Långström *et al* (1992), and is hence not discussed here.

Altogether, the above results indicate that pruning on different occasions prior to beetle attack had not, after all, differentially altered the trees' susceptibility to bark beetles. Similar results have been obtained for drought-stressed or pruned Norway spruce (*Picea abies* L (Karst)) (Christiansen, 1992; Christiansen and Fjone, 1993). On the other hand, removal of ≈ two-thirds of the foliage resulted in one-third of the trees left to grow over the summer being killed by beetle attack. This would hardly have happened with trees carrying intact foliage (*cf* Långström *et al,* 1992; and references therein). Thus, the pruning treatment substantially increased the susceptibility of the trees to beetle attack. The reduced defence capacity was also reflected in the comparatively low starch levels of the inner bark in trees felled on 1 June (*cf* Långström *et al,* 1992). Similar results have been obtained for Norway spruce, *Picea abies*, when pruned and inoculated with blue-stain fungi (Christiansen and Fjone, 1993).

These results, as well as those obtained for drought-stressed Norway spruce (Christiansen, 1992), lead to the conclusion that the momentary vigour, *ie* the physiological condition of the tree at the very moment of beetle attack is much more important than the historical vigour which is usually measured. If so, the observed significant difference in cambial electrical resistance, measured at the time of attack, between trees that were going to survive and those that eventually died, indicates some important difference between the 2 batches of trees. However, the observed result showing higher CER for surviving trees is illogical since CER was also negatively correlated with tree vigour (Christiansen, 1981; Lieutier and Ferrel, 1988; Filip *et al,* 1989). Other studies indicate that CER may reflect differences in tree vitality due to factors such as defoliation (Piene *et al,* 1984a), thinning (Piene *et al,* 1984b; Matson *et al,* 1987) and root rot (Lindberg and Johansson, 1989).

The poor beetle performance even in successfully colonised trees is in full agreement with our earlier results in the area, and hence is not discussed here (Långström and Hellqvist, 1988, 1993; Långström *et al,* 1992). The same applies to the observation that the sapwood of dead trees was heavily blue-stained, indicating that these trees may have been killed by the beetle-vectored blue-stain fungi rather than the beetles (Solheim and Långström, 1991; Solheim *et al,* 1993). On the other hand, sapwood occlusion (indicating fungal growth) had barely started on 1 June when egg galleries were fully grown. It is also worth noting that sapwood occlusion did not occur below all beetle galleries (*cf* fig 6B). This is consistent with the findings that only a fraction of the beetle galleries contain blue-stain fungi (Lieutier *et al,* 1988, 1989b; Solheim and Långström, 1991).

In conclusion, the present study confirmed earlier observations on beetle performance and induced defence reactions in young Scots pine. It also yielded new data regarding beetle attack and behaviour, lesion formation and sapwood occlusion. However, we failed to demonstrate differences in resistance between trees of different vigour indices, nor did we find valid criteria for describing host resistance. Hence, further studies are needed to develop methods of identifying and measuring even short-term changes in host susceptibility to bark beetles. The physical or chemical properties of the phloem could be a trait to pursue, as indicated by the measurements of cambial electrical resistance, despite conflicting results.

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