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Distribution of pine shoot beetle attacks within the crown of Scots pine

Märgborreangreppens fördelning i tallkronan

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Abstract

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The seasonal and spatial distribution of pine shoot beetle attacks was studied at Simonstorp in southern Sweden. Scots pine of 15—46 years age and 4—14 m height were felled during the period 1972—1974. Samples of attacked shoots were also collected from standing pines of about 2—3 m height. In 1974, attacks were also counted and labelled individually on preselected pines throughout the growing season.

The results indicate a seasonal change in the age distribution of attacked shoots. The average diameter of damaged shoots was about 4.5 mm, ranging from 2 to 6 mm. The spatial distribution of attacks coincided with the distribution of suitable sized shoots, but the attack pattern was modified by the density of attacks per tree. Multiple attacks were frequently observed which indicated a relative shortage of suitable shoots, especially in upper whorls. More than 50 % of all current shoots were affected in upper whorls, whereas a far smaller proportion of the shoots was damaged in lower whorls.

Key words: Scolytidae, *Tomicus* spp., *Pinus sylvestris* L., attack pattern, intensity of attacks.

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Contents

1 Introduction

The pine shoot beetles, *Tomicus piniperda* (L.) and *T. minor* (Hart.) (Col., Scolytidae), are amongst the most destructive forest insect pests in Europe. These bark beetles breed in fresh pine wood and may occasionally attack standing pines of low vigour. However, the main damage is caused when the beetles bore into the shoots of healthy pines. Severe attacks cause great losses of foliage, which in turn will result in growth losses and eventually in reduced vigour of the attacked trees. Nilsson (1975) has estimated the yearly growth losses in the early 1970s to be of the magnitude of 2—6 million cubic metres. In individual stands, pine shoot beetle attacks have caused growth reductions ranging from 20 to 45 % during a period of up to 10 years and occasionally even longer (Michalski & Witkowski 1962, Bergman 1964, Andersson 1974, Nilsson 1974).

Hundreds of studies have been published on various aspects of the biology and control of the pine shoot beetles. Older references have been compiled by Escherich (1923) and more recent ones by Postner (1974). Most of the papers published since then have been reviewed by Långström (1980a).

Although the destructive feeding behaviour of the pine shoot beetles has been known ever since the days of Linnaeus (Ratzeburg 1839), very few systematic studies exist on the seasonal and spatial distribution of attacks within pine crowns. There are many general observations indicating that shoot-feeding mainly occurs in the upper part of the crowns (see e.g. Trägårdh 1921, Escherich 1923). Detailed information on the vertical distribution of pine shoot beetle attacks has been provided by Sylvén (1916), Nilsson & Karlsson (1971), Führer & Kerck (1978), Löyttyniemi (1978) and Långström (1980a). Some of the abovementioned papers also describe the size of attacked shoots. In two of these, some evidence was found pertaining to different attack patterns between *T. piniperda* and *T. minor* (Sylvén 1916, Långström 1980a). It was concluded that the former species may prefer young or middle-aged pines for its maturation feeding, whereas the latter one was more frequently found in the crowns of mature pines. When the two species occurred together, the majority of *T. minor* was found in lower whorls, whereas *T. piniperda* was concentrated to the upper part of the crown (Långström 1980a).

The occurrence of attacks in shoots of different ages has been observed by several authors (see e.g. Holmgren 1867, Ritchie 1917, Trägårdh 1921, Greese 1926 and Salonen 1973), but only a few studies exist on the age distribution of attacked shoots (Šrot 1968, Långström 1980a). Obviously there is a connection between the age distribution of attacked shoots, and the seasonal course of the shoot-feeding. It has long been known that in early summer one-year-old shoots may frequently be attacked by the parent generation after the period of oviposition, but there is also some evidence that shoot-feeding may take place in early spring at the time of flight and oviposition (see e.g. Ritchie 1917, Salonen 1973). These two feeding periods of the parent beetles, as well as the maturation feeding of the new generation, have been studied and discussed by Långström (1980a).

In the present study, the seasonal and spatial distribution of pine shoot beetle attacks within the pine crowns is described. Furthermore, an attempt is made to estimate the number of shoots which are affected by these attacks. This study is a continuation of earlier investigations where the life cycles of *T. piniperda* and *T. minor*, as well as the specific attack patterns of the two species, have already been described and discussed (Långström 1980a).

2 Material and Methods

Since the general procedure of the present study has been described by Långström (1980a), only a brief recapitulation is needed here. Field data were collected from 1972 to 1974 at Simonstorp, southern Sweden (N 58°47′ latitude, E 16°10′ longitude, about 65 m above sea level). Pines were felled in a young stand (Ålgöl) during the period 1972—1973, and in an older stand (Tegnetorp) in 1974 and 1975. The age of the trees varied from 15 to 20 and 15—46 years in the former and latter stands, respectively. The corresponding height ranges were 4.5—6.5 and 6.5—12 m. Tree data are given in appendices 2 and 3 in Långström (1980a). These sample trees were felled throughout the growing seasons, at least one tree per month, and each tree was carefully examined whorl by whorl and branch by branch. During this procedure notes were kept on the vertical and horizontal position of each attacked shoot within the crown. All damaged shoots were collected in plastic bags, and taken to the laboratory within 24 hours, where they were stored in a freezer (−18°C) prior to subsequent handling.

The position of each attack within the crown was recorded according to the following system: the relative position of an attack in the vertical direction was indicated by a "branch whorl number", and the relative horizontal position within each whorl was expressed as a "second-order whorl number" along each branch. By branch whorls are meant primary branches which arise from the main stem in a particular year. These whorls were numbered downwards as 1, 2, 3 etc., the current year being known as 1, previous year's whorl as 2 etc. The numbering continued to the last living branches. Second-order whorls (or twig whorls) originate from primary branches and consist of secondary shoots, arising from lateral buds of a certain age. Second-order whorls were numbered from the branch tip to the base as follows:

A, A + 1, A + 2, etc., with A meaning the current year, A + 1 the lateral buds of the previous year etc. Each second-order whorl also included the terminal shoot of that particular year. The principles governing these positions are shown in Figure 1. A similar but more detailed system where shoots were classified according to "orders" and "positions" has been developed by Flower-Ellis et al. (1976). Whorls are numbered in the same way in both studies, but the second-order whorls in the present paper include shoots of different orders in a certain position according to the terminology used by Flower-Ellis et al. (1976).

In order to describe the relative intensity of the shoot-feeding, current shoots were counted on four pines which were felled in September and October of 1974 in Tegnetorp (for tree data, see Appendix 3, Långström 1980a). However, in the lower part of the crown, where few attacks occurred, only current shoots of 5 cm in length or longer were counted. A current shoot was also considered "damaged" when the entrance hole was found proximally on the twig in another internode. Thus, one attack in an older shoot often affected several current shoots, and consequently the number of broken and fallen current shoots could not be estimated exactly. Each remaining shoot fragment was counted as one lost shoot. This was a systematic under-estimation of the number of damaged shoots, but since these fragments generally constituted less than 30 % of the total number of attacks, the under-estimation was moderate (Långström in prep.).

Information concerning the seasonal attack pattern was obtained in the two fol-

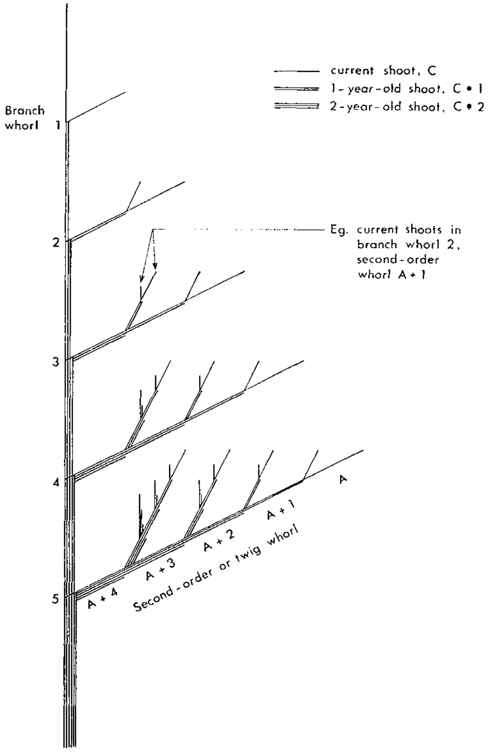


Figure 1. Age classification and position of shoots within the pine crown. Further information obtainable in the text.

lowing ways: throughout the growing season of 1973, samples of attacked shoots were collected at random from young pines of about 3 m height (Klinta and Tegnetorp). In 1974, the course of attacks was followed on preselected young pines of 2 to 2.5 m height at Tegnetorp. From April to October, all new attacks on 30 pines were marked with plastic labels. New attacks were also removed continuously from a similar group of 15 pines in the same stand. Hereafter, these two experiments are referred to as "shoot labelling" and "shoot removal", respectively. For detailed information, see Långström (1980a).

In the laboratory, all shoots were classified according to their age as follows: current, one-year-old or older shoots. A shoot was called "current" during the remainder of the calendar year in which it had developed. In accordance with Flower-Ellis et al. (1976), the age of the shoot was indicated by C (current), C+1 (one-year-old) but the age classes of older shoots were taken as one group C>1 (should strictly speaking read >C+1).

The shoot-diameter was measured to the nearest millimetre at the entrance hole to the feeding tunnel, and the number of entrance holes in each shoot was counted in order to estimate the frequency of multiple attacks. Notes were also kept on several other variables, but these results are given elsewhere (Långström 1980a, in prep.).

3 Results

3.1 Age of attacked shoots

The age distribution of attacked shoots was studied during the growing seasons 1972—1974. The average results for each study area are shown in Table 1, and the age distribution (in relation to time) in Figure 2, which also shows the average diameter of the shoot samples with the exception of the labelling experiment at Tegnetorp in 1974.

The age distribution of the damaged shoots varied greatly between the different study areas (Table 1). For the year 1973, at Klinta as well as Tegnetorp very few attacks were observed in current shoots, whereas the corresponding percentage in other study areas varied from one third to two-thirds. Attacks in older shoots (C > 1) were rare, with the exception of the felled trees at Ålgöl in 1972, where 26 % of all attacks occurred in this age class.

These observed differences between the study areas become even more apparent when the age distribution of attacks is seen in relation to time (Figure 2). At Klinta and Tegnetorp 1973, there were no seasonal changes in the age distribution of attacked shoots. In the other study areas there was

Table 1. Age distribution (%) of infested shoots in current (C), one-year-old (C + 1) and older (C > 1) shoots in different study areas. Further information obtainable in the text.

Study area and period of sampling		Age distribution, %			Total number of shoots	Mean diameter mm	Remarks
		C	C + 1	C > 1			
Ålgöl	1972 (6.7—23.11)	33.8	40.2	26.0	769	4.4	14 felled pines (average height 5.5 m, age appr. 17 years)
Klinta	1973 (8.5—8.11)	1.5	98.5	0.0	520	4.6	12 shoot samples from standing pines of appr. 2.5 m height
Tegnetorp	1973 (4.4—7.11)	1.7	98.2	0.1	765	4.6	15 shoot samples from standing pines of appr. 2.5 m height
Tegnetorp	1974 (6.6—30.10)	39.5	51.1	9.4	1640	4.2	13 felled pines (height 6—12 m, age 15—46 years)
Tegnetorp	1974 (5.7—3.10)	67.3	31.5	1.2	257	3.7	Continuous removal of attacked shoots on 15 pines of appr. 3 m in height
Tegnetorp	1974 (13.5—3.10)	45.0	54.4	0.6	171	—	Continuous labelling of attacked shoots on 30 pines of appr. 3 m height

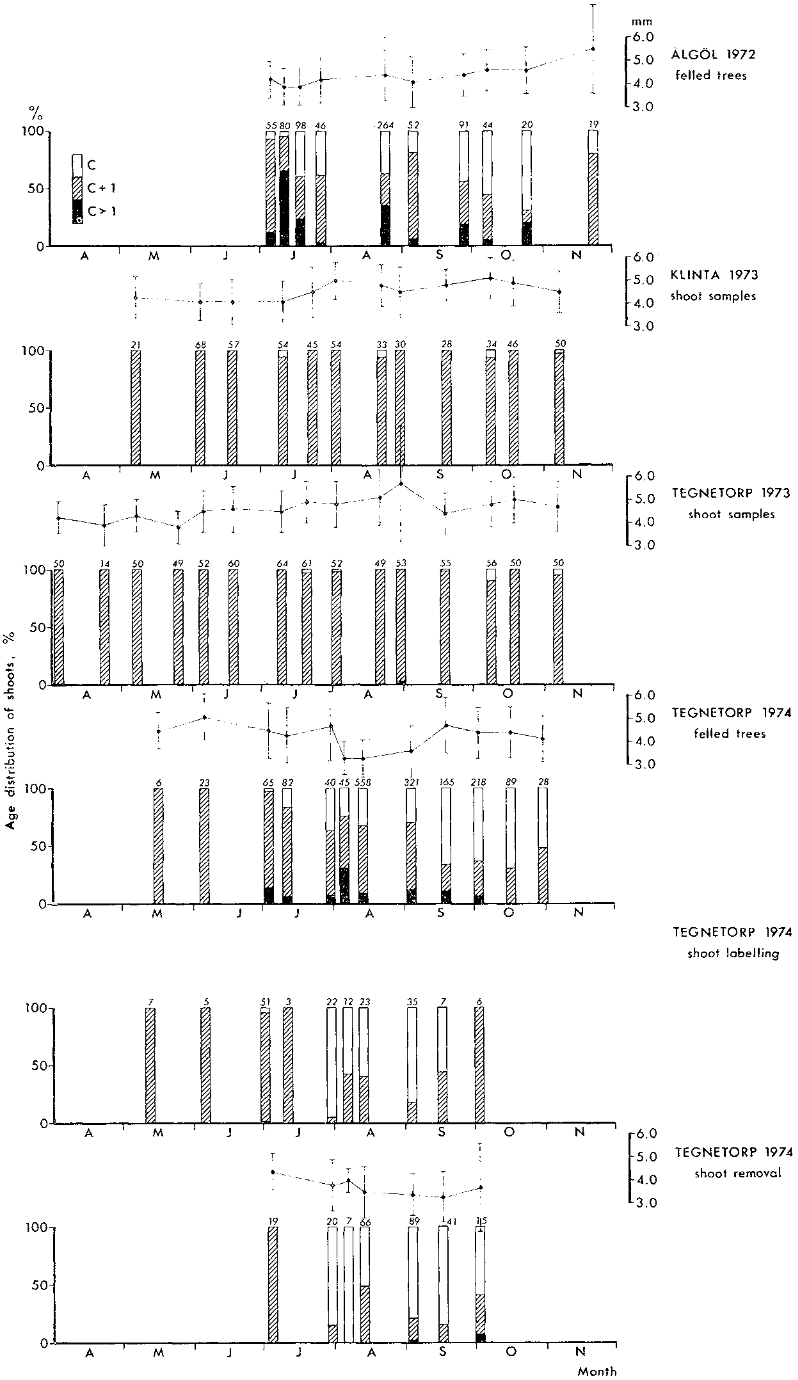


Figure 2. Age distribution and diameter of attacked shoots according to date of sampling, study area and year. The shoots were known as current (C) in their first year of growth, one-year-old (C+1) during the course of the second year and older (C>1) in later years. The average diameters of shoot samples are given in mm and the vertical lines indicate standard deviations of means. The numbers indicate sample sizes. For further information, see the text.

Table 2. Spatial distribution of pine shoot beetle attacks in the crowns of two pines felled at Ålgöl in 1972.

Whorl	Second-order whorls						Total	
	A (1972)	A+1 (1971)	A+2 (1970)	A+3 (1969)	A+4 (1968)	A+5 (1967)	n	%
1 (1972)	31						31	5.1
2 (1971)	27	3					30	4.9
3 (1970)	6	16					22	3.6
4 (1969)	22	26	26				74	12.2
5* (1968)	30	36	44	68	5		183	30.1
6* (1967)		16	30	36	57		139	22.9
7* (1966)			22	40	25	5	92	15.1
8* (1965)			15	11	7	4	37	6.1
9* (1964)							0	
Sum	116	97	137	155	94	9	608	
%	19.1	15.9	22.5	22.5	15.5	1.5		100.0

* Only two branches in each whorl were studied, numbers adjusted for all branches.

a clear increase in the percentage of attacks in current shoots during the progression of the growth period. In this context, it should be remembered that felled trees and random shoot samples reflect the accumulated attack situation, i.e. all attacks from the beginning of the growth period up to the time of inspection are included. The continuous counting and marking of new attacks at Tegnetorp in 1974 provide—in principle—more reliable results, although some of the attacks may have been overlooked when they first occurred. The removal of damaged shoots may have affected the attack pattern, firstly because beetles were removed, and secondly, since the number of available shoots decreased after each cutting. Thus, the labelling experiment probably reflects the natural attack pattern better than the other methods used.

The above results show clearly that current shoots were not attacked during the main phase of shoot elongation in June. The first attacks in current shoots occurred in early July, and thereafter an increasing percentage of attacks took place in these shoots. However, older shoots still became attacked when the current shoots were fully grown.

3.2 **Diameter of attacked shoots**

The average diameter of attacked shoots varied around 4.5 mm, with the exception of the shoot-removal experiment (Table 1). In all study areas and all shoot samples, there was a large variation in the diameter of the damaged shoots (Figure 2). No consistent seasonal changes in mean diameters were observed. However, in the shoot-removal experiment there was a successive decrease in average shoot diameter, but this result could also be an effect of the shoot clipping itself (i.e. that the available number of optimum-sized shoots decreased after each clipping).

3.3 **Spatial distribution of attacks within the crown**

The spatial distribution of pine shoot beetle attacks is shown in Tables 2 and 3. The former is based upon two trees at Ålgöl, felled on 19 July and 25 August, 1972, respectively, and the latter table concerns four trees from Tegnetorp in 1974. (For tree data, see Långström 1980a.)

The vertical distribution of beetle attacks is shown whorl by whorl, and the horizontal distribution within each whorl is given ac-

Table 3. Spatial distribution of pine shoot beetle attacks in crowns of four pines felled at Tegnetorp in 1974. Further information obtainable in the text.

Whorl	Second-order whorls							Total	
	A (1974)	A+1 (1973)	A+2 (1972)	A+3 (1971)	A+4 (1970)	A+5 (1969)	A+6 (1968)	n	%
1 (1974)	23							23	4.6
2 (1973)	65	3						68	13.6
3 (1972)	72	74						146	29.2
4 (1971)	25	29	12					66	13.2
5 (1970)	24	13	22	10				69	13.8
6 (1969)	1	9	11	37	23			81	16.2
7 (1968)		1	1	7	13	7		29	5.8
8 (1967)		4			9	2		15	3.0
9 (1966)							3	3	0.6
Sum	210	133	46	54	45	9	3	500	
%	42.0	26.6	9.2	10.8	9.0	1.8	0.6		100.0

Table 4. Occurrence of multiple attacks on sample trees at Tegnetorp 1974. The figures indicate the distribution (in per cent) of attacked shoots according to the number of entrance holes per shoot, as well as the mean value per sample.

Date of sampling	Per cent frequency of number of entrance holes per attacked shoot							Sum	Number of shoots	Average number of entrance holes per shoot
	1	2	3	4	5	6	7			
1974										
06-06	100.0							100.0	6	1.00
07-04	84.6	13.9		1.5				100.0	65	1.17
07-12	92.3	6.2	1.5					100.0	65	1.09
07-31	83.9	9.7	6.4					100.0	31	1.23
08-07	77.1	22.9						100.0	35	1.23
08-14	67.8	27.4	4.8					100.0	248	1.37
09-04	69.3	21.5	6.9	1.5	0.8			100.0	130	1.43
09-18	73.9	17.1	4.5	3.4	1.1			100.0	88	1.41
10-03	62.5	26.8	8.9	0.9			0.9	100.0	112	1.53
10-17	60.4	33.3	2.1	2.1		2.1		100.0	48	1.54
10-30	65.0	20.0	10.0	5.0				100.0	20	1.55
Total	71.9	21.8	4.8	1.1	0.2	0.1	0.1	100.0	848	1.37

cording to the second-order whorls (for explanations, see Figure 1). In both tables a similar pattern can be observed. Moving downwards through the crown, the main points of attack change from the outer second-order whorls in towards the main stem. At Ålgöl, attacks were concentrated to whorls 5 and 6, while whorl 3 was the most intensely attacked one in Tegnetorp. In 1972 many more attacks were found in the inner second-order whorls as compared with the trees from 1974.

These observed differences in the spatial as well as in the age distribution of attacks

Table 5. Vertical distribution of multiple attacks expressed as the average number of entrance holes per damaged shoot in different whorls. Sample trees from Tegnetorp 1974.

Whorl number	Number of entrance holes	Number of attacked shoots	Average number of entrance holes per attacked shoot
1 (1974)	53	32	1.65
2 (1973)	102	64	1.59
3 (1972)	199	134	1.48
4 (1971)	75	53	1.41
5 (1970)	69	52	1.33
6 (1969)	159	120	1.32
7 (1968)	100	74	1.35
8 (1967)	125	94	1.33
9 (1966)	90	73	1.23
10 (1965)	57	47	1.21
Total	1029	743	1.39

between Ålgöl and Tegnetorp may indicate that the attack pattern can be modified, eg. by a shortage of suitable shoots. However, there is a need for further studies to test this hypothesis.

3.4 **Occurrence of multiple attacks**

By "multiple attack" is meant that more than one entrance hole is present in the same shoot during the same year, i.e. that several pine shoot beetles burrow into the same internode, or that one beetle makes several tunnels in the same shoot. Multiple attacks were frequently observed during the course of the study, but not until 1974 were they studied systematically in felled trees at Tegnetorp (see Table 4).

The average number of attacks per damaged shoot was approximately 1.4, but there was a clear increase of multiple attacks with the passing of time. Shoots with more than one entrance hole were to be found on all sampling occasions. The highest number observed was seven entrance holes in one shoot, but taken as a whole, shoots with more than two holes accounted for less than 10 % of the total.

The vertical distribution of multiple attacks was also studied. In Table 5, data from trees felled in 1974 have been arranged according to the frequency of multiple attacks in different whorls.

The above table clearly shows that the frequency of multiple attacks was at its highest in the upper whorls, and steadily decreased downwards in the crown. It is likely that the frequency and distribution of multiple attacks reflect the beetles' preference for shoots in the upper part of the crown, as well as competition for those preferred shoots.

3.5 **Attack pattern in relation to density of attacks**

In 1974, the attack pattern was analysed in relation to the number of attacks per felled tree (Figures 3a—c). Only those trees which were felled after the termination of the growth period were included, i.e. five pines which were felled in September and October (see Appendix 3, Långström 1980a).

The relation between the density of attacks and the age distribution of the damaged shoots is shown in Figure 3a. The result indicates a weak negative correlation (not significant at 5 % risk level, $P > 0.05$) between the percentage of attacks in current shoots and the number of attacks per tree.

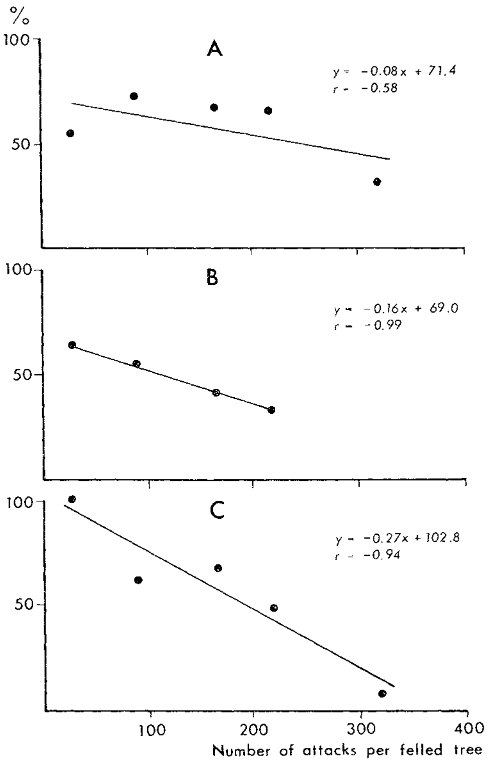


Figure 3. The relationship between the number of attacks per tree and the percentage of attacks in: a) current shoots, b) second-order whorl A, and c) branch whorls 1—4. Further information obtainable in the text.

A much stronger negative correlation was found when the number of attacks was compared with the relative distribution of attacks in horizontal as well as vertical direction (Figures 3b—c). With increasing attack density, the percentage of attacks decreased in the outermost second-order whorl (A) and uppermost whorls (1—4).

3.6 **Attack pattern in relation to shoot size**

The spatial distribution of attacks together with the average diameter of the attacked shoots, justify the assumption that this attack pattern may be governed by the distribution of suitable shoots within the crown.

To test this hypothesis, two pines of the same size as the sample trees were felled in a stand adjoining Tegnetorp in 1974. Within each whorl two branches were taken at random. Shoot lengths and diameters were measured in the second-order whorls A, A + 1 and A + 2 in shoots of first and second order *(sensu stricto)*. Within each category, one shoot, selected at random, was measured to an accuracy of 1 cm and 0.5 mm in length and diameter, respectively. Similar measurements were made on four felled pines at Åsele. The results are shown in Figures 4a—b.

In both study areas, the length and diameter of any shoot decreased downwards in the crown notwithstanding its position, compared with a corresponding shoot in higher whorls. Unfortunately some whorls were incomplete owing to previous attacks by pine shoot beetles.

At Tegnetorp, shoots on first-order branches in upper whorls were generally much thicker than the optimum diameter range (3—6 mm), while most shoots on second-order branches were of a more suitable size. In whorls 8 to 11, shoot diameter of first-order branches was suitable, while shoots of second-order branches were generally below 3 mm in thickness. In whorls 12—16 shoots even of first-order branches were thinner than 3 mm.

A similar pattern can be seen in the change in shoot length in relation to whorl level. In the lower part of the crown, scarcely any shoots on first-order branches extended to 5 cm in length, while very few shoots in the upper part of the crown were shorter than that. At Tegnetorp shoots on second-order branches below whorl 11 were only 1—2 cm long or non-existent. In the upper part of the crown, even these second-order shoots were longer than 5 cm.

Although the pines felled at Åsele belong to another phenotype, similar changes in shoot length and diameter were observed on them (Figure 4b). However, the crown in the northern type was longer and the shoots were clearly shorter than those of the southern type. There was a more even distribution of shoot diameter and length in the former type than in the latter.

Regarding the horizontal distribution, shoots of optimum diameter were frequent

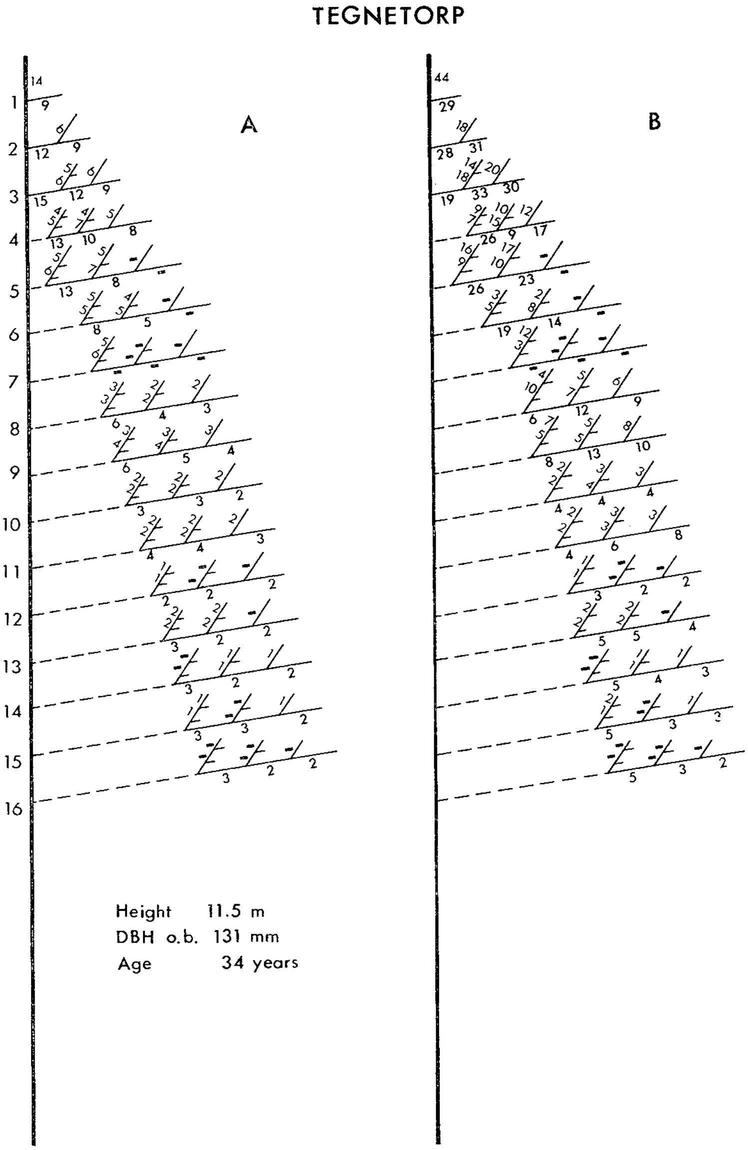
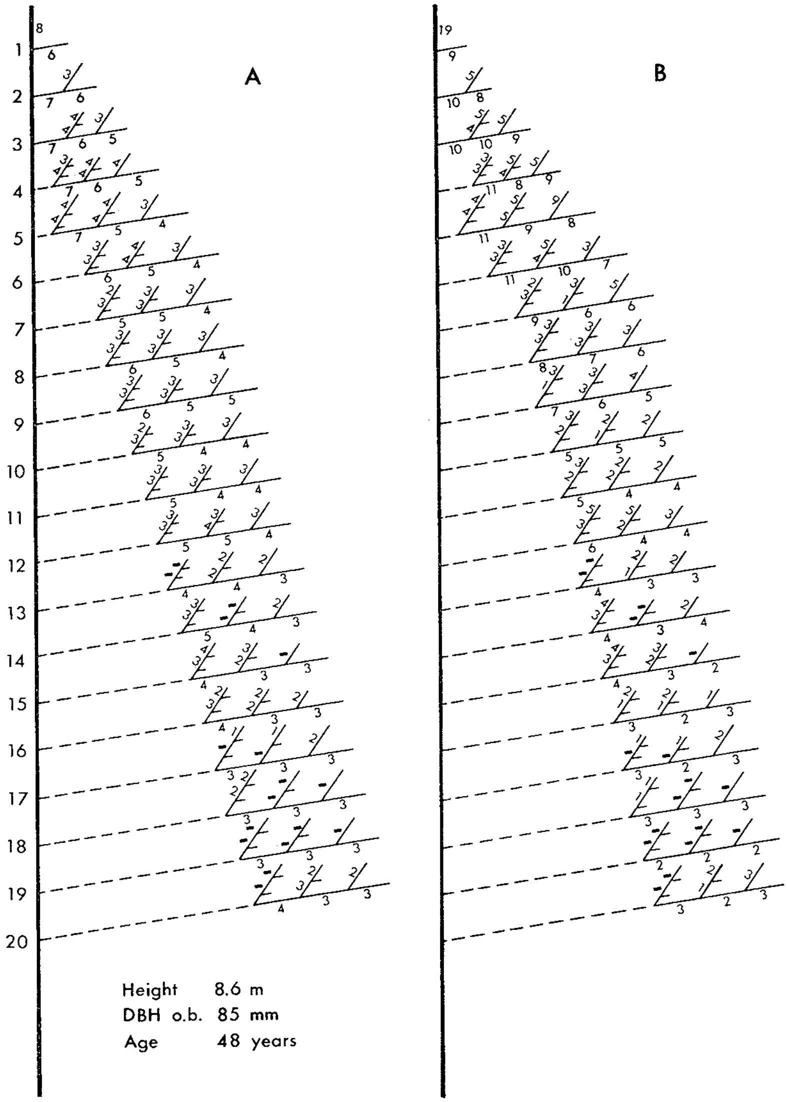


Figure 4. The relation between shoot size and position within the pine crown. The average shoot diameters (A), and lengths (B) are rounded to the nearest mm and cm, respectively. Data derive from two and four pines at Tegnetorp and Åsele, respectively. Within each whorl two branches were taken at random, and thereafter one shoot of each category was sampled and measured per branch. Further information obtainable in the text.

ÅSELE



in all second-order whorls in the upper crown, whereas these shoots in lower whorls were only to be found amongst older shoots in inner second-order whorls. As can be seen from the shoot lengths, this does not necessarily mean that the beetles have to go deeper into the crown to find suitable shoots. Since the length of first-order increments decreases downwards in the crown, the distance from an entrance hole in e.g. second-order whorl A + 3, whorl 10 to the tip of the branch may be as short as, or even shorter than the corresponding distance in e.g. A + 1, whorl 3 (cf. Flower-Ellis et al. 1976).

Although the above picture is incomplete, it still gives som support to the hypothesis that the attack pattern may be linked to the distribution of shoots of suitable size.

Table 6. Estimated extent of shoot damage caused by pine shoot beetle attacks on four sample trees at Tegnetorp 1974. Shoot counts refer to current shoots of 5 cm in length or longer, whereas each feeding tunnel or entrance hole was counted as one attack.

Date of felling	Percentage of damaged current shoots	Total number of current shoots	Number of attacks	Average number of damaged current shoots per attack
1974				
09-15	53.7	361	165	1.18
10-03	46.7	546	218	1.17
10-17	22.2	406	89	1.01
10-30	27.1	181	28	1.75
Total	39.1	1494	500	1.18

Table 7. Vertical distribution of estimated shoot damage in four sample trees at Tegnetorp 1974. For further information, see legend to table 6.

Whorl	Total number of current shoots >5 cm	Percentage of damaged current shoots	Number of attacks	Number of attacks/ damaged shoot	Number of current shoots/ attack
1 (1974)	24	62.5	23	1.5	1.0
2 (1973)	110	50.0	68	1.2	1.6
3 (1972)	305	53.8	146	0.9	2.1
4 (1971)	189	43.4	66	0.8	2.9
5 (1970)	217	37.3	69	0.8	3.1
6 (1969)	356	40.4	81	0.6	4.4
7 (1968)	205	12.7	29	1.1	7.1
8 (1967)	71	25.3	15	0.8	4.7
9 (1966)	17	17.7	3	1.0	5.7
Total	1494	39.4	500	0.8	3.0

3.7 The estimated significance of shoot damage

In 1974, the relative intensity of the pine shoot beetle attacks was studied on four pines at Tegnetorp. Table 6 shows the number of current shoots damaged in relation to the total number of current shoots of 5 cm in length or longer. The observed number of pine shoot beetle attacks is also given, as well as the average number of damaged shoots per attack.

Nearly 40 % of the current shoots (over 5 cm) were affected by the attacks. The figures varied from about 20 to 50 %, according to the attack level on each particular tree. If the number of damaged shoots is compared with the number of attacks, it can be seen that, on an average one attack affected 1.2 current shoots. In terms of shoot availability for the attacking beetles, it can be seen that according to attack level, there were about 3 current shoots per beetle, ranging from 2 to 6. However, as can be seen below, the attacks were not evenly distributed and, consequently the effects varied according to the crown level.

Table 8. Horizontal distribution of shoot damage along the first-order shoot axis from the apical (A) to the basal (A + n) end, in four sample trees at Tegnetorp 1974. For further information, see legend of Table 6.

	Second-order whorls						Total
	A (1974)	A + 1 (1973)	A + 2 (1972)	A + 3 (1971)	A + 4 (1970)	A + 5 (1969 and older)	
Total number of current shoots > 5 cm	325	409	193	200	271	96	1494
Percentage of damaged current shoots	46.5	54.3	25.9	47.0	21.0	14.6	39.4
Number of attacks	210	133	46	54	45	12	500
Number of attacks/ damaged shoot	1.4	0.6	0.9	0.6	0.8	0.9	0.8
Number of current shoots/attack	1.5	3.1	4.2	3.7	6.0	8.0	3.0

The vertical distribution of damaged shoots is shown in Table 7. It can clearly be seen that the upper whorls were severely damaged, while the attack level in the lower part of the crown was moderate. Since the total number of current shoots (per branch) increases greatly below the upper whorls, this result would have been even more pronounced, if all the current shoots had been included. The proportion of damaged shoots would thus have decreased to a fraction of the figures in the table.

In whorls 1—3, 50 % or more of the current shoots were attacked. On two of the trees, the leading shoots were also damaged. The total number of current shoots per attacking beetle increased steadily downwards in the crown. If all current shoots had been included without size restriction, this increase would have been much greater. These figures clearly indicate that the relative severity of the attacks is much more pronounced in the upper than in the lower whorls.

In the horizontal direction, a similar pattern was to be found when the data were arranged according to second-order whorls (Table 8). The current shoots of the outer (apical) second-order whorls were damaged to a higher degree than the shoots of the inner (basal) ones. The number of current shoots per attack increased with the age of the second-order whorl, whereas the frequency of multiple attacks in the damaged shoots followed the opposite pattern. This result indicates a competitive situation for the outermost shoots.

4 Discussion

It must be borne in mind when discussing these results, that they are derived from only a few trees in central Sweden, and may therefore not be uncritically generalized. However, they seem to offer some clues to a functional explanation of the attack pattern of the pine shoot beetles.

The age distribution of attacked shoots showed a seasonal variation. Until the middle of July, most attacks occurred in one-year-old and older shoots. From the end of that month the majority of the new attacks occurred in current shoots, although some attacks were still to be seen in older shoots.

The remarkable differences in the age distribution of attacked shoots between the study areas were probably due to structural differences in local beetle populations. In 1973, the lack of attacks in current shoots can be explained by the fact that no population increase took place in these study areas and, consequently nearly all attacks were caused by the parent generation æstivating in the shoots (cf. Långström 1980a). At Ålgöl, a high percentage (26 %) of attacks was observed in two-year-old and older shoots ($C > 1$). In this area the population increase had already started in 1971, and many current shoots were lost for that year. Therefore, the result may reflect a relative shortage of one-year-old shoots at the time when the parent beetles were leaving the brood logs for their regeneration feeding. At that time the parent beetles were confined to older shoots, since current shoots were not fully grown, and only occasional attacks had been observed in them during the phase of shoot elongation. Thus, a high proportion of parent beetles in the local population may result in extensive attacks in old shoots early in the growth period (cf. Långström 1979, 1980a). Since each attack in one-year-old shoots normally affects several potential current shoots, it is evident that these early attacks may significantly reduce the biomass of the pines. According to Sylvén (1916), on an average three current shoots were lost for every attacked one-year-old shoot.

Although the results do not directly prove this, it can be surmised that the major part of the maturation feeding of the new generation takes place in current shoots. The age distribution of attacked shoots may, however, vary from case to case according to the availability of suitable shoots. Observations regarding this phenomenon are lacking in the literature, although Holmgren (1867) and Altum (1881) were already aware of the fact that shoot-feeding occurred in early summer in one-year-old shoots and later mainly in current shoots. Similar observations have been made by other authors (see e.g. Sylvén 1916, Trägårdh 1921, Šrot 1968, Nilsson & Karlsson 1971 and Salonen 1973), but none of them has systematically studied the age distribution of attacked shoots.

As could be seen in this study, the average thickness of attacked shoots was ca 4 mm, but there was a considerable range in shoot diameters. Part of these data have also been evaluated elsewhere with reference to beetle species, shoot age and diameter (Långström 1980a). The results showed significant differences in mean diameters between the age groups, but no specific preferences were observed concerning shoot age or size between *T. piniperda* and *T. minor*. The mean diameter of these shoots ($n = 193$) was 3.5 mm, ranging from 2 to 6 mm.

These figures are lower than the means reported by Löyttyniemi (1978), but the range in shoot diameter is of the same magnitude. He found that the mean diameter of broken and unbroken attacked shoots was 5.1 and 6.9 mm, respectively. According to Führer & Kerck (1978), the average diameters of attacked shoots varied from 2 to 6 mm, being highest in whorl 1 and decreasing downwards in the crown. Furthermore they noticed that the attacked shoots in all whorls were clearly thicker than the undamaged ones.

Although the preferred shoot diameter seems to be in the range of 2 to 6 mm, much thicker shoots may occasionally be attacked. In Löyttyniemi's (1978) study, attacks were recorded to a diameter of 13 mm. Vigorous leading shoots may frequently be attacked, but not always killed or broken (see e.g. Hanson 1937, Löyttyniemi 1978). According to Nilsson (1974) half of the trees included in his study had lost their leaders owing to beetle attacks.

The observed spatial distribution of attacks is in agreement with the findings of other authors in regard to the vertical distribution (Nilsson & Karlsson 1971, Führer & Kerck 1978, Löyttyniemi 1978). Concerning horizontal distribution, there are no earlier results to use in comparison.

Although based upon only a few trees, the present results strongly indicate that the spatial distribution of attacks is correlated with the density of attacks, and that the beetles colonize the crown from the upper whorls downwards and from the periphery inwards. Führer & Kerck (1978) observed a similar correlation in the vertical distribution of attacks. They found that the number of attacked shoots in the lower part of the crown was positively correlated to the attack density in the upper crown.

The observed occurrence of multiple attacks also indicates that there is a strong preference for certain shoots, and furthermore that this coincides with the vertical attack pattern. A similar distribution of multiple attacks can be deduced from the figures in Nilsson & Karlsson (1971). Multiple attacks, especially in leading shoots, have been observed by e.g. Trägårdh (1921) and Löyttyniemi (1978). According to Hanson (1937) vigorous shoots may sometimes contain more than 10 feeding tunnels.

Altogether it is evident that the attacks are not randomly distributed over the pine crown. The general attack pattern seems to coincide with the observed distribution of suitable-sized shoots (cf. Flower-Ellis et al. 1976). However, density of attacks and availability of suitable shoots may often modify the general pattern.

These results are interesting from the ethological point of view, as very little is known about how the beetles find their way into the pine shoots. It is commonly thought that the orientation is merely visual (see e.g. Eidmann 1977), but so far no detailed studies have been conducted on pine shoot beetles to explain this phenomenon. Studies with North American *Scolytus*-species, which resemble pine shoot beetles in their habit of feeding on twigs of healthy trees, have given interesting results regarding their way of dispersal. It has been observed that the flying beetles of *S. quadrispinuosus* Say. disperse at random in the crowns of host *(Carya ovata)* and non-host trees *(Quercus alba)* (Goeden & Norris 1965). Furthermore, the presence of chemicals which arrest locomotion and stimulate feeding of another *Scolytus*-species, *(S. multistriatus)*, has been demonstrated in 2 and 4 year old twigs, but not in current twigs of its host tree *(Ulmus sp.)* (Loschiavo et al. 1963, see Norris & Baker 1967). These results provide a logical basis for the orientation mechanisms which in principle could be applicable also to the pine shoot beetles.

The above discussion has so far approached the attack pattern from the entomological point of view. If we consider the present results in terms of lost current shoots, it becomes evident that the upper whorls are more severely attacked than the lower ones. These results compare well with those of other authors. Nilsson & Karlsson (1971) analysed two pines of 5 and 8 m in height, respectively. They found that the majority of current shoots in the upper half of the crown was damaged by attacks, whereas only a fraction of those in the lower part was affected. Of the total number of current shoots, 39 and 22 %, respectively, were damaged on the two pines included in their study. These figures include those tiny shoots on lower branches which neither are attacked nor contribute to the net photosynthesis of the tree (as will be seen below). The level of damage was very high, with over 70 % of the current shoots in the upper part of the crown being affected by attacks on both trees. Führer & Kerck (1978) report a similar vertical distribution of damaged shoots on six 32—38 year old pines. The average percentage of damaged shoots decreased from 100 % in whorl 1 to 40 % in whorl 5, and to 2 % in whorl 10. No attacks were found below whorl 15. Sylvén (1916) studied several pines of different sizes, though his results cannot be compared with the abovementioned ones, since the damage referred to different shoot orders which cannot be traced. However, he found higher percentages of damaged shoots in orders 1—2 as compared with orders 3—7.

These detailed studies have proved the validity of the commonly accepted impression that the shoot-feeding mainly affects shoots in the uppermost part of the crown. Furthermore, the present study has shown that the outer secondary whorls within each whorl lose a larger percentage of current shoots than the inner ones.

If these results are compared with the assimilating efficiency of shoots of different ages and crown positions, it becomes clear that the shoot-feeding mainly affects shoots of vital photosynthetic significance. Troeng & Linder (1978) have shown that great variations in photosynthetic efficiency occurred within the crown of a 20-year-old Scots pine. Generally, net photosynthesis decreased downwards in the crown. This was probably the effect of a lower "light saturation" in the lower whorls compared with that of the upper ones. Similar results were obtained on sitka spruce by Woodman (1971). The photosynthetic rate of conifer needles of different ages has been studied by Freeland (1952). In Scots pine, he observed the highest photosynthetic rate in mature current needles, whereas it was approximately 20 % lower in one-year-old and 30 % lower in two-year-old needles.

Although little is known about the physiological mechanisms governing the stem growth of Scots pine, it is likely that the observed growth losses mainly derive from the greatly reduced photosynthetic capacity of the attacked pines. However, it has been hypothesized that the observed slow recovery to normal growth may be an effect of decreased nitrogen uptake owing to extensive root mortality (Fagerström et al. 1978). Several tentative hypotheses on the effect of defoliation upon growth processes of pine have been formulated and discussed by Ericsson et al. (1980). These hypotheses were supported by results from artificial defoliations which amongst other results, indicated the existence of compensating mechanisms and a seasonal variation in growth response to defoliation. It has recently been shown in a pilot study that an early pine shoot beetle attack affects the net photosynthetic production of a current shoot more seriously than a similar attack later in the season (Troeng et al. 1979). In experiments with artificial shoot-pruning intended to simulate pine shoot beetle attacks, no significant reductions in diameter growth could be observed (Långström 1980b). It was evident that the artificial shoot-pruning did not affect the growth processes in the same way as beetle attacks of a corresponding intensity would have done. All these results stress the need for future research into the physiological impact of insect attacks on tree growth.

5 Summary

The present study deals with different aspects of the attack pattern of the pine shoot beetles (*Tomicus* spp., Col. Scolytidae) within the crowns of Scots pine (*Pinus sylvestris* L.). During the period 1972—1974, field studies were made in pine stands in Simonstorp, southern Sweden. Information regarding the age and diameter of attacked shoots, as well as the spatial distribution of attacks within the pine crowns, was collected. The results were related to: 1) the progress of the growth period, 2) the intensity of attacks, and 3) the shoot size in different crown layers. Furthermore, the relative significance of the shoot damage was studied in relation to the number of shoots suitable for attack at different crown levels.

This study is a continuation of Långström (1980a), in which a detailed description of the general procedure as well as the study areas has been given.

The main results can be summarized in the following conclusions:

1. Pine shoot beetle attacks were observed in current, one-year-old and older shoots. However, there was a remarkable variation in the age distribution of attacked shoots between the study areas. For example, the average percentage of attacks in current shoots varied from a few per cent to about two-thirds of the total number. These results reflect different seasonal attack patterns, but may also imply a relative shortage of suitable shoots.

2. The diameter range of attacked shoots was 2 to 6 mm, the mean in most study areas being approximately 4.5 mm. No clear seasonal changes in the diameter of attacked shoots were observed.

3. The spatial distribution of attacks within the crown was found to coincide with the distribution of optimum shoot size. In general, the attacks were concentrated to the upper whorls, but when moving downwards in the crown, the main point of attack within each whorl changed from outer to inner second-order whorls.

4. The frequency of multiple attacks, i.e. more than one feeding tunnel per shoot, was found to increase from spring to autumn, whereas its vertical distribution followed the general attack pattern, and decreased downwards in the crown.

5. Correlations were observed between the number and the spatial distribution of attacks. With an increasing number of attacks per tree, the percentage of attacks in upper and outer secondary whorls decreased. A similar tendency was observed with regards to the frequency of attacks in current shoots.

6. The relative impact of the attacks upon the new foliage varied in different crown levels. In upper whorls a large percentage (over 50 %) of all current shoots (over 5 cm in length) was affected by the attacks, whereas in lower whorls only a fraction of all current shoots was affected. A similar tendency was to be observed in the horizontal direction, with outer secondary whorls being more severely affected than inner ones.

7. The results were discussed from ecological, ethological and physiological points of view. The conclusions were as follows: 1) By attacking shoots of vital importance, the pine shoot beetles greatly reduce the photosynthetic capacity of the pine. 2) The beetles colonize the crowns from the top downwards and from the periphery inwards. 3) The attack pattern may be modified by a relative shortage of suitable shoots.

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7 Sammanfattning

Syftet med denna undersökning var att beskriva och analysera märgborreangreppens fördelning i tallkronorna. Fältförsök utfördes under åren 1972—74 i tallbestånd i Simonstorp i södra Sverige. Information om märgborreangreppens rumsliga fördelning samt de angripna skottens ålder och grovlek insamlades och analyserades med hänsyn till angreppstidpunkt, populationsnivå och skottstorlek i olika kronskikt. Dessutom uppskattades den relativa skadeeffekten på barrmassan i olika kronskikt. Undersökningen är en direkt fortsättning på ett tidigare arbete och metodiken och försöksplatserna har därför beskrivits i detalj i det sammanhanget (Långström 1980a).

De viktigaste resultaten kan sammanfattas i följande slutsatser:

1. Märgborreangrepp förekom i års- och fjolårsskott men även i äldre skott. Mellan försöksplatserna observerades emellertid betydande skillnader i de angripna skottens åldersfördelning. Den genomsnittliga angreppsnivån i årsskotten varierade t.ex. från några få procent till ca två tredjedelar av antalet angripna skott. Denna variation avspeglade dels skillnader i märgborreangreppens tidsmässiga förlopp dels relativ brist på lämpliga årsskott.

2. De angripna skottens diameter (vid ingångshålet) varierade mellan 2 och 6 mm. I flertalet fall låg medeltalen omkring 4.5 mm. Ingen klar tendens till ändring av medeldiametern kunde observeras under vegetationsperioden.

3. Märgborreangreppens rumsliga fördelning visade god överensstämmelse med förekomsten av skott av optimal diameter i tallkronan. Angreppen var generellt koncentrerade till de övre grenvarvens yttersta kvistkransar. I de lägre grenvarven återfanns angreppen i huvudsak i de äldre (inre) kvistkransarna.

4. Förekomsten av multipla angrepp dvs. mer än ett ingångshål per skott ökade med tiden och var högst i de översta grenvarven.

5. Ett samband mellan angreppstätheten och angreppsmönstret kunde observeras. Med ökande antal angrepp per träd minskade andelen angrepp i de översta grenvarven respektive i den yttersta kvistkransen. En liknande men svagare tendens kunde även ses beträffande angreppsfrekvensen i årsskotten i relation till angreppstätheten.

6. Angreppens relativa betydelse för barrmassan varierade med kronskiktet. I de övre grenvarven drabbades mer än 50 % av årsskotten, medan skadeeffekten i de nedre grenvarven var mindre påtaglig. En liknande tendens kunde observeras horisontellt i kronan, där de yttre kvistkransarna drabbades hårdare än de inre.

7. Resultaten diskuterades från ekologisk, etologisk och fysiologisk utgångspunkt. Följande slutsatser drogs: 1) genom att angripa skott av vital betydelse reducerar märgborrarna tallens fotosynteskapacitet drastiskt, 2) märgborrarna koloniserar tallkronan uppifrån nedåt och utifrån inåt och 3) angreppsmönstret kan påverkas av relativ brist på lämpliga skott.

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