

Shoot damage and growth losses following three years of *Tomicus*-attacks in Scots pine stands close to a timber storage site

Bo Långström & Claes Hellqvist

TIIVISTELMÄ: YTIMENNÄVERTÄJIEN AIHEUTTAMAT KASVAIN TUHOT JA KASVUTAPPIOT PUUTAVARAVARASTON LÄHEISYYDESSÄ SIJAITSEVISSA MÄNNIKÖISSÄ KOLMIVUOTISEN VARASTOINNIN JÄLKEEN

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Shoot losses due to maturation feeding by pine shoot beetles (*Tomicus piniperda* (L.) and *T. minor* (Hart.), Col., Scolytidae) and subsequent growth losses were studied in pine stands growing at different distances from a timber yard, where pine timber was stored during the years 1982–1984. In autumn 1985, pine trees were felled at 20, 40, 80, 500 and 1500 m distance from the timber yard, five trees in each distance class. Trees were analysed for beetle attack, needle biomass and growth. In autumn 1988, increment cores were taken from 20 trees in each distance class.

In 1985, different damage estimates showed that beetle damage was more than 10-fold in the crowns of pine trees growing close to the timber yard as compared to less damaged trees at greater distance. Crude needle biomass estimates indicated that the trees attacked most had lost more than half of the total foliage. Following three years of attack, basal area growth decreased for 2–3 years and recovered during the subsequent 3 years, the total period of loss thus being 5–6 years. The loss in volume growth during 1983–1985 was ca 70, 40, 20 and 10 percent at 20, 40, 80 and 500 m distance from the beetle source, respectively, as compared to the stand at 1500 m. Growth losses did not occur until the number of beetle-attacks, “pegs”, exceeded ca. 200 per tree. The highest observed growth losses occurred in trees with more than 1000 pegs per tree.

Ytimennävertäjien (*Tomicus piniperda* (L.) ja *T. minor* (Hart.), Col., Scolytidae) ravintosyönnin seurauksena syntyviä kasvaintuhoja ja kasvutappioita tutkittiin Etelä-Ruotsissa sijaitsevan puutavaravaraston ympäröimissä männiköissä. Mäntypinotavaraa varastoitiin vuosina 1982–1984. Syksyllä 1985 mitattiin kaatokoeputia 20, 40, 80, 500 ja 1500 m etäisyydellä puutavaravarastosta. Kultakin etäisyydeltä kaadettiin viisi mäntyä, joista arvioitiin kasvaintuhojen määrä, neulamassa ja puiden kasvu. Syksyllä 1988 kairattiin 20 puuta kussakin etäisyysryhmässä.

Vuonna 1985 erilaiset kasvaintuhoarviot osoittivat ytimennävertäjätuhojen olevan noin 10-kertaiset puutavaravaraston lähituntumassa kasvavissa ja vakavasti vaurioituneissa männyissä etäisimpiin ja lievästi vaurioituneisiin puihin verrattuina. Karkeat neulamassa-arviot viittasivat siihen että suurimman tuhon kärsineet männyt olivat menettäneet yli puolet neulamassastaan. Kolmivuotisen tuhokauden seurauksena pohjapinta-alan kasvu pieneni 2–3 vuoden ajan ja toipui seuraavien 3 vuoden aikana. Kasvutappio kesti täten 5–6 vuotta. Tilauuskasvu oli vuosina 1983–1985 20, 40, 80 ja 500 m etäisyydellä noin 70, 40,

20 ja 10 % pienempi kuin etäisimmän (eli 1500 m etäisyydellä kasvavan) metsikön kasvu. Kasvutappioita ei esiintynyt ennenkuin tuhoutuneiden versontynkien lukumäärä puuta kohti ylitti noin 200. Suurimmat tappiot todettiin puissa joissa tynkiä oli yli 1000.

Keywords: *Pinus sylvestris*, forest damage, estimates, growth, shoots, *Tomicus piniperda*, *Tomicus minor*.
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Authors' address: Swedish University of Agricultural Sciences, Division of Forest Entomology, S-770 73 Garpenberg, Sweden.

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1 Introduction

The pine shoot beetles, *Tomicus piniperda* (L.) and *T. minor* (Hart.) (Col., Scolytidae), are unique among European bark beetles in causing considerable growth losses to Scots pine (*Pinus sylvestris* L.) by destroying young shoots (Nilsson 1976). The beetles breed in fresh pine wood (e.g. storm-felled trees, pulp wood, moribund trees etc.) and the emerging young beetles as well as the surviving beetles of the parent generation feed on young shoots of living pine trees (for details regarding the biology of the species, see e.g. Långström 1983). This shoot-feeding results in loss of foliage, and at high population levels considerable growth losses have been observed (Michalski and Witkowski 1962, Andersson 1973, 1974, Nilsson 1974b, 1976, Stroink 1982, Långström and Hellqvist 1990).

However, conclusive demonstration of insect impact on tree growth is a difficult task requiring careful estimation of damage levels and growth reactions as well as consideration of potential biasing factors such as site and stand differences, weather conditions, etc. The accumulated

empirical data are conflicting, and experimental data obtained under controlled conditions indicate that some of the older studies may have underestimated the damage levels (Långström et al. 1990 and references therein). Thus, further studies have been considered necessary in order to clarify the relationships between attack level, foliage loss and growth loss.

The aim of the present study was to estimate shoot damage levels and growth losses in pine stands surrounding a timber yard following three years of timber storage, and to establish whether the observed impact could be attributed to pine shoot beetles developing in the stored timber.

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2 Materials and methods

2.1 Study site

The study area was situated at Aneby in southern Sweden (57°50' N. lat.; 14°45' E. long.; 230 m above sea level). In the early 1980s, large amounts of conifer pulp wood were stored at a timber yard previously used mainly for birch wood (B. Carlsson, pers. comm.). Timber storage began in 1982, and in May 1985 no timber

was stored any longer at the yard, but at that time adjacent pine stands displayed mis-shaped crowns with the characteristic appearance of trees heavily attacked by *Tomicus*-beetles (Fig. 1a), while similar pine stands further away were apparently less attacked. Thus, the area was suitable for impact studies.

The severely damaged pine forest adjoining the timber yard was growing on the eastern

slope of a low moraine ridge, extending in north-south direction. The forests on the western slope had escaped attack. The whole land area from the timber yard to the most distant study stand at 1500 m was forested with pine-dominated stands, and there was no treeless space in the study area. On the eastern side of the timber yard, the landscape was flat with young pine plantations intermingled with agricultural land and urban areas at some distance.

Forest management and protection practice in the area were good, leaving the beetles with no or few breeding grounds, other than the timber stored at the yard. No extreme weather conditions occurred during the study period, that could have affected beetle development or tree growth abnormally. In 1988, thinnings were carried out in the study area, making further impact studies in the area meaningless due to altered structure in experimental stands.

2.2 Field procedures

In September 1985, stand data were recorded on relascope plots (8 plots per row) laid out in three rows at 20, 40 and 80 m distance from and parallel with the edge of the forest adjoining the timber yard (hereafter referred to as "stands" A, B, and C, respectively). In addition, two similar sets of plots were established in the less damaged stands growing at 500 m (stand D) and 1500 m (stand E) from the timber yard, respectively. There was some variation in stem number and basal area between the stands (Table 1).

On 24–26 September 1985, a total of 25 sample trees (5 trees in each stand) were selected at random (i. e. the nearest tree at 20 m intervals

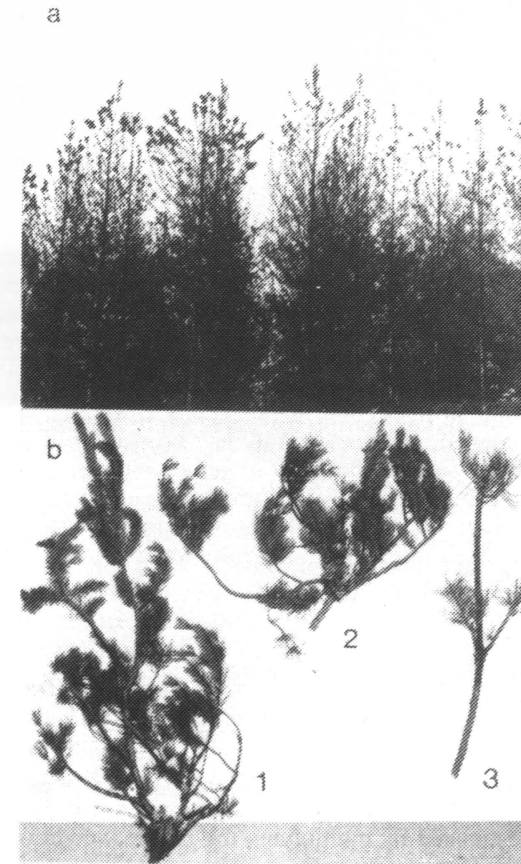


Fig. 1. (a) Mis-shaped upper crowns of Scots pine due to intensive shoot-feeding by pine shoot beetles during 1982–1984; (b) Typical examples of branches in branch damage classes (BDC): 1, 2 and 3 (undamaged and dead branches are missing; photo: BL).

Table 1. Stand data at Aneby in 1985 (estimated from 8 relascope plots per stand).

Variable	Stand				
	A	B	C	D	E
Distance to beetle source, m	20	40	80	500	1500
Site index, m ^a	T29	T29	T28	T28	T28
Basal area, m ² per ha	23	25	22	23	20
Stems per ha	1000	1900	1700	2000	1500
Pine, % of stem number	80	90	80	90+	90+
Stand age at stump, years ^b	40	32	34	27	33

^a For a legend to site index, see Hägglund and Lundmark 1977

^b Estimated from trees felled in 1985, see Table 2

Table 2. Description of trees felled at Aneby in 1985 (n = 5; numbers in brackets are standard deviations of means).

Variable	A	B	Stand C	D	E
Diameter at breast height (over bark), mm	185 (21)	131 (24)	149 (22)	140 (17)	133 (17)
Tree height in 1985, m	16.9 (2.0)	15.3 (1.0)	15.2 (0.8)	11.9 (0.5)	14.0 (1.3)
Number of live whorls	14.6 (0.9)	12.4 (0.9)	13.2 (1.3)	12.0 (1.2)	14.8 (0.5)
Live crown length, m	7.0 (1.3)	6.7 (0.9)	6.8 (1.3)	6.5 (0.7)	7.3 (1.2)
Stem volume in 1985, dm ³	186 (51)	97 (31)	104 (31)	77 (13)	84 (23)
Competing basal area at 50 m ² , m ²	0.12 (0.07)	0.14 (0.05)	0.12 (0.05)	0.10 (0.02)	0.07 (0.03)

along the rows of relascope plots) among the dominant or codominant trees growing in the study stands, and felled (Table 2).

After felling, all *Tomicus*-attacks, i.e. broken shoots and other visible signs of pine shoot beetle attacks (hereafter referred to as "pegs"), were counted on 19 trees (3, 3, 3, 5 and 5 trees in stands A, B, C, D and E, respectively) whorl by whorl for all living branches back to and including whorl 1971. In addition, the branch damage class (BDC) was determined for each branch of all 25 felled trees as: 0 = undamaged, normal branch, 1 = slight damage, branch architecture still close to normal, 2 = intermediate damage, branch architecture clearly distorted, 3 = severe damage, branch severely stunted, and 4 = branch dead due to beetle pruning. Typical examples of branch damage classes 1–3 are shown in Fig. 1b.

Sample branches were collected for needle biomass estimates from 15 trees (the peg-counted ones mentioned above excluding 2 trees in each of stands D and E). On whorls 1974, 1977, 1980 and 1983, representing different crown fractions, the diameter at the base was measured (over bark) for each branch before they were clipped down in plastic bags, and taken to the laboratory for needle biomass estimates. If present, secondary shoots developing from interfascicular buds to replace destroyed original branches were also collected.

Field measurements also included total tree length, crown length, leader lengths back to 1971. Stem discs were taken at the stump, breast height (1.3 m), 5 m, and at internodes 1974 and 1980. For all sample trees, the distance to and the diameter of the nearest neighbour was measured, and all competitors growing within a 50 m² circle plot were counted and calipered at breast height.

On 14 September 1988, the stands were re-

inspected. Increment cores were taken at breast height from 20 pine trees in stands A–E. At the time of inspection, stands D and E were being thinned, and stands A–C had been thinned in early summer. In order to get an impression of the recovery in height growth, leader lengths were measured on felled crown tips in the stands (although they were not fully representative of the stands).

2.3 Laboratory procedures

Within a few days after felling, all needles were picked off the sample branches and needle dry mass was determined after drying (24 h at 105 °C). The total crown needle biomass was then estimated by multiplying the needle weight of the four whorls by the ratio between the number of weighed branches and the total number of live branches per tree, assuming that these whorls were representative for their corresponding crown section.

Ring widths were measured with 0.01 mm accuracy along two opposite radii on the discs, and annual radial growth was expressed as a mean of the two measurements. Using mean ring widths and diameter under bark at breast height, radial and basal area growths were calculated for each tree and year.

Annual volume growth was obtained by calculating total stem volume for each tree and year by sectioning, i.e. by applying Smalian's formula for a truncated cone to each stem section stepping back ring by ring and internode by internode (see e.g. Thomson and Van Sickle 1980).

In order to compensate for initial differences in tree size (Table 2), different expressions for relative growth rates and potential growth for basal area as well as volume were calculated.

This technique has been widely used when calculating fertilization effects (for references, see Lipas 1979), as well as in impact studies (Thomson and Van Sickle 1980, Ericsson et al. 1985, Laurent-Hervouët 1986, Björkdahl and Eriksson 1989).

Periodic growth rates (PGR) were calculated for basal area and volume growth as a measure of relative increment of each tree according to the following formula:

$$PGR = I_i / I_{ref}$$

where I_i was the basal area or volume increment for a given year during the damage period 1983–1985, and I_{ref} was the corresponding average increment of the same tree during the reference period 1980–1982. In addition, the average relative increment for the damage period was calculated using the average ring width during 1983–1985 instead of that for a given year. Climatic effects can be corrected by using weather-corrected ring widths (Jonsson and Stener 1986), but we used uncorrected ring widths, since the comparisons of relative growth rates between stands were independent of whether we used uncorrected or corrected ring widths.

In order to normalize the periodic growth rates to the growth level of control trees (stand E), we calculated another growth ratio, used by Eriksson (internal report) in fertilization studies and often referred to as the growth response or response index:

$$RI = 100 (PGR_{dam} / PGR_{con}),$$

where the response index (RI) is the above PGR of a damaged stand (PGR_{dam}) for a given year or period divided by that of the undamaged control

stand (PGR_{con}) and multiplied by 100 to get a percentage expression.

Relative growth expressions based on quotients have been compared to other growth response estimates, and found to give reliable results for the first 5-year period of comparison (Lipas 1979 and references therein). One general weakness with quotients, however, is that they assume growth trends to be similar for the periods under comparison, except for the factor studied. In order to test the validity of this assumption for our data, we fitted different linear and exponential equations based on basal areas or basal area growth percentages to the data sets for the pre-damage period. Using the true basal area development of stand E as a reference, we found that a simple linear regression was the best predictor, underestimating total basal area in 1988 and basal area growth 1983–1988 by 0.8 % and 3.4 %, respectively. Since linear regression gave a good fit for the pre-damage period for the other four stands as well, it seemed appropriate to use the above quotient techniques to estimate the growth reduction.

2.4 Statistics

Interactions between growth and damage variables were analysed using correlation, linear and non-linear regression analysis (Zar 1974, SAS 1987). The dependence of growth and damage variables on the distance to the timber yard was analysed using regression analyses. Finally, step-wise linear regressions were computed in order to explain the variation in growth loss as a function of beetle damage, distance to timber yard, needle biomass and inter-tree competition.

3 Results

3.1 Beetle damage

Both the peg-counting, branch damage classification and different expressions derived from these, showed that the beetles' shoot-feeding caused severe damage in the trees growing close to the edge of the timber yard, and decreased with increasing distance to the beetle source (Table 3, see also Fig. 7A). The most and least

attacked trees differed by more than one order of magnitude regardless of the way of expressing the damage.

3.2 Needle biomass

The estimated total needle biomass was considerably lower in stands A and B than in D and E,

Table 3. Description of beetle damage on trees felled in 1985 (n = 5; numbers in brackets are standard deviations of means).

Variable	A	B	Stand C	D	E
Number of pegs ^a	1152 (294)	449 (161)	357 (115)	95 (58)	63 (17)
Mean branch damage class	2.77 (0.24)	2.13 (0.37)	1.62 (0.14)	0.15 (0.02)	0.31 (0.10)
Number of damaged branches ^b	56.8 (10.7)	37.4 (4.6)	29.4 (5.0)	2.2 (0.8)	4.2 (2.2)
Percentage of damaged branches, % ^b	88.8 (6.1)	62.7 (10.0)	50.4 (6.3)	3.7 (1.4)	5.6 (2.3)
Number of damaged whorls ^c	11.0 (1.7)	6.8 (0.8)	5.4 (1.1)	0	0
Damaged crown length, m ^c	4.79 (1.59)	3.39 (0.66)	2.64 (0.72)	0	0
Percentage damaged crown length, % ^c	69.2 (19.9)	50.0 (5.9)	39.4 (9.5)	0	0
Needle biomass, kg d.w. ^d	2.21 (1.09)	2.28 (0.92)	3.07 (1.72)	4.63 (0.67)	4.39 (1.51)

^a Pegs counted only on 3 trees in stand A–C; all other means based on 5 trees

^b Branch damage class 2 or larger

^c Whorls with branch damage class 2 or larger

^d n = 3 in all stands

whereas C was intermediate (Table 3). The trees at the stand edge were, however, larger than the others (Table 2) and would hence have carried more needles than the control trees if not attacked by the beetles. Thus, more than half of the foliage was probably lost due to beetle attack in stand A. The results indicate further that stands B and C may have lost close to 50 and 30 percent, respectively, as compared to D and E. However, the estimation technique was a very crude one, and thus, these results should be seen only as indications of possible levels of needle loss.

3.3 Annual growth

3.3.1 Radial growth

Radial growth decreased in 1983–1985 in the stands (A–C) close to the timber yard as compared with the two less damaged stands (Fig. 2). This applied to both batches of trees, although the growth reduction was somewhat larger in the 1988-trees in stand A during 1983–1985 than for the trees felled in 1985, whereas the opposite pattern occurred in stand B. The 1988-trees show that trees started to recover in 1986 and had almost recovered by 1988.

3.3.2 Basal area growth

The basal area growth at breast height was similar in all stands until 1981–1982 (Fig. 3). During 1983–1985, growth of all trees in the

stands close to the timber yard decreased, and started to recover in 1986, reaching pre-damage levels by 1988. Thus, three years of damage seems to have caused a reduction in basal area growth during 6 years in the stand attacked most. It looks as if the growth decline was less abrupt in stands B and C but that the bottom was reached in 1985, as in stand A, and the recovery process was similar in all three stands.

3.3.3 Height growth

Height growth (Fig. 4) followed a pattern similar to that of basal area growth. For trees close to the timber yard, height growth declined drastically in 1983 and started to recover in 1986. For other trees, height growth was not particularly affected, indicating that leader shoots were not commonly attacked by the beetles. However, the decrease in stand B from 1982 to 1984 could just as well be a result of beetle attack.

Judging from field notes and the annual height growths of individual trees felled in 1985 (data not shown), all five of the A-trees were attacked in the leader shoots, two already in 1982 and three in 1983. Among the B-trees, one was attacked in 1983 and three in 1984, whereas none of the C–E-trees suffered damage to their leaders. The trees attacked most might have suffered recurrent leader attacks but the frequency of multiple attacks could not be traced. In 1985, i.e. after the attack had ceased, none of the leader shoots outgrown that year was attacked, nor were there any reduced leader lengths in the years prior to attack. Thus, reduced height growth

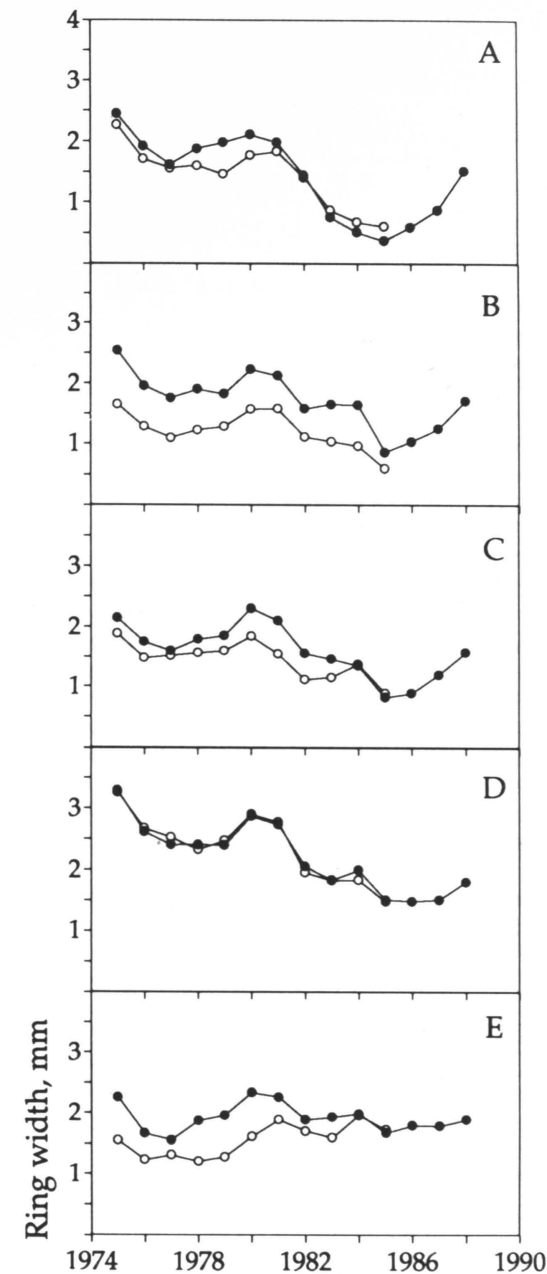


Fig. 2. Mean annual radial growth of study trees at breast height (white = trees felled in 1985, n = 5 in each stand; black = increment cores taken in 1988, n = 20 in each stand) growing at different distances (stand A–E) from the timber yard. For stand descriptions, see Table 1.

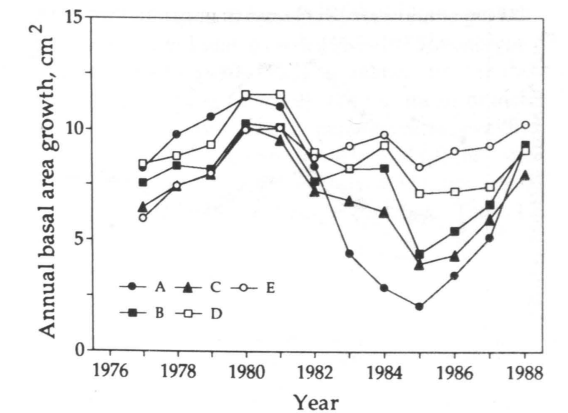


Fig. 3. Mean annual basal area growth at breast height during 1977–1988 based on increment cores from 20 trees per stand. For stand descriptions, see Table 1.

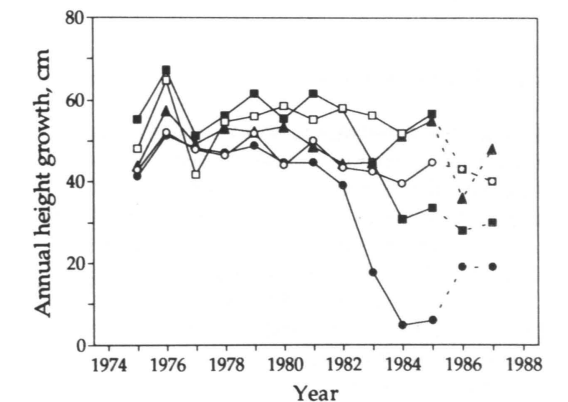


Fig. 4. Mean annual height growth during 1975–1985 for trees felled in 1985. Dotted lines indicate additional data obtained from trees thinned in 1988. For stand symbols and descriptions, see Fig. 3 and Table 1, respectively.

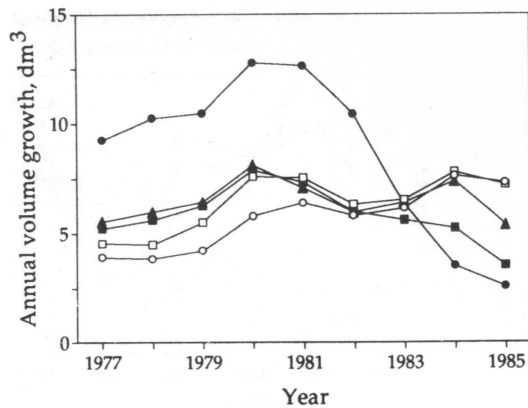


Fig. 5. Mean annual volume growth during 1977–1985 for trees felled in 1985. For stand symbols and descriptions, see Fig. 3 and Table 1, respectively.

was always a result of leader destruction due to beetle attack.

3.3.4 Volume growth

During the pre-damage period, the annual volume growth was considerably higher in stand A than in other stands (Fig. 5). This was due to initial differences in tree size (Table 2). There is, however, no mistaking the fact that a massive growth decline occurred in stand A during 1983–1985, a smaller decline in stand B and possibly a decline in stand C in 1985. A further analysis will have to rely on relative growth variables (see below).

3.4 Total impact

For the trees attacked most, different growth loss expressions showed a reduction in basal area growth during 1983–1988 ranging from 51 to 66 percent, and correspondingly the volume growth loss during 1983–1985 varied from 42 to 70 percent (Table 4 and Fig. 7b). The growth difference percentages were not, however, corrected for initial differences in tree size, whereas the quotient expressions (PGR and RI) gave similar loss estimates. For basal area growth, a larger reduction occurred in C- than in B-trees, the opposite being the case for volume growth.

3.5 Relationship: damage–growth

The periodic growth rates (PGR) for volume growth during 1983–1985 were negatively correlated with different expressions of beetle damage and positively correlated with needle biomass (Fig. 6). Both mean branch damage class (calculated as a crown mean for all live branches) and the percentage of damaged crown length (calculated as the percentage of crown length with whorls having a mean branch damage class of 2 or higher) showed almost as high correlations with the periodic growth rate as the traditionally used peg-counting. The comparatively poor correlation between growth reduction and crown needle biomass (Fig. 6d) may be due to the crude manner of estimating needle biomass or to differences in tree size.

A step-wise linear regression analysis (SAS 1987) including different damage variables for the 15 trees with needle biomass data as well as a measure for inter-tree competition (competing basal area at a 50 m² circle plot centred at the stump of the felled tree), showed that the number of pegs explained 77 % of the variation in volume PGR. Mean branch damage class was entered as the second variable and the number of severely damaged whorls as third variable into the model, and increased the level of explanation to 0.86. Since inter-tree competition did not explain any significant proportion of the variation in growth, we conclude that this factor was not biasing our growth loss estimates.

Table 4. Relative losses (%) in basal area growth during 1983–1988 (n = 20) and volume growth during 1983–1985 (n = 5) according to different growth loss expressions.

Variable	Stand				
	A	B	C	D	E
Loss in basal area growth 1983–1988					
Growth difference of stand E	51	25	38	14	0
Relative PGR ^a	66	24	33	25	3
Relative RI ^b	65	22	32	23	0
Loss in volume growth 1983–1985					
Growth difference of stand E	42	33	11	2	0
Relative PGR ^a	65	33	10	0	-16
Relative RI ^b	70	42	22	13	0

^a Relative PGR = 100(1-PGR); PGR = periodic growth rate

^b Relative RI = 100-RI; RI = response index

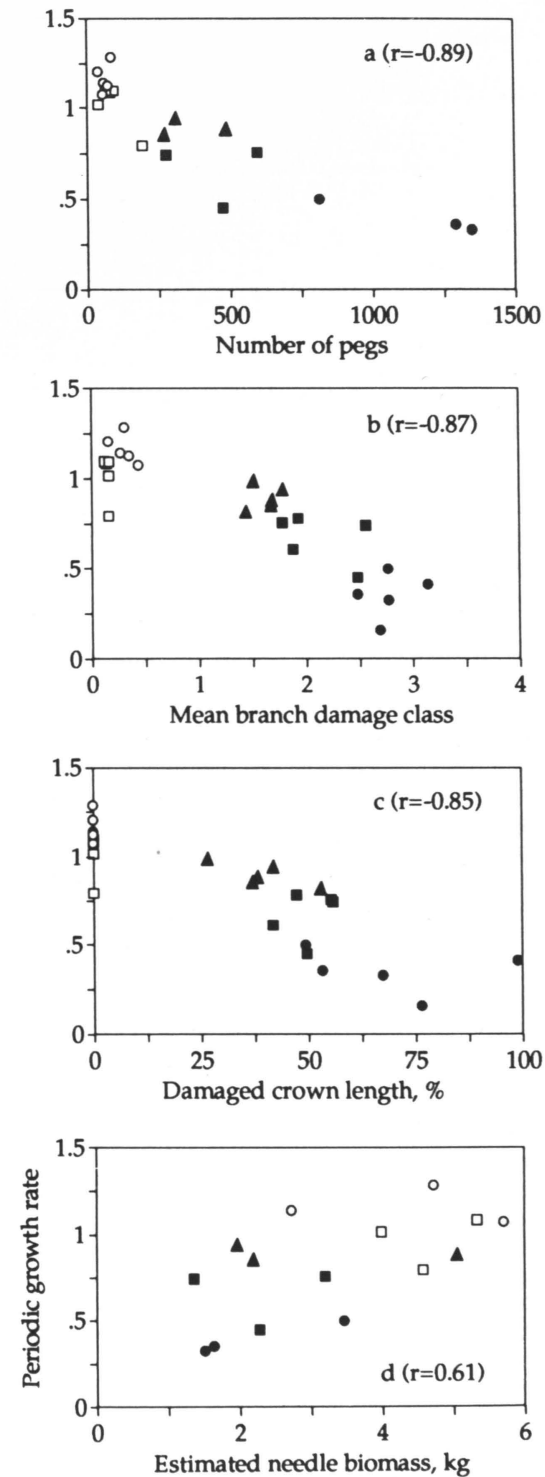


Fig. 6. Periodic growth rate (PGR) for volume growth (i.e. mean volume growth 1983–1985/mean volume growth 1980–1982) as related to: (a) the number of pegs (n = 19), (b) the mean branch damage class (n = 25), (c) percentage of severely damaged crown length (n = 25), and (d) the estimated crown needle biomass (n = 15). For stand symbols and descriptions, see Fig. 3 and Table 1, respectively.

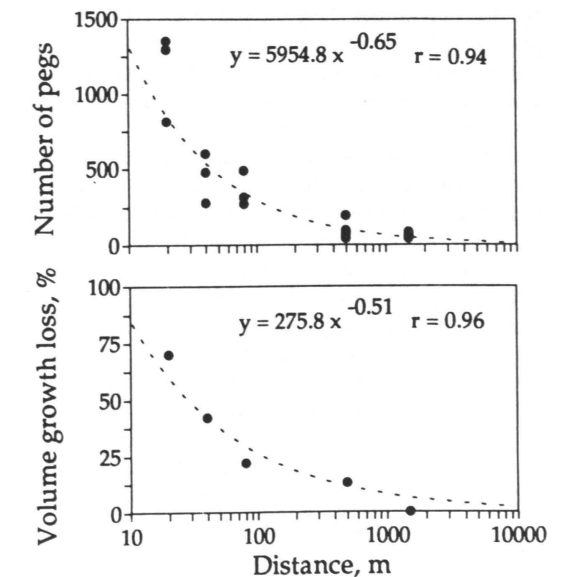


Fig. 7. Beetle attack estimated as the number of pegs per tree (a) and the average loss in volume growth expressed as relative response index (b) as a function of the distance from the timber yard.

4 Discussion

4.1 Beetle damage and needle loss

Presumably, most (if not all) shoot-feeding was caused by the common pine shoot beetle, *T. piniperda*. The lesser pine shoot beetle, *T. minor* is less frequent in southern Sweden (Lekander et al. 1977), and does not readily attack pulp wood in stacks (Långström et al. 1984 and references therein).

Although few trees were felled, the consistent pattern in crown damage strongly suggests that shoot losses were due to beetles emerging from stored timber. Crown damage, however, quickly decreased with increasing distance to the beetle source, as summarized in Fig. 7A. In this respect, the observed pattern resembled more that of a single year of attack (Nilsson 1974a, Sauvard et al. 1987), than the wide-spread damage observed after many years of recurrent beetle damage (Haagensen 1978, Långström and Hellqvist 1990).

In the stand most attacked, the observed shoot losses corresponded to about 100 fallen shoots per m² (assuming 1 shoot per peg, 1000 pegs per tree, Table 3, and 1000 trees per hectare, Table 1) during the whole period of damage. The corresponding figures were 85, 60, 20 and 10 shoots per m² for the stands at 40, 80, 500 and 1500 m distance, respectively. These figures compare well with those of Stroink (1982), but he did not measure shoot losses beyond 200 m. Even higher figures, around 100 shoots per m² in a single year were found in the most severely attacked stands at Mönsterås (Långström and Hellqvist 1990). Since pine shoot beetles are more or less ubiquitous, zero-values cannot be expected even in well-managed forests, but the base level of damage should be well below one shoot per m² (Stroink 1982, Sauvard et al. 1987, Långström and Hellqvist unpubl.). Thus, we conclude that the E-trees at 1500 m were, in fact, also affected by beetle damage, probably emanating from the timber yard.

Although the approach used to estimate needle biomass was crude, we believe that the estimates indicate the magnitude sufficiently accurately to allow us to conclude that the A-, B- and C-trees had suffered substantial needle losses, being short of more than half, close to half and about one third of their foliage, respec-

tively, at the time of felling, whereas the loss in the D- and E-trees was negligible. Considering the attack level and tree size, these figures compare well with those obtained in experimentally pruned trees (Ericsson et al. 1985, Långström et al. 1990), and in naturally attacked trees (Stroink 1982). In a Dutch study, 56 shoots per m² were found to correspond to a 20 % foliage loss in a young pine stand (Doom and Luitjes 1971). These figures are low, however, when compared to needle losses caused by defoliators, often exceeding 50 % and not seldom approaching 100 % in a single year (e.g. Piene 1980, MacLean 1981, Alfaro et al. 1982, Austarå 1984, Austarå et al. 1987, Alfaro and Shepherd 1991).

4.2 Growth losses

In the most severely attacked trees, the reduction in radial and basal area growth began in 1983, i.e. one year after the first attack, culminated in 1985 and had recovered in 1988, thus resulting in a 6-year-period of reduced growth. For the less attacked B- and C-trees, the same pattern can be seen but the growth decline started later, culminated in the same year, and recovery paralleled that of the A-trees.

The observed pattern with an equally long period of decline and recovery was very similar to that described for defoliation of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Alfaro et al. 1982, Alfaro and Shepherd 1991), or Norway spruce (*Picea abies* (L.) Karst.) (Austarå 1984). On Scots pine, needle losses caused by sawfly defoliation (Brantseg 1962) and a needle cast (*Lophoderma sulcigena* (Rostrup) Höhnelt) (Jalkanen 1986) have also resulted in a similar decline-recovery pattern. On the other hand, Balsam fir (*Abies balsamea* (L.) Mill.) responded with different recovery patterns depending on defoliation intensity and number of years with defoliation (Piene 1989). For Scots pine, Austarå et al. (1987) found an extended period of recovery following two years of sawfly defoliation. There are also indications of increased growth of surviving trees after completed recovery as a result of lower competition (Mattson and Addy 1975, Wickman 1980). Thus, the interaction between the pest, host, site, cli-

mate etc. is extremely complex.

Altogether, the estimated loss in basal area growth during the 6-year-period of decline and recovery was about 60 % in the most severely attacked A-trees, 25–35 % in the less attacked B- and C-trees, but also about 25 % in the even less attacked D-trees, when the least attacked E-trees were used as a reference. However, the growth reduction in the younger D-trees was a gradual decline resulting from increasing competition, although some beetle impact cannot be excluded. The site of the C-trees is drier and the trees may have suffered comparatively more than the B-trees. Since no damage data are available for the trees studied in 1988, these growth results cannot be evaluated further.

The decline in height growth accompanied that of radial growth, but our data do not allow a conclusion on when recovery would have been completed, although they indicate a pattern similar to that of radial growth. The total loss in height growth during 1983–1987 was about 1.5 and 0.5 m in the A- and B-trees and nil in the others.

Following one year of leader loss, we have observed complete recovery to normal height growth within 2–3 years (Långström and Hellqvist 1992); a result conforming with the present findings (see also Piene 1989). In contrast, Andersson (1974) and Nilsson (1974b) report periods of significant height growth reduction extending about more than 10 years after one year of beetle attack. Regardless of these conflicting results concerning the length of the recovery period, all the above-mentioned studies, as well as the present one, are in agreement that height growth losses occur only when the leader shoot itself is damaged by the beetles (see also Ericsson et al. 1985). Actually, a tendency towards increased height growth has been observed for damaged trees with intact leaders (Andersson 1974, Nilsson 1974b, Ericsson et al. 1985, Långström et al. 1990). This finding is in contrast with the effects of a pure needle loss (defoliation, needle cast) which invariably reduces height growth if intensive enough to affect growth (e.g. Brantseg 1962, Ericsson et al. 1980, Jalkanen 1986), but can be explained in terms of different sink-source relations (Ericsson et al. 1985, Långström et al. 1990, Långström and Hellqvist 1991).

Although leader shoots are often thicker than the preferred shoot diameter (Långström 1980), they may frequently become attacked when beetles are abundant. For example, Nilsson

(1974b) reported leader attacks in 9, 41, 54, 56, and 83 % of the trees in five stands. No information is, however, available about the frequency of recurrent leader attacks in the same tree during consecutive years. Obviously, recurrent attacks must occur, and these could explain the extremely long recovery periods reported by Andersson (1974) and Nilsson (1974b).

The volume growth losses during 1983–1985 decreased from about 70 to 10 percent for stands A to D with E as the reference (Fig. 7B and Table 4). Judging from the decline-recovery pattern of radial, basal area and height growth (Figs 2–4), it is not unreasonable to assume approximately the same reduction level for the recovery period as well.

For individual trees, the volume growth losses were closely related to the different expressions of beetle damage (Fig. 6). However, the damage levels required for a measurable change in growth rate were much higher than those reported by Nilsson (1974b). In our material, less than 100 pegs per tree caused little or no change in the periodic growth rate, and more than 200 pegs resulted in considerable growth reduction. This finding is in accordance with results obtained in a shoot-pruning experiment on similar-sized trees (Långström et al. 1990), but contrasts to Nilsson's (1974b) conclusion that 150 lost shoots may be enough to cause maximum growth losses. According to Jalkanen (1986), young Scots pines tolerate a 10–20 % needle loss without growth losses, whereas a corresponding amount of lost shoots resulted in a measurable but transient growth reduction (Ericsson et al. 1985, Långström et al. 1990).

In comparison with growth losses reported after defoliation, *Tomicus*-attacks seem to cause larger losses considering the amount of foliage destroyed. For example, during a sawfly outbreak in Norway, defoliation on Scots pine was about 75 % during two consecutive years, and this defoliation resulted in approximately 30 % loss in basal area and volume growth during a 9-year period (Austarå et al. 1987). In Finland, young Scots pines severely diseased by a needle cast lost 29 % of their volume growth during a 5-year period (Jalkanen 1986). Similar defoliation effects are reported for many conifers from different geographical regions (Kulman 1971).

The different growth response of pine to *Tomicus*-attacks as compared with defoliation, could at least in part be due to the fact that beetle attacks mainly affect the upper whorls, which are photosynthetically most important

(Troeng and Linder 1982), whereas defoliation often is distributed all over the crown. Furthermore, the concomitant destruction of buds as well as needles is probably impairing carbohydrate dynamics more than a pure needle loss (Ericsson et al. 1980, Ericsson et al. 1985, Långström et al. 1990). When leader shoots are killed, growth regulation by phytohormones (IAA) could also be affected (Sandberg and Ericsson 1987 and references therein).

The maximum growth loss observed in this study was higher than in other cases studied with recurrent beetle attack (Långström and Hellqvist 1990 and references therein), but the growth losses did not, in contrast to the above-mentioned study, extend far into the forest, probably not beyond 100–200 m. However, we cannot exclude the possibility that the growth decline of the trees at 500 m distance from the timber yard was in part caused by the beetle attack, but growth pattern as well as stand conditions indicate this to be an effect of increasing competition rather than beetle attack. The growth

pattern of the least attacked trees at 1500 m distance indicated that they were not at all affected by the beetle attack, although some shoots had been lost. A comparison with the expected volume growth percentage for this county and tree size (Jacobsson 1979) revealed that these trees were growing even better than the average.

In conclusion, the coincidence in time of the growth decline with that of timber storage, as well as the spatial pattern in beetle attack followed by a concomitant growth loss pattern strongly suggest that the beetle damage emanated from the stored timber. Thus, timber storage practice should be modified in order to avoid severe growth losses in pine stands adjoining storage sites. We also conclude that, for practical purposes, damage estimates can be based on different expressions describing the proportion of the severely damaged crown which are easier to obtain than the tedious peg-counting, and could perhaps even be assessed visually for standing trees.

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