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Genetic Variation in Progeny Tests of Scots Pine (*Pinus silvestris* L.)

Ärftlig variation i avkommeförsök med tall

by

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Introduction

The inheritance and genetic variation of quantitative and qualitative characters in conifers have been studied in progenies obtained from individual trees after open and controlled pollination, as well as in clone trials (SYRACH LARSEN, 1937, 1947, 1956; DENGLER, 1939; LANGNER, 1952; MERGEN, 1953, 1955, 1959; FIELDING, 1953, 1960; STERN, 1953; NILSSON, 1955; ARNBORG and HADDERS, 1957; TODA, 1955, 1958, TODA *et al.* 1959; ERICSON, 1960; CALLAHAM and HASEL, 1961; ZOBEL 1960, 1961). The quantitative characters are strongly influenced by environmental factors. The genetic part of the variation is recognized from the observation that the variation within progenies or clones generally is smaller than the variation between them.

The present investigation concerns seedlings and young trees of *Pinus silvestris* L. obtained by artificial crossing or open pollination. Height, branch length, branch angle, number of branches, size of the terminal bud and other morphological features were recorded. Differences in the development and variation of these characters among the progenies have been studied. The external resemblance of the progenies to their parent trees has been analyzed, as well as the influence of environmental factors on the tree development. In a few suitable cases it was possible to make direct comparisons between clone individuals of the parent trees and the parent offspring. The effect of inbreeding was studied in progenies obtained after self-pollination. Finally, abnormalities in the formation of buds and branches (EHRENBERG and GUSTAFSSON, 1957; EHRENBERG, 1958) have been examined with regard to penetrance and expressivity as defined by TIMOFÉEFF-RESSOVSKY (1934, 1940) and ALLARD (1960).

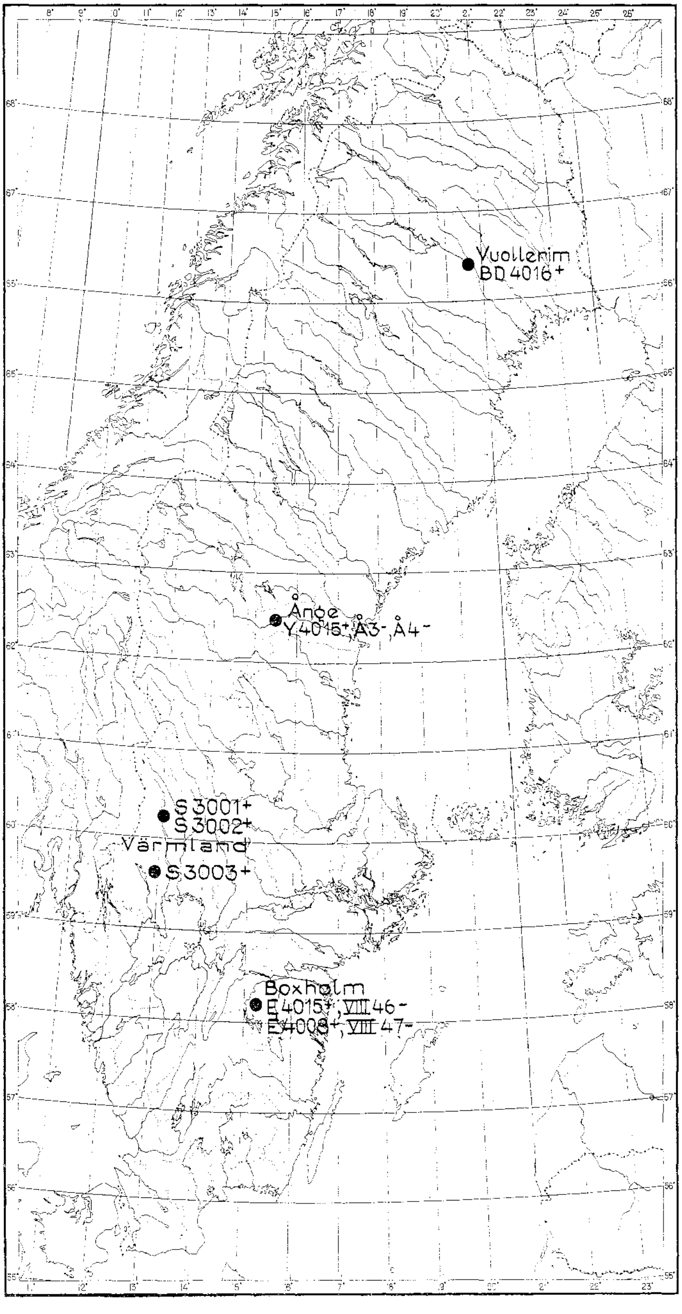


Figure 1. Localities of plus and minus trees used as parents.

Material and methods

1. *Parent trees*

The twelve parent trees studied in the experiments reported here were phenotypically classified as distinct plus trees or minus trees. Four of the trees were selected in a stand at Boxholm in the province of Östergötland, four in a stand south of Ånge in the province of Medelpad, three in different localities in the province of Värmland and one at Vuollerim in the parish of Jokkmokk in the province of Lapland (Fig. 1). Data of the trees and the localities are presented in Table 1.

The plus trees at Boxholm have superior height growth, straight, slowly tapering stems, a narrow fine-limbed crown, and almost right-angled branching. They are 5 to 10 years older than the minus trees growing in the same locality. Although one minus tree, VIII: 46$^-$, has a diameter equalling that of the plus tree E 4015$^+$, it is characterized by slow height growth, a rapidly tapering stem, a wide, coarse-limbed crown, and almost right-angled branching. The second minus tree, VIII: 47$^-$, is also marked by slow height growth, whereas the diameter growth is rapid. The crown is wide, the branches are coarse, and the branch angle is intermediate. Both minus trees show poor natural pruning (Fig. 2).

The plus trees at Ånge were chosen for the experiment on account of their superior height growth, good stem form and narrow, fine-limbed crowns. The branch angles of both trees are intermediate. Primarily, the minus trees are characterized by their acute branch angle, in Å 4$^-$ extremely acute, and by their wide, coarse-limbed, long crowns. Although their height growth is slow, their diameter increment is good. In 1948 the age of three trees was about 90 years, while the fourth tree, Å 4$^-$, was some ten years younger.

Among the pines studied in the province of Värmland, S 3002$^+$ differs from the others by an acute branch angle, relatively low height and a small diameter, poor natural pruning and intermediate crown width. In 1948 this tree was over 150 years old. Tree S 3001$^+$ has a particularly narrow crown and fine limbs, whereas tree S 3003$^+$ is distinguished by good growth in regard to height and diameter. The branch angle of both of the trees is right.

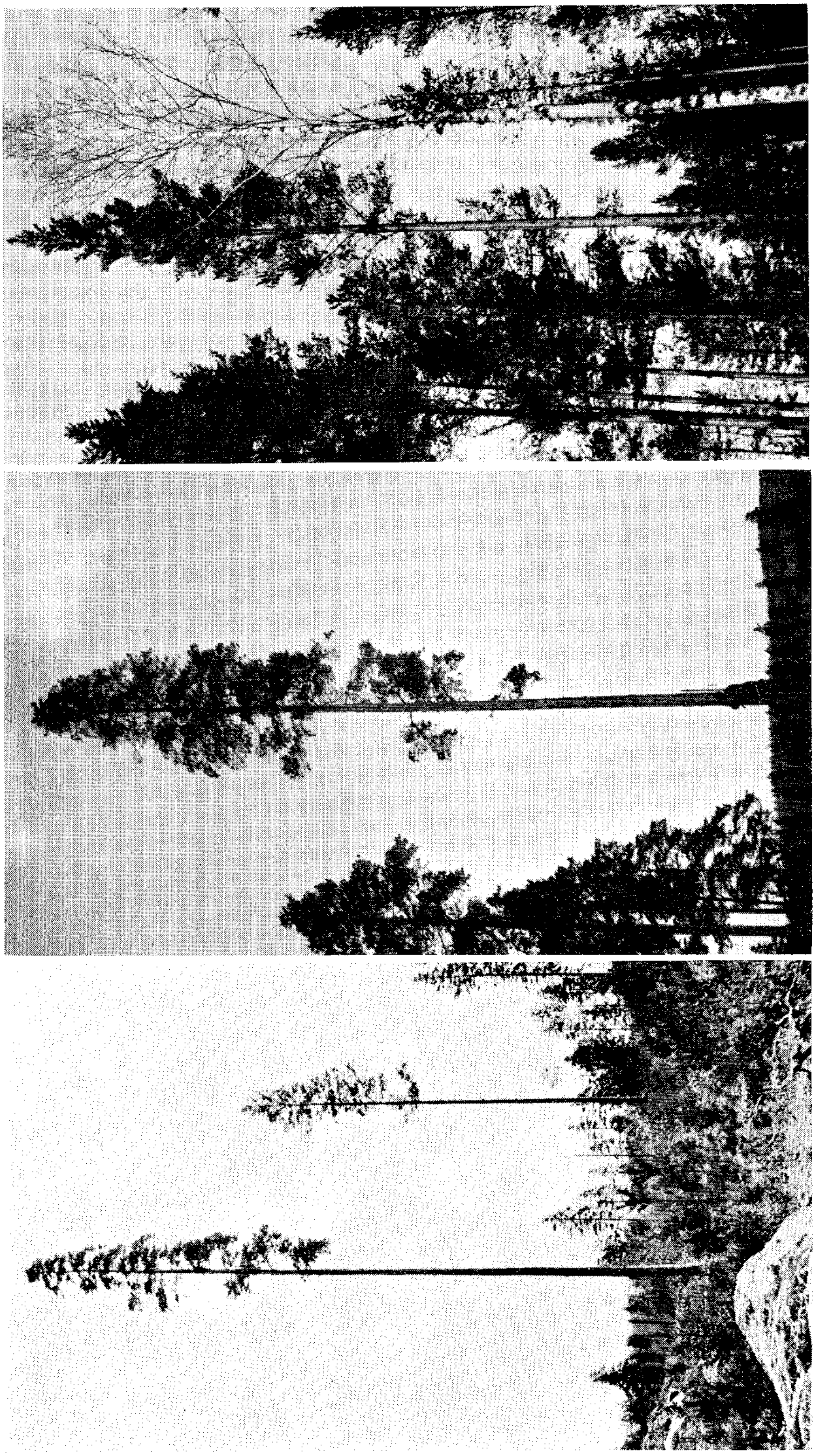
The plus tree at Vuollerim, BD 4016$^+$, is approximately 100 years old. It has a narrow, regular, fine-limbed crown with right-angled branching.

Age has been determined by counting the number of annual rings on increment cores extracted at breast height. The height and distance from the ground to the lowermost green limb of the crown has been measured by tape, and the diameter at breast height (DBH) by caliper. The crown type

Table 1. Parent trees. Data on localities and tree characteristics.

Tree No.[1]	Locality and Province	Latitude	Altitude (m)	Site	Fenotype plus-tree: + minus-tree: –	Year of measurement	Age years	Height (m)	Diameter, breast height (mm)	Crown type	Crown radius (longest) (m)	Crown height (m)	Crown ratio, per cent	Branch type	Branch angle
E 4015^{+}	Boxholm Östergötland	58°07′	180	fresh, moraine	+	1949	123	28.0	420	narrow	3.8	15.5	45	fine	right
E 4008^{+}					+	1949	118	30.5	460	narrow	2.8	15.5	49	fine	right
VIII 46^{-}					–	1949	113	22.8	486	broad	4.3	8.5	63	coarse	intermediate
VIII 47^{-}					–	1949	113	19.0	418	broad	3.7	6.6	65	coarse	intermediate
Y 4015^{+}	Ånge Västernorrland	62°25′	275	moist, moraine	+	1948	88	25.5	283	narrow	1.8	13.2	48	fine	intermediate
Å 2^{+}					+	1948	90	26.5	335	narrow	2.1	13.2	50	fine	intermediate
Å 3^{-}					–	1948	89	20.5	437	broad	3.7	10.0	51	coarse	acute
Å 4^{-}					–	1948	78	20.0	425	broad	4.2	4.7	77	coarse	extremely acute
S 3001^{+}	Vägsjöfors Värmland	60°22′	157	dry, sandy moraine	+	1948	85	25.0	310	extremely narrow	1.7	11.5	54	extremely fine	right
S 3002^{+}		60°19′	208	fresh, moraine	+	1948	152	24.0	330	narrow-intermediate	2.0	5.5	73	fine	acute
S 3003^{+}	Brunsberg Värmland	59°37′	118		+	1948	112	28.5	405	narrow	2.0	16.5	42	fine	right
BD4016^{+}	Vuollerim Norrbotten	66°25′	110	dry, sand	+	1949	98	18.8	298	narrow	2.0	6.5	65	fine	right

[1] *Explanations of symbols.* The letters E, Y, S and BD refer to the provinces (»län»). VIII and Å stand for local districts.



a) Plus tree E 4015$^+$, Boxholm. b) Plus tree E 4008$^+$, Boxholm. c) Plus tree Y 4015$^+$, Ånge.

Fig. 2. a—c *The plus trees* have straight stems, narrow fine-limbed crowns and almost right to intermediate branch angles.

d) Minus tree VIII 46⁻, Boxholm. e) Minus tree VIII 47⁻, Boxholm.

Fig. 2 d—e. The *minus trees* show rapidly tapering stems with long bends and poor pruning, wide coarse-limbed crowns and intermediate to acute branch angles.

has been recorded by measurements of the largest crown radius; the branch type and the branching angle having been judged ocularly. Plus trees assigned a national registration number (province letter and serial number, *e.g.* E 4015$^+$), are intended to be used as parent trees in seed orchards. They have been propagated by grafting on a large scale. Grafts from all the trees listed in Table 1 have been planted in clonal experiments for the purpose of investigating the growth and form of each of the selected trees in different surroundings. The branch length and branch angle have been measured on only a few of these clonal trees. The measurements will be extended as soon as more grafts have reached an appropriate age.

Fig. 2 f. Plus tree Y 4015^{+}. The stem is straight and well pruned. g) Minus tree Å 4^{-}, Ånge. Lowermost part of the stem showing the poor pruning and the acute branch angles.

2. *Crossings*

The techniques of crossing and selfing have been described earlier (Plym Forshell, 1953; Ehrenberg and Simak, 1957). The crossings were carried out in 1948 and 1949. Seeds after open pollination were collected at the same time as the artificially produced seeds. The various seed-lots were all treated in the same way from harvest to sowing. Empty seeds were separated from filled seeds by the fanning method (Huss, 1951), and the percentage of filled seeds was determined by counting the number of seeds in the two seed groups.

Table 2. Provenances, cross combinations, number of trees per progeny and percentage of dead trees in 1955 to 1960.

Experiment	Provenance	Combination		No. of trees	Percentage of dead trees			
				1954	1955 3)	1956	1958 3)	1960
X	Boxholm	E 4015^{+} × E 4008^{+}	+ × +	210	1.9	2.4	1.0	1.4
		E 4008^{+} × E 4015^{+}	+ × +	210	9.5	10.0	9.5	8.1
		VIII 46^{-}	i 1)	210	5.7	16.2	33.8	38.6
		VIII 46^{-} × VIII 47^{-}	− × −	210	3.3	6.7	13.3	8.1
	Ånge	Y 4015^{+} × Å 2^{+}	+ × +	210	5.7	7.1	1.4	2.4
	Värmland	S 3001^{+}	o. p. 2)	210	1.4	6.7	2.9	3.3
G	Boxholm	E 4015^{+}	o. p.	648	2.8	8.2	1.9	2.9
		E 4008^{+}	o. p.	324	1.9	8.3	4.6	4.0
		VIII 46^{-} × E 4015^{+}	− × +	324	1.9	8.3	6.5	2.5
		VIII 46^{-}	o. p.	324	0.6	4.9	4.3	6.5
		VIII 47^{-}	o. p.	648	4.8	15.9	4.0	6.3
	Ånge	Y 4015^{+}	o. p.	324	0.6	6.2	2.2	3.4
		Å 3^{-}	o. p.	324	1.9	8.0	4.3	6.2
		Å 4^{-} × Å 3^{-}	− × −	324	0.3	1.2	0.3	0.6

1) Selfed. 2) Open pollinated. 3) The inventory made in the spring immediately before the fill-in planting.

The various cross combinations are presented in Tables 2 and 3. With regard to the phenotypes of the parent trees, the combinations can be grouped in the following way:

Type of combination:	+ × +	+ × −	− × +	− × −	Selfing (i)		Open pollination (o.p.)	
Number of					+	−	+	−
combinations:	4	5	2	3	6	2	7	4

The materials from Boxholm, Ånge, and Vuollerim were sown in 1951, transplanted in 1953, and planted in field experiments in 1954. The percentage of germinated seeds and the seedling and tree mortality in various years has been recorded.

The seeds from the trees in the province of Värmland obtained after open pollination and after selfing were sown in 1950. The seedlings were planted in the same years as the other materials. The number of seedlings of Värmland origin was low, varying between 8 and 56, except for the progeny of S 3001^{+} o.p., which consisted of more than 300 individuals. Seedlings of the latter were included in one of the field experiments, X. It should be borne in mind, however, that they are one year ahead in development.

Table 3. Experiment O. Provenances, cross combinations, number of trees per progeny and percentage of dead trees in 1958 and 1960.

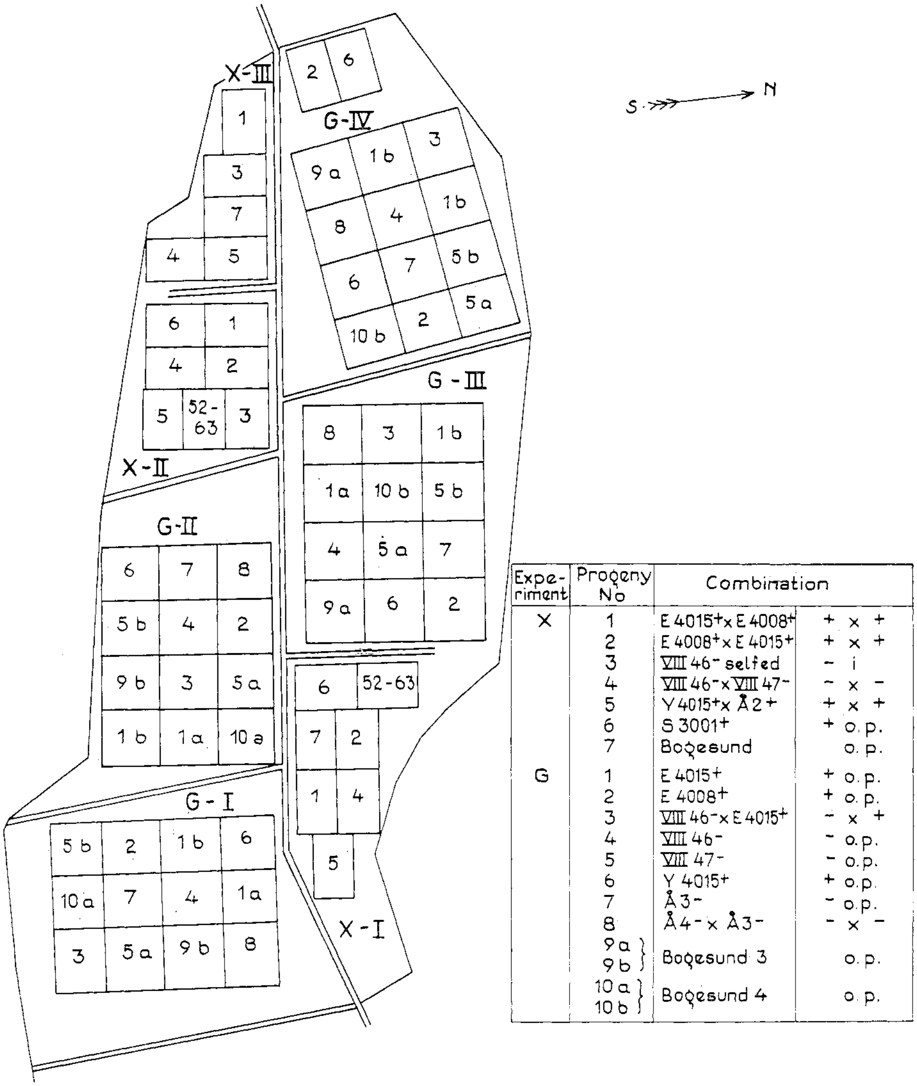
Provenance	Combination		No. of trees	Percentage of dead trees	
			1954	1958	1960
Boxholm	E 4015$^+$	o. p.¹)	34	5.9	5.9
	E 4015$^+$	i²)	18	11.1	11.1
	E 4015$^+$ × E 4008$^+$	+ × +	24	4.2	4.2
	E 4015$^+$ × VIII 46$^-$	+ × −	24	8.3	8.3
	E 4008$^+$	o. p.	24	4.2	4.2
	E 4008$^+$ × E 4015$^+$	+ × +	19	0.0	0.0
	E 4008$^+$ × VIII 46$^-$	+ × −	25	0.0	0.0
	VIII 46$^-$	o. p.	25	4.0	4.0
	VIII 46$^-$	i	48	10.4	12.5
	VIII 46$^-$ × E 4015$^+$	− × +	24	0.0	0.0
	VIII 46$^-$ × VIII 47$^-$	− × −	25	0.0	0.0
	VIII 47$^-$	o. p.	25	4.0	4.0
Ånge	Y 4015$^+$	o. p.	25	4.0	4.0
	Y 4015$^+$ × Å 2$^+$	+ × +	24	8.3	8.3
	Y 4015$^+$ × Å 4$^-$	+ × −	25	0.0	0.0
	Å 2$^+$	o. p.	23	0.0	0.0
	Å 2$^+$ × Y 4015$^+$	+ × +	25	4.0	4.0
	Å 3$^-$	o. p.	50	2.0	8.0
	Å 3$^-$	i	15	0.0	0.0
	Å 3$^-$ × Å 4$^-$	− × −	50	4.0	6.0
	Å 4$^-$	o. p.	32	6.7	6.7
	Å 4$^-$ × Y 4015$^+$	− × +	25	4.0	4.0
	Å 4$^-$ × Å 3$^-$	− × −	25	0.0	1.0
Värmland	S 3001$^+$	o. p.	25	8.0	8.0
	S 3001$^+$	i	27	7.4	7.4
	S 3002$^+$	o. p.	13	0.0	15.4
	S 3002$^+$	i	16	12.5	12.5
	S 3003$^+$	o. p.	25	8.0	8.0
	S 3003$^+$	i	7	0.0	0.0
Vuollerim	BD 4016$^+$	i	7	0.0	0.0

¹) Open pollinated. ²) Selfed.

3. *Field experiments*

I. *Field experiment* X. (Fig. 3). This experiment with seven progenies was laid out in three blocks. The number of specimens in each plot was 7 × 10 = 70 with a spacing of 1.5 × 1.5 metres. The control material, (field No. X 7), representing the local provenance, originated from a pine tree at Bogesund near Stockholm. This material showed poor development. Comprehensive fill-in planting was necessary in 1955 and in 1958, one entire plot being replanted with other stock (field No. 52—63). So far, this progeny has been excluded from the measurements and the analysis of the data.

The progeny obtained from the minus tree VIII: 46$^-$ at Boxholm after selfing also grew slowly, and had a high mortality. Fill-in planting was done in the blocks II and III, but in block I this progeny had to be replaced with



Experiment	Progeny No	Combination	
X	1	E 4015^{+} x E 4008^{+}	+ x +
	2	E 4008^{+} x E 4015^{+}	+ x +
	3	VIII 46^{-} selfed	− i
	4	VIII 46^{-} x VIII 47^{-}	− x −
	5	Y 4015^{+} x Å 2^{+}	+ x +
	6	S 3001^{+}	+ o. p.
	7	Bogesund	o. p.
G	1	E 4015^{+}	+ o. p.
	2	E 4008^{+}	+ o. p.
	3	VIII 46^{-} x E 4015^{+}	− x +
	4	VIII 46^{-}	− o. p.
	5	VIII 47^{-}	− o. p.
	6	Y 4015^{+}	+ o. p.
	7	Å 3^{-}	− o. p.
	8	Å 4^{-} x Å 3^{-}	− x −
	9 a 9 b	Bogesund 3	o. p.
	10 a 10 b	Bogesund 4	o. p.

Fig. 3. Design of field experiment X and G, Södermyra. Experiment X laid out in three blocks, experiment G in four blocks.

other stock (field No. 52—63). Consequently only two replications of it are available for analysis.

Experiment X was established quite close to experiment G, and the same site differences occur in both experiments (see below). The site conditions thus vary within blocks as well as between blocks.

II. *Field experiment G.* (Fig. 3). In this experiment ten progenies were laid out in randomized blocks with four replications. Each plot contains 9 × 9 = 81 trees with a spacing of 1.5 × 1.5 metres. There were two plots of the progenies E 4015^{+} o. p. and VIII: 47^{-} o.p. in each block. For comparison with the local provenance, the experiment included materials obtained after open pollination from two pine trees growing in the neighbourhood (field Nos. G 9 and G 10). These progenies were reared in a nursery together with the rest of the experimental material; but part of them were transplanted on another occasion. Unfortunately, these progenies proved to be considerably inferior to the rest of the material, their growth being slow in the first years, and the mortality unusually high. In three plots, most of the original individuals had to be replaced with new material. The progenies G 9 and G 10, therefore, have not been included in the present statistical analysis.

Although the experimental field is quite plane, the soil conditions vary to a great extent. In the years prior to the trial layout, the area, a clay farm field, was covered with grass. In the autumn before planting it was ploughed. Seepages in the blocks I, III, and IV were eliminated by trenching. In the blocks II and III each seedling was fertilized with 22.5 g superphosphate and 7.5 g potassium sulphate immediately after the planting. The same amounts were given to both blocks in conjunction with fill-in planting in the spring of 1955. The blocks I and IV were left unfertilized. The site differences are in parts considerable, both between and within some of the blocks.

The experimental area is located on a tenant farm on the state-owned Bogesund estate in the vicinity of Stockholm.

III. *Observation experiment O* comprises eighteen progenies obtained after selfing and open pollination, and twelve type crossings. The number of seedlings in the different combinations varied from 7 to 50 (Table 3). Each progeny was planted in a row without replications, except for the progenies consisting of 50 seedlings which were planted in two rows. No fill-in planting was done. The purpose of this experiment was to observe the development of the individual trees, and no statistical processing of the data was intended. The experiment was established on an old farm field with heavy clay soil at the Bogesund field station.

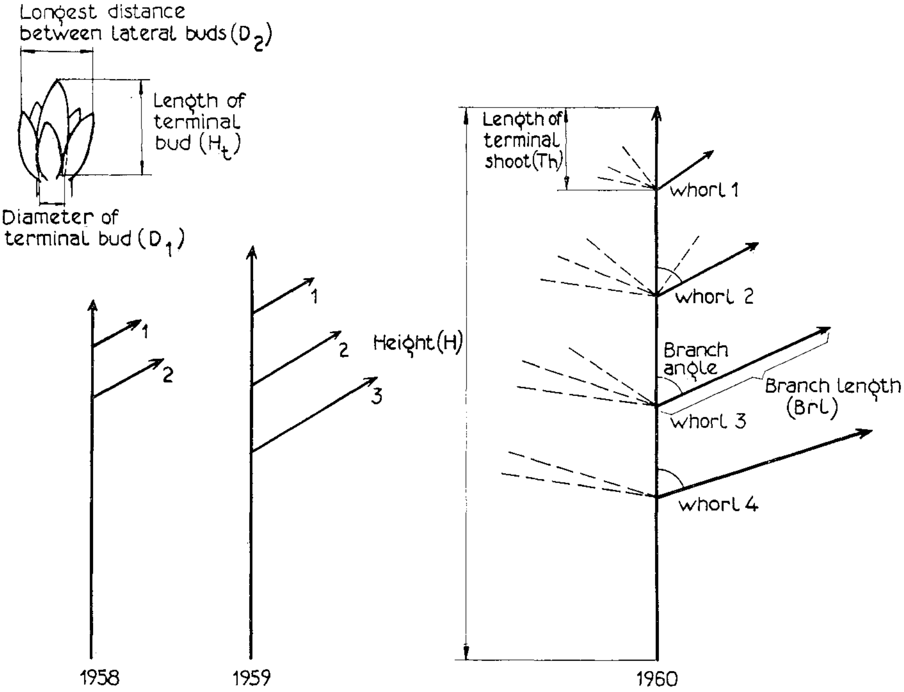


Fig. 4. Characters analyzed in the years 1958 to 1960.

4. *Properties investigated and methods of measurement*

The following characteristics of the young trees have been analyzed (Fig. 4).

a) *Tree height (H).* The height was measured on the three-year-old seedlings in the nursery in the autumn prior to planting. In the field experiments measurements were taken on all trees after the termination of the growing season in 1956, 1958, 1959 and 1960.

b) *The length of the terminal shoot (Th)* was recorded for all trees in the years 1958—1960.

c) *Branch length (Brl).* The branch length has been determined by measuring the three longest branches in each whorl. Only dominant, well developed branches were measured, even if they numbered less than three. The whorls are numbered consistently from the top downwards as whorl No. 1, 2, 3, and 4.

d) *Branch angles.* The upper angle between the stem and the branches measured for length was determined with a special protractor.

e) *The number of branches* in each whorl were counted.
f) *The length (Ht) and diameter (D_1)* of the apical bud were measured with a steel ruler graded in millimetres and a slide gauge respectively.
g) *The lateral buds of the terminal shoot.* The longest distance (D_2) between the opposite lateral buds was determined. The biggest three lateral buds were also measured in length (Hs).
h) Each individual was studied with regard to *the occurrence of irregularities* in growth, such as abnormal development of buds and branches, mechanical defects, damage by fungi or animals.

The 20 tallest undamaged trees in each plot were selected for the registration of the properties c—g analyzed in the experiments X and G. The height values obtained from these 20 trees were used in computing the relationship between height and branch length. In the statistical analyses the mean values of plots and progenies were used for comparison of the progenies (SNEDECOR, 1946, p. 266, 268, 318 *et seq.*).

In *experiment X* a constructed value had to be used in the analysis of variance instead of the value missing from the progeny VIII: 46^- selfed (X 3). One degree of freedom has been subtracted from the total sum of squares and from the error sum of squares (KEMPTHORNE 1952, p. 173). The preliminary test having revealed significant differences between progenies or between blocks, an exact test of the significance was made.

In *experiment G* the plot G 5 *a* in block IV had to be excluded. Instead, measurements were made on the trees in plot G 5 *b* of block II. This plot replaces G 5 *a* of block IV in the statistical treatment of the data. In consequence, progeny G 5 has probably been slightly favoured in comparison with the other progenies in block IV.

Results

1. Characteristics of the parent trees of importance for the development of the seedlings

In previous investigations, cone and seed characters have proved to be characteristic of the individual parent trees (PLYM FORSHELL, 1953; EHRENBERG *et al.*, 1955). It was concluded that the differences in the length of cones, seed morphology, and the ability of the trees to produce seed after selfing, are to a large extent genetically conditioned. Since the 1,000-grain weight is correlated with the cone size (SIMAK, 1953), and the minus trees generally produce larger cones than the plus trees of the same provenance, seeds from the minus trees generally have a higher 1,000-grain weight. Filled seeds obtained after selfing have a 1,000-grain weight equalling that of seeds obtained from the same tree after open pollination. Nevertheless seedlings grown from selfed seeds display inferior growth. This seems to be due to disturbances in embryo development such as polyembryony and a high percentage of seeds in the embryo classes II—III. Inbreeding phenomena are thus manifested at an early stage, and continue to reduce vigour at later stages of growth.

Table 4 gives a summary of data published by PLYM FORSHELL in 1953 on cones and seeds collected in 1949 or 1950, and used for obtaining the materials analyzed in this investigation.

Seven trees at Boxholm, Ånge, and Vuollerim have been analyzed in regard to the following characteristics:

1) *The cone size* (mean value of two years) is characteristic of each parent tree, but shows some annual variation. It is not influenced by various types of pollination. The ranking of the trees at Boxholm with regard to cone length was as follows: VIII: $46^{-} > $ VIII: $47^{-} > $ E $4015^{+} > $ E 4008^{+}. The cones of the two minus trees are consistently larger than those of the plus trees. The same relationship is observed in the Ånge trees, where the ranking is: Å $4^{-} > $ Å $3^{-} > $ Å $2^{+} > $ Y 4015^{+}. The cone length varies within the same size-range for both the provenances. The cones of the pine BD 4016^{+} from the northerly provenance at Vuollerim are smaller than those of all the other trees.

2) *The selfing ability* expressed as the percentage of filled seeds is low in two of the Boxholm trees, while the tree VIII: 46^{-} produced more than 50 per cent filled seeds. The only tree at Ånge, Å 3^{-}, from which selfed seeds were available in 1949, had a low percentage of full seeds. Later analyses have shown that, on an average, the trees at Ånge have a higher ability for

Table 4. Cross combinations and data on cones and seeds, collected in 1949 and 1950 and used to obtain the materials for the progeny tests.

Provenance	Combination	Year of pollination	Length of cones (mm)	Per cent filled seeds	No. of filled seeds per cone	1,000 grain weight	Per cent germinated seeds
Boxholm	E 4015^{+} o.p.1)	1949	35	85.7	19.6	4.5	99.0
	i 2)		36	15.3	1.9	5.5	75.0
	× E 4008^{+}		34	87.7	12.6	4.9	64.4
	× VIII 46^{-}		35	76.7	13.3	4.8	55.9
	E 4008^{+} o. p.		31	64.2	12.2	4.2	85.0
	i3)		30	2.9	0.3	3.7	66.7
	× E 4015^{+}		33	81.3	12.8	4.4	64.4
	× VIII 46^{-}		32	65.3	11.9	3.9	67.5
	VIII 46^{-} o. p.		36	78.3	12.3	4.6	68.7
	i		37	54.2	9.1	4.4	64.7
	× E 4015^{+}		38	83.5	15.5	4.4	86.3
	× VIII 47^{-}		38	47.0	7.4	4.7	68.4
	VIII 47^{-} o. p.		32	66.3	13.9	4.4	50.2
Ånge	Y 4015^{+} o. p.	1948	32	72.2	12.1	4.9	
	× Å 2^{+}		32	78.9	13.9	5.1	48.7
	× Å 4^{-}		32	86.9	13.2	5.1	57.3
	Å 2^{+} o. p.	1949	48 4)	79.0	16.0	6.4	69.6
	× Y 4015^{+}		34	54.7	7.5	5.0	71.0
	Å 3^{-} o. p.		34	77.6	14.5	5.4	56.0
	i		32	8.1	1.2	4.6	48.1
	× Å 4^{-}		33	62.3	7.4	6.2	72.9
	Å 4^{-} o. p.	1948	37	71.7	4.9	5.6	82.9
	× E 4015^{+}		38	59.3	4.3	5.7	44.0
	× Å 3^{-}		35	90.9	10.2	5.4	75.6
Värmland	S 3001^{+} o. p		36			4.6	77.2
	i		36				
	S 3002^{+} o. p.		27				
	i		27				
	S 3003^{+} o. p.		23				
	i		25				
Vuollerim	BD 4016^{+} i	1949	29	10.6	0.3	5.7	70.0

1) Open pollinated. 2) Selfed. 3) Not included in later analyses. 4) Four cones only.

seed production after selfing than the trees at Boxholm. Tree BD 4016^{+} at Vuollerim equals tree Y 4015^{+} at Ånge in this respect. Seeds from trees with a high selfing ability generally germinate better than the seeds from the other trees.

3) *The seed morphology.* The form and details in the structure of the seeds and the basic colour of the seed coat vary but little in any one tree (Simak, 1953), whereas the size of the seed varies with the external conditions, such as climate, cone size, etc. A summary of the data from the trees used in this investigation is to be found in Plym Forshell's paper of 1953. Significant differences in these characters have been established among the mother trees.

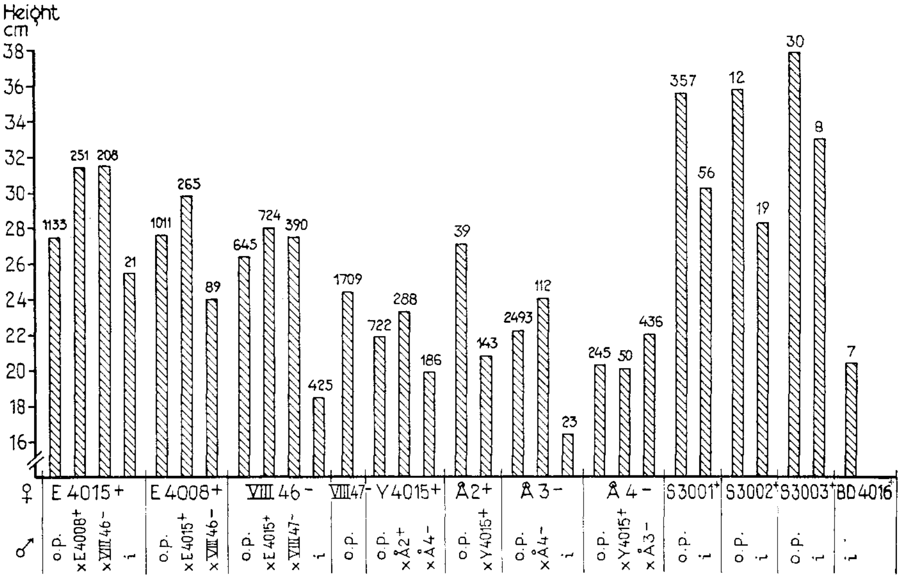


Fig. 5. Average seedling height of the progenies in 1953. The number of seedlings measured given above the bars.

2. *Seedling heights in 1953*

The average seedling height of the progenies in 1953 after three growing seasons is presented in Fig. 5. The main results of this investigation have been discussed earlier (Ehrenberg *et al.*, 1955, pp. 339—346). Hence only a short review will be given here.

In the *open pollinated* materials from Boxholm, the progenies from the plus trees were superior in growth to those obtained from the minus trees. In the Ånge group, too, the plus tree progenies, when grouped together, showed the best growth and decidedly surpassed the minus ones.

The *cross-pollinated* materials were arranged in four groups:

1) plus trees × plus trees
2) plus trees × minus trees
3) minus trees × plus trees, and
4) minus trees × minus trees.

Of the Boxholm progenies, the plus × plus combinations were tallest, distinctly superior to the other three groups. The plus × plus progeny from Ånge equalled the minus × minus combination in height, but was superior to the plus × minus and minus × plus progenies.

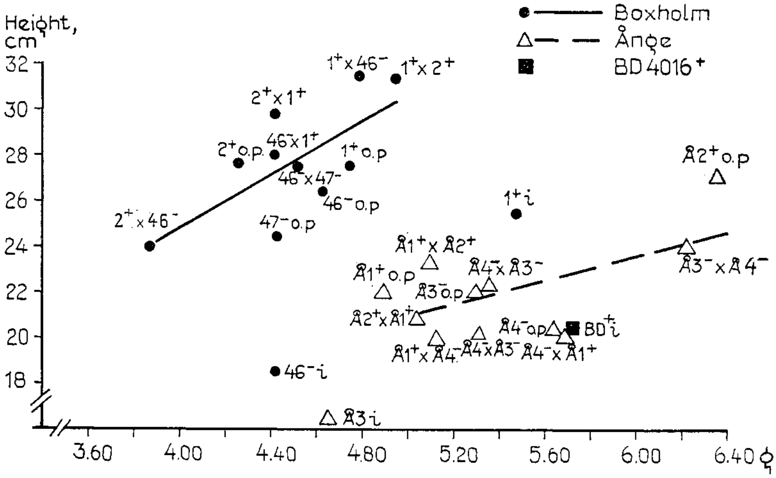


Fig. 6. Relation between 1,000-grain weight and average seedling height in 1953.

The superiority of the plus × plus combinations, when compared with other combinations of the same provenance, is evident. In addition, the greater seedling height of the Boxholm material is of interest, considering the lower average 1,000-grain weight of this material. There is a correlation between grain weight and juvenile growth in Scots pine (EHRENBERG *et al.*, 1955, p. 338). In the material investigated here, a correlation is found only between the average 1,000-grain weight and the average height of the three-year-old seedlings within each provenance group (Fig. 6). The correlation does not hold good when all the progenies are pooled. In spite of their heavier seed, the Ånge progenies were smaller. This inferiority in growth is not due to defective embryo development or poor endosperm, but is determined by the genotypes of the progeny.

The important part played by the genetic factors in the height of the seedlings is further stressed by the comparatively slow growth of the progenies from the minus trees VIII: 47^- and Å 4^- after open pollination. Both trees have rather high 1,000-grain weight. The conclusion was drawn that the inferior growth of many minus trees—"the minus type of growth"—is genotypically conditioned and is often apparent already at a juvenile stage.

The seven *progenies obtained after forced self-fertilization* were markedly retarded in growth—on an average by about 20 per cent—in comparison with materials obtained after open pollination and cross pollination. The selfed plus tree progenies were less inhibited than those of the minus trees. The differences in growth rate between the various pollination types and between selfed progenies from plus trees and minus trees are not correlated with differences in seed weight. As previously mentioned, the 1,000-grain weight is characteristic for a mother tree and is strongly correlated with the cone weight (PLYM FORSHELL, 1953). This also applies to seeds obtained after selfing, their 1,000-grain weight being equal to that of seeds obtained from cones of the same size after open pollination or after crossings (*cf.* BINGHAM and SQUILLACE, 1955). Hereditary factors with a semilethal or viability-reducing effect were assumed to be more frequent in the minus trees than in the plus trees. Some of these factors may be effective also in the heterozygous state. Such factors are active also at early stages of embryo development, as evidenced from the high percentage of seeds with poor embryos and endosperm (embryo class II—III) found in selfed material. These seeds usually develop into weak and slow-growing trees. The conclusions drawn were as follows: Self-fertilization seems to lead to more disastrous effects on embryo development in the minus trees than in the plus trees. Hereditary factors are largely responsible for the "minus type of growth". Progenies of minus trees obtained after open and cross pollination as well as after selfing often show a stunted juvenile growth. Progenies obtained after self-fertilization of plus trees are on an average less affected by inbreeding than those of minus trees.

A few more facts that were not discussed in the previous paper may be added here.

The 1,000-grain weights of the different combinations from tree Y 4015^+ were about equal. The same was the case with the seed lots from the tree Å 4^- whereas the values for the trees Å 2^+ and Å 3^- differed from one combination to another.

The variation in the grain weight in Å 2^+ is no doubt a consequence of the striking differences between the cone lengths of the two combinations in the year of cone collection (*cf.* Table 4). The cones obtained from Å 3^- after selfing were considerably smaller than those obtained after open pollination and crossing. This in turn caused a low 1,000-grain weight of the seeds produced after selfing. Dissimilarities in cone length, however, cannot explain the differences in 1,000-grain weight between the other two combinations (Å 3^- o. p. and Å $3^- \times$ Å 4^-).

Concerning the four-year-old seedlings (1953) obtained from three of the Scots pine trees in the province of Värmland, there are no data available except on cone length and seedling height, and — for the tree S 3001^+ — on germinability of the seed and 1,000-grain weight. A slight negative correla-

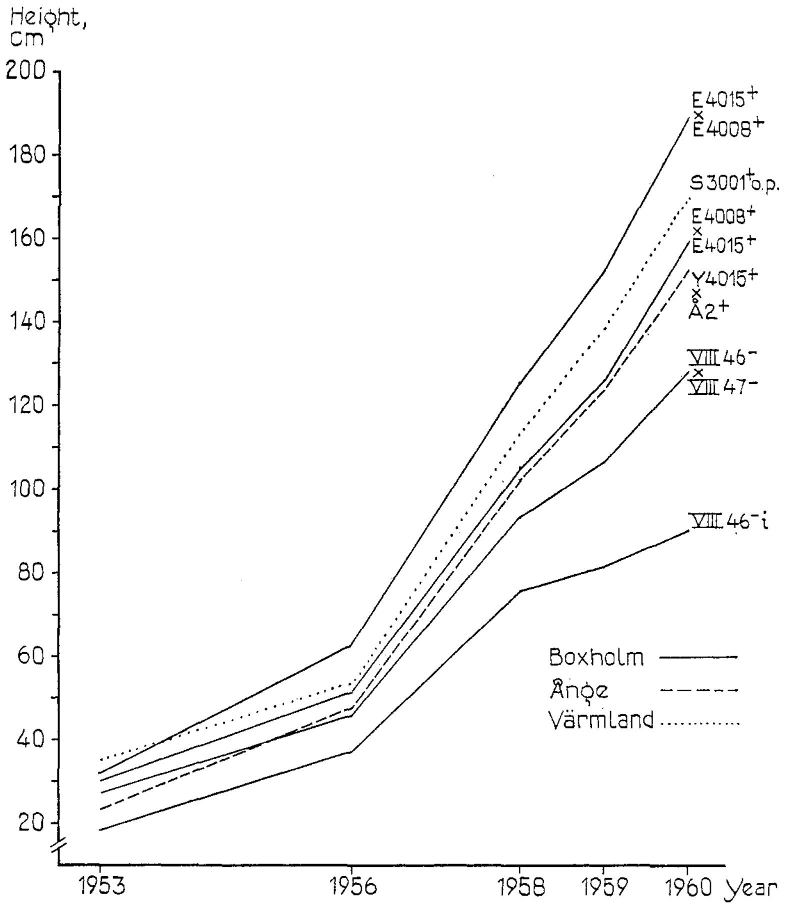


Fig. 7. *Experiment X.* Mean heights of the progenies in the years 1953, 1956 and 1958 to 1960.

tion appears between cone length and seedling height. This negative correlation is spurious, however, and is due to the fact that the progenies obtained from S 3003+ after open pollination and selfing were taller than those of the other four progenies, in spite of the small cones of S 3003+ (*cf.* SIMAK, 1953).

3. Properties analyzed in 1957 to 1960

a) *Height (H)*

The height values of the six (experiment X), eight, nine, and ten-year-old progenies (experiments X, G, and O) are presented in Tables 5, 6 and I (see appendix) and in Figures 7, 8 and 10—12.

Table 5. Mean heights of the progenies in 1956 to 1960.

Experiment	Combination	Year							
		1956		1958		1959		1960	
		Number of trees	Height (cm)	Number of trees	Height (cm)	Number of trees	Height (cm)	Number of trees	Height (cm)
X	E 4015$^+$ × E 4008$^+$	210	62.8 ± 0.90	206	125.6 ± 1.65	208	152.2 ± 2.11	206	189.3 ± 2.77
	E 4008$^+$ × E 4015$^+$	200	51.1 ± 0.84	185	105.5 ± 1.75	193	126.2 ± 2.29	193	159.6 ± 2.85
	VIII 46$^-$ i.	192	37.1 ± 0.72	111	75.9 ± 1.52	131	81.4 ± 1.86	127	90.5 ± 2.22
	VIII 46$^-$ × VIII 47$^-$	210	45.9 ± 0.79	180	93.3 ± 1.67	194	106.9 ± 2.20	192	128.3 ± 2.57
	Y 4015$^+$ × Å 2$^+$	208	47.5 ± 0.84	204	102.5 ± 1.70	208	124.5 ± 2.11	206	153.1 ± 2.50
	S 3001$^+$ o. p.	210	53.8 ± 0.80	198	113.7 ± 2.08	205	138.9 ± 2.47	202	171.1 ± 2.92
G	E 4015$^+$ o. p.			616	106.6 ± 1.02	631	129.2 ± 1.32	628	161.5 ± 2.17
	E 4008$^+$ o. p.			306	117.2 ± 1.63	313	141.3 ± 2.20	310	177.8 ± 2.77
	VIII 46$^-$ × E 4015$^+$			301	105.5 ± 1.35	316	122.3 ± 2.03	313	148.2 ± 2.11
	VIII 46$^-$ o. p.			298	102.3 ± 1.58	312	118.8 ± 2.03	300	144.5 ± 2.28
	VIII 47$^-$ o. p.			568	92.7 ± 1.16	609	108.5 ± 1.53	597	135.0 ± 1.81
	Y 4015$^+$ o. p.			311	103.8 ± 1.38	314	124.5 ± 1.70	312	153.6 ± 2.06
	Å 3$^-$ o. p.			303	97.8 ± 1.36	306	116.0 ± 2.06	303	142.1 ± 2.46
	Å 4$^-$ × Å 3$^-$			320	104.8 ± 1.27	323	126.5 ± 1.56	321	153.8 ± 1.76

Table 6. Heights of the progenies. Significance of the differences between progenies and between blocks.

Experiment	Year	Source of variation	df	Mean Square	F
X	1958[1])	Progenies	5	601.64	20.31***
		Blocks	2	410.39	13.86**
		Error	9	29.62	
	1959[1])	Progenies	5	1,241.29	27.51***
		Blocks	2	945.89	20.97***
		Error	9	45.11	
	1960[1])	Progenies	5	2,392.81	21.67***
		Blocks	2	1,727.68	15.65**
		Error	9	110.42	
G	1958	Progenies	9	360.59	3.18**
		Blocks	3	1,186.54	10.46***
		Error	27	113.44	
	1959	Progenies	9	681.40	3.17*
		Blocks	3	2,279.94	10.60***
		Error	27	215.16	
	1960	Progenies	9	1,089.58	3.38**
		Blocks	3	3,328.53	10.34***
		Error	27	321.89	

[1]) Corrected for missing value.

In *experiment X*, which includes both a progeny obtained after inbreeding and a progeny one year older than the rest of the material, thus a somewhat heterogeneous material, the differences in height among the progenies were great from the very beginning (Table 5, Fig. 7). The mutual order in height among the progenies was constant from 1953 to 1960, with the exception of the minus crossing VIII: 46^- × VIII: 47^- which moved down from fourth to fifth place between the age of three and six years, and the o. p. progeny of S 3001^+, which declined in growth rate and fell to second place. Statistically significant differences in height between the progenies were established in the years 1958—1960 (Table 6). The mean height of the progeny obtained from the minus crossing VIII: 46^- × VIII: 47^- was lower than that of all the others, except for the selfed progeny VIII: 46^- *i*, the growth of which was even slower. The differences between the blocks within the progenies were significant every year (Table 6). They reveal considerable influence of the varying site conditions.

Experiment G (Fig. 8) is of a somewhat different composition. It contains progenies of the four pine trees at Boxholm after open pollination (two plus trees and two minus trees), of one plus tree and one minus tree at

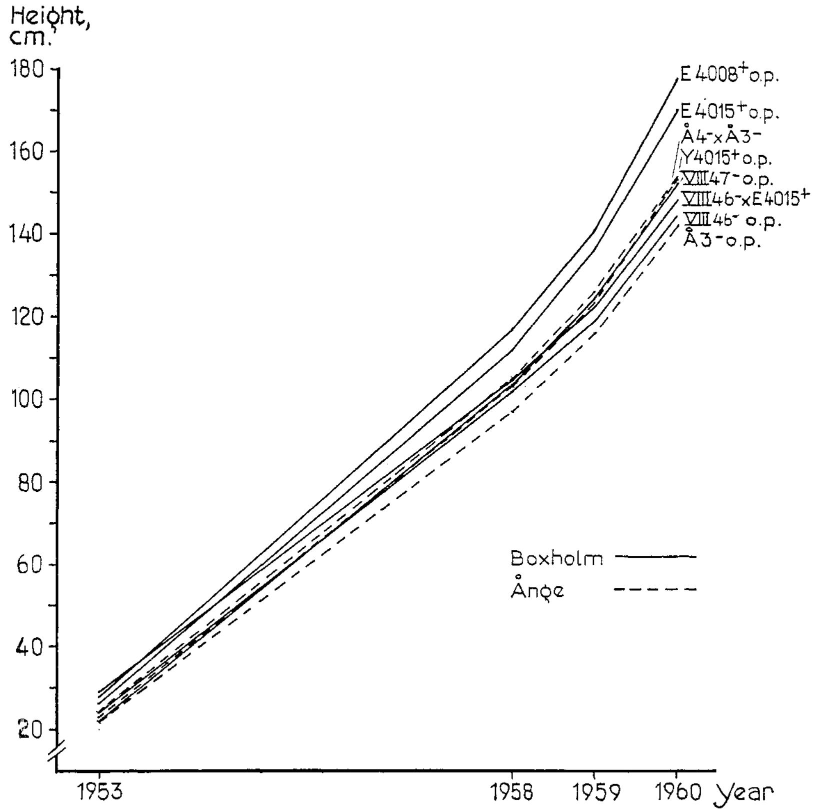


Fig. 8. *Experiment G.* Mean heights of the progenies in the years 1953 and 1958 to 1960.

Ånge, as well as of one minus × plus crossing (Boxholm), and one minus × minus crossing (Ånge).

On an average there was no difference between the Boxholm and Ånge groups in regard to height during the last three years of measurement, *i.e.* the mean values of the height of the Ånge progenies ranked between the lowest (— o.p.) and the second highest (+ o.p.) of the Boxholm progenies. This is in contrast to the order in 1953, the year prior to planting out in the field, when the mean height of the Ånge seedlings was about 83 per cent of that of the Boxholm material.

The differences among the Boxholm progenies were not significant in 1958 and 1959. In 1960 the two plus progenies (o.p.) showed superior growth, and there was a distinct difference in their mean values of height and those of the other three progenies ($P = 0.05 - 0.01$).

The ranking in height of the progenies was the same during the last three

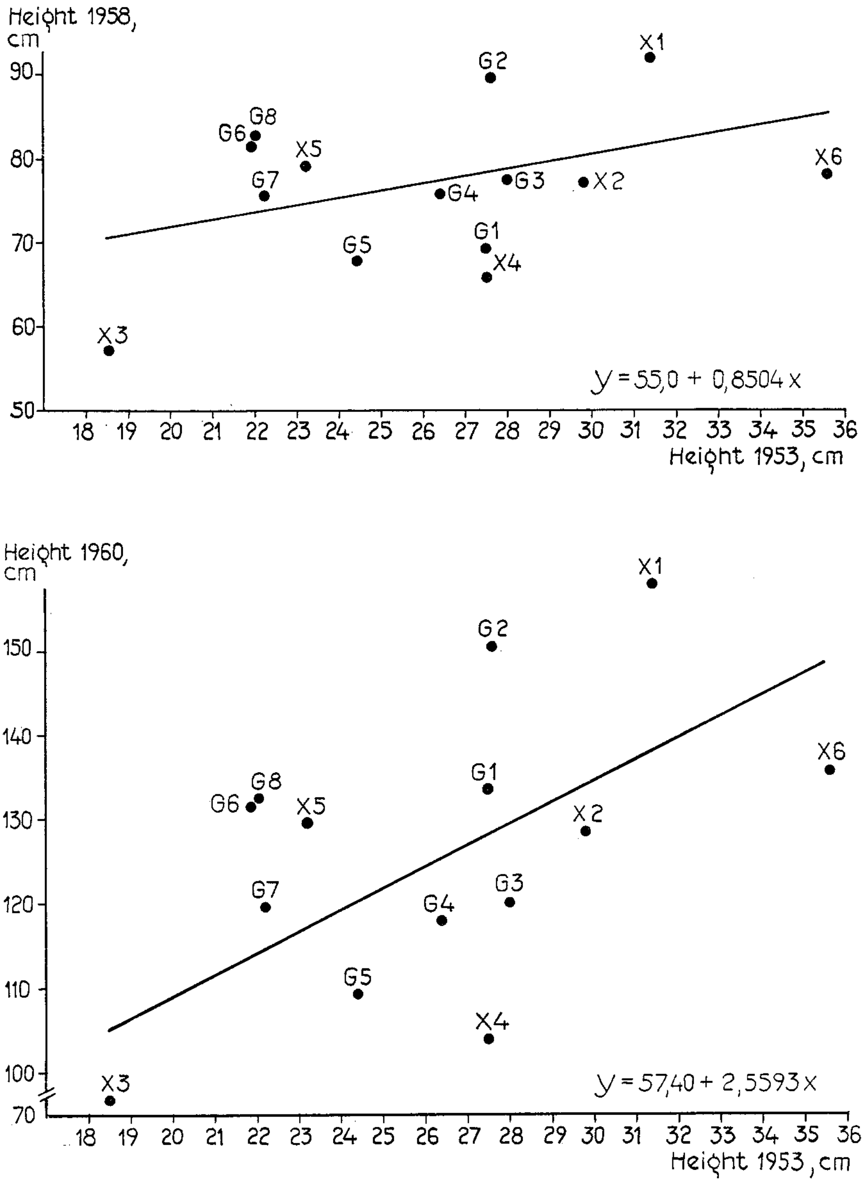
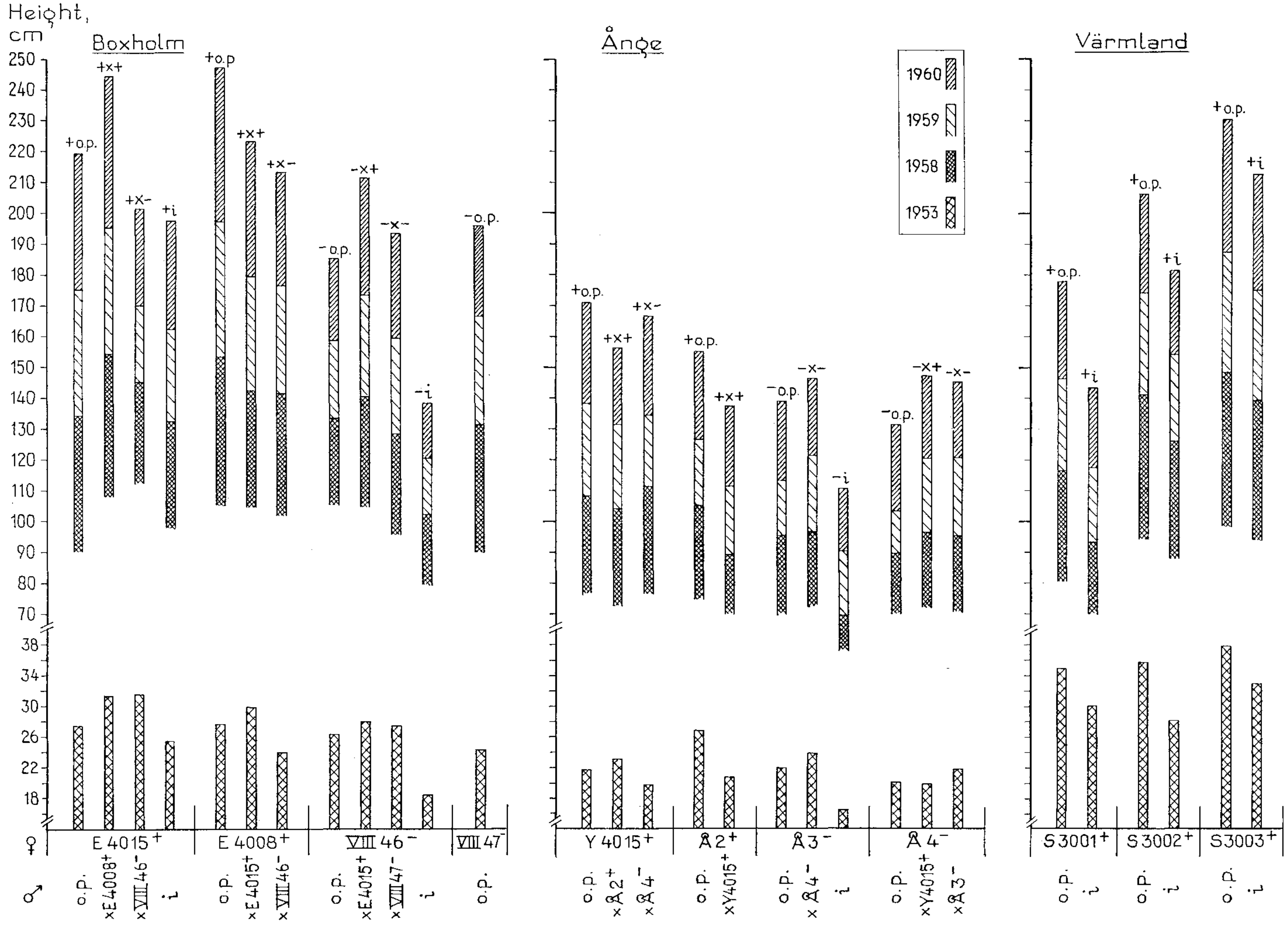


Fig. 9. Relation between mean heights of the progenies in 1953 and the increase in height from 1953 to 1958 (above) and from 1953 to 1960 (below). X1: E 4015^+ × E 4008^+, X2: E 4008^+ × E 4015^+, X3: VIII 46^- *i*, X4: VIII 46^- × VIII 47^-, X5: Y 4015^+ × Å 2^+, X6: S 3001^+ o.p., G1: E 4015^+ o.p., G2: E 4008^+ o.p., G3: VIII 46^- × E 4015^+, G4: VIII: 46^-o.p., G5: VIII 47^- o.p., G6: Y 4015^+ o.p., G7: Å 3^- o.p., G8: Å4^- × Å3^-.



Figs. 10—12. *Experiment O.* Mean heights of the progenies in the years 1953 and 1958 to 1960. 10. Boxholm progenies. 11. Ånge progenies. 12. Värmland progenies.

years of measurements, *viz.* E 4008^+ o.p. > E 4015^+ o.p. > VIII: 47^- o.p. > VIII: 46^- × E 4015^+ > VIII: 46^- o.p. The crossing minus × plus thus ranked between the two minus progenies.

The mean height of the minus-crossing Å 4^- × Å 3^- in the Ånge group was slightly higher than that of the plus tree progeny Y 4015^+ o.p. from 1953 up to 1960, when the mean values were equal. The third progeny in this group, Å 3^- o. p., was slightly superior in height in 1953. Since 1958, however, this progeny has been lagging behind the others by a few centimetres every year. The difference in 1960, however, was not yet significant.

As mentioned previously, the differences between the blocks were great in both experiments, and the variation between the plots of each progeny was also considerable. A striking example of the influence of the site variation is shown by the duplicated progenies E 4015^+ o.p. and VIII: 47^- o.p. Although large, the difference between the mean height values of the parallel plots (*a* and *b*) of the former progeny was not significant. In the latter progeny, however, the plots differed significantly ($P = 0.001$ in 1960).

A rather strong correlation was established between the mean heights of the progenies in 1953 on the one hand, and in 1958 and 1960 on the other ($r = 0.70$ and 0.67 respectively), when all the progenies in the two *experiments X and G* were considered together (Fig. 9). Thus, *on an average*, the most rapidly growing progenies in 1953 were also the tallest ones in 1960. The irregularities that occurred, however, were great enough anyhow, so that any attempt to estimate which of the progenies in the nursery beds would be the best growers in the years to follow would in many cases have failed. For instance, the four progenies E 4008^+ o. p., E 4015^+ o. p., VIII: 46^- × E 4015^+ and VIII: 46^- × VIII: 47^- were of about the same height in the nursery, and intermediate as compared with the rest. Seven years later, in 1960, the progeny E 4008^+ o.p. was next tallest of all the progenies, and the minus crossing next lowest, the difference in their mean heights having increased by about 50 cm. A comparison of the progenies VIII: 46^- × E 4015^+ and Y 4015^+ o.p. offers another example. The latter was the lowest of the two progenies in 1953, on an average six centimetres lower. In 1960 it was superior in height. If the material had been sown with replications in the nursery according to a proper design, the ranking of the three-year-old progenies might have been different and have given a more reliable indication of the inherent growth rates of the individual progenies.

With regard to the progenies of the *observation experiment O*, measurements were made in 1958, 1959, and 1960 (Table I [see appendix], Figs. 10—12). As the number of trees is small, and since the design of this experiment does not allow any statistical analysis, only the general trends in the mutual order of the progenies will be discussed.

Ten progenies obtained after crossing, and two progenies produced by selfing at Boxholm are presented (Fig. 10). The progenies obtained from the four plus-tree combinations E 4008^{+} o.p., E 4015^{+} × E 4008^{+}, E 4008^{+} × E 4015^{+}, and E 4015^{+} o.p. were superior in height, and they have remained in the order now mentioned for the last three years (1958—1960). Next in order came the crossings plus × minus and their reciprocal combination, closely followed by the minus-tree progeny VIII: 47^{-} o.p. and the only minus × minus crossing VIII: 46^{-} × VIII: 47^{-}. The lowest mean value was found in the progeny of the minus tree VIII: 46^{-} o.p. Of the two progenies obtained after selfing, E 4015^{+} *i* and VIII: 46^{-} *i*, the former showed relatively good growth, its mean height slightly exceeding that of VIII: 47^{-} o.p. in 1960. The latter, VIII: 46^{-} *i*, however, had a remarkably slow growth, its mean height in 1960 being less than 75 per cent of that achieved by the progenies obtained from the same tree after open pollination.

The mutual order of the progenies in respect of mean height varied in the different years of measurement. The plus-tree progenies (+ × +, + × −, − × +, + o.p.), however, were with one exception the tallest of the lot during the entire period investigated (seven years). The crossing E 4008^{+} × VIII: 46^{-} constituted an exception. It showed the lowest mean height value in 1953, but ranked fifth in 1960 (*cf.* Fig. 6, seedling height in relation to 1,000-grain weight). Two other progenies obtained from the tree E 4008^{+} — used either as mother or father tree — in combination with E 4015^{+} (+ × +) ranked second and third both in 1953 and in 1960. The fourth progeny of this tree, E 4008^{+} o.p., ranked sixth at an age of three years, whereas in 1960 it was the tallest progeny of all. Four other combinations in which VIII: 46^{-} was included as a parent tree showed quite another trend of growth. The progenies grew fairly rapidly up to 1953, when their order of ranking was 1 (+ × −), 4 (− × +), 7 (− × −), and 8 (− o.p.), but their subsequent development was quite slow. In 1960 they ranked 7, 6, 10, and 11, respectively. The growth of the progeny obtained from this tree after inbreeding was markedly slow. The height of the other progeny obtained after inbreeding, E 4015^{+} *i*, was lower than that of the progenies obtained from the same tree after crossing, but higher than those of the combinations − × − and − o.p. (1960).

The progenies obtained when the plus tree E 4008^{+} was used as one of the parent trees were thus superior in height during the years 1958—1960. The trees with the comparatively poorest growth originated from the minus tree VIII: 46^{-}. The same relationship was observed in field experiment G (*cf.* Fig. 8), in which some of these combinations participated.

The Ånge group comprises eleven progenies (Fig. 11). Of these the combinations + o.p., + × +, + × −, and − × + were the tallest (except for Å 2^{+} × Y 4015^{+} which was planted on a marshy part of the experimental field). Next in height were the two progenies obtained after the crossing − × −. The poorest of the progenies were the − o.p. As in the Boxholm group, the order in mean height of the progenies was largely constant during the last three years (1958—1960), though completely reversed in comparison with the status of 1953. The progenies Å 2^{+} o.p. and Å 3^{-} × Å 4^{-} (high 1,000-grain weight, *cf.* Table 4), which at the age of three were by far the tallest ones, ranked fourth and sixth respectively at the age of ten. While ranking only sixth in 1953, the progeny Y 4015^{+} o.p. showed the greatest mean height of all in 1960, and the crossing Y 4015^{+} × Å 4^{-}, which was eleventh in 1953, was the next tallest in 1960. The progeny obtained after inbreeding, Å 3^{-} *i*, was still inferior to the others.

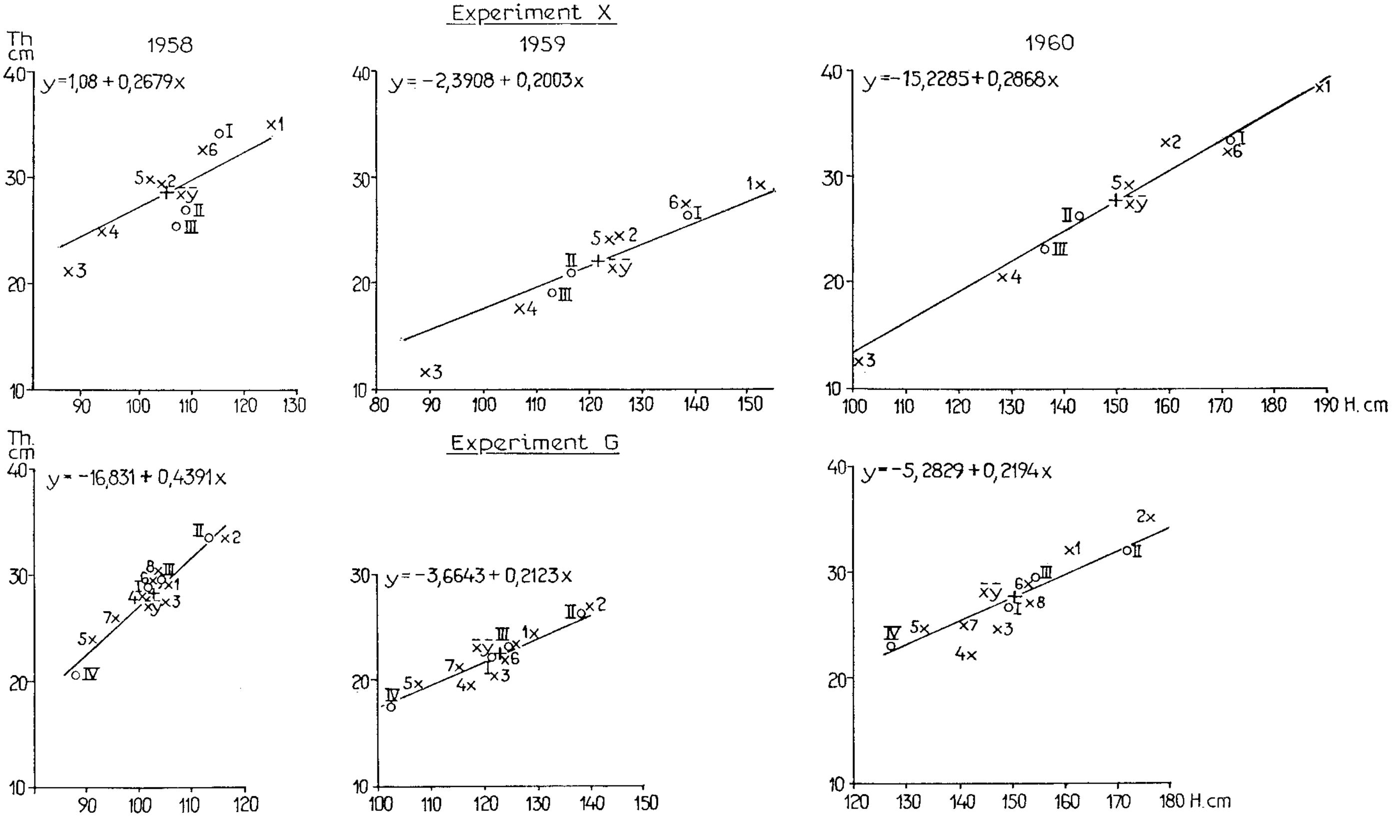
The third group in the observation experiment comprises progenies obtained after open pollination and selfing from three plus trees in the province of Värmland (Fig. 12). In 1953 the ranking of the progenies in the nursery was as follows: S 3003^{+} o.p. > S 3002^{+} o.p. > S 3001^{+} o.p. > S 3003^{+} *i* > S 3001^{+} *i* > S 3002^{+} *i*.

When measured in 1960, they ranked differently. The three progenies obtained after selfing were still shorter than the progenies obtained from the same mother tree after open pollination, but the progeny S 3003^{+} *i* was taller than both the progenies (o.p. and *i*) from S 3002^{+} and these in turn taller than the two progenies from S 3001^{+}. Thus, the highest progeny obtained after inbreeding originated from the tree with the tallest o.p. progeny.

b) *The length of the terminal shoot (Th)*

A strong correlation between the length of the terminal shoot and the height of the young tree was obtained from the measurements made in 1958 ($r = 0.83$ in experiment X, $r = 0.97$ in experiment G, all specimens). The length of the terminal shoot thus varied parallel with the tree height. Strongly significant differences between the mean shoot values were obtained in experiment X, slightly significant differences in experiment G, and strongly significant differences between the blocks in both the X and G experiments (Table II, 23 and 24).

The regression of terminal shoot length on the mean height of the individual progenies is shown in Fig. 13. No significant difference was found between the slopes of the regression lines, *i.e.* the average increase in the terminal shoot length at an one-centimetre increase in the tree height of the progenies in each experiment was approximately equal in 1958 (0.27 cm in experiment X, 0.44 cm in experiment G).



13. Average regression of terminal shoot length on tree height in 1958 to 1960. Experiment X 1: E 4015^{+} × E 4008^{+}, 2: E 4008^{+} × E 4015^{+}, 3: VIII 46^{-} i, 4: VIII 46^{-} × VIII 47^{-}, 5: Y 4015^{+} × Å 2^{+}, 6: S 3001^{+} o.p. Experiment G. 1: E 4015^{+} o.p., 2: E 4008^{+} o.p., 3: VIII 46^{-} × E 4015^{+}, 4: VIII 46^{-} o.p., 5: VIII 47^{-} o.p., 6: Y 4015^{+} o.p., 7: Å 3^{-} o.p., 8: Å 4^{-} × Å 3^{-}. I—IV: block numbers.

Table 7. Heights (x) and length of terminal shoots (y). Comparison between adjusted progeny means of y.

Experiment	Year	Source of variation	df	Mean Square	F
X	1958	Progenies Error	5 8	3.519 4.676	0.752
	1959	Progenies Error	5 8	8.102 0.730	11.099**
	1960	Progenies Error	5 8	6.871 2.276	3.02
G	1958	Progenies Error	7 28	4.669 1.953	2.391*
	1959	Progenies Error	7 28	4.700 0.626	7.508***
	1960	Progenies Error	7 28	16.609 3.038	5.467***

The differences between the progenies in the mean length of the annual shoots not only depend on the correlation between annual shoot length and tree height, but must also be ascribed to inherent differences (experiment X: F = 0.752, experiment G: F = 2.391*, Table 7). In *experiment X* the mean value of the terminal shoot length of the progeny obtained by selfing, VIII: 46^- *i*, deviated distinctly from the other mean values. In *experiment G* the case was the same with the progeny VIII: $46^- \times$ E 4015^+. In both instances, as seen, VIII: 46^- was used as the mother tree.

The development of the progenies in various respects with increasing age is shown by the results of measurements in 1959 and 1960. Strongly significant differences between the progenies as regards the length of the terminal shoot were evident in both years in both experiments. The block differences were still great (Tables II, 23 and 24).

The correlation between the tree height and terminal shoot length continued to be strong (experiment X: r = 0.87 in 1959, and 0.87 in 1960; experiment G: r = 0.88 in 1959, and 0.85 in 1960).

As in 1958, the differences in the slopes of the regression lines in *experiment X* were not significant in 1959. The average increase in terminal shoot length at one centimetre increase in tree height amounted to 0.21 cm in the six progenies of the experiment.

In *experiment G* there were slightly significant differences between the slopes of the regression lines (F = 2.81*). The progenies of VIII: $46^-(- \times +$,

– o.p.), and the minus crossing Å 4^- × Å 3^- increased their terminal shoot length at increasing tree height slightly less than the other progenies.

Irrespective of the correlation with the tree height, the differences in the terminal shoot length of the progenies were strongly significant in both experiments (Table 7). The lowest mean values of the terminal shoot length were found among the progenies of VIII: 46^- in all the combinations (selfing, – × – in experiment X; – × + and – o.p. in experiment G).

In 1960 the increase in the terminal shoot length with increasing tree height was significantly lower in the progenies of the minus tree VIII: 46^- (– × –, – *i*) than in the four plus-tree progenies in *experiment X* (F = 4.38*). The regression lines of the reciprocal combinations between the Boxholm trees E 4015^+ and E 4008^+ were almost parallel, and slightly steeper than the corresponding lines for Y 4015^+ × Å 2^+ and S 3001^+ o.p. The differences in slope, however, were not significant.

The differentiation between the progenies that was slightly discernible in 1958, resulted in 1960 in a clear division of the material into two groups of progenies: those from VIII: 46^- on the one hand and the plus-tree progenies on the other.

The same trend appeared in *experiment G.* The differentiation of the progenies in respect of the differences in the regression of length of the terminal shoots on tree height was more distinct in the ten-year-old (F = 4.43***) than in the eight-year-old (F = 1.48) material. Moreover, the change in the mutual order between the progenies, which was slight in 1959, was more distinct in 1960, *i.e.* the grouping of the progenies according to the parent-tree types was clear (Fig. 13). The smallest increase in terminal shoot length with rising tree height was shown by the progenies of the minus tree VIII: 46^- (– o.p. and – × +) and by the minus crossing Å 4^- × Å 3^-. The increase was greatest in the plus-tree progenies obtained after open pollination at Boxholm (E 4015^+, E 4008^+) and Ånge (Y4015^+). In both experiments that part of the variation in the terminal shoot length which did not depend on the variation in height was great, and the differences between the progenies were statistically significant (Table 7). Here, too, the progenies of the minus tree VIII:46^- formed a deviating group. The minus crossing Å 4^- × Å 3^- also had a lower mean value of the terminal shoot length than *e.g.* Y 4015^+ o.p. at an equal mean height.

c) *Branch length* (*Brl*)

The evaluation of the branch length in the various whorls was made on the basis of measurements of the three longest branches in each whorl, *i.e.* the branches that most likely would be the last ones to dry and fall off. The

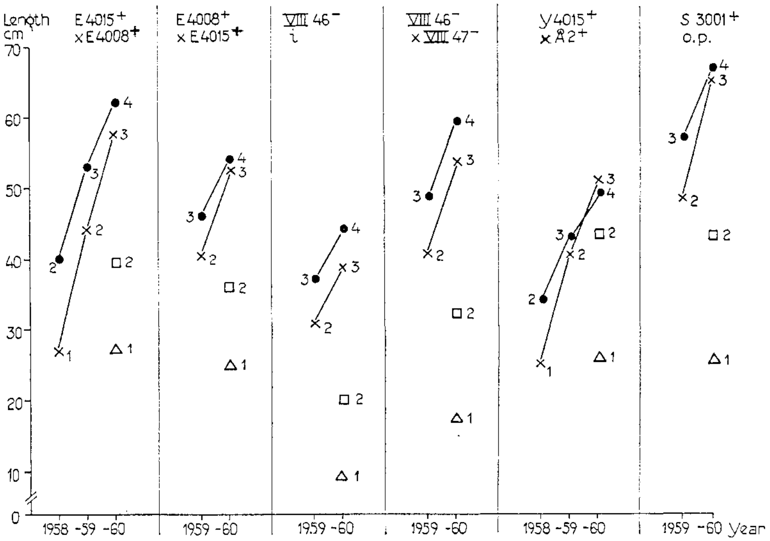


Fig. 14. *Experiment X.* Length of branches in different whorls in 1958 to 1960. × = whorl 1 in 1958 = whorl 2 in 1959 = whorl 3 in 1960. ● = whorl 2 in 1958 = whorl 3 in 1959 = whorl 4 in 1960. △ = whorl 1 in 1960. □ = whorl 2 in 1960.

one-year-old branches in whorl 1 varied only slightly in length. A clear differentiation into stronger and weaker branches was first visible in whorl 2, and increased in the older whorls. The mean length of the three branches measured in each whorl was used for a comparison of the progenies and for an evaluation of the relationship between tree height and branch length.

In 1958 the branches were measured in whorls 1 and 2, in 1959 in whorls 2 and 3, and in 1960 in whorls 1 to 4. Each progeny is represented by 3 × 20 = 60 trees in experiment X and by 4 × 20 = 80 trees in experiment G. The crossing combinations measured and the results of measurements in the different years are presented in Tables 8—10, 23, 24 and IV—VI and in Figures 14—18.

The absolute branch length varied strongly within each progeny. The correlation between tree height and branch length in the individual trees of a progeny is evident. The variation in the branch length is therefore a natural consequence of the variation in the tree height. The branch length is equally as sensitive as the tree height to variations in site conditions within and between plots and blocks (Tables 23, 24 and IV).

The two progenies in *experiment X*, which were first measured in detail in 1958 (Fig. 14), were produced by crossings between plus trees, in one case

Table 8. Experiment X. Summary of correlations between tree height and branch length in 1958 and 1960. Correlation coefficients (r).

Combination	Correlation coefficients (r)					
	1958 Whorl No.		1960 Whorl No.			
	1	2	1	2	3	4
E 4015^{+} × E 4008^{+}	0.45	0.79	0.63	0.64	0.60	0.46
E 4008^{+} × E 4015^{+}			0.68	0.69	0.73	0.71
VIII 46^{-} i			0.37	0.57	0.69	0.83
VIII 46^{-} × VIII 47^{-}			0.70	0.76	0.81	0.85
Y 4015^{+} × Å 2^{+}	0.69	0.78	0.71	0.72	0.75	0.72
S 3001^{+} o.p.			0.41	0.45	0.42	0.45

r value required for	df = 2	df = 6
5 % level	0.950	0.707
1 % level	0.990	0.834

between the trees E 4015^{+} and E 4008^{+}, both from Boxholm, and in the second case between the trees Y 4015^{+} and Å 2^{+} from Ånge. They were thus of the same crossing type, although of different provenance. There was no significant difference between the two progenies in mean tree height (20 trees per plot, Table III) nor in branch length of whorl 1. In whorl 2 the difference between the mean values was slightly significant. When tested by analysis of variance, the ratio between tree height and branch length $\left(\frac{H}{Brl}\right)$ was found to be the same in both progenies (Table 23).

The measurements made in the following years (1959 and 1960) gave a slightly different picture of the relationships between these two progenies. In 1959 the differences in height were significant, but in the second whorl the branch lengths as well as the ratios of height to branch length were equal. In whorl 3 the cross E 4015^{+} × E 4008^{+} had significantly longer branches than the Ånge progeny both as regards absolute length and the ratio $\frac{H}{Brl}$. In 1960, finally, the differences in absolute branch length had increased in all four whorls, whereas the ratio of tree height over branch length was equal (Table V).

Consequently these two progenies, both of them results of the same pollination type, $+ \times +$, showed a similar development in tree height and branch length up to their ninth year, when definite differences in the absolute branch length appeared.

Other progenies included in experiment X, and measured in 1959 and 1960, are the plus-tree combination E 4008^{+} × E 4015^{+}, one progeny obtained

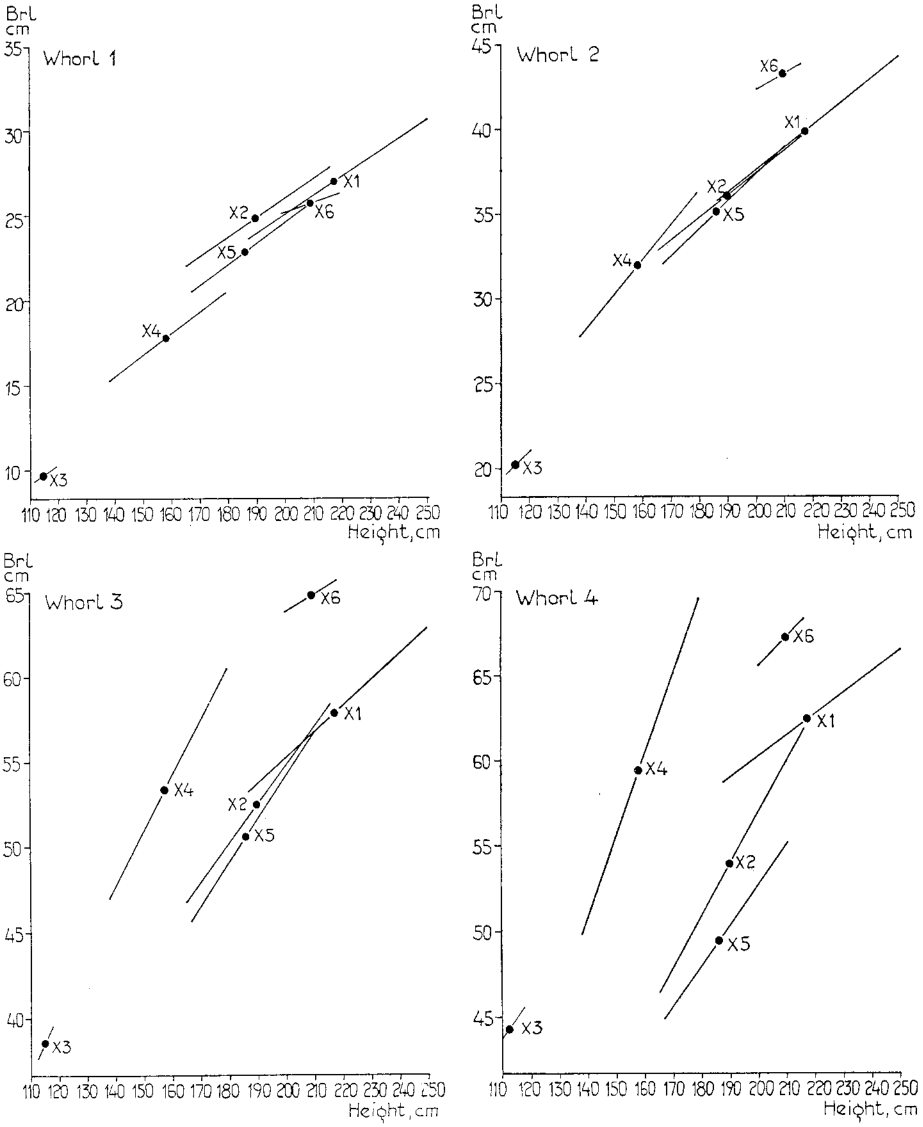


Fig. 15. *Experiment X.* Regression of mean branch length on mean tree height in 1960. X1: E 4015^{+} × E 4008^{+}, X2: E 4008^{+} × E $4015^{\div}$, X3: VIII 46^{-} *i*, X4: VIII 46^{-} × VIII 47^{-}, X5: Y 4015^{+} × Å $2^{\div}$, X6: S 3001^{+} o.p.

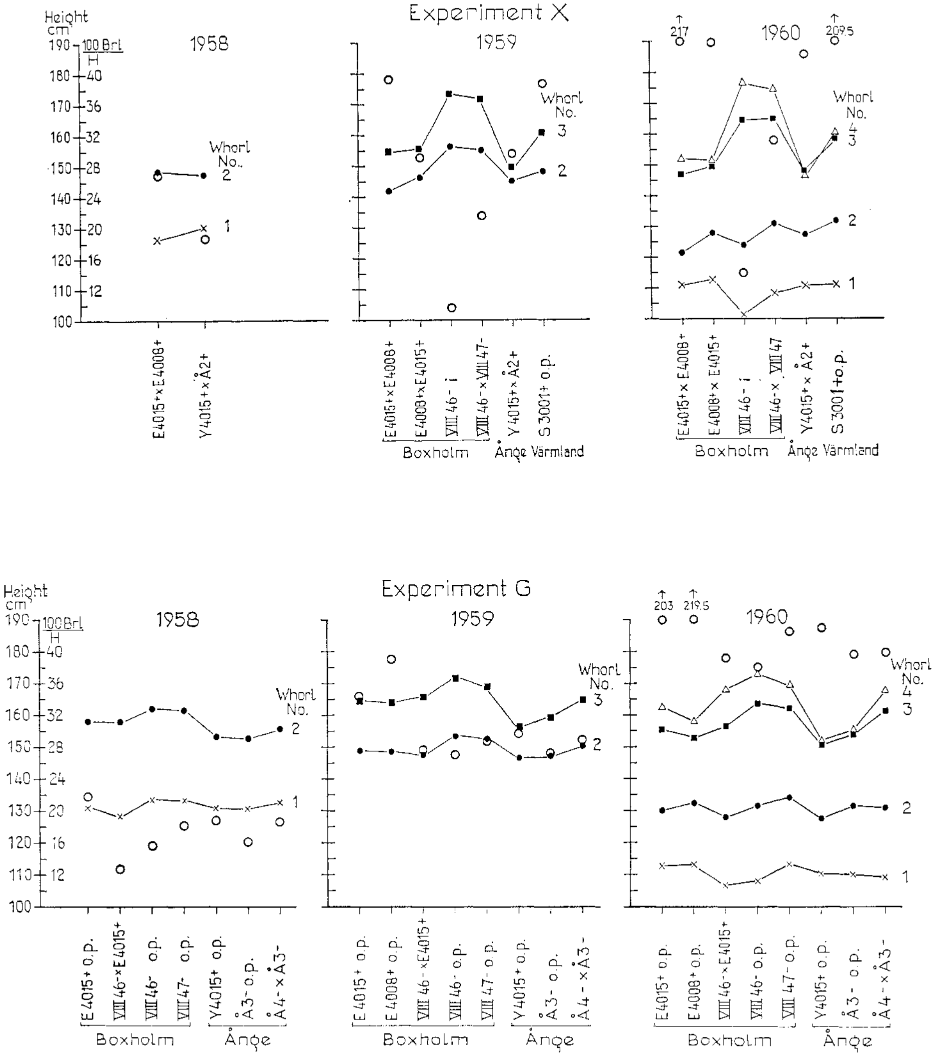


Fig. 16. Ratios between branch length and tree height $\left(\frac{100\ \mathrm{Brl}}{\mathrm{H}}\right)$ in different whorls in 1958 to 1960. ○ = Mean tree height.

from the tree S 3001$^+$ after open pollination, one from the minus tree VIII: 46$^-$ after selfing, and finally one minus × minus crossing, VIII: 46$^-$ × VIII: 47$^-$ (Fig. 14). Significant differences between the progenies in tree height and absolute branch length appeared in both years (Table 23). Progenies that were superior in height also had longer branches, while progenies with a slow growth developed shorter branches.

As mentioned above, the branch length was strongly correlated with the tree height. The strength of this relationship varied between the years, as also between the whorls and the progenies. The difference between the progenies was evident in 1958, and still more striking in 1960. In the last-mentioned year, the strength of the correlation was constant from one whorl to another in the four plus-tree progenies (Table 8). It was considerably weaker in one of the progenies, S 3001^+ o.p. In the minus crossing VIII: 46^- × VIII: 47^-, as well as in the progeny obtained from the same mother tree after selfing, the strength of the correlation increased gradually from whorl 1 to whorl 4. In the last-mentioned progeny the two uppermost whorls showed a particularly weak correlation between the mean branch length and tree height.

For a given whorl the progenies also differed in respect of the average increase in branch length per one centimetre increase in tree height. In 1959 there was no significant difference in the slopes of the regression lines representing whorls 2 and 3. In 1960 (Fig. 15), when the measurements comprised the whorls 1 to 4, no distinct differences occurred in the three uppermost whorls. In whorl 4, however, the two progenies from the minus tree VIII: 46^- deviated from the plus-tree progenies by showing a significantly greater increase in branch length per one centimetre increase of tree height ($P < 0.01$).

A similar grouping of plus-tree progenies on the one hand, and the progenies of the minus tree VIII: 46^- on the other, can be made concerning the relative branch lengths expressed by the ratios of height over branch length (Fig. 16 and Table V). In 1959 the measurements of whorls 2 and 3 produced lower ratios for the minus progenies, *i.e.* the minus progenies had in these whorls longer branches in relation to their height than the plus progenies. The differences were significant ($P < 0.01$, whorl 2; $P < 0.001$, whorl 3). In the last year of measurement (1960), the progenies from VIII: 46^- (selfing and – × –), manifested, in comparison with the plus-tree progenies, a weak height increment in combination with short branches in whorl 1, and rather long branches in the whorls 3 and 4.

Of the plus-tree progenies, S 3001^+ o.p. developed the widest crown, with relatively long and strong branches in the whorls 3 and 4. The plus × plus cross from Ånge, Y 4015^+ × Å 2^+, showed a crown relatively narrow at the base due to the poor growth of the fourth whorl.

In contrast to the tree height and absolute branch length, the ratios $\frac{H}{Brl}$ varied only slightly with the differences in the site conditions ($P>0.05$ for block differences, Table 23).

As early as in 1959 clear differences between the progenies examined in experiment X were found with regard to the branch length of various whorls, the branch length in relation to tree height, and the average increase in branch length per one centimetre increase in height. The differences became greater with increasing age of the trees. In 1960, when the progenies were ten years old, each offspring had developed a characteristic average crown type of its own. The *plus-tree progenies* were characterized by their narrow crowns, where the branch lengths increased greatly from whorl 1 to whorl 3, and less in whorl 4 than in whorl 3. With regard to the relative branch lengths $\left(\frac{H}{Brl}\right)$ in the various whorls, the variation between the plus-tree progenies was slight, except in S 3001^{+} o.p., which had longer branches in the lower whorls than the other progenies. The correlation between branch lengths and tree heights and the regression of the branch lengths over the heights were approximately equal in all these progenies.

The average individual of the *minus crossing* VIII: $46^{-} \times$ VIII: 47^{-} was of an entirely different type. Compared to the plus-tree progenies, its height growth was weaker, the average branch in the whorls 1 and 2 was shorter, and in the whorls 3 and 4 it was longer in relation to the height of the tree. A similar average type was found in the progeny obtained from the same mother tree, VIII: 46^{-}, after selfing. In relation to their height, the young trees had short branches in whorl 1, and very long ones in the whorls 3 and 4. Both these latter progenies developed a dense crown with a wide base, and sharply tapered from the base towards the top.

In *experiment G* the measurements of 1958 comprised four progenies from Boxholm and three from Ånge. No significant differences in the mean heights of the progenies were established this year (Table III). The absolute branch lengths of the whorls 1 and 2 were of the same order of magnitude in all of the seven progenies (Fig. 17 and Tables 24 and IV). No significant differences between the progenies of plus trees and minus trees were found. Nor were any differences between the provenances detected when the Boxholm group of progenies was compared with the Ånge group (Table VI).

Some differentiation between the progenies was noticeable in whorl 3 in 1959. In that year the mean heights also differed to a certain degree. The open-pollinated plus progenies from Boxholm showed longer branches than the minus tree crossings of the same provenance. A slightly significant difference appeared between the Boxholm group and the Ånge group. On an average, the trees in the latter group had shorter branches (Fig. 17).

In 1960 there was a significant difference in the mean height of the progenies, and hence also in the length of their branches. With regard to the branch length of the whorls 1 and 2, the two progenies from VIII: 46^{-}

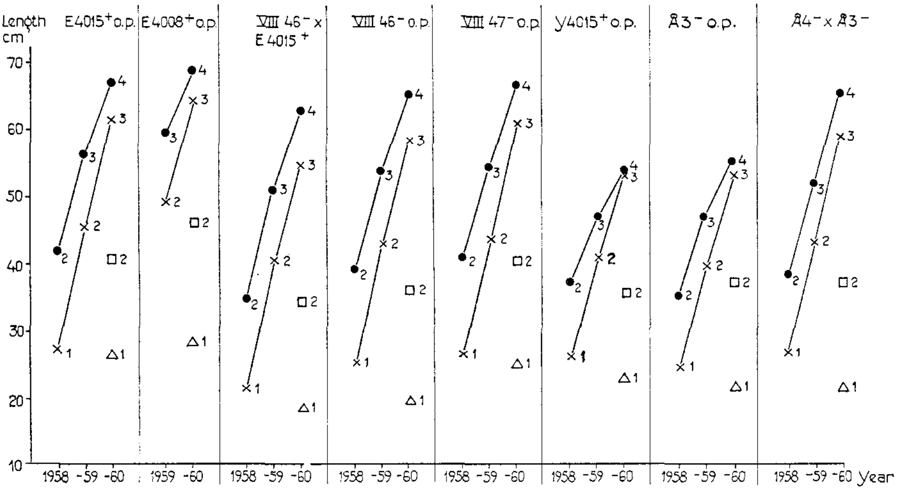


Fig. 17. *Experiment G.* Length of branches in different whorls in 1958 to 1960. x = whorl 1 in 1958 = whorl 2 in 1959 = whorl 3 in 1960. ● = whorl 2 in 1958 = whorl 3 in 1959 = whorl 4 in 1960. △ = whorl 1 in 1960. □ = whorl 2 in 1960.

(– × +, and – o.p.) showed the lowest mean values, and the plus-tree progenies E 4015+ o.p. and E 4008+ o.p. the highest. The corresponding values of the fifth Boxholm progeny, VIII: 47- o.p., and of the three Ånge progenies were intermediate (Fig. 17). No significant differences were established in whorl 3. In whorl 4 the branch length of Y 4015+ o.p., Ånge, was lower than that of the plus-tree progenies in the Boxholm group. Treated as two groups, the two provenances showed a certain difference in this whorl only (Table VI).

The correlation between tree height and branch length and the average increase in branch length per one centimetre increase in tree height is presented in Table 9 and Fig. 18. The strength of the relationship varied slightly from one year to another in the different progenies and whorls. Thus, a comparison of the correlation coefficients of all the whorls during the three years shows that those of whorl 2 were consistently lowest in 1959. In 1960 the r-values of all the progenies and all the whorls were between 0.70 and 0.93 (except in one case, where r = 0.60). No regular increase in the strength of this correlation seemed to occur with increasing height and age.

A regression analysis gave no indication of any significant differences between the progenies in the regression of the branch length on height in any of the whorls measured in any one year (*cf.* b-coefficients, Table 10). The eight regression lines within each whorl are thus largely parallel in regard to slope (Fig. 18).

Table 9. Experiment G. Summary of correlations between tree height and branch length in 1958 and 1960. Correlation coefficients (r).

Combination	Correlation coefficients (r)					
	1958 Whorl No.		1960 Whorl No.			
	1	2	1	2	3	4
E 4015$^+$ o.p.	0.53	0.69	0.80	0.77	0.76	0.77
E 4008$^+$ o.p.			0.83	0.81	0.84	0.83
VIII 46$^-$ × E 4015$^+$	0.69	0.74	0.79	0.86	0.84	0.76
VIII 46$^-$ o.p.	0.87	0.86	0.76	0.85	0.89	0.86
VIII 47$^-$ o.p.	0.87	0.90	0.86	0.87	0.93	0.87
Y 4015$^+$ o.p.	0.75	0.79	0.79	0.80	0.79	0.75
Å 3$^-$ o.p.	0.87	0.88	0.83	0.88	0.88	0.90
Å 4$^-$ × Å 3$^-$	0.84	0.82	0.60	0.78	0.76	0.71

r value required for	df = 6	df = 7
5 % level	0.707	0.666
1 % level	0.834	0.798

The data obtained in 1960 from the measurements of four whorls indicate that the slope of the regression lines rises from whorl 1 to whorl 4 within each progeny (Fig. 18). There were great differences between the progenies with regard to the branch length at equal tree height, particularly in the whorls 3 and 4. As far as whorl 4 is concerned, four of the minus progenies had higher mean values than those of the other progenies in this respect. The differences were significant.

The ratios of tree height over branch length $\left(\frac{\mathrm{H}}{\mathrm{Brl}}\right)$ are given in Table V. In Fig. 16 the inverted values multiplied by 100 $\left(\frac{100\ \mathrm{Brl}}{\mathrm{H}}\right)$ are graphically shown. In 1958 there were significant differences between the progenies in whorl 2 only. The progenies of the Boxholm group showed in this whorl a mean value that was distinctly lower than that of the Ånge group, *i.e.* the branches of the Boxholm progenies were longer in relation to the tree height than those of the Ånge group (Table 24).

In the following year (1959) there were clear differences between the progenies within each of the provenance groups. In the Boxholm group, the branches of the two minus progenies VIII: 46$^-$ o.p. and VIII: 47$^-$ o.p. were longer in relation to the tree height than the branches of the progenies obtained from the plus trees. In the Ånge group, too, the minus-tree progenies Å 3$^-$ o.p. and Å 4$^-$ × Å 3$^-$ were of a different and more long-branched type than the plus progeny Y 4015$^+$ o.p. This applied to both whorl 2 and whorl 3. No differences *between* the provenance groups appeared in whorl 2,

Table 10. Experiment G. Regression of mean branch length on mean tree height. Regression coefficients. Significance of the differences between progenies and between blocks.

Year	Whorl No.	Source of variation	df	Mean Square	F
1958	2	Progenies	6	0.0048	0.23
		Blocks	3	0.0089	0.43
		Error	18	0.0208	
1959	2	Progenies	6	0.0076	1.52
		Blocks	3	0.0117	2.34
		Error	18	0.0050	
1960	1	Progenies	7	0.0026	2.36
		Blocks	3	0.0034	3.09*
		Error	21	0.0011	
	2	Progenies	7	0.0059	1.11
		Blocks	3	0.0057	1.08
		Error	21	0.0053	
	3	Progenies	7	0.0054	1.35
		Blocks	3	0.0147	3.68*
		Error	21	0.0040	
	4	Progenies	7	0.0273	1.07
		Blocks	3	0.0158	0.62
		Error	21	0.0256	

since the mean values of the three progenies from Ånge were covered by the range of variation of the mean values of the Boxholm material. A slightly significant difference between the provenances occurred in whorl 3, with the highest mean value of the ratios in the Ånge group, *i.e.* the trees in this group had the shortest branches in relation to height (Table 24).

In 1960 the ten-year-old material was further differentiated with regard to the crown type. In the Boxholm group the two progenies of VIII: 46^- ($- \times +$, $-$ o.p.) had relatively *short* branches in whorl 1 compared to the plus-tree progenies, and long branches in whorls 3 and 4. The differences were significant. The minus progeny VIII: 47^- o.p. equalled the plus-tree progenies as regards whorl 1, but behaved as the minus progenies of VIII: 46^- as regards the lower whorls. In the Ånge group the two minus progenies likewise differed from the plus-tree progeny by having a relatively short-branched upper whorl and distinctly longer branches in the whorls below.

On an average, the Boxholm group had longer branches in relation to tree height than the Ånge group. The differences, however, were not significant.

To sum up: in experiment X as well as in experiment G the progenies of the plus-tree combinations were of a different type to those of the minus combinations. In the plus combinations, individuals with vigorous growth and a

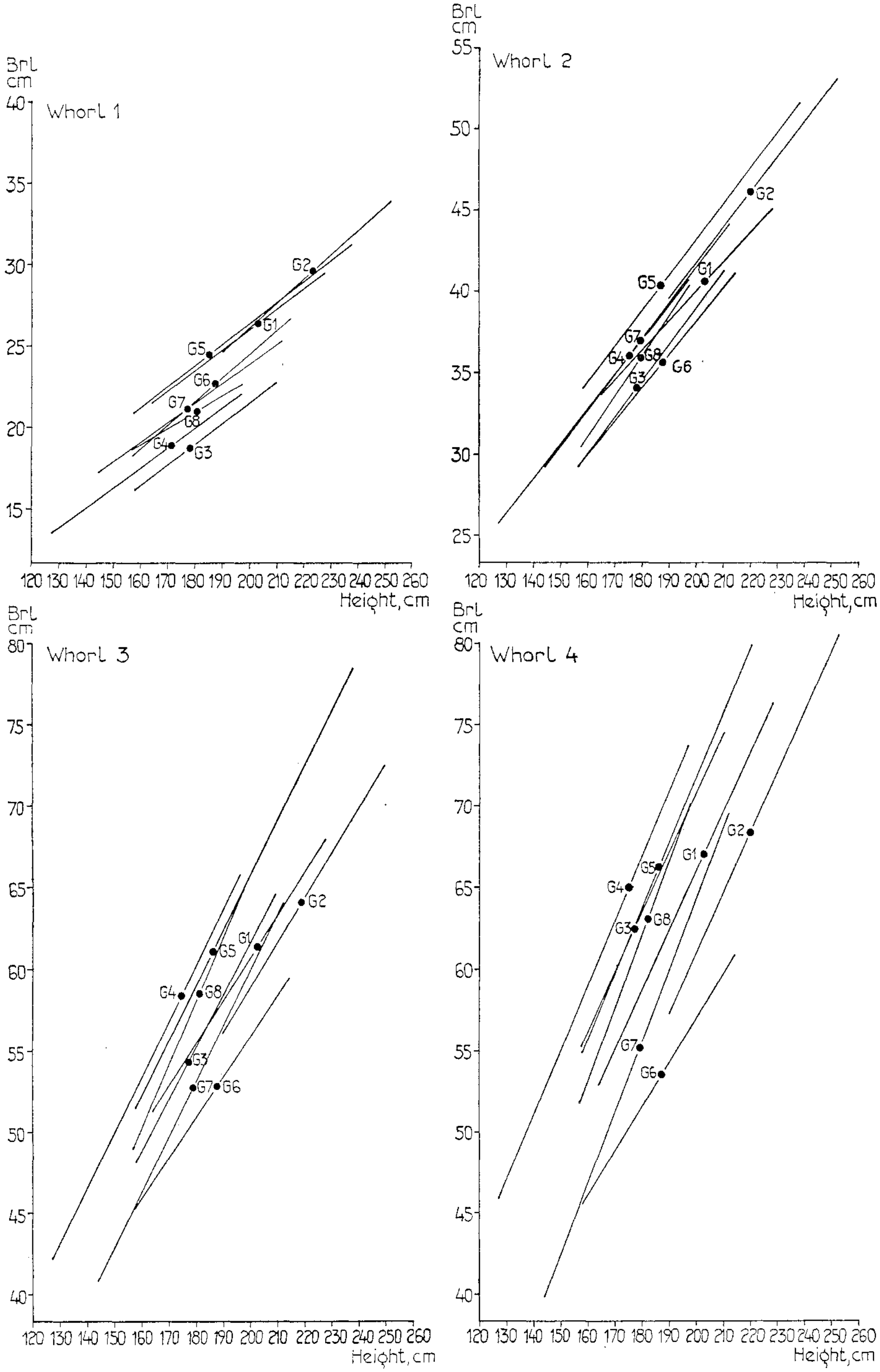


Fig. 18. *Experiment G.* Regression of mean branch length on mean tree height in 1960. G1: E 4015^+ o.p., G2: E 4008^+ o.p., G3: VIII 46^- × E 4015^+, G4: VIII 46^- o. p., G5: $VIII47^-$ o.p., G6: Y 4015^+ o.p., G7: Å 3^- o.p., G8: Å 4^- × Å 3^-.

Table 11. Experiment X. Angles of branches. Significance of the differences between individual progenies.

1 = $E\,4015^{+} \times E\,4008^{+}$, 2 = $E\,4008^{+} \times E\,4015^{+}$, 3 = VIII 46^{-}i, 4 = VIII $46^{-} \times$ VIII 47^{-}, 5 = $Y\,4015^{+} \times Å\,2^{+}$, 6 = $S3001^{+}$ o.p.

Year	Whorl No.	Significance of difference														
		1—2	1—3	1—4	1—5	1—6	2—3	2—4	2—5	2—6	3—4	3—5	3—6	4—5	4—6	5—6
1958	1				o											
	2				o											
1959	2	o			*	o			*	o						o
	3	*			o	o			o	o						o
1960	2	o	***	***	o	o	***	***	o	o	o	***	***	***	***	o
	3	o	*	o	**	o	*	o	**	o	**	***	*	**	o	**
	4	*	o	o	o	o	o	o	o	o	o	o	o	o	o	o

° No significance. * Significant at 5 % level. ** Significant at 1 % level. *** Significant at 0.1 % level.

crown relatively narrow at the base were most common. In the minus combinations the average tree developed a crown with a long-branched base and relatively short branches in the first whorl. These minus progenies generally displayed rather slow height growth as well. The variation in the tree type was greater among the five progenies from Boxholm than among those from Ånge. The Boxholm progeny VIII: $46^{-} \times E\,4015^{+}$ $(- \times +)$ ranked in between the plus-tree progenies and the minus-tree progenies from the same provenance in regard to the character of the branches. As the branch length is correlated with tree height, it is strongly influenced by the environmental conditions. The relative branch length, $\frac{H}{Brl}$, however, varied less with differences in environment.

d) *Branch angle*

In young Scots pines the branches usually form a regular whorl with three big branches evenly distributed around the stem and the rest of the branches situated slightly below. Disturbances in this common type of branching are frequently encountered. In the present material deviations in this respect were found especially in the progenies originating from the minus tree VIII: 46^{-} at Boxholm. In these progenies the normal branching was disturbed with regard to the formation of buds and branches (*cf.* p. 70 *et seq*), and the variation in the branch angle within the whorls increased. The disturbances were most extensive in trees with rapid height growth.

The mean of the three angles measured in each whorl was used as an ex-

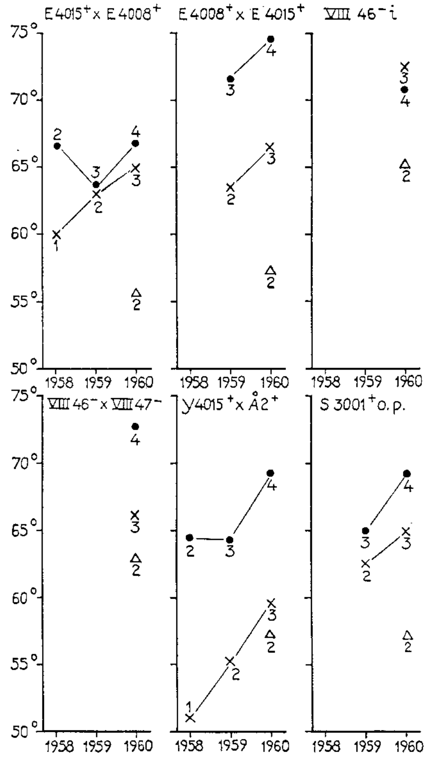


Fig. 19. *Experiment X*. Mean branch angles in different whorls in 1958 to 1960. x = whorl 1 in 1958 = whorl 2 in 1959 = whorl 3 in 1960. ● = whorl 2 in 1958 = whorl 3 in 1959 = whorl 4 in 1960. △ = whorl 2 in 1960.

pression of the branch angle of the whorl. The measurements are given in Table VII and the significance of the differences between individual progenies in Tables 11 and 12. As mentioned above, branch lengths and branch angles were measured simultaneously on the same individuals (1 to 3 branches per whorl). Generally the size of the branch angle increased with the age of the whorl in all the progenies, but there was a wide difference between them in the degree of the increase.

Experiment X (Table 11 and Fig. 19). In 1958 there were no significant differences between the two plus progenies E 4015+ × E 4008+ and Y 4015+ × Å 2+ in the size of the branch angles in the two youngest whorls, 1 and 2 (Table 11).

In 1959 all four plus-tree progenies of this experiment were measured with regard to the branch angles of whorls 2 and 3. The angles of the various progenies were about the same within the whorls concerned. However, the crossing Y 4015+ × Å 2+ had more acute angles in whorl 2 than the other three plus-tree combinations. The angles in whorl 3 in the cross E 4008+ ×

Table 12. Experiment G. Angles of branches. Significance of the differences between individual progenies.

1 = E 4015^+ o.p., 2 = E 4008^+ o.p., 3 = VIII 46^- × E 4015^+, 4 = VIII 46^- o.p., 5 = VIII 47^- o.p., 6 = Y 4015^+ o.p., 7 = Å 3^- o.p., 8 = Å 4^- × Å 3^-.

Year	Whorl No.	Significance of difference													
		1—2	1—3	1—4	1—5	1—6	1—7	1—8	2—3	2—4	2—5	2—6	2—7	2—8	3—4
1958	1		***	**	o	**	o	*							***
	2		o	**	o	o	***	***							***
1959	2	o			o	***	o	*			o	***	o	o	
	3	**			o	o	**	***			**	**	o	o	
1960	2	**	o	o	o	*	o	o	***	**	***	***	*	o	o
	3	*	***	o	o	*	o	***	***	*	*	***	o	o	***
	4	***	*	o	o	o	**	***	***	*	***	***	o	o	***

Year	Whorl No.	Significance of difference													
		3—5	3—6	3—7	3—8	4—5	4—6	4—7	4—8	5—6	5—7	5—8	6—7	6—8	7—8
1958	1	***	***	***	***	***	o	***	***	***	o	o	***	***	o
	2	**	**	***	***	o	*	o	**	o	**	***	**	***	o
1959	2									***	o	*	***	***	*
	3									o	**	***	**	***	o
1960	2	o	o	*	*	o	o	o	o	o	o	o	**	**	o
	3	***	*	***	***	o	*	*	***	**	o	***	***	***	o
	4	o	o	***	***	*	**	o	***	o	**	***	***	***	*

o No significance * Significant at 5 % level. ** Significant at 1 % level. *** Significant at 0.1 % level.

E 4015^+ were larger than those in the other progenies. In one case only were the differences slightly significant (Table 11).

In 1960 measurements of the two minus progenies of VIII: 46^- were included. These two progenies were equal in whorl 2, but differed from the plus-tree progenies by having significantly larger angles. The progeny obtained after selfing (VIII: 46- *i*) showed relatively large branch angles in whorl 3. In whorl 4, however, no differences between the progenies were observed. The lowest and the highest mean values of the branch angles in this whorl were recorded for the two reciprocal Boxholm plus-tree combinations.

Significant block differences did not occur in any whorl or progeny (Table 23).

Experiment G (Table 12 and Fig. 20). Marked differences between the progenies were observed in each year of measurement. In the Boxholm group the plus-tree progeny E 4015^+ o.p., had throughout wider branch angles in the whorls 2 to 4 than the progeny from the other plus-tree at Boxholm,

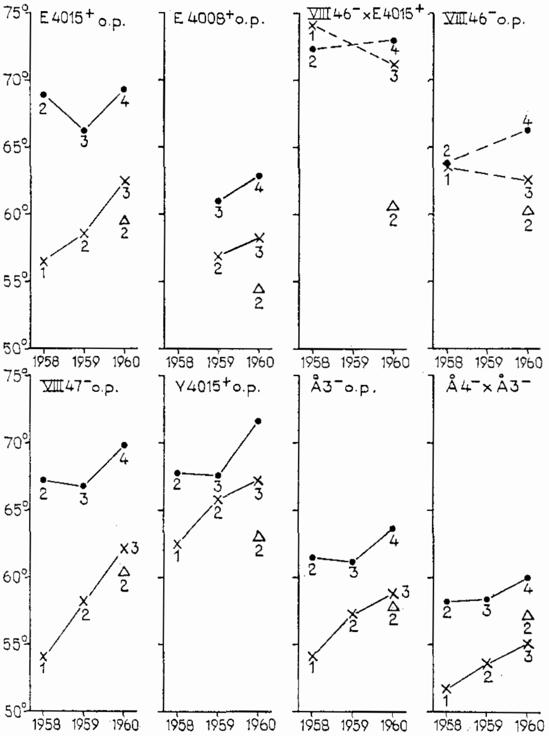


Fig. 20. *Experiment G.* Mean branch angles in different whorls in 1958 to 1960. x = whorl 1 in 1958 = whorl 2 in 1959 = whorl 3 in 1960. ● = whorl 2 in 1958 = whorl 3 in 1959 = whorl 4 in 1960. △ = whorl 2 in 1960.

E 4008+ o.p. The angles of all whorls in the progeny of E 4015+ o.p. were more acute than those in the crossing VIII: 46− × E 4015+. Significant differences were found in whorl 1 in 1958 and in whorl 3 and 4 in 1960. In comparison with the progeny VIII: 46− o.p., significant differences occurred in the whorls 1 and 2 in 1958; the angles of the progeny of E 4015+ being smaller in whorl 1, but larger in whorl 2. Two years later the differences had disappeared. Although the progeny VIII: 47− o.p. was entirely different to E 4015+ o.p. in other characteristics, both had the same branch angles in all the whorls.

The plus-tree progeny E 4008+ o.p. showed consistently smaller branch angles than the other progenies, and the combination VIII: 46− × E 4015+ consistently larger ones. The minus-tree progenies VIII: 46− o.p. and VIII: 47− o. p. were equal except in whorl 1 in 1958.

The order in size of the branch angle of the three progenies in the Ånge group was constant. The plus-tree progeny Y 4015^{+} o.p., with its larger branch angles, clearly deviated from the two minus progenies (Fig. 20). The offspring of Å 3^{-} o.p. had consistently the least acute angles of the minus progenies, although the difference is not statistically significant.

The block differences were significant for each whorl of all the progenies every year (Table 24).

No average difference occurred between the two provenance groups Boxholm and Ånge. In 1960 the Ånge progeny Y 4015^{+} showed branch angles equal in size to those of the Boxholm crossing $- \times +$. The combination Å 4^{-} × Å 3^{-} had more acute branch angles than any other progeny. Upon comparison of the plus-tree progenies with the minus-tree progenies, a wide range of variation in branch angle was found within each group. The parents of the plus-tree group are characterized by right to intermediate branch angles. Progenies obtained from these parent trees after open pollination differed considerably. The minus-tree group is represented by progenies of the Boxholm trees VIII: 46^{-} and VIII: 47^{-}, which were selected as minus trees primarily on account of poor stem form, wide crowns, and coarse limbs. The branch angles are intermediate to right. The progenies of these minus-trees obtained after open pollination have branch angles that are larger than those of the corresponding plus-tree progenies or equal to them. The other two minus-tree progenies in the group originate from the Ånge trees Å 3^{-} and Å 4^{-}, which have acute to extremely acute branch angles in all whorls in addition to other minus characters. The angles of the progeny Å 3^{-} o.p., and particularly those of the crossing Å 4^{-} × Å 3^{-}, were also acute, and in 1960 they increased less in size from whorl 2 to whorl 4 than, for instance, those of the plus-tree progeny from the same provenance, Y 4015^{+} o.p.

The age of the trees played a certain role in the formation of the branch angles (Figs. 19 and 20). The angles of whorl 1 were measured only in 1958. In seven of the nine progenies they were then more acute than those in whorl 2. In the two progenies with the minus-tree VIII: 46^{-} as mother, whorl 1 had angles equal to whorl 2, or larger. In all the progenies measured in 1958, the angles of whorl 2 were larger in that year than in 1959. The size of the angle thus was more acute in whorl 2 as the trees aged. After another year of growth this decrease had ceased in some of the progenies, but continued in others, *i.e.* the angle in whorl 2 of the ten-year-old trees (1960) was either larger or smaller than that of whorl 2 in the previous year or equal to it. There was no regular difference between the plus-tree and minus-tree progenies in this respect.

On an average, the branch angles of whorl 3 were larger in 1959 than in 1960. There was no regular difference between the plus-tree progenies and

Table 13. Experiment X. Number of branches per whorl. Significance of the differences between individual progenies. (For explanation of progeny numbers see Fig. 21.)

Year	Whorl No.	Significance of difference														
		1—2	1—3	1—4	1—5	1—6	2—3	2—4	2—5	2—6	3—4	3—5	3—6	4—5	4—6	5—6
1958	1				°											
	2				°											
1959	1	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
	2	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
	3	**	***	***	**	***	**	°	°	°	**	**	*	°	°	*
1960	1	°	***	**	*	°	**	*	°	°	*	*	**	°	°	°
	2	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
	3	°	°	°	°	°	°	°	°	°	°	°	°	°	°	°
	4	**	***	***	*	***	*	°	°	°	°	**	°	°	°	*

° No significance. * Significant at 5 % level. ** Significant at 1 % level. *** Significant at 0.1 % level.

the minus-tree progenies, nor were there any consistent differences between the two provenance groups.

The changes in the size of the branch angle in individual whorls during the growth of the tree is also shown in Figs. 19 and 20. As mentioned above, the mean size of the branch angles differed in the various combinations, but the fixation of the angles was parallel in the two whorls of seven progenies, regarding which data from several years are available. The 1958 angle of whorl 1 increased steadily during the next two years. The second whorl of 1958 showed an unchanged or slightly decreased branch angle in the following year. The most distinct decrease in angle size appeared in the two progenies E 4015^{+} o.p. and E 4015^{+} × E 4008^{+}, both progenies of the same mother tree, but with different fathers. A similar parallel change in the angle in progenies with common mother trees but different fathers occurred in Y 4015^{+} o.p. and Y 4015^{+} × Å 2^{+}. In 1960, when the branches were four years old, the angle had again increased in all the progenies.

e) *The number of branches*

The number of branches per whorl was registered for the whorls 1 and 2 in 1958, 1 to 3 in 1959, and 1 to 4 in 1960 (Tables 13, 14 and VIII). In both experiments the course of all the progenies ran parallel from year to year in regard to the variation in the number of branches in whorl 1 and the reduction in the number of branches in whorls 2 to 4 (Figs. 21 and 22).

In 1958 the number of branches in whorl 2 of each progeny was about half of that in whorl 1. In the one-year-older trees of 1959 the differences between

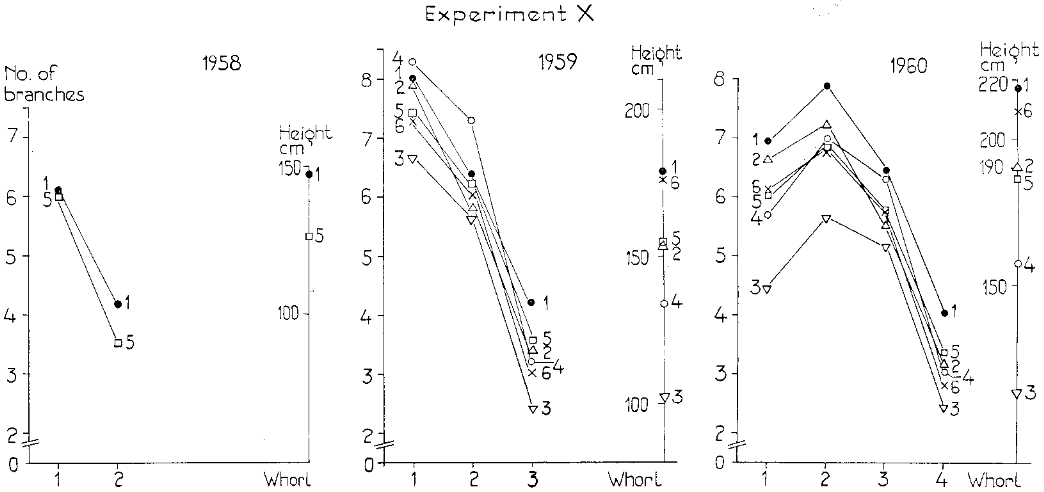


Fig. 21. *Experiment X.* Mean number of branches in different whorls and mean heights of the progenies in 1958 to 1960. 1: E 4015+ × E 4008+, 2: E 4008+ × E 4015+, 3: VIII 46− *i*, 4: VIII 46− × VIII 47−, 5: Y 4015+ × Å 2+, 6: S 3001+ o.p.

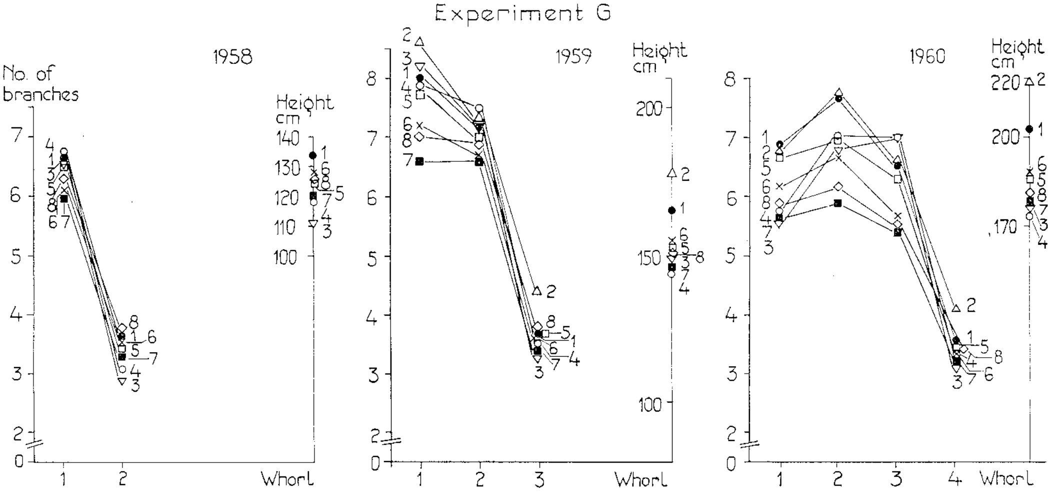


Fig. 22. *Experiment G.* Mean number of branches in different whorls and mean heights of the progenies in 1958 to 1960. 1: E 4015+ o.p., 2: E 4008+ o.p., 3: VIII 46− × E 4015+, 4: VIII 46− o.p., 5: VIII 47− o.p., 6: Y 4015+ o.p., 7: Å 3− o.p., 8: Å 4− × Å 3−.

these two whorls were less, but the great difference between whorls 1 and 2 of 1958 remained as a similar great difference between whorls 2 and 3 of 1959. In all the progenies a relatively low number of branches in whorl 1 was formed in 1960. That year the number of branches in whorl 2 had been only slightly reduced. Whorl 3 showed a slight decrease in the number of branches, on an average one aborted branch per tree throughout the entire material. The distinct difference between whorls 3 and 4 in the number of branches was a consequence of the difference in branch numbers between the whorls 1 and 2 in 1958.

Significant differences between the progenies were established by a whorl-by-whorl comparison in different years (Table 13). The differences increased as the trees grew older. In 1958 the progenies obtained from the two Boxholm and Ånge plus-tree crossings in *experiment* X, had on an average an equal number of branches in whorl 1 (Fig. 21). In whorl 2 the number was slightly lower in the Ånge progeny. In 1959, too, the variation between the six progenies analyzed was slight in whorls 1 and 2. Whorl 3 of the Boxholm crossing E $4015^+ \times$ E 4008^+ differed significantly from other crossings by retaining a large number of branches. In the progeny VIII: $46^- i$, obtained after selfing, the number of branches was distinctly reduced (Table 13). Compared to the other progenies in 1960, VIII: $46^- i$ showed fewer branches in all the whorls (significant differences in the whorls 1, 2, and 4). In the same year the reciprocal plus-tree crossings E $4015^+ \times$ E 4008^+ and E $4008^+ \times$ E 4015^+ had a relatively large number of branches in whorls 1 and 2. The first-mentioned crossing also showed the largest number of branches in whorls 3 and 4 of all the progenies, whereas the number in E $4008^+ \times$ E 4015^+ was heavily reduced. The minus crossing VIII: $46^- \times$ VIII: 47^-, which developed the largest number of branches in whorl 1 in 1959, showed in 1960 fewer branches in this whorl than the other progenies, with the exception of the progeny obtained after selfing.

In *experiment G* (Fig. 22) there were no significant differences between the progenies in 1958 in regard to whorls 1 and 2. On an average the three progenies from Ånge had a lower number of branches in whorl 1 than the Boxholm progenies. In whorl 2 no significant differences between the provenances were found. In the following year (1959) the provenances differed significantly as regards whorls 1 and 2, the Ånge group showing the lowest mean number of branches. The variation within each group was slight. The differences between the provenances had almost disappeared in whorl 3. Instead, there was a difference between the Boxholm progenies in this whorl, E 4008^+ o.p. maintaining the largest number of branches, and the crossing VIII: $46^- \times$ E 4015^+ the lowest number.

In the ten-year-old material (1960) the Ånge group had in whorls 2 and 3

Table 14. Experiment G. Number of branches per whorl. Significance of the differences between individual progenies. (For explanation of progeny numbers see Fig. 22.)

Year	Whorl No.	Significance of difference													
		1—2	1—3	1—4	1—5	1—6	1—7	1—8	2—3	2—4	2—5	2—6	2—7	2—8	3—4
1958	1		o	o	o	o	o	o							o
	2		o	o	o	o	o	o							o
1959	1	o	o	o	o	o	**	*	o	o	o	**	***	*	o
	2	o	o	o	o	o	o	o	o	o	o	o	o	o	o
	3	*	o	o	o	o	o	o	***	**	*	*	**	o	o
1960	1	o	**	*	o	o	**	*	**	*	o	o	**	*	o
	2	o	o	o	o	o	**	**	o	o	o	*	**	**	o
	3	o	o	o	o	*	*	*	o	o	o	*	**	*	o
	4	o	o	o	o	o	o	o	o	o	o	o	o	o	o

Year	Whorl No.	Significance of difference													
		3—5	3—6	3—7	3—8	4—5	4—6	4—7	4—8	5—6	5—7	5—8	6—7	6—8	7—8
1958	1	o	o	o	o	o	o	o	o	o	o	o	o	o	o
	2	o	o	o	o	o	o	o	o	o	o	o	o	o	o
1959	1	o	o	**	*	o	o	*	*	o	*	o	o	o	o
	2	o	o	o	o	o	o	o	o	o	o	o	o	o	o
	3	o	o	o	o	o	o	o	o	o	o	o	o	o	o
1960	1	*	o	o	o	o	o	o	o	o	*	o	o	o	o
	2	o	o	o	o	o	o	*	o	o	*	o	o	o	o
	3	o	**	**	**	o	**	**	**	o	*	o	o	o	o
	4	o	o	o	o	o	o	o	o	o	o	o	o	o	o

o No significance. * Significant at 5 % level. ** Significant at 1 % level. *** Significant at 0,1 % level.

a lower number of branches per whorl than the Boxholm progenies. The differences were significant. Among the individual progenies the ranking changed from one whorl to another (Fig. 22, Table 14). The vigorous plus-tree progenies from Boxholm had the relatively largest number of branches in whorls 1, 2 and 4. The two slow-growing progenies with VIII: 46^{-} as their mother tree showed relatively few branches in whorl 1, an intermediate number in whorl 2, the largest number of all the progenies in whorl 3, and again a low number in whorl 4.

The number of branches in whorl 1 varied from one year to another within a progeny (Fig. 23). In the total material the mean values ranged between 6 and 6.8 in 1958, between 6.6 and 8.6 in 1959, and between 5.5 and 6.8 in 1960. Fluctuations in the climate at the bud setting in the year before the shoot development, as well as the climatic conditions in the year when

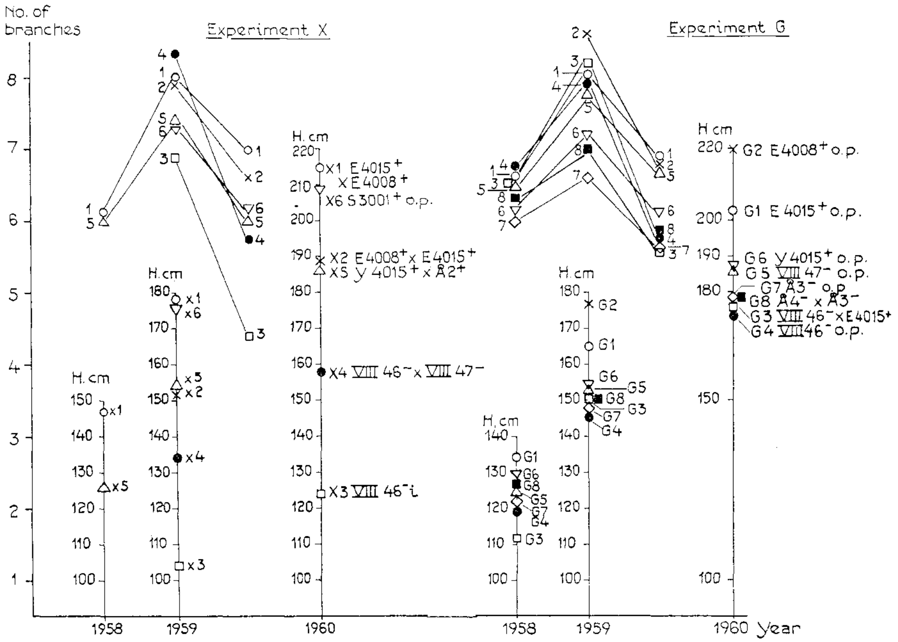


Fig. 23. Mean number of branches in whorl 1 and mean tree height (H) of the progenies in 1958 to 1960.

whorl 1 was forming, may have caused a great part of this annual variation. No regular correlation with age or tree height was found.

The changes occurring in the number of branches in a whorl with increasing age (for instance, from whorl 1 of 1958 to whorl 2 of 1959) showed a parallel course in all the progenies (Figs. 24 and 25). Only two progenies in *experiment X* deviated in this respect. In VIII: 46− × VIII: 47− the average difference between whorl 1 of 1959 and whorl 2 of 1960 was 1.3 branch per tree, and the difference between whorl 2 of 1959 and whorl 3 of 1960 was one branch. On an average, the second deviating progeny, VIII: 46− *i*, had lost one branch in the 1959 whorl 1 when this whorl was registered as whorl 2 in 1960. In the rest of the material the reduction in the number of branches in these two whorls varied between 0.1 and 0.7 and between *nil* and 0.4, respectively.

In *experiment G* the number of branches in the second whorl of 1958 was largely constant during the next two years, but whorl 2 of 1960 showed 0.7 branches less per tree than it did as whorl 1 in 1959. Whorl 2 of 1959 had 0.8 branches less as whorl 3 in 1960. The difference between whorl 3 of 1959 and whorl 4 of 1960 was 0.2 per tree.

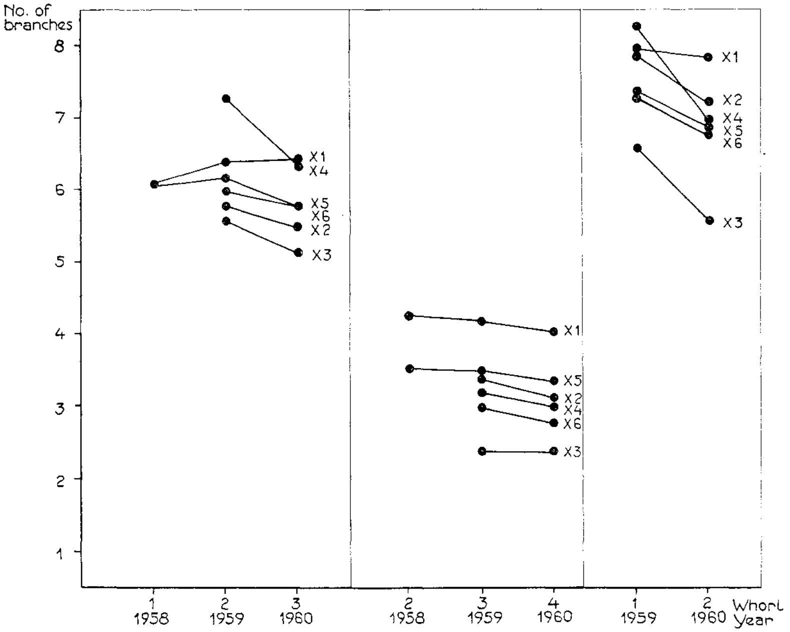


Fig. 24. *Experiment X.* Mean number of branches in the whorls with increasing age of whorl. X1: E 4015^{+} × E 4008^{+}, X2: E 4008^{+} × E 4015^{+}, X3: VIII 46^{-} *i*, X4: VIII 46^{-} × VIII 47^{-}, X5: Y 4015^{+} × Å 2^{+}, X6: S 3001^{+} o.p.

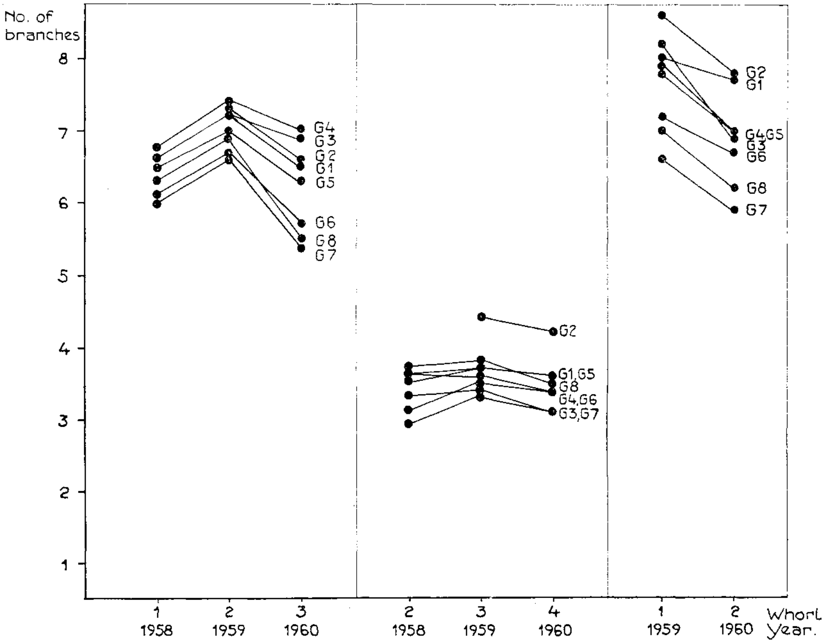


Fig. 25. *Experiment G.* Mean number of branches in the whorls with increasing age of whorl. G1: E 4015^{+} o.p., G2: E4008^{+} o.p., G3: VIII 46^{-} × E 4015^{+}, G4: VIII 46^{-} o.p., G5: VIII 47^{-} o.p., G6: Y 4015^{+} o.p., G7: Å 3^{-} o.p., G8: Å 4^{-} × Å 3^{-}.

Table 15. Form of apical buds. Ratios between length (Ht) and longest diameter (D_1) of buds in 1958.

Experiment	Combination	Ratio Ht/D_1
X	E 4015^{+} × E 4008$^{\div}$.......	1.99
	Y 4015$^{\div}$ × Å 2$^{\div}$	2.03
G	E 4015^{+} o. p............	1.95
	VIII 46^{-} × E 4015$^{\div}$......	2.09
	VIII 46^{-} o. p...........	2.24
	VIII 47^{-} o. p...........	2.05
	Y 4015$^{\div}$ o. p...........	2.22
	Å 3^{-} o. p................	2.25
	Å 4^{-} × Å 3^{-}.............	2.21

An increase in the number of branches was recorded between whorl 1 of 1958 and whorl 2 of 1959, and in some progenies between whorl 2 of 1958 and whorl 3 of 1959 (Fig. 25). The reason for this increase may be found in the classification by branch size applied in the registration of the number of branches. Very weak, tender and short shoots were classified as "accessory shoots", and were not included in the total number of branches of each whorl. There has possibly been some inconsistency in selecting the branches that were to be regarded as belonging to this group, *i.e.* an experimental error. It is also likely that some of these accessory shoots developed during the following year to an extent which then caused them to be classified as "branches". There was no such increase in the number of branches from whorl 1 to whorl 2 in the one-year-older trees in 1959.

A consistent difference between the two provenance groups could be shown in respect of the loss of branches in the years 1959—1960 (Fig. 25). In the Boxholm progenies the number was most heavily reduced from whorl 1 to whorl 2, slightly less from whorl 2 to whorl 3 and by a mere 0.1 branch per tree from whorl 3 to whorl 4. In the Ånge group, however, the greatest decrease occurred between whorl 2 and whorl 3, and it was more than twice as great as the decrease in the Boxholm trees. Between whorl 3 and whorl 4, the loss was three times that of the Boxholm trees in the corresponding whorls.

The varying site conditions in the experimental field were manifested by the large variation in the same progeny from one plot to another in the mean number of branches per whorl. The block differences were significant in the uppermost whorls in 1958, 1959 and 1960 as well as in the lower whorls in 1960 (Tables 23 and 24).

Table 16. Form of apical bud (Ht/D_1). Significance of the differences between progenies and between blocks.

Experiment	Source of variation	df	Mean Square	F
X	Progenies	1	0.0024	0.86
	Blocks	2	0.0044	0.78
	Error	2	0.0028	
G	Progenies	6	0.06050	7.23***
	Blocks	3	0.08573	10.25***
	Error	18	0.00837	

f) *The apical bud*

The *form of the apical bud* is defined as the ratio between its length and largest diameter (Ht/D_1), and was investigated in 1958 (Tables 15 and 16).

In *experiment X* the two progenies measured were of different provenance but of the same crossing type, + × +. The form of the apical buds was about the same in both progenies and the variation between the trees was slight. In *experiment G* the average apical buds were wider in three of the Boxholm progenies than in the three progenies of the Ånge provenance. The fourth progeny from Boxholm, VIII: 46^- o.p., deviated significantly from the other Boxholm progenies by having relatively slim buds, very similar in form to the apical bud in the Ånge group. The apical bud of the progeny E 4015^+ o.p. was slightly wider than in the other Boxholm progenies. The plus-tree progeny in the Ånge group, Y 4015^+ o.p., had apical buds of the same form as those of the two minus-tree progenies in this group. In this material, therefore, the form of the apical bud is independent of provenance or parent tree type.

The length of the apical bud (Ht) in the various progenies during different years is presented in Fig. 26 and Table IX. Although the progeny Y 4015^+ × Å 2^+ had in all years smaller apical buds than the other plus-tree progenies measured in *experiment X*, the differences were significant only in 1958. In each year the length of the terminal shoot was about equal in these progenies. The length of the apical bud in the two progenies of the minus tree VIII: 46^- (*i*, − × −) was measured in one year only (1960). The apical buds and the terminal shoots were smaller than those of the plus-tree progenies. In *experiment G* the plus-tree progeny E 4008^+ o.p. had the longest apical buds and terminal shoots of all progenies. The apical buds of the

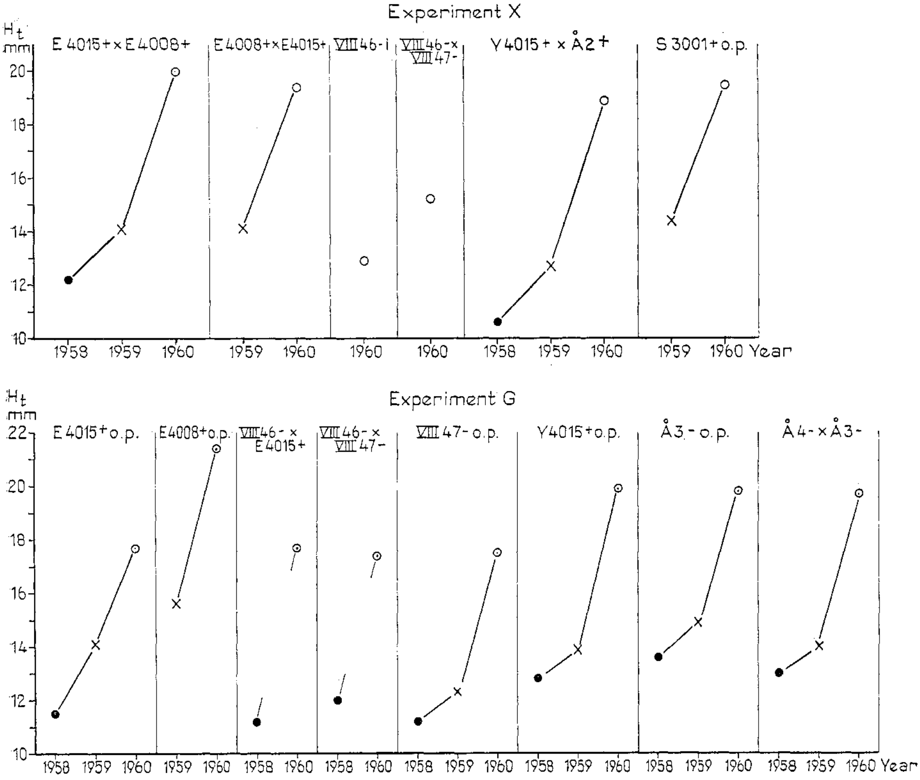


Fig. 26. Mean length of the apical buds in 1958 to 1960.

Table 17. Summary of correlations between length of terminal shoot and length of apical bud in 1958. Correlation coefficients (r) significant at the 1 % level.

Experiment	Combination	r
X	E $4015^{+}\times$ E 4008^{+}	0.79
	Y $4015^{+}\times$ Å 2^{+}	0.58
G	E 4015^{+} o. p.	0.65
	VIII $46^{-}\times$ E 4015^{+}	0.49
	VIII 46^{-} o. p.	0.57
	VIII 47^{-} o. p.	0.67
	Y 4015^{+} o. p.	0.65
	Å 3^{-} o. p.	0.79
	Å $4^{-}\times$ Å 3^{-}	0.66

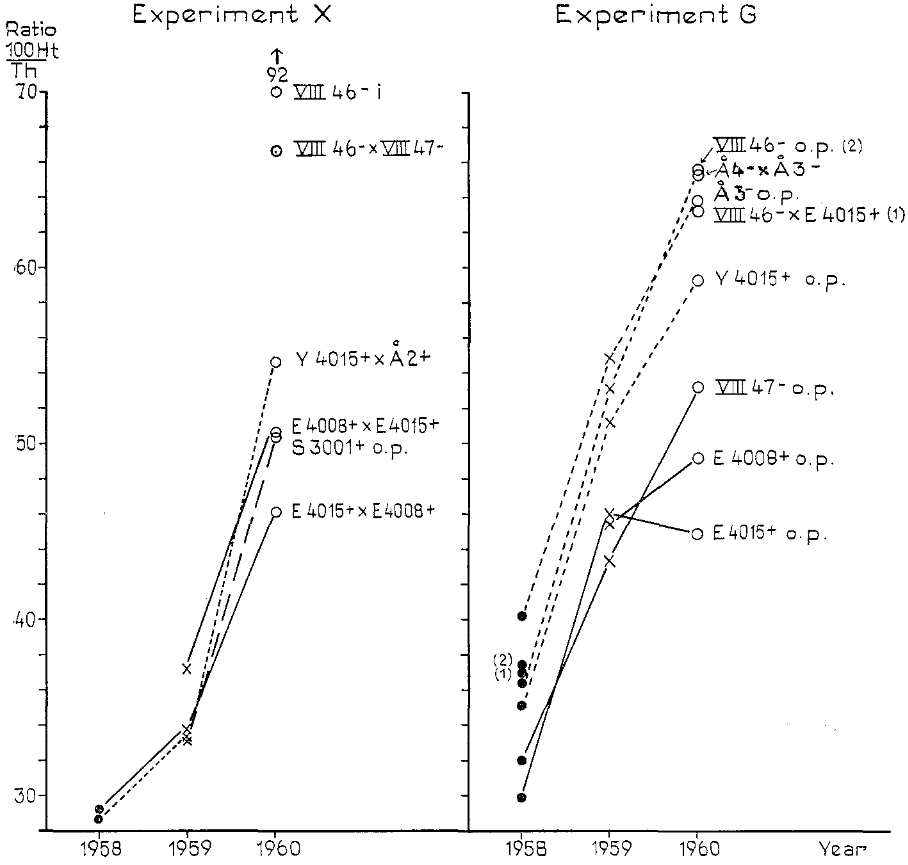


Fig. 27. Ratios between length of apical buds (Ht) and length of terminal shoots (Th) in 1958 to 1960. (——— Boxholm - - - - - - Ånge — — — Värmland)

three Ånge progenies were of equal length in spite of the different length of the terminal shoot. They were longer than those of the Boxholm progenies (with the exception of E 4008^{+} o.p.). The two progenies of the tree VIII:46^{-} showed apical buds of about the same size as those of the other Boxholm progenies.

The variations in the environment strongly affected the length of the apical buds, as shown by the significant block differences in each year (Tables 23 and 24).

The length of the apical bud was positively correlated with the length of the terminal shoot in the same year, and varied accordingly as the shoot varied ($r = 0.61$ in experiment X, $r = 0.63$ in experiment G, 1958). The correlation coefficients of the individual progenies are given in Table 17.

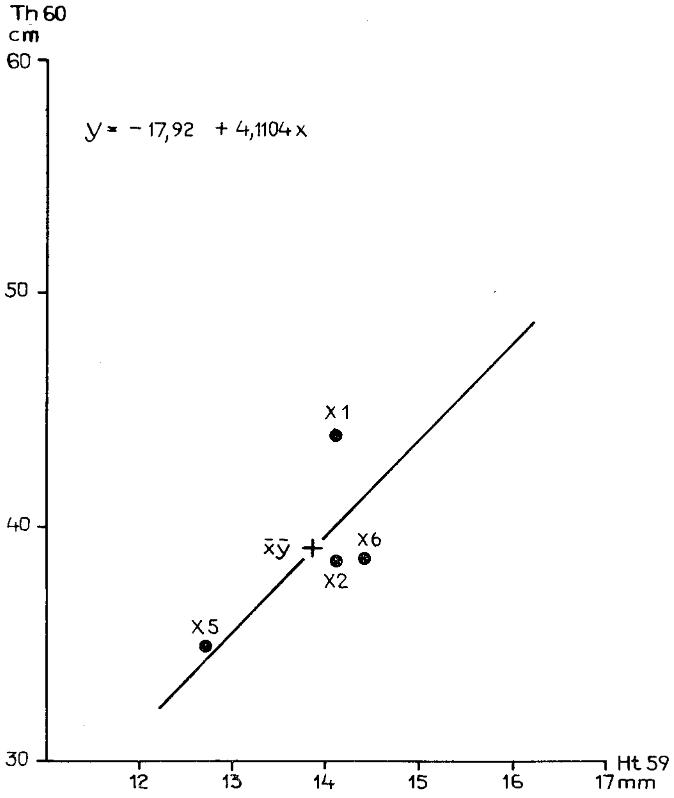


Fig. 28. *Experiment X.* Average regression of mean length of terminal shoot in 1960 (Th 60) on mean length of apical bud in 1959 (Ht 59). X1: E $4015^+ \times$ E 4008^+, X2: E $4008^+ \times$ E 4015^+, X5: Y $4015^+ \times$ Å 2^+, X6: S 3001^+ o.p.

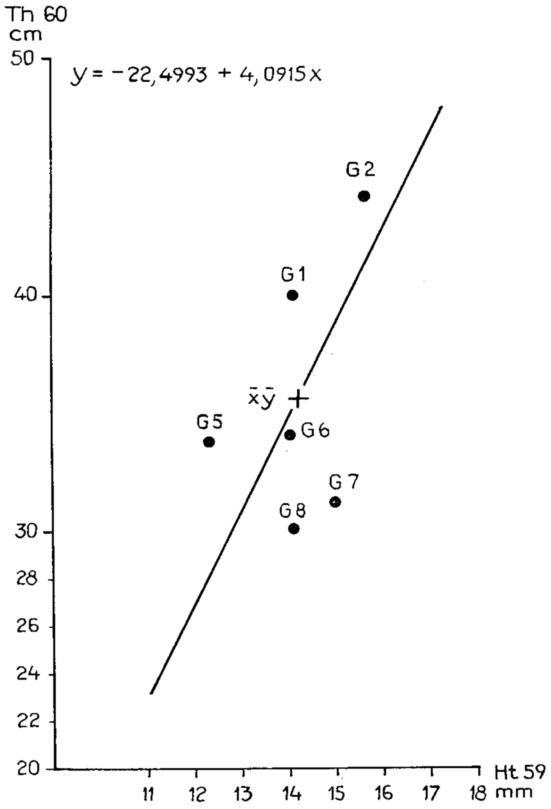


Fig. 29. *Experiment G.* Average regression of mean length of terminal shoot in 1960 (Th 60) on mean length of apical bud in 1959 (Ht 59) G1: E 4015^+ o.p., G2: E 4008^+ o.p., G5: VIII 47^- o.p., G6: Y 4015^+ o.p., G7: Å 3^- o.p., G8: Å $4^- \times$ Å 3^-.

Table 18. Length of apical bud (x) and length of terminal shoot (y). Comparison between adjusted progeny means of y.

a. 1958 (x) and 1959 (y)

Experiment	Source of variation	df	Mean Square	F
X	Progenies	1	0.227	0.95
	Error	1	0.238	
G	Progenies	6	26.252	5.10**
	Error	17	5.151	

b. 1959 (x) and 1960 (y)

Experiment	Source of variation	df	Mean Square	F
X	Progenies	3	21.526	3.80
	Error	5	5.657	
G	Progenies	5	107.753	27.81***
	Error	14	3.875	

In 1958 the mean bud length of the Boxholm crossing in *experiment X* increased by 0.9 mm for each centimetre of increase in the terminal shoot. In the Ånge crossing the corresponding value was 0.5 mm. In *experiment G*, this relative increase in the mean bud length was greatest in the Ånge progeny Å 3^- o.p. (0.9 mm) and smallest in the Boxholm progeny E 4015^+ o.p. (0.5 mm). On an average it was greater in the Ånge group than in the Boxholm group. Significant differences were established in each year.

The ratio of the *length of the apical bud to the length of the terminal shoot* (100 Ht/Th) varied strongly between the progenies (Fig. 27). Among the plus-tree progenies in *experiment X* the variation was slight in each year of measurement, regardless of crossing type and provenance. In 1960 they differed significantly from the two progenies obtained from VIII: 46^- (*i*, $- \times -$) which were characterized by a larger ratio than those obtained from the plus trees. In *experiment G*, the two progenies with VIII: 46^- as mother tree differed from the other Boxholm progenies by a larger ratio of the length of the apical bud to the terminal shoot, being similar to those of the minus progenies in the Ånge group in 1960. In both provenances the plus-tree progenies had lower ratios than the minus tree progenies, *i.e.* small apical buds compared to their terminal shoot length.

The length of the terminal shoot in one year was dependent on the size of the apical bud in the preceding year (Table 18, Figs. 28 and 29). In the

Table 19. Longest distance between the points of opposite lateral buds (D_2) in 1958.

Experiment	Combination	Mean Distance (mm)
X	E 4015^{+} × E 4008^{+}.......	16.9 ± 0.24
	Y 4015^{+} × Å 2^{+}..........	13.6 ± 0.24
G	E 4015^{+} o. p............	16.2 ± 0.23
	VIII 46^{-} × E 4015^{+}......	15.7 ± 0.29
	VIII 46^{-} o. p...........	16.0 ± 0.36
	VIII 47^{-} o. p...........	15.5 ± 0.26
	Y 4015^{+} o. p...........	15.4 ± 0.23
	Å 3^{-} o. p................	15.9 ± 0.23
	Å 4^{-} × Å 3^{-}.............	15.9 ± 0.21

individual trees of one progeny the most vigorous shoots developed from the longest buds. On the other hand, different progenies with buds of an equal average size did not produce the same average length of shoots from these buds. The Boxholm progenies E 4015^{+} o.p. and E 4008^{+} o.p., for instance, developed stronger terminal shoots in 1960 than the three progenies of the Ånge group, although the former had the smaller buds in 1959. The case was the same with the crossing E 4015^{+} × E 4008^{+}. Its apical buds were equal in size to those of the other plus-tree progenies in experiment X in 1959, but the terminal shoots were longer in 1960.

g) *The lateral buds of the terminal shoot*

The longest distance (D_2) between the points of opposite lateral buds (Table 19) was measured in 1958. In some of the progenies, *e.g.* E 4015^{+} × E 4008^{+}, the lateral buds were turned outwards. In others, *e.g.* Y 4015^{+} × Å 2^{+}, they seemed to be more crowded around the apical bud. The distance, D_2, however, was not significantly different between any of the progenies ($0.2 > P > 0.05$ in experiment X, $P > 0.2$ in experiment G). This distance is only in part dependent on the diameter of the apical bud, D_1 (Table 20). Clear differences between the progenies in regard to the ratio of D_1/D_2 were established (Table 24). In the progeny VIII: 46^{-} o.p., for instance, D_2 was long in relation to the diameter of the apical bud, whereas in Å3^{-} o.p. it was comparatively short.

The *length* of the lateral buds (Hs), defined as the mean length of the largest three buds, was recorded in 1959 and 1960 (Tables 21, 23 and 24). In 1959 there was no significant difference between the progenies in any of the two *experiments X and G.* That year the progenies with VIII: 46^{-} as

Table 20. Diameter of apical bud (x) and longest distance between opposite lateral buds (y). Comparison between adjusted progeny means of y in 1958.

Experiment	Source of variation	df	Mean Square	F
G	Progenies	6	0.992	4.48**
	Error	17	0.221	

Table 21. Mean length of lateral buds (Hs) in 1959 and 1960.

Experiment	Combination	Length (mm)	
		1959	1960
X	E 4015^{+} × E 4008^{+}	10.0 ± 0.24	17.1 ± 0.26
	E 4008^{+} × E 4015^{+}	10.7 ± 0.24	16.7 ± 0.31
	VIII 46^{-} i.		11.3 ± 0.27
	VIII 46^{-} × VIII 47^{-}		13.5 ± 0.25
	Y 4015^{+} × Å 2^{+}	9.5 ± 0.17	16.0 ± 0.26
	S 3001^{+} o. p.	11.4 ± 0.16	16.4 ± 0.28
G	E 4015^{+} o. p.	11.0 ± 0.21	15.4 ± 0.24
	E 4008^{+} o. p.	12.1 ± 0.25	18.1 ± 0.27
	VIII 46^{-} × E 4015^{+}		14.9 ± 0.30
	VIII 46^{-} o. p.		14.3 ± 0.26
	VIII 47^{-} o. p.	10.6 ± 0.12	14.9 ± 0.19
	Y 4015^{+} o. p.	11.2 ± 0.23	16.2 ± 0.22
	Å 3^{-} o. p.	11.3 ± 0.19	16.3 ± 0.28
	Å 4^{-} × Å 3^{-}	11.2 ± 0.18	15.7 ± 0.29

Table 22. Ratios between apical bud length (Ht) and length of lateral buds (Hs) in 1959 and 1960.

Experiment	Combination	Ratio Ht/Hs	
		1959	1960
X	E 4015^{+} × E 4008^{+}	1.33	1.18
	E 4008^{+} × E 4015^{+}	1.32	1.16
	VIII 46^{-} i.		1.14
	VIII 46^{-} × VIII 47^{-}		1.13
	Y 4015^{+} × Å 2^{+}	1.34	1.18
	S 3001^{+} o. p.	1.27	1.19
G	E 4015^{+} o. p.	1.28	1.15
	E 4008^{+} o. p.	1.29	1.18
	VIII 46^{-} × E 4015^{+}		1.19
	VIII 46^{-} o. p.		1.22
	VIII 47^{-} o. p.	1.14	1.18
	Y 4015^{+} o. p.	1.24	1.23
	Å 3^{-} o. p.	1.32	1.21
	Å 4^{-} × Å 3^{-}	1.25	1.25

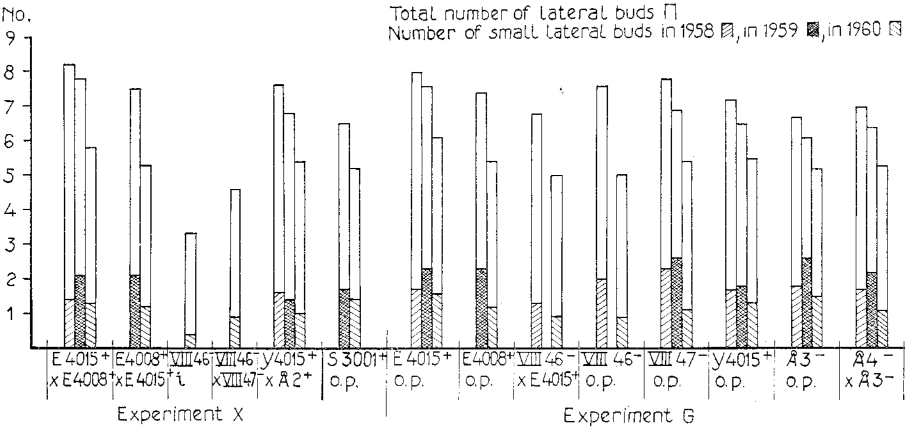


Fig. 30. Total number of lateral buds per tree and number of small lateral buds per tree in 1958 to 1960.

the mother tree were not included in the records. In 1960 the values of the two progenies from VIII: 46⁻ measured in *experiment* X (*i*, – × –) deviated distinctly from those of the other progenies, in that both their lateral and apical buds were relatively small and the terminal shoots were short. In *experiment G*, however, the lateral buds of VIII: 46⁻ × E 4015⁺ and VIII: 46⁻ o.p. were equal in length to those of five of the other progenies. The sixth progeny, E 4008⁺ o.p., deviated already in 1959 by having larger lateral buds and at the same time longer terminal shoots than the other progenies. This difference was still more marked and significant in 1960.

The degree of dominance of the apical bud over the lateral buds can be recognized from the ratios between apical bud length and lateral bud length (Ht/Hs) (Tables 22, 23 and 24). In the four plus-tree progenies in *experiment* X measured in 1959 and 1960, and in the two progenies of VIII: 46⁻ measured in 1960 only, the relationship between the apical bud and the lateral buds was about the same. In *experiment G* the progenies differed significantly in 1959, relatively large lateral buds occurring in the progeny VIII: 47⁻ o.p. and relatively small ones in Å 3⁻ o.p. In 1960 the differences between the individual progenies were slight, but the provenance groups showed different mean ratios. The progenies from Ånge had definitely more dominating apical buds than those from Boxholm. The difference is significant on the 5 per cent level.

The number of lateral buds was recorded in the years 1958—1960 (Fig. 30) and the mean values per tree for each progeny and year are given in Table XI.

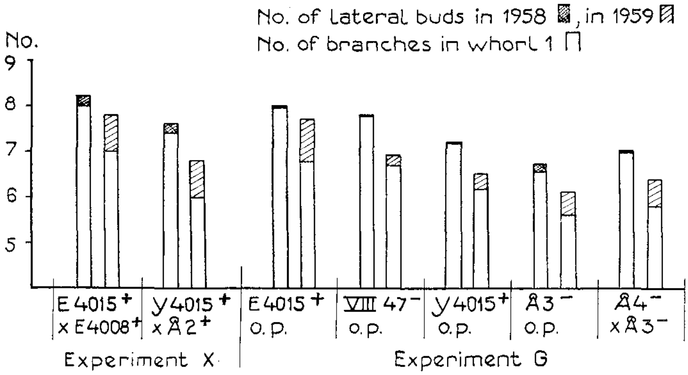


Fig. 31. Mean number of lateral buds in 1958 and 1959 and mean number of branches in whorl 1 in the year next.

Among the plus-tree progenies in *experiment* X, the southerly ones from Boxholm showed a slightly larger number of lateral buds in the first two years than the progenies from Ånge and Värmland. The difference in 1959 was significant on the 5 % level. In 1960 the progenies obtained from VIII: 46$^-$ (*i*, – × –) produced fewer lateral buds—two and one buds less per tree respectively—than the other progenies ($P < 0.001$). In *experiment G* the trend was similar, *viz.* a larger number of lateral buds in the plus-tree progenies in the Boxholm group compared to the Ånge progeny Y 4015$^+$ o.p. during the first two years, but in one progeny only, E 4015$^+$ o.p., in the last year of measurement (1960). The minus-tree progenies in the two provenance groups showed fewer lateral buds than the plus-tree progenies of the same provenance. Significant differences between the provenance groups were recorded in 1959 only ($P < 0.05$). That year the Ånge progenies had, on an average, one lateral bud less than the Boxholm progenies.

The average number of lateral buds per terminal shoot decreased with increasing age of the progenies (Fig. 30). The greatest decrease in the number of buds from 1958 to 1960 occurred in the minus progenies VIII: 46$^-$ o.p. and VIII: 47$^-$ o.p.

The number of lateral buds that developed branches in the following year decreased as the progenies grew older (Fig. 31). In 1959 shoots developed from almost all lateral buds formed in the previous year. In 1960, however, the number of branches in whorl 1 was about 10 per cent less than the number of lateral buds set in 1959. Damage by insects or fungi may have been partly responsible for this decrease. However, since the tendency was

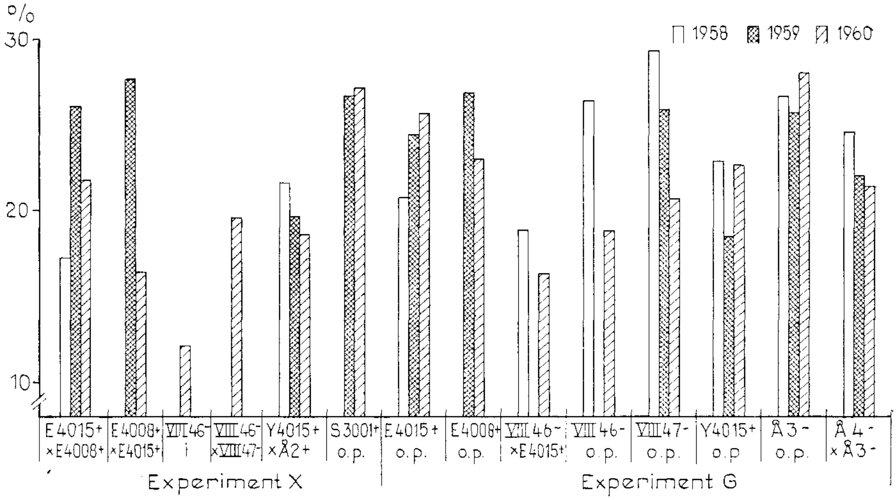


Fig. 32. Percentage of small lateral buds in 1958 to 1960.

the same in all the progenies, there is reason to assume a true abortion of poorly developed buds.

A differentiation in the size of the lateral buds of the terminal shoot is characteristic of *Pinus silvestris*. In the present material the lateral buds were classified into three groups: large, small, and accessory. Buds in the last-mentioned group were small, weak and irregularly distributed in the bud cluster. If they developed at all, they produced weak, short branches, and they have not been included in the compilation of the present data. No regular relationship could be found between the total number of lateral buds per tree and the percentage of small lateral buds. For instance, the progenies VIII: 46^- × E 4015^+ and Å 3^- o.p. had, on an average, an equal number of lateral buds, whereas the frequency of small buds differed entirely in the two progenies (Fig. 32). Neither was there any regular increase or decrease in the percentage of small buds with increasing age of the progenies. Consequently the order of the progenies in regard to this character varied from one year to another. Exceptions were the progeny VIII: 46^- × E 4015^+, where the percentage was consistently low, and Å 3^- o.p. where it was relatively high in all three years. The progeny with the slowest growth, VIII: 46^- *i*, was observed only in 1960. It then showed a very low percentage of small buds, as well as a low total number of buds.

The effect of differences in environment was evidenced by the strongly significant block differences in every character of the apical and lateral buds referred to above (Tables 23 and 24).

Table 23. Experiment X. Characters studied in 1958 to 1960. Significance of the differences between progenies and between blocks.

Character	1958[1]) between		1959 between		1960 between	
	progenies	blocks	progenies	blocks	progenies	blocks
All trees						
Height (H)	***	**	***	***	***	**
Length of terminal shoot (Th)	**	**	***	***	***	**
Length of terminal shoot/Height (100 Th/H)			***	**	***	**
60 trees						
Height	o	o	***	**	**	*
Length of terminal shoot	o	o	***	***	***	**
Length of branches (Brl) Whorl No. 1	o	o			***	**
2	*	*	**	**	***	**
3			**	**	**	**
4					**	**
Height/Length of branches (H/Brl) Whorl No. 1	o	o			***	o
2	o	o	**	o	o	o
3			***	o	***	o
4					**	o
Branch angle Whorl No. 1	o	o				
2	o	o	o	o	***	o
3			o	o	***	o
4					o	o
No. of branches per whorl 1	o	o	o	*	**	**
2	o	o	o	o	o	***
3			***	o	o	*
4					**	*
Form of apical bud	o	o				
Length of apical bud (Ht)	*	o	o	*	**	*
Length of apical bud/Length of terminal shoot (100 Ht/Th)	o	o	o	o	***	*
Length of apical bud/Diameter of apical bud (Ht/D_1)	o	o				
Diameter of apical bud (D_1)	o	o				
Distance between opposite lateral buds (D_2)	o	o				
Diameter of apical bud/Distance between opposite lateral buds (D_1/D_2)	o	o				
Length of lateral buds (Hs)			o	o	**	o
Length of apical bud/Length of lateral buds (Ht/Hs)			o	o	o	*
No. of lateral buds	o	o	*	o	***	*
No. of big lateral buds	o	o				
Percentage of small lateral buds					o	o

° No significance. * Significant at 5 % level. ** Significant at 1 % level. *** Significant at 0.1 % level.

[1]) Two progenies.

Table 24. Experiment G. Characters studied in 1958 to 1960. Significance of the differences between progenies, between blocks, between provenances and between plus and minus groups.

Character	1958 between			
	progenies	blocks	provenances	plus and minus groups
All trees				
Height (H)	**	***	o	o
Length of terminal shoot (Th)	*	***	o	o
Length of terminal shoot/Height (100 Th/H)	o	***		
80 trees				
Height	o	***		
Length of terminal shoot	o	***		
Length of branches (Brl)				
Whorl No. 1	o	***	o	o
2	o	***	o	o
3				
4				
Height/Length of branches				
(H/Brl) Whorl No. 1	o	**	o	o
2	**	***	*	o
3				
4				
Branch angle				
Whorl No. 1	***	**	o	
2	***	***		
3				
4				
No. of branches per whorl 1	o	*	**	o
2	o	o	o	o
3				
4				
Form of apical bud	***	***		
Length of apical bud (Ht)	*	***	**	o
Length of apical bud/Length of terminal shoot (100 Ht/Th)	*	**	o	o
Length of apical bud/Diameter of terminal bud (Ht/D_1)	***	***	o	o
Diameter of apical bud (D_1)	*	o	o	o
Distance between opposite lateral buds (D_2)	o	***		
Diameter of apical bud/Distance between opposite lateral buds (D_1/D_2)	***	o	o	
Length of lateral buds (Hs)				
Length of apical bud/Length of lateral buds (Ht/Hs)				
No. of lateral buds	*	***	o	o
No. of big lateral buds	**	**		
Percentage of small lateral buds				

o No significance. * Significant at 5 % level.** Significant at 1 % level. *** Significant at 0.1 % level.

Table 24 (continued).

1959 between				1960 between			
progenies	blocks	provenances	plus and minus groups	progenies	blocks	provenances	plus and minus groups
*	***	o	*	**	***	o	o
**	***	o		***	***	o	o
***	***	o	o	***	o	o	o
o	***			*	***		
**	***			**	**		
				***	***	o	*
o	***	o	o	**	***	o	o
*	***	*	o	o	***	o	o
				o	***	*	o
				***	o	o	o
*	**	o	o	**	*	o	o
***	***	*	o	***	**	o	o
				***	***	o	o
***	***	o	o	**	**	o	o
***	***	o	o	***	***	o	o
				***	***	o	o
**	**	**	o	*	**	o	o
o	*	**	o	*	*	*	o
*	o	o	o	**	*	***	o
				o	o	o	o
*	**	o	o	**	*	o	o
***	**	**	o	***	o	o	o
o	**	o	o	**	*	o	
***	*	o	o	o	o	*	
**	*	*	o	o	**	o	o
				*	o	o	o

h) *Abnormalities*

Various disturbances in the development of buds and branches occurring in the progenies analyzed in the present work have been partly reported in previous papers (EHRENBERG *et al.*, 1955; EHRENBERG, 1958, 1961).

The abnormalities are of two different types:

1. Disturbances in bud and shoot formation (Figs. 33—35). They seem to be caused by one or a few dominant genes with varying penetrance and expressivity.
   These disturbances may be divided into the following types:
   a. Apical bud divided into two, three, or four parts within one bud sheath.
   b. Two, three, or four separate apical buds of equal size.
   c. Forks on the annual shoots.
   d. Fasciation, *i.e.* a flattening of the upper part of the annual shoot and a formation of several apical buds in a row at the top of the shoot.
2. Disturbances in the buds already developed. The phenomenon of prolepsis belongs to this type of disturbance. The buds developed on the annual shoots at the end of the growing season burst again in the same year, producing short shoots with new apical and lateral buds (Fig. 36). The number of branches in the first whorl is often increased in the following year.

In addition, trees with short, thick needles or other rare deviations from the normal type were found occasionally (see below p. 82).

Data from the observations made in various years are presented in Tables 25 and 37. Table 25 is taken from EHRENBERG (1961) but it has been extended to include some results of the inventories in 1957 and 1961. The four progenies of the Boxholm minus tree VIII: 46^- showed an exceptionally high frequency of individuals with abnormalities of the type 1 a—d. A detailed analysis of the frequency and type of abnormalities was confined to these progenies.

1. The percentage of specimens with *abnormalities of the type 1 a—d* varied markedly in the different progenies and years without any clear relation to the age of the progeny (Table 25).

As stated previously (EHRENBERG and GUSTAFSSON, 1957), these abnormalities were largely restricted to progenies with VIII: 46^- as a parent. The occurrence of abnormal shoots in the other progenies was more or less sporadic. In progenies obtained from the plus trees E 4015^+ and E 4008^+

Fig. 33. Abnormalities of the type 1a and b. Two or more apical buds within one bud sheath or many separate apical buds.

Fig. 34. Forks developing on young annual shoots. a) The tip of the shoot is flattened out. b) Ten days later the fork is clearly seen.

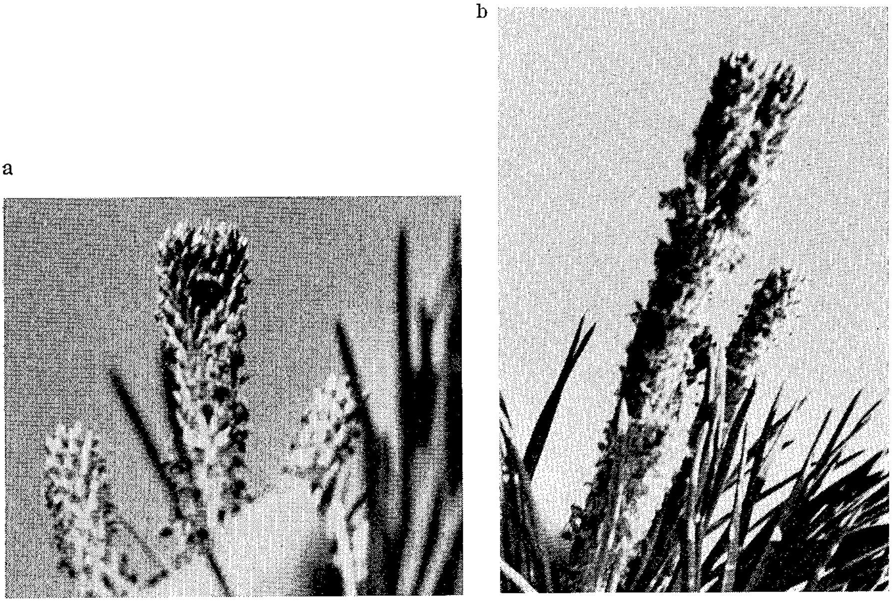


Table 25. Percentage of trees showing abnormalities of type 1 a—d in the annual shoots in 1957 to 1961.

Experiment	Combination	Year									
		1957		1958		1959		1960		1961	
		Number of trees	Per cent abnormal trees	Number of trees	Per cent abnormal trees	Number of trees	Per cent abnormal trees	Number of trees	Per cent abnormal trees	Number of trees	Per cent abnormal trees
X	E 4015^{+} × E 4008^{+}	133		208	1.9	208	0.5	207		207	
	E 4008^{+} × E 4015^{+}	122		195	1.5	194		193	0.5	191	
	VIII 46^{-} i.	137	2.8	137	26.3	131	8.4	129	7.0	129	11.6
	VIII 46^{-} × VIII 47^{-}	117	1.6	200	26.0	194	22.7	193	18.2	193	22.8
	Y 4015^{+} × Å 2^{+}	121		208		208	0.5	205		205	0.5
	S 3001^{+} o. p.	131		206		205	1.0	203	0.5	202	
G	E 4015^{+} o. p.	237	0.2	632	2.7	629	4.4	629	2.5	628	2.1
	E 4008^{+} o. p.	221	0.4	316	0.9	313	3.5	311	0.3	311	0.3
	VIII 46^{-} × E 4015^{+}	251	9.4	318	43.6	316	34.5	316	49.1	316	35.8
	VIII 46^{-} o. p.	228	4.9	311	44.7	309	38.2	303	42.9	301	40.5
	VIII 47^{-} o. p.	215	0.4	618		610	2.1	607	0.3	607	0.3
	Y 4015^{+} o. p.	219		319		314	1.9	313		312	
	Å 3^{-} o. p.	76		315	0.3	306	3.9	304		303	
	Å 4^{-} × Å 3^{-}	227		323	0.3	323	2.2	322		321	
Provenance											
	Boxholm										
	except progenies from VIII 46^{-}	928	0.2	1969	1.4	1954	2.1	1947	0.7	1944	0.5
	progenies from VIII 46^{-}	729	4.7	966	35.2	950	26.0	941	29.3	939	27.7
	Ånge	643		1165	0.2	1151	2.1	1144		1141	
	Värmland	131		206		205	1.0	203	0.5	202	

Table 26. Percentage of trees with abnormalities showing forking, fasciation or divided apical buds in different years.
Numbers in brackets based on less than five trees.

Experiment	Combination	Forking				Fasciation				Several apical buds				Total number of abnormal trees			
		1958	1959	1960	1961	1958	1959	1960	1961	1958	1959	1960	1961	1958	1959	1960	1961
X	E 4015^{+} × E 4008^{+}	(75)	(100)							(25)				4	1		
	E 4008^{+} × E 4015^{+}	(100)		(100)										3		1	
	VIII 46^{-} i.	69.4	90.9	44.5	33.3	2.8		22.2		27.8	9.1	33.3	66.7	34	11	8	12
	VIII 46^{-} × VIII 47^{-}	50.0	45.5	48.6	20.4	30.8	29.5	22.9	18.2	19.2	25.0	28.5	61.4	46	34	36	38
	Y 4015^{+} × Å 2^{+}		(100)												1		1
	S 3001^{+} o. p.		(100)	(100)											2	1	
G	E 4015^{+} o. p.	47.0	89.3	56.3	46.1	17.6	7.1	25.0	7.8	35.3	3.6	18.7	46.1	13	26	12	9
	E 4008^{+} o. p.	(50.0)	(66.7)	(100)	(100)					(50.0)	(33.3)			4	3	1	1
	VIII 46^{-} × E 4015^{+}	51.4	55.0	49.7	29.2	17.4	19.3	23.9	10.6	31.2	25.7	26.4	60.2	112	85	118	93
	VIII 46^{-} o. p.	53.2	58.2	52.3	32.0	20.1	18.6	30.8	13.1	26.6	22.9	16.9	54.9	116	89	98	93
	VIII 47^{-} o. p.		(33.3)				(33.3)	(50.0)	(50.0)		(33.3)	(50.0)	(50.0)		3	2	2
	Y 4015^{+} o. p.																
	Å 3^{-} o. p.	(100)	83.3				16.7							1	6		
	Å 4^{-} × Å 3^{-}	(100)	100											1	6		
	Total	54.1	61.0	50.9	30.0	18.4	18.0	26.3	12.3	27.5	21.0	22.9	57.7	334	267	270	249

Table 27. Expressivity of abnormalities 1 a—d in four progenies from the minus tree VIII 46^- and the mean tree heights of the progenies in 1960 and 1961.

Experiment	Year	Combination	Sum of points			Sum total	No. of trees	No. of points per tree	Mean Height (cm)
			Forking	Fasciation	Several apical buds				
X	1960	VIII 46^- i.........	8	6	4	18	8	2.3	90.5±2.22
		VIII 46^- × VIII 47^-	40	24	13	77	36	2.2	128.3±2.57
G	1960	VIII 46^- × E 4015^+ .	208	117	41	366	118	3.1	148.2±2.11
		VIII 46^- o. p......	190	129	22	341	98	3.5	144.5±2.28
X	1961	VIII 46^- i.........	12		14	26	12	2.2	105.1±2.88
		VIII 46^- × VIII 47^-	20	27	27	74	38	1.9	152.7±3.51
G	1961	VIII 46^- × E 4015^+ .	72	36	78	186	93	2.0	182.4±2.25
		VIII 46^- o. p......	80	51	71	202	93	2.2	174.7±2.73

after open pollination, however, abnormal specimens were recorded regularly every year, the frequency usually being several times higher in the progeny of E 4015^+. The lowest frequency of abnormalities was recorded in the seven-year-old material in 1957.

Fasciation (1 d) was in most years the type of anomaly least frequent in the entire material, as well as in each individual progeny (Table 26). Trees with fork formation (1 c) were frequent in the first years, while the number of individuals with divided apical buds (1 a—b) dominated in 1961. A rough estimate of the *expressivity* (the degree of manifestation of a gene, TIMOFÉEFF-RESSOVSKY, 1934; ALLARD, 1960) was made for the four progenies of VIII: 46^- in 1960 and 1961. Fasciation was classified as three points, fork formation as two points, and divided apical buds as one point. If any of the three types was repeatedly recorded in the same individual, the scoring of the feature was doubled. The results are given in Table 27. Expressivity in the slow-growing progenies (*i*, − × −) was lowest in 1960, fork formation and fasciation being rare in these progenies. The progenies with the most vigorous growth, − × + and − o.p., also had the highest mean values in points, *i.e.* expressivity was highest in vigorous trees. In the following year (1961) divided apical buds were the abnormality most commonly occurring even in vigorously growing trees, and the expressivity was therefore about equal in weak and vigorous progenies that year. In addition to this variation between the years, probably caused by climatic factors, there were other environmental factors that influenced the development of the buds and shoots. As mentioned before, the site conditions varied in both experiments. The effect of these dissimilarities was expressed by

Table 28. Influence of environment on expressivity of the abnormalities 1 a—d. Mean points per tree in different plots of four progenies in 1960 and 1961.

Experiment	Combination	1960				1961			
		Block				Block			
		I	II	III	IV	I	II	III	IV
X	VIII 46^- i.	—	2.0	3.0	—	—	2.3	1.5	—
	VIII 46^- × VIII 47^-	2.8	2.3	2.0	—	2.1	2.0	1.6	—
G	VIII 46^- × E 4015^+	3.6	3.1	3.3	2.7	2.4	2.0	2.0	1.8
	VIII 46^- o. p.	3.4	3.3	4.2	2.3	2.0	2.4	2.3	2.1

Table 29. Penetrance. Trees with abnormalities of type 1 a—d in one to four years in per cent of the total number of abnormal trees.

Numbers in brackets based on less than five trees.

Experiment	Combination	No. of abnormal trees	Number of years				Percentage of abnormal trees
			1	2	3	4	
X	E 4015^+ × E 4008^+	4	(100)				1.9
	E 4008^+ × E 4015^+	4	(100)				2.1
	VIII 46^- i.	42	64.3	21.4	4.8	9.5	30.7
	VIII 46^- × VIII 47^-	80	50.0	23.8	15.0	11.2	40.0
	Y 4015^+ × Å 2^+	1	(100)				0.5
	S 3001^+ o. p.	3	(100)				1.4
G	E 4015^+ o. p.	33	63.6	12.1	9.1	15.2	5.2
	E 4008^+ o. p.	4	(50.0)	(25.0)	(25.0)		1.3
	VIII 46^- × E 4015^+	198	38.4	29.3	15.7	16.7	62.3
	VIII 46^- o. p.	176	33.5	23.3	21.6	21.6	56.6
	VIII 47^- o. p.	6	100				1.0
	Y 4015^+ o. p.	1	(100)				0.3
	Å 3^- o. p.	8	100				2.5
	Å 4^- × Å 3^-	7	(100)				2.2

Table 30. Penetrance of abnormalities of type 1 a—d in 1958 to 1961. Percentage of total number of abnormal trees.

Experiment	Combination	Percentage			
		1958	1959	1960	1961
X	VIII 46^- i.	80.9	28.6	19.0	28.6
	VIII 46^- × VIII 47^-	57.5	42.5	38.8	46.3
G	VIII 46^- × E 4015^+	57.6	42.9	59.6	47.0
	VIII 46^- o. p.	65.9	50.0	55.7	52.8
	E 4015^+ o. p.	39.4	78.8	36.4	27.3

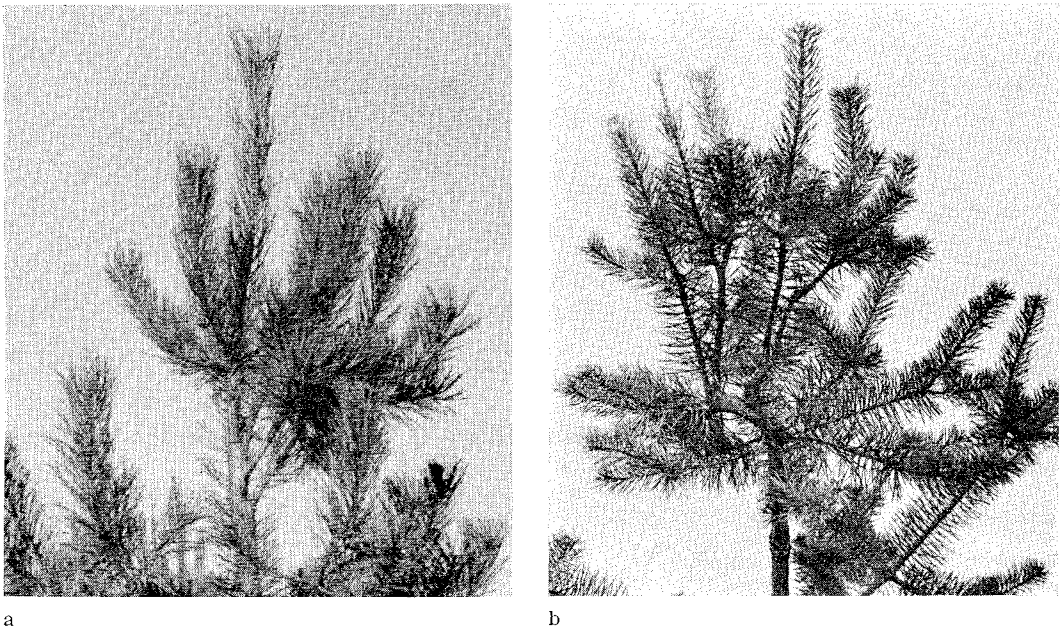


Fig. 35. Trees with fasciation take on a bushy, irregular shape. a) Fasciation and forking of the terminal shoot in one year results in heavy branches between two branch whorls in the year next. b) Several leading shoots developed out of a fasciated terminal shoot compete.

the variation in the point values per tree obtained in the different plots within each progeny (Table 28). In experiment G the lowest mean point-value occurred in block IV, where the trees were inferior in growth to those in the other three plots in blocks I—III.

Malformations occurred in some specimens every year. In others they appeared only in one or two of the four years (Table 29). The *penetrance* (the ability of a gene to be expressed in individuals carrying it, Timoféeff-Ressovsky, 1934; Allard, 1960) was apparently incomplete, and varied in the different progenies. The progeny obtained from VIII: 46^{-} after selfing thus had a total of 42 abnormal individuals out of 137 (30.7 per cent). Of these 42 individuals only 6 (*i.e.* 14 per cent) showed abnormalities in more than two years. Growth in this progeny was slow, and vigour was depressed. In the progenies VIII: $46^{-} \times$ E 4015^{+} and VIII: 46^{-} o.p., which produced high frequencies of abnormal trees (62 and 57 per cent respectively), malformations were observed in about two-thirds of the abnormal trees during several years.

In the progenies with a low percentage of deformed specimens, malformations generally occurred only one year in the same tree (Table 29). The

Table 31. Comparison between length of terminal shoots in trees with abnormalities 1 a—d (Th$_a$) and in normal trees (Th).

Experiment	Combination	Year	Terminal shoot	Number of trees	Mean Length (cm)	Significance of the differences t
X	VIII 46$^-$ i	1959	Th$_a$	12	12.1 ± 1.30	0.67
			Th	118	11.1 ± 0.73	
		1960	Th$_a$	8	15.6 ± 1.75	2.04*
			Th	118	12.0 ± 0.25	
		1961	Th$_a$	12	25.4 ± 1.56	4.61***
			Th	116	17.2 ± 0.85	
	VIII 46$^-$ × VIII 47$^-$	1959	Th$_a$	34	24.7 ± 0.84	5.84***
			Th	158	19.2 ± 0.44	
		1960	Th$_a$	31	27.9 ± 0.26	6.20***
			Th	160	21.8 ± 0.95	
		1961	Th$_a$	37	38.9 ± 0.80	6.55***
			Th	157	31.9 ± 0.70	
G	VIII 46$^-$ × E 4015$^+$	1959	Th$_a$	85	25.0 ± 0.55	4.82***
			Th	231	21.6 ± 0.44	
		1960	Th$_a$	118	29.8 ± 0.68	6.60***
			Th	194	24.9 ± 0.30	
		1961	Th$_a$	93	39.1 ± 0.68	1.97*
			Th	222	37.4 ± 0.53	
	VIII 46$^-$ o. p.	1959	Th$_a$	89	25.7 ± 0.58	6.06***
			Th	212	21.0 ± 0.51	
		1960	Th$_a$	98	28.0 ± 0.62	5.41***
			Th	203	23.5 ± 0.57	
		1961	Th$_a$	99	36.5 ± 0.84	2.60**
			Th	201	33.6 ± 0.74	

progeny E 4015$^+$ o.p. deviated slightly. Although it had a low frequency of abnormal individuals (5.2 per cent), no less than 36 per cent of these produced malformed shoots or buds in more than one year.

The penetrance varied in the individual progenies from one year to another (Table 30). In the progeny obtained after selfing, VIII: 46$^-$ *i*, abnormalities thus appeared in 34 out of 42 individuals in 1958 (81 per cent) but only in 8 individuals in 1960 (19 per cent). A similar great variation occurred in E 4015$^+$ o.p., while the corresponding values in the other progenies varied between 66 and 39 per cent.

As a consequence of disturbances in the formation of buds and shoots, the individuals generally took on a bushy and irregular appearance.

Table 32. Length of terminal shoots in 1961. Comparison between trees with abnormalities 1 a—d in 1960 (Th_{a60}) and the progeny mean (Th).

Experiment	Combination	Terminal shoot	No. of trees	Mean length (cm)
X	VIII 46⁻ i.	Th_{a60} Th	8 128	26.9 ± 2.66 17.9 ± 0.75
	VIII 46⁻ × VIII 47⁻ . .	Th_{a60} Th	31 194	37.7 ± 1.48 33.1 ± 0.75
G	VIII 46⁻ × E 4015⁺. . .	Th_{a60} Th	118 315	38.3 ± 0.61 37.9 ± 0.28
	VIII 46⁻ o. p.	Th_{a60} Th	97 300	37.8 ± 0.76 34.6 ± 0.57

Particularly the uppermost part of the young tree deviated markedly from the normal appearance by displaying several terminal shoots, or a flattened shoot with a large number of buds. The number of lateral branches in whorl 1 as well, was usually larger than normal. Two or several terminal shoots in one year resulted in either a maintenance of several leading shoots, or in a leading terminal, with the other terminal shoots reduced to heavy lateral branches next year (Fig. 35). Double or redoubled annual shoots on the branches of the various whorls also contributed to the deformation of the trees.

The abnormalities generally occurred in the individuals of a progeny growing most vigorously. Thus, trees with abnormalities had, on an average, longer terminal shoots than individuals that had no malformations during the same year (Table 31). Abnormal shoot development did not impede the growth of the leading shoot next year (Table 32).

2. *Prolepsis.* The occurrence of proleptic shoots had a similar effect on the appearance of the trees, whether developed from apical or from lateral buds (EHRENBERG and GUSTAFSSON, 1957). In the first case, double sets of branches were formed in whorl 1 upon the development of shoots in the following year. In the latter case the tree developed strong lateral branches which competed heavily with the terminal shoot (Fig. 36). SCHLÜTER (1956) made similar observations in his study on abnormal shoot development in Scots pine.

Prolepsis occurred every year in all the Boxholm progenies in the *experiments X and G.* Its frequency varied strongly between the progenies and between the years (Table 33). The average percentage of proleptic trees was highest in 1957 and decreased when the trees grew older. The progeny ob-

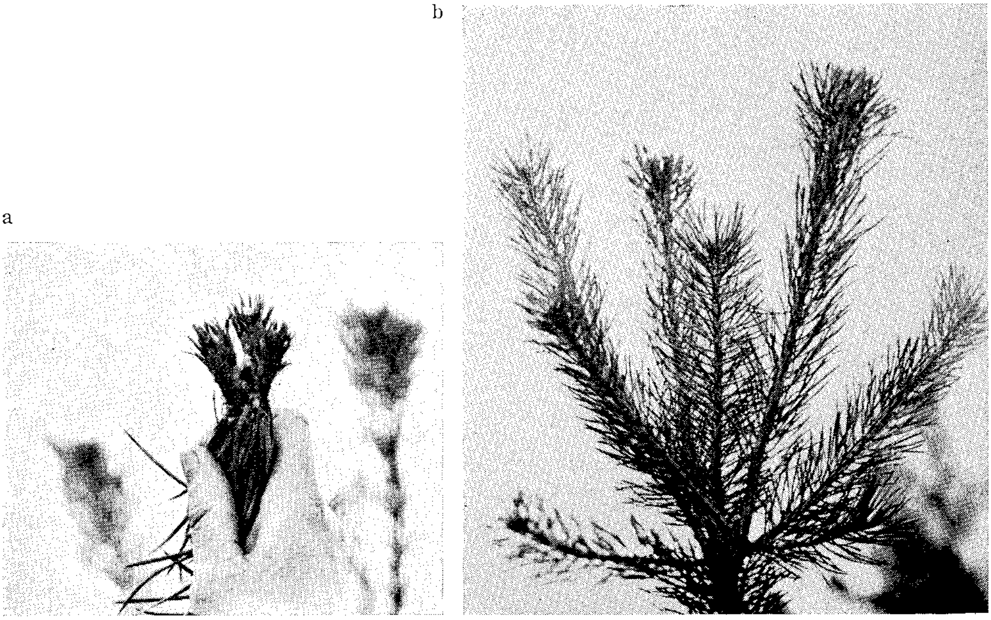


Fig. 36. a) Prolepsis developed from lateral buds. b) Strong lateral branches developed from proleptic lateral buds compete heavily with the terminal shoot.

tained after inbreeding, VIII: 46^- *i* (not recorded in 1957), had the lowest frequency of individuals with prolepsis in 1959 (0.8 per cent).

The conspicuous differences between the progenies are further evident from the great variation in penetrance of the character (Table 34). The strongly varying values indicate great dissimilarities in the genetic constitution of the progenies. A predisposition for prolepsis must consequently be considered to exist to a large extent in the progenies of the parent trees E 4015^+ and VIII: 46^-, where 14 to 24 per cent of the individuals showed prolepsis, irrespective of whether the progenies had been produced by controlled crossings or open pollination. The crossing between these two trees, VIII: 46^- × E 4015^+, resulted in a progeny in which over 43 per cent of the young trees showed prolepsis. The percentage of individuals with recurrent prolepsis was also higher in this progeny than in the others.

The trait was usually observed only one year, and very seldom four years in the same individual. In the progenies E 4008^+ o.p. and VIII: 47^- o.p., for instance, 85 to 90 per cent of the abnormal trees developed proleptic shoots in one year only. The same phenomenon, though still more pronounced, appeared in the progenies from Ånge and Värmland. In these, pro-

Table 33. Percentage of trees with proleptic shoots in 1957 to 1961.

Experiment	Combination	Year									
		1957		1958		1959		1960		1961	
		Number of trees	Per cent proleptic trees	Number of trees	Per cent proleptic trees	Number of trees	Per cent proleptic trees	Number of trees	Per cent proleptic trees	Number of trees	Per cent proleptic trees
X	E 4015^{+} × E 4008^{+}	133	23.3	208	5.8	208	8.6	207	0.9	207	2.4
	E 4008^{+} × E 4015^{+}	122	23.8	195	11.0	194	8.2	193	1.6	191	3.7
	VIII 46^{-} i	137	—	137	4.4	131	0.8	129	2.3	129	3.9
	VIII 46^{-} × VIII 47^{-}	117	30.8	200	8.0	194	7.7	193	4.2	193	3.6
	Y 4015^{+} × Å 2^{+}	121		208		208		205		205	2.8
	S 3001^{+} o.p.	131		206		205		203		202	0.5
G	E 4015^{+} o. p.	237	19.0	632	6.6	629	9.4	629	2.4	628	1.8
	E 4008^{+} o. p.	221	9.5	316	1.6	313	2.6	310	0.3	311	5.8
	VIII 46^{-} × E 4015^{+}	251	55.4	318	20.1	316	29.7	316	10.4	316	12.0
	VIII 46^{-} o. p.	228	36.4	311	10.6	309	9.4	303	4.6	301	5.0
	VIII 47^{-} o. p.	215	11.2	618	1.1	610	2.6	607	1.2	607	0.8
	Y 4015^{+} o. p.	219	0.9	319		314	0.6	313		312	5.1
	Å 3^{-} o. p.	76	3.9	315	0.9	306	0.3	304		303	4.6
	Å 4^{-} × Å 3^{-}	227		323	0.3	323		322		321	2.2

Provenance

Boxholm										
except progenies from VIII 46^{-}	928	17.4	1969	5.2	1954	6.3	1946	1.3	1944	2.9
progenies from VIII 46^{-}	729	32.4	966	10.8	950	11.9	941	5.4	939	6.1
Ånge	643	1.2	1165	0.3	1151	0.2	1144		1141	3.7
Värmland	131		206		205		203		202	0.5

Table 34. Penetrance. Trees with prolepsis in one to four years in per cent of the total number of proleptic trees. Numbers in brackets based on less than five trees.

Experiment	Combination	No. of proleptic trees	Number of years				Percentage of proleptic trees
			1	2	3	4	
X	E 4015^{+} × E 4008^{+}	30	73.3	26.7			14.4
	E 4008^{+} × E 4015^{+}	38	68.4	28.9	2.7		19.5
	VIII 46^{-} i.	13	76.9	15.4	7.7		9.5
	VIII 46^{-} × VIII 47^{-}	46	76.1	17.4	2.2	4.3	23.5
	Y 4015^{+} × Å 2^{+}	5	100				2.4
	S 3001^{+} o. p.	1	(100)				0.5
G	E 4015^{+} o. p.	91	71.4	22.0	5.5	1.1	14.4
	E 4008^{+} o. p.	27	85.2	11.1	3.7		8.5
	VIII 46^{-} × E 4015^{+}	139	54.0	33.1	8.6	4.3	43.7
	VIII 46^{-} o. p.	65	64.6	32.3	3.1		20.9
	VIII 47^{-} o. p.	30	90.0	6.7			4.9
	Y 4015^{+} o. p.	18	94.4	5.6			5.6
	Å 3^{-} o. p.	18	100				5.7
	Å 4^{-} × Å 3^{-}	8	100				2.5

lepsis was lacking entirely in some years (*e. g.* in 1960), and in nearly all the abnormal trees recorded, it appeared only once.

Within a progeny, prolepsis occurred more frequently in vigorous trees than in slow-growing individuals. On an average, the proleptic trees had longer terminal shoots than the normal trees in the same progeny (Table 35). There was no indication that prolepsis in one year had any inhibiting effect on the growth during the following year (Table 36).

As mentioned above, the frequency of trees with prolepsis was also high in the progenies in which abnormalities of the type 1 a—d (fork formation, fasciation, etc.) occurred at a relatively high frequency. The two kinds of anomalies occurred in the same individuals more often than would have been expected if they had been entirely independent of each other. Comparisons were made between 13 pairs of percentages (Snedecor 1946 p. 447 *et seq.*, angle transformation). Average of 13 differences (in degrees):

$$8.506 \pm 2.278,\ t = \frac{8.506}{2.278} = 3.73^{**}.\ \mathrm{Df} = 12.$$

The great variation in the frequency and occurrence of prolepsis was also conditioned by the varying environmental factors contributing to the large block variations observed in each progeny in the same year.

The results obtained in the *observation experiment O* were similar to those obtained in the experiments X and G (Table 37). The percentage of trees with abnormalities of the type 1 a—d was high in the progenies that originated from the minus tree VIII: 46^{-} as the mother or father tree. No

Table 35. Comparison between length of terminal shoots in trees with prolepsis (Th_p) and in normal trees (Th).

Experiment	Combination	Year	Terminal shoot	Number of trees	Mean Length (cm)	Significance of the differences t
X	VIII 46^- i...........	1959	Th_p Th	1 129	25.0 11.1 ±0.46	
		1960	Th_p Th	2 124	30.0 11.6 ±0.44	
		1961	Th_p Th	5 124	29.0 ±2.92 17.3 ±0.75	3.89***
	VIII 46^- × VIII 47^- ..	1959	Th_p Th	17 175	25.6 ±1.12 19.6 ±0.42	5.00***
		1960	Th_p Th	8 183	28.8 ±2.80 22.5 ±0.48	2.22*
		1961	Th_p Th	7 187	41.4 ±3.03 32.9 ±0.76	2.72*
G	VIII 46^- × E 4015^+...	1959	Th_p Th	94 222	27.4 ±0.49 20.4 ±0.39	11.25***
		1960	Th_p Th	33 279	26.1 ±1.17 26.8 ±0.47	0.55
		1961	Th_p Th	36 279	39.7 ±1.34 37.6 ±0.45	1.49
	VIII 46^- o.p	1959	Th_p Th	30 271	26.3 ±1.24 22.1 ±0.42	3.20**
		1960	Th_p Th	14 287	27.1 ±1.94 24.9 ±0.46	1.11
		1961	Th_p Th	16 284	39.4 ±2.50 34.4 ±0.57	1.95*

such abnormal individuals occurred in the other progenies included in the experiment. A high percentage of prolepsis was recorded among the same progenies as in experiments X and G. The influence of *i.a.* the climate during the different years was evident, since the frequencies of both types of abnormalities varied strongly from one year to another. In the slowgrowing and weak progeny VIII: 46^- *i*, the frequency of abnormal individuals was low.

i) *Other irregularities in the development of the young trees*

A few individuals with *short, thick and stiff needles* were recorded in the selfed progenies (Tables 38, 39 and Fig. 37). Trees with short needles occurred

Table 36. Length of terminal shoots in 1960 and 1961 in trees with prolepsis in 1959 and 1960 respectively (Th$_{p59}$ and Th$_{p60}$) compared with the mean length of terminal shoots of the progenies (Th).

Experiment	Combination	Year	Terminal shoot	Number of trees	Mean Length (cm)
X	VIII 46^{-} × VIII 47^{-}	1960	Th$_{p59}$ Th	17 191	29.1 ± 1.67 22.7 ± 0.48
		1961	Th$_{p60}$ Th	8 194	36.9 ± 4.21 33.1 ± 0.75
G	VIII 46^{-} × E 4015^{+}.......	1960	Th$_{p59}$ Th	94 312	31.1 ± 0.75 26.7 ± 0.45
		1961	Th$_{p60}$ Th	33 315	37.1 ± 1.23 37.9 ± 0.28
	VIII 46^{-} o. p.............	1960	Th$_{p59}$ Th	30 301	28.8 ± 1.35 25.0 ± 0.45
		1961	Th$_{p60}$ Th	14 300	33.6 ± 2.64 34.6 ± 0.57

Table 37. Experiment O. Percentage of trees with abnormalities 1 a—d and with prolepsis in 1958 to 1960.

Combination	No. of trees	Percentage of trees					
		1958		1959		1960	
		1 a—d	Prolepsis	1 a—d	Prolepsis	1 a—d	Prolepsis
E 4015^{+} o. p.........	32				9.4		6.3
E 4015^{+} × E 4008^{+}....	23				13.0		8.7
E 4015^{+} i...........	16		6.3		12.5	6.3	6.3
E 4008^{+} o. p.........	23				4.3		8.7
E 4008^{+} × E 4015^{+}....	19		5.3		26.3		
VIII 46^{-} o. p........	24	66.7	8.3	70.8	41.7	79.2	4.2
VIII 46^{-} × E 4015^{+}...	24	41.7	29.2	75.0	70.8	69.6	8.7
E 4015^{+} × VIII 46^{-}...	22	90.9	22.7	86.4	54.5	90.9	22.7
E 4008^{+} × VIII 46^{-}...	24	58.3	16.7	88.0	52.0	64.0	24.0
VIII 46^{-} × VIII 47^{-} ..	24	29.2		72.0	36.0	68.0	8.0
VIII 46^{-} i..........	43	46.5	2.3	44.2	4.7	27.9	
VIII 47^{-} o. p........	24						
Y 4015^{+} × Å 4^{-}.......	24		4.0				4.0
BD 4016^{+} i..........	7		42.9				

Ten progenies from Ånge and six from Värmland showed no abnormalities 1 a—d and no prolepsis.

Table 38. Percentage of trees with short needles, sinuous shoots and young cones in 1960 and 1961.

Experiment	Combination	Percentage of trees					
		Short needles		Sinuous shoots		Young cones	
		1960	1961	1960	1961	1960	1961
X	E 4015$^+$ × E 4008$^+$....				29.9		0.5
	E 4008$^+$ × E 4015$^+$....				17.3	0.5	
	VIII 46$^-$ i...........	0.6	0.6				0.8
	VIII 46$^-$ × VIII 47$^-$ ..					1.6	0.5
	Y 4015$^+$ × Å 2$^+$.......					35.1	29.8
	S 3001$^+$ o. p.........				2.5	4.4	6.8
G	E 4015$^+$ o. p.........			0.6	3.3		1.1
	E 4008$^+$ o. p.........			13.2	16.4	1.3	1.3
	VIII 46$^-$ × E 4015$^+$...	0.6	0.6		0.3	0.3	0.6
	VIII 46$^-$ o. p........	0.3	0.3				
	VIII 47$^-$ o. p........			0.2	0.3	0.3	1.2
	Y 4015$^+$ o. p........				2.2	24.3	20.8
	Å 3$^-$ o. p.............				0.3	9.9	7.6
	Å 4$^-$ × Å 3$^-$..........			0.3		3.7	2.6

now and then in other progenies, too, but there the needles were of a different and weaker type than those of the short-needled, selfed trees. Schröck (1957), in analyzing a progeny obtained from a pine with abnormally high cone production, records some individuals with short, thickened needles. He ascribes their rare occurrence to a recessive gene. The occurrence of such short-needled individuals in the selfed progenies in the present material is an indication that the abnormality is due to the homozygotization of recessive

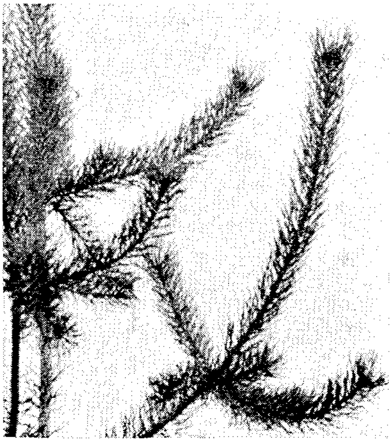


Fig. 37. In the selfed progeny E 4015$^+$ *i* trees with short stiff needles occurred.

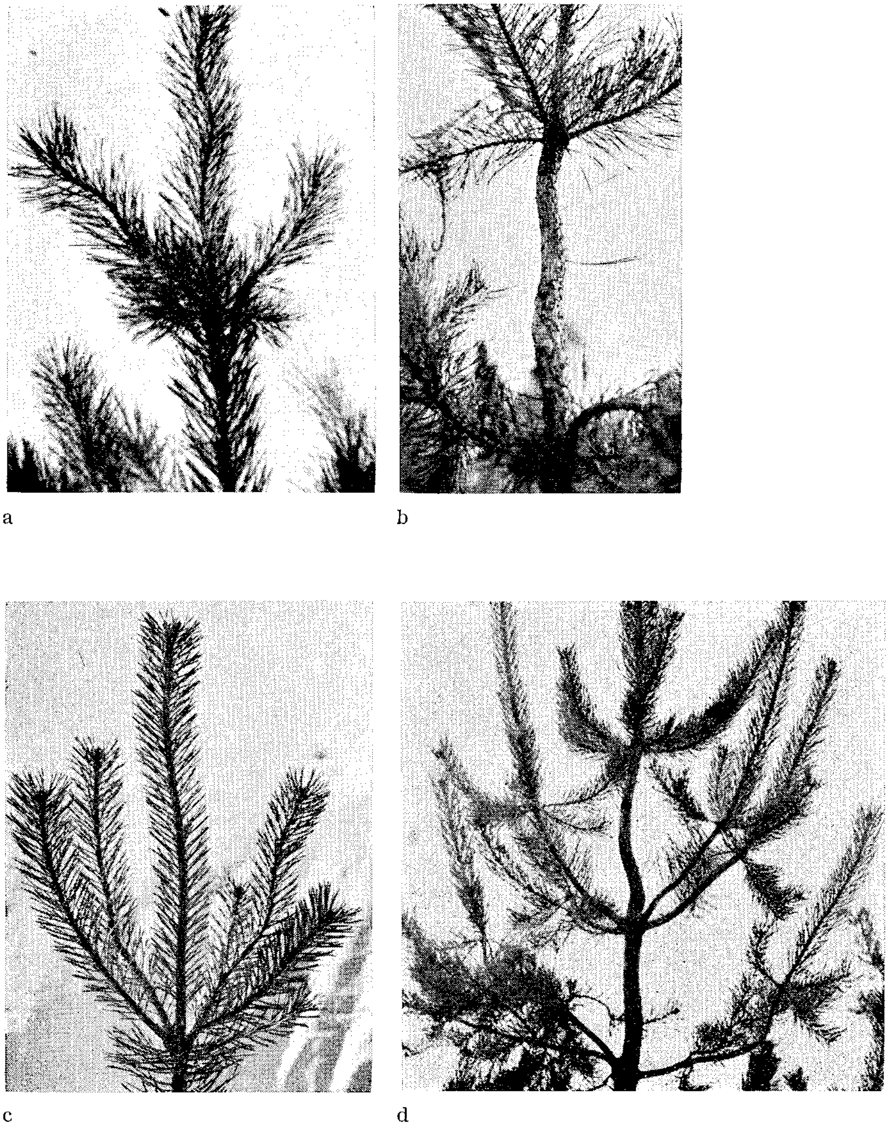


Fig. 38. Trees with sinuous shoots occurred in the grafts as well as in the progenies of the plus tree E 4008^{+}. a) Graft of E 4008^{+}. Terminal shoot and branches in whorl 1 with bends in 1960. b) The same graft in 1962 with the bends remaining in the three-year old stem and branches. c) Young tree of the crossing E $4008^{+} \times$ E 4015^{+}. Terminal shoot and branches of whorl 1 in 1960. d) The same tree two years later still showing the bends and crooks formed in 1960.

Table 39. Experiment O. Percentage of trees with short needles, sinuous shoots and young cones in 1960.

Combination	No. of trees	Percentage of trees			Combination	No. of trees	Percentage of trees		
		Short needles	Sinuous shoots	Young cones			Short needles	Sinuous shoots	Young cones
E 4015$^+$ o. p.	32		25.0		Å 2$^+$ o. p.	21			4.3
E 4015$^+$ × E 4008$^+$	23		78.3		Å 2$^+$ × Y 4015$^+$	23		4.2	20.8
E 4015$^+$ i.	16	12.5	6.3		Å 3$^-$ o. p.	49			2.2
E 4008$^+$ o. p.	23		43.5		Å 3$^-$ × Å 4$^-$	48			
E 4008$^+$ × E 4015$^+$	19	5.3	52.6		Å 3$^-$ i.	15			
VIII 46$^-$ o. p.	24		4.2	4.2	Å 4$^-$ o. p.	30			3.3
VIII 46$^-$ × E 4015$^+$	24		17.4		Å 4$^-$ × Y 4015$^+$	24			
E 4015$^+$ × VIII 46$^-$	22		4.5		Å 4$^-$ × Å 3$^-$	25			
E 4008$^+$ × VIII 46$^-$	24		20.0		S 3001$^+$ o. p.	23			
VIII 46$^-$ × VIII 47$^-$	24			4.0	S 3001$^+$ i.	25			4.0
VIII 46$^-$ i.	43	11.6			S 3002$^+$ o. p.	11		27.3	
VIII 47$^-$ o. p.	24				S 3002$^+$ i	14	14.3	50.0	9.1
Y 4015$^+$ o. p.	24			4.2	S 3003$^+$ o. p.	23			21.7
Y 4015$^+$ × Å 2$^+$	22			9.1	S 3003$^+$ i	7		8.7	28.6
Y 4015$^+$ × Å 4$^-$	24	4.0			BD 4016$^+$ i.	7	14.3	14.3	28.6

factors present in the mother trees. This is in accordance with the view expressed by SCHRÖCK.

Trees with markedly *sinuous* terminal shoots and branches (Fig. 38) occurred in 10 to 30 per cent of the progenies of E 4008$^+$ in 1960 and 1961 in the *experiments X and G* (Table 38). Similar, though less markedly sinuous terminal shoots were observed in some other progenies, but in these cases the shoots eventually became straight as the lignification proceeded. In the first-mentioned progenies the stems remained slightly crooked, as did also the branches. In the *observation experiment O*, too, the percentage of trees with sinuous annual shoots and deformed stems was considerably higher in the progenies of E 4008$^+$ (o.p., $+\times+$, $+\times-$) than in the other progenies (Table 39).

Four grafts of E 4008$^+$ growing close to the experimental fields, and grafted in 1950, exhibited the same winding of the terminal shoots, crooked stems and sinuous branches. Another 37 grafts of E 4008$^+$ growing partly in a plus-tree archive, and partly in a clone trial near Boxholm, were studied in this respect. In 1961 these grafts were eight years old, and 28 of them showed more or less winding stems and branches. In seven of the grafts the branches only were deformed. In one specimen the malformation was limited to the stem and terminal shoot. Finally, one graft had a straight stem and normal branches. Four grafts of E 4015$^+$, growing in the same locality, were normal.

The plus tree E 4008+ itself has a straight, well pruned stem. If the tree had sinuous shoots and a crooked stem in its youth, then the bends must have straightened out later. Since sinuous terminal shoots occur in grafts as well as among the progeny trees of E 4008+, the character probably exists in the plus tree itself and is transmitted to the offspring. In slash pine (*Pinus Elliottii* var. *Elliottii* ENGELM.), according to MERGEN (1955), similar malformations occur in young trees obtained from a parent tree with "cork-screw stem" after controlled pollinations. MERGEN considers this character to be partly due to environmental influences. A very rapid growth of the terminal shoots combined with a slow lignification of the cells may mean that "the weight of the leader bends the new growth", and further, "if lignification sets in while the new candles are crooked, they will maintain this form". Both the time when lignification starts and the speed at which it proceeds vary with the climate of the year. The significant differences between the progenies with regard to the frequency of crooked trees, however, are proof of genetic differences. "The tendency to form sweeps or crooks in the boles of slash pine is under genetic control."

The results obtained in *Pinus silvestris* in the present investigation evidently lead to the same conclusions (*cf*. DENGLER, 1939; SCAMONI, 1950; PERRY, 1960; DUFFIELD, 1962).

j) *Age of flowering*

The cone production was recorded every year at the same time as the other characters. The age at which the first cones were set varied strongly between the progenies. There was also considerable variation among the individuals in a progeny. In the years 1957 to 1959 a few cones were observed in some trees of the Ånge progenies. In 1960 two progenies of Y 4015+, used as the mother tree, contained 35 and 25 per cent respectively of trees with first-year cones (Table 38). The two other progenies from Ånge, Å 3− o.p. and Å 4− × Å 3−, as well as the progeny from Värmland, S 3001+ o.p., had beetween 3 and 10 per cent trees with cones. In the Boxholm progenies, cones were practically lacking. Similar results were obtained in 1961.

The northern progenies thus produced cones at an earlier age than the southern ones. Similar conditions were found by LANGLET (1943). According to him, the transplanting of northern provenances southwards facilitates female flowering at an early age, whereas he found the male flowering to be more irregular. Recently he has pointed out that a variation in the age of flowering may occur also in the native locality of the northern provenances (personal communication). The age of flowering would thus depend on

Table 40. Percentage of trees attacked by Melampsora pinitorqua in 1958 to 1961.

Experiment	Combination	Percentage of trees			
		1958	1959	1960	1961
X	E 4015^{+} × E 4008^{+}	55.3	29.4	0.5	
	E 4008^{+} × E 4015^{+}	35.6	24.8	1.0	1.0
	VIII 46^{-} i.	13.7	13.1		
	VIII 46^{-} × VIII 47^{-}	23.2	13.2	0.5	0.5
	Y 4015^{+} × Å 2^{+}	31.7	43.1	0.5	2.9
	S 3001^{+} o. p.	28.3	27.4	1.0	0.5
G	E 4015^{+} o. p.	37.8	37.8	1.7	1.1
	E 4008^{+} o. p.	46.3	56.2	0.6	1.0
	VIII 46^{-} × E 4015^{+}	27.2	15.8	0.6	0.3
	VIII 46^{-} o. p.	37.2	20.7		1.0
	VIII 47^{-} o. p.	20.3	41.0	1.2	2.1
	Y 4015^{+} o. p.	55.4	45.8	4.5	3.8
	Å 3^{-} o. p.	40.2	40.1	2.3	4.0
	Å 4^{-} × Å 3^{-}	52.0	43.1	2.2	4.4

inherent factors characteristic of each progeny, although some effect of the transplanting is also noticeable.

Besides this difference between the provenances, the progenies in the Ånge group differed markedly *inter se*. The frequency of cone-producing individuals was up to eight times higher in the progenies of Y 4015^{+} than in the other two Ånge progenies. Also the number of cones per tree was more abundant in the Y 4015^{+} progenies. A similar great difference between progenies and between trees of a progeny was found by SCHRÖCK (1949) in *Pinus silvestris*, FIELDING (1960) in *Pinus radiata*, JOHNSSON (1949) and STERN (1961) in *Betula* species.

The high frequency of early-flowering specimens in some of the progenies indicates that the ability to flower at an early age is genetically controlled (*cf.* MATTHEWS, 1950; MERGEN, 1961). The mode of inheritance cannot be established. SCHRÖCK (1949) in *Pinus silvestris* suggested this character to be due to a dominant gene.

Judging from the density of needles on the branches, male flowering has so far been very scarce in all the progenies (*cf.* SYLVÉN, 1908; LANGLET, 1943).

k) *Damage caused by fungi*

Widespread infection with pine twisting rust (*Melampsora pinitorqua* (Braun) Rostrup) was observed in 1958 and 1959, when the trees were eight and nine years old (Tables 40 and 41). The damages were recorded when

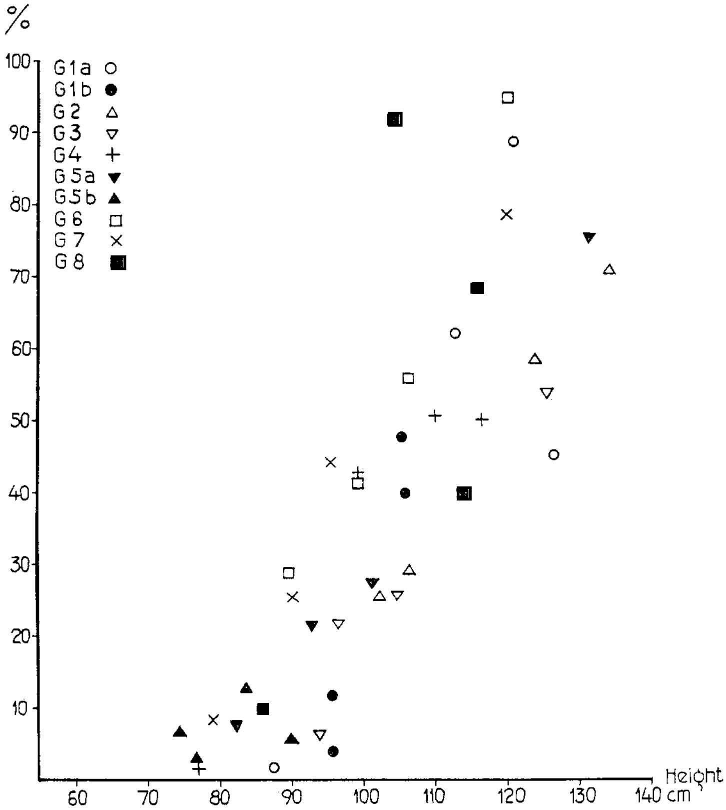


Fig. 39. *Experiment G.* Percentage of trees infected by *Melampsora pinitorqua* in different plots of each progeny in 1958. G1 a and b: E 4015⁺ o.p., G2: E 4008⁺ o.p., G3: VIII 46⁻ × E 4015⁺, G4: VIII 46⁻ o.p., G5 a and b: VIII 47⁻ o.p., G6: Y 4015⁺ o.p., G7: Å 3⁻ o.p., G8: Å 4⁻ × Å 3⁻.

the trees were measured in September. The percentage of individuals clearly showing the characteristic yellow spore masses on the annual shoots ranged between 1 and 94. In 1960 and 1961 the infection was slight ($<$ 5 per cent). Probably the variation was mainly due to differences in tree height, since in each progeny there was a clear connection between the average tree height of a plot and the percentage of infected individuals (Fig. 39, *cf.* SYLVÉN, 1917). The distance from the source of infection also seemed to be of importance. There were young aspens growing alongside a ditch running right through the experimental field, and the infection was heaviest in the plots adjoining the ditch (Fig. 40).

Table 41. Experiment O. Percentage of trees attacked by Melampsora pinitorqua in 1958 to 1960.

Combination	No. of trees	Percentage of trees			Combination	No. of trees	Percentage of trees		
		1958	1959	1960			1958	1959	1960
E 4015^{+} o. p.	32	53.1	12.5		Å 2^{+} o. p.	23	38.1	56.5	8.7
E 4015^{+} × E 4008^{+}	23	82.6	13.0	8.7	Å 2^{+} × Y 4015^{+}	24	34.8	45.8	8.3
E 4015^{+} i	16	37.5	6.3	6.3	Å 3^{-} o. p.	46	42.9	63.8	6.5
E 4008^{+} o. p.	23	87.0	30.4	26.1	Å 3^{-} × Å 4^{-}	47	39.6	66.7	
E 4008^{+} × E 4015^{+}	19	84.2	21.1	36.8	Å 3^{-} i	15	26.7	40.0	
VIII 46^{-} o. p.	24	66.7	20.8	8.3	Å 4^{-} o. p.	30	26.7	60.0	3.3
VIII 46^{-} × E 4015^{+}	23	54.2	12.5	8.7	Å 4^{-} × Y 4015^{+}	24	33.3	79.2	4.2
E 4015^{+} × VIII 46^{-}	22	45.5	4.5	4.5	Å 4^{-} × Å 3^{-}	24	48.0	45.8	8.3
E 4008^{+} × VIII 46^{-}	25	75.0	16.0	12.0	S 3001^{+} o. p.	23	52.2	43.5	4.3
VIII 46^{-} × VIII 47^{-}	25	70.8	20.0		S 3001^{+} i	25	36.0	44.0	
VIII 46^{-} i	43	32.6	4.7		S 3002^{+} o. p.	11	30.8	36.4	18.2
VIII 47^{-} o. p.	24	54.2	16.7		S 3002^{+} i	14	42.9	50.0	14.3
Y 4015^{+} o. p.	24	58.3	45.8	8.3	S 3003^{+} o. p.	23	21.7	13.0	4.3
Y 4015^{+} × Å 2^{+}	22	45.5	54.5		S 3003^{+} i	7	14.3	14.3	
Y 4015^{+} × Å 4^{-}	25	68.0	72.0		BD 4016^{+} i	7	50.0	57.1	14.3

Significant differences between the progenies in *experiment G* were recorded in 1958, but not in 1959. In *experiment X* the two progenies with the slowest growth (VIII: 46^{-} × VIII: 47^{-}, VIII: 46^{-} *i*) also showed the lowest percentage of infected specimens. It is difficult to determine whether this variation in resistance is really due to genetic factors. GAVRIS (1939), RENNERFELT (1953), BERGMAN (1953) and KLINGSTRÖM (1963) are inclined to believe in the existence of genetic differences.

4. *Estimation of heritability*

In 1960 estimates of heritability ("narrow sense", LUSH 1949) of tree height, ratio between tree height and branch length, branch angle and number of branches per whorl were made for the material in *experiments X* (VIII: 46^{-} *i* excluded) and *G*. The estimates are based on the variance components, calculated from the mean squares of the analysis of variance of the different characters (KEMPTHORNE 1952, p. 110 *et seq.*). The estimation of the genotypic variance, σ_g^2, was calculated from the components of variance with consideration given to the number and type of combinations (controlled crossing, open pollination) included in each experiment. An example is given below of the estimation of the heritability of height growth in *experiment G.*

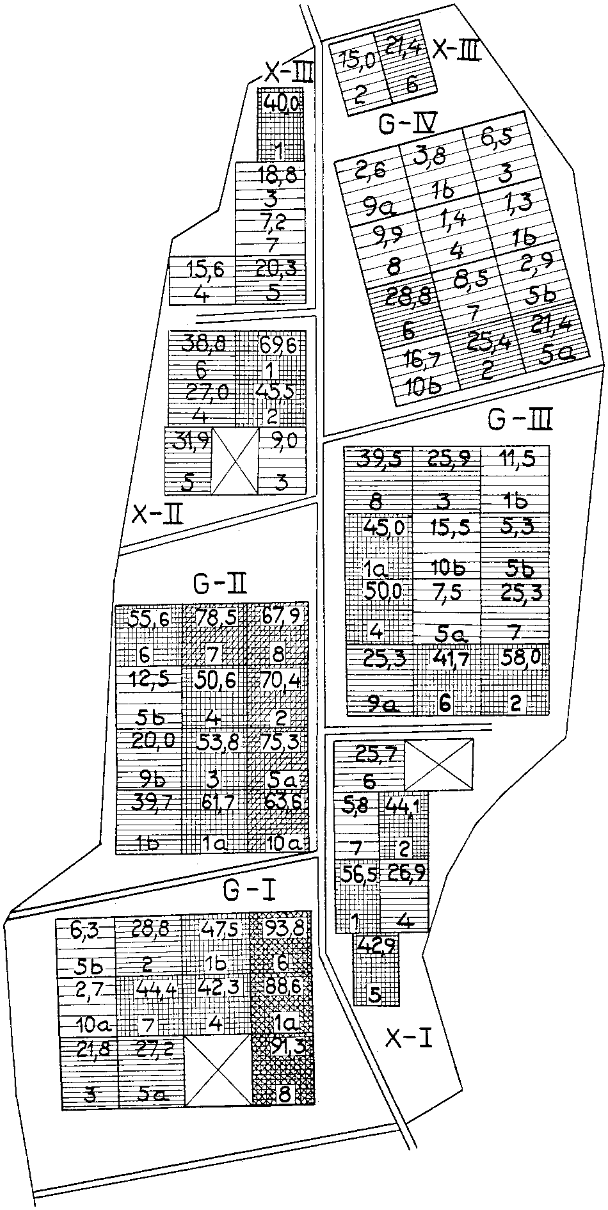


Fig. 40. The percentage of infected trees was highest in the plots adjacent to the ditch with young aspens.

1) *Analysis of variance of plot means*

Source of variation	df	M.S.
Progenies	7	1089.58
Blocks	3	3328.53
Error	21	321.89

Number of progenies = 8

2) *Variance between trees within plots* $\left(s_{pl}^2\right)$

$$s_{pl}^2 = 1104.31 \qquad \text{df} = 2476$$

3) *Components of variance*

From 1) is estimated the components of variance for:

Progenies, $s_t^2 = \dfrac{1089.58-321.89}{4} = 191.92$

Blocks, $s_b^2 = \dfrac{3328.53-321.89}{8} = 375.83$

Plots within blocks, $s_{pa}^2 = 321.89 - \dfrac{1104.31}{77.10} = 307.57$

Trees within plots, $s_{pl}^2 = 1104.31$

4) *Genetic variance* $\left(\sigma_g^2\right)$

The component of variance of s_t^2 has an expected value equalling

$$\alpha \cdot \sigma_g^2$$

where the value of α depends on the type of the combinations included.

Hence, as an estimation of σ_g^2 the expression

$$\sigma_g^2 = s_t^2 / \alpha$$

can be used.

In the experiment treated here

$$\alpha = \frac{1}{4\,(t-1)\,t}\,[k_1(t-k_1) + k_2(t-k_2) + \ldots . k_n(t-k_n)]$$

where n = number of parent trees, t = number of progenies, k_i = the number of progenies in which the i:th tree appears as parent. Applying the above formula we find $\alpha = 2/7$ in experiment G.

Thus

$$s_g^2 = \frac{7}{2} \cdot 191.92 = 671.72$$

5) *Environmental variance*

The components of variance s_b^2 and s_{pa}^2 are assumed to be due exclusively to environmental influence, whereas s_{pl}^2 may be divided further in one portion due to genetical and one portion due to environmental influences. Let the environmental effect be σ_e^2 then the expectation of s_{pl}^2 is

$$\sigma_e^2 + \beta\sigma_g^2.$$

Here $\beta = \frac{1}{t}\left(t_1 \cdot \frac{3}{4} + t_2 \cdot \frac{1}{2}\right)$

t_1 = number of progenies of open pollinated origin = 6

t_2 = number of progenies of cross pollinated origin = 2

We thus find $\beta = 11/16$ and σ_e^2 can be estimated as

$$s_{pl}^2 - \beta \cdot s_g^2 = 1104.31 - \frac{11}{16} \cdot 671.72 = 642.50$$

We now have three different estimates of the environmental variance (within a plot, within a block and total respectively)

$$s_e^2 = 642.5$$

$$s_e^2 + s_{pa}^2 = 642.5 + 307.57 = 950.07$$

$$s_e^2 + s_{pa}^2 + s_b^2 = 950.07 + 375.03 = 1325.90$$

6) *Estimation of heritability ("narrow sense")*

$$h^2 = \frac{s_g^2}{s_g^2 + s_e^2 + s_{pa}^2} = \frac{671.72}{671.2 + 950.07} = 0.41$$

The estimates of heritability correspond to the assumptions that 1) the block effects are added to the effects of the progenies, 2) the genetic effects are additive and 3) the obtained height values of a plot are a simple random sample from a population, the mean of which is the true mean of the progeny on the plot.

The method used is applicable only to experiments of the type studied

Table 42. Estimates of heritability (narrow sense) for four characters of the ten-year-old progenies (per cent).

Character	Heritability	
	Experiment X	Experiment G
Tree height (all trees)........	65	~~41~~ 46
Ratio height/Branch length		
Whorl 1..................	14	87
2..................	25	30
3..................	74	68
4..................	83	89
Branch angle Whorl 2........	39	36
3........	26	96
4........	14	81
Number of branches Whorl 1..	18	34
2..	9	33
3..	9	41
4..	43	14

here. The estimation of h^2 may be regarded as rather inaccurate since only eight progenies are included (five in experiment X).

The estimates of heritability of the four characters analyzed are given in Table 42.

If the above mentioned assumptions are accepted, then the estimates indicate a higher heritability of tree height than that estimated by TODA (1958) for Scots pine ($h^2 =$ about 24 %). In *Cryptomeria* the estimates of heritability for the same character were similar or about 25 % (TODA *et al.* 1959). On the other hand, the results obtained in experiment G in the present material are in agreement with the estimates of heritability of *Pinus ponderosa* height growth calculated by CALLAHAM and HASEL (39 %, 1961) and SQUILLACE and SILEN (36 %, 1962).

Selection gain

The estimates of heritability can be used to indicate the expected selection gains. An example will be given below.

The selection of the best growing progeny in experiment G—in this case E 4008+ o.p.—may lead to an estimated improvement of about thirteen per cent compared to the mean population height growth. This selection gain was calculated from the estimates of heritability given above and taking into consideration the type of combination The selection intensity was 12.5 per cent (one progeny out of eight). The selection gain in height (centimetres) was estimated as

$$k\sqrt{s_t^2+\varepsilon^2}\cdot\frac{s_t^2}{s_t^2+\varepsilon^2}$$

where $k = 1.65$ (*cf.* ALLARD, 1960 p. 93 *et seq.*), $s_g^2 = 191.92, \varepsilon^2 = \frac{321.89}{4} =$ 80.47.

An improvement in height growth of more than twelve per cent, through selection of the best growing progeny, must be considered rather good.

The estimated values of the heritability for crown width $\left(\frac{\mathrm{H}}{\mathrm{Brl}}\right)$ in both experiments and branch angle (experiment G) were fairly large, especially in the two lowermost whorls. Selections of progenies displaying relatively narrow crowns and wide branch angles will probably be effective and lead to improvement in these characters.

Estimates of heritability of the number of branches per whorl were of similar magnitude as heritability estimates for height growth (experiment G) in some of the whorls but conspicuously lower in others. There was no consistent increase or decrease of the values from whorl 1 to whorl 4 (*cf.* Campbell 1961). Despite the varying estimates of heritability in different whorls, the values may be considered high enough to indicate a possible gain, through selection, in this character.

Zobel (1961) points out that heritability "*is not* a constant factor for all conditions, and will change with tree environment and with tree age". Environmental variance accounted for a great part of the total variance in this material. Still the magnitude of the genetic portion of the variance is considerable and indicates great possibilities for improvement through selection. Estimates of heritability based on data from the progeny tests studied here when the trees have grown older may not be similar to those obtained to-day.

It should perhaps be emphasized once again that the precision of the estimates of heritability given above is rather low owing to the small number of progenies. Further these progenies cannot be regarded as a sample from an ordinary population of Scots pine.

Discussion

A thorough analysis of the progenies studied reveals:

1) A great variability within and between the progenies in regard to the quantitative and qualitative characters.
2) A varying degree of environmental influence on the characters studied.
3) An influence of the age of the young trees on the establishment of a habit characteristic of a particular progeny.
4) A striking overall phenotypical resemblance of the progenies to their parent trees.

The variation in different characters. The progenies differed significantly in tree height, length of terminal shoots, branch length, branch angle, number of branches per whorl, length and form of the apical bud, and length and number of the lateral buds of the terminal shoots. The variation in the ratios between terminal shoot length and tree height, between tree height and branch length and between apical bud length and terminal shoot length is controlled genetically. Each progeny thus developed a highly characteristic average habitus (Figs. 41—44).

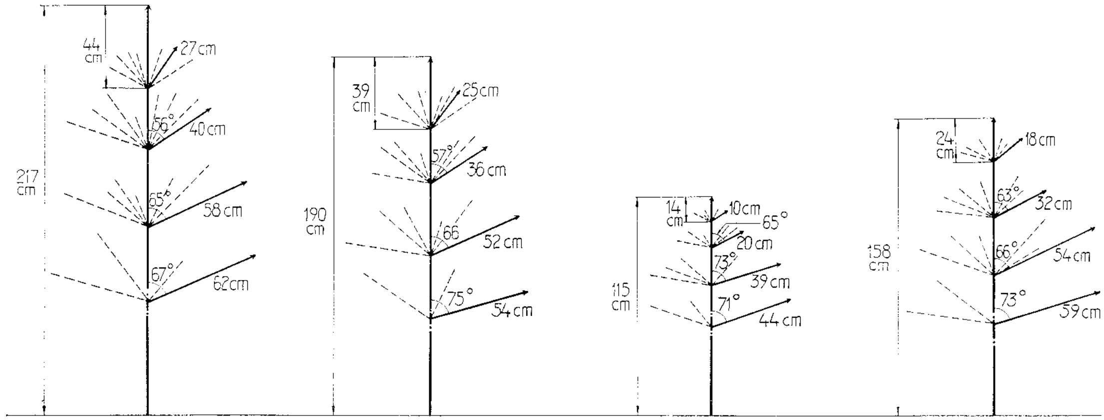
The present results agree with those obtained in other investigations into quantitative characters in conifers, where progenies from open pollination or of controlled crossings as well as clones have been studied (for literature and review up to 1959 see SCHÜTT, 1959; ROHMEDER und SCHÖNBACH, 1959; ZOBEL, 1960). FIELDING (1953), in working with *Pinus radiata* Don., established clear-cut differences between clones in their rate of growth, resistance to diseases and insects, wood density, trunk form, size and angle of the branches, flowering time, length of flowering period, and in their cone- and seed-characteristics. He ascribes a great part of these differences to inherent variation. In a later work (1960) the same author analyzed the branching characteristics in plantations of *Pinus radiata* ranging in age up to 33 years. The variations in the number of whorls, the number of branches on the annual shoots, the length of the internodes, the number of branches in the whorl, and the angle of the branches, are considered by him to be largely determined by differences in their genetic constitution. JOHNSSON (1954) reports from a 15-year-old provenance test with Scots pine that whether the seed is of northern or southern origin is of decisive importance for the subsequent growth of the trees, but that at the same time the genetic constitution of the individual progenies plays an important rôle. This is in agreement with the results of the numerous provenance tests analyzed by SCHOTTE (1923), LANGLET (1936, 1959), PETRINI (1959), and others.

Analyses of growth rate in progenies obtained through wind-pollination of *Pinus ponderosa* Laws., made by CALLAHAM and HASEL (1961), showed that "about 39 per cent of the variation in 15 years heights could be attributed to heritable genetic differences between progenies". Significant differences in tree height, stem girth, stem taper, crown diameter, bark thickness and angle of the longest branch were established by TODA (1958) in a seedling population of *Cryptomeria*. In progeny tests, using control-pollinated and wind-pollinated progenies of rust-resistant western white pine phenotypes (*Pinus monticola* Dougl.) along with wind-pollinated progenies from non-resistant phenotypes, BINGHAM *et al.* (1960) found highly significant differences between progenies of different mating types and between progenies of the same mating type.

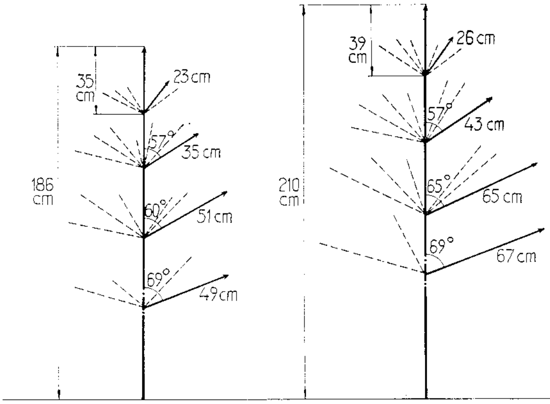
The progenies studied in the present investigation originate from plus and minus trees of widely different phenotype and provenance. Consequently great differences were to be expected between the progenies of the various crossing types. Considering each character separately the following facts may be discussed.

Height

Regarding the variation in height, the investigation of the material in 1953 (EHRENBERG *et al.* 1955) lead to a discussion of the relationship between the 1,000-grain weight and the height of the three-year-old seedlings, of the differences in height of the plus-tree progenies on the one hand and the minus-tree progenies on the other, and, finally, of the effect of self-fertilization on the offspring of plus and minus trees. Already at that age the genotypic influence on height growth was predominant, the effect of the 1,000-grain weight on seedling growth being less pronounced, though still noticeable. In general the influence of the weight of the seed will last for two to four years in pine. After that differences due to seed development vanish and the tree's own genotypic constitution is expressed (ROHMEDER und SCHÖNBACH, 1959). In the present material the plus-tree progenies within each provenance were on an average superior in height to the minus-tree progenies at three years of age, and remained superior up to the age of ten in 1960. The few exceptions in 1953, where progenies of minus crossings were superior or equal to progenies of plus crossings, had disappeared by 1960. The plus-tree progenies with a retarded growth in 1953 were among the best growing ones at the age of ten. Most of the changes in the ranking list occurred before the trees reached the age of eight, but the progenies of the minus tree VIII:



X1 E 4015$^+$ × E 4008$^+$ X2 E 4008$^+$ × E 4015$^+$ X3 VIII 46$^-$ i   X4 VIII 46$^-$ × VIII 4



X5 Y 4015$^+$ × Å2$^+$ X6 S 3001$^+$ o.p.

Fig. 41 a. *Experiment X*. Average tree type of the 20 tallest undamaged trees of each progeny in 1960.

46$^-$ (o.p., $- \times +$, $- \times -$) still fell behind also after that age. Similarly the minus cross from Ånge, Å 4$^-$ × Å 3$^-$, which was slightly superior in mean height to the plus-tree progeny from the same provenance, Y 4015$^+$ o.p., up to 1959, seemed in 1960 to grow less than the plus-tree progeny. The 20 tallest trees in the latter progeny, chosen for measurements of branching and top-bud characteristics, were significantly higher than those in the minus crossing, though the total mean heights were about the same in both progenies.

The progenies were not grown in replicates in the nursery beds, and hence it was not possible to sort out the environmental influences. Differences in

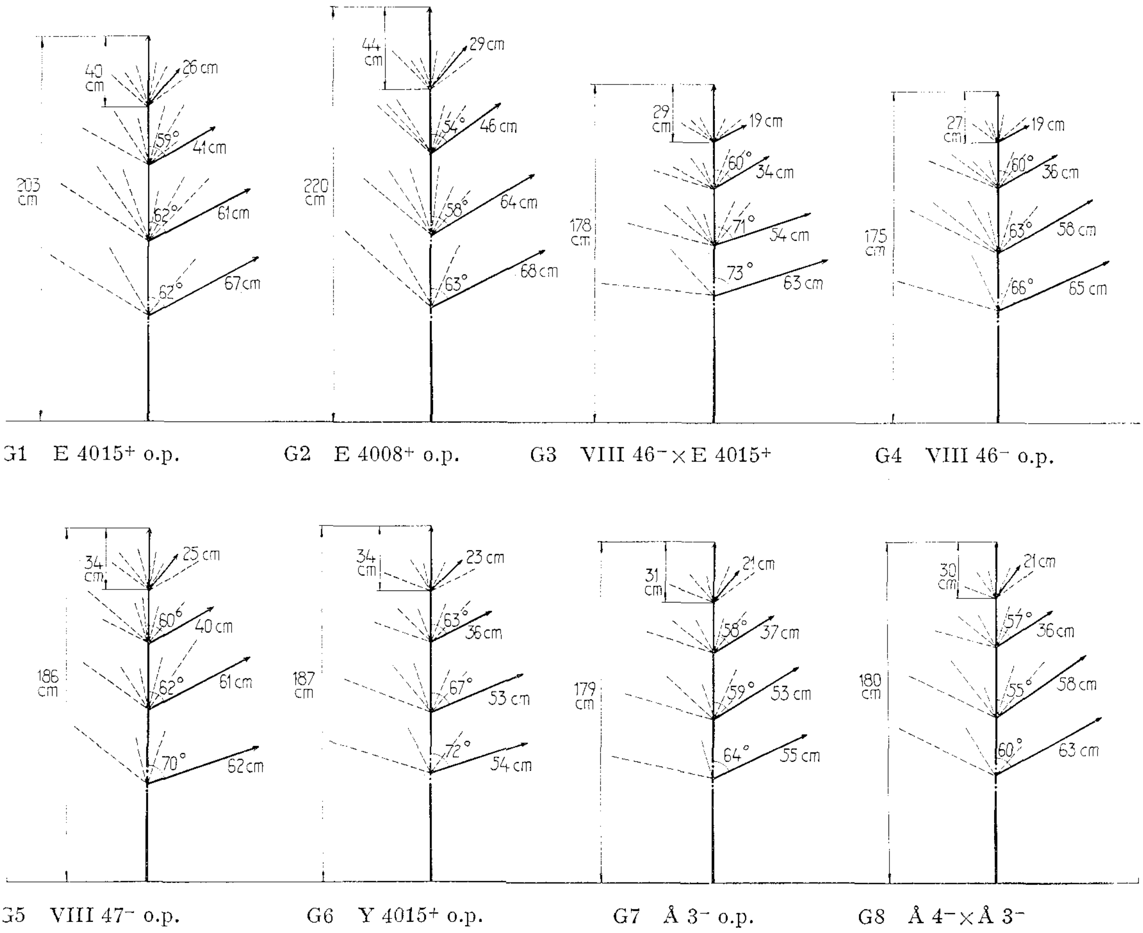


Fig. 41 b. *Experiment G.* Average tree type of the 20 tallest undamaged trees of each progeny in 1960.

site conditions may be responsible for the exceptions from the rule that the plus-tree progenies were superior in height to the minus-tree progenies. As some irregularities still existed when the trees had reached the age of ten, the possibilities of selecting the best growing progenies before this age seem doubtful. Discussing these problems in *Pinus ponderosa*, Callaham and Hasel (1961) conclude that "differences in inherent growth potentialities of progenies can be recognized in two-year-old seedlings. Fast growing seedlings on the average proved to be the fastest growing trees 13 years later". Schröck und Stern (1952) assume that an estimate of the future height growth of individual trees or progenies may be possible after eight to ten

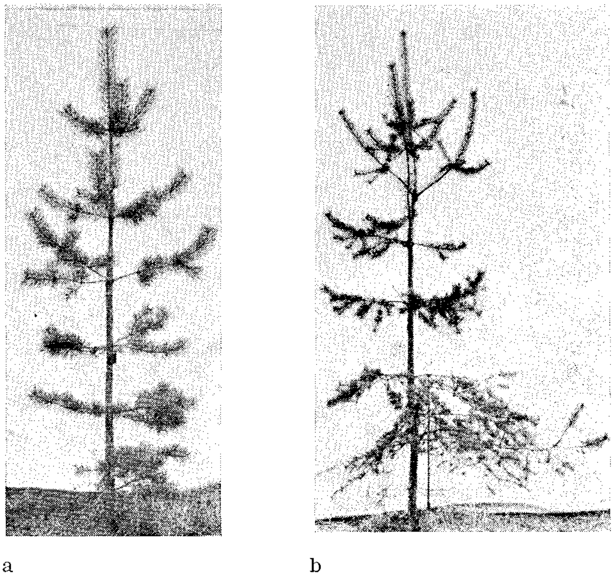


Fig. 42. Grafts and typical progeny trees originating from the plus trees at Boxholm. a) Graft of E 4015+. b) Young tree obtained after self-fertilization of E 4015+ with short needles and depressed growth compared to crossing seedlings.

years, or earlier provided that height values are available from repeated measurements and that no disturbances in the development of the trees occur (*cf.* SCHRÖCK, 1956, 1957). NILSSON (1956) considers it likely that the state of ten-year-old trees may be typical for the later development of the trees, while MÜNCH (1949) is of the opinion that nothing could be said about the final development and ranking of the progenies in his material before they reach the age of 20. He thinks it probable, however, that progeny tests can give an overall picture of the final state of the material after 10 to 13 years.

When compared as units, the two provenance groups Boxholm and Ånge did not differ significantly in height. Among the plus-tree progenies, those from Ånge had consistently the lowest mean height, although the difference was not significant. Among the minus-tree progenies, the highest and the lowest ones were the two from Ånge, the Boxholm progenies being intermediate. Thus the transfer of the northern Ånge material to the latitude of Stockholm did not cause it to grow slower than the southern material transferred northwards.

The decisive factor in the ten-year-old material was the parental background, whether plus or minus, which seemed to determine the rate of growth.

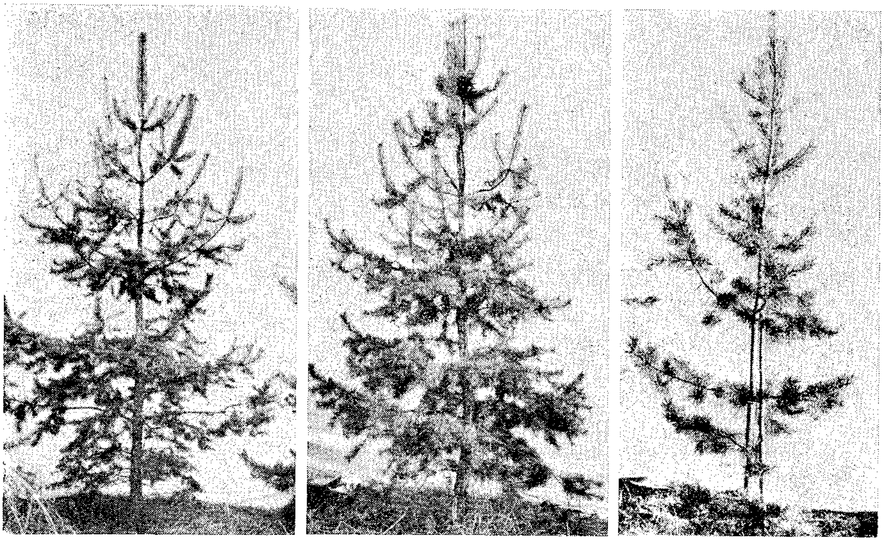


Fig. 42. c) and d) Young trees of plus × plus origin. e) Graft of E 4008+.

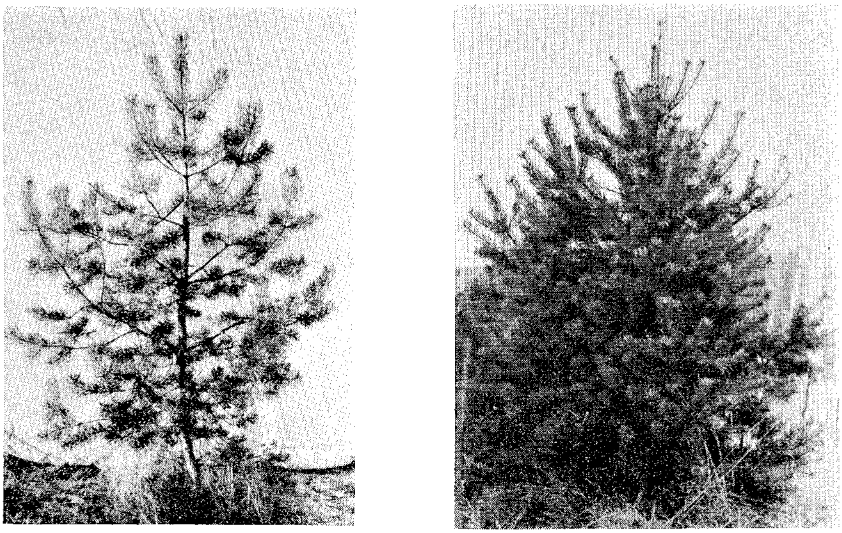
Crown width

The same parental influence holds good for the crown width. The progenies originating from the wide-crowned minus trees had relatively long branches in the lower whorls, but often comparatively short branches in whorl 1. The progenies of the minus tree VIII: 46⁻ in particular showed a wide crown in all combinations. A similar tendency was noticeable in the other minus progenies.

Among the plus-tree progenies, those from Ånge had by far the most slender crowns, indicating genetic differences between the provenances in this character.

The different types of crown in the various progenies were already clearly visible when the trees were seven years old. With increasing age the crown characteristics of the progenies became more pronounced.

Evidence from other pine species, too, indicates a strong genetic control of this characteristic manifesting itself already in the seedling stage. In slash pine, *Pinus Elliottii*, BARBER *et al.* (1955) reported distinct differences in crown width between different lots of three-year-old seedlings originating from mother-trees with slender or wide crowns after open pollination. Similar results with open pollinated material were obtained in a progeny test with *Pinus radiata* (SHERRY, 1947), in which the mother trees differed in regard



a b

Fig. 43. Graft and typical progeny trees originating from the minus trees atBoxholm. a) Graft of VIII 46^-. b) Young tree obtained after open pollination of VIII 46^-.

to crown type. The progenies were measured at the age of seven, and a high percentage of the young trees showed a marked resemblance to the maternal parent. The data indicated that the genes responsible for the slender branching and the short internodes are dominant in character.

Branch angle

With regard to the branch angle, a distinct genetic variation between the progenies was found. A strong genetic influence on this character was likewise demonstrated by Fielding in *Pinus radiata* (1953).

In general, each whorl in a progeny had a characteristic branch angle in relation to the other progenies, but significant differences between two progenies in one whorl did not imply significant differences in the whorl below or above. A progeny could even possess relatively acute branch angles in one whorl and less acute angles in another. This was particularly the case in the eight-year-old progenies in 1958, when only the two uppermost whorls were measured.

The ranking of the progenies in regard to the branch angle can thus turn out to be quite different depending on which whorls are compared. Evidently, the character of the branching is so variable in young trees that a fully

c d

Fig. 43 c) Young tree of minus × minus origin. d) Young tree of the progeny VIII 47⁻ o.p.

reliable estimation of the branch angle for a special progeny cannot be made before the trees have passed the age of ten or eleven.

The resemblance of the progenies to their parents was strong in the Ånge group, where the parent trees were chosen for crossing experiments primarily because of the great differences in their branching. The plus trees had right branch angles in contrast to the very acute ones of the minus trees. In the progenies the branch angles were of the same type as that of their respective parents. Even in the young trees this resemblance was pronounced (Fig. 44).

In the Boxholm group, on the other hand, the type of the branch angle was not the deciding factor, when the trees were chosen as parent trees, the branch angle types varying within a much smaller range than in the Ånge trees. Nonetheless a classification was made, the two plus trees being classified as "right angled" and the two minus trees as "intermediate". No regular similarity could be established between parent tree and offspring in respect of the branch angle. Of the two progenies of the plus tree E 4008^{+}, the one obtained after open pollination had more acute branch angles in every whorl than the other progenies. The second progeny of this tree, obtained from the $+\times+$ crossing, had very large branch angles. The progenies of the minus tree VIII: 46^{-} had the largest branch angles of all.

This apparent discrepancy between the type of the parent trees and the type of their offspring in the Boxholm material could possibly be due to

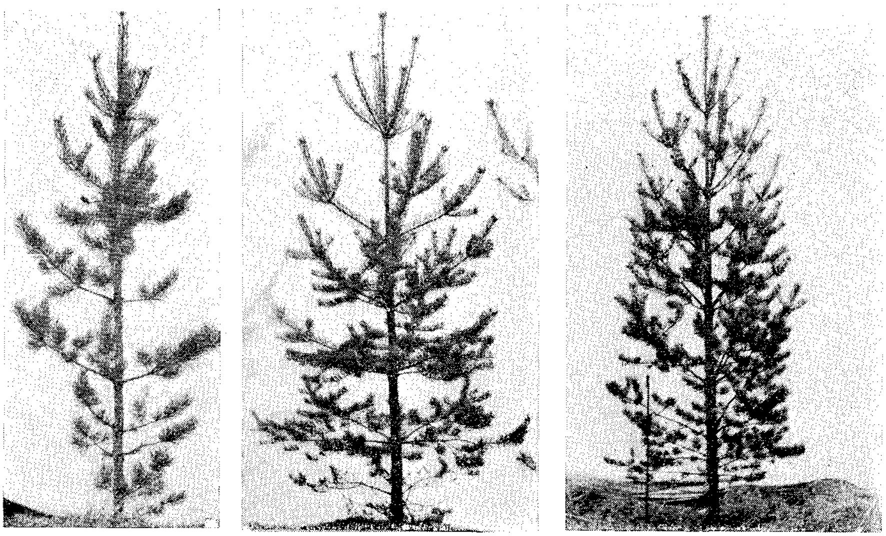
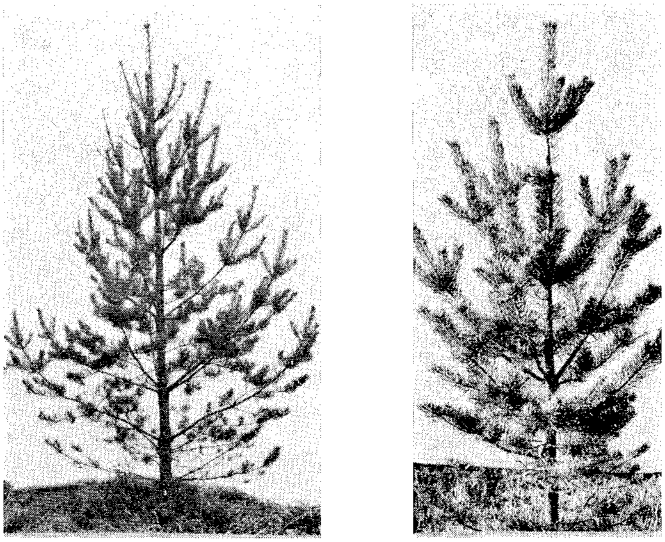


Fig. 44. Grafts and typical young trees originating from plus and minus trees at Ånge. a) Graft of Y 4015+. b) and c) Young trees from the crossings plus × plus and plus × minus, respectively.

gene recombination. The most probable explanation, however, is an unreliable estimation of the type of branch angle of the parent trees. Ocularly estimated, the plus tree E 4008+ showed right branch angles, but in a clonal test, grafts from this tree had more acute branch angles than those of the other right-angled plus tree, E 4015+. In other clonal tests with *Pinus silvestris* (Nilsson, 1955; Arnborg and Hadders, 1957) there exists a positive correlation between the mother tree and the graft in regard to the type of the branch angle. Similar results have been obtained in *Pinus radiata* by Fielding (1953), who reports a definite resemblance of the clones to the mother trees in the angle of branching. It would seem therefore, that the type of branch angle in the plus tree E 4008+ should have been classified as "intermediate" instead of "right", and that it should have been distinguished from the plus tree E 4015+ in this character. If the latter was indeed the case, the branching characteristics of the two plus trees were reflected in their progenies as well.

Phenotypically the minus tree VIII: 46− from Boxholm was classified as "intermediate" in branch angle. Considering the branch-angle types of the progenies, it reacts genotypically as a wide-angled tree. The progeny obtained after self-fertilization displayed very wide branch angles and the cross VIII: 46− × E 4015+ showed in each whorl and each year larger branch angles than the progenies from these trees when crossed with other trees. Either



d e

Fig. 44 d) Young tree obtained after open pollination of Å 3^-. e) Young tree of minus × minus origin.

the classification of the mother tree was incorrect, or the genotype of the mother tree did not reveal itself properly in the actual phenotype.

The increase of the branch angle from whorl 1 to whorl 4 was not as consistent in the present material as described by Fielding (1960) in the case of the Monterey pine. According to Fielding a very acute branch angle was found in the top-most whorl, and the angle widened as the branch aged. This was not the case in the progenies studied here. It is true that the branch angles of the fourth whorl were the widest ones in comparison with the angles of the whorls 1—3 in the same year, thus, an increase with increasing age of the *tree*. The angles did not, however, widen regularly as the *branch* grew older. Nor did whorl 2 or 3 always show a larger branch angle than the whorl above them. In some of the minus-tree progenies, for instance, where the branch angles on the whole developed in a more irregular fashion, the branch angles of whorl 2 were mostly wider than those of whorl 1, but the angles of the whorls 3 and 4 were sometimes equal or even more acute than those of the whorl immediately above. The age of the branches, at which the greatest increase in angle size took place, varied considerably between the progenies. In some progenies the differences in branch angle were greater between whorls 2 and 3 than between whorls 3 and 4, in others the greatest differences were recorded between whorls 3 and 4. In general, the minus-tree progenies displayed a comparatively small increase in the size of the branch angle from whorl 2 to whorl 4, irrespective of whether they were acute-angled or wide-angled.

Hence, at an age of ten years the progenies differed significantly in characteristic development of the branch angles. They could not be divided up into one typical plus-tree and one minus-tree progeny group, owing to the fact that the parent trees of the plus or minus groups were not selected according to one principle only. For the same reason the two provenance groups, treated as units, did not differ distinctly from one another. Decisive for the progeny's type of branching were the characteristics of the parent trees.

Apical and lateral buds

The characters relating to the apical and lateral buds of the terminal shoot likewise varied greatly among the progenies. Significant differences were found in the length of the apical buds and the lateral buds, the form of the apical bud, the ratio between the length of the apical bud and the length of the terminal shoot, the total number of lateral buds, and the percentage of small lateral buds. Generally the plus-tree progenies had comparatively small apical buds in relation to the length of the terminal shoot and a larger number of lateral buds. The other characters did not seem to be typical for anyone combination type. In experiment X the variation between the plus-tree progenies was small, and was not associated with differences in geographic origin.

Abnormalities

The abnormalities recorded in some progenies were evidently due to one or a few dominant genes. The frequency of abnormal trees as well as the degree of abnormal development in each individual (double apical bud—forking—fasciation) varied strongly between the years and sites. This variation indicates a strong environmental influence on the expression of these characters (*cf.* SCHRÖCK, 1957). EICHE (1955) studying chlorophyll defects in pine seedlings, reports a similar great variation in the expressivity of that character.

In general, fasciation arises by fusion of separate organs or by lateral expansion of an organ at its growing point (REED, 1912). The latter type of fasciation becomes morphologically apparent by a gradual flattening out of the distal part of the stem (SCHOUTE, 1936). Only this type was observed in the present material. Fasciation occurs in all vascular plants as a rare anomaly (SCHOUTE *l.c.*). In conifers it has been observed in *Picea abies* (SYLVÉN, 1916), *Pinus silvestris* (SYLVÉN, 1916; SCHLÜTER, 1956; SCHRÖCK, 1957; EHRENBERG, 1958), *Pinus Elliottii* (MERGEN, 1955, 1959), *Pinus* *radiata* (FIELDING, 1953). According to SCHOUTE (*l.c.*) the typical fasciation "is due to a disharmonic growth, the central zones of the vegetative cone being dilated by tangential growth of the surrounding zone of differentiating organs". In several species this type of abnormality is under direct genetic control (DE VRIES, 1884; KNOX, 1908; GEORGESCU, 1927; MERGEN, 1959). From non-isolated flowers of a 19-year old tree of *Pinus silvestris*, SCHRÖCK (1957) obtained a progeny with abnormally high cone production and great variation in vigour and growth. Deformities such as forking of the terminal and lateral shoots also occurred. The mother tree itself showed early fertility, abnormally high cone production, and a stem with small crooks and bends. The appearance of progeny trees defective in other characters is assumed to result from spontaneous self-fertilization. These deformities were considered to be conditioned by recessive genes. The repeated crooks and bends in the stem of the mother tree are supposed by SCHRÖCK to be due to repeated "Zwieselbildungen", *i.e.* the formation of two leading shoots in one year. One shoot disappears later on or forms a strong side branch. A small bend of the remaining leading shoot will be the result of this. Nothing is said by SCHRÖCK about the cause of the formation of two leading shoots. Considering the results in the present material, the formation of two terminal shoots may be caused by the occurrence of double apical buds. If that was the case in the mother tree studied by SCHRÖCK, the abnormality may be due to a dominant gene, already manifesting itself in the mother tree and appearing as forking in the progeny. On the other hand several traits, such as reduced seed yield of the mother tree and pronounced growth depression in the progeny, support the assumption that self-fertilization has occurred. A recessive mode of inheritance of the trait is then possible.

In the present material the abnormalities appeared in progenies obtained after open pollination as well as from controlled crossings and self-fertilization of the minus tree VIII: 46^-. Moreover, when this tree was used as the male parent in crossings, abnormal trees occurred in the offspring. The dominant mode of inheritance cannot be doubted in this case.

The strong influence of environmental factors on the variation of this character was clearly demonstrated. The penetrance and expressivity varied from year to year and also differed in the different plots of a progeny in the same year. This was evident, for instance, in the inbred offspring of VIII: 46^-, where the progeny trees are generally depressed in vigour and growth.

Fasciation may also be produced by mechanical injuries to the growing point, or by insects or fungi (KNOX, 1908; REED, 1912), but only specimens with inherent tendencies of developing the malformations will do so when injured (GEORGESCU, 1927). No injuries on the deformed trees were observed in the present material, and the development of the deformities must be ascribed to a disharmonic growth, caused in these instances by one (or more) dominant genes. A condition favouring the appearance of fasciation is superabundant nourishment (GOEBEL, 1928). Generally fasciation, forking and double apical buds occurred in the most vigorously growing trees in a progeny. This confirms the statement, mentioned above, that vigorous growth favours the development of deformities.

The other type of abnormalities recorded here, *prolepsis*, occurred in all the progenies in a varying degree. Genetic differences between the individual progenies and between provenances were established, and the great influence of the environment on the occurrence of prolepsis was observed. Special, partly unknown seasonal conditions, as well as high nutrition, favoured the development of proleptic shoots. Similar results were obtained by SCHLÜTER (1956) in *Pinus silvestris*, by FIELDING (1960) in *Pinus radiata* and by RUDOLPH (1962) in *Pinus banksiana.* No significant differences between provenances in the frequency of proleptic trees appeared in the provenance tests of *Pinus silvestris,* described by DENGLER (1938) and SCHMIDT (1940), but the individual progenies of one and the same provenance varied to a great extent. The provenance difference established in the present material, with rare occurrence of prolepsis in the northern progenies from Ånge, may be due to general provenance differences, as well as to individual differences between the parent trees irrespective of geographic origin. The number of progenies is too small, however, to allow any general conclusions, particularly as the environmental influence was profound. Several years of observation are necessary before a reliable opinion can be formed of the degree of variation within and between the progenies. The character is undoubtly genetically conditioned, but no conclusions regarding the mode of inheritance or the number of genes involved can be drawn at present. The occurrence of prolepsis and abnormalities of type 1 a—d in the same individuals somewhat more frequent than would have been expected if they had been entirely independent of each other may be explained in different ways, for instance by assuming that their gene loci in part are on the same chromosomes.

Effect of inbreeding

The effect of forced inbreeding (selfing) was evident in the progenies obtained from self-fertilization. In addition to a pronounced lethality in the nursery beds and during the first years after planting, the young trees displayed depressed vigour and retarded growth. Aberrations such as chlorophyll defects or abnormally short needles were also recorded.

Inbreeding depression and the occurrence of deformed individuals in inbred progenies have been observed in many coniferous species (DENGLER, 1939; v. WETTSTEIN, 1940; LANGLET, 1940; JOHNSSON, 1945; SCAMONI, 1950; MERGEN, 1954; BINGHAM and SQUILLACE, 1955; Ruden, 1957; SCHRÖCK, 1957; LANGNER, 1958; DIMPFLMEIER, 1959). Generally all individuals in a selfed progeny are depressed, but exceptions also occur. MERGEN (1954) reports that in slash pine, "a few individual inbred seedlings were as tall as cross- or wind-pollinated ones". In the present material some vigorously growing trees appeared also in the inbred progenies. Offhand it was assumed that they were the result of unsuccessful isolation and consequent fertilization by foreign pollen. Further experiments will decide whether this was the case, or whether a considerable variation in vitality and growth ability may exist also *within* a selfed progeny.

Such a variation undoubtly exists *between* selfed progenies from different mother trees (DORMAN, 1952 in *Pinus Elliottii;* BINGHAM and SQUILLACE, 1955 in *Pinus monticola;* LANGNER, 1958 in *Larix japonica*, and ORR-EWING, 1954 in Douglas Fir). This was clearly demonstrated in the present experiments too, where there was a marked difference in the height and vigour of the selfed progenies of three plus trees from Värmland. Compared to the wind-pollinated progeny from the same mother tree, the mean height of the selfed progeny was lower. The tallest inbred and the tallest open-pollinated progeny originated from one and the same mother tree. Likewise the open-pollinated and selfed progenies that were most inferior in height, sprung from another mother tree. It has been stated previously that the capability of self-fertilization varies widely in Scots pine (PLYM FORSHELL, 1953; EHRENBERG and SIMAK, 1957). Evidently the capacity of producing viable and well growing offspring after self-fertilization varies considerably too.

Variation caused by environmental factors

The great influence of environmental factors on the characters recorded was manifested by the significant block differences occurring every year and in nearly all characters. This influence is particularly clear in experiment G, where the site conditions in one of the blocks (IV) are very poor. Height, as well as the characters strongly correlated with height, for instance, the length of the terminal shoot and branch length, vary more with site conditions than the branch angle and properties related to the apical bud and lateral buds of the terminal shoot. Some form indexes, for instance the ratio between the tree height and branch length, between the length of the apical bud and the length of the terminal shoot, between the length of the apical bud and the length of the lateral buds of the terminal shoot, so characteristic for each progeny, varied only slightly with differences in the environment. According to RICHENS (1945) "sufficient evidence has now been obtained to confirm the assumption that the genotype has an important effect on crown shape, and the only question that can be profitably discussed is the relative importance and the mode of interaction of the environment and the genotypes". The height and the length of the branches are no doubt very sensitive to environmental influences, but the relationship between them is fairly static and the proportion of the variation contributed by environmental factors relatively small (*cf.* BARBER, DORMAN and JORDAN, 1955; SHERRY, 1947). A similar condition was found in seed of Scots pine as regards length and width of the seeds and the ratio between them (SIMAK, 1953). The seed *size* was greatly influenced by climatic factors, by the weight of the cone, and by the position of the seed in the cone, varying strongly from one tree to another and even in the tree itself. The *shape* of the seed, on the other hand, was fairly constant, and characteristic of the individual tree. Even more fixed are the *seed details* as described by SIMAK and GUSTAFSSON (1954).

Discussing the possibilities of a genetic improvement of forest trees, SCHREINER (1958) presents estimates of heritability and improvement procedures for different characters. The improvement procedures are the following:

1) Genetical improvement.
2) Genetical improvement followed by some degree of silvicultural control.
3) Genetical improvement and silvicultural control of equal importance.
4) Silvicultural control plus genetic research to determine the possibilities of genetical improvement, and, finally,
5) Silvicultural control.

Out of 13 characteristics relating to growth rate, optimum stem form and optimum branching, only one, the minimum numbers of branches, is supposed to be under such a considerable genetic control that improvement may be achieved mainly through selection and breeding. The other characters can be widely influenced by environmental factors, which have to be controlled carefully. In characteristics affecting wood quality, for instance, or physical-chemical and anatomical properties, a few may be subject to genetical improvement exclusively, since the influence of the environment is supposed to be weak. Sufficient heritability indices to justify genetical improvement was supposed to be present in 29 out of 39 characters recorded in the two groups.

A comparison between the estimates of heritability reviewed by SCHREINER and those calculated for some of the characters analyzed in the present material reveals a rather good agreement as regards the characters height growth and branch angle. Evidently height growth may be improved by selection in combination with strong silvicultural control, as SCHREINER assumes. The wide branch angle, indispensable for elimination of large knots in the stem, seems to be even more strongly genetically controlled and so may be improved mainly by selection and breeding. As regards the numbers of branches per whorl, which is of importance for the number and distribution of knots, there is "evidence for sufficient heritability to justify genetical improvement" in this character without silvicultural control, according to SCHREINER. Judging from the results obtained in the present material improvement by selection is possible but some degree of silvicultural control seems to be necessary. Finally, the estimates of heritability for the slightly varying ratio between tree height and branch length indicate great possibilities for improvement by selection. Some stem form characteristics mentioned by SCHREINER, such as crooks and forks, are shown to be inherited in the present material. Although no estimation of heritability has been made for these characters here, the conclusion is certainly justified that stem form may be improved by selection and breeding.

It has been pointed out before (p. 95) that the precision of the estimates of heritability is low (Table 42). The good agreement with the results reviewed by SCHREINER indicates, however, that these estimates are meaningful even though they were obtained from such a small and varying sample.

Relationship between parent trees and offspring

The relationship between the parent trees and the progenies in the present material has not been statistically analyzed. As mentioned before (p. 7) the parent trees were classified as plus or minus trees according to their phenotypes. Some characters were measured as exactly as possible (*e.g.* height, diameter). As the trees had reached the age when the height growth slowly ceases, and as the crowns had been damaged by the repeated collection of scions and by the erection of scaffoldings around them for the purpose of making crossings, the values obtainable for other characters (branch lengths, branch angles) were considered unreliable and not representative of the trees. The damages made may also have influenced the development of other characters and may thus have rendered the comparison between parent trees and offspring, based on exact measurements, still more uncertain. Besides these interferences in the crown development, the widely differing environments of the plus- and minus trees on the one hand, and those of their progenies on the other, must be taken into consideration. In the present material, where the parent trees grow at different latitudes and altitudes, in different climates, and on different sites, an elimination of the effects of the environment in order to make the values from the parent trees and their offspring comparable, must be considered very difficult. Furthermore, the plus trees at Boxholm are now growing in a clear cut area, and no trees of the same age are available in the neighbourhood for comparison and calculation of the relative values of the plus trees. The classification is based on the general appearance of the trees and on the comparison with other plus trees growing on to all appearance similar sites in the surrounding forests.

Under the circumstances, a comparison between the parent trees and their offspring as to details hardly seems justified, and consequently no calculation of the strength of the correlation between them has been made.

There is no doubt that the never-ceasing influence of the environment during the life-time of a tree, and its important rôle in the formation of the final tree type must be taken into account when estimating the phenotypic characteristics of a tree. This is emphasized by KIELLANDER (1956) when discussing the difficulties in selecting plus trees of *Picea abies*. He concludes that "to a much wider extent than hitherto supposed, the dimensions of the mother trees would be the result of environmental than of hereditary factors", and further, that "the influence of the hereditary factors would thus on forest land in Norway spruce be more or less eliminated by a number of environmental factors in the never-ceasing interaction between heredity and environment". ANDERSSON (1962) further stresses the need of a thorough analysis of the environment in conjunction with the selection of plus trees and in estimating the correlation between parent trees and their offspring. Such an estimate is justified only if the influence of environment has been eliminated to the greatest possible extent. Differences between parent trees and between parent trees and progenies in latitude, altitude, temperature, sites and age always exist, and a correct adjustment may be difficult. To circumvent these difficulties various methods are recommended, for instance clonal tests of the parent trees in connection with progeny tests on the same localities, progeny tests in the immediate neighbourhood of the stand where the parent trees grow, and comparisons of cuttings from the parent trees with progenies from the same parent trees under strictly uniform conditions, for instance in a phytotron. SQUILLACE and BINGHAM (1954) used special methods for measuring the mother trees in order to eliminate differences in environment and age between them and the progenies. They point out, however, that "the method may not be satisfactory on trees where growth in upper crown has decreased appreciably or ceased (probably trees over 100 years old)".

In this connection a work by ROHMEDER (1961) may be mentioned. He studied progenies obtained after wind-pollination, of *Picea abies* (two stands, 59 and 22 mother trees respectively), *Pinus silvestris* (two stands, 35 and 31 trees), and *Quercus petraea* (one stand, 31 trees). The progenies were planted in five experimental fields in different localities, and were measured at ages ranging between 9 and 20 years (spruce), 6 and 9 years (pine) and 1 and 9 years (oak). The average ages of the mother trees were in spruce 85 and 97 years, in pine 113 and 120 years, and in oak 150 years. The mother trees in each stand were divided up into three groups according to their heights or timber yield. Group I included the phenotypical "plus" trees, group II the intermediate ones, and group III the trees inferior in height and yield. The mean values of each group were compared with the mean height values of the progenies originating from the corresponding group of mother trees. No correlations between the mother-tree groups and the corresponding progeny groups in height or timber yield could be established. On an average the progenies from the inferior mother trees (group III) had reached the same heights as the progenies from the mother trees in group I. He concludes that a cursory selection of the best yielding trees, the so-called "plus trees" in a stand, the harvesting of the seed exclusively from these trees, and the establishment of new stands from these seed collections do not result in increased timber yield in the next generation (*cf.* WRIGHT, BINGHAM and DORMAN, 1958, p. 805). A single tree selection, on the other hand, combined with progeny tests, may result in a considerable increase in timber yield, since a great variation in this character occurs among the mother trees as well as between the individual progenies in a group.

To draw any general conclusions as to the correlation between the yield of the "plus" trees and the yield of their progenies in these experiments seems hardly justified for the following reasons. No adjustment for the differences in environment and age between the mother trees *inter se* and between the mother trees and the progenies has been attempted. The classification of the mother trees may be based on purely accidental differences caused by environment. Furthermore the mother trees and the progenies are growing on widely differing sites and in different climates. For these reasons a comparison between them is not very reliable. To use the term "plus" tree in this connection must be considered misleading. As the term is now generally defined, it means a tree, superior to trees growing on the same site and of the same age as regards timber yield (height and diameter), stem form, branching habit, wood quality and wood density. Plus trees must also be superior to the mean values of the whole stand (ANDERSSON, 1962). The environmental influences on the development of a tree nominated as a "plus" tree must be very carefully analyzed, and environmental factors favouring or impeding it must be taken into account. These indispensable conditions being fulfilled, very few trees in a stand will be approved as "plus" trees *sensu stricto*. The expected correlation between the three groups of mother trees and the corresponding groups of progenies which failed to appear in the progeny trials reported by ROHMEDER, may be explained by the *cursory* selection of the mother trees without making an allowance for environmental factors. A selection of *individual* trees superior in height and yield, on the other hand, may render superior progenies, as also pointed out by ROHMEDER (*l.c.*).

In the present progeny tests the great influence of the environment on the phenotypic development is acknowledged, as well as its varying effect on distinct part-characters. A great variation due to genetic differences between the progenies was also established, as well as a general resemblance of the offspring to their parent trees. On the whole the "plus" trees produced "plus" progenies, with rapid growth, straight stems and narrow crowns. Progenies from the minus trees displayed the same minus characters as their parent trees. Thus the estimation of the genotype on the basis of the phenotype of the parent trees has given a very satisfactory result in this investigation.

Summary

The inheritance and genetic variation of quantitative and qualitative characters have been studied in progenies of *Pinus silvestris,* obtained from individual trees by open or controlled pollination.

The characters studied are height, branch length, branch angle, number of branches, size of the apical bud, size and number of the lateral buds of the terminal shoot and other morphological features.

The external resemblance of the progenies to their parent trees has been analyzed, as well as the influence of environmental factors on tree development.

The twelve trees used as parents were classified as distinct plus trees or minus trees. Two plus and two minus trees grow in a stand at Boxholm (Lat. 58°07′), two plus and two minus trees in a stand near Ånge (Lat. 62°25′), three plus trees in different localities in the province of Värmland (Lat. 59°37′—60°22′) and one plus tree at Vuollerim (Lat. 66°25′).

The plus trees generally show superior height growth, straight, slowly tapering stems, a narrow fine-limbed crown, and right to intermediate branch angles.

The minus trees are characterized by slow height growth, a rapidly tapering stem, a wide, coarse-limbed crown, and very poor natural pruning. The branch angles of the minus trees at Boxholm are right to intermediate whereas the minus trees at Ånge have acute to extremely acute branch angles.

On an average the *plus-tree progenies* were characterized by vigorous growth, a relatively narrow crown, widely varying branch angles, small apical buds in relation to the length of the terminal shoot, a relatively large number of branches in the whorls 1 and 2, variations in the form of the apical bud, and a relatively large number of lateral buds.

The *minus-tree progenies* generally displayed a rather slow height growth. They developed a crown with a long-branched base and relatively short branches in whorl 1. The branch angles were acute or right depending on the type of the parent trees' branch angle. The number of branches in the two uppermost whorls was relatively low. The form of the apical bud varied independently of the parent tree type. The apical buds were large in relation to the length of the terminal shoot. The number of lateral buds was relatively small.

A comparison of the two provenance groups Boxholm and Ånge showed distinct differences between them in regard to tree height in 1953, the mean height of the Ånge progenies being about 83 per cent of that of the Boxholm progenies. In the years 1958—1960, on an average, no differences between

the mean heights of the groups were recorded as the minus tree progenies from Boxholm were inferior in height to the three Ånge progenies. The progenies in the Ånge group had significantly shorter branches in whorl 4 only. The branches of the Boxholm group were distinctly longer in relation to the tree height than those of the Ånge group in 1958 (whorl 2) and 1959 (whorl 3). In 1960 the same differences still remained, but were not significant. No average difference was established in regard to the branch angles. The Ånge progenies had a significantly lower number of branches in whorl 1 in 1958–1960, in whorl 2 in 1959 and 1960, and in whorl 3 in 1960. A consistent difference between the two groups was observed in respect of the loss of branches, the Ånge group showing a decrease between whorl 2 and 3 more than twice as great as the decrease in the Boxholm trees, and between whorls 3 and 4 more than three times as great as in the Boxholm group. The form of the apical bud was independent of the provenance. The apical buds of the Boxholm progenies were generally shorter than those of the Ånge progenies, and less dominating compared with the lateral buds. The number of lateral buds was significantly lower in the Ånge group in 1959 only, on an average one lateral bud less per tree than in the Boxholm group.

The effect of inbreeding was studied in progenies obtained after selfpollination. In addition to a pronounced lethality in the nursery beds and during the first years after planting, the young trees showed depressed vigour and retarded growth. Differences in vitality and growth ability were found between the selfed progenies of different mother trees. Aberrations such as chlorophyll defects and abnormally short thick needles were recorded.

Abnormalities in the formation of buds and branches such as forking, fasciation and prolepsis have been examined with regard to penetrance and expressivity and their genetical background has been discussed.

Sinuous terminal shoots and branches occurred in some of the progenies. The deformity remained as crooks and bends on the stem and branches. The character seems to be transmitted from the parent tree to the offspring.

The age at which the first cones were set varied greatly between the progenies as well as among the individuals within a progeny. The progenies in the Ånge group produced cones at an earlier age than those in the Boxholm group. The ability to flower at an early age seems to be strongly genetically controlled.

Widespread infection with pine twisting rust (*Melampsora pinitorqua*) was observed when the material was eight and nine years old. A clear connection between the average tree height of a plot and the percentage of infected specimens was established. Probably the great differences in height and vigour between both progenies and plots contributed to the great variation in the degree of damage in the material caused by the fungus. The distance from the source of infection also appeared to be of significance. The variation in resistance may be due to genetic factors or may be created entirely by differing environmental conditions.

The great influence of the environmental factors was manifested by the significant block differences occurring every year and in nearly all the characters. Height, and characters correlated with height, for instance the length of the terminal shoot and the branch length, varied more with the site conditions than was the case with the branch angle and the length of the apical and lateral buds of the terminal shoot. Some form indexes, for instance the ratio between tree height and branch length and between the length of the apical bud and that of the lateral buds, varied only slightly with differences in environment.

The age of the young trees at which the development of the properties characteristic for each progeny can be properly estimated is discussed. The differences between the progenies became greater with increasing age of the trees, and the characteristic habit of each progeny was more pronounced in the ten-year-old trees in 1960 than in the eight-year-old trees in 1958.

Estimates of heritability ("narrow sense") were made for the characters tree height, ratio between tree height and branch length, branch angle and number of branches per whorl. The estimates are based on the variance components, calculated from the mean square of analysis of variance of different characters in 1960. It is emphasized, that the precision of the estimates of heritability is rather low owing to the small number of progenies. Further these progenies cannot be regarded as a sample from an ordinary population of Scots pine. Still the magnitude of the genetic portion of the variance is considerable and indicates great possibilities for improvement through selection.

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Sammanfattning

Ärftlig variation i avkommeförsök med tall

Utvecklingen och variationen av kvantitativa och kvalitativa egenskaper hos tall, *Pinus silvestris*, har undersökts hos åtta—tioåriga avkommor från enskilda träd efter fri avblomning eller kontrollerad korsning. Planthöjd, grenlängd, grenvinkel, antal grenar per grenvarv, längd och diameter hos toppskottets topp- och sidoknoppar liksom antalet sidoknoppar på toppskottet har registrerats hos de enskilda avkommorna och variationen mellan och inom avkommorna analyserats.

Tolv träd, klassificerade som typiska plus- eller minusträd, har använts som föräldraträd, därav två plus- och två minusträd i ett bestånd vid Boxholm (lat. 58°07′), två plus- och två minusträd i ett bestånd vid Ånge (lat. 62°25′), tre plusträd i olika bestånd i Värmland (lat. 59°37′—60°22′) och ett plusträd vid Vuollerim (lat. 66°25′).

Plusträden karakteriseras av god höjdtillväxt, rak långsamt avsmalnande stam, fingrenig smal krona, räta till intermediära grenvinklar och god kvistrensning.

Minusträden har relativt långsam höjdtillväxt, god diametertillväxt, hastigt avsmalnande stam, grovgrenig, vid krona och dålig kvistrensning. Grenvinklarna hos minusträden i Boxholm är räta till intermediära, medan minusträden i Ånge har spetsiga till extremt spetsiga vinklar.

Plusträdsavkommorna utmärkes i genomsnitt av god höjdtillväxt, jämförelsevis smal krona, varierande grenvinkelstorlek, små toppknoppar i förhållande till toppskottslängden, relativt stort antal grenar i varv 1 och 2, varierande toppknoppsform och ett relativt stort antal sidoknoppar på toppskottet.

Minusträdsavkommorna karakteriseras av genomsnittligt lägre planthöjd och bredare krona än plusträdsavkommorna, räta eller spetsiga grenvinklar beroende på föräldraträdens grenvinkeltyp och korta relativt få grenar i de två översta grenvarven. Toppknopparna var stora i förhållande till toppskottets längd och av varierande form. Antalet sidoknoppar på toppskottet var jämförelsevis litet.

Avkommorna inom Ånge-gruppen uppnådde efter tre tillväxtperioder (1953) en medelhöjd på ca 80 % av Boxholmsgruppens. Fem till sju år senare (1958—1960) registrerades ingen signifikant skillnad i medelhöjd mellan grupperna. Minusträdsavkommorna från Boxholm hade då lägre plantmedelhöjd än avkommorna från Ånge. Ingen skillnad mellan grupperna observerades beträffande grenlängden i varv 1—3, medan grenarna i varv 4 var signifikant kortare hos Ångeavkommorna än hos Boxholmsavkommorna. I förhållande till planthöjden var grenarna hos Boxholmsgruppen jämfört med Ångegruppen längre i varv 2 år 1958 och i varv 3 år 1959. 1960 var tendensen i varv 4 liknande men skillnaderna icke signifikanta. Ingen genomsnittlig olikhet mellan provenienserna förelåg beträffande grenvinklarna. Avkommorna från Ånge hade ett lägre antal grenar i varv 1 under åren 1958—1960, i varv 2 år 1959 och 1960 och endast i varv 3 år 1960. Inom Ångegruppen var skillnaden i antalet grenar mellan grenvarven 2 och 3 dubbelt så stor och mellan varv 3 och 4 tre gånger så stor som inom Boxholmsgruppen år 1960. Toppknoppens form varierade oberoende av avkommornas proveniens. Boxholmsavkommorna hade i allmänhet mindre toppknoppar och relativt toppknoppen större sidoknoppar än Ångeavkommorna. Antalet sidoknoppar på toppskottet var 1959 signifikativt lägre inom Ångegruppen, i genomsnitt en knopp mindre per planta, än inom Boxholmsgruppen.

Effekten av *inavel* undersöktes hos avkommor erhållna efter självbefruktning. Dessa avkommor utmärktes av hög plantavgång i plantskolan såväl som under de första åren efter utplantering i fältförsök, svag höjdtillväxt och dålig vitalitet. Skillnader i vitalitet och medelhöjd mellan inavelsavkommor från olika moderträd konstaterades. Plantor med klorofylldefekter eller korta, tjocka barr registrerades hos vissa inavelsavkommor.

Abnormt utbildade knoppar och årsskott (fasciation, gaffelbildning, dubbla knoppar, prolepsis) förekom i hög frekvens hos avkommor efter minusträdet VIII 46⁻ från Boxholm. Dessa missbildningars penetrans och expressivitet har analyserats och deras genetiska bakgrund diskuterats.

Abnormt krokiga årsskott observerades hos en stor procent av plantorna i avkommor efter plusträdet E 4008⁺. Abnormiteten kvarstod efter förvedningen av skotten två till flera år som stamkrökar och slingriga grenar. Egenskapen synes vara ärftligt betingad då samma företeelse återfanns hos ympar av föräldraträdet E 4008⁺.

Kottsättningen hos de olika avkommorna registrerades. Avkommorna från Ångeträden producerade kott vid tidigare ålder än avkommorna från Boxholm. Stora skillnader i procenten kottbärande individ per avkomma förelåg inom Ångegruppen liksom i antalet kottar per träd inom en avkomma.

Starka angrepp av *knäckesjuka, Melampsora pinitorqua,* förekom år 1959 och 1960. Någon genomgående skillnad mellan avkommorna i procenten infekterade träd kunde inte fastställas. Ett samband mellan parcellernas plantmedelhöjd och procenten angripna plantor konstaterades, d. v. s. med ökad medelhöjd ökade frekvensen angripna plantor. Frekvensen infekterade plantor var även större i de parceller, som låg närmast infektionskällan än i längre bort belägna parceller. Variationen i graden av infektion i materialet kan bero på ärftliga skillnader mellan avkommorna eller vara helt miljöbetingad.

Miljöns starka inflytande på utformningen av de analyserade karaktärerna framgår av de signifikanta skillnaderna mellan blocken, som förelåg varje år. Planthöjden liksom med denna korrelerade egenskaper, såsom toppskottets och grenarnas längd, syntes mera påverkade av miljöförhållandena än t. ex. grenvinkeln eller topp- och sidoknopparnas storlek. Vissa index-värden, t. ex. förhållandet mellan planthöjd och grenlängd, varierade också mindre med miljön.

Skillnaderna mellan avkommorna ifråga om genomsnittlig planttyp ökade med ökad ålder. Den för den enskilda avkomman karakteristiska planttypen var mera utpräglad i det tioåriga materialet än hos de åttaåriga plantorna.

En skattning av heritabiliteten (”narrow sense”) för höjd, förhållandet mellan höjd och grenlängd, grenvinkel och antal grenar per varv utfördes med data från mätningarna 1960. Skattningarna måste anses ganska otillförlitliga, beroende på det ringa antalet avkommor i försöken. Ytterligare en osäkerhetsfaktor utgör det förhållandet, att avkommorna inte kan betraktas som ett stickprov ur en normalpopulation. De relativt höga värden, som erhållits för heritabiliteten för de olika egenskaperna, tyder dock på en möjlig positiv effekt vid urvalsförädling.

APPENDIX

Tables I—XI

Table I. Experiment O. Heights of the progenies in 1958 to 1960.

Combination	1958		1959		1960	
	No. of trees	Height (cm)	No. of trees	Height (cm)	No. of trees	Height (cm)
E 4015^{+} o. p.	32	134.4±0.84	32	175.1± 4.72	32	219.6± 8.61
E 4015^{+} i.	16	132.9±0.89	16	162.6± 5.44	16	197.7± 6.69
E 4015^{+} × E 4008^{+}.	23	154.5±1.27	23	195.4± 8.16	23	244.7±10.06
E 4015^{+} × VIII 46^{-}.	22	145.4±0.89	22	170.1± 7.52	22	201.9± 8.45
E 4008^{+} o. p.	23	153.6±1.03	23	197.2± 7.33	23	247.4± 9.84
E 4008^{+} × E 4015^{+}.	19	142.4±1.18	19	179.4± 7.74	19	223.5±10.87
E 4008^{+} × VIII 46^{-}.	24	141.8±1.00	25	176.6± 5.83	25	213.4± 6.87
VIII 46^{-} o. p.	23	133.4±0.77	24	158.8± 5.85	24	185.2± 7.34
VIII 46^{-} i.	43	102.2±0.64	43	120.6± 3.90	42	138.4± 4.96
VIII 46^{-} × E 4015^{+}.	24	140.7±0.91	24	173.5± 5.61	23	211.4± 5.98
VIII 46^{-} × VIII 47^{-}	24	128.6±0.94	25	159.8± 5.65	25	193.7± 7.24
VIII 47^{-} o. p.	24	131.1±0.94	24	166.4± 5.70	24	196.0± 8.01
Y 4015^{+} o. p.	24	108.2±1.16	24	138.3± 7.29	24	171.1± 8.87
Y 4015^{+} × Å 2^{+}.	22	104.1±1.31	22	131.5± 8.63	22	156.6±10.32
Y 4015^{+} × Å 4^{-}.	24	110.4±0.86	25	134.5± 5.44	25	166.9± 6.63
Å 2^{+} o. p.	21	105.1±0.82	23	126.9± 7.13	23	155.4± 8.10
Å 2^{+} × Y 4015^{+}[1].	22	89.4±1.26	24	111.5± 7.38	24	137.8± 9.18
Å 3^{-} o. p.	47	95.7±0.80	47	113.5± 4.69	46	139.1± 5.98
Å 3^{-} i.	15	69.7±1.11	15	90.3± 6.59	15	110.9± 8.09
Å 3^{-} × Å 4^{-}.	48	96.6±0.70	48	121.5± 4.20	47	146.7± 5.07
Å 4^{-} o. p.	30	89.8±0.90	30	110.1± 5.71	30	131.7± 6.51
Å 4^{-} × Y 4015^{+}.	23	96.9±1.06	24	120.5± 6.35	24	147.5± 6.31
Å 4^{-} × Å 3^{-}.	23	95.4±1.03	24	120.8± 6.65	24	145.6± 8.34
S 3001^{+} o. p.	22	116.9±1.15	23	146.2± 7.32	23	178.0± 8.86
S 3001^{+} i.	25	93.6±1.42	24	117.6± 9.26	25	143.8±11.56
S 3002^{+} o. p.	13	141.1±1.17	11	174.3± 8.29	11	206.3±13.32
S 3002^{+} i.	14	126.2±1.54	14	154.3± 9.31	14	181.8±10.86
S 3003^{+} o. p.	23	148.4±0.93	23	187.8± 5.42	23	230.7± 9.78
S 3003^{+} i.	7	139.4±1.78	7	175.0±10.98	7	212.9±13.54
BD 4016^{+} i.	6	95.7±7.35	7	107.1±10.05	7	126.7±14.01

[1]) Growing on a marshy part of the field.

Table II. Mean length of terminal shoots (Th) in 1958 to 1960.

Experiment	Combination	Length (cm)					
		1958		1959		1960	
		No. of trees	Th	No. of trees	Th	No. of trees	Th
X	E 4015^{+} × E 4008^{+}..	206	35.5 ± 0.57	208	28.2 ± 0.22	206	38.7 ± 0.78
	E 4008^{+} × E 4015^{+}..	185	29.9 ± 0.74	193	24.5 ± 0.52	193	33.4 ± 0.77
	VIII 46^{-} i	111	18.9 ± 0.79	131	9.0 ± 0.46	127	9.9 ± 0.44
	VIII 46^{-} × VIII 47^{-}	180	25.1 ± 0.60	194	17.8 ± 0.44	192	20.4 ± 0.48
	Y 4015^{+} × Å 2^{+}.....	204	29.9 ± 0.64	208	24.2 ± 0.46	206	29.3 ± 0.59
	S 3001^{+} o. p.	198	32.8 ± 0.80	205	27.6 ± 0.55	202	32.6 ± 0.62
G	E 4015^{+} o. p.......	616	29.2 ± 0.44	631	24.5 ± 0.31	628	32.2 ± 0.42
	E 4008^{+} o. p.......	306	33.8 ± 0.68	313	27.1 ± 0.50	310	35.6 ± 0.72
	VIII 46^{-} × E 4015^{+} .	301	27.8 ± 0.51	316	20.5 ± 0.36	313	24.9 ± 0.44
	VIII 46^{-} o. p.	298	28.7 ± 0.67	312	20.1 ± 0.42	300	23.1 ± 0.44
	VIII 47^{-} o. p.	568	24.2 ± 0.45	609	17.0 ± 0.54	597	25.0 ± 0.38
	Y 4015^{+} o. p.	311	29.7 ± 0.55	314	22.2 ± 0.39	312	28.8 ± 0.49
	Å 3^{-} o. p.	303	26.3 ± 0.68	306	21.4 ± 0.49	303	25.2 ± 0.51
	Å 4^{-} × Å 3^{-}........	320	30.8 ± 0.51	323	23.3 ± 0.31	321	27.0 ± 0.32

Table III. Progenies, selected for analysis of the properties c—g and mean heights of the selected trees in different years.

No. of trees per progeny: Experiment X = 60. Experiment G = 80.

Experiment	Combination	Height (cm)		
		1958	1959	1960
X	E 4015^{+} × E 4008^{+}....	147.4 ± 1.62	178.2 ± 2.12	217.0 ± 4.29
	E 4008^{+} × E 4015^{+}....		152.8 ± 2.81	189.6 ± 3.71
	VIII 46^{-} i[1])		100.4 ± 2.40	114.8 ± 2.24
	VIII 46^{-} × VIII 47^{-} ..		134.0 ± 2.29	157.8 ± 2.70
	Y 4015^{+} × Å 2^{+}.......	126.6 ± 2.28	154.0 ± 2.66	185.7 ± 3.51
	S 3001^{+} o. p.........		176.6 ± 1.84	209.5 ± 3.58
G	E 4015^{+} o. p.	134.4 ± 2.11	165.1 ± 2.68	203.0 ± 3.48
	E 4008^{+} o. p.		177.5 ± 2.81	219.5 ± 3.61
	VIII 46^{-} × E 4015^{+} ...	111.8 ± 1.92	149.1 ± 2.31	177.8 ± 2.90
	VIII 46^{-} o. p.	119.1 ± 2.44	147.5 ± 2.85	175.0 ± 3.72
	VIII 47^{-} o. p.	125.5 ± 2.51	152.8 ± 3.12	186.2 ± 4.10
	Y 4015^{+} o. p.	127.4 ± 1.88	154.2 ± 2.28	187.4 ± 2.85
	Å 3^{-} o. p.	120.4 ± 2.59	148.1 ± 2.94	179.0 ± 3.49
	Å 4^{-} × Å 3^{-}..........	126.5 ± 1.61	152.2 ± 2.04	180.0 ± 2.74

[1]) 40 trees.

Table IV. Mean length of branches in different whorls in 1958 to 1960.

Experiment	Combination	Length (cm)							
		1958		1959		1960			
		Whorl No.		Whorl No.		Whorl No.			
		1	2	2	3	1	2	3	4
X	E 4015$^+$ × E 4008$^+$....	27.2 ±0.45	40.2 ±0.70	44.2 ±0.68	53.3 ±1.26	27.0 ±0.74	39.9 ±0.91	57.9 ±1.08	62.4 ±1.14
	E 4008$^+$ × E 4015$^+$....			40.6 ±0.69	46.3 ±1.26	24.7 ±0.60	36.1 ±0.71	52.4 ±1.15	54.0 ±1.48
	VIII 46$^-$ i			30.6 ±0.84	37.4 ±1.20	9.7 ±0.52	20.2 ±0.71	38.6 ±1.09	44.2 ±1.44
	VIII 46$^-$ × VIII 47$^-$ ..			40.3 ±0.78	49.1 ±1.13	17.8 ±0.47	32.0 ±0.74	53.5 ±1.10	59.4 ±1.53
	Y 4015$^+$ × Å 2$^+$.......	25.3 ±0.68	34.1 ±0.78	40.2 ±0.89	42.8 ±0.91	22.9 ±0.60	35.1 ±0.77	50.6 ±1.18	49.4 ±1.14
	S 3001$^+$ o. p.........			48.3 ±0.69	57.0 ±1.03	25.7 ±0.45	43.4 ±0.63	64.9 ±0.91	67.3 ±1.36
G	E 4015$^+$ o. p.........	27.4 ±0.56	41.8 ±0.92	45.3 ±0.86	56.2 ±1.28	26.4 ±0.54	40.6 ±0.78	61.4 ±1.18	67.0 ±1.67
	E 4008$^+$ o. p.........			48.5 ±0.81	59.4 ±1.14	29.1 ±0.64	46.0 ±0.95	64.0 ±1.14	68.4 ±1.62
	VIII 46$^-$ × E 4015$^+$...	21.7 ±0.46	34.7 ±0.91	40.2 ±0.71	50.9 ±1.04	18.9 ±0.46	34.2 ±0.87	54.5 ±1.09	62.6 ±1.40
	VIII 46$^-$ o. p........	25.5 ±0.69	39.1 ±1.03	43.3 ±0.99	53.8 ±1.33	19.5 ±0.57	36.0 ±0.88	58.4 ±1.33	65.0 ±1.60
	VIII 47$^-$ o. p........	26.7 ±0.62	40.9 ±1.04	43.9 ±1.03	54.2 ±1.31	24.7 ±0.58	40.3 ±1.03	61.0 ±1.48	66.3 ±1.90
	Y 4015$^+$ o. p........	26.0 ±0.56	37.1 ±0.70	40.8 ±0.72	47.3 ±0.88	22.6 ±0.54	35.6 ±1.45	52.9 ±0.90	53.7 ±1.03
	Å 3$^-$ o. p...........	24.3 ±0.69	34.9 ±1.05	39.8 ±0.98	46.7 ±1.28	21.4 ±0.49	36.9 ±0.88	52.8 ±1.35	55.1 ±1.70
	Å 4$^-$ × Å 3$^-$..........	26.6 ±0.61	38.2 ±0.82	42.8 ±0.90	51.8 ±1.14	21.0 ±0.37	36.5 ±0.74	58.5 ±1.10	62.9 ±1.48

Table V. Ratios between tree height (H) and branch length (Brl) in different whorls in 1958 to 1960.

Experiment	Combination	Ratio H/Brl							
		1958		1959		1960			
		Whorl No.		Whorl No.		Whorl No.			
		1	2	2	3	1	2	3	4
X	E 4015$^{\div}$ × E 4008^{+}..	5.41	3.66	4.03	3.35	8.04	5.43	3.75	3.48
	E 4008^{+} × E 4015^{+}..			3.77	3.30	7.68	5.25	3.61	3.51
	VIII 46^{-} i.........			3.28	2.68	11.82	5.67	2.97	2.60
	VIII 46^{-} × VIII 47^{-}			3.33	2.73	8.87	4.93	2.95	2.65
	Y 4015$^{\div}$ × Å 2^{+}.....	5.00	3.72	3.84	3.60	8.12	5.29	3.67	3.76
	S 3001^{+} o. p.......			3.66	3.10	8.15	4.83	3.23	3.11
G	E 4015^{+} o. p.......	4.91	3.22	3.64	2.94	7.68	5.00	3.31	3.03
	E 4008^{+} o. p.......			3.66	2.99	7.55	4.77	3.43	3.21
	VIII 46^{-} × E 4015^{+}.	5.15	3.22	3.71	2.96	9.40	5.20	3.26	2.84
	VIII 46^{-} o. p......	4.67	3.05	3.41	2.74	8.98	4.86	2.99	2.69
	VIII 47^{-} o. p......	4.70	3.06	3.48	2.82	7.54	4.62	3.05	2.81
	Y 4015^{+} o. p......	4.91	3.43	3.78	3.26	8.28	5.26	3.54	3.49
	Å 3^{-} o. p..........	4.95	3.45	3.72	3.17	8.35	4.85	3.39	3.25
	Å 4^{-} × Å 3^{-}.........	4.76	3.31	3.56	2.95	8.57	4.93	3.08	2.86

Table VI. Length of branches. Significance of the differences between provenances.

Experiment	Year	Provenance	No. of progenies	Whorl No.	Mean Length (cm)	Significance of the differences[1]
G	1958	Boxholm Ånge	4 3	1	25.3 25.2	o
		Boxholm Ånge	4 3	2	39.1 36.8	*
	1959	Boxholm Ånge	5 3	2	44.2 41.1	o
		Boxholm Ånge	5 3	3	54.8 48.6	*
	1960	Boxholm Ånge	5 3	1	23.7 21.7	o
		Boxholm Ånge	5 3	2	39.4 36.3	o
		Boxholm Ånge	5 3	3	59.8 54.7	o
		Boxholm Ånge	5 3	4	65.8 57.3	*

[1] Significance of the differences between provenances calculated in the following way.

Year	Whorl No.	Source of variation	df	Mean Square	F
1958	1	Between provenances	1	72.6185	1.277°
		Within provenances	6	56.8723	3.936**
		Error	21	14.4477	

$$\text{Quotient: } \frac{72.6185}{56.8723} = 1.277^{\circ} \qquad \frac{56.8723}{14.4477} = 3.936^{**}$$

Table VII. Angles of branches in different whorls in 1958 to 1960.

Experiment	Combination	Branch angles (degrees)						
		1958		1959		1960		
		Whorl No.		Whorl No.		Whorl No.		
		1	2	2	3	2	3	4
X	E 4015$^+$ × E 4008$^+$	60.0 ± 1.22	66.6 ± 1.03	63.0 ± 1.10	63.7 ± 0.93	55.8 ± 0.72	64.7 ± 0.93	66.8 ± 0.94
	E 4008$^+$ × E 4015$^+$			63.5 ± 1.23	71.6 ± 1.27	57.2 ± 0.94	66.5 ± 1.10	74.7 ± 1.22
	VIII 46$^-$ i.					65.2 ± 1.61	72.7 ± 1.25	70.9 ± 1.64
	VIII 46$^-$ × VIII 47$^-$					63.1 ± 1.20	66.2 ± 1.00	72.9 ± 1.10
	Y 4015$^+$ × Å 2$^+$	51.0 ± 0.88	64.5 ± 0.97	55.4 ± 0.98	64.2 ± 1.01	57.2 ± 0.73	59.8 ± 0.82	68.9 ± 1.04
	S 3001$^+$ o. p.			62.7 ± 0.89	65.1 ± 0.95	57.0 ± 0.73	64.8 ± 0.87	69.2 ± 0.90
G	E 4015$^+$ o. p.	56.4 ± 1.08	68.9 ± 1.08	58.5 ± 1.04	66.2 ± 0.98	59.4 ± 0.71	62.4 ± 0.85	69.3 ± 0.70
	E 4008$^+$ o. p.			56.8 ± 0.96	61.0 ± 0.91	54.4 ± 0.77	58.2 ± 0.81	62.9 ± 0.81
	VIII 46$^-$ × E 4015$^+$	74.1 ± 1.08	72.3 ± 1.05			60.6 ± 1.32	71.2 ± 0.99	73.0 ± 0.86
	VIII 46$^-$ o. p.	63.5 ± 1.25	63.8 ± 1.11			60.2 ± 0.86	62.6 ± 0.98	66.3 ± 0.99
	VIII 47$^-$ o. p.	54.0 ± 1.27	67.2 ± 1.27	58.2 ± 1.17	66.8 ± 1.13	60.4 ± 0.82	62.2 ± 1.01	69.8 ± 1.10
	Y 4015$^+$ o. p.	62.6 ± 1.10	67.8 ± 1.48	65.8 ± 1.04	67.6 ± 1.05	63.0 ± 0.83	67.2 ± 0.82	71.6 ± 0.99
	Å 3$^-$ o. p.	54.2 ± 0.96	61.5 ± 1.03	57.3 ± 0.87	61.2 ± 0.93	57.8 ± 0.82	58.8 ± 0.78	63.7 ± 0.89
	Å 4$^-$ × Å 3$^-$	51.7 ± 0.96	58.2 ± 0.82	53.6 ± 0.88	58.4 ± 0.80	57.2 ± 0.84	55.1 ± 0.80	60.0 ± 0.80

Table VIII. Number of branches per whorl in 1958 to 1960.

Experiment	Combination	1958		1959			1960			
		Whorl No.		Whorl No.			Whorl No.			
		1	2	1	2	3	1	2	3	4
X	E 4015$^+$ × E 4008$^+$..	6.1 ± 0.17	4.3 ± 0.16	8.0 ± 0.17	6.4 ± 0.16	4.2 ± 0.17	7.0 ± 0.17	7.9 ± 0.19	6.4 ± 0.18	4.1 ± 0.16
	E 4008$^+$ × E 4015$^+$..			7.9 ± 0.23	5.8 ± 0.18	3.4 ± 0.14	6.6 ± 0.18	7.2 ± 0.23	5.5 ± 0.17	3.1 ± 0.13
	VIII 46$^-$ i.........			6.6 ± 0.35	5.6 ± 0.25	2.4 ± 0.12	4.4 ± 0.19	5.6 ± 0.29	5.2 ± 0.16	2.4 ± 0.15
	VIII 46$^-$ × VIII 47$^-$			8.3 ± 0.51	7.3 ± 0.33	3.2 ± 0.11	5.7 ± 0.29	7.0 ± 0.39	6.3 ± 0.20	3.0 ± 0.12
	Y 4015$^+$ × Å 2$^+$.....	6.1 ± 0.14	3.5 ± 0.12	7.4 ± 0.14	6.2 ± 0.15	3.5 ± 0.12	6.0 ± 0.20	6.9 ± 0.19	5.8 ± 0.17	3.4 ± 0.12
	S 3001$^+$ o. p.......			7.3 ± 0.17	6.0 ± 0.13	3.0 ± 0.12	6.2 ± 0.16	6.8 ± 0.21	5.8 ± 0.15	2.8 ± 0.11
G	E 4015$^+$ o. p.......	6.6 ± 0.13	3.6 ± 0.10	8.0 ± 0.16	7.2 ± 0.17	3.7 ± 0.11	6.8 ± 0.19	7.7 ± 0.18	6.5 ± 0.14	3.6 ± 0.14
	E 4008$^+$ o. p.......			8.6 ± 0.18	7.3 ± 0.17	4.4 ± 0.15	6.8 ± 0.18	7.8 ± 0.22	6.6 ± 0.18	4.2 ± 0.15
	VIII 46$^-$ × E 4015$^+$.	6.6 ± 0.20	2.9 ± 0.12	8.2 ± 0.26	7.2 ± 0.20	3.3 ± 0.15	5.6 ± 0.16	6.8 ± 0.24	6.9 ± 0.25	3.1 ± 0.13
	VIII 46$^-$ o. p......	6.8 ± 0.17	3.1 ± 0.11	7.9 ± 0.30	7.4 ± 0.29	3.5 ± 0.11	5.8 ± 0.24	7.0 ± 0.29	7.0 ± 0.28	3.4 ± 0.14
	VIII 47$^-$ o. p......	6.5 ± 0.16	3.5 ± 0.14	7.8 ± 0.20	7.0 ± 0.22	3.7 ± 0.13	6.7 ± 0.15	7.0 ± 0.18	6.3 ± 0.13	3.6 ± 0.13
	Y 4015$^+$ o. p......	6.1 ± 0.14	3.6 ± 0.12	7.2 ± 0.13	6.7 ± 0.18	3.6 ± 0.12	6.2 ± 0.11	6.7 ± 0.12	5.7 ± 0.12	3.4 ± 0.13
	Å 3$^-$ o. p..........	6.0 ± 0.16	3.3 ± 0.11	6.6 ± 0.18	6.6 ± 0.20	3.4 ± 0.11	5.6 ± 0.13	5.9 ± 0.14	5.4 ± 0.12	3.1 ± 0.10
	Å 4$^-$ × Å 3$^-$........	6.3 ± 0.15	3.7 ± 0.10	7.0 ± 0.14	6.9 ± 0.17	3.8 ± 0.10	5.8 ± 0.13	6.2 ± 0.12	5.5 ± 0.11	3.5 ± 0.10

Table IX. Mean length of apical buds (Ht) in 1958 to 1960.

Experiment	Combination	Length of apical bud (mm)		
		1958	1959	1960
X	E 4015^{+} × E 4008^{+}	12.2 ± 0.22	14.1 ± 0.28	20.0 ± 0.36
	E 4008^{+} × E 4015^{+}		14.1 ± 0.31	19.4 ± 0.43
	VIII 46^{-} i.			12.9 ± 0.32
	VIII 46^{-} × VIII 47^{-}			15.2 ± 0.30
	Y 4015^{+} × Å 2^{+}	10.6 ± 0.20	12.7 ± 0.26	18.9 ± 0.32
	S 3001^{+} o. p.		14.4 ± 0.23	19.5 ± 0.30
G	E 4015^{+} o. p.	11.5 ± 0.20	14.1 ± 0.29	17.7 ± 0.32
	E 4008^{+} o. p.		15.6 ± 0.38	21.4 ± 0.37
	VIII 46^{-} × E 4015^{+}	11.2 ± 0.25		17.7 ± 0.32
	VIII 46^{-} o. p.	12.0 ± 0.30		17.4 ± 0.35
	VIII 47^{-} o. p.	11.2 ± 0.28	12.3 ± 0.25	17.5 ± 0.25
	Y 4015^{+} o. p.	12.8 ± 0.24	13.9 ± 0.27	19.9 ± 0.32
	Å 3^{-} o. p.	13.6 ± 0.30	14.9 ± 0.29	19.8 ± 0.36
	Å 4^{-} × Å 3^{-}	13.0 ± 0.26	14.0 ± 0.24	19.7 ± 0.33

Table X. Ratios between length of apical buds (Ht) and length of terminal shoots (Th) in 1958 to 1960 (100 Ht/Th).

Experiment	Combination	Ratios 100 Ht/Th		
		1958	1959	1960
X	E 4015^{+} × E 4008^{+}	29.2	33.7	46.1
	E 4008^{+} × E 4015^{+}		37.2	50.6
	VIII 46^{-} i.			91.6
	VIII 46^{-} × VIII 47^{-}			65.9
	Y 4015^{+} × Å 2^{+}	28.7	33.3	54.6
	S 3001^{+} o. p.		33.2	50.5
G	E 4015^{+} o. p.	29.9	46.0	44.9
	E 4008^{+} o. p.		45.4	49.2
	VIII 46^{-} × E 4015^{+}	37.0		63.2
	VIII 46^{-} o. p.	37.4		65.5
	VIII 47^{-} o. p.	32.0	43.4	53.2
	Y 4015^{+} o. p.	35.1	51.2	59.3
	Å 3^{-} o. p.	40.2	54.8	63.8
	Å 4^{-} × Å 3^{-}	36.4	53.1	65.4

Table XI. Mean number of lateral buds per terminal shoot in 1958 to 1960.

Experiment	Combination	Mean Number		
		1958	1959	1960
X	E 4015^{+} × E 4008^{+}	8.2 ± 0.16	7.8 ± 0.16	5.8 ± 0.15
	E 4008^{+} × E 4015^{+}		7.5 ± 0.13	5.3 ± 0.12
	VIII 46^{-} i.			3.3 ± 0.16
	VIII 46^{-} × VIII 47^{-}			4.6 ± 0.14
	Y 4015^{+} × Å 2^{+}	7.6 ± 0.13	6.8 ± 0.13	5.4 ± 0.10
	S 3001^{+} o. p.		6.5 ± 0.14	5.2 ± 0.13
G	E 4015^{+} o. p.	8.0 ± 0.14	7.6 ± 0.13	6.1 ± 0.14
	E 4008^{+} o. p.		7.4 ± 0.12	5.4 ± 0.10
	VIII 46^{-} × E 4015^{+}	6.8 ± 0.16		5.2 ± 0.16
	VIII 46^{-} o. p.	7.6 ± 0.28		5.0 ± 0.16
	VIII 47^{-} o. p.	7.8 ± 0.18	6.9 ± 0.12	5.4 ± 0.10
	Y 4015^{+} o. p.	7.2 ± 0.12	6.5 ± 0.11	5.5 ± 0.12
	Å 3^{-} o. p.	6.7 ± 0.16	6.1 ± 0.15	5.2 ± 0.12
	Å 4^{-} × Å 3^{-}	7.0 ± 0.14	6.4 ± 0.09	5.3 ± 0.11

Corrections to Carin Eklundh Ehrenberg: Genetic Variation in Progeny tests of Scots Pine (Pinus silvestris L.)

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Page

6 Fig. 1. "Å 2^{+}" should be added to Ånge.

7 Line 11. Substitute "VIII:46^{-}" by "VIII:47^{-}" on line 14 and vice versa.
Line 13. "almost right-angled branching" should read "intermediate branch-angles".

12 Line 7. Number of combinations. For "$\underset{6}{+ \times -}$" read "$\underset{3}{+ \times -}$" and for "$\underset{\underset{6}{+}}{\text{selfing}}$" read "$\underset{\underset{5}{+}}{\text{selfing}}$".

13 Table 3. *Columns 5 and 6, 10th line from bottom.* For "6.7" read "8.2".
Column 6, 7th line from bottom. For "1.0" read "4.0".

14 Fig. 3. Block G IV, 2nd row, 3rd column. "1b" should read "1a".

19 Table 4. Column 2, 9th line from bottom. "x E 4015" should read "x Y 4015".

26 Fig. 8. VIII:47^{-} o.p. ranks below Å 3^{-} o.p., according to the height-values for VIII:47^{-} o.p. in Table 5, page 24.

27 Fig. 9. (above). G1 should be moved upwards to 79.1 cm height, 1958.

29 Line 1. VIII:47^{-} o.p. should be moved down to the 2nd line after VIII:46^{-} o.p.
Line 3. For "two" read "plus and".

32 Fig. 13. Experiment G, 1959. Progeny number "8" should be placed at the "x" immediately above "6". Text below the figure. For "13" read "Fig. 13".

33 4th line from bottom. For "0.21" read "0.20".

36 Text below Table 8 should read:

r value required for	df=58
5 % level	0.250
1 % level	0.325

37 Text below Table 15. Delete "mean" in both places.

42 Text below Table 9 should read:

r values required for	df=78
5 % level	0.217
1 % level	0.283

43 Text above Table 10. Delete "mean" in both places.

44 Text below Fig. 18. Delete "mean" in both places.

61 Bottom line. Delete "Table 18".

67 Note 1) under Table 23. For "two progenies" read "All trees: 6 progenies; 60 trees: 2 progenies.

91 Fig. 40. Block G IV, 2nd row 3rd column. "1b" should read "1a".

92 Line 1. 1) Analysis of variance of plot means.

For "M.S."	read "M.S."
1089.58	632.57
3328.53	3591.76
321.89	349.44

These values of M.S. should be entered in the formulae on pp. 92-93. As a consequence the estimated heritability of "tree height (all trees)" will be 16 instead of 41 per cent in experiment G (Table 42, p. 93), and the estimated selection gain (p. 94, *7th line from bottom*) will be six per cent. In addition, the statement on lines 5-12, p. 94, should refer to the average heritability of both experiments, X and G.

92 2nd formula under 4). For "α_{g}^{2}" read "s_{g}^{2}".

Page	
93	Table 42. Tree height (all trees). Experiment G. For "41" read "16".
94	9th line from bottom. For "s_g^2 " read "s_t^2 ".
95	Line 3. For "lower" read "higher".
97	Line 14. For "phenotype and provenance" read "phenotypes and provenances".
98	Text below Fig. 41a. For "20" read "60".
99	Fig. 41b. Progeny 47^{-} o.p. Whorl 4. Branch length should be 66 cm.
	Text below Fig. 41b. For "20" read "80".
100	Lines 13 to 15. For "and the lowest ... being intermediate" read "one was from Ånge and the lowest one from Boxholm".
119	Line 28. For "An introduction to genetic statistics" read "The design and analysis of experiments".

The author is indepted to Docent N. Nybom and Mr B. Ericson, Lic. of Forestry, for drawing her attention to several of the above corrections.