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# Parent-Progeny Relationship in Scots Pine (*Pinus silvestris* L.)

Results from three progeny tests with plus and minus tree progenies in southern Sweden

*Sambandet mellan föräldraträd och avkommor hos tall (Pinus silvestris L.)*

*Resultat från avkommeförsök med plus- och minusträdsavkommor vid Remningstorp, Västergötland*

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Fig. 1. Plus trees at Boxholm.

# Introduction

A previous paper dealing with the genetic variation in Scots pine, *Pinus silvestris* L. (Eklundh Ehrenberg, 1963) set out the significant differences between progenies after controlled pollination, after wind pollination and after selfing as regards height growth, branch length, branch angles and some bud characteristics. Abnormalities in the development of buds and shoots were reported and the genetic background of these characteristics was discussed. The genetic part of the variance was calculated. The effect of selfing was manifested in low cone and seed set, in low germination capacity of the seeds, in different degrees of plant mortality at different ages, and in slow height growth and low vitality.

It was found that progenies obtained from crosses between plus trees or even crosses between a plus tree and a minus tree of the same provenance were superior in height growth to minus tree progenies; also the crowns were narrower and the branches had right to intermediate angles. Progenies from parent trees with narrow branch angles had comparably narrow angles, too.

In order to test still further the results obtained in the experiments mentioned above, similar inventories and measurements were made in three other field experiments which were established in 1956 and included progenies from the same types of crossing. Measurements were made for the first time in 1960 and repeated during the following years.

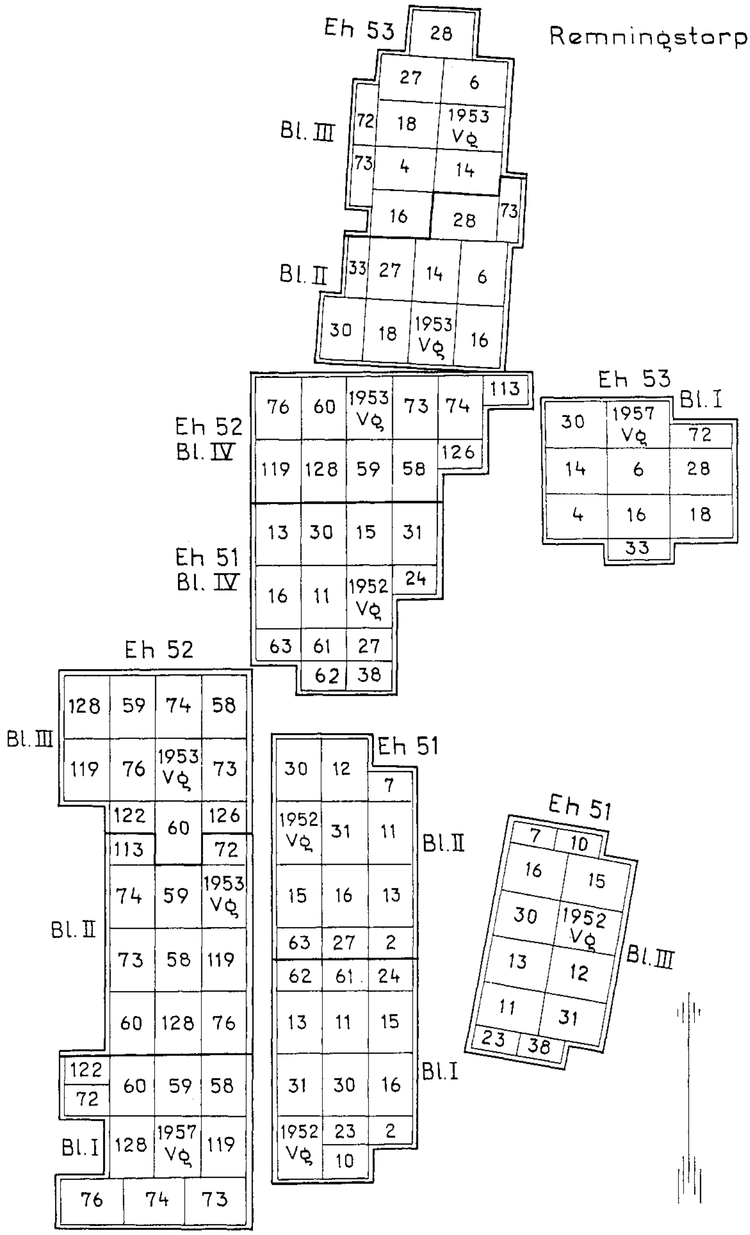


Fig. 2. Design of field experiments Eh 51—53 at Remningstorp.

## Material and Methods

The number and data of the parent trees included in the experiments are summarised in Table 4 and the various cross combinations in Tables 1—3. The pollination techniques used were the same as described by EHRENBERG and SIMAK (1957). The seedlings available for field experiment Eh 51 were sown in 1952, the ones in experiments Eh 52 and Eh 53 in 1953. All three experiments were planted in 1956 on former farmland belonging to the Remningstorp Experimental Forest in the county of Västergötland (Lat. 58° 30′ N).

Due to the varying number of seedlings available of each progeny, simple block designs had to be used. Each progeny was replicated two to four times (Fig. 2). Consequently, the progeny mean had to be adjusted according to the group of blocks in which the progeny in question occurred. The analysis of variance and the comparison of the individual progenies were made with allowance for the non-orthogonality of the designs.

In experiment Eh 51 (Table 1) progenies obtained after crosses between plus and minus trees of the same provenance or after open pollination or self-pollination (one progeny) of these trees are included. Four provenances are represented, namely Boxholm (E or VIII), Värmland (S), Aspan (Z or Y), and Ånge (Y or Å). (Fig. 3.) The same types of crossing are represented in experiment Eh 52 (Table 2), including progenies of selected trees in stands at Boxholm, Värmland and Ockelbo (X or 11). One provenance cross and one inbred progeny are added. Experiment Eh 53 (Table 3) is composed partly of progenies obtained after crosses between trees of widely different origin (provenance crosses), partly of open pollinated progenies from the same parent trees. One of the progenies originates from a cross between parents of the same provenance. Provenances represented are Boxholm, Ockelbo, Ånge and Vuollerim (BD).

When comparing the data obtained from the various measurements, the materials are arranged in provenance groups and comparisons are made between progenies of the same provenance as well as between all the progenies in one experiment. Each comparison between any progeny means was made by an individual t-test. Owing to the non-orthogonality of the designs, existing multiple range tests are not applicable.

One progeny from a local stand, Västergötland (Vg), is included in each of the three experiments. The progenies of *Pinus banksiana* and *Pinus contorta*, planted in experiments Eh 51 and Eh 52 were not included in the investigation.

**Table 1. Experiment Eh 51. Provenances, cross combinations, number of plots and number of trees per progeny.**

| Progeny No. | Cross combination | | No. of plots | No. of trees planted 1956 | No. of trees measured[1]) 1964 |
|---|---|---|---|---|---|
| | *Boxholm* | | | | |
| 52— 2 | E 4015 × E 4008 | + × + | 2 | 80 | 80 |
| 7 | E 4008 × E 4015 | + × + | 2 | 80 | 63 |
| 10 | E 4008 | o.p.[2]) | 2 | 80 | 78 |
| 11 | VIII 46⁻ | i[3]) | 4 | 320 | 201 |
| 12 | VIII 46⁻ × VIII 47⁻ | − × − | 2 | 160 | 143 |
| 13 | VIII 46⁻ | o.p. | 4 | 320 | 316 |
| 15 | VIII 47⁻ × VIII 46⁻ | − × − | 4 | 320 | 288 |
| 16 | VIII 47⁻ | o.p. | 4 | 320 | 292 |
| | *Aspan* | | | | |
| 23 | Z 4401 × Z 4406 | + × + | 2 | 80 | 59 |
| 24 | Z 4401 × Z 4400 | + × + | 2 | 80 | 75 |
| 27 | Y 37⁻ × Y 38⁻ | − × − | 2 | 80 | 75 |
| 30 | Y 38⁻ × Z 4401 | − × + | 4 | 320 | 278 |
| 31 | Y 38⁻ × Y 37⁻ | − × − | 2 | 320 | 307 |
| | *Ånge* | | | | |
| 38 | Å 3⁻ | o.p. | 2 | 80 | 77 |
| | *Värmland* | | | | |
| 61 | S 3003 | o.p. | 2 | 80 | 79 |
| Vg | Local provenance | | 4 | 320 | 277 |

[1]) Height and terminal shoot  [2]) Open pollination  [3]) Selfed

**Table 2. Experiment Eh 52. Provenances, cross combinations, number of plots and number of trees per progeny.**

| Progeny No. | Cross combination | | No. of plots | No. of trees planted 1956 | No. of trees measured[1]) 1964 |
|---|---|---|---|---|---|
| | *Ockelbo* | | | | |
| 53—58 | 11:18⁻ × X 2021 | − × + | 4 | 320 | 318 |
| 59 | 11:18⁻ × X 2030 | − × + | 4 | 320 | 292 |
| 60 | 11:18⁻ × 11:19⁻ | − × − | 4 | 320 | 297 |
| 113 | 11:18⁻ | o.p.[3]) | 2 | 80 | 72 |
| | *Boxholm* | | | | |
| 72 | E 4008 | o.p. | 2 | 80 | 80 |
| 73 | VIII 46⁻ × VIII 46⁻ | i[4]) | 4 | 320 | 188 |
| 74 | VIII 46⁻ × Sib | − × Sib[2]) | 4 | 320 | 298 |
| 76 | VIII 46⁻ | o.p. | 4 | 320 | 297 |
| | *Värmland* | | | | |
| 119 | S 3003 | o.p. | 4 | 320 | 301 |
| 126 | S 3001 × S 6210 | + × + | 2 | 80 | 74 |
| 128 | S 3001 | o.p. | 4 | 320 | 297 |
| Vg | Local provenance | | 3 | 240 | 217 |

[1]) Height and terminal shoot  [3]) Open pollination
[2]) Provenance cross  [4]) Selfed

**Table 3. Experiment Eh 53. Cross combinations, number of plots and number of trees per progeny.**

| Progeny No. | Cross combination | | No. of plots | No. of trees | |
|---|---|---|---|---|---|
| | | | | planted 1956 | measured[1]) 1964 |
| 53— 4 | BD 4016 × E 4008... | $+ \times +$[2]) | 2 | 160 | 146 |
| 6 | BD 4016............ | o.p.[3]) | 3 | 240 | 215 |
| 14 | E $67^-$ × VIII $46^-$.... | $- \times -$[2]) | 3 | 240 | 233 |
| 16 | E $67^-$ × BD 4016.... | $- \times +$ | 3 | 240 | 231 |
| 18 | E $67^-$............... | o.p. | 3 | 240 | 224 |
| 27 | Å $3^-$ × VIII $46^-$..... | $- \times -$[2]) | 2 | 160 | 159 |
| 28 | Å $3^-$ × 11:$18^-$....... | $- \times -$[2]) | 3 | 240 | 237 |
| 30 | Å $3^-$................ | o.p. | 2 | 160 | 148 |
| 33 | Å $4^-$ × VIII $46^-$..... | $- \times -$[2]) | 2 | 80 | 78 |
| 72 | E 4008.............. | o.p. | 2 | 80 | 65 |
| 73 | VIII $46^-$............ | i[4]) | 2 | 80 | 34 |
| Vg | Local provenance..... | | 2 | 160 | 139 |

[1]) Height and terminal shoot
[2]) Provenance cross
[3]) Open pollination
[4]) Selfed

The number of seedlings per progeny planted in 1956 varied between 40 and 320 (Tables 1—3). The mortality was low in all three experiments during the years up to 1964, i.e. less than ten per cent, except in the inbred progenies 52—11 and 53—73 (VIII $46^-$ i) where the percentage of surviving trees per progeny was 62 and 38 respectively.

The characteristics analysed are as follows:

a) Tree height (H), and
b) Length of the terminal shoot (Th).

Measurements were made in all plots after the termination of the growing season in the years 1960—1964. Damaged trees and trees growing on exceptional sites were excluded from the data used in the processing.

c) Branch length (Brl), and
d) Branch angle.

The length and the angle of the three longest branches in each whorl were measured and the mean values of these were used when computing the mean plot value. Only dominant, well-developed branches were measured even if they numbered less than three. The whorls were numbered consistently from the top downwards as whorl 1, 2, 3 and 4.

e) Number of branches in each whorl
f) Length of the apical bud
g) Length of the lateral buds, and
h) Number of lateral buds.

The characteristics f—h refer to the terminal shoot.

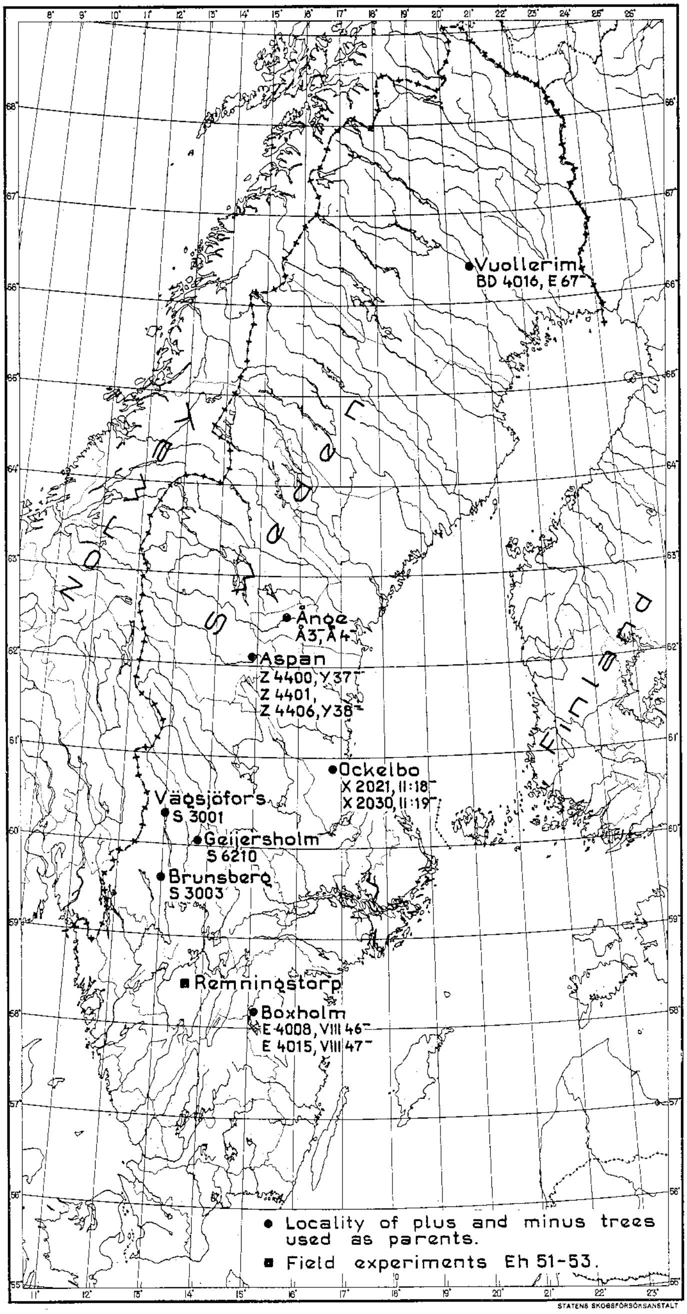


Fig. 3. Localities of plus and minus trees used as parents.

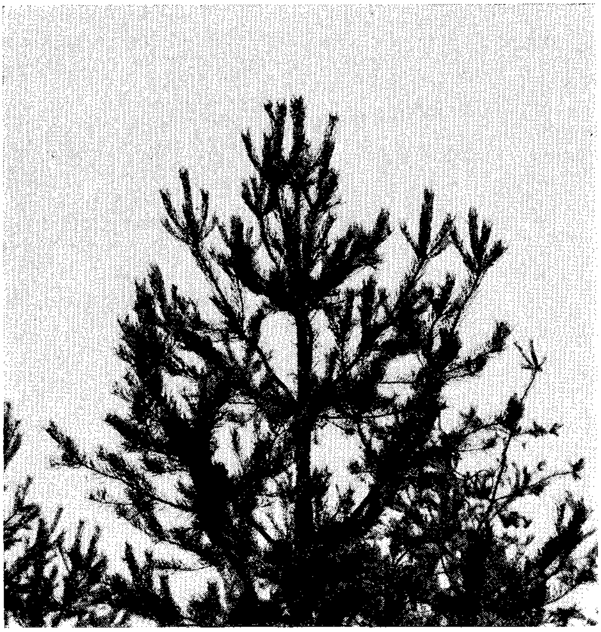

Fig. 4. Graft of the plus tree E 4008 at Boxholm.
The branch angles are intermediate to acute.

For the analyses of the properties c—h in 1960 and 1961 a limited number of the progenies was used. The data obtained are presented in Tables 5 and 6. The 20 tallest undamaged trees in each registered plot were selected for the investigation and the mean values of plots and progenies were used in the analyses of variance. Adjusted progeny means were used when comparing the progenies with one another. After a preliminary test had revealed significant differences between progenies, an exact test of the significance of the differences between individual progenies was made.

## The Characteristics of the Parent Trees

When selecting the plus and minus trees for this investigation the main principle was to find extreme phenotypes of either type growing at different latitudes and altitudes. The *plus trees* should be superior in height and diameter compared to the check trees growing nearby, the stems should be straight and even, the crowns narrow, the branches fine and the branch angles right or nearly right (Fig. 1). No trees with damages of any kind should be selected (ANDERSSON, 1948).

**Table 4. Parent trees. Data on**

| Tree No. | Phenotype plustree: + minus tree: – | Locality and Province | Latitude | Altitude m | Site | Year of measurement | Age at breast height c:a |
|---|---|---|---|---|---|---|---|
| E 4015 | + | Boxholm, Östergötland | 58° 7′ | 180 | normally drained moraine | 1949 | 121 |
| E 4008 | + | | | | | | 116 |
| VIII 46⁻ | — | | | | | | 111 |
| VIII 47⁻ | — | | | | | | 113 |
| S 3001 | + | Vägsjöfors, Värmland | 60° 22′ | 157 | normally drained moraine | 1948 | 79 |
| S 3003 | + | Brunsberg, Värmland | 59° 38′ | 118 | | 1948 | 107 |
| S 6210 | + | Geijersholm, Värmland | 60° 4′ | 200 | | 1946 | 108 |
| X 2021 | + | Ockelbo, Gästrikland | 60° 56′ | 150 | normally drained moraine | 1951 | 83 |
| X 2030 | + | | | | | | 87 |
| 11:18⁻ | — | | | | | | 58 |
| 11:19⁻ | — | | | | | | 79 |
| Z 4400 | + | Aspan, Jämtland | 62° 5′ | 300 | normally drained moraine | 1951 | 82 |
| Z 4401 | + | | | | | | 93 |
| Z 4406 | + | | | | | | 96 |
| Y 37⁻ | — | | | | | | 72 |
| Y 38⁻ | — | | | | | | 102 |
| Å 3⁻ | — | Ånge, Västernorrland | 62° 25′ | 275 | moderately drained moraine | 1948 | 89 |
| Å 4⁻ | — | | | | | | 78 |
| BD 4016 | + | Vuollerim, Norrbotten | 66° 25′ | 110 | well drained sandy soil | 1949 | 98 |
| E 67⁻ | — | | | | | | 58 |

[1]) AB: pass with distinction; Ba: pass with credit; B: satisfactory

The *minus trees* were chosen mainly for their slow height growth, strongly tapering stems, broad crowns and thick branches. The branch angles were intermediate to right-angled in some of the trees, and acute in others.

**localities and characteristics.**

| Characteristics | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Crown | | | | Branches | | |
| Height m | Diameter, breast height o. b. mm | Type | Radius (longest) m | Limit m | Ratio per cent | Type | Angle | Credit[1]) |
| 28.0 | 420 | narrow | 3.8 | 15.5 | 45 | fine | right | Ba |
| 30.5 | 460 | narrow | 2.8 | 15.5 | 49 | fine | right | AB— |
| 22.8 | 486 | broad | 4.3 | 8.5 | 63 | coarse | inter-mediate | |
| 19.0 | 418 | broad | 3.7 | 6.6 | 65 | coarse | inter-mediate | |
| 25.0 | 310 | extremely narrow | 1.7 | 11.5 | 54 | extremely fine | inter-mediate | Ba |
| 28.5 | 405 | narrow | 2.0 | 16.5 | 42 | fine | right | Ba— |
| 28.5 | 410 | narrow | 2.4 | 9.5 | 67 | fine | right | Ba+ |
| 21.5 | 305 | extremely narrow | 1.6 | 9.9 | 54 | fine | right | AB |
| 24.5 | 315 | narrow | 2.2 | 9.8 | 60 | fine | right | AB |
| 15.8 | 305 | broad | 3.0 | 5.6 | 64 | coarse | inter-mediate | |
| 20.6 | 425 | broad | 4.5 | 7.6 | 63 | coarse | acute | |
| 24.6 | 328 | narrow | 1.7 | 10.9 | 56 | extremely fine | inter-mediate | B+ |
| 24.2 | 314 | narrow | 2.2 | 7.5 | 69 | extremely fine | inter-mediate | B+ |
| 25.3 | 300 | narrow | 1.4 | 9.7 | 62 | fine | inter-mediate | Ba— |
| 19.9 | 380 | broad | 3.0 | 7.7 | 61 | coarse | inter-mediate | |
| 22.4 | 320 | broad | 3.5 | 5.2 | 77 | coarse | inter-mediate | |
| 20.5 | 437 | broad | 3.7 | 10.0 | 51 | coarse | acute | |
| 20.0 | 425 | broad | 4.2 | 4.7 | 77 | coarse | extremely acute | |
| 18.8 | 298 | narrow—inter-mediate | 2.0 | 6.5 | 65 | fine | inter-mediate—right | B+ |
| 16.5 | 330 | broad | 3.6 | 10.5 | 64 | coarse | inter-mediate | |

The original selection of the plus trees was made mainly by the Society of Forest Tree Breeding, Uppsala and by the Forest Tree Breeding Association, Brunsberg, Värmland, (now united into one organization).

The first estimates and measurements of the trees selected were made in 1948—1951 and the trees were classified according to the data obtained (Table 4). A second check of the trees in 1952—1953 corresponded to the previous assessments of the tree types on the whole, with the exception of the trees at Aspan (Z). In this provenance the two selected plus trees Z 4400 and Z 4401 were not recognised as extreme plus types and a special note was made as to their inferiority of growth compared to other plus trees on the same sites and latitudes. Furthermore, one of the trees, Z 4401, was attacked by the fungus *Peridermium pini*. They were not to be used in further breeding work. The two minus trees in the same stand were still classified as minus types as regards stem and crown, but as 'normal' as regards height growth. Furthermore, clone tests revealed that the classification of the plus tree E 4008 as right-angled was probably incorrect. This tree was analysed in three clone trials on different sites and on different stock material (*cf.* HOFFMANN, 1963). The branch angles of the ramets were intermediate to acute in all cases. (Fig. 4.)

# Results

## Characteristics of the Progenies

### 1. Tree height (H)

The variation in total height and yearly height growth was analysed for all progenies for five years (Fig. 5—10). Each year significant differences between progenies were found in every experiment.

Owing to the inefficient designs of the experiments no estimate of heritability was made for the present material. In other studies, the heritability values (narrow-sense) reported for height growth varied between 16 and 65 per cent in *Pinus silvestris*, (TODA, 1958; EKLUNDH EHRENBERG 1963). The broad-sense heritability values recorded in various tests are about 81 per cent (WRIGHT, 1963). In other pine species, for instance *Pinus monticola* (SQUILLACE ET AL., 1960), the narrow-sense heritability calculated varies between — 0.08 and 0.21 (for review of literature, see SZIKLAI, 1964). This variation is to a great extent due to the methods used for estimating heritability and to the design of the experiments studied. HATTEMER (1963) emphasised the fact 'that $h^2$ in plant breeding is a parameter of a field trial rather than a genetic parameter'.

| Year | 1960 | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | Z | E | E | Z | Z | E | E | E | E | Y | Z | E | Z | S |
| Combination | -selfed | +x+ | -x- | -x- | -x+ | +x+ | -o.p. | +x+ | -o.p. | +o.p. | -o.p. | -x- | +x+ | -x- | +o.p. |
| Progeny No. | 11 | 23 | 15 | 12 | 30 | 24 | 16 | 7 | 13 | 10 | 38 | 31 | 2 | 27 | 61 |
| Height, cm | 60 | 68 | 71 | 78 | 86 | 87 | 87 | 91 | 94 | 100 | 101 | 103 | 103 | 117 | 118 |

| Year | 1964 | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | Z | E | E | Z | Z | E | Vg | E | Z | E | Y | E | Z | E | S |
| Combination | -selfed | +x+ | -x- | -x- | -x+ | +x+ | -o.p. | | -o.p. | -x- | +x+ | -o.p. | +x+ | -x- | +o.p. | +o.p. |
| Progeny No. | 11 | 23 | 15 | 12 | 30 | 24 | 13 | | 16 | 31 | 7 | 38 | 2 | 27 | 10 | 61 |
| Height, cm | 147 | 172 | 187 | 199 | 206 | 229 | 233 | 235 | 238 | 242 | 244 | 267 | 273 | 276 | 280 | 318 |

Fig. 5. Experiment Eh 51. Range and significance of the differences between progenies in height in the years 1960 and 1964. The arrows indicate progenies, which markedly changed place in ranking from 1960 to 1964. Any two means not underscored by the same line are significantly different (individual t-test).

## *11. Experiment Eh 51*

A comparison between all the progenies in *experiment Eh* 51 (Fig. 5) did not reveal any regular trend in the range in height among the plus and minus tree progenies. One plus tree progeny from Värmland, 52—61, was among the tallest in 1960 and by far the tallest in 1964. The next one in range in 1960 was a minus × minus crossing of the Z-provenance. This progeny was followed by one plus × plus progeny of Boxholm (E) origin, another minus crossing from Aspan (Z), and one progeny of a minus tree from Ånge (Y). The progenies most inferior in height were two minus crossings from Boxholm and a plus × plus crossing from Aspan. The lowest progeny was the only inbred offspring in the experiment, VIII 46⁻ selfed (52—11). In 1964 the range had changed so far that some of the minus tree progenies had increased relatively little in height, for instance 52—31 (– × –, Z) ranking fourth in 1960 and seventh in 1964, and 52—13 (– o. p., E), which also ranked lower in 1964 than in 1960. Two of the plus tree progenies from Boxholm, Nos. 7 and 10, ranked higher in 1964 than in 1960. Especially the last one had gained conspicuously in height and was the tallest but one in 1964. Thus, in 1964 there were still both plus and minus tree progenies among the tallest as well as among the smallest.

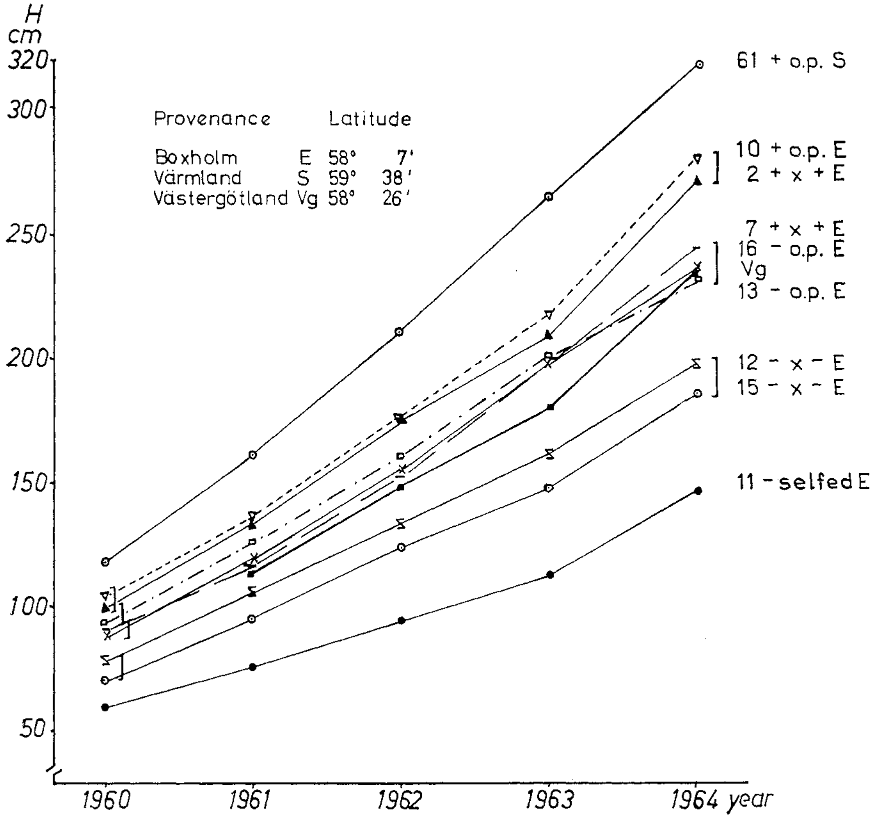


Fig. 6. a Experiment Eh 51. Mean heights of the progenies in the years 1960 to 1964. Any two means not included within the same line appearing at the right of each set of data are significantly different.

*a) The Boxholm provenance*

A different picture is obtained if the various provenances are separately analysed (Fig. 6 a). Within the Boxholm provenance two of the plus tree progenies, Nos. 2 and 10, were superior in height from 1960 to 1964. In the latter year the differences between them and the other six progenies were significant at the 5 to 0.1 per cent level. The third plus tree progeny, No. 7, ranked between two minus tree progenies obtained from open pollination in 1960, but had surpassed the tallest of these in 1964. The two minus × minus crosses included had a comparatively slow height growth. The same results were found in the previous investigation of some Boxholm progenies obtained after crosses between the same parent trees (EKLUNDH EHRENBERG, 1963).

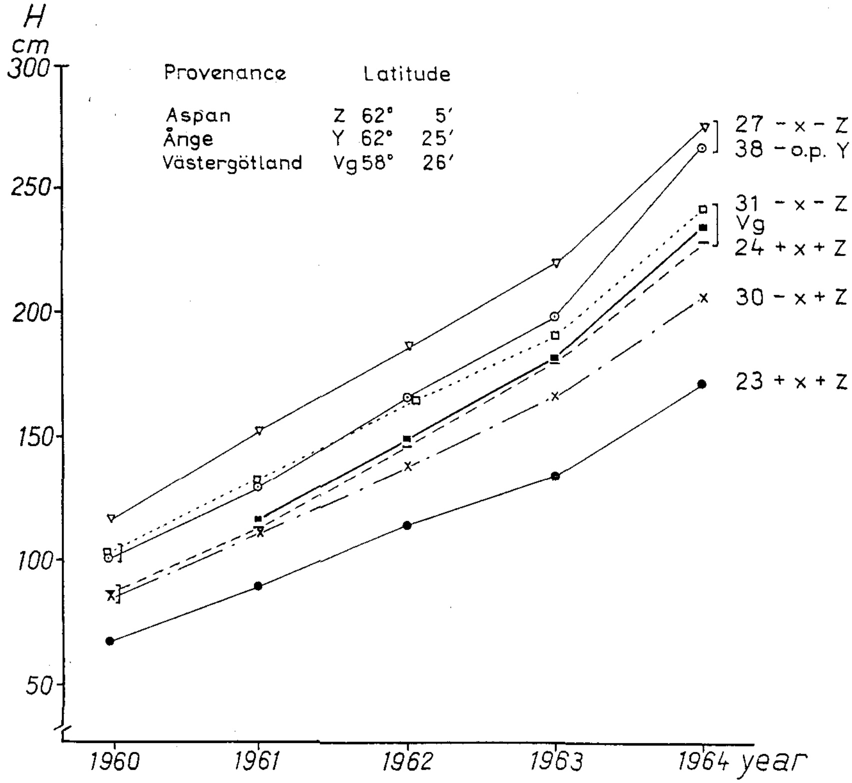


Fig. 6 b. Experiment Eh 51. Mean heights of the progenies in the years 1960 to 1964. Any two means not included within the same line appearing at the right of each set of data are significantly different.

*b) The Aspan provenance*

Quite the reverse condition prevailed within the provenance of Aspan (Fig. 6 b), where the two minus × minus crosses dominated as regards height, and the three plus tree progenies, including one minus × plus cross, were by far the smallest. One plus tree, Z 4401, is a common parent to these progenies, and used either as a mother or a father tree. A possible explanation of the slow growth of its offspring could be a poor special combining ability. A more probable cause, however, is the fact that the plus trees in Aspan, selected for crossing purposes, were wrongly classified as 'plus' as regards growth capacity when chosen in 1951. A later check of the trees in 1953 revealed their comparatively poor ability of volume production (*cf.* p. 4). The behaviour of the progenies thus seems to confirm the estimated genotypes of the parent trees.

*c) Reciprocal crosses*

Three pairs of reciprocal crosses are included in this experiment. Two are of Boxholm origin, where the two plus trees and the two minus trees respectively were crossed in both directions. The third pair includes the two minus trees at Aspan. No significant differences in height between the two minus tree progenies at Boxholm were established in any of the years 1960—1964. The two reciprocal plus tree crosses of the same provenance differed significantly every year. Also there were significant differences between the reciprocal minus crosses from Aspan. Differences in seed weight or in the treatment of the seedlings have not been recorded in either case.

## *12. Experiment Eh 52*

In *experiment Eh* 52, mainly including progenies of similar type as those in experiment Eh 51, namely crosses between trees within provenances (Table 2), plus and minus tree progenies were found among the tallest as well as among the smallest in 1960. The range of the progenies and the significance of the differences in height are presented in Figs. 7 and 8. In 1964 the progenies ranked in a slightly different order and there was a clear tendency for the plus tree progenies to gain more in height than the minus tree progenies. For instance, Nos. 53—128 (+ o.p., S) and 53—113 (– o.p., X) had changed places. The minus tree progeny, No. 113, ranking third in 1960, was now number six in order, and the plus tree progeny, No. 128, had moved in the opposite direction. The differences between the two progenies were not significant in either year, however.

The height differences were less marked in 1960 than in 1964. In 1964, there were significant differences between the two plus tree progenies from Värmland, Nos. 126 and 119, on the one hand, and the group of progenies ranking next in height (Nos. 128—113) on the other, the latter representing three different provenances and both plus and minus tree progenies obtained from open pollination or crosses. A third group, Nos. 76, 58 and 74, differing significantly in height from the rest, is also composed of progenies of varying origin. Finally, progeny No. 60 with a comparatively slow height growth in all years is the minus × minus progeny from Ockelbo.

The selfed progeny, No 73, was obtained from the same minus tree, VIII 46⁻, at Boxholm, as the progeny No. 11 in experiment Eh 51. In general, both show poor vitality and slow growth. In 1964 the progeny No. 73 had reached a height less than half of that achieved by the tallest progeny in experiment Eh 52, No. 126 (120 and 290 cm respectively).

| Year | 1960 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | X | Exprov. | X | E | S | X | E | X | S | S |
| Combination | -selfed | -x- | -xsib. | -x+ | -o.p. | +o.p | -x+ | +o.p. | -o.p. | +o.p. | +x+ |
| Progeny No. | 73 | 60 | 74 | 58 | 76 | 128 | 59 | 72 | 113 | 119 | 126 |
| Height, cm | 46 | 66 | 74 | 77 | 77 | 83 | 84 | 85 | 86 | 90 | 96 |

| Year | 1964 | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | X | Vǫ | E | X | E | X | X | E | S | S | S |
| Combination | -selfed | -x- | | -xsib. | -x+ | -o.p. | -o.p. | -x+ | +o.p. | +o.p. | +o.p. | +x+ |
| Progeny No. | 73 | 60 | | 74 | 58 | 76 | 113 | 59 | 72 | 128 | 119 | 126 |
| Height, cm | 120 | 177 | 199 | 200 | 205 | 208 | 235 | 239 | 249 | 253 | 274 | 290 |

Fig. 7. Experiment Eh 52. Range and significance of the differences between progenies in height in the years 1960 and 1964. The arrows indicate progenies, which markedly changed place in the ranking from 1960 to 1964. Any two means not underscored by the same line are significantly different (individual t-test).

*a) The Värmland and Boxholm provenances*

Analysing each provenance separately (Fig. 8 a), the plus tree cross No. 126, *Värmland*, was superior in height to the two open pollinated plus tree progenies of the same provenance in all years. The difference was significant only in relation to progeny No. 128. The ranking of the four *Boxholm* progenies was in agreement with that obtained in every experiment where crosses from the selected Boxholm trees were included. In the present case the plus tree offspring, No. 72, dominated all years, and more as the trees grew older. As mentioned above, the selfed progeny, No. 73, was comparatively weak and slow-growing.

*b) The Ockelbo provenance*

The four progenies of the provenance Ockelbo (X) (Fig. 8 b) are especially interesting as they all originate from the same mother tree, 11:18⁻. The male parents are two plus trees and one minus tree and, as regards the open-pollinated progeny No. 113, are probably pines of various types in the immediate neighbourhood (*cf.* Wright, 1962, for review of literature on

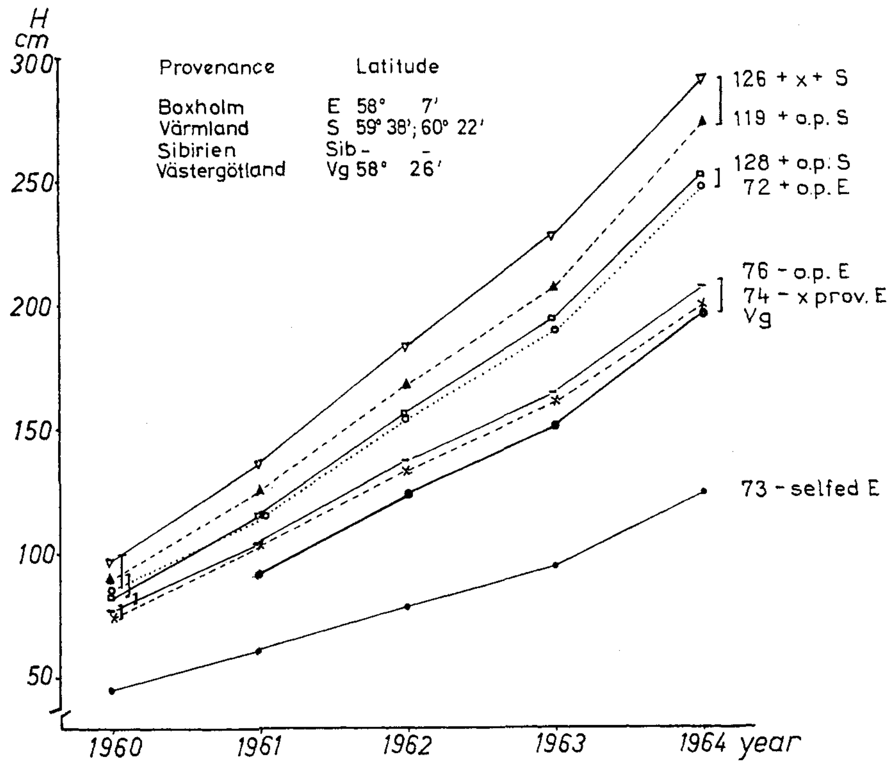


Fig. 8 a. Experiment Eh 52. Mean heights of the progenies in the years 1960 to 1964. Any two means not included within the same line appearing at the right of each set of data are significantly different.

pollen dispersion). No significant differences in height were found between the progenies Nos. 113, −o.p., 59, −×+, and 58, −×+, in 1960, whereas the fourth progeny, No. 60, −×−, was significantly lower. In 1964, the last year of measurement, the progenies Nos. 59 and 113 ranked first in height. The other minus × plus progeny, No. 58, had lagged behind and was at this age significantly lower than the two which ranked first. The minus cross No. 60 was still the progeny of slowest growth.

Unfortunately, the design of the experiment, the small number of progenies from the tree 11:18⁻ and the lack of reciprocal crosses or of a diallell system of crossing do not allow a detailed analysis of the components of variance or a calculation of the heritability of this property to be made. The results obtained indicate that there are inherent differences between the male plus parents in height growth or differences between the two plus trees in combining ability with the common female minus tree 11:18⁻. They also indicate that the classification of the parent trees as plus or minus types was correct as regards this property.

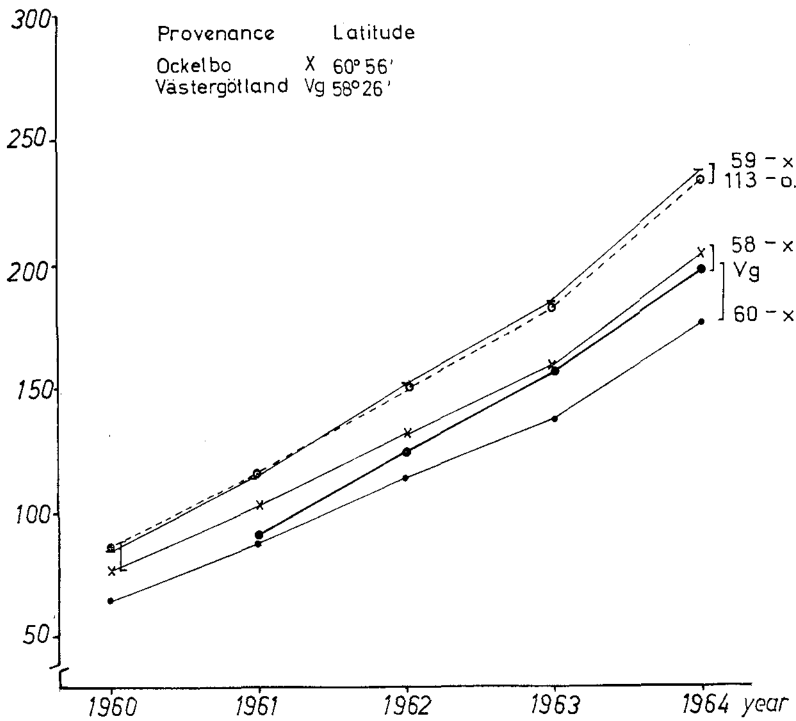


Fig. 8 b. Experiment Eh 52. Mean heights of the progenies in the years 1960 to 1964. Any two means not included within the same line appearing at the right of each set of data are significantly different.

## *13. Experiment Eh 53*

In the third *experiment, Eh* 53 (Table 3 and Figs. 9 and 10) involving progenies of widely differing origin, there is one progeny, No. 4, of special interest. This progeny is a cross between a plus tree, BD 4016, of the northern provenance Vuollerim and a plus tree from Boxholm, E 4008, in southern Sweden. It was superior in height to the open-pollinated progenies from the two parent trees in the first years of measurement (Fig. 9). The differences were significant at the 0.1 and 5 per cent level respectively. In 1964 the open-pollinated progeny from the male parent, E 4008, had caught up with the provenance hybrid, but the female parent offspring after open pollination, No. 6, was still the next to lowest one in the experiment.

The rest of the material, mainly of the same height in 1960, was more differentiated in 1964 (Fig. 9). In that year all the progenies (except No. 4), originating from the two Vuollerim trees as female parents, were inferior in height to the progenies of a more southern origin irrespective of the male parents. The transfer of seeds or plants of a very northern origin to a local-

| Year | 1960 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | BD | Y | Y×E | Y×X | BD | BD | BD×E | E | Y×E | BD×E |
| Combination | -selfed | +o.p. | -o.p. | -x- | -x- | -x+ | -o.p. | -x- | +o.p. | -x- | +x+ |
| Progeny No. | 73 | 6 | 30 | 33 | 28 | 16 | 18 | 14 | 72 | 27 | 4 |
| Height, cm | 39 | 60 | 66 | 68 | 70 | 72 | 73 | 73 | 77 | 82 | 106 |

| Year | 1964 | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | BD | BD | BD | Y×E | BD×E | Y×X | Y | Vg | Y×E | E | BD×E |
| Combination | -selfed | +o.p. | -o.p. | -x+ | -x- | -x- | -x- | -o.p. | | -x- | +o.p. | +x+ |
| Progeny No. | 73 | 6 | 18 | 16 | 33 | 14 | 28 | 30 | | 27 | 72 | 4 |
| Height, cm | 102 | 148 | 172 | 179 | 184 | 189 | 190 | 191 | 204 | 208 | 249 | 274 |

Fig. 9. Experiment Eh 53. Range and significance of the differences between progenies in height in the years 1960 and 1964. The arrows indicate progenies which markedly changed place in ranking from 1960 to 1964. Any two means not underscored by the same line are significantly different (individual t-test).

ity far south usually results in a lowered volume production as compared to that of the provenances adapted to the southern climate and latitude (Langlet, 1948). This might be the explanation of the inferiority in height of the BD-progenies in this case.

No significant differences between the four *Ånge* crosses were established in either year (Figs. 9 and 10). The three provenance hybrids (Nos. 27, 28 and 33) did not exceed the open-pollinated progeny from Å 3⁻ (No. 30) in height. In all the crosses only minus trees were used as parents.

Among the progenies from the two mother trees at *Vuollerim* the provenance cross No. 4, BD 4016 × E 4008, was the fastest-growing progeny, as already mentioned (*cf.* p. 8), exceeding the open-pollinated progeny, No. 6, from the same mother tree by 126 cm, and the other provenance hybrid E 67⁻ × VIII 46⁻, No. 14, by a little less than one metre in 1964 (Figs. 9 and 10). The other two progenies in this group, E 67⁻ × BD 4016, No. 16, and E 67⁻ o.p., No. 18, ranked close to No. 14 in all years. The difference in height between No. 16, minus × plus, and No. 6, plus o.p., was significant in 1964.

There are two progenies in common in the experiments Eh 52 and Eh 53, namely No. 72, E 4008 o.p., and the local provenance, Vg. The first-mentioned, E 4008 o.p,. displayed about the same mean height in both experiments in

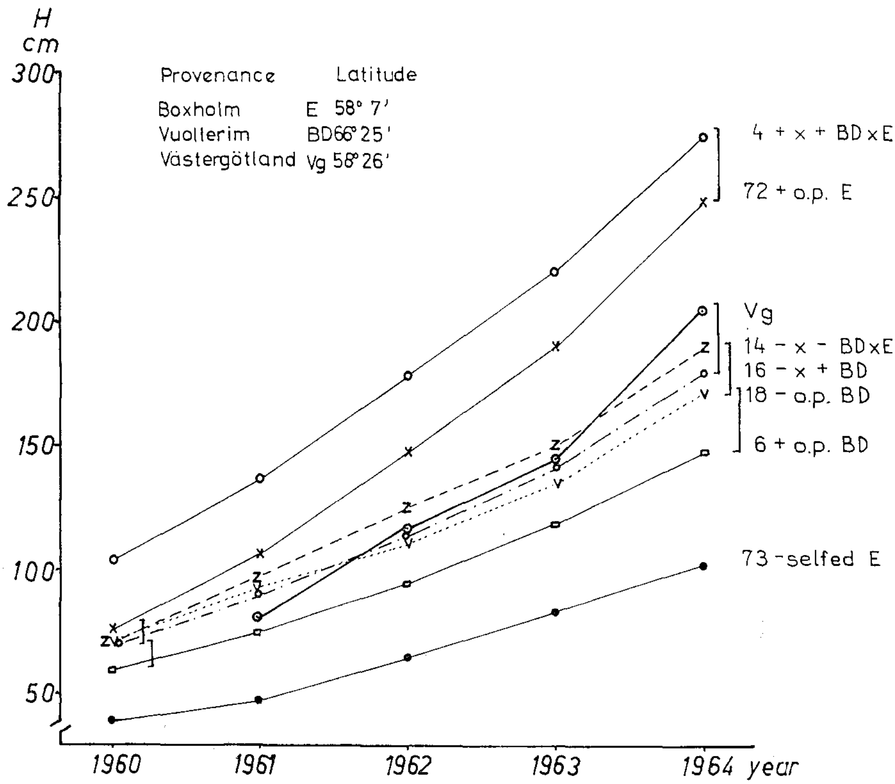


Fig. 10 a. Experiment Eh 53. Mean heights of the progenies in the years 1960 to 1964. Any two means not included within the same line appearing at the right of each set of data are significantly different.

1960 and exactly the same height in 1964. The Vg-progeny, too, was about equal in height in the two test plots. Using these progenies as a basis for comparison between progenies of both experiments, the provenance hybrid in experiment Eh 53, No. 4, apparently is of the same vigorously growing type as the tallest plus tree progenies from Värmland in experiment Eh 52. No other cross between plus trees of so widely differing origin was available when these field trials were planted. The provenance hybrids obtained from minus tree combinations were of about the same height as the local provenance and the open-pollinated progenies from the northernmost parent.

Another interesting comparison can be made between the progenies obtained from the plus tree No. S 3003 after open pollination in two different years, and the rest of the material in experiments Eh 51 and Eh 52 respectively. In both tests the offspring of this tree is by far superior as regards height growth, increasing in height by about two metres in five years. This may be

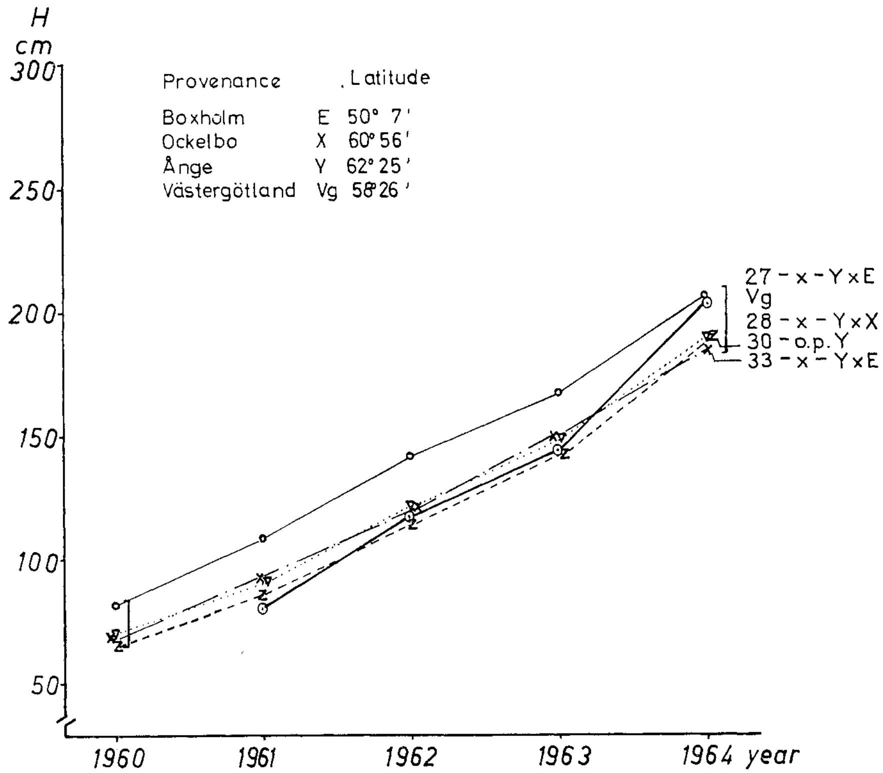


Fig. 10 b. Experiment Eh 53. Mean heights of the progenies in the years 1960 to 1964. Any two means not included within the same line appearing at the right of each set of data are significantly different.

regarded as proof of the very good genotype of the female parent, correctly estimated as a plus tree in terms of growth rate.

The local provenances, Vg, measured only in the years 1961—1964, usually varied about the total mean of all progenies in each experiment (Figs. 5, 7 and 9). The seedlings were in a rather bad condition when planted in 1956, and this was the reason for excluding them from the investigations in the first years. From the diagrams of the growth (Figs. 6, 8 and 10) it can be seen that the Vg-progeny sown in 1952, experiment Eh 51, had increased most in height during the last year, i.e. 1964. Even in the one-year-younger material, sown in 1953, experiments Eh 52 and Eh 53, there seemed to be a slightly steeper gradient of the increase in height for the last year. Their final position among the progenies in the three test plots may be perceptibly changed in the years to follow, if the tendency to faster growth in 1964 is a sign of better inherent growth capacity than that shown earlier.

There was a strong correlation between the length of the terminal shoots

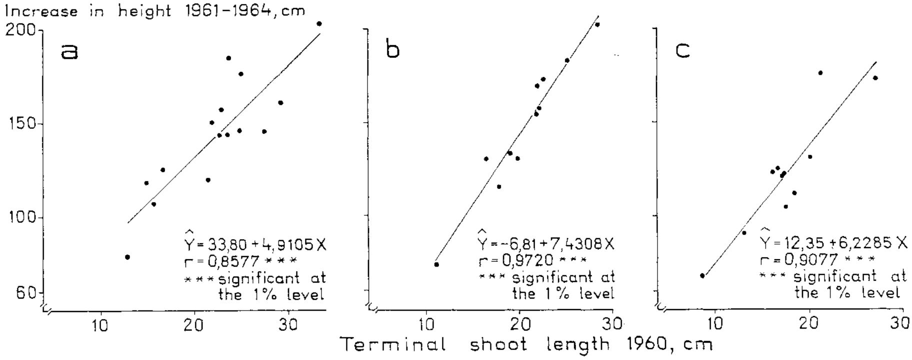


Fig. 11. Relation between the mean terminal shoot length of the progenies in 1960 and the increase in height from 1961 to 1964. a. Experiment Eh 51. b. Experiment Eh 52. c. Experiment Eh 53.

in 1960 and the increase in height in 1961 to 1964 (Figs. 11). Simple correlation analyses using progeny means as items were made to determine the coefficients of correlation and of regression. In each experiment the correlation was significant at the 0.1 per cent level. This indicates a possibility of selecting future rapidly growing progenies from this material as early as the eighth growing season, if the selection is based on the superiority of the terminal shoot length. The same high correlations were obtained when total height values for 1960 and 1964 were used (*cf.* TODA, 1958; CALLAHAM and HAZEL, 1961; CALLAHAM and DUFFIELD, 1963). However, later changes in range among the progenies, that is, after 14 years of age, might occur, and nothing can be said, as yet, about the relative position of the progenies in terms of total height at the end of the rotation (*cf.* MATÉRN, 1959; LANGLET, 1960; STERN and HATTEMER, 1963).

## 2. Branch and bud characteristics (c—h) analysed in 1960 and 1961

The progenies analysed, the number of plots and trees per progeny, as well as the mean values of the recorded properties in 1960 and 1961, are presented in Tables 5 and 6. The range and the significance of the differences between progenies in the various characteristics are shown in Figs. 12—18. For various reasons certain plots had to be left out, and only a limited number of plots per progeny was measured in 1960 in experiments Eh 51 and Eh 53; also the two progenies in experiment Eh 51 deviating most in height, S 3003 o.p. and VIII 46⁻ selfed, were excluded. In 1961 the choice of progenies to be analysed was slightly different and only some progenies were measured in both years.

**Table 5. Progenies selected for analysis of the properties**

| Experiment No. | Progeny No. | Cross combination | | Height cm | Terminal shoot cm | Branch length cm Whorl No. | | |
|---|---|---|---|---|---|---|---|---|
| | | | | | | 1 | 2 | 3 |
| | | *Boxholm* | | | | | | |
| Eh 51 | 52— 2 | E 4015 × E 4008... | + × + | 113.8 | 27.2 | 18.3 | 30.2 | 33.7 |
| | 7 | E 4008 × E 4015... | + × + | 124.5 | 36.7 | 25.3 | 37.2 | 44.0 |
| | 10 | E 4008........... | o. p.[1]) | 109.7 | 24.8 | 18.1 | 30.5 | 34.2 |
| | 12 | VIII $46^-$ × VIII $47^-$ | − × − | 95.3 | 23.9 | 18.9 | 31.5 | 37.1 |
| | 13 | VIII $46^-$......... | o. p. | 116.2 | 28.6 | 20.4 | 36.9 | 43.4 |
| | 15 | VIII $47^-$ × VIII $46^-$ | − × − | 88.1 | 19.2 | 14.1 | 26.2 | 29.9 |
| | 16 | VIII $47^-$......... | o. p. | 119.8 | 30.8 | 22.2 | 37.2 | 42.1 |
| | | *Aspan* | | | | | | |
| | 23 | Z 4401 × Z 4406... | + × + | 91.2 | 22.1 | 16.1 | 23.6 | 24.4 |
| | 24 | Z 4401 × Z 4400... | + × + | 101.9 | 28.6 | 19.4 | 27.4 | 26.7 |
| | 27 | Y $37^-$ × Y $38^-$..... | − × − | 135.4 | 34.4 | 22.9 | 39.2 | 47.6 |
| | 30 | Y $38^-$ × Z 4401.... | − × + | 114.0 | 31.0 | 21.2 | 33.2 | 39.1 |
| | 31 | Y $38^-$ × Y $37^-$..... | − × − | 129.7 | 31.8 | 20.9 | 36.5 | 42.3 |
| | | *Ånge* | | | | | | |
| | 38 | Å $3^-$............. | o. p. | 115.3 | 30.4 | 20.5 | 33.1 | 38.4 |
| Eh 53 | 53— 4 | BD 4016 × E 4008 . | + × + | 127.4 | 33.9 | 23.4 | 36.5 | 43.1 |
| | 6 | BD 4016......... | o. p. | 81.6 | 19.2 | 13.1 | 19.9 | 24.2 |
| | 14 | E $67^-$ × VIII $46^-$.. | − × − | 98.3 | 24.6 | 17.0 | 29.8 | 37.0 |
| | 16 | E $67^-$ × BD 4016.. | − × + | 100.5 | 26.4 | 17.7 | 27.6 | 31.9 |
| | 18 | E $67^-$............ | o. p. | 95.8 | 24.0 | 16.6 | 25.8 | 32.9 |
| | 72 | E 4008........... | o. p. | 89.1 | 24.3 | 17.5 | 28.9 | 34.5 |

## *21. Results in 1960*

*Experiment Eh 51*

No significant differences between the progenies were established as regards the following properties

| | |
|---|---|
| Length of branches | whorl 1 |
| Angle of branches | whorl 2 and whorl 3 |
| Number of branches | whorl 2 |
| Ratio between branch length and tree height | whorl 1 and whorl 2. |

As to the remaining properties analysed, and comparing all the progenies in the experiment irrespective of the various provenances, there was no grouping of plus tree progenies in one unit and minus tree progenies in another (Fig. 12). The only characteristic in which a tendency to such grouping was discernible was the number of branches in whorl 3, and here the plus tree progenies ranked lowest. However, there was one exception, namely the minus cross No. 15, − × −, with comparatively few branches.

Some features characteristic of the individual progenies can be emphasised. The four progenies ranking lowest in height (20 trees per plot) were the two reciprocal minus crosses from Boxholm, Nos. 12 and 15, and two plus tree

**c-h in 1960. Mean values of the recorded properties.**

| Ratio $\frac{100\ Brl}{H}$ Whorl No. | | | Branch angle Whorl No. | | No. of branches Whorl No. | | | Length of apical bud mm | Length of lateral buds mm | No. of lateral buds | Ratio $\frac{100\ Ht}{Th}$ | No. of trees | No. of plots |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 2 | 3 | 1 | 2 | 3 | | | | | | |
| 16.1 | 26.7 | 29.5 | 54.5 | 67.7 | 5.3 | 4.7 | 3.0 | 14.6 | 12.5 | 4.7 | 5.4 | 40 | 2 |
| 20.3 | 30.2 | 35.3 | 60.8 | 69.9 | 6.6 | 5.1 | 3.2 | 17.1 | 15.0 | 5.9 | 4.5 | 20 | 1 |
| 16.6 | 28.1 | 31.4 | 53.1 | 64.0 | 4.5 | 4.4 | 3.1 | 15.6 | 13.6 | 4.0 | 6.2 | 20 | 1 |
| 19.6 | 33.3 | 38.8 | 59.0 | 69.5 | 5.9 | 4.7 | 3.6 | 14.2 | 12.6 | 3.8 | 5.4 | 20 | 1 |
| 17.4 | 33.9 | 37.2 | 53.7 | 62.2 | 5.8 | 5.3 | 3.6 | 16.8 | 14.9 | 4.5 | 6.0 | 80 | 4 |
| 16.1 | 29.6 | 34.2 | 57.6 | 69.3 | 5.0 | 4.1 | 2.9 | 13.1 | 11.8 | 3.7 | 6.8 | 60 | 3 |
| 18.5 | 30.8 | 35.0 | 53.0 | 63.7 | 6.3 | 5.2 | 3.7 | 16.4 | 14.7 | 5.0 | 5.4 | 60 | 3 |
| 17.8 | 26.3 | 26.9 | 53.9 | 64.9 | 3.9 | 3.2 | 2.3 | 15.3 | 12.4 | 3.9 | 6.9 | 20 | 1 |
| 19.0 | 26.5 | 26.6 | 51.4 | 60.4 | 4.9 | 4.0 | 3.1 | 15.9 | 13.2 | 4.4 | 5.6 | 40 | 2 |
| 16.7 | 28.5 | 34.7 | 52.0 | 61.5 | 5.1 | 4.7 | 3.9 | 19.2 | 15.6 | 4.8 | 5.7 | 40 | 2 |
| 18.5 | 28.8 | 34.2 | 55.1 | 63.2 | 4.9 | 4.7 | 3.3 | 16.8 | 13.9 | 4.7 | 5.4 | 60 | 3 |
| 16.1 | 28.1 | 32.5 | 53.8 | 62.4 | 5.0 | 4.5 | 3.3 | 18.2 | 15.0 | 4.8 | 5.8 | 80 | 4 |
| 17.5 | 28.2 | 32.6 | 56.2 | 62.1 | 5.4 | 5.1 | 3.8 | 17.4 | 14.8 | 4.7 | 5.8 | 40 | 2 |
| 18.4 | 28.5 | 33.6 | 58.5 | 69.8 | 6.2 | 6.1 | 5.3 | 18.6 | 15.0 | 5.6 | 5.5 | 40 | 2 |
| 15.9 | 24.4 | 29.5 | 67.7 | 81.0 | 4.6 | 5.5 | 3.9 | 12.0 | 10.3 | 4.4 | 6.3 | 60 | 3 |
| 17.3 | 30.3 | 37.7 | 67.1 | 77.0 | 5.2 | 5.1 | 3.4 | 12.9 | 11.6 | 4.5 | 5.3 | 40 | 2 |
| 17.5 | 27.4 | 31.8 | 67.4 | 81.1 | 5.1 | 5.0 | 3.9 | 13.7 | 11.6 | 4.1 | 5.3 | 40 | 2 |
| 17.3 | 27.0 | 34.5 | 67.9 | 78.5 | 4.4 | 4.7 | 4.2 | 13.0 | 11.3 | 4.1 | 5.5 | 40 | 2 |
| 19.7 | 32.5 | 38.7 | 61.8 | 76.4 | 5.6 | 5.1 | 3.2 | 13.4 | 12.1 | 4.8 | 5.5 | 40 | 2 |

crosses from Aspan, Nos. 23 and 24. The progeny No. 12 had the longest branches in relation to height of all progenies in whorl 3 and a high number of branches in whorl 1 and whorl 3. This progeny differed significantly from No. 15 as regards the first and the last-mentioned characteristics. At this age (8 years) the progenies with the broadest crowns, as estimated by the relative length of the branches in whorl 3, were three minus and one plus tree progeny from Boxholm and one minus × minus offspring from Aspan. At the other extreme of the range were four plus tree progenies, two from Boxholm and two from Aspan, all with comparatively narrow crowns.

The progeny No. 15 had a very large apical bud in relation to the length of the terminal shoot, despite the fact that this progeny is one of the slowest-growing in the experiment. The progeny No. 23, ranking lowest, or lowest but one in all the other analysed properties, also had a relatively large apical bud. The opposite was the case in the fast-growing progenies from Boxholm, Nos. 2, 7 and 16, all three of which had small apical buds.

Hannover (1963) reported a strong positive correlation between dormant terminal bud length and total seasonal elongation in a 45-year-old *Pinus ponderosa* provenance test. The same general relationship was reported in the present material of Scots pine. The ratio between apical bud length

Boxholm E  Aspan Z  Ånge Y

Height (H)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | Z | E | Z | E | Z | E | Y | E | E | E | Z | Z |
| Combination | -x- | +x+ | -x- | +x+ | +o.p. | -x+ | +x+ | -o.p. | -o.p. | -o.p. | +x+ | -x- | -x- |
| Progeny No. | 15 | 23 | 12 | 24 | 10 | 30 | 2 | 38 | 13 | 16 | 7 | 31 | 27 |
| cm | 88 | 91 | 95 | 102 | 110 | 114 | 114 | 115 | 116 | 120 | 124 | 130 | 135 |

Length of terminal shoot (Th)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | E | Z | E | E | E | Z | E | Y | E | Z | Z | Z | E |
| Combination | -x- | +x+ | -x- | +o.p. | +x+ | +x+ | -o.p. | -o.p. | -o.p. | -x+ | -x- | -x- | +x+ |
| Progeny No. | 15 | 23 | 12 | 10 | 2 | 24 | 13 | 38 | 16 | 30 | 31 | 27 | 7 |
| cm | 19 | 22 | 24 | 25 | 27 | 28 | 29 | 30 | 31 | 31 | 32 | 34 | 37 |

Length of branches (Brl)

Whorl 2

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | Z | E | Z | E | E | E | Y | Z | E | Z | E | E | Z |
| Combination | +x+ | -x- | +x+ | +x+ | +o.p. | -x- | -o.p. | -x+ | +x+ | -x- | -o.p. | -o.p. | -x- |
| Progeny No. | 23 | 15 | 24 | 2 | 10 | 12 | 38 | 30 | 7 | 31 | 13 | 16 | 27 |
| cm | 24 | 26 | 27 | 30 | 30 | 32 | 33 | 33 | 37 | 36 | 37 | 37 | 39 |

Whorl 3

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | Z | Z | E | E | E | E | Y | Z | Z | E | E | E | Z |
| Combination | +x+ | +x+ | -x- | +x+ | +o.p. | -x- | -o.p. | -x+ | -x- | -o.p. | +x+ | -o.p. | -x- |
| Progeny No. | 23 | 24 | 15 | 2 | 10 | 12 | 38 | 30 | 31 | 16 | 7 | 13 | 27 |
| cm | 24 | 27 | 30 | 34 | 34 | 37 | 38 | 39 | 42 | 42 | 44 | 43 | 48 |

Ratio between branch length and height $\left(\frac{100\,Brl}{H}\right)$

Whorl 3

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Provenance | Z | Z | E | E | Z | Y | Z | E | Z | E | E | E | E |
| Combination | +x+ | +x+ | +x+ | +o.p. | -x- | -o.p. | -x+ | -x- | -x- | -o.p. | +x+ | -o.p. | -x- |
| Progeny No. | 24 | 23 | 2 | 10 | 31 | 38 | 30 | 15 | 27 | 16 | 7 | 13 | 12 |
| Ratio | 26.6 | 26.9 | 29.5 | 31.4 | 32.5 | 32.6 | 34.2 | 34.2 | 34.7 | 35.0 | 35.3 | 37.2 | 38.8 |

Fig. 12. Experiment Eh 51. Range and significance of the differences between progenies in height and branch and bud characteristics (c-h) in 1960. 13 progenies. 20 trees (*Continued p. 29*)

Number of branches

Whorl 1

| Provenances | Z | E | Z | Z | Z | E | Z | E | Y | E | E | E | E |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Combination | +x+ | +o.p. | −x+ | +x+ | −x− | −x− | −x− | +x+ | −o.p. | −x− | −o.p. | −o.p. | +x+ |
| Progeny No. | 23 | 10 | 30 | 24 | 31 | 15 | 27 | 2 | 38 | 12 | 13 | 16 | 7 |
| Number | 3.9 | 4.5 | 4.9 | 4.9 | 5.0 | 5.0 | 5.1 | 5.3 | 5.4 | 5.9 | 5.8 | 6.3 | 6.6 |

Whorl 3

| Provenance | Z | E | E | E | Z | E | Z | Z | E | E | E | Y | Z |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Combination | +x+ | −x− | +x+ | +o.p. | +x+ | +x+ | −x+ | −x− | −x− | −o.p. | −o.p. | −o.p. | −x− |
| Progeny No. | 23 | 15 | 2 | 10 | 24 | 7 | 30 | 31 | 12 | 13 | 16 | 38 | 27 |
| Number | 2.3 | 2.9 | 3.0 | 3.1 | 3.1 | 3.2 | 3.3 | 3.3 | 3.6 | 3.6 | 3.7 | 3.8 | 3.9 |

Length of apical bud (Ht)

| Provenance | E | E | E | Z | E | Z | E | Z | E | E | Y | Z | Z |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Combination | −x− | −x− | +x+ | +x+ | +o.p. | +x+ | −o.p. | −x+ | −o.p. | +x+ | −o.p. | −x− | −x− |
| Progeny No. | 15 | 12 | 2 | 23 | 10 | 24 | 16 | 30 | 13 | 7 | 38 | 31 | 27 |
| mm | 13 | 14 | 15 | 15 | 16 | 16 | 16 | 17 | 17 | 17 | 17 | 18 | 19 |

Ratio between apical bud and terminal shoot $\left(\frac{100\ Ht}{Th}\right)$

| Provenance | E | E | E | Z | E | Z | Z | Z | Y | E | E | Z | E |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Combination | +x+ | −o.p. | +x+ | −x+ | −x− | +x+ | −x− | −x− | −o.p. | −o.p. | +o.p. | +x+ | −x− |
| Progeny No. | 7 | 16 | 2 | 30 | 12 | 24 | 27 | 31 | 38 | 13 | 10 | 23 | 15 |
| Ratio | 4.5 | 5.4 | 5.4 | 5.4 | 5.4 | 5.6 | 5.7 | 5.8 | 5.8 | 6.0 | 6.2 | 6.9 | 6.8 |

Length of lateral buds (Hs)

| Provenance | E | Z | E | E | Z | E | Z | E | Y | E | Z | E | Z |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Combination | −x− | +x+ | +x+ | −x− | +x+ | +o.p. | −x+ | −o.p. | −o.p. | −o.p. | −x− | +x+ | −x− |
| Progeny No. | 15 | 23 | 2 | 12 | 24 | 10 | 30 | 16 | 38 | 13 | 31 | 7 | 27 |
| mm | 12 | 12 | 12 | 13 | 13 | 14 | 14 | 15 | 15 | 15 | 15 | 15 | 16 |

Number of lateral buds

| Provenance | E | E | Z | E | Z | E | E | Z | Y | Z | Z | E | E |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Combination | −x− | −x− | +x+ | +o.p. | +x+ | −o.p. | +x+ | −x+ | −o.p. | −x− | −x− | −o.p. | +x+ |
| Progeny No. | 15 | 12 | 23 | 10 | 24 | 13 | 2 | 30 | 38 | 27 | 31 | 16 | 7 |
| Number | 3.7 | 3.8 | 3.9 | 4.0 | 4.4 | 4.5 | 4.7 | 4.7 | 4.7 | 4.8 | 4.8 | 5.0 | 5.9 |

per plot. Any two means not underscored by the same line are significantly different (individual t-test).

# Boxholm E

### Height (H)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | -x- | +o.p. | +x+ | -o.p. | -o.p. | +x+ |
| Progeny No. | 15 | 12 | 10 | 2 | 13 | 16 | 7 |
| cm | 88 | 95 | 110 | 114 | 116 | 120 | 124 |

### Length of terminal shoot (Th)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | -x- | +o.p. | +x+ | -o.p. | -o.p. | +x+ |
| Progeny No. | 15 | 12 | 10 | 2 | 13 | 16 | 7 |
| cm | 19 | 24 | 25 | 27 | 29 | 31 | 37 |

### Length of branches (Brl)

Whorl 2

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | +x+ | +o.p. | -x- | -o.p. | +x+ | -o.p. |
| Progeny No. | 15 | 2 | 10 | 12 | 13 | 7 | 16 |
| cm | 26 | 30 | 30 | 32 | 37 | 37 | 37 |

Whorl 3

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | +x+ | +o.p. | -x- | -o.p. | +x+ | -o.p. |
| Progeny No. | 15 | 2 | 10 | 12 | 16 | 7 | 13 |
| cm | 30 | 34 | 34 | 37 | 42 | 44 | 43 |

### Ratio between branch length and height $\left(\frac{100\ Brl}{H}\right)$

Whorl 3

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | +x+ | +o.p. | -x- | -o.p. | +x+ | -o.p. | -x- |
| Progeny No. | 2 | 10 | 15 | 16 | 7 | 13 | 12 |
| Ratio | 29.5 | 31.4 | 34.2 | 35.0 | 35.3 | 37.2 | 38.8 |

### Number of branches

Whorl 1

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | +o.p. | -x- | +x+ | -x- | -o.p. | -o.p. | +x+ |
| Progeny No. | 10 | 15 | 2 | 12 | 13 | 16 | 7 |
| Number | 4.5 | 5.0 | 5.3 | 5.9 | 5.8 | 6.3 | 6.6 |

Whorl 3

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | +x+ | +o.p. | +x+ | -x- | -o.p. | -o.p. |
| Progeny No. | 15 | 2 | 10 | 7 | 12 | 13 | 16 |
| Number | 2.9 | 3.0 | 3.0 | 3.2 | 3.6 | 3.6 | 3.7 |

### Length of apical bud (Ht)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | -x- | +x+ | +o.p. | -o.p. | -o.p. | +x+ |
| Progeny No. | 15 | 12 | 2 | 10 | 16 | 13 | 7 |
| mm | 13 | 14 | 15 | 16 | 16 | 17 | 17 |

### Ratio between apical bud and terminal shoot $\left(\frac{100\ Ht}{Th}\right)$

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | +x+ | -x- | +x+ | -o.p. | -o.p. | +o.p. | -x- |
| Progeny No. | 7 | 12 | 2 | 16 | 13 | 10 | 15 |
| Ratio | 4.5 | 5.4 | 5.4 | 5.4 | 6.0 | 6.2 | 6.8 |

### Length of lateral buds

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | +x+ | -x- | +o.p. | -o.p. | -o.p. | +x+ |
| Progeny No. | 15 | 2 | 12 | 10 | 16 | 13 | 7 |
| mm | 12 | 12 | 13 | 14 | 15 | 15 | 15 |

### Number of lateral buds

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| Combination | -x- | -x- | +o.p. | -o.p. | +x+ | -o.p. | +x+ |
| Progeny No. | 15 | 12 | 10 | 13 | 2 | 16 | 7 |
| Number | 3.7 | 3.8 | 4.0 | 4.5 | 4.7 | 5.0 | 5.9 |

Fig. 13. Experiment Eh 51. Range and significance of the differences between progenies in height and branch and bud characteristics (c-h) in 1960. Seven progenies of Boxholm provenance. 20 trees per plot. Any two means not underscored by the same line are significantly different (individual t-test).

## Aspan Z Ånge Y

### Height (H)

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Z | Y | Z | Z |
| Combination | +x+ | +x+ | -x+ | -o.p. | -x- | -x- |
| Progeny No. | 23 | 24 | 30 | 38 | 31 | 27 |
| cm | 91 | 102 | 114 | 115 | 130 | 135 |

### Length of terminal shoot (Th)

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Y | Z | Z | Z |
| Combination | +x+ | +x+ | -o.p. | -x+ | -x- | -x- |
| Progeny No. | 23 | 24 | 38 | 30 | 31 | 27 |
| cm | 22 | 29 | 30 | 31 | 32 | 34 |

### Length of branches (Brl)

Whorl 2

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Y | Z | Z | Z |
| Combination | +x+ | +x+ | -o.p. | -x+ | -x- | -x- |
| Progeny No. | 23 | 24 | 38 | 30 | 31 | 27 |
| cm | 24 | 27 | 33 | 33 | 36 | 39 |

Whorl 3

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Y | Z | Z | Z |
| Combination | +x+ | +x+ | -o.p. | -x+ | -x- | -x- |
| Progeny No. | 23 | 24 | 38 | 30 | 31 | 27 |
| cm | 24 | 27 | 38 | 39 | 42 | 48 |

### Ratio between branch length and height $\left(\frac{100\,Brl}{H}\right)$

Whorl 3

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Z | Y | Z | Z |
| Combination | +x+ | +x+ | -x- | -o.p. | -x+ | -x- |
| Progeny No. | 24 | 23 | 31 | 38 | 30 | 27 |
| Ratio | 27 | 27 | 32 | 33 | 34 | 35 |

### Number of branches

Whorl 1

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Z | Y | Z | Z |
| Combination | +x+ | +x+ | -x+ | -x- | -x- | -o.p. |
| Progeny No. | 23 | 24 | 30 | 31 | 27 | 38 |
| Number | 3.9 | 4.9 | 4.9 | 5.0 | 5.1 | 5.4 |

Whorl 3

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Z | Z | Y | Z |
| Combination | +x+ | +x+ | -x+ | -x- | -o.p. | -x- |
| Progeny No. | 23 | 24 | 30 | 31 | 38 | 27 |
| Number | 2.3 | 3.1 | 3.3 | 3.3 | 3.8 | 3.9 |

### Length of apical bud ($H_t$)

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Y | Z | Z | Z |
| Combination | +x+ | +x+ | -o.p. | -x+ | -x- | -x- |
| Progeny No. | 23 | 24 | 38 | 30 | 31 | 27 |
| mm | 15 | 16 | 17 | 17 | 18 | 19 |

### Ratio between apical bud and terminal shoot $\left(\frac{100\,H_t}{T_h}\right)$

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Z | Z | Y | Z |
| Combination | -x+ | +x+ | -x- | -x- | -o.p. | +x+ |
| Progeny No. | 30 | 24 | 27 | 31 | 38 | 23 |
| Ratio | 5.4 | 5.6 | 5.7 | 5.8 | 5.8 | 6.9 |

### Length of lateral buds ($H_s$)

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Z | Y | Z | Z |
| Combination | +x+ | +x+ | -x+ | -o.p. | -x- | -x- |
| Progeny No. | 23 | 24 | 30 | 38 | 31 | 27 |
| mm | 12 | 13 | 14 | 15 | 15 | 16 |

### Number of lateral buds

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | Z | Z | Y | Z | Z | Z |
| Combination | +x+ | +x+ | -o.p. | -x+ | -x- | -x- |
| Progeny No. | 23 | 24 | 38 | 30 | 27 | 31 |
| Number | 3.9 | 4.4 | 4.7 | 4.7 | 4.8 | 4.8 |

Fig. 14. Experiment Eh 51. Range and significance of the differences between progenies in height and branch and bud characteristics (c-h) in 1960. Six progenies of Aspan (Z) and Ånge (Y) provenances. 20 trees per plot. Any two means not underscored by the same line are significantly different (individual t-test).

Boxholm E Vuollerim BD

Height (H)

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD | E | BD | BD×E | BD | BD×E |
| Combination | +o.p. | +o.p. | -o.p. | -x- | -x+ | +x+ |
| Progeny No. | 6 | 72 | 18 | 14 | 16 | 4 |
| cm | 82 | 89 | 96 | 98 | 100 | 127 |

Length of terminal shoot (Th)

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD | BD | E | BD×E | BD | BD×E |
| Combination | +o.p. | -o.p. | +o.p. | -x- | -x+ | +x+ |
| Progeny No. | 6 | 18 | 72 | 14 | 16 | 4 |
| cm | 19 | 24 | 24 | 25 | 26 | 34 |

Length of branches (Brl)

Whorl 1

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD | BD | BD×E | E | BD | BD×E |
| Combination | +o.p. | -o.p. | -x- | +o.p. | -x+ | +x+ |
| Progeny No. | 6 | 18 | 14 | 72 | 16 | 4 |
| cm | 13 | 17 | 17 | 18 | 18 | 23 |

Whorl 2

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD | BD | BD | E | BD×E | BD×E |
| Combination | +o.p. | -o.p. | -x+ | +o.p. | -x- | +x+ |
| Progeny No. | 6 | 18 | 16 | 72 | 14 | 4 |
| cm | 20 | 26 | 28 | 29 | 30 | 36 |

Whorl 3

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD | BD | BD | E | BD×E | BD×E |
| Combination | +o.p. | -x+ | -o.p. | +o.p. | -x- | +x+ |
| Progeny No. | 6 | 16 | 18 | 72 | 14 | 4 |
| cm | 24 | 32 | 33 | 34 | 37 | 43 |

Branch angles

Whorl 2

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD×E | E | BD×E | BD | BD | BD |
| Combination | +x+ | +o.p. | -x- | -x+ | +o.p. | -o.p. |
| Progeny No. | 4 | 72 | 14 | 16 | 6 | 18 |
| Degree | 58 | 62 | 67 | 67 | 68 | 68 |

Whorl 3

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD×E | E | BD×E | BD | BD | BD |
| Combination | +x+ | +o.p. | -x- | -o.p. | +o.p. | -x+ |
| Progeny No. | 4 | 72 | 14 | 18 | 6 | 16 |
| Degree | 70 | 76 | 77 | 78 | 81 | 81 |

Number of branches

Whorl 2

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | BD | BD | BD×E | E | BD | BD×E |
| Combination | -o.p. | -x+ | -x- | +o.p. | +o.p. | +x+ |
| Progeny No. | 18 | 16 | 14 | 72 | 6 | 4 |
| Number | 4.7 | 5.0 | 5.1 | 5.1 | 5.5 | 6.1 |

Whorl 3

| | | | | | | |
|---|---|---|---|---|---|---|
| Provenance | E | BD×E | BD | BD | BD | BD×E |
| Combination | +o.p. | -x- | -x+ | +o.p. | -o.p. | +x+ |
| Progeny No. | 72 | 14 | 16 | 6 | 18 | 4 |
| Number | 3.2 | 3.4 | 3.9 | 3.9 | 4.2 | 5.3 |

Fig. 15. Experiment Eh 53. Range and significance of the differences between progenies in height and branch and bud characteristics (c-h) in 1960. Six progenies of Boxholm (E) and Vuollerim (BD) provenances. 20 trees per plot. Any two means not underscored by the same line are significantly different (individual t-test).

and length of terminal shoot, however, was obviously higher in some of the slow-growing progenies than in the more rapidly growing ones. Thus large apical buds, (large as compared with the length of the leading shoot), do not necessarily indicate superior average growth of a progeny.

In the main, the development of the various characteristics was parallel in the three pairs of reciprocal crosses included in the investigation, Nos. 2 and 7 (+ × +) and 12 and 15 (− × −) from Boxholm (Fig. 13) and Nos. 27 and 31 (− × −) from Aspan (Fig. 14). The reciprocal plus tree crosses from Boxholm differed significantly only in the ratio between branch length and height, whorl 3, and in the numbers of branches, whorl 1. The differences were significant at the five per cent level. As mentioned above, the reciprocal minus tree progenies had apical buds of very different sizes. Furthermore, the number of branches in whorl 3 as well as the ratio $\frac{100 \text{ Brl}}{\text{H}}$, whorl 3, were significantly higher in the progeny No. 12 as compared to No. 15. The reciprocal Aspan crosses had significantly different numbers of branches in whorl 3 (the difference significant at the five per cent level), in which whorl the progeny No. 27, Y 37⁻ × Y 38⁻, retained more branches than any other progeny in the experiment.

The six progenies measured in *experiment Eh* 53 in 1960 (Table 5, Fig. 15), representing combinations of parent trees from Vuollerim (Lat. 66° N) and Boxholm (Lat. 58° N), varied only slightly as regards the number of branches in whorl 1, the length and number of lateral buds, the ratio of branch length to height in whorls 1—3 and the ratio of apical bud length to length of terminal shoot. The differences displayed between the progenies were not significant in any case. This means, for instance, that the crown shape was of much the same type in all the progenies at this age irrespective of the various crown types of the parent trees.

The vigorously growing provenance hybrid No. 4 (BD 4016 × E 4008) differed significantly from all or nearly all of the other progenies analysed in height, in lenght of branches in whorls 1—3 and in the number of branches in whorls 2 and 3 (Fig. 15). The hybrid was predominant in these properties. As regards the branch angles in whorls 2 and 3, it had the most acute angles of all. The open-pollinated progeny from the same mother tree, BD 4016, was a rather slow-growing progeny with relatively short branches and was intermediate as to size of branch angles as well as in number of branches in the various whorls. The apical bud was comparatively large. The open-pollinated progeny from the male parent tree, E 4008, was intermediate in height in 1960, but ranked second in 1964, when the difference between this progeny and the provenance cross No. 4 was nonsignificant (all trees, Fig. 10 a). This indicates that the growth capacity of progeny No. 72 is greater than that shown in 1960 and does not differ greatly from that of the hybrid. Moreover, progeny No. 72 had comparatively acute branch angles, which was also the case with No. 4. In all other properties it ranked intermediately, except in the number of branches, whorl 3, where its mean value was the lowest of all.

**Table 6. Progenies selected for analysis**

| Experiment No. | Progeny No. | Cross combination | | Height cm | Terminal shoot cm | Branch length, cm Whorl No. | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1 | 2 | 3 | 4 |
| | | *Boxholm* | | | | | | | |
| Eh 51 | 52—13 | VIII $46^-$ | o. p.[1]) | 149.6 | 38.9 | 29.4 | 42.6 | 55.4 | 57.4 |
| | 15 | VIII $47^- \times$ VIII $46^-$ | $- \times -$ | 118.6 | 31.6 | 24.3 | 33.9 | 43.0 | 44.2 |
| | 16 | VIII $47^-$ | o. p. | 157.0 | 41.6 | 31.3 | 43.8 | 55.1 | 54.2 |
| | | *Aspan* | | | | | | | |
| | 30 | Y $38^- \times$ Z 4401 | $- \times +$ | 141.4 | 33.3 | 24.9 | 38.2 | 45.3 | 47.3 |
| | 31 | Y $38^- \times$ Y $37^-$ | $- \times -$ | 163.9 | 39.7 | 29.2 | 40.1 | 51.4 | 52.3 |
| | | *Ockelbo* | | | | | | | |
| Eh 52 | 58 | $11{:}18^- \times$ X 2021 | $- \times +$ | 127.0 | 33.5 | 25.7 | 35.6 | 44.0 | 47.4 |
| | 59 | $11{:}18^- \times$ X 2030 | $- \times +$ | 149.4 | 40.7 | 30.3 | 42.7 | 51.3 | 56.0 |
| | 60 | $11{:}18^- \times 11{:}19^-$ | $- \times -$ | 118.1 | 31.9 | 24.9 | 35.0 | 42.0 | 45.3 |
| Eh 53 | 4 | BD 4016 × E 4008 | $+ \times +$ | 162.5 | 39.9 | 29.4 | 44.2 | 52.4 | 54.8 |
| | 6 | BD 4016 | o. p. | 107.4 | 24.7 | 17.3 | 25.1 | 30.0 | 33.8 |
| | 16 | E $67^- \times$ BD 4016 | $- \times +$ | 123.9 | 27.7 | 20.3 | 30.6 | 36.0 | 38.5 |
| | 18 | E $67^-$ | o. p. | 123.0 | 27.8 | 20.6 | 32.0 | 36.1 | 40.7 |
| | 28 | Å $3^- \times 11{:}18^-$ | $- \times -$ | 115.6 | 28.6 | 22.2 | 29.9 | 37.9 | 39.7 |
| | 72 | E 4008 | o. p. | 120.6 | 38.8 | 26.0 | 35.4 | 43.3 | 47.0 |

[1]) Open pollination

Comparing the three half-sib progenies from the minus tree E $67^-$, Nos. 14, 16 and 18, no significant differences between them could be established for any characteristics, except in the number of branches, whorl 3. Thus the provenance hybrid E $67^- \times$ VIII $46^-$ developed in very much the same way as the progenies E $67^- \times$ BD 4016 and E $67^-$ o.p., i.e. crosses between trees of the same provenance. Similarly, in this case the type of the male parent—plus or minus—did not influence the development of the progenies to any measurable degree.

## *22. Results in 1961*

*Experiment Eh 51*

The five progenies studied in experiment Eh 51 (Table 6, Fig. 16) represent three minus tree progenies from Boxholm, one minus × plus and one minus × minus cross from Aspan. Significant differences between the progenies were established for all the characteristics analysed, except for branch length, whorl 2, and number of branches, whorl 4.

A comparison between the data obtained in 1960 and the data obtained in 1961 from the same five progenies showed a clear tendency towards greater differentiation of the progenies in the latter year in the case of 17 out of 21 characteristics measured (Tables 5 and 6). Especially interesting is the occurrence of significant differences between the progenies in branch angles,

**of the properties c-h in 1961. Mean values of the recorded properties.**

| Ratio $\frac{100\,\mathrm{Brl}}{\mathrm{H}}$ Whorl No. | | | | Branch angle degree Whorl No. | | | Number of branches Whorl No. | | | | Length of | | No. of lateral buds | Ratio $\frac{100\,\mathrm{Ht}}{\mathrm{Th}}$ | No. of trees | No. of plots |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 2 | 3 | 4 | 2 | 3 | 4 | 1 | 2 | 3 | 4 | apical bud mm | lateral buds mm | | | | |
| 19.6 | 28.3 | 37.0 | 38.3 | 60.5 | 61.2 | 69.2 | 4.6 | 5.8 | 5.2 | 3.6 | 22.1 | 19.2 | 6.5 | 5.7 | 80 | 4 |
| 20.4 | 28.5 | 36.2 | 37.3 | 64.0 | 65.9 | 74.0 | 3.8 | 4.9 | 4.2 | 3.2 | 18.5 | 16.9 | 5.8 | 5.9 | 80 | 4 |
| 19.9 | 27.7 | 34.9 | 35.0 | 56.8 | 59.2 | 69.6 | 4.8 | 6.1 | 5.2 | 3.6 | 20.9 | 19.3 | 7.7 | 5.0 | 80 | 4 |
| | | | | | | | | | | | | | | | | |
| 17.6 | 26.8 | 31.8 | 33.1 | 58.3 | 61.4 | 68.6 | 5.1 | 5.3 | 4.6 | 3.4 | 22.3 | 18.6 | 6.6 | 6.7 | 80 | 4 |
| 17.8 | 24.4 | 31.4 | 32.3 | 57.3 | 59.7 | 67.3 | 4.9 | 5.4 | 4.6 | 3.2 | 22.7 | 18.6 | 6.6 | 5.7 | 80 | 4 |
| | | | | | | | | | | | | | | | | |
| 20.2 | 28.0 | 34.6 | 37.3 | 66.4 | 66.1 | 77.5 | 5.0 | 5.7 | 5.6 | 4.6 | 24.4 | 22.6 | 7.9 | 7.3 | 80 | 4 |
| 20.2 | 28.6 | 34.3 | 37.5 | 65.1 | 68.3 | 75.9 | 5.0 | 6.0 | 6.0 | 4.8 | 24.1 | 22.5 | 7.8 | 5.9 | 80 | 4 |
| 21.0 | 29.6 | 35.6 | 38.3 | 69.6 | 70.8 | 77.5 | 4.8 | 5.2 | 5.1 | 3.5 | 21.6 | 18.3 | 7.0 | 6.8 | 80 | 4 |
| | | | | | | | | | | | | | | | | |
| 18.1 | 27.1 | 32.1 | 33.7 | 62.1 | 61.6 | 69.2 | 5.4 | 6.0 | 5.7 | 5.1 | 24.9 | 20.4 | 7.8 | 6.2 | 40 | 2 |
| 16.0 | 23.4 | 27.9 | 31.4 | 70.7 | 71.7 | 82.5 | 5.3 | 4.6 | 4.8 | 3.9 | 19.7 | 15.7 | 5.7 | 7.7 | 60 | 3 |
| 16.3 | 24.6 | 29.0 | 31.1 | 75.0 | 73.2 | 84.8 | 4.8 | 4.9 | 4.4 | 3.9 | 19.5 | 16.4 | 5.2 | 7.1 | 60 | 3 |
| 16.7 | 26.0 | 29.3 | 33.0 | 73.6 | 74.7 | 82.9 | 4.9 | 4.9 | 4.7 | 4.2 | 19.4 | 16.6 | 5.4 | 7.0 | 60 | 3 |
| 19.2 | 25.9 | 32.8 | 34.3 | 68.2 | 68.8 | 76.5 | 4.7 | 4.8 | 5.0 | 3.9 | 21.2 | 18.8 | 5.5 | 7.4 | 60 | 3 |
| 21.6 | 29.3 | 35.9 | 38.9 | 70.0 | 67.0 | 75.4 | 4.8 | 5.4 | 4.7 | 2.8 | 19.9 | 17.4 | 6.2 | 5.9 | 40 | 2 |

whorls 2 and 3, and crown shape ($\frac{100\,\mathrm{Brl}}{\mathrm{H}}$ whorls 1 and 2) in 1961 (Fig. 16). In that year progeny No. 15, – × – Boxholm, had significantly larger branch angles in whorls 2—4 than the other four progenies included. As regards crown shape, there was a marked difference between the two provenances: the three Boxholm progenies, Nos. 13, 15 and 16, had broader crowns than the northern progenies from Aspan, Nos. 30 and 31. There were significant differences, too, in the ratio between branch length and height between the Boxholm progenies in whorls 3 and 4 and between the two Aspan progenies in whorl 2.

The ranking of the progenies in respect of the various characteristics was about the same in both years, 1960 and 1961, with progeny No. 15 consistently ranking lowest as regards height, length of terminal shoot and apical as well as lateral buds, branch lengths and number of branches. But this progeny ranked first as regards the branch angles which were nearly right, and it had a large apical bud in relation to the length of the terminal shoot. The crown width increased relatively more in this progeny than in the others.

The only property in which the range of the progenies was markedly changed from 1960 to 1961 was the number of branches in whorl 1, where the progeny ranking lowest in 1960 (No. 30) had a significantly higher number of branches than the rest in 1961, and the progeny No. 16 with a high number in 1960 ranked third in 1961.

# Boxholm E Aspan Z

## Height (H)

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | E | E | Z |
| Combination | -x- | -x+ | -o.p. | -o.p. | -x- |
| Progeny No. | 15 | 30 | 13 | 16 | 31 |
| cm | 119 | 141 | 150 | 157 | 164 |

## Length of terminal shoot (Th)

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | E | Z | E |
| Combination | -x- | -x+ | -o.p. | -x- | -o.p. |
| Progeny No. | 15 | 30 | 13 | 31 | 16 |
| cm | 32 | 33 | 39 | 40 | 42 |

## Length of branches (Brl)

### Whorl 1

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -x- | -x+ | -x- | -o.p. | -o.p. |
| Progeny No. | 15 | 30 | 31 | 13 | 16 |
| cm | 24 | 25 | 29 | 29 | 31 |

### Whorl 2

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -x- | -x+ | -x- | -o.p. | -o.p. |
| Progeny No. | 15 | 30 | 31 | 13 | 16 |
| cm | 34 | 38 | 40 | 43 | 44 |

### Whorl 3

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -x- | -x+ | -x- | -o.p. | -o.p. |
| Progeny No. | 15 | 30 | 31 | 16 | 13 |
| cm | 43 | 45 | 51 | 55 | 55 |

### Whorl 4

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -x- | -x+ | -x- | -o.p. | -o.p. |
| Progeny No. | 15 | 30 | 31 | 16 | 13 |
| cm | 44 | 47 | 53 | 55 | 57 |

## Branch angles

### Whorl 2

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -o.p. | -x- | -x+ | -o.p. | -x- |
| Progeny No. | 16 | 31 | 30 | 13 | 15 |
| Degree | 57 | 57 | 58 | 60 | 64 |

### Whorl 3

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | E | Z | E |
| Combination | -o.p. | -x- | -o.p. | -x+ | -x- |
| Progeny No. | 16 | 31 | 13 | 30 | 15 |
| Degree | 59 | 60 | 61 | 61 | 66 |

### Whorl 4

| | | | | | |
|---|---|---|---|---|---|
| Provenance | Z | Z | E | E | E |
| Combination | -x- | -x+ | -o.p. | -o.p. | -x- |
| Progeny No. | 31 | 30 | 13 | 16 | 15 |
| Degree | 67 | 69 | 69 | 70 | 74 |

Ratio between branch length and height $\left(\frac{100\ Brl}{H}\right)$

Whorl 1

| | | | | | |
|---|---|---|---|---|---|
| Provenance | Z | Z | E | E | E |
| Combination | -x+ | -x- | -o.p. | -o.p. | -x- |
| Progeny No. | 30 | 31 | 13 | 16 | 15 |
| Ratio | 17.6 | 17.8 | 19.6 | 19.9 | 20.4 |

Whorl 2

| | | | | | |
|---|---|---|---|---|---|
| Provenance | Z | Z | E | E | E |
| Combination | -x- | -x+ | -o.p. | -o.p. | -x- |
| Progeny No. | 31 | 30 | 16 | 13 | 15 |
| Ratio | 24.4 | 26.8 | 27.7 | 28.3 | 28.5 |

Whorl 3

| | | | | | |
|---|---|---|---|---|---|
| Provenance | Z | Z | E | E | E |
| Combination | -x- | -x+ | -o.p. | -x- | -o.p. |
| Progeny No. | 31 | 30 | 16 | 15 | 13 |
| Ratio | 31.4 | 31.8 | 34.9 | 36.2 | 37.0 |

Whorl 4

| | | | | | |
|---|---|---|---|---|---|
| Provenance | Z | Z | E | E | E |
| Combination | -x- | -x+ | -o.p. | -x- | -o.p. |
| Progeny No. | 31 | 30 | 16 | 15 | 13 |
| Ratio | 32.3 | 33.1 | 35.0 | 37.3 | 38.3 |

Number of branches

Whorl 1

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | E | E | Z | Z |
| Combination | -x- | -o.p. | -o.p. | -x- | -x+ |
| Progeny No. | 15 | 13 | 16 | 31 | 30 |
| Number | 3.8 | 4.6 | 4.8 | 4.9 | 5.1 |

Whorl 2

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -x- | -x+ | -x- | -o.p. | -o.p. |
| Progeny No. | 15 | 30 | 31 | 13 | 16 |
| Number | 4.9 | 5.3 | 5.4 | 5.8 | 6.1 |

Whorl 3

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -x- | -x- | -x+ | -o.p. | -o.p. |
| Progeny No. | 15 | 31 | 30 | 13 | 16 |
| Number | 4.2 | 4.6 | 4.6 | 5.2 | 5.2 |

Length of apical bud ($H_t$)

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | E | E | Z | Z |
| Combination | -x- | -o.p. | -o.p. | -x+ | -x- |
| Progeny No. | 15 | 16 | 13 | 30 | 31 |
| mm | 18 | 21 | 22 | 22 | 23 |

Ratio between apical bud and terminal shoot $\left(\frac{100\ H_t}{H}\right)$

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | E | E | Z |
| Combination | -o.p. | -x- | -o.p. | -x- | -x+ |
| Progeny No. | 16 | 31 | 13 | 15 | 30 |
| Ratio | 5.0 | 5.7 | 5.7 | 5.9 | 6.7 |

Length of lateral buds ($H_s$)

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | Z | Z | E | E |
| Combination | -x- | -x+ | -x- | -o.p. | -o.p. |
| Progeny No. | 15 | 30 | 31 | 13 | 16 |
| mm | 17 | 19 | 19 | 19 | 19 |

Number of lateral buds

| | | | | | |
|---|---|---|---|---|---|
| Provenance | E | E | Z | Z | E |
| Combination | -x- | -o.p. | -x+ | -x- | -o.p. |
| Progeny No. | 15 | 13 | 30 | 31 | 16 |
| Number | 5.8 | 6.5 | 6.6 | 6.6 | 7.7 |

Fig. 16. Experiment Eh 51. Range and significance of the differences between progenies in height and branch and bud characteristics (c-h) in 1961. Five progenies of Boxholm (E) and Aspan (Z) provenances. 20 trees per plot. Any two means not underscored by the same line are significantly different (individual t-test).

Ockelbo X

Height (H)

| Combination | -x- | -x+ | -x+ |
|---|---|---|---|
| Progeny No. | 60 | 58 | 59 |
| cm | 118 | 127 | 149 |

Length of terminal shoot (Th)

| Combination | -x- | -x+ | -x+ |
|---|---|---|---|
| Progeny No. | 60 | 58 | 59 |
| cm | 32 | 34 | 41 |

Branch angles

Whorl 2

| Combination | -x+ | -x+ | -x- |
|---|---|---|---|
| Progeny No. | 59 | 58 | 60 |
| Degree | 65 | 66 | 70 |

Whorl 3

| Combination | -x+ | -x+ | -x- |
|---|---|---|---|
| Progeny No. | 58 | 59 | 60 |
| Degree | 66 | 68 | 71 |

Number of branches

Whorl 3

| Combination | -x- | -x+ | -x+ |
|---|---|---|---|
| Progeny No. | 60 | 58 | 59 |
| Number | 5.2 | 5.6 | 6.0 |

Whorl 4

| Combination | -x- | -x+ | -x+ |
|---|---|---|---|
| Progeny No. | 60 | 58 | 59 |
| Number | 3.6 | 4.6 | 4.8 |

Length of apical bud (H

| Combination | -x- | -x+ | -x |
|---|---|---|---|
| Progeny No. | 60 | 59 | 5 |
| mm | 22 | 24 | 2 |

Ratio between apical bud ar
terminal shoot $\left(\frac{100\ H_b}{Th}\right)$

| Combination | -x+ | -x- | -x |
|---|---|---|---|
| Progeny No. | 59 | 60 | 5 |
| Ratio | 5.9 | 6.8 | 7. |

Length of lateral bud

| Combination | -x- | -x+ | -x |
|---|---|---|---|
| Progeny No. | 60 | 59 | 5 |
| mm | 18 | 22 | 2 |

Fig. 17. Experiment Eh 52. Range and significance of the differences between progenies in height and branch and bud characteristics (c-h) in 1961. Three progenies of Ockelbo (X) provenance. 20 trees per plot. Any two means not underscored by the same line are significantly different (individual t-test).

*Experiment Eh 52*

Three progenies were analysed in 1961 (Table 6, Fig. 17), all of them obtained from crosses of the minus tree 11:18⁻, Ockelbo, with two plus trees, X 2021 and X 2030, and one minus tree, 11:19⁻, i.e. intraprovenance combinations. None of them was analysed for the properties c—h in 1960.

Significant differences between the progenies were stated in nine of the 21 characteristics studied (Fig. 17). The most rapidly growing progeny 11:18⁻ $\times$ X 2030 (No. 59) had a small apical bud in relation to the terminal shoot length and a comparatively high number of branches in whorls 3 and 4. It had more acute branch angles in whorls 2 and 3 than the minus $\times$ minus progeny No. 60. The latter combination originates from the minus trees 11:18⁻ and 11:19⁻ classified as "intermediate" and "acute" respectively as regards the branch angles. The two plus trees in the stand, X 2021 and X 2030, are classified as "right-angled". The minus $\times$ minus offspring having the least acute branch angles among the three crosses compared indicates that the ocular estimate of the branch angles of the parent trees was incorrect, but the age of the progenies may be too low to permit a reliable estimation of the final type of branch angles. As shown previously (EKLUNDH EHRENBERG, 1963) the branch angles generally increase in size with the age of the whorl and, furthermore, there is a decrease in the size of branch angles in the upper most whorls with increasing age of the young trees. Further changes in the ranking of the progenies as regards the branch angles which are characteristic of the individual progenies may by reported in the material for a more advanced age.

There was only a slight variation among the three progenies in respect of crown shape. The ratio between branch length and tree height did not differ significantly in any of the whorls measured. One of the plus trees, X 2021, used as male parent in the progeny No. 58, is a pine with an extremely narrow crown and fine branches, while the two minus trees have long coarse branches and consequently conspicously broad crowns (*cf.* Table 4). Evidently at this age of the progenies the wide differences in crown types of the parent trees were not apparent in either of their offspring. The same slight variation in crown shape was reported among the progenies in experiments Eh 51 and Eh 53 in 1960 (*cf.* pp. 26 and 33). One year later there were highly significant differences between the progenies in these experiments in respect of this property. One may reasonably expect an increased differentiation in the three progenies analysed in experiment Eh 52 as the trees grow older.

*Experiment Eh 53*

The differentiation of the progenies in respect of the various characteristics was on the whole more pronounced than in the previous year, the most striking increase of variation occurring in the development of the crowns (Fig. 18). The open-pollinated progeny from Boxholm, No. 72, had a significantly higher ratio between branch length and tree height than the rest in whorls 1, 3 and 4, while the three intra-provenance crosses from Vuollerim ranked lowest in the same whorls. The vigorously growing provenance hybrid No. 4 ranked third in these whorls, thus being of a more narrow-crowned type than the open-pollinated offspring from its southern male parent, E 4008. Both these progenies, Nos. 4 and 72, were characterised by long vigorous terminal shoots and relatively small apical buds as well as comparatively acute branch angles. Almost right-angled branches were found in the narrow-crowned progenies from Vuollerim in whorl 4 (*cf.* BARBER, 1964).

No significant differences have yet been established between the two half-sib progenies Nos. 16 and 18. Likewise the half-sib progenies Nos. 6 (+ o.p.) and 16 (– × +), which were of very similar type, differed significantly only in height and length of branches, whorls 2—4.

# Boxholm E   Ockelbo X   Ånge Y   Vuollerim BD

## Height (H)

| Provenance | BD | Y×X | E | BD | BD | BD×E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x- | +o.p. | -o.p. | -x+ | +x+ |
| Progeny No. | 6 | 28 | 72 | 18 | 16 | 4 |
| cm | 107 | 116 | 121 | 123 | 124 | 162 |

## Length of terminal shoot (Th

| Provenance | BD | Y×X | E | BD | E | BD×E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x- | -o.p. | -o.p. | +o.p. | +x+ |
| Progeny No. | 6 | 16 | 18 | 28 | 72 | 4 |
| cm | 25 | 28 | 28 | 29 | 34 | 40 |

## Length of branches (Brl)

### Whorl 1

| Provenance | BD | BD | BD | Y×X | E | BD×X |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x+ | -o.p. | -x- | +o.p. | +x+ |
| Progeny No. | 6 | 16 | 18 | 28 | 72 | 4 |
| cm | 17 | 20 | 21 | 22 | 26 | 29 |

### Whorl 2

| Provenance | BD | Y×X | BD | BD | E | BD×X |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x- | -x+ | -o.p. | +o.p. | +x+ |
| Progeny No. | 6 | 28 | 16 | 18 | 72 | 4 |
| cm | 25 | 30 | 31 | 32 | 35 | 44 |

### Whorl 3

| Provenance | BD | BD | BD | Y×X | E | BD×E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x+ | -o.p. | -x- | +o.p. | +x+ |
| Progeny No. | 6 | 16 | 18 | 28 | 72 | 4 |
| cm | 30 | 36 | 36 | 38 | 43 | 52 |

### Whorl 4

| Provenance | BD | BD | Y×X | BD | E | BD×E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x+ | -x- | -o.p. | +o.p. | +x+ |
| Progeny No. | 6 | 16 | 28 | 18 | 72 | 4 |
| cm | 34 | 38 | 40 | 41 | 47 | 55 |

## Ratio between branch length and height $\left(\frac{100\,Brl}{H}\right.$

### Whorl 1

| Provenance | BD | BD | BD | BD×E | Y×X | E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x+ | -o.p. | +x+ | -x- | +o.p. |
| Progeny No. | 6 | 16 | 18 | 4 | 28 | 72 |
| Ratio | 16.0 | 16.3 | 16.7 | 18.1 | 19.2 | 21.6 |

### Whorl 2

| Provenance | BD | BD | Y×X | BD | BD×E | E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x+ | -x- | -o.p. | +x+ | +o.p. |
| Progeny No. | 6 | 16 | 28 | 18 | 4 | 72 |
| Ratio | 23.4 | 24.6 | 25.9 | 26.0 | 27.1 | 29.3 |

### Whorl 3

| Provenance | BD | BD | BD | BD×E | Y×X | E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x+ | -o.p. | +x+ | -x- | +o.p. |
| Progeny No. | 6 | 16 | 18 | 4 | 28 | 72 |
| Ratio | 27.9 | 29.0 | 29.3 | 32.1 | 32.8 | 35.9 |

### Whorl 4

| Provenance | BD | BD | BD | BD×E | Y×X | E |
|---|---|---|---|---|---|---|
| Combination | -x+ | +o.p. | -o.p. | +x+ | -x- | +o.p. |
| Progeny No. | 16 | 6 | 18 | 4 | 28 | 72 |
| Ratio | 31.1 | 31.4 | 33.0 | 33.7 | 34.3 | 38.9 |

### Branch angles

Whorl 2

| Provenance | BD×E | Y×X | E | BD | BD | BD |
|---|---|---|---|---|---|---|
| Combination | +x+ | -x- | +o.p. | +o.p. | -o.p. | -x+ |
| Progeny No. | 4 | 28 | 72 | 6 | 18 | 16 |
| Degree | 62 | 68 | 70 | 71 | 74 | 75 |

Whorl 3

| Provenance | BD×E | E | Y×X | BD | BD | BD |
|---|---|---|---|---|---|---|
| Combination | +x+ | +o.p. | -x- | +o.p. | -x+ | -o.p. |
| Progeny No. | 4 | 72 | 28 | 6 | 16 | 18 |
| Degree | 62 | 67 | 69 | 72 | 73 | 75 |

Whorl 4

| Provenance | BD×E | E | Y×X | BD | BD | BD |
|---|---|---|---|---|---|---|
| Combination | +x+ | +o.p. | -x- | +o.p. | -o.p. | -x+ |
| Progeny No. | 4 | 72 | 28 | 6 | 18 | 16 |
| Degree | 69 | 75 | 76 | 82 | 83 | 85 |

### Number of branches

Whorl 2

| Provenance | BD | Y×X | BD | BD | E | BD×E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x- | -x+ | -o.p. | +o.p. | +x+ |
| Progeny No. | 6 | 28 | 16 | 18 | 72 | 4 |
| Number | 4.6 | 4.8 | 4.9 | 4.9 | 5.4 | 6.0 |

Whorl 4

| Provenance | E | BD | Y×X | BD | BD | BD×E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -x+ | -x- | +o.p. | -o.p. | +x+ |
| Progeny No. | 72 | 16 | 28 | 6 | 18 | 4 |
| Number | 2.8 | 3.9 | 3.9 | 3.9 | 4.2 | 5.1 |

### Length of apical bud ($H_t$)

| Provenance | BD | BD | BD | E | Y×X | BD×E |
|---|---|---|---|---|---|---|
| Combination | +o.p. | -o.p. | -x+ | +o.p. | -x- | +x+ |
| Progeny No. | 6 | 18 | 16 | 72 | 28 | 4 |
| mm | 19 | 19 | 20 | 20 | 21 | 25 |

### Ratio between apical bud and terminal shoot $\left(\frac{100\,H_t}{Th}\right)$

| Provenance | E | BD×E | BD | BD | Y×X | BD |
|---|---|---|---|---|---|---|
| Combination | +o.p. | +x+ | -o.p. | -x+ | -x- | +o.p. |
| Progeny No. | 72 | 4 | 18 | 16 | 28 | 6 |
| Ratio | 5.9 | 6.2 | 7.0 | 7.1 | 7.4 | 7.7 |

Fig. 18. Experiment Eh 53. Range and significance of the differences between progenies in height and branch and bud characteristics (c-h) in 1961. Six progenies of Boxholm (E), Ockelbo (X), Ånge (Y) and Vuollerim (BD) provenances. 20 trees per plot. Any two means not underscored by the same line are significantly different (individual t-test).

## Discussion

In the same way as in the previous study of the genetic variation of progenies obtained from crosses between extreme plus and minus types of Scots pine (EKLUNDH EHRENBERG, 1963), the progenies included in the present investigation also displayed great variation in the properties analysed. Evidently this variation is genetically controlled to a great extent, but the varying environmental factors also exert a strong influence upon the development of the plants and trees. In experiments Eh 51 and Eh 52, for instance, the variation in soil conditions was indicated by the significant block differences reported in each experiment for height growth in all years and for the other properties analysed in 1960 and 1961. In the experiments previously analysed the ratio between branch length and tree height seemed to be less affected by changes in the environment than did the other characteristics. In the present material no such trend could be established.

In the third experiment, Eh 53, the block differences were non-significant in 19 out of 20 properties investigated, indicating fairly even site conditions in the three blocks.

The plus tree progenies from Boxholm showed a superior growth rate when compared with the minus tree progenies from the same provenance. This superiority in height was established for the plus $\times$ plus as well as for the open-pollinated plus tree progenies in all years, and confirms the results obtained in the previously mentioned experiments, where the same types of crosses were studied (see p. 1). Obviously the phenotypes of the parent plus and minus trees in this case were correctly estimated as a true expression of the genotypes of the trees selected. The self-fertilised progeny of the minus tree VIII 46$^-$, which grows exceptionally slowly and shows a very varying and poor development of the crown, reveals especially the inherent minus characteristics of this tree. The degree of homozygosity is increased in a selfed progeny and the effects of deleterious or lethal recessive genes of the parent tree may be expected to manifest themselves clearly in the offspring. Evidently the genotype of the minus tree VIII 46$^-$ is inferior as regards growth ability and general vitality.

The reverse condition, i.e. minus tree progenies growing more rapidly than plus tree progenies of the same provenance, as found among the progenies from Aspan (Z), stresses the necessity for scrupulous checking of the phenotypes of the selected trees. As mentioned before (p. 4), the two plus trees in

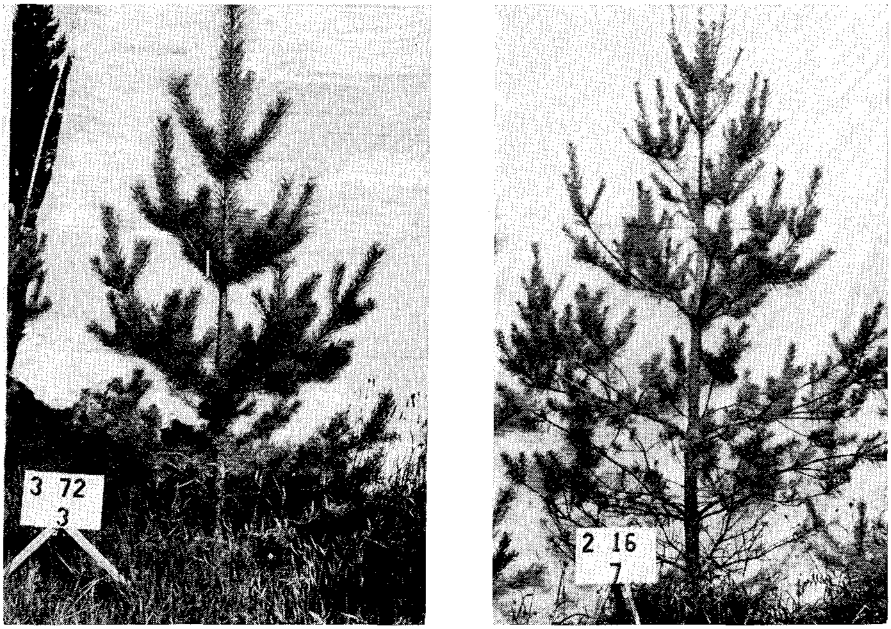


Fig. 19. Young trees obtained after open pollination of the plus tree E 4008 *(left)* and the minus tree VIII 47⁻ *(right)* at Boxholm.

this provenance had a comparatively high rating when first selected for crossing purposes, but were not approved as seed orchard trees when carefully checked for height growth and volume production two years later. The stem form and the crown characteristics were still considered to be typically "plus". The minus trees had broad crowns, thick branches and a rapidly tapering stem, but at least one of them, Y $37^-$, was considered to possess better inherent growth capacity than was estimated previously. Considering the performance of the progenies, the classification of the parent trees made by the later check was shown to be the more correct. The plus tree progenies were inferior in growth rate but had slender crowns and good stem form, while the minus tree progenies grew vigorously and had broad crowns.

The provenance Värmland is represented by one plus × plus and three open-pollinated plus tree progenies. Two of the latter are from the same tree, though the seeds were harvested in different years. These four progenies were by far the most superior as regards height growth during the last three years, the controlled plus × plus cross being at the top of the ranking list every year. No comparison with minus tree progenies from the same provenance was possible, as such progenies were not available. None of the Värmland progenies was included in the detailed analyses of the branch and bud characteristics in either of the years 1960 and 1961, but by ocular estimation of

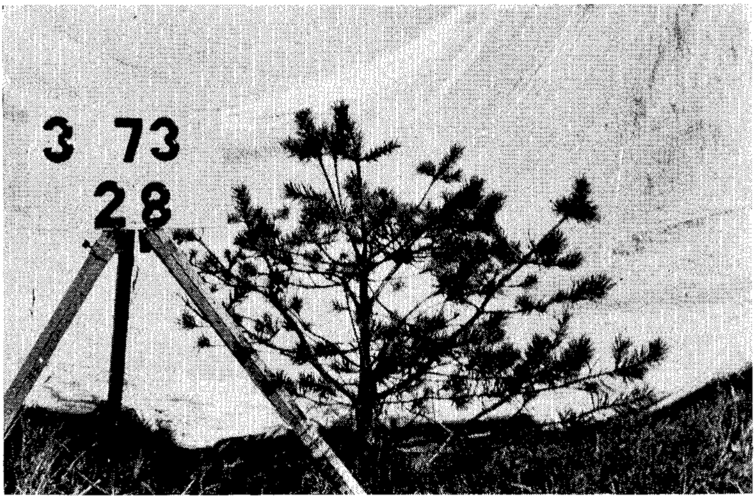



Fig. 20. Typical progeny trees obtained after self-fertilization of the minus tree VIII 46⁻. *Above:* a poorly developed specimen. *Below:* a vigorous but slow-growing type.

crown and stem shape it was established that in general these progenies had straight stems and that they had somewhat broader crowns than the Boxholm plus tree progenies. The good phenotypes of the parent trees thus seem to be a true manifestation of their good genotypes as regards growth potentials as judged by the progeny tests.

Among the progenies originating from combinations of the four type trees at Ockelbo the minus × minus cross ranked last in height in all years.

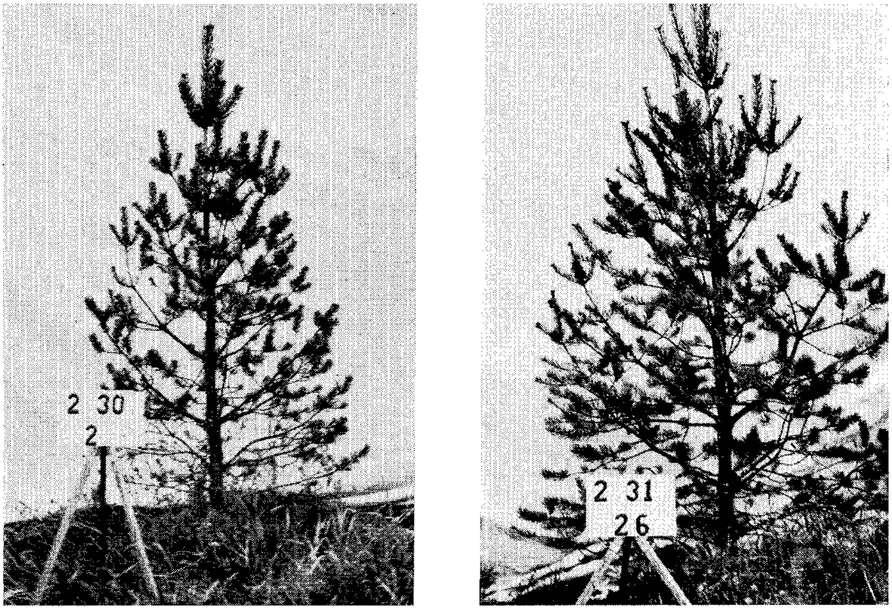


Fig. 21. Young trees obtained after crosses between the minus tree Y 38⁻ at Aspan and the plus tree Z 4401 *(left)* and the minus tree Y 37⁻ *(right)*.

As all the progenies had the mother tree $11{:}18^-$ in common, it was concluded that the significant differences established between the progenies were due both to the different genotypes of the male parents or to the male parents having different combining ability with the common female tree, and to differences between plus and minus trees. If this conclusion is correct then inherent differences must exist between the two plus trees as regards growth capacity. Both trees were rated highly in the phenotype check but the one yielding the slower-growing progeny of the two minus × plus combinations, tree X 2021, has lower height and diameter values than the other plus tree. Furthermore, it has an extremely narrow crown and very fine, right-angled branches. It was selected as a plus tree particularly for its very good quality. But the height which it had attained at the age of 83 years (age at breast height) surpassed by barely a metre that of the minus tree $11{:}19^-$ which was four years younger. The lower growth capacity of this tree seems to be indicated by the lower growth rate of its progeny. Also the minus × minus combination reveals the minus type of the parent trees as regards height growth. As to the only open-pollinated progeny of the tree $11{:}18^-$, No. 113, both plus and normal trees growing in the neighbourhood might have functioned as male parents, thus counteracting the low growth capacity inherited from the mother tree.

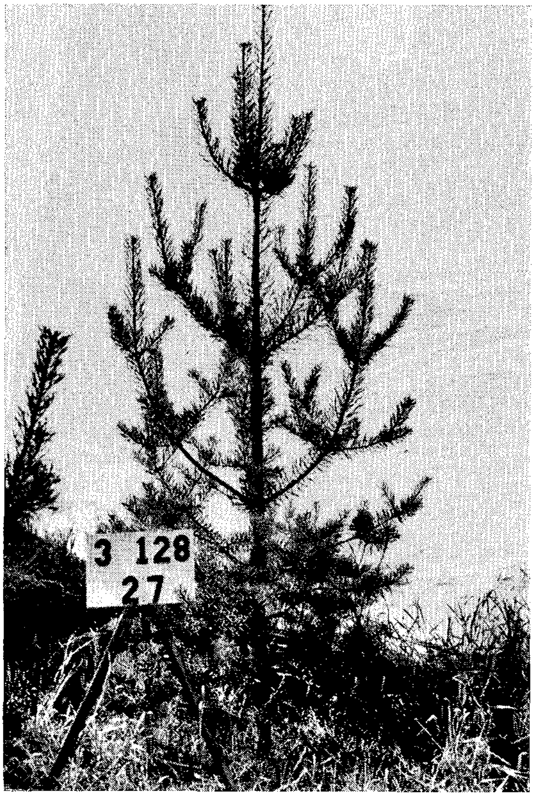


Fig. 22. Young tree obtained after open pollination of the plus tree S 3001, Värmland.

Of the two pairs of reciprocal crosses (one from Boxholm and one from Aspan) which differed significantly in height, the reciprocal Boxholm combinations were studied earlier in the progeny test at Södermyra in 1958—1960 (Eklundh Ehrenberg, 1963). Significant differences between the progenies were reported in this experiment, the cross E 4015 × E 4008 being the superior in all cases. Provided that there was no contamination at pollination through technical errors, this indicates a maternal influence on the growth rate of the offspring. The fact that the crosses were repeated in two different years and the fact that the progenies were planted in experiments situated in widely differing areas exclude the possibility that extraordinarily great differences in environment, favouring by chance only one of the progenies, should be the reason for the differences in height. But the progeny obtained after open pollination of E 4008 and analysed at the Södermyra test plot displayed a very superior height growth. Different combining ability may be the explanation for this, and thus, the genotype of the tree can not be considered inferior as regards growth capacity in general. Differing reciprocal crosses have been reported e.g. in *Larix* by LANGNER (1951) and in *Pseudotsuga* by SZIKLAI (1964). The latter author studied various seed and seedling characteristics in polyallelic crosses between four Douglas firs, and obtained different results in reciprocal combinations in, for instance, seedling mortality, length of epicotyl, length of branches and number of branches. He ascribed this diversity to seed parent or pollen parent effect. As to the total growth and the yearly height growth, the two reciprocal combinations studied did not differ significantly, although one of the crosses was on the average taller than the other.

As regards the properties c—h studied in the present material, no difference or only slight differences between the reciprocal crosses were established for any of the characteristics analysed.

One of the five provenance hybrids included in experiment Eh 53 exceeded in height the open-pollinated progenies from the female as well as the male parent in all years. This was a cross between two plus trees. The other four hybrid progenies were all combinations between minus trees of various provenances and did not display the same superiority in growth rate as the plus tree combination. The cross between two individuals of widely differing origin will result in an increased heterozygosity in the offspring. A probable explanation of the positive effect of species or provenance hybrids reported in various cases, for instance in *Larix* (LANGNER, 1951; SYRACH LARSEN, 1956; ROHMEDER, 1963) and *Populus* (JOHNSSON, 1953; *cf.* SCHÖNBACH, 1961) is the combination of dominant growth genes by crossing dissimilar genotypes. The effect on quantitative characteristics, which are due to many co-ordinated genes, should be especially evident. In the present material, where only one of the provenance hybrids showed heterosis effect, the statement made by ROHMEDER and SCHÖNBACH (1959) and ROHMEDER (1963) that the type of the parent trees as regards growth capacity is of great importance, is applicable in this connection. Consequently a combination of two plus trees should result in better growing offspring than a cross between two minus trees.

As already known, the branch angle size is a variable trait in young trees of Scots pine due to environmental influences as well as to genetical differences between the trees. The same great variation is found in other pine species (*cf.* BARBER, 1964; WOESSNER, 1965). A reliable estimate of the branch angle type of a progeny may not be obtainable from the progeny at ten years of age or younger. This may be the reason for the occurrence of some of the discrepancies in branch angle type between parents and offspring in the present material. But the ocular classification of the parent trees by different branch angle types may have been incorrect (see p. 14) and the size

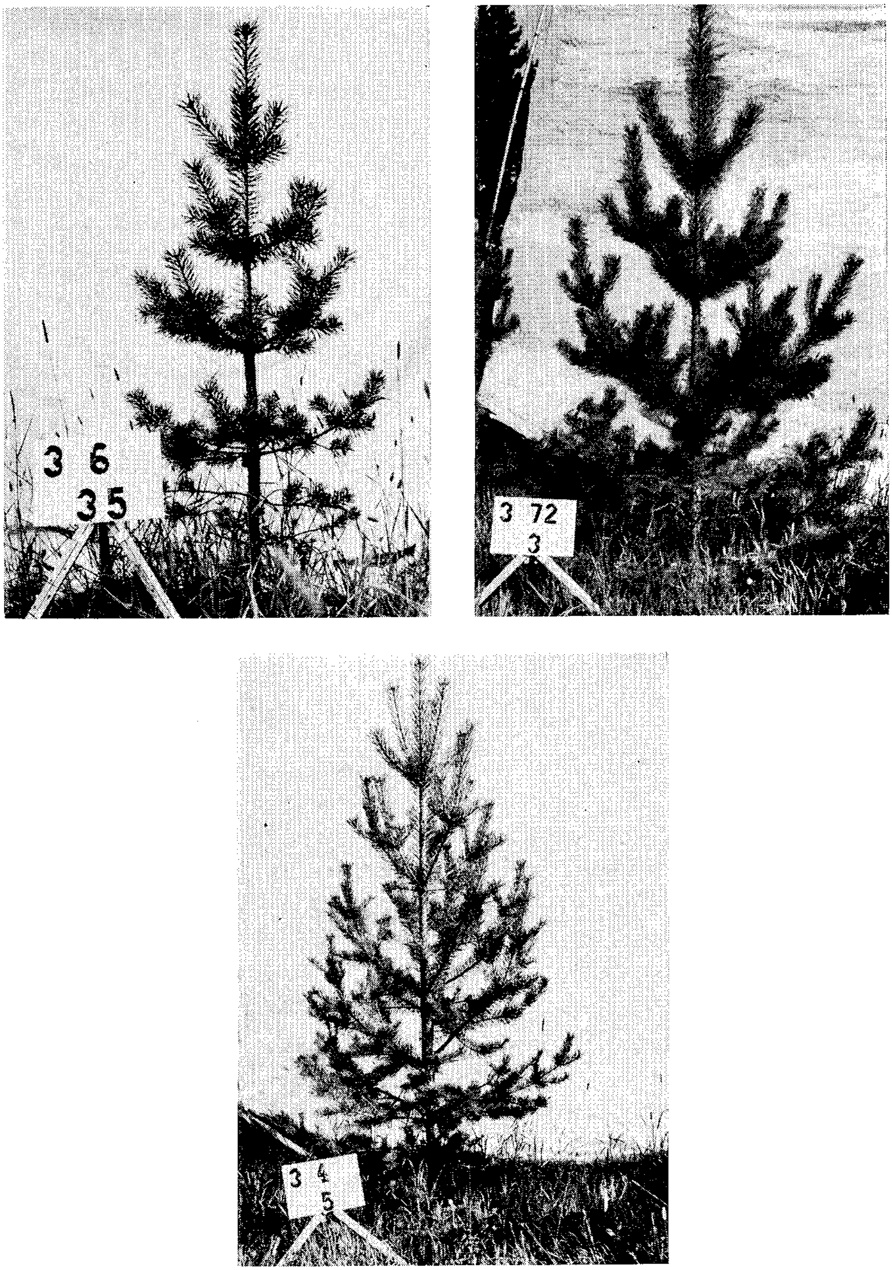


Fig. 23. Typical progeny trees originating from the two plus trees BD 4016 at Vuollerim and E 4008 at Boxholm. *Above left:* Young tree obtained after open pollination of BD 4016. *Above right:* Open pollinated progeny tree from E 4008. *Below:* A typical tree of the provenance cross BD 4016 × E 4008.

of the branch angles established in the progenies might be the true expression of the parental genotypes although deviating widely from the phenotypes of the parents. Nevertheless, the analyses of variance indicated inherent differences between the progenies in this trait. A strong genetic influence on the branch angle size has been reported in, for instance, *Pinus silvestris* by NILSSON (1956), ARNBORG and HADDERS (1957), EKLUNDH EHRENBERG (1963); in *Pinus radiata* by FIELDING (1960); in *Pinus elliottii* by BARBER (1964); in *Pinus monticula* by CAMPBELL (1964); in *Cryptomeria* by TODA (1958). Obviously there is a need for better methods of estimating the branch angle type of old trees. Also a further investigation should be undertaken to establish the age and developmental stage of young trees at which an evaluation of the branch angle can be made with accuracy. Moreover, experiments to establish a sound basis for comparison of mature trees and their offspring should be carried out on a large scale.

Because of the heterogeneous composition of the experiments as regards the types of crosses included (self-fertilisation, controlled crossings between trees of different types and provenances, open pollination and seed lots from natural stands), which increased the variation within the experiments, and because of the rather inefficient design of individual experiments (different number of trees per plot, varying number of plots per progeny), depending on the material available, no attempt has been made to estimate the genetical components or the heritability values for the various characteristics. The results of such estimates were considered to be rather unreliable and of little use for evaluating the inherent nature of the progenies, the genetical background of the individual characteristics, and the possibility of determining the relative importance of heredity and environment (*cf.* ALLARD, 1960; WRIGHT, 1963; GUSTAFSSON and MERGEN, 1964; SZIKLAI, 1964). The comparisons between progenies and the conclusions drawn are thus based mainly on the data obtained by the analyses of variance made for each property.

On the whole, the phenotypes of the 20 selected plus and minus trees used as parents in the experiments appeared to be closely related to the performance of their offspring as regards height growth capacity. The relationship between parent trees and offspring for the branching characteristics seemed to be less well defined. Reliable methods for comparison between young and mature trees are definitely needed; this has been emphasised by CALLAHAM and HAZEL (1961), HANNOVER and BARNES (1963), BARBER (1964), and others.

## Summary

Three progeny tests with Scots pine (*Pinus silvestris* L.) including progenies from phenotypical plus and minus trees growing at different latitudes and altitudes were analysed.

The progenies were obtained from crosses between the various tree types in a stand, between trees of different provenances, and after wind pollination and selfing.

The characteristics analysed were total height, yearly height growth, branch length and branch angle, number of branches per whorl, length of apical bud, and length and number of lateral buds. The variation among the progenies seemed to be genetically controlled to a large extent but the varying environmental factors exerted a strong influence on the development of the young trees as well.

No regular trend in the range among the plus and minus tree progenies in height growth was established when all progenies in each individual experiment were compared. Plus tree progenies were superior in height growth when compared to minus tree progenies of the same provenance. In two cases, plus tree progenies were inferior in growth rate. This was explained by an incorrect classification of the parent trees.

In two out of three reciprocal crosses, significant differences in height between the reciprocal pairs were reported. Different combining ability or maternal influence are discussed as possible reasons for the differences.

Four progenies obtained from the same mother tree after crosses with two plus trees, one minus tree, and after open pollination differed significantly in height. A great part of the variation between progenies is ascribed to the diversity of the male plus trees, in addition to the differences between plus and minus trees.

One provenance cross between two plus trees of widely differing origin was superior in height growth to the open-pollinated progenies of the female as well as of the male parent tree. Four other provenance hybrids obtained from crosses between various minus trees did not exceed the open-pollinated progenies from the northernmost female parents in height. It is shown that the growth capacity of the parent trees used in provenance crosses is of great importance. A combination of two plus trees should result in better growing offspring than a cross between two minus trees.

There was a strong correlation between the length of the terminal shoot in 1960 and the increase in height in 1961—1964. This indicates the possibility of selecting the best growing progeny at an early age.

Significant differences between progenies were established in most of the branch and bud characteristics analysed, indicating genetical control of these properties. The differences increased with increasing age of the progenies. There was a tendency for the plus tree progenies to have more slender crowns and fewer branches per whorl in the lower whorls as compared with minus tree progenies. The effect of inbreeding was manifested in slow height growth and poor vitality of the plants.

No grouping by provenances was reported in the range of the progenies as regards branch and bud characteristics except in one experiment, where minus tree progenies of northern origin had narrower crowns than minus tree progenies from the southern provenance.

On the whole, the phenotypes of the 20 selected plus and minus trees used as parents appeared to be closely related to the performance of their offspring as regards height growth ability. The relationship between parent trees and offspring with respect to branching characteristics seemed to be less well defined. Correlations between parents and offspring in these characteristics cannot be estimated with the methods available at present.

## LITERATURE


ALLARD, R. W. 1960. Principles of plant breeding. — New York, London.

ANDERSSON, E. 1948. The Association of Forest Tree Breeding. — Svensk Papperstidn. 1—3, p. 1—12.

BARBER, J. C. 1964. Inherent variation among slash pine progenies at the Ida Cason Callaway Foundation. — U.S. Forest Serv. Res. Paper SE-10. Southeastern Forest Expt. Sta. N.C.

CALLAHAM, R. Z. & DUFFIELD, J. W. 1963. Heights of selected ponderosa pine seedlings during 20 years. — Proc. Forest Genet. Workshop, Macon, Ga. Southern Forest Tree Improvement Comm. Publ. 22, p. 10—13.

CALLAHAM, R. Z. & HAZEL, A. A. 1961. *Pinus ponderosa.* Height growth of wind-pollinated progenies. — Silvae Genet. 10, p. 33—42.

CAMPBELL, P. K. 1964. Recommended traits to be improved in a breeding program for Douglas-fir. — Weyerhaeuser Comp. Forest Note 57, p. 1—19.

EHRENBERG, C. EKLUNDH 1963. Genetic variation in progeny tests of Scots pine (*Pinus silvestris* L.). — Studia Forestalia Suecica 10, p. 1—135.

GODDARD, R. E., BROWN, C. L. & CAMPBELL, T. E. 1959. An evaluation of growth and form in 5-year-old open-pollinated progeny from selected loblolly pine. — Southern Forest Tree Improvement Conf. Proc. 5, p. 35—43.

GUSTAFSSON, Å. & MERGEN, F. 1964. Some principles of tree cytology and genetics. — Unasylva 18, p. 1—14.

HANNOVER, J. W. 1963. Geographic variation in ponderosa pine leader growth. — Forest Sci. 9, p. 86—95.

HANNOVER, J. W. & BARNES, B. V. 1962. Heritability of height growth in year-old western white pine. — Proc. Forest Genet. Workshop, Macon, Ga. Southern Forest Tree Improvement Comm. Publ. 22, p. 71—76.

HATTEMER, H. H. 1963. Estimates of heritability published in forest tree breeding research. — Proc. World Consultation Forest Genet. Tree Improvement FAO, Stockholm. 2 a/3.

HOFFMAN, K. 1965. Möglichkeiten der Pfropfklonprüfung zur Beurteilung von Auslesebäumen. — Tagungsberichte. Deut. Akad. Landwirtschaftswiss. Berlin 69, p. 12—36.

JOHNSSON, H. 1956. Heterosiserscheinungen bei Hybriden zwischen Breitengradrassen von *Populus tremula*. — Z. Forstgenet. Forstpflanzenzücht. 5, p. 156—160.

LANGLET, O. 1943. Photoperiodismus und Provenienz bei der gemeinen Kiefer (*Pinus silvestris* L.). — Medd. Statens Skogsförsöksanst. 33, p. 295—330.

— 1960. Mellaneuropeiska granprovenienser i svenskt skogsbruk. (Mitteleuropäische Fichte in Schweden, nach den Ergebnissen des internationalen Provenienzversuches von 1938.) — Kgl. Skogs-Lantbruksakad. Tidskr. 5—6, p. 259—329.

LANGNER, W. 1951. Kreuzungsversuche mit *Larix europaea* D.C. und *Larix leptolepis* Gord. — Z. Forstgenet. Forstpflanzenzücht. 1, p. 2—18 & 40—56.

LARSEN, C. S. 1956. Genetics in silviculture. — London.

MATÉRN, B. 1959. Några synpunkter på extrapolation av höjdutvecklingskurvor. (Some remarks on the extrapolation of height growth.) — Forest Res. Inst. Sweden. Statistical Office Rept. 2, p. 1—3.

NILSSON, B. 1956. Kvalitets- och produktionsförhållanden i ett klonförsök av tall. — Svenska Skogsvårdsfören. Tidskr. 54, p. 61—74.

ROHMEDER, E. 1963. Experiments on forest tree hybrids in Bavaria from 1936 to 1962. — Proc. World Consultation Forest Genet. Tree Improvement FAO, Stockholm 2 b/1.

ROHMEDER, E. & SCHÖNBACH, H. 1959. Genetik und Züchtung der Waldbäume. — Hamburg & Berlin.

SCHÖNBACH, H. 1962. Ergibt die Kreuzung *Populus tremula* × *Populus alba* (und reziprok) luxurierende Bastarde? (Ein Beitrag zum Heterosisproblem bei Waldbäumen.) — Silvae Genet. 11, p. 3—11.

SQUILLACE, A. E. & BINGHAM, R. T. 1960. Heritability of juvenile growth rate in western white pine. — Abstr. of semi-formal research papers in Forest Genet. Proc. Soc. Am. Forestry 1959.

STERN, K. & HATTEMER, H. H. 1964. Problems involved in some models of selection in forest tree breeding. — Silvae Genet. 13, p. 27—32.

SZIKLAI, O. 1964. Variation and inheritance of some physiological and morphological traits in *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*. — Faculty of Forestry, University of British Columbia.

TODA, R. 1958. Variation and heritability of some quantitative characters in *Cryptomeria*. — Silvae Genet. 7, p. 87—93.

— 1964. A brief review and conclusions of the discussion on seed orchards. — Ibid. 13, p. 1—4.

WOESSNER, R. A. 1965. Growth, form and disease resistance in four-year-old control- and five-year-old open-pollinated progeny of loblolly pine selected for use in seed orchards. — Forest Tree Improvement Program. Tech. Rept. 28. School of Forestry, N.C.

WRIGHT, J. W. 1962. Genetics of forest tree improvement. — FAO, Rome.

— 1963. Genetic variation among 140 half-sib Scots pine families derived from 9 stands. — Silvae Genet. 12, p. 83—89.

# Sammanfattning

## Sambandet mellan föräldraträd och avkommor hos tall (*Pinus silvestris* L.)

*Resultat från avkommeförsök med plus- och minusträdsavkommor vid Remningstorp, Västergötland.*

Avkommor från fenotypiska plus- och minusträd av tall (*Pinus silvestris* L.) undersöktes i tre avkommeförsök utlagda på Remningstorps försöksskog, Västergötland. Föräldraträden utvaldes under åren 1948—1951 i bestånd på olika latituder och olika höjd över havet.

I försöken ingår avkommor efter kontrollerade korsningar mellan plus- och minusträd i samma bestånd eller av olika proveniens. Dessutom ingår avkommor efter fri avblomning och efter självbefruktning från de utvalda träden samt avkommor från två normalbestånd i Västergötland.

Mätningar av planthöjd och årsskottslängd utfördes under åren 1960—1964. Inom vissa avkommor mättes grenlängd, grenvinkel, antalet grenar per grenkrans, toppknoppens längd och antalet sidoknoppar på toppskottet på de 20 högsta plantorna inom varje parcell åren 1960 och 1961.

Plusträdsavkommorna var i allmänhet överlägsna minusträdsavkommorna från samma proveniens i höjdtillväxt. Jämfördes samtliga avkommor inom ett försök förelåg ingen gruppering i plus- och minusavkommor.

Inom proveniensen Aspan hade plusträdsavkommorna långsammare tillväxt än minusträdsavkommorna. Den första klassningen av föräldraträden som plus- eller minusträd har bedömts som felaktig. Vid en senare kontroll av respektive träd konstaterades att plusträden icke var överlägsna jämförelseträden beträffande höjdtillväxt. Beträffande övriga egenskaper såsom kron- och stamtyp var de av pluskaraktär.

Hos två av tre reciproka korsningar förelåg signifikanta skillnader mellan de två avkommorna inom ett korsningspar. Olikheter i »Combining ability» och maternell nedärvning diskuteras som orsak till skillnaderna.

Fyra avkommor från ett och samma minusträd visade signifikanta skillnader i höjd. Avkommorna härstammade från korsningar med två plusträd, ett minusträd, samt efter fri avblomning. Den stora variationen mellan avkommorna kan tillskrivas genotypiska skillnader mellan de två plusträden såväl som mellan plus- och minusträd i tillväxtförmåga.

Provenienshybrider med föräldraträd växande på geografiskt vitt skilda lokaler varierade starkt sinsemellan i höjdtillväxt. Endast en av hybridavkommorna, framställd vid korsning mellan två plusträd, var markant överlägsen avkommor efter fri avblomning från respektive föräldraträd. Fyra andra provenienskorsningar mellan minusträd hade ungefär samma höjdtillväxt som

jämförbara avkommor efter fri avblomning eller korsning. Någon generell heterosisverkan efter provenienskorsningar förelåg inte. Vikten av att plusträd användes vid framställning av provenienshybrider betonas.

Stark korrelation förelåg mellan årsskottets längd 1960 och tillväxten i höjd 1961—1964. Möjligheten att med någorlunda säkerhet utvälja de i framtiden bäst växande avkommorna redan efter tio växtsäsonger diskuteras.

Genetiskt betingade skillnader i gren- och knoppegenskaper förelåg mellan det begränsade antal avkommor, som undersökts i dessa karaktärer. Skillnaderna ökade med ökad plantålder. Hos plusträdsavkommorna förelåg en tydlig tendens till smalare kronor och färre antal grenar per grenkrans i jämförelse med minusträdsavkommorna.

Effekten av inavel var tydlig hos den enda avkomman efter självbefruktning, som ingick i försöken. Hos denna avkomma var plantavgången hög, höjdtillväxten långsam och vitaliteten hos plantorna i allmänhet låg.

Någon generell gruppering av avkommorna efter provenienser i fråga om utvecklingen av gren- och knoppegenskaper förelåg icke. I ett av försöken märktes dock en klar tendens till smalare kronor hos avkommor med nordligt ursprung jämfört med avkommor med sydlig härstamning.

Föräldraträdens klassificering som plus- eller minusträd beträffande höjdtillväxt syntes i de flesta fall vara korrekt att döma efter resultaten från avkommeprövningen. Svagare samband tycktes föreligga mellan föräldraträds och avkommors fenotyp i fråga om övriga undersökta egenskaper. Säkrare metoder för skattning av sambanden mellan föräldraträd med hög ålder och unga avkommeplantor bör utarbetas i speciella försök.