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Crown development of Scots pine trees following thinning and nitrogen fertilization

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Studia Forestalia Suecica
No. 188 · 1993

ISSN 0039-3150
ISSN 91-576-4694-5

Abstract

Valinger, E. 1993. Crown development of Scots pine trees following thinning and nitrogen fertilization. *Studia Forestalia Suecica 188*, 12 pp. ISSN 0039-3150, ISBN 91-576-4694-5.

The effects of thinning and nitrogen fertilization, singly and in combination, on the growth of 45-year-old Scots pine (*Pinus sylvestris* L.) trees in northern Sweden, were studied from 1983-1988 inclusive. Sixteen trees were examined each year for crown development. The number of branches, shoot axes and buds produced, branch elongation on main axes, and dry weight production of shoot axes, needles, buds, cones, and dead material on live branches, were determined destructively on four trees per treatment.

Both thinning and fertilization influenced the number of crown components produced annually. Branch elongation was increased by fertilization, and decreased by thinning. The weights of the components studied were increased more by fertilization than by thinning. Thinning promoted the distribution of growth to the lower crown, while fertilization promoted growth in the upper crown. Combined thinning and fertilization increased the weight of shoot axes, needles and buds more rapidly than did thinning or fertilization applied individually.

Key words: biomass, branches, cones, growth distribution, *Pinus sylvestris*, production, urea fertilizer.

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Contents

MS. received 1 July 1992
MS. accepted 7 January 1993

Typeset and Printed by The Charlesworth Group, Huddersfield, UK, 0484 517077

Introduction

Nitrogen fertilization in connection with commercial thinning is increasingly practised in Sweden. A better understanding of the effects of these treatments on the distribution of growth within Scots pine (*Pinus sylvestris* L.) trees is therefore needed.

The photosynthetic capacity of a tree depends on the amount and distribution of foliage in the crown. Burger (1948) and Satoo (1971) suggested that there is a positive relationship between foliar mass and stem growth. Brix (1981) stated that photosynthesis depends not only on the amount of needles, but also on light relationships, temperature, water transport and CO^2-concentration within the canopy, which are in turn influenced by the distribution of needles (cf. Kira et al., 1969; Satoo, 1971; Farmer, 1976). To understand how different silvicultural treatments affect tree growth, it is necessary to understand how these treatments affect the amount of needles, their photosynthetic capacity, and their distribution within the tree crown.

A field experiment was carried out from 1983 to 1988, to establish how thinning and nitrogen fertilization affect annual growth, and its distribution in Scots pine trees. This paper describes changes in crown development, including: numbers of branches, shoot axes and buds produced, branch elongation on main axes, production of shoot axes, needles, buds, cones, and dead material on live branches, and distribution of growth to the upper crown.

Materials and methods

The Scots pine trees used in this study were growing in a well-stocked, even-aged stand at Vindeln (64° 14′N, 19° 46′E, 200 m a.s.l.) in northern Sweden. In 1939, the stand was established through artificial seeding and natural regeneration. By 1983, mean age at breast-height (1.3 m) was 30 years, and dominant height 12 m; this indicates a site index of SI100 = 24 (dominant height 24 m at 100 years of age; Hägglund & Lundmark, 1982). The soil was a mesic sandy-silty till. The ground vegetation was dominated by *Vaccinium vitis-idaea* L. and *Vaccinium myrtillus* L. At the start in 1983, stand density was 1350 stems ha^{-1}, mean diameter at 1.3 m (DBH) was 13.7 cm, basal area was 20 m^2 ha^{-1}, and total stem volume, calculated according to Näslund (1941), was 116 m^3 ha^{-1}.

A 2 × 2 factorial design was used, with 10 replications (blocks). The treatments were control (F_oT_o), fertilization with 150 kg N per ha (F_{150}), thinning (T_{40}), involving the removal of 40 per cent of the basal area (46 per cent of the stems), and fertilization × thinning ($F_{150}T_{40}$). Thinning was carried out on the T_{40}- and $F_{150}T_{40}$-plots in autumn 1983. Urea was applied by hand on the F_{150}- and $F_{150}T_{40}$-plots in spring 1984. The experiment consisted of a rectangular grid of adjacent plots, the gross plot area being 0.09 ha (30 × 30 m) and the net plot area 0.04 ha (20 × 20 m), giving a 10 m treated buffer zone between net plots. Plots were ranked by basal area and assorted into 10 blocks of 4. Plots within each block varied in basal area by less than 1 m^2 ha^{-1}. The 4 treatments were randomized within the blocks, giving 10 replications of each treatment.

In 1983, all trees within the gross plots were numbered and measured at breast height. For each net plot, eight trees with a basal area as close as possible to the tree of mean basal area on the gross plot, were identified in the list of numbered trees. Two of these eight trees were then randomly selected. The difference in DBH between each pair of trees, and the DBH corresponding to the tree of mean basal area on the gross plots, was less than 1 cm for all plots. For a period of five years, commencing in 1984, eight pairs from two randomly selected blocks were sampled each autumn. In whorls produced in the period 1980–1988, all branches were sampled. From older whorls, one branch from every second whorl was sampled. To ensure that all compass directions were equally represented, the crowns were divided into quadrants. The first living branch encountered in a randomized starting quadrant was selected as sample branch. The quadrants were then rotated clockwise down through the crown. Living branches in each whorl were counted. Dead branches were not included.

Branches were stored in plastic bags for about

Table 1. *Total number of branches per whorl produced during the 1983–1988 period, and relative accumulated branch production (per cent). Differences compared using t-test. Results significantly different from the control are indicated by * ($p<0.05$), ** ($p<0.01$), or *** ($p<0.001$)*

Treatment	Year 1984	1985	1986	1987	1988	$\bar{x}$	Σ	%
F_oT_o	4.66	4.45	4.07	4.35	3.90	4.28	21.4	100
F_{150}	5.04	5.03	5.43***	5.65**	4.40	5.11	25.6	120
T_{40}	4.54	4.93	4.17	5.30*	3.90	4.57	22.9	107
$F_{150}T_{40}$	4.90	4.60	5.63**	6.20*	4.60	5.18	25.9	121

one month at a temperature of +4°C while awaiting laboratory processing.

On each sample branch, total length of the main axis and length of the latest shoot on the main axis were measured to the nearest centimetre. Branches were then separated into current year's shoots, older shoots, and attached dead material.

On current shoots, the number of shoot axes, current cones, and buds were counted. On shoots from the preceding year, the number of two-year-old cones was counted. All branch material was then dried for 24 hours at 85°C in preparation for further analysis and to prevent decomposition.

After drying, current shoots were separated into shoot axes, needles, one-year-old cones, and buds. Older shoots were separated into needles, axes, and two-year-old cones. The material was then re-dried for 24 hours at 85°C.

The whole material, except the buds, was weighed to the nearest 0.1 g. The buds were weighed to the nearest 0.01 g.

For whorls with only one sample branch, the values for each component were multiplied by the number of branches in the whorl, and doubled to represent two whorls of branches.

To study the annual distribution of growth by components within the crown, the proportion of a component in the upper eight branch whorls (upper crown) was calculated.

When analyzing the number of branches produced per whorl during the experimental period, the whole sample tree material was used. Thus there were data for branches formed in 1988 from 4 trees per treatment, and for branches formed in 1984, from 20 trees per treatment. All other calculations were restricted to the 4 trees per treatment and year.

Multiple pairwise comparisons between treatments were made using Tukey's studentized test on all main effect means. If $p<0.05$, the result of the statistical analysis was regarded as significant.

Results

Number of branches

A larger number of branches was produced annually, compared with control trees, on F_{150}- and $F_{150}T_{40}$-trees in 1986 and 1987, and on T_{40}-trees in 1987 (Table 1). Mean annual branch production was not significantly affected by treatments. The increase in branch production for the entire five-year period studied was ca 20 per cent in treatments which included fertilization.

In 1987, F_oT_o-trees had fewer live branches than $F_{150}T_{40}$-trees (Table 2). Trees on treated plots tended to have more live branches than control trees, from the third year onwards. The proportion of live branches in the upper crown did not change during the period studied (Fig. 1). There were indications, however, that trees on fertilized plots had proportionately more branches in the upper crown than did F_oT_o trees, in the years 1985 to 1987.

Table 2. *Total number of branches per tree. Data in the same column not followed by the same letter are significantly different ($p<0.05$)*

Treatment	Year 1984	1985	1986	1987	1988
F_oT_o	83.1a	78.6a	76.3a	71.3a	82.5a
F_{150}	75.5a	85.5a	82.8a	82.6ab	87.3a
T_{40}	74.5a	71.8a	86.5a	87.8ab	89.5a
$F_{150}T_{40}$	74.8a	75.3a	80.3a	93.5b	90.3a

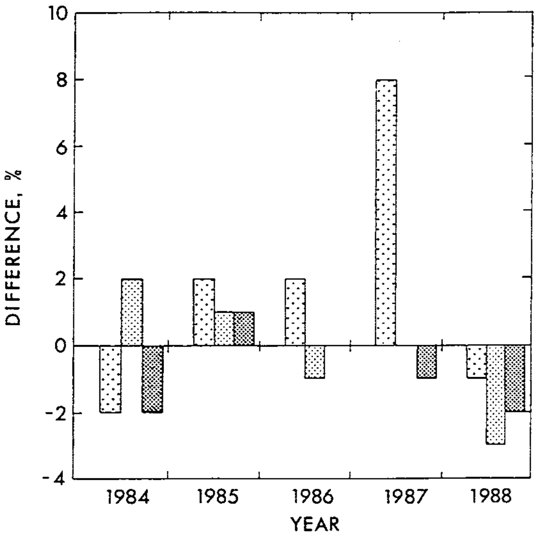

Fig. 1. Relative difference in proportion of live branches in the upper crown (upper eight whorls of branches) between treated trees and control (0 %). F_{150}-, T_{40}-, $F_{150}T_{40}$-trees.

Branch elongation

In 1986, the total annual branch elongation of T_{40}-trees was lower than that of F_{150}-trees, and in 1987 significantly lower than that of all the other treatments (Table 3). Mean annual branch elongation of T_{40}-trees was lower than that of trees from treatments which included fertilization. Thinning reduced the relative accumulated branch elongation by almost 20 per cent, while both F_{150}- and $F_{150}T_{40}$-trees had branches which elongated more than those of the control. The proportion of the total branch elongation on main axes in the upper crown was higher in F_{150}-trees than in other treatments in 1987 (Fig. 2). Both of the treatments which included thinning had a lower proportion of branch elongation in the upper crown than did the control, in the three years 1985, 1987, and 1988.

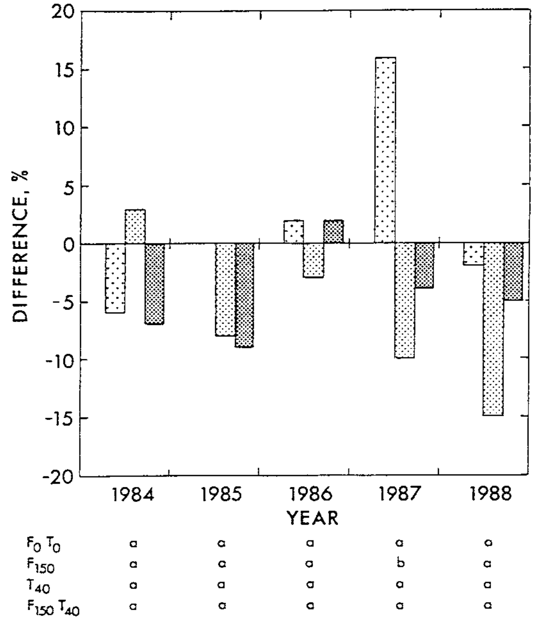

Fig. 2. Relative difference in proportion of annual branch length growth on main axes in the upper crown (upper eight whorls of branches) between treated trees and control (0 %). For notation see Fig. 1. Data from the same year not followed by the same letter are significantly different ($p < 0.05$).

Number of shoot axes

In 1987, T_{40}- and $F_{150}T_{40}$-trees produced more shoot axes than did F_oT_o- and F_{150}-trees (Table 4). The accumulated number of shoot axes produced increased in all treatments, as compared to the control, although the increase was not statistically significant. The number of shoot axes distributed to the upper crown was larger in F_{150}-trees, as compared to F_oT_o-trees, in the years 1985 to 1987 (Fig. 3). Compared

Table 3. *Sum of annual branch elongation per tree (m) on main axes and relative accumulated branch elongation (per cent). Data in the same column not followed by the same letter are significantly different ($p < 0.05$)*

Treatment	Year 1984	1985	1986	1987	1988	$\bar{x}$	Σ	%
F_oT_o	7.09a	5.72a	6.74ab	5.90a	4.35a	5.96ab	29.8	100
F_{150}	6.60a	7.14a	8.62b	6.62a	5.64a	6.92a	34.6	116
T_{40}	6.20a	5.63a	4.40a	3.64b	4.41a	4.86b	24.3	82
$F_{150}T_{40}$	6.93a	6.80a	6.40ab	7.22a	5.80a	6.63a	33.2	111

Table 4. *The number of shoots produced per tree and relative accumulated production (per cent). Data in the same column not followed by the same letter are significantly different ($p < 0.05$)*

	Year							
Treatment	1984	1985	1986	1987	1988	$\bar{x}$	Σ	%
F_0T_0	3 510a	5 400a	3 270a	3 830a	3 720a	3 950a	19 700	100
F_{150}	4 470a	4 120a	4 990a	2 700a	5 110a	4 280a	21 400	109
T_{40}	4 080a	5 510a	4 360a	6 110b	4 820a	4 780a	24 900	126
$F_{150}T_{40}$	4 320a	5 010a	3 860a	5 940b	4 330a	4 690a	23 500	119

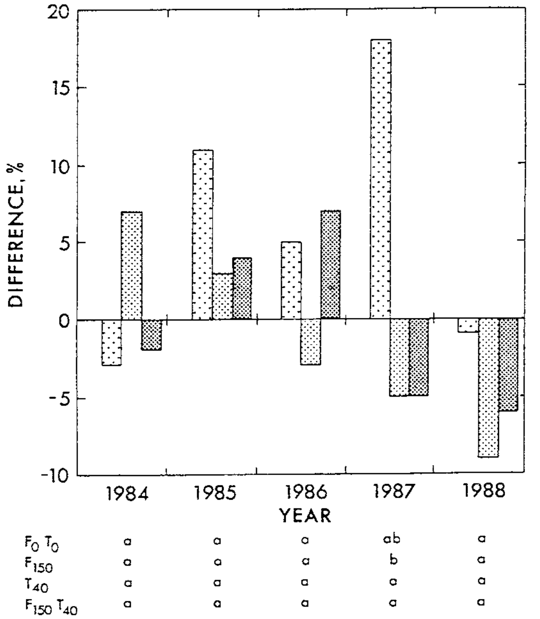

Fig. 3. Relative difference in proportion of annual number of shoot axes produced in the upper crown (upper eight whorls of branches) between treated trees and control (0 %). For notation see Fig. 1. Data from the same year not followed by the same letter are significantly different ($p < 0.05$).

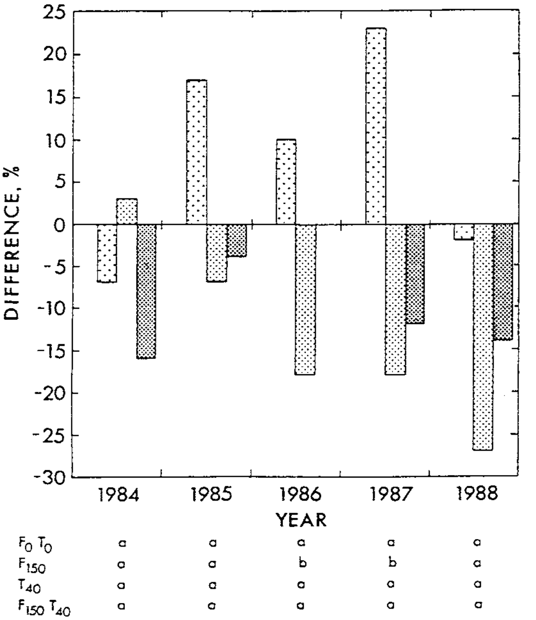

Fig. 4. Relative difference in proportion of annual weight of shoot axes produced in the upper crown (upper eight whorls of branches) between treated trees and control (0 %). For notation see Fig. 1. Data from the same year not followed by the same letter are significantly different ($p < 0.05$).

with F_0T_0-trees, the T_{40}-trees tended to have fewer shoot axes distributed to the upper crown, throughout the period studied.

Weight of shoot axes

In 1987, the shoot axis biomass of $F_{150}T_{40}$-trees was larger than that of trees in the other treatments (Table 5). The mean annual dry weight production was 44 per cent higher for $F_{150}T_{40}$-trees, as compared with T_{40}-trees. The production of shoots in the upper crown of F_{150}-trees tended to be larger than that in other treatments, in the years 1985 to 1987 (Fig. 4). The distribution by weight of new shoot axes to the upper crown of T_{40}-trees tended to decrease in comparison with that in F_0T_0-trees, throughout the period studied.

Weight of needles

With the exception of 1987, there were no statistically significant differences in the total dry weight of needles produced annually (Table 6). In that year, $F_{150}T_{40}$-trees produced a larger weight of needle than did trees on F_0T_0- and T_{40}-plots. The mean annual dry weight of needles produced increased by 56 per cent in $F_{150}T_{40}$-trees, compared with the control. In F_{150}-trees in 1986, more needle dry weight was distributed to the upper crown, as compared with F_0T_0- and T_{40}-trees. In 1987, the F_{150}-trees

Table 5. *Total dry weight (g) of current shoot axes produced per tree and relative accumulated production (per cent). Data in the same column not followed by the same letter are significantly different (p<0.05)*

Treatment	Year 1984	1985	1986	1987	1988	x̄	Σ	%
F_oT_o	181a	236a	202a	173a	138a	186ab	930	100
F_{150}	233a	194a	288a	215a	211a	228ab	1140	123
T_{40}	202a	193a	174a	124a	165a	172b	858	92
$F_{150}T_{40}$	221a	239a	241a	346b	194a	248a	1240	133

Table 6. *Total dry weight (kg) of current needle production per tree and relative accumulated production (per cent). Data in the same column not followed by the same letter are significantly different (p<0.05)*

Treatment	Year 1984	1985	1986	1987	1988	x̄	Σ	%
F_oT_o	1.03a	0.98a	1.01a	0.69a	0.73a	0.89a	4.44	100
F_{150}	1.35a	1.15a	1.44a	0.74ab	1.06a	1.15ab	5.74	129
T_{40}	1.16a	1.23a	1.01a	0.65a	1.07a	1.02ab	5.12	115
$F_{150}T_{40}$	1.39a	1.69a	1.53a	1.22b	1.13a	1.39b	6.96	157

distributed more dry weight to the upper crown than trees in all other treatment (Fig. 5). In 1985, too, F_{150}-trees distributed more needle dry weight to the upper crown than did those

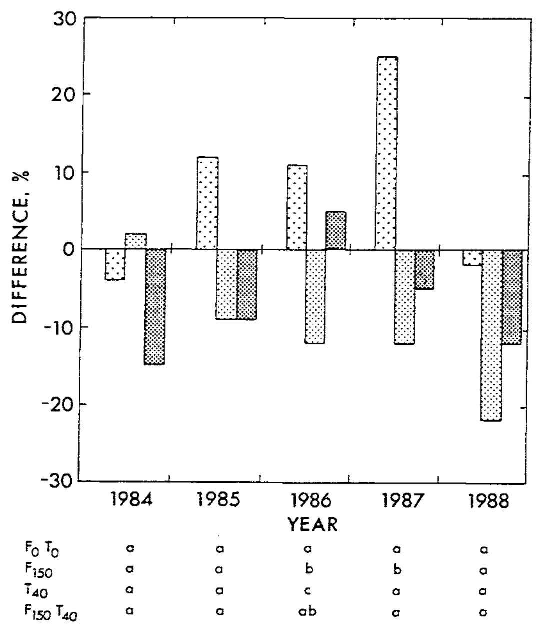

Fig. 5. Relative difference in proportion of annual needle weight produced in the upper crown (upper eight whorls of branches) between treated trees and control (0 %). For notation see Fig. 1. Data from the same year not followed by the same letter are significantly different ($p<0.05$).

in other treatments, but the difference was not statistically significant. The T_{40}-trees had a lower distribution of needles to the upper crown in 1986, compared to trees from all other treatments. The T_{40}- and $F_{150}T_{40}$-trees tended, overall, to produce a smaller proportion of their needles in the upper part of the crown.

Number of buds

In 1987, T_{40}- and $F_{150}T_{40}$-trees produced more buds than F_oT_o- and F_{150}-trees, and F_{150}-trees less than F_oT_o-trees (Table 7). The accumulated number of buds produced was positively affected by thinning and fertilization. In 1987, there was a lower proportion of the total number of buds in the upper crown in T_{40}- and $F_{150}T_{40}$-trees than in F_{150}-trees (Fig. 6). The T_{40}-trees tended to have a decreasing proportion of the total number of buds in the upper crown, and F_{150}-trees tended to have a higher proportion, as compared with the control.

Weight of buds

No differences were detected in the annual dry weight of buds produced (Table 8). The weight tended, however, to be higher in trees on treated plots than in those on control plots. The accumulated dry weight of buds was approxi-

Table 7. *The number of buds produced per tree and relative accumulated production (per cent). Data in the same column not followed by the same letter are significantly different ($p<0.05$)*

	Year							
Treatment	1984	1985	1986	1987	1988	x̄	Σ	%
F_oT_o	3 600a	5 200a	3 520a	3 760a	3 990a	4 010a	20 100	100
F_{150}	4 810a	4 230a	5 200a	2 740c	5 490a	4 490a	22 500	112
T_{40}	4 610a	5 770a	4 850a	4 940b	5 550a	5 140a	25 700	128
$F_{150}T_{40}$	4 890a	5 340a	4 240a	5 450b	4 830a	4 950a	24 800	123

Table 8. *Total dry weight (g) of current bud production per tree and relative accumulated production (per cent). Data in the same column not followed by the same letter are significantly different ($p<0.05$)*

	Year							
Treatment	1984	1985	1986	1987	1988	x̄	Σ	%
F_oT_o	48.9a	48.2a	38.4a	28.2a	68.7a	46.5a	232	100
F_{150}	58.8a	49.5a	52.7a	40.7a	63.7a	53.1a	265	114
T_{40}	52.8a	48.9a	48.4a	31.6a	88.9a	54.1a	271	117
$F_{150}T_{40}$	59.8a	57.3a	51.6a	88.8a	85.5a	68.6a	343	148

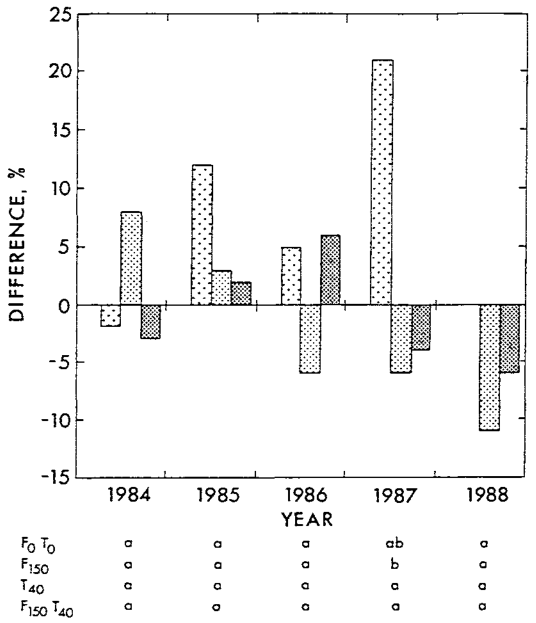

Fig. 6. Relative difference in proportion of annual number of buds produced in the upper crown (upper eight whorls of branches) between treated trees and control (0 %). For notation see Fig. 1. Data from the same year not followed by the same letter are significantly different ($p<0.05$).

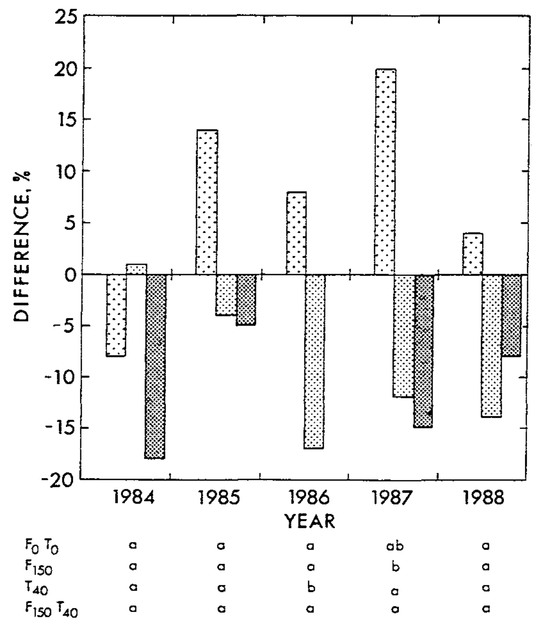

Fig. 7. Relative difference in proportion of annual weight of buds produced in the upper crown (upper eight whorls of branches) between treated trees and control (0 %). For notation see Fig. 1. Data from the same year not followed by the same letter are significantly different ($p<0.05$).

mately 10 per cent higher for F_{150}- and T_{40}-trees than for F_oT_o-trees, and in $F_{150}T_{40}$-trees, almost 50 per cent higher. The T_{40}- and $F_{150}T_{40}$-trees had a lower proportion of their total bud weight in the upper crown than did F_oT_o-trees (Fig. 7). With the exception of 1984, the F_{150}-trees had a higher proportion of their total bud weight in the upper crown.

Weight of cones

In 1986, the dry weight of current cones was lower in F_oT_o-trees than in $F_{150}T_{40}$-trees

Table 9. *Total dry weight (g) of current cone production per tree, relative accumulated production (per cent), and proportion (per cent) in the upper crown (upper eight whorls of branches). Data for each variable in the same row not followed by the same letter are significantly different (p<0.05)*

	Total weight (g)				Proportion in upper crown (%)			
Year	F_0T_0	F_{150}	T_{40}	$F_{150}T_{40}$	F_0T_0	F_{150}	T_{40}	$F_{150}T_{40}$
1984	1.7a	2.0a	3.6a	3.1a	100a	100a	91a	74a
1985	11.0a	4.7a	1.5a	7.0a	85a	100a	100a	74a
1986	0.2a	0.4ab	0.4ab	0.8b	100a	100a	100a	100a
1987	0.2a	0.2a	2.2a	1.9a	100a	100a	100a	56a
1988	0.0a	0.0a	0.3a	0.0a	0a	0a	100a	0a
$\bar{x}$	2.6a	1.5a	1.6a	2.6a				
Σ	13.1	7.3	8.0	12.8				
%	100	56	61	98				

Table 10. *Total dry weight (g) of two-year-old cone production per tree, relative accumulated production (per cent), and proportion (per cent) of two-year-old cones in the upper crown (upper eight whorls of branches). Data for each variable in the same row not followed by the same letter are significantly different (p<0.05)*

	Total weight (g)				Proportion in upper crown (%)			
Year	F_0T_0	F_{150}	T_{40}	$F_{150}T_{40}$	F_0T_0	F_{150}	T_{40}	$F_{150}T_{40}$
1984	90a	30a	43a	28a	99a	100a	100a	63a
1985	196a	96ab	3b	76ab	77a	80a	100a	94a
1986	221a	141a	113a	278a	65a	99a	96a	90a
1987	15a	35a	30a	58a	53a	72a	76a	98a
1988	0a	2a	14a	0a	0a	58a	75a	0a
$\bar{x}$	104a	61a	41a	88a				
Σ	522	304	203	440				
%	100	58	39	84				

(Table 9). The summed dry weight of cones was lower for all treatments, compared with the control. The current cones were concentrated in the upper part of the crown in all treatments. In 1985, two-year-old cones of T_{40}-trees weighed less than those of F_0T_0-trees (Table 10). The summed dry weight of two-year-old cones was lower on all treated plots, as compared with the control. Two-year-old cones were concentrated in the upper part of the crown.

Table 11. *Mean total dry weight (kg) of all current crown components per tree (dead material excluded) produced during the 1983–1988 period and relative accumulated production (per cent). Data in the same column not followed by the same letter are significantly different (p<0.05)*

Treatment	$\bar{x}$	Σ	%
F_0T_0	1.23a	6.14	100
F_{150}	1.49ab	7.46	121
T_{40}	1.29a	6.46	105
$F_{150}T_{40}$	1.80b	9.00	146

Weight of all current crown components

The mean total dry weight of all current crown components increased by ca 40 per cent in $F_{150}T_{40}$-trees, compared to F_0T_0- and T_{40}-trees (Table 11).

Weight of attached dead material

The total dry weight and mean annual dry weight of attached dead material on living branches was unaffected by thinning and fertilization during the period of study (Table 12). Dead material on live branches was concentrated to the lower part of the tree crowns.

Discussion

The sample trees on each plot were selected as mean basal area trees to represent the trees of

Table 12. *Total dry weight (g) of dead material on living branches per tree, relative accumulated weight (per cent), and proportion (per cent) of dead material in the upper crown (upper eight whorls of branches). Data in the same row not followed by the same letter are significantly different ($p < 0.05$)*

Year	Total weight (g)				Proportion in upper crown (%)			
	F_oT_o	F_{150}	T_{40}	$F_{150}T_{40}$	F_oT_o	F_{150}	T_{40}	$F_{150}T_{40}$
1984	267a	222a	282a	187a	1a	1a	2a	1a
1985	291a	192a	212a	195a	2a	0a	1a	4a
1986	310a	387a	278a	283a	0a	2a	2a	3a
1987	279a	296a	251a	492a	6a	6a	9a	1a
1988	374a	371a	346a	285a	2a	1a	2a	2a
$\bar{x}$	304a	294a	274a	288a				
Σ	1 520	1 470	1 370	1 440				
%	100	97	90	95				

their plots as closely as possible. Differences in crown size between trees within plots were not taken into consideration when sampling. For this reason, a high proportion of the differences between control trees and treated trees in a particular year can probably be ascribed to the initial crown size of the sample tree, and not to treatment. When analysing the data, the GLM procedure within the SAS package (SAS Institute Inc., 1989) was used. The only effects on crown development that were significantly different from zero, were the main effects of treatments. Therefore, only the effects of treatments are presented.

There was no effect of treatment on the numbers of each component studied during the first year after treatment. This was as expected, as buds were initiated in the previous year (cf. Junttila, 1986).

According to Persson (1976) and Kellomäki (1986), thinning promotes retention of lower branches. If the number of branches produced at the top is not affected by the treatment, this would lead to proportionately fewer branches in the upper crown for the two thinning treatments. This study indicates, however, that the number of new branches produced at the top during the period 1983–1988 increased after both thinning and fertilization (Table 1). The annual proportion of branches produced in the upper eight whorls of branches was thus not significantly affected (Fig. 1). The retention of lower branches following thinning might be detectable after a longer period of study. Because of the larger proportion of branches retained in the upper crown, trees can respond quickly to changed light relationships as stand density increases some years after thinning. In competition with neighbouring trees, this behavior is certainly of importance.

According to Flower-Ellis et al. (1976), there is a negative correlation between the number and mean length of second-order shoots. In the present study, thinning increased the number of shoot axes produced in the whole crown, probably because of the increased influx of light in the lower crown. The lower branches had a high proportion of the total number of shoot axes. The shoots produced after thinning were shorter and weighed less than shoots produced on F_oT_o- and F_{150}-trees. The increase in number was not followed by an equal increase in weight of shoot axes.

The proportion of needles produced in the lower part of the canopy was higher in both of the treatments that included thinning (cf. Magin, 1952; Brix, 1981). Fertilization, on the other hand, promotes needle production in the upper crown (cf. Albrektson et al., 1977; Brix, 1981). Trees in unthinned stands compete for light: failure to compete leads to suppression and to a redistribution of growth gradients (Forward & Nolan, 1961). It is therefore important for trees to maintain the production of photosynthetic organs high up in the crown, in order to grow and survive. Initially, this is not necessary for trees in thinned stands, because of the increase in light reaching the lower parts of the crown.

Thinning increased bud production in the entire crown, but the number of buds produced did not represent proportionately the same weight (cf. shoot axes). Buds produced on fertilized trees were heavier.

Fertilization promoted a shift of growth within the crown from the lower to the upper crown, while thinning promoted a shift of growth to the lower section of the crown (cf. Brix, 1981). After thinning, the proportion of growth in the upper part decreased each year. The effect of treatments on stem growth in the same experiment (Valinger, 1992), indicates a similar distribution pattern as for crown development: Nitrogen fertilization promotes height growth, and increased radial growth along the whole bole (cf. dry weight increase of the studied crown components, mainly distributed to the upper crown), while thinning promotes lower bole growth. The combined treatment promotes an increased radial growth along the entire bole—most pronounced in the lower bole—and a retained height growth.

During the period of study, there were two years of high cone production (1984 and 1985), but no clear treatment effects could be detected (cf. Sweet & Hong, 1978). This may depend on the low level of fertilizer application (cf. Heidmann, 1984), on the irregularity of cone production, attributable both to the age of the trees studied (Albrektson & Valinger, 1985), and to the cyclicity of cone production (Bergman, 1976).

The accumulated dry weight of all current crown components indicates that a more rapid increase in dry weight production was associated with the combined thinning and fertilization treatment than with thinning or fertilization alone. This effect may be a consequence of the expansion of the crown indicated in Table 3, and of the increased influx of light in the lower crown. The trees also had additional nitrogen available from the first year (cf. Nason et al., 1990), which made possible an increased growth of shoot axes, needles, and buds in the whole crown. Brix & Ebell (1969) and Linder & Rook (1984) state that an increased weight of the crown, i.e. of needles, is a requirement for an increase in stem growth. From an analysis of the total aboveground biomass growth of the same sample tree material, Valinger (1993) suggested that the increased biomass growth following fertilization depended on both increased needle efficiency and increased needle weight.

Conclusions

- Crown development was affected by both thinning and nitrogen fertilization.
- Initially, thinning, both singly and in combination with fertilization, caused changes in the distribution of growth within the crown, by promoting growth in the lower crown, while fertilization promoted upper crown growth.
- The weight of the studied components was increased more by fertilization than by thinning.
- The combined treatment not only promoted growth in the lower crown, but also led to increased weight of the crown components studied. Although the increase was not statistically significant, the weight of crown components increased more than the sum of the individual effects of thinning and fertilization.

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Acknowledgements

This study was supported financially by the Swedish Council for Forestry and Agricultural Research.