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Effects of Spacing and Fertilization on Four Grafted Clones of Scots Pine

Inverkan av förband och gödsling på utvecklingen av tallympar av fyra olika kloner

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Abstract

ODC 165.44:147.4 Pinus silvestris: *181.65*

An experiment was made with grafts of four different clones of Scots Pine (Pinus silvestris) *planted in 1963 in poor sandy soil, with two different spacings and with and without an annual supply of fertilizers from 1964 onwards. The nutrient status of the pines was followed by foliar analysis of needles sampled every autumn. Measurements of a great number of traits (dimensions of tree stems and top-shoots, dimensions and number of branches, branch angles, cone frequencies, etc.) were made in 1967 and 1969 and subsequent statistical analyses showed that both clones and treatment had significant effects on tree properties. Fertilizer strongly affected many properties, such as diameter, branch length and diameter, cone setting and needle length. In this early phase of stand development spacing had less effect on growth than did fertilizer, but branch and stem diameters were affected. Clone influence was very strong in branch angle (one of the four clones was characterized by acute branch angles) but also appeared in some dimensional relations and cone numbers.*

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1 Introduction

In 1963, the Departments of Plant Ecology and Forest Genetics at the Royal College of Forestry, Stockholm, initiated a study of the significance of plant genotype and reaction to spacing and full fertilization. The scope of the experiment was restricted to a small number of genotypes and a small number of applied treatments. It was intended mainly as a pilot study for more detailed experimentation. However, in the early development a considerable variation in growth and vigour was evident between grafts, showing that the techniques used were not as satisfactory as expected for the purpose: to quantify the importance of genetic, as opposed to environmental factors, to the development of plots with forest trees. Consequently, further experiments have been postponed, pending a better technique for vegetative propagation developed in recent years.

The original plans for the experiment, and for the revisions in 1967 and 1969, were drawn up by E. Andersson[1] and C. O. Tamm,[1] while most of the data evaluation has been made by H. H. Hattemer.[1] The vegetative propagation was carried out at the Röskär Experimental Park, Bogesund, of the Royal College of Forestry, under the supervision of B. Jansson. Planting, fertilization, and foliar sampling were carried out by the staff of the Department of Forest Ecology, under the supervision of H. Burgtorf. Chemical analyses were carried out at the same department by B. Hultin and collaborators. The investigation was supported by the Research Council for Forestry and Agriculture.

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2 Material and methods

2.1 Material

Four grafted clones were chosen to represent some genetic variability in the study. The scions were taken either from adult indigenous trees in central Sweden (Kopparbergs Län and Gävleborgs Län) or from existing grafts of these. This heterogeneity in the experimental material could have little influenced the comparisons made between clones (cf. Andersson and Hattemer 1975); this was confirmed by testing the differences in growth between the two types of grafts. The four ortets (cf. Table 1) differed markedly in traits related to economic value; three of the trees were so-called plus-trees (Andersson 1966) and one was a minus-tree. Ortet B was described by Lindquist (1946). The method applied for producing the grafts was veneer-side-grafting.

Growth of the grafts in the field experiment was slow and their general development only moderate.

Thorin and Nömmik (1973) have studied the variability of the monoterpenes of cortical oleoresin. They did not find any differences between fertilized and control plots, but they did find variation among clones. One of the clones, for instance, lacked the compounds Δ^3-carene, α-terpinene, and terpinolene, while the other clones synthesized these compounds at least as traces. There were quantitative differences among the clones in other compounds.

Table 1. The ortets; letters A to D are identical to clone labels in later tables.

Symbol	Name	Reg. no.	Crown form	Cone setting
A	Växbotallen	X 2201	small	abundant
B	Brändbotallen	X 4400	slender	average
C	Evertsbergstallen	W 4013	very slender	average
D	Siljansfors	W 5003	very broad	single cones

2.2 Experimental site

The material was planted 20 km SW of Stockholm in the Lindhov State Forest at latitude 59°14′N in the spring of 1963. The area is a square of 78×78 m surrounded by adult pine stands. The two photographs in Figure 1a and 1b show the condition of the experiment in the autumn of 1970, i.e. eight vegetation periods after planting.

The topography of the experimental area is almost flat (very slightly sloping towards the West) not far from the top of a glacifluvial eskar. The soil material is a deep sand, very low in clay. The soil type is a podzol with a humus layer of mor type and a relatively thin but highly variable A_2 horizon. The site index is low (T · 24 in the H_{100} system), as is expected precipitation (550 mm annually). Some further data on the site have been published by Nömmik and Popović (1971), who carried out another investigation just outside this experimental area.

2.3 Types of treatment

The four different types of treatment applied were the combinations of close and wide spacing (1.3 m×1.3 m and 1.95 m×1.95 m) with or without fertilization (cf. Table 2). A combined fertilizer ('Väx-Upp' 10-10-15) was applied repeatedly: 30 g per tree in May of the two years following establishment of the experiment, and then 500 kg annually on a per ha basis from 1966 to 1972. The composition of the fertilizer (with respect to macronutrients) was

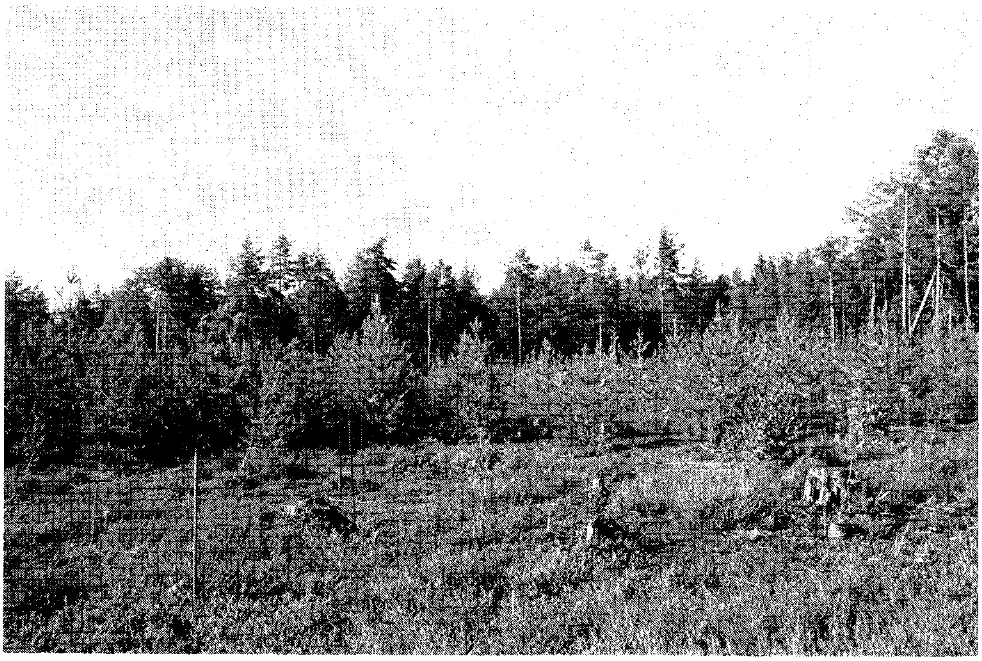


Figure 1a. The experimental area from the south-east. (Photo C. O. Tamm 1970-09-04.)

Figure 1b. Close-up of grafts set back in growth by the severe drought in the summer of 1969. (Photo C. O. Tamm 1970-09-04.)

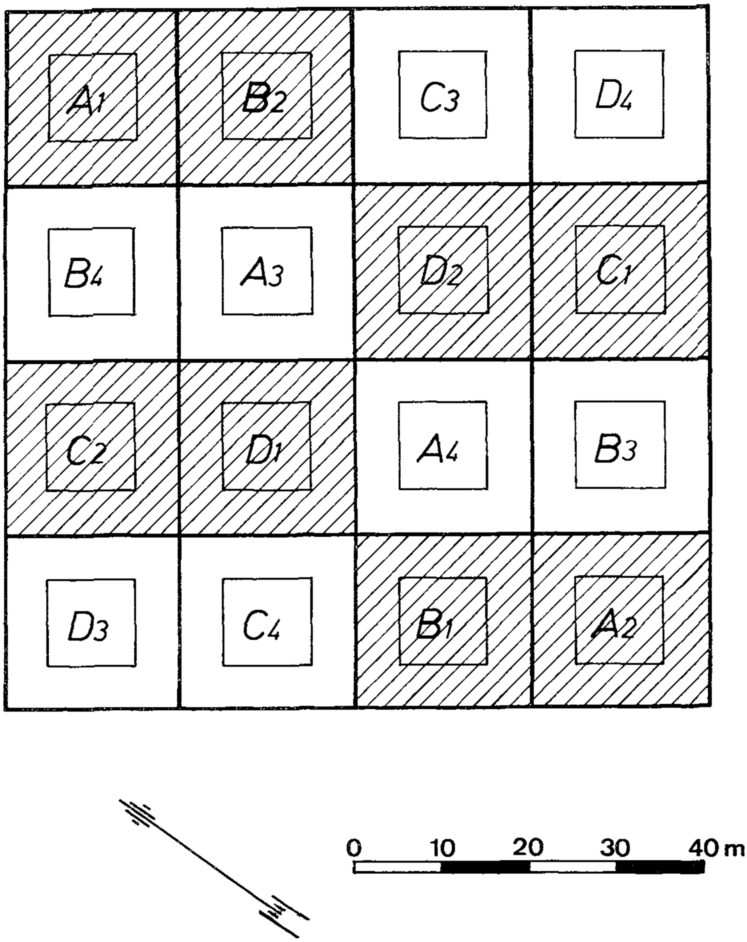


Figure 2. Layout of the experiment. The 16 plots are surrounded by isolation strips that have three times the area of the plots themselves. Fertilized plots (treatment 1 and 2) are denoted by hatching.

Table 2. Treatments.

No.	Spacing	Fertilization
1	close	yes
2	wide	yes
3	close	no
4	wide	no

as follows: 10 % nitrogen, 4.4 % phosphorus, 12.4 % potassium, 11.5 % calcium, 0.4 % magnesium, and 6 % sulphur.

2.4 Lay-out and methods of analysis

The design used was that of a Graeco-Latin square with $n = 4$. The design and its analysis are described in statistical texts, e.g. Peng (1967). Figure 2 shows the 16 plots as they were arranged in the field.

Fertilized plots are denoted by hatching. The square plots have a size of 380 m^2, only one quarter of which (i.e. 100 m^2) was regarded as containing the real measurement plots bearing the grafts. Three quarters of the area thus served as isolation strips, planted with seedling pines of local origin (planted as 2+1 seedlings in the spring, 1963). The margins of measurement plots assigned to different treatments are 10 m apart.

Figure 2 displays a regular pattern of fertilized and control plots in spite of the randomization made; this regularity is due to the small number of treatments (the other alternative had been a checkerboard-like pattern).

The model,

$$y_{ijkl} = \mu + a_i + b_j + c_k + d_l + e_{ijkl}$$

Table 3. Analysis of variance for evaluating treatment effects (fixed-effects model).

Source	d.f.	s.s.	expected m.s.
Rows	3	$4\sum_{i}(\bar{y}_i-\bar{y})^2$	
Columns	3	$4\sum_{j}(\bar{y}_j-\bar{y})^2$	
Clones	3	$4\sum_{k}(\bar{y}_k-\bar{y})^2$	$\sigma^2+\frac{4}{3}\sum_{k} g_k{}^2$
Treatment	3	$4\sum_{l}\sum_{m}(\bar{y}_{lm}-\bar{y})^2$	
Spacing	1	$8\sum_{l}(\bar{y}_l-\bar{y})^2$	$\sigma^2+8\sum_{l} s_l{}^2$
Fertilizer	1	$8\sum_{m}(\bar{y}_m-\bar{y})^2$	$\sigma^2+8\sum_{m} f_m{}^2$
Interaction	1	$4\sum_{l}\sum_{m}(\bar{y}_{lm}-\bar{y}_l-\bar{y}_m+\bar{y})^2$	$\sigma^2+4\sum_{l}\sum_{m}(sf)_{lm}{}^2$
Error	3	$\sum_{i}\sum_{j}\sum_{k}\sum_{l}\sum_{m}(y_{ijklm}-\bar{y}_i-\bar{y}_j-\bar{y}_k-\bar{y}_{lm}+3\bar{y})^2$	σ^2

The dot notation for means, e.g. $\bar{y}_{i....}$ or $\bar{y}_{...lm}$ was simplified to $\bar{y}_i$ and $\bar{y}_{lm}$, respectively.

implies that there are no interactions between the four factors and that the arrangement of the experimental units is a square; μ stands for the general mean, and e is an independently and normally distributed random variable, independent of the four factors, with variance σ^2 and zero expectation. In the present case, a and b may represent rows and columns (blocks) in the field, c and d the clones and treatments. The linear effects as such possessed the primary interest; also, the treatments applied were not fundamentally different as regards plant growth and development. This justified the choice of the present model, which helped to attain greater economy as regards the size of the field experiment.

The above model was then detailed to the following model of analysis of variance for evaluating treatment effects:

$$y_{ijklm}=\mu+r_i+c_j+g_{(k)}+s_{(l)}+f_{(m)} + (sf)_{(lm)}+e_{ijklm}$$

where μ is the overall mean; r, c, and g are the effects of rows, columns, and clones, respectively; s and f are the effects of spacing and fertilization; (sf) is the interaction between these two effects; and e represents the experimental error deviation in the aforementioned properties.

The plot means of the trees measured were subjected to the unweighted analysis of Table 3; this analysis was made for simplicity, although the number of trees varied between 15 and 37 among plots (there were 390 trees in all).

The sum of squares for the various types of treatment was partitioned into three orthogonal contrasts with 1 degree of freedom each: one reflects the effect of spacing $\frac{1}{8}(y_{...1.}-y_{...2.})^2$, and one reflects the fertilizer effect $\frac{1}{8}(y_{....1}-y_{....2})^2$. The last one was computed as a residual and reflects interaction between the two effects.

2.5 Traits measured

A large number of traits were measured in the experimental trees (i.e. the grafts). In Tables 4 and 5 these traits are listed together with some information about the scales of measurement. Some of the traits were also assessed in the seedlings growing in the isolation strip surrounding each plot.

Some branch lengths, branch diameters, and branch angles were measured in a typical branch representing that particular whorl (numbers 19, 23 and 27 in Table 4);

Table 4. Traits measured in the experimental trees (grafts).

No.	Trait	Year	Unit of measurement
a)	*Tree dimensions*		
1	tree height	1963	cm
2	tree height	1964	cm
3	tree height	1965	cm
4	tree height	1966	cm
5	tree height	1967	cm
6	tree height	1968	cm
7	tree height	1969	cm
8	leader growth	1964	cm
9	leader growth	1965	cm
10	leader growth	1966	cm
11	leader growth	1967	cm
12	leader growth	1968	cm
13	leader growth	1969	cm
14	leader growth	1963 through 1967	cm
15	leader growth	1966 through 1969	cm
16	stem diameter at breast height	1969	mm
17	branch length (whorl 1)	1967	cm
18	branch length (whorl 2)	1967	cm
19	branch length (whorl 1)	1969	cm
20	branch length (whorl 3)	1969	cm
21	branch diameter (whorl 1)	1967	mm
22	branch diameter (whorl 2)	1967	mm
23	branch diameter (whorl 1)	1969	mm
24	branch diameter (whorl 3)	1969	mm
b)	*Growth habit*		
25	branch angle (whorl 1)	1967	degrees
26	branch angle (whorl 2)	1967	degrees
27	branch angle (whorl 1)	1969	degrees
28	branch angle (whorl 3)	1969	degrees
29	number of branches (whorls 1 through 4)	1967	
30	number of branches (whorls 1 and 2)	1969	
31	number of branches (whorls 1 through 6)	1969	
32	percentage of coarse branches (whorls 1 through 4)	1967	%
33	as before	1969	%
34	ratio of branch and stem diameter	1969	
35	ratio of branch and leader growth	1967	
36	ratio of branch and leader growth	1968	
37	ratio of branch and leader growth	1969	

in the other instances these traits were reported as the respective average observations in the three longest (and presumably thickest) branches of the whorl indicated. The branch angle was taken at about 10 cm from the point of insertion between a 'representative' branch and the stem above. The whorls were numbered from top to bottom so that no. 1 was the youngest whorl of a tree, no. 3 was two years older. The percentage of coarse branches was computed after classifying all branches in the whorls as coarse, medium, or fine; the classification was to be absolute among all plots of the experiment rather than relative to the branches of single trees. The ratio between branch and stem diameter (trait no. 34) was computed as the ratio between trait numbers 24 and 16. The other ratios reported in Table 4 as traits 35 through 37 were assessed in 1969; the three longest branches in whorl number 3 were measured, keeping

Table 5. Traits measured in the experimental trees (grafts).

No.	Trait	Year	Unit of measurement
c) *Buds*			
38	length of the terminal bud	1967	mm
39	length of the terminal bud	1969	mm
40	length of lateral buds	1967	mm
41	length of lateral buds	1969	mm
42	same as 38 in whorl no. 1	1967	mm
43	same as 40 in whorl no. 1	1967	mm
44	number of lateral buds in leader	1967	
45	number of lateral buds in whorl no. 1	1967	
d) *Foliage*			
46	needle length in present year's foliage	1967	mm
47	needle length in previous year's foliage	1967	mm
e) *Cone setting*			
48	number of 1-year-old cones	1967	
49	number of 2-year-old cones	1967	
50	number of 1-year-old cones	1969	
51	number of 2-year-old cones	1969	
52	number of 1-year-old cones	1975	
53	number of 2-year-old cones	1975	
f) *Nutrient content of foliage*			
54—60	nitrogen	annually 1966 through 1972	% of dry matter
61—67	phosphorus	annually 1966 through 1972	% of dry matter
68—74	potassium	annually 1966 through 1972	% of dry matter
75—81	calcium	annually 1966 through 1972	% of dry matter
82—88	magnesium	annually 1966 through 1972	% of dry matter

the three annual shoots separate. These were then related to terminal growth.

2.6 Repeated measurements

Some traits were remeasured in a sample of 10 identical trees per plot by the same persons[1] some months later, in order to obtain some idea of the errors of measurement involved in this type of experimentation. The statistical model for such observations was the following model of hierarchic analysis of variance for estimating variance components between and within plots:

$$y_{ijk} = \mu + a_i + b_{j(i)} + e_{k(ji)}$$

where μ is the grand mean; a and b are the effects of all plots and of trees within plots ($i = 1, 2, \ldots, 16$; $j = 1, 2, \ldots, 10$); and e is the deviation of repeated measurements within trees from their mean ($k = 1, 2$). Table 6 shows the analysis of variance run for each of the respective traits.

Table 6. Analysis of variance for estimating components of variance within plots.

Source	d.f.	s.s.	expected m.s.
Plots	15	$20\sum_{i}(\bar{y}_i - \bar{y})^2$	$\sigma^2 + 2\sigma_t^2 + 20\sigma_p^2$
Trees	144	$2\sum_{i}\sum_{j}(\bar{y}_{ij} - \bar{y}_i)^2$	$\sigma^2 + 2\sigma_t^2$
Error of measurement	160	$\sum_{i}\sum_{j}\sum_{k}(y_{ijk} - \bar{y}_{ij})^2$	σ^2

[1] The help received from Mr. Sven Andersson and Mr. Verner Åkerbrand is greatly acknowledged.

3 Results and discussion

3.1 Treatment effects on morphology and cone-set

A summary of tests made on various aspects of treatment effects is given in Tables 7 and 8. If there are significant differences between all types of treatment, this condition is due to the fertilization, either alone or in connection with other causes. In the two extreme-right columns, the means of the unfertilized and the fertilized plots are therefore reported. Tree height was initially the same for fertilized and unfertilized plots; it was only some years after outplanting that differences in total height arose. This was reflected in the annual measurements of leader growth. Only after 1967 is there a significant, but small, difference between fertilized and control plots. But there was a substantial increase in breast-height diameter due to fertilization, and also in length and thickness of branches. This increase was very consistent over the various years and whorls measured. However, the percentage of coarse branches was unaffected, as was the whole group of traits related to growth habit (the increases in the number of branches and the number of lateral buds in various parts of the trees were small). The length of the buds may to some extent be regarded as an expression of general vigour, which might explain the fact that the fertilized trees had slightly larger buds.

The diameter of the branches was larger in the widely-spaced plots, even though the branch tips of the trees hardly touched in any plot at this early age. In 1967 the closely-spaced grafts had branches 5.1 mm in diameter in whorl 2 (in 1969 the diameter of the youngest branches was 4.6 mm); the widely-spaced grafts had branches 5.6 mm in diameter (5.0 in 1969). But the differences among the spacings were always larger in the unfertilized plots. This led to a significant interaction mean square in 1967. It is remarkable that not only the older and therefore lower branches showed a cumulated reaction to spacing, but also the upper branches which all received full light.

Tree height and diameter in the two most recent years differed not only as a result of spacing or fertilization alone, but there was also a significant interaction between the two factors. According to the cell means in Table 9, the spacing does not have an effect on growth if there is no lack of nutrients, but in the unfertilized plots the reduction of the area per tree to less than one half brings about a marked depression in tree growth. This tendency is consistent with the diameter of the grafts. One must not forget, however, that these cell means possess large error variances.

Zobel and Roberds (1970) and Goddard, Zobel and Hollis (1974) describe and discuss genotype-related differential growth response of forest trees to fertilizer treatment. In various other reports, such as Goddard (1973), examples are given indicating that the potential response to various silvicultural treatments might have a genetic component. If one extrapolates experience drawn from perennial crops, one would expect such interactions to exist between genotypes and almost any treatment applied. As stated before, this problem cannot be studied in the present experiment.

The largest F-values in Tables 7 and 8 occur with the number of cones. This number was sometimes increased six-fold by fertilization. In 1967 the differences were not yet as pronounced, since the grafts were even smaller and had just started flower production. The increase in flower and cone-set after fertilization is not

Table 7. Significance tests of treatment and clone effects on tree morphology.

No.	Trait	F-values					Means	
		treatm.	fert.	spacing	int.	clones	control	fertilized
1	tree height 1963	.52	.01	.03	1.53	8.54	41	41
2	tree height 1964	8.93	7.25	2.27	17.27*	35.73**	52	50
3	tree height 1965	2.47	1.56	.11	5.73	5.36	76	74
4	tree height 1966	.44	.01	.53	.77	1.32	105	105
5	tree height 1967	2.62	3.35	1.64	2.88	2.34	135	142
6	tree height 1968	12.48*	18.63*	5.87	12.93*	9.04	161	173
7	tree height 1969	42.58**	90.03**	17.24*	20.45*	13.62*	191	210
8	leader growth 1964	.71	1.45	.24	.42	2.49	11	9
9	leader growth 1965	.65	.22	.04	1.69	1.44	25	24
10	leader growth 1966	4.06	7.49	.01	4.68	1.71	30	33
11	leader growth 1967	20.85*	52.41**	2.90	7.23	12.45*	30	36
12	leader growth 1968	9.17	16.94	2.28	8.30	8.61	26	31
13	leader growth 1969	43.68**	122.40**	8.56	.06	1.78	30	38
14	leader growth 1963 to 1967	1.43	1.81	.05	2.41	1.72	100	105
15	leader growth 1966 to 1969	22.61*	58.46**	4.57	4.79	7.30	86	106
16	breast height diameter 1969	66.43**	153.19**	26.98*	19.12*	31.20**	12.8	17.9
17	branch length whorl 1 (1967)	20.85*	56.08**	.12	6.35	2.66	18	24
18	branch length whorl 2 (1967)	19.03*	50.00**	.21	11.89*	56.36**	31	37
19	branch length whorl 1 (1969)	49.19**	138.04**	8.51	1.02	3.21	16	22
20	branch length whorl 3 (1969)	10.16*	23.71*	6.01	.75	10.86*	37	48
21	branch diameter whorl 1 (1967)	25.70*	63.97**	7.25	5.88	12.95*	4.0	5.1
22	branch diameter whorl 2 (1967)	54.94**	115.52**	36.39**	12.89*	60.27**	4.9	5.8
23	branch diameter whorl 1 (1969)	47.73**	131.84**	10.84*	.50	14.11*	4.0	5.4
24	branch diameter whorl 3 (1969)	20.50*	51.89**	9.00	.60	7.01	7.2	9.9
25	branch angle whorl 1 (1967)	.47	.30	.18	.93	68.86**	50	51
26	branch angle whorl 2 (1967)	.69	.94	.97	.15	23.08*	54	57
27	branch angle whorl 1 (1969)	3.55	10.49	.11	.03	61.53**	42	48
28	branch angle whorl 3 (1969)	1.94	5.52	.17	.13	29.98**	61	66
29	no. branches (1 to 4) (1967)	3.18	1.90	.61	7.03	13.25*	14	14
30	no. branches (1 and 2) (1969)	22.21*	54.78**	8.85	2.99	23.23*	8	10
31	no. branches (1 to 6) (1969)	.56	.99	.01	.69	2.79	22	23
32	% coarse branches (1967)	3.07	7.76	1.40	.05	8.49	46	42
33	% coarse branches (1969)	.23	.03	.12	.56	33.70**	30	30
34	branch/stem diameter	.89	.96	.04	1.67	.84	.59	.56
35	branch/leader growth 1967	5.49	12.48	2.92	1.39	19.48*	.54	.57
36	branch/leader growth 1968	2.08	3.49	1.95	.81	45.65**	.43	.45
37	branch/leader growth 1969	.73	.14	1.17	.89	22.74*	.33	.34

Values of test statistics denoted by * are significant at the 0.05 level, those by ** at the 0.01 level and those by *** at the 0.001 level.

unique. Kleinschmit (1958, 1961), Andersson (1965), and more recently Remröd (1973) reported such an increase; compare also the review by Bleymüller (1973). A glance at Table 10 shows that fertilization increased the number of cones by unequal amounts in the various clones.

The clones thus reacted to fertilization or some other factor in very different ways. The resulting interaction between clones and one treatment component (though it cannot be estimated in this experiment) must have inflated the experimental error and was presumably also responsible for the failure to detect a significant fertilizer effect. Apart from this, the amount of increase in the number of cones per graft with fertilization was remarkable.

Table 8. Significance tests of treatment and clone effects on bud morphology, needle length and cone setting.

No.	Trait	F-values					Means	
		treatm.	fert.	spacing	int.	clones	control	fertilized
38	terminal bud length 1967	5.78	13.27*	.11	3.95	11.35*	17.7	20.3
39	terminal bud length 1969	.99	.47	.65	1.87	6.31	12.9	13.3
40	lateral bud length 1967	2.77	5.20	.03	3.09	3.89	13.5	15.7
41	lateral bud length 1969	.74	.22	.05	1.95	11.16*	10.5	10.3
42	terminal bud, whorl 1 1967	5.06	11.38*	.06	3.75	2.68	13.3	15.7
43	lateral bud, whorl 1	3.95	8.16	.11	3.58	2.51	9.1	11.3
44	no. lateral buds (leader)	3.45	8.32	.03	2.06	3.45	4.5	5.1
45	no. lateral buds (whorl 1)	3.11	8.23	.04	1.06	4.76	3.2	3.7
46	needle length (current year)	9.44*	24.61*	1.16	2.55	4.54	44	53
47	needle length (previous year)	7.42	21.82*	.17	.28	9.14	52	63
48	no. 1-year-old cones 1967	4.47	12.59*	.26	.56	4.86	3.4	7.3
49	no. 2-year-old cones 1967	.79	.72	1.58	.06	.16	.1	.2
50	no. 1-year-old cones 1969	152.10***	448.59***	6.86	.87	44.47**	1.8	9.8
51	no. 2-year-old cones 1969	3.91	10.94*	.76	.05	3.00	9.4	18.9
52	no. 1-year-old cones 1975	28.08*	70.79**	6.05	7.39	27.77*	1.6	9.8
53	no. 2-year-old cones 1975	8.44	21.69*	1.23	2.41	6.18	1.3	6.5

Table 9. Treatment means for tree height and diameter at breast height.

a) tree height, 1969, in cm (trait no. 7)

	control	fertilized	mean
close spacing	182	211	197
wide spacing	200	211	205
mean	191	211	

b) tree diameter, 1969, in mm (trait no. 16)

	control	fertilized	mean
close spacing	11	18	14
wide spacing	15	18	16
mean	13	18	

It should be mentioned in this context that the number of cones, and particularly the number of mature cones, does not necessarily reflect the number of flowers produced. The number of cones might be strongly affected by the differential rate of cone abscission among clones and/or environmental factors. But the above results may also be interpreted as a shortcoming of the present experiment as a pilot study.

3.2 Differences among clones

In addition to differences in the number of cones, there were also significant differences in bud length among clones, in most of the measurements describing crown form, and in height and diameter growth. However, differentiation in height growth was due to the fact that clone A gained some superiority during the period of observation, while the others formed a homogeneous group. All clonal means are reported in Tables 11 and 12. There are some similarities between the description of the ortets in Table 1 and the means of the vegetative offspring: clone A had the smallest branch angle (the angle in the uppermost whorl is probably not comparable to that of the ortet because the 'branches' are not loaded with much weight as yet). The least acute branch angle was found in the ramets of the Siljansfors tree, which also had the longest and thickest branches; incidentally, this clone grows fastest and its branches might also

Table 10. Average number of cones per graft by clones and fertilizer treatment.

48) One-year-old cones in 1967

	clones				
	A	B	C	D	mean
control	3.5	1.1	6.7	2.1	3.4
fertilized	7.9	3.5	9.7	8.1	7.3
mean	5.7	2.3	8.2	5.1	

49) Two-year-old cones in 1967

	clones				
	A	B	C	D	mean
control	.3	.1	.1	0	.1
fertilized	.1	.1	.3	.8	.2
mean	.1	.1	.2	.1	

50) One-year-old cones in 1969

	clones				
	A	B	C	D	mean
control	1.2	.8	3.4	1.8	1.8
fertilized	10.2	4.5	15.1	9.2	9.8
mean	5.7	2.6	9.2	5.5	

51) Two-year-old cones in 1969

	clones				
	A	B	C	D	mean
control	7.1	2.9	22.1	5.4	9.4
fertilized	25.7	13.3	18.0	18.5	18.9
mean	16.4	8.1	20.0	12.0	

52) One-year-old cones in 1975

	clones				
	A	B	C	D	mean
control	0	0.5	4.5	1.5	1.6
fertilized	5.5	1.5	20.5	11.5	9.8
mean	2.8	1.0	12.5	6.5	

53) Two-year-old cones in 1975

	clones				
	A	B	C	D	mean
control	1.0	1.0	2.5	0.5	1.3
fertilized	4.5	2.5	13.5	5.5	6.5
mean	2.8	1.8	8.0	3.0	

be larger by physiological correlation. The abundance of cones did not resemble that of the ortet tree; moreover, the latter was based on few observations.

3.3 Nutrient content in the foliage

Autumn samples of current needles for chemical analysis were collected annually in 1966—1972. The samples were taken from the second whorl (20) and analysed for nitrogen, phosphorus, potassium, calcium, and magnesium at the Department of Forest Ecology. The results are expressed as percentage dry weight.

Right from the start of the foliar analyses the uptake of nitrogen and phosphorus was consistently higher in the fertilized plots.

This is true for the grafts and for the seedlings in the surrounding strips, as shown by the tests of significance in Tables 13 and 14, and in the averages put together in Table 15. Something similar can be observed with potassium, though not all of the differences are significant. It has to be borne in mind that the number of test statistics reported in these tables is rather large and that one has to expect some to lie within the rejection region of zero hypotheses (type I errors).

In the case of calcium and magnesium, where the amounts added with the fertilizer were moderate (57 kg per hectare calcium) or small (2 kg magnesium), no clear effects of fertilization can be expected.

It was shown in Table 9 that spacing affected tree height and diameter in unfertilized plots only. An influence of spacing on nutrient levels would therefore appear likely, at least in unfertilized plots. There is

Table 11. Clonal means (tree morphology).

No.	Trait	Clones A	B	C	D
1	tree height 1963	47	36	41	40
2	tree height 1964	57	49	49	48
3	tree height 1965	82	71	71	75
4	tree height 1966	110	104	99	108
5	tree height 1967	140	136	132	145
6	tree height 1968	166	163	161	179
7	tree height 1969	199	197	197	212
8	leader growth 1964	10	13	8	8
9	leader growth 1965	25	23	22	27
10	leader growth 1966	30	31	31	34
11	leader growth 1967	30	32	34	37
12	leader growth 1968	26	27	29	33
13	leader growth 1969	33	34	35	34
14	leader growth 1963 to 1967	101	104	97	107
15	leader growth 1966 to 1969	89	93	98	105
16	breast height diameter	18	18	11	15
17	branch length whorl 1 (1967)	20	20	21	23
18	branch length whorl 2 (1967)	40	27	31	38
19	branch length whorl 1 (1969)	19	20	18	18
20	branch length whorl 3 (1969)	47	35	38	50
21	branch diameter whorl 1 (1967)	4.0	4.2	4.8	4.1
22	branch diameter whorl 2 (1967)	5.3	4.6	5.1	6.2
23	branch diameter whorl 1 (1969)	4.2	4.5	5.2	5.0
24	branch diameter whorl 3 (1969)	7.9	7.6	8.9	9.8
25	branch angle whorl 1 (1967)	34	46	56	66
26	branch angle whorl 2 (1967)	36	51	66	69
27	branch angle whorl 1 (1969)	48	48	42	43
28	branch angle whorl 3 (1969)	50	62	69	73
29	no. branches (1 to 4) (1967)	14	13	15	13
30	no. branches (1 and 2) (1969)	8	9	10	9
31	no. branches (1 to 6) (1969)	8	8	10	9
32	percentage of coarse branches (1967)	37	25	24	34
33	percentage of coarse branches (1969)	45	39	43	47
34	branch/stem diameter	.60	.60	.55	.55
35	branch/leader growth 1967	.59	.59	.54	.52
36	branch/leader growth 1968	.59	.34	.39	.48
37	branch/leader growth 1969	.46	.22	.24	.42

very little evidence of such influence in Table 13. The trees may adjust their growth very closely to the amounts of nutrients available (Tamm 1975), so that the more severe competition for nutrients at close spacing depresses growth to the exact extent needed to maintain the same nutrient level.

Table 15, however, provides other interesting information, viz. the variation in nutrient levels from year to year. In most nutrients there is no clear trend, except perhaps a tendency for the contents of nitrogen, phosphorus and potassium to decrease with time in unfertilized plots. In 1969, which had a very dry summer, high concentrations of the elements mentioned were evident in *fertilized* plots, but concentrations of calcium and magnesium were low throughout the experiment. This table does not show any striking difference between grafts and seedlings as to the effect of fertilizer quantity on foliar nutrient concentrations.

Figure 3. Number of 1-year-old cones in 1969 plotted against the number of such cones in 1967. Triangles refer to fertilized plots, circles and dots to controls: wide spacing is denoted by empty symbols, narrow spacing by solid symbols. The letters refer to the clones.

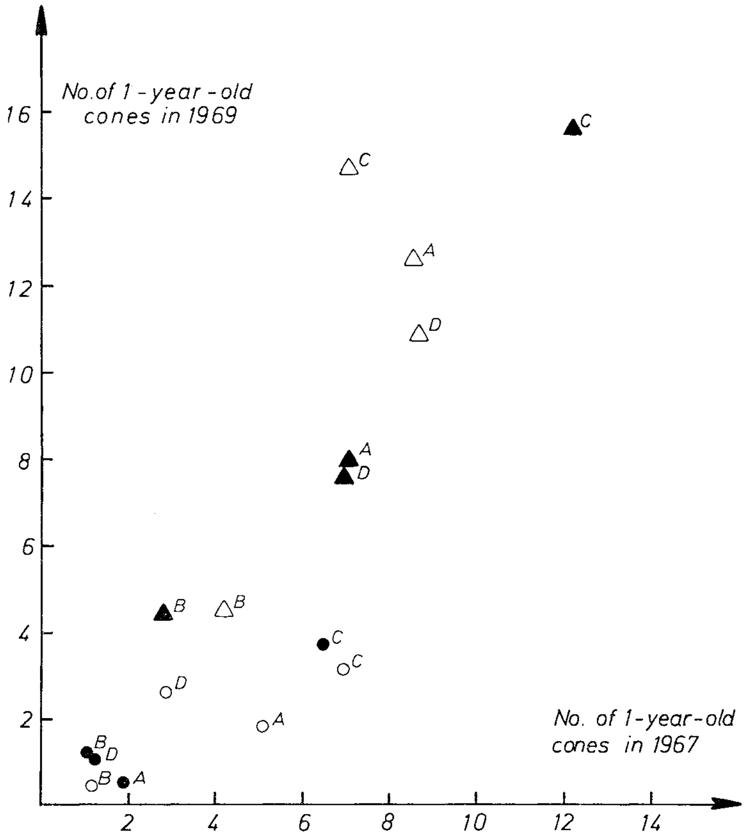


Table 12. Clonal means (bud morphology, needle length and cone setting).

No.	Trait	Clones			
		A	B	C	D
38	length of the terminal bud	16.2	18.0	20.9	21.0
39	length of the terminal bud	11.0	13.2	14.0	14.4
40	length of lateral buds	12.9	13.2	16.5	16.0
41	length of lateral buds	8.3	9.8	11.9	11.7
42	same as 38 in whorl no. 1	13.2	13.8	15.2	15.8
43	same as 40 in whorl no. 1	9.5	8.8	11.4	11.0
44	number of lateral buds in leader	4.3	4.8	5.0	5.2
45	number of lateral buds in whorl no. 1	3.1	3.1	3.8	3.8
46	needle length in present year's foliage	50	43	49	53
47	needle length in previous year's foliage	53	53	58	67
48	number of 1-year-old cones	5.7	2.3	8.2	5.1
49	number of 2-year-old cones	.1	.1	.2	.1
50	number of 1-year-old cones	5.7	2.6	9.2	5.5
51	number of 2-year-old cones	16.4	8.1	20.0	12.0
52	number of 1-year-old cones	2.8	1.0	12.5	6.5
53	number of 2-year-old cones	2.8	1.8	8.0	3.0

Table 13. Summary of analyses of variance of nutrient contents during seven successive years: F-values.

Element	Year	Treatments	Fertilizer	Spacing	Interaction	Clones
N	1966	17.85*	50.58**	2.61	.37	2.34
	1967	16.73*	49.74**	.31	.13	3.53
	1968	11.79*	28.45*	2.69	4.22	1.57
	1969	141.86***	410.48***	7.15	7.96	8.22
	1970	43.42**	122.76**	5.37	2.15	1.10
	1971	67.49**	201.86***	.01	.60	2.59
	1972	81.84**	243.29***	.77	1.48	2.26
P	1966	8.30	24.75	.01	.13	9.08
	1967	7.42	21.49*	.01	.74	5.34
	1968	19.41*	55.29**	.74	2.21	1.84
	1969	254.08***	745.61***	15.48*	1.15	54.50**
	1970	220.64***	660.97***	.97	.00	30.04*
	1971	115.96**	347.44***	.13	.31	23.47*
	1972	20.30*	53.51**	3.01	4.40	3.05
K	1966	4.51	4.64	8.49	.40	25.43*
	1967	13.20*	22.42*	14.69*	2.49	89.68**
	1968	5.74	15.52*	1.07	.65	.40
	1969	.70	2.09	.01	.01	.93
	1970	7.55	22.59*	.04	.04	2.01
	1971	4.48	11.79*	.24	1.24	3.59
	1972	8.77	20.27*	2.25	3.78	2.59
Ca	1966	1.78	3.70	.12	1.50	7.12
	1967	1.45	2.64	1.64	.07	1.25
	1968	6.59	11.64*	6.26	1.86	.62
	1969	1.00	1.93	.21	.86	4.00
	1970	.63	.88	.39	.61	.04
	1971	2.73	2.88	.53	4.76	3.82
	1972	4.69	13.96*	.00	.12	4.00
Mg	1966	1.84	.72	1.03	3.79	1.59
	1967	.41	.58	.28	.37	1.40
	1968	10.58*	30.10*	.91	.74	2.12
	1969	21.57*	62.49**	2.14	.09	16.54*
	1970	.40	.05	.32	.83	5.90
	1971	9.99*	16.85*	.79	12.34*	1.19
	1972	3.26	1.10	1.25	7.43	1.70

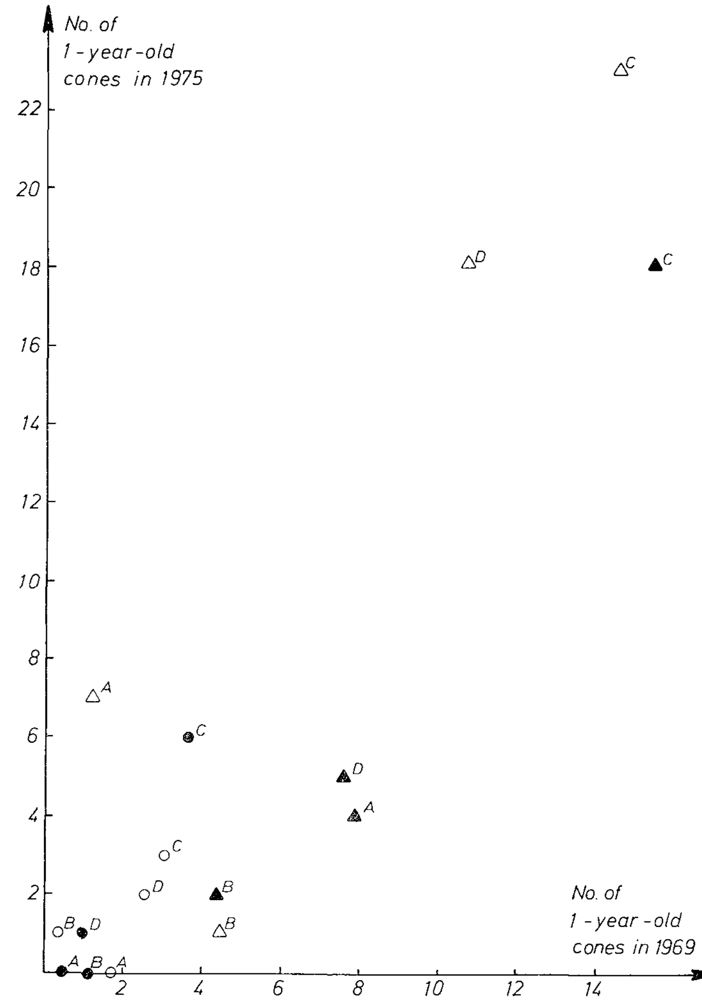
For explanation of asteriscs see Table 7.

The effect of the clones is sometimes significant, but mostly it is not. In making the tests on the seedling data, it turned out that the F-values for clones were all (as they should be) within the acceptance region. In this respect the experiment reduces to a normal Latin square.

3.4 Correlations among traits

The design of the experiment does not provide means for efficiently estimating correlation coefficients among the numerous traits assessed. There are, for instance, only three degrees of freedom left for the error variances. As an alternative, the correlations among all plot means were computed since they represent some provisional information. There are also a few instances where both treatment and clone effects are absent so that these main effects then might not inflate the covariances. A condition that may reduce correlations among traits measured in different years is the

Figure 4. Number of 1-year-old cones in 1975 plotted against the number of such cones in 1969. For explanation of symbols see Fig. 3.



fact that a tree sampled in 1967 did not necessarily enter the respective 1969 plot mean.

The data on height growth in various years are strongly correlated, when there are only one or two periods of growth in between (r around 0.95). There is a regular decrease with the length of the period (r is as low as 0.2 between 1963 and 1969). The height increment data are not as strongly correlated as one might expect; the correlation coefficients range between 0 and 0.7 but do not display any regular pattern.

The plot means in branch length, branch diameter and branch angle are strongly correlated (r above 0.9) among whorls indicating a certain repeatability of such traits among parts of the trees formed in different years. The four cone counts also possess positive correlations, though r varies between 0.1 and 0.85. Fig. 3 shows a plot of the numbers of 1-year-old cones in 1967 and 1969, which makes it clear that the differences between treatment and clones both contribute to such a correlation. The number of cones not only reveals some consistency by clones in time (see also Figs. 3 and 4), but is, of course, influenced by other traits, such as the number of branches. Although the branches were counted right at the stem, the numbers of branches may give some indication of the number of

Table 14. Summary of analyses of variance of nutrient contents in the seedlings growing in the isolation strips during three successive years: F-values.

Element	Year	Fertilizer	Spacing	Interaction
N	1966	15.18*	1.59	.76
	1967	63.86**	.21	.54
	1968	30.89*	.06	.35
P	1966	68.62**	.14	5.10
	1967	100.49**	1.86	.03
	1968	37.82**	.93	2.33
K	1966	77.82**	4.41	14.29*
	1967	1.37	.65	3.43
	1968	2.68	.19	.27
Ca	1966	2.16	.32	.01
	1967	2.10	.20	<.01
	1968	.14	.85	.24
Mg	1966	<.01	3.50	.14
	1968	8.48	1.91	.63

For explanation of asteriscs see Table 7.

Table 15. Average nutrient contents (% of foliage dry matter) of control and fertilized plots.

Element	Year	Grafts		Seedlings	
		control	fertilized	control	fertilized
N	1966	1.32	1.72	1.23	1.56
	1967	1.40	1.85	1.39	1.74
	1968	1.42	1.71	1.37	1.94
	1969	1.40	2.09		
	1970	1.12	1.83		
	1971	1.23	1.87		
	1972	1.21	1.79		
P	1966	.152	.176	.130	.157
	1967	.157	.188	.145	.181
	1968	.139	.171	.150	.188
	1969	.147	.205		
	1970	.131	.177		
	1971	.143	.189		
	1972	.135	.190		
K	1966	.62	.64	.54	.59
	1967	.60	.63	.55	.57
	1968	.52	.65	.64	.69
	1969	.58	.61		
	1970	.54	.63		
	1971	.54	.60		
	1972	.54	.50		
Ca	1966	.17	.20	.17	.19
	1967	.17	.19	.18	.15
	1968	.18	.14	.20	.19
	1969	.13	.12		
	1970	.17	.18		
	1971	.21	.22		
	1972	.26	.29		
Mg	1966	.079	.081	.077	.077
	1967	.086	.084		
	1968	.086	.071	.089	.076
	1969	.059	.055		
	1970	.100	.101		
	1971	.113	.101		
	1972	.118	.115		

shoot tips that can bear flowers (there are close correlations among the numbers of lateral buds in the leader and the branch tips). The onset of cones was only moderate, due to the young age and small size of the trees, and the variation in branch number was not very large; nonetheless Fig. 5 displays some relationship between cone and branch number. The uppermost whorl was included in the counting of the latter, in order to provide a more reliable measure of branchiness.

There are some relations worthy of observation among the content of various nutrient elements. Nitrogen, for instance, is predominantly positively correlated with all other compounds except magnesium; the coefficients are largest among N and P (r between 0.6 and 0.95) but negative among N and Mg (r between 0 and −0.8). The fertilizer used contained N, P, K and Ca in considerable quantities, but very little Mg (see Section 2.3). This may explain the positive correlations between most nutrient concentrations. The negative N/Mg correlation may be a so-called dilution effect; application of nitrogen (and other nutrients) increases growth more than magnesium uptake, resulting in low magnesium concentrations. Correlations among other such groups of measurements are not at all consistent, since they change their signs in successive years. For example, the correlations among nitrogen and calcium are positive in 1966 and 1967, but then fall below zero.

Particular interest should be paid to the correlations between nutrient levels and traits of economic interest. But, in general, these are moderate as far as growth is

Figure 5. Number of 1-year-old cones in 1967 plotted against the total number of branches in the four uppermost whorls counted in the same year. For explanation of symbols see Fig. 3.

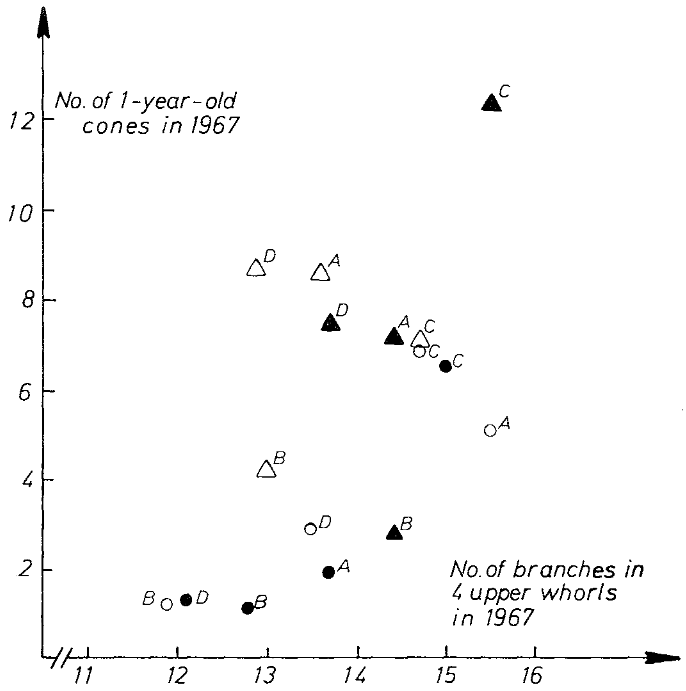


Table 16. Results of repeated measurements of several traits.

No.	Trait	Variance components (% of their sum)			s	Mean
		plots	trees	error		
1	leader growth 1967	43	64	2	1.1	33
2	leader growth 1968	27	45	28	5.6	29
3	leader growth 1969	22	50	28	5.8	33
4	leader growth 1966 to 1969	37	62	1	2.7	96
5	tree height 1966	13	85	2	2.9	105
6	tree height 1967	15	83	1	2.7	138
7	tree height 1968	20	76	4	5.9	167
8	tree height 1969	23	77	< 1	1.4	201
9	breast height diameter	30	69	1	.8	15
10	branch length whorl 1	40	50	10	2.0	19
11	branch length whorl 3	44	43	13	5.4	43
12	branch diameter whorl 1	42	39	19	.6	5
13	branch diameter whorl 3	50	44	6	.6	9
14	percentage coarse branches	14	42	44	4.1	44
15	branch angle whorl 1	60	13	27	7.4	45
16	branch angle whorl 3	45	49	6	3.2	63
21	length of terminal bud	20	73	7	.9	13
22	longest lateral bud	22	68	10	.9	10

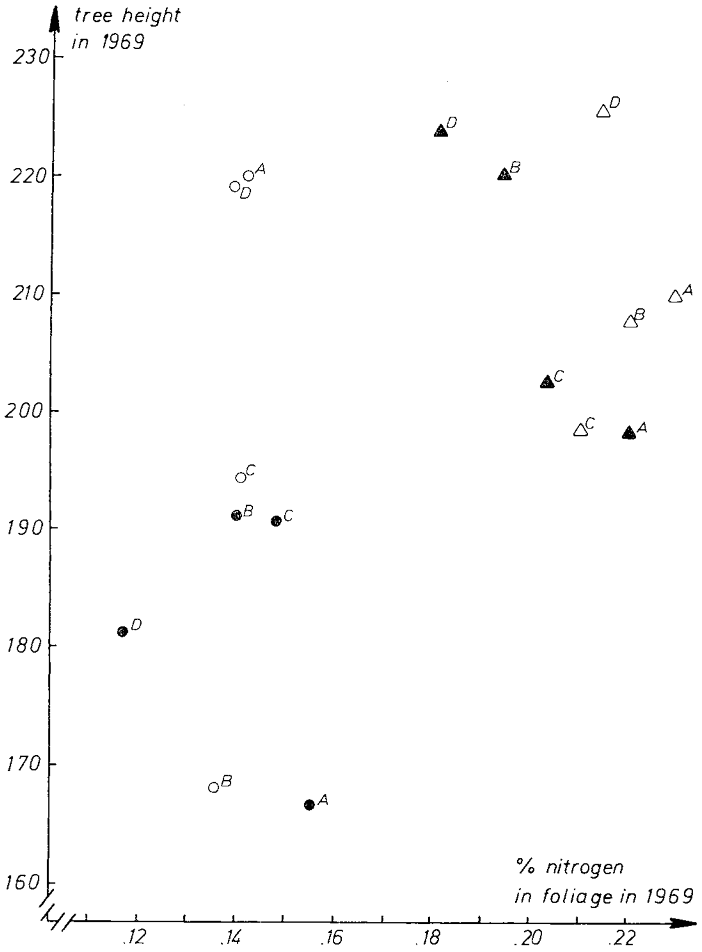


Figure 6. Tree height in 1969 plotted against nitrogen concentration in the foliage, measured in 1969. For explanation of symbols see Fig. 3.

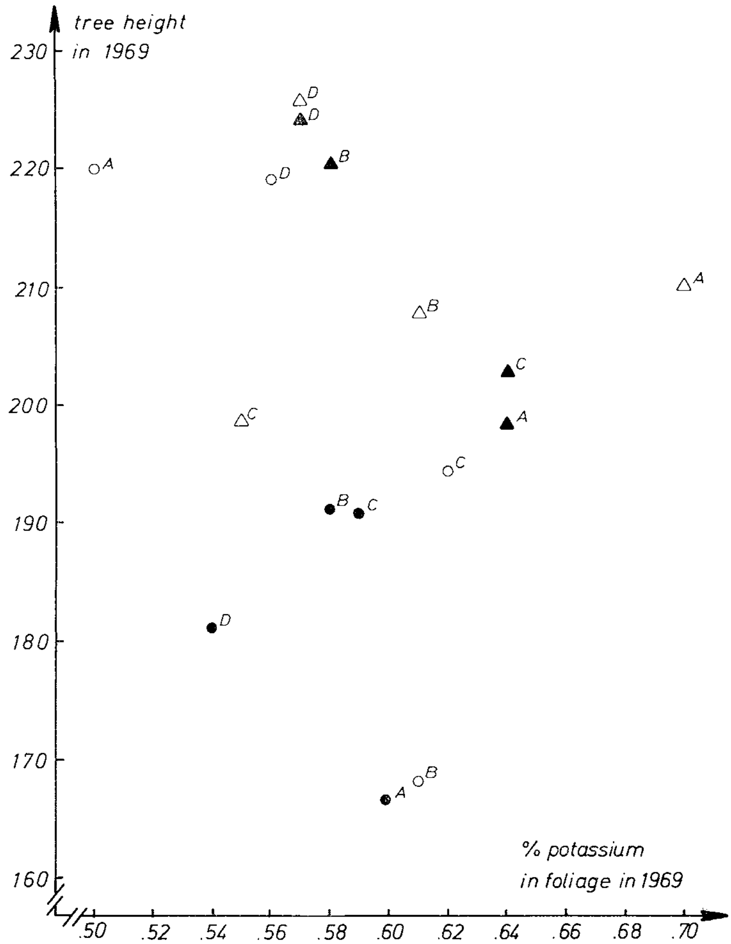
concerned. Again a few examples, such as height, will be given up to 1969, and the contents in the five elements measured. They are mostly positive (r essentially between 0 and 0.7 except with magnesium where they are around −0.4). Figures 6 through 10 show plot diagrams of the relation between nutrient concentrations measured in 1969 and tree growth expressed in tree height up to 1969.

The correlations between cone production and nutrient concentration in the foliage have a similar pattern. Figures 11 and 12 give some idea of the common influence of clones and treatment on this correlation (note that, particularly in Fig. 11, the pairs of symbols denoting combinations of clones and fertilizer treatment have similar positions in the diagrams). These correlations were similar among the years studied, but it appeared to be more reasonable to plot cone counts against nutrient concentrations in earlier years.

3.5 Repeated measurements

The estimates of variance components for the three sources, all plots, trees within plots, and error of measurement, were converted to percentages of their respective sums. These percentages are reported in Table 16 and prove that with few exceptions the error component is the smallest;

Figure 7. Tree height in 1969 plotted against potassium concentration in the foliage, measured in 1969. For explanation of symbols see Fig. 3.



the assessment of these traits turned out to be highly repeatable. Both the variance between trees and among all plots proved to be significant in all traits.

The last two columns show the absolute value of the standard error, i.e. the square root of the error mean square, and the mean for purposes of comparison. The mean was computed from the trees used for the analysis of treatment effects that, nevertheless, might closely indicate the mean of the 160 trees measured twice. Even in traits like the percentage of coarse branches, the absolute error appears to be sufficiently small. This condition is underlined by the small size of the between-plot differences; furthermore, this error has two components: erroneous counting and varying classification of branches as coarse or not. In addition, the error of branch thickness actually has two components: failure to detect the three longest branches by inspection, and errors in measuring their diameters. The height increments (the first four traits) were derived only in the computer; they do not indicate that their variances are manifolds of the basic items (traits 4 to 7).

The distribution of the error deviations in most cases represented almost classical normal distribution. But there were also some rare outliers that may be attributable to misunderstandings between crew members, etc. In all, the precision of measurements proved to be sufficient.

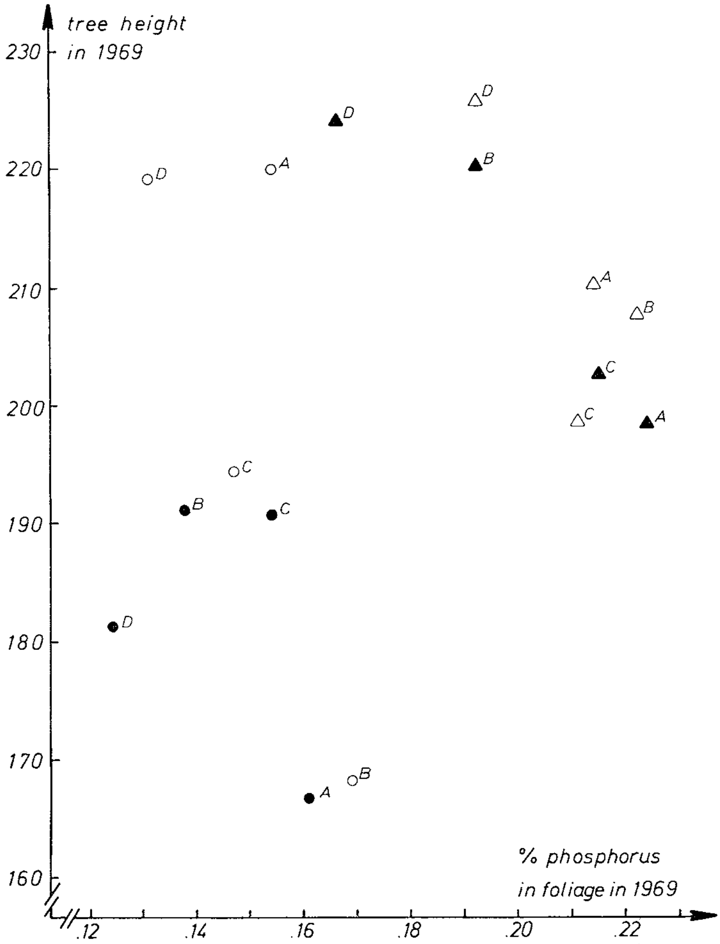
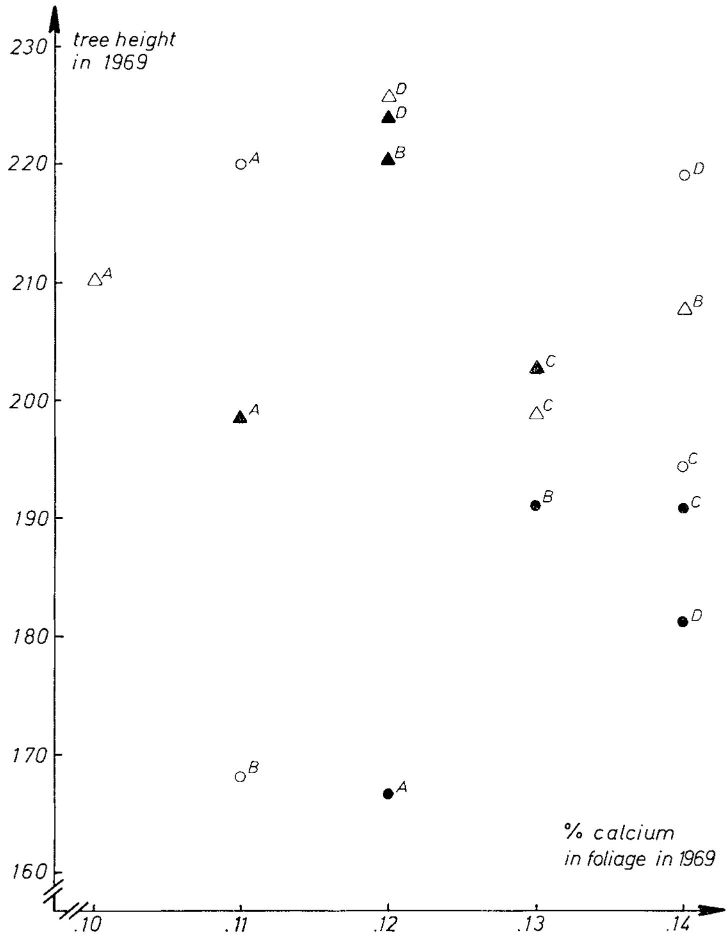


Figure 8. Tree height in 1969 plotted against phosphorus concentration in the foliage, measured in 1969. For explanation of symbols see Fig. 3.

Figure 9. Tree height in 1969 plotted against calcium concentration in the foliage, measured in 1969. For explanation of symbols see Fig. 3.



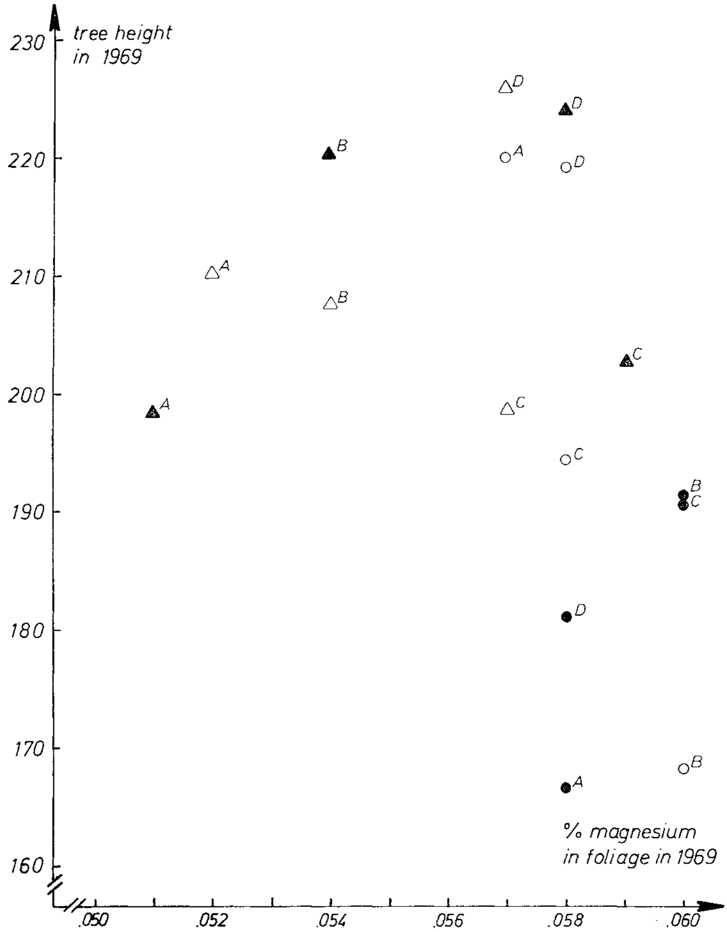
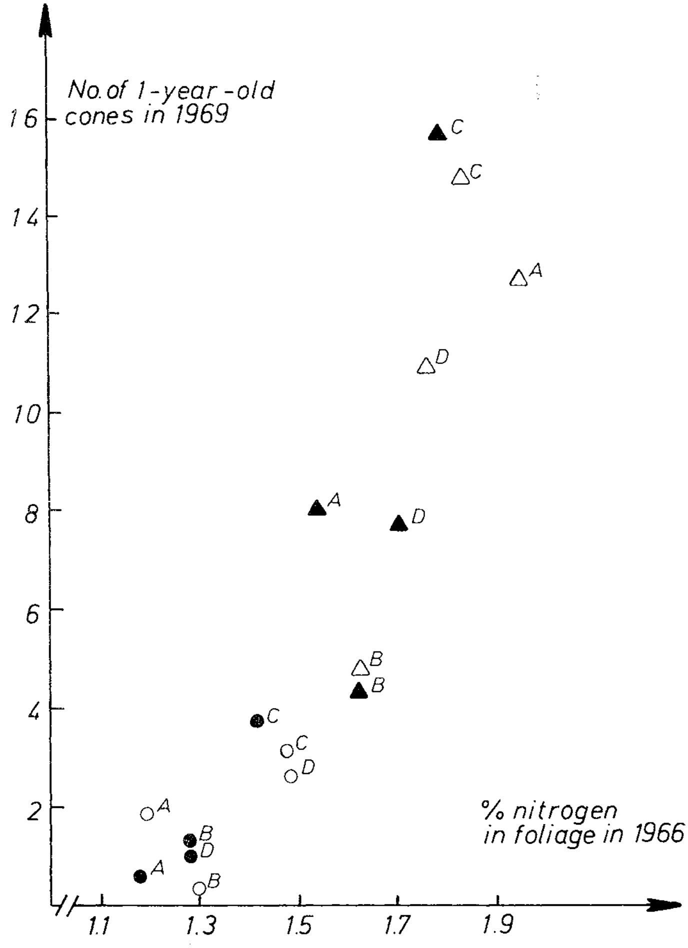


Figure 10. Tree height in 1969 plotted against magnesium concentration in the foliage, measured in 1969. For explanation of symbols see Fig. 3.

Figure 11. Number of 1-year-old cones in 1969 plotted against the percentage of nitrogen in foliage dry matter measured in 1966. For explanation of symbols see Fig. 3.



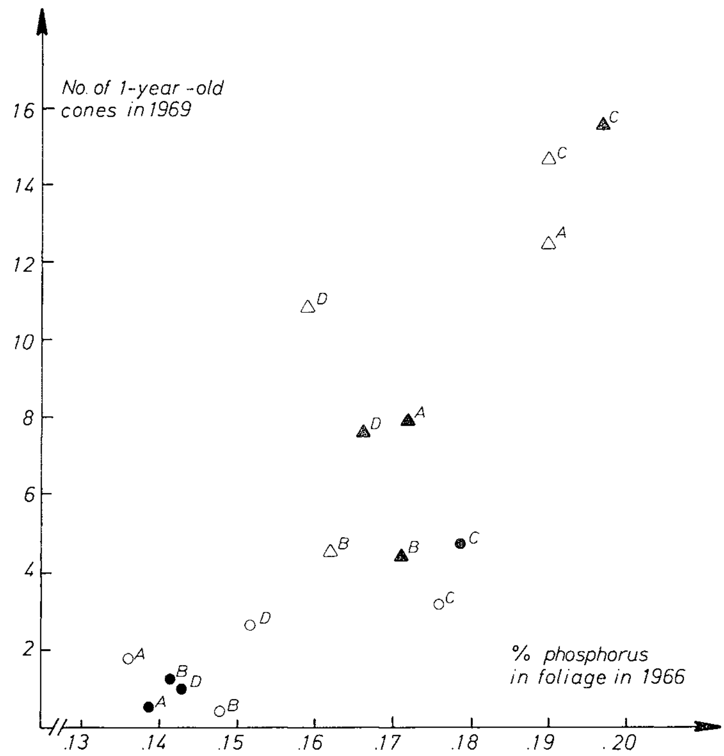


Figure 12. Number of 1-year-old cones in 1969 plotted against the percentage of phosphorus in foliage dry matter measured in 1966. For explanation of symbols see Fig. 3.

4 Summary

1. Four clones represented by grafts were treated by either wide or close spacing, and by applying a combined fertilizer or not. The field experiment was designed as a Graeco-Latin square.
2. Both treatments (spacing and fertilization) and genotypes differed in a large number of variables measuring tree dimensions, growth habit and branch morphology, number and size of buds, needle length, and cone-set. At the age of 7 years the effect of spacing was manifest in tree height and diameter. However, wide spacing meant larger tree dimensions only in the unfertilized control plots; conversely, the effect of fertilization was more pronounced in close spacing.
3. The number of cones was considerably higher among the fertilized grafts than in the control material (cf. Table 10).
4. There was a pronounced fertilizer effect on the nitrogen and phosphorus content of the foliage. The effect on potassium, calcium, and magnesium content was also sometimes present but varied between years during the 7-year period of observation.
5. The error of measurement estimated in 18 morphological characteristics turned out to be tolerable both in terms of absolute and relative size.

5 Sammanfattning

Ett planteringsförsök med ympar av fyra olika kloner av tall och med fyra olika behandlingar anlades 1963 på en sandmark sydväst om Stockholm, Krp Lindhov. Behandlingarna bestod i årlig tillförsel av gödselmedel fr.o.m. 1964 (under de två första åren till de enskilda plantorna, sedan bredspritt) samt tätt respektive glest förband. Varje parcell med klonplantor omgavs av en fem meter bred lika behandlad skyddsremsa med fröplantor.

Näringstillståndet i tallplantorna följdes genom årlig barranalys. 1967 och 1969 gjordes omfattande tillväxtmätningar varvid ett stort antal trädegenskaper registrerades. Signifikanta skillnader erhölls både mellan behandlingar och mellan kloner. Signifikanta gödslingseffekter kunde konstateras i många egenskaper, t.ex. stamdiameter, grenlängd, grendiameter, kottantal och barrlängd. Effekten av förbandet visade sig bl.a. i att ogödslade träd i det större förbandet hade större höjd och diameter 1969 i glest förband än i tätt. Gödslingseffekten var mera utpräglad i det täta förbandet. Naturligt nog ökade kväve- och fosforinnehållet i barren efter gödslingen medan effekterna på innehållet av kalium, kalcium och magnesium var mera varierande. Kloninflytandet visade sig i några kvantitativa egenskaper som stamdiameter och grendimensioner men slog igenom särskilt hårt i fråga om grenvinkel, huvudsakligen därför att en av de ingående klonerna utmärktes av mycket spetsig grenvinkel.

Det uppskattade mätfelet i 18 olika morfologiska egenskaper var måttligt både i absoluta och relativa termer. Det är därför angeläget att försök av detta slag upprepas med ett vidare spektrum av kloner och behandlingar, eftersom det är ont om undersökningar där det är möjligt att kvantitativt väga genetiska inflytanden mot miljöpåverkanden.

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