

Coastal and inland provenance  
trials in *Pinus sylvestris* L.

Proveniensförsök med kust-  
och inlandstall

by

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## ABSTRACT

ODC 232.12 — 174.7 *Pinus sylvestris* (485)

Stands of Scots pine (*Pinus sylvestris*) along the south-eastern coast of Sweden differ from inland stands at the same latitude as regards frequency of trees with broad crowns and crooked stems. In order to investigate the nature and extent of the differences, a provenance trial was established with material of coastal and inland origin. The experimental design involved testings at two sites (coastal and inland), at two spacings at each site and with two methods of establishment (sowing and planting).

Differences between provenances were established as regards germination, survival, occurrence of prolepsis and some branching characteristics. Inland pines were less well adapted to coastal conditions than were coastal pines to inland environment. The stem form of the inland trees was superior to that of the coastal ones. A strong effect of differences in spacing was demonstrated as well as an influence of different methods of establishment. A strong relationship between the various growth characteristics within the individual trees was manifested. The branch angle was negatively correlated with branch size. The variation in stem form was independent of the variation in other traits. The conclusion was drawn that genetical differences between the parent stands existed as regards crown form and especially stem straightness.

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Coastal pine stand.



Inland pine stand.

## 1. Introduction

Stands of Scots pine (*Pinus sylvestris* L.) along the south-eastern coast of Sweden are characterized by a high frequency of trees with coarse branches, wide flat crowns and more or less crooked stems. Inland stands 50 to 100 km west of the coast at the same latitude and at slightly higher elevations have in general a high frequency of trees with more slender branches, straight stems and intermediate or narrow crowns.

The development of a "coastal" type, adapted to the climate and the sites at the coast is considered to be the result mainly of natural selection (Lindquist 1946). Selective felling of the best timber trees near village settlements is mentioned as a further cause of the inferior quality of the coastal pine. The great variation within such stands, and the high frequency of aberrant trees has been explained by Nordström (1954) as resulting from the late migration of pine to the outer coast and the archipelago as land elevation proceeded. According to this assumption, a high degree of inbreeding has occurred, which has added to the obvious phenotypic variation.

For centuries different kinds of selection have certainly acted on the coastal and the inland pine populations, and the genetic constitution of the stands along the coast might now greatly differ from that of the inland pine stands. In order to investigate the nature and extent of the presumed differences, a provenance trial was established with material from one coastal and one inland provenance,<sup>1</sup> both at the same latitude ( $57^{\circ} 50'$ ), but separated by a distance of about 55 km (long.  $15^{\circ} 50'$  and  $16^{\circ} 46'$  respectively). The experimental design involved testings at two sites (coast and inland), at two spacings at each site and with two methods of establishment (sowing and planting). The experiment was carried out jointly by the County Forestry Board (Västervik) and the Department of Forest Genetics, Royal College of Forestry, Stockholm.

## 2. Material and experimental design

Cones were collected during the winter of 1949/50. At the coast cones were collected from felled trees on the opening up of an old stand; thus some negative selection probably occurred (Waesterberg, personal communica-

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<sup>1</sup> Another two provenances were planted at the coastal site one year later (see below).

**Table 1. Data for provenances included in test plantations Eh 86 and Eh 87.**

Provenance (place and parish)	Stand type	Latitude	Longitude	Site	Age	Mean height	Vol/ha
Hansehult, Vimmerby	inland (I)	57°43'N	15°50'E	mesic dwarf- shrub type	Ca.130	25	250a300
Byvik and Ås- kedal, Lofta- hammar (1950)	coastal (K)	57°54'N	16°46'E	dry dwarf- shrub type	Ca.90	?	?
Hallmare, Lof- tahammar (1951)							

tion). The inland stand was clear-felled and the cones collected from felled trees. Data for the two stands are presented in Table 1. No characteristics of the individual trees in the stands were registered. All seed from the trees in each stand was mixed and used as one seed lot.

Two test sites were chosen, one near the coast, "Horn" (Eh 86) and one inland, "Fågelhem" (Eh 87), about 55 km west of Horn (Table 2). The design of the experiment is shown in Figure 1. The seed lots from each provenance were divided into two before sowing in spring 1950:

- 1) for direct patch sowing (S/50) on prepared spots
- 2) for sowing in the nursery (P/52)

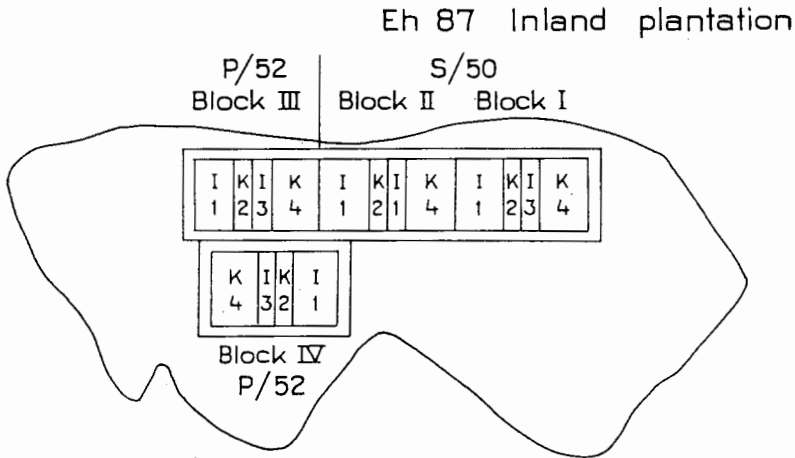
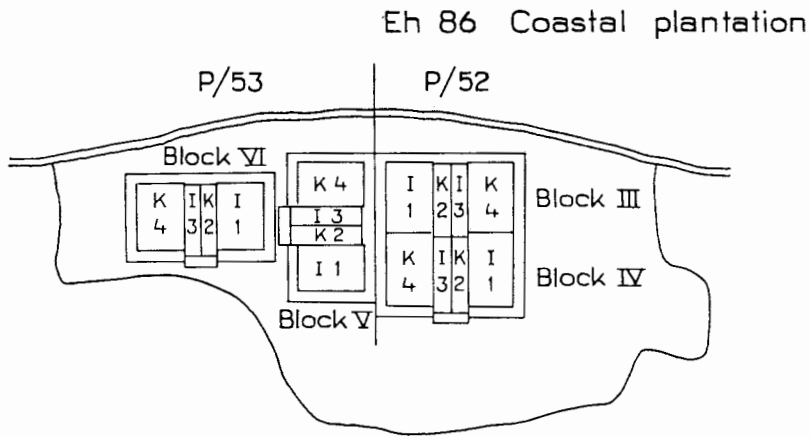
The two-year old nursery plants (2/0) were planted in the spring of 1952. The two blocks sown directly at Eh 86 "Horn" were discarded in 1952, owing to poor germination and survival. Two other stands were used as seed sources in 1951 and plants grown from these seeds were planted in 1953 (P/53, Figure 1). In general the results from the later plantation confirm those from the rest of the material, and are therefore discussed only where they markedly deviate. A comparison between the two test plantations Horn and Fågelhem is possible only for the two blocks planted in 1952 (P/52).

In 1958 release cutting was carried out in the two blocks sown (S/50, Eh 87). In sown patches with more than one plant all except the tallest were removed.

**Table 2. Data on experimental sites. Test plantations Eh 86 and Eh 87.**

Planta- tion	Place	Latitude	Longitude	Climatic area	Soil type	Establish- ed method/ year <sup>1</sup>	Blocks
Eh 86 Coastal	Horn	57°43'	16°40'	coast	sandy field	P/1952 P/1953	III + IV V + VI
Eh 87 Inland	Fågelhem	57°41'	15°50'	inland	blocky till	S/1950 P/1952	I + II III + IV

<sup>1</sup> S = sown P = planted



I = Inland provenance  
K = Coastal provenance

Spacing: 2.0 x 2.0 m plot 1 and 4  
1.3 x 1.3 m " 2 " 3

No of plants / plot: 228 (plot 1 and 4)  
232 ( " 2 " 3)

Figure 1. Experimental layout and initial number of plants on coastal (Eh 86) and inland (Eh 87) site.

**Table 3. Test plantations Eh 86 and Eh 87. Characteristics analysed.**

Characteristic	Year		
	1959	1961	1967
<i>All trees</i>			
Height	*	*	*
Leading shoot length	*	*	*
Diameter at 1.3 m (D. B. H.)			*
Stem form			*
<i>20 trees/plot</i>			
Branch length, whorls 2 and 3 <sup>2</sup>	*1		
"    1—5		*	
"    3 and 6 (7)			*
Branch angle, whorls 2 and 3	*1		
"    2—5		*	
"    3 and 6 (7)			*
Branch diameter, whorls 3 and 6 (7)			*
(ca. 5 cm from branch base)			
Number of branches/whorl, whorls 1—3	*1		
"    1—5		*	
"    2—7			*
Crown form. Branch length/height, %			
whorls 2 and 3	*1		
"    1—5		*	
<i>Covariation</i>			
Branch length — branch angle			*
— branch diameter			*
Branch angle — branch diameter			*
— no. of branches/whorl			*
Branch diameter — no. of branches/whorl			*
Height — stem diameter			*
Stem diameter — branch angle, whorl 6 (7)			*
— branch diameter, whorl 6 (7)			*

\* = measurements made in 1959, 1961 and 1967 respectively

<sup>1</sup> = P/53 (blocks V and VI) not measured

<sup>2</sup> = whorls numbered from top downwards

Owing to differences in germination, to beeting and to differences in survival, the remaining trees were exposed to varying competition during the first eight years after sowing. Since this variation was apparently evenly distributed over the two blocks, independently of spacing and provenance, no attempt has been made to correct for differences in competition when processing the results. The trees were measured in the autumns of 1959 and 1961 and in spring 1967 (Table 3). Height, leading shoot length and stem diameter were measured on all trees. The branching characteristics were measured on 20 dominant trees in each plot. The mean of three branches in each of two to five whorls per tree was used for calculating the plot means. The whorls were numbered from the top downwards.



The stem form was estimated ocularly when the trees were measured in 1967. Class 0 denotes straight and class 3 very crooked stems. Deaths, insect and fungal damage, and growth abnormalities were continuously registered.

The statistical analyses of data are based on plot means, except for the calculation of the correlation between branch and stem characteristics. Here the individual branch values were used. The computer program BHK23 of the Royal College of Forestry, Stockholm, was used for making the analysis of covariance. The Department of Forest Biometry and the Computer Centre, RCF, Stockholm, have worked out the models.

Significant differences between the values of measurement are given as follows: \* significant at 5 per cent level; \*\* significant at 1 per cent level; \*\*\* significant at 0.1 per cent level.

### 3. Results and discussion

#### 3.1. Germination

The germination percentage of the coastal seed in laboratory tests was slightly lower than that of the inland seed. Also the frequency of blank sown patches was higher in the coastal plots (13 per cent against 5 per cent in the inland plots in 1950), indicating a difference in seed quality between the provenances.

#### 3.2. Damages

Insect and fungal damage was rare in the material, except for a severe attack of grey needle cast [*Hypodermella sulcigena* (Rost.) Tub.] on the coastal test plantation in 1962 (Table 4). The disease appeared all over the area, irrespective of provenance and spacing and gradually disappeared during the next few years.

**Table 4. Per cent trees with prolepsis and grey needle cast 1958 and 1962.**

Test plantation	Established method/year	Provenance	Prolepsis		Grey needle cast	Test plantation	Established method/year	Provenance	Prolepsis	
			1958 %	1962 %					1958 %	1962 %
					1962 %					
Eh 86 Coastal	P/52	I	13.6	12.3	58.8	Eh 87 Inland	S/50	I	3.0	2.2
		K	12.8	8.4	54.0			K	2.7	1.0
	P/53	I	24.6	26.5	47.5		P/52	I	3.7	2.6
		K	15.8	19.0	70.6			K	4.0	2.8

### 3.3. Abnormalities

Abnormalities such as forking of shoots occasionally occurred in both provenances. Prolepsis (lammas shoots) was registered in 1958 and 1962 (Table 4). In the inland plantation the percentage of trees with prolepsis was low in both provenances ( $< 5$  per cent), and on the average four to eight times lower than in the coastal plantation. In the latter, about 14 per cent of the trees of coastal origin and more than 19 per cent of the inland trees exhibited prolepsis in one or both years. This indicates a different influence of the two local environments on this character and also a slightly different reaction of the provenances to the coastal climate, the inland provenance being the more sensitive of the two.

### 3.4. Survival

Differences between the *provenances* as regards survival were clearly observed only in the coastal plantation (Eh 86, Figure 2). The percentage of plants lost<sup>1</sup> was consistently greater in the inland than in the coastal provenance from 1955 onwards, but the differences were not significant up to the last year of registration, 1967 ( $0.2 > P > 0.05$ ).

In this plantation an effect of *spacing* was also shown (Figure 3). With increasing age, the inland provenance seemed to be more sensitive to the increased competition in the dense plots than the coastal provenance. In

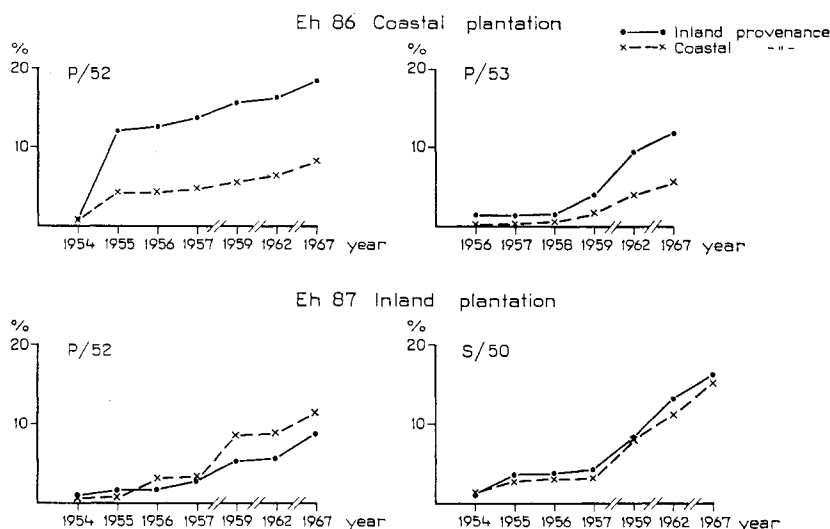


Figure 2. Plant losses recorded after last beeting 1954 and 1956.

<sup>1</sup> Cumulative mortality; cf Eiche 1966

1967 more than 23 per cent of the inland trees in the dense plots were lost compared with 8 per cent of the coastal trees. The difference, however, is not significant. No such differences in reaction for different spacing were found in the inland plantation, the percentage of trees lost being about the same in both provenances (13 per cent) and slightly greater in the blocks sown than in those planted (16 and 8 per cent respectively,  $0.2 > P > 0.05$ ). The varying treatment of the plants in the sown blocks, mentioned earlier, may have had a negative effect on survival.

In general, Scots pine is highly sensitive to changes in the overall climate and to variations in the microclimate (Eiche 1966). When studying the variation in mortality of some provenances growing near the inland seed stand used as seed source in the present investigation, Eiche (personal communication) found an extraordinarily high sensitivity in these provenances, in contrast to that found in provenances growing near the coast. In connection with a study of the inherent growth rhythm of provenances, Langlet (1945) discussed the effect on resistance and growth when seeds and plants are removed from their native habitat to other latitudes and altitudes. According to him, a transfer along the same latitude is fairly safe. He points out, however, that in regions with a particularly dry or moist climate, seeds from areas with similar climatic conditions should be used. The great variability of *Pinus sylvestris* in physiological traits, for instance hardiness and drought resistance, is well established and may be the reason for their swift response to changes in the environment also in this case.

In the present experiment the inland provenances are less well adapted to

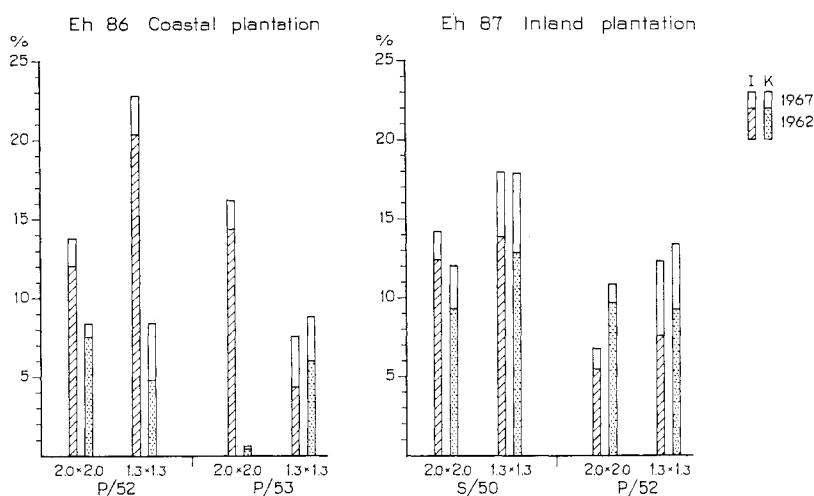


Figure 3. Plant losses by spacing and provenance, 1962 and 1967.

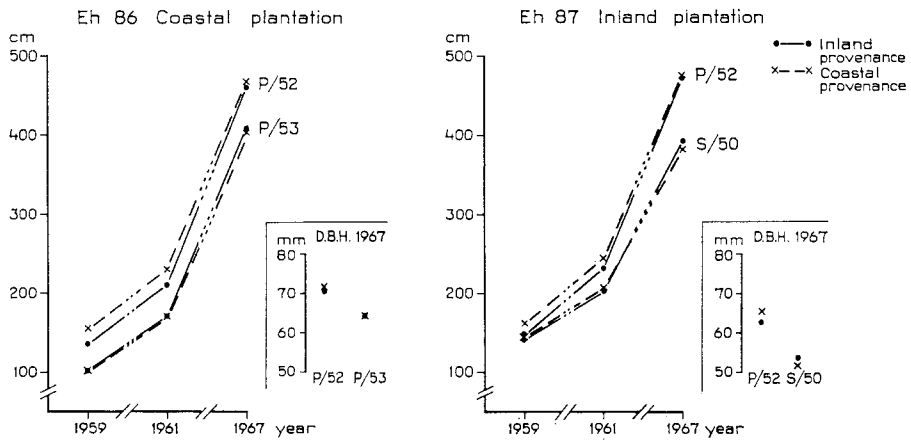


Figure 4. Mean height of provenances in different years. Mean diameter (DBH) in 1967

site and climate at the coast, than is the coastal provenance to inland conditions. The increasing competition between trees with age affected the survival and vitality of the trees, suppressing the weak individuals in the dense plots at a younger age than in the widely spaced plots. This factor of selection acted most efficiently on the inland provenance at the coast.

### 3.5. Growth characteristics

Tree height and the length of the leading shoot of all trees were measured in 1959, 1961 and 1967. In the last year also the diameter at breast height was included. The results from the measurements in different years are presented in Figures 4 and 5. Only the analyses of variance of the data from 1967

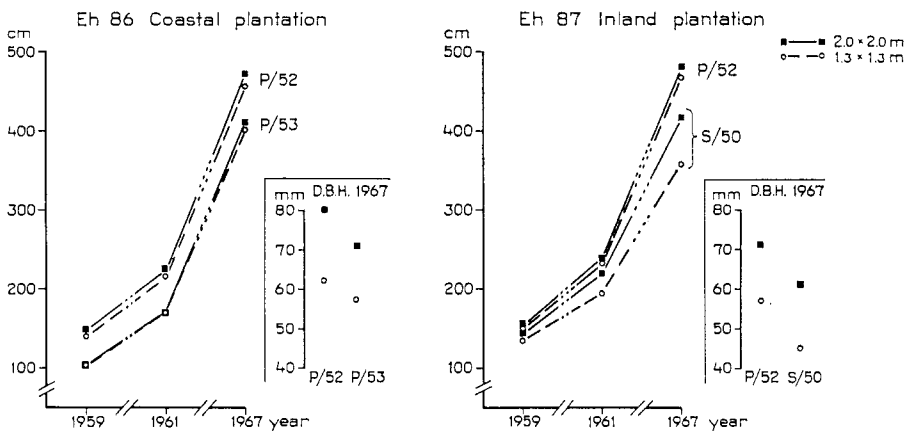


Figure 5. Mean height of trees at spacings 2.0x2.0 and 1.3x1.3 m respectively, in different years. Mean diameter (DBH) in 1967.

are given (App. I and II). The results from 1959 and 1961 corresponded as a rule to those from 1967 as regards the significance of the differences between provenances, between spacings and between methods of establishment. There were, however, some exceptions. The effect of different spacing on growth and branching characteristics increased with increasing age of the trees in both test plantations ( $2.0 \times 2.0 \text{ m} > 1.3 \times 1.3 \text{ m}$ ). In the inland plantation significant differences *between provenances* in height were recorded in 1959 ( $K > I$ ;  $P = 0.05$ ), and between *methods of establishment* in the length of the leading shoot in 1961 ( $P > S$ ;  $P = 0.05$ ). These differences were not significant in 1967.

### *Height and diameter growth (all trees)*

#### *Coastal plantation (Eh 86)*

No significant differences between *provenances* were recorded in mean height or diameter, but the coastal provenance in section P/52 was consistently the taller in all years after planting. Different nursery conditions or differences in germination rate and growth rate of the two provenances at the seedling stage may be the reason for this.

No effect on height growth of differences in *spacing* was demonstrated in either provenance in this plantation. Diameter growth, on the other hand, was strongly influenced by differences in tree density, and both coastal and inland provenances reacted in a similar way to the greater competition, *i.e.* with slower growth in the dense plots. The difference was highly significant in section P/52 ( $P = 0.01$ ).

#### *Inland plantation (Eh 87)*

As in plantation Eh 86, the coastal *provenance* was superior in growth in the first years of measurement. In 1967, however, the inland provenance was slightly taller and had significantly longer leading shoots than the coastal provenance ( $P = 0.05$ ). The mean breast height diameter was similar in both provenances. Thus the coastal and inland trees grew somewhat differently up to the age of 18 years, the inland provenance gaining more in height than the coastal provenance. The differences were, however, not significant.

An increasing effect of different *spacing* on growth was registered from 1959 to 1967. The mean values of the dense plots were the lowest in all years of measurement, but significantly lower only in 1967. The differences were highly significant for leading shoot lengths and diameters ( $2.0 \times 2.0 \text{ m} > 1.3 \times 1.3 \text{ m}$ ,  $P = 0.01$  and  $0.001$  respectively). No interactions could be demonstrated between provenances and spacing, both provenances reacting in the same way to increased density.

Differences in growth between the two *methods of establishment* used in this plantation were also demonstrated. In the sown section (P/50, blocks I and II) mean tree height and stem diameter were consistently smaller than those in the planted section (P/52, blocks III och IV). The differences were significant in 1967, irrespective of provenance and spacing. In 1955 the trees in the two sections were of about the same mean height (56 cm). The later difference in growth rate may be due to the fact that 40—60 per cent of the trees in the sown section had grown under more or less crowded conditions in the sown patches up to the age of eight years, when all trees except the tallest one in each spot were removed.

Similar results were obtained in an experiment with Scots pine, established in 1906 in Västergötland, Sweden, by Maass (1910), and reported on by Langlet (1937), Näslund (1944) and Eklund (1956).

### 3.6. Branching characteristics

The 20 trees per plot, selected in each provenance in each plantation for the study of branch characteristics, were dominant, healthy trees of about the same mean height and diameter in both provenances. The results obtained in the two test plantations generally agreed, but some differences were observed, as is shown below.

#### *Coastal plantation (Eh 86)*

In 1959 and 1961 significant differences between *provenances* were established for a few of the characteristics, but only in the oldest section, P/52. They may be summarized as follows: The inland trees had, in comparison with the coastal trees, more open branch angles in whorl 5 in both years, longer branches in relation to height in whorls 1 and 2, but relatively shorter in whorl 5 in 1961; a lower number of branches in whorl 1 in 1959 and a higher number in whorl 2 in 1961.

In 1967 (App. II. 1 and 2), the only significant differences registered in section P/52 referred to the number of branches in whorls 2 and 5 ( $I > K$ ,  $P = 0.01$  and  $0.05$  respectively). In general the inland trees in this section were characterized by slightly longer branches as well as by a higher number of branches in the uppermost whorls. They also had a more open branch angle in the lower whorls in all years (significantly greater only in 1959). As the branch angle size is strongly genetically controlled in *Pinus sylvestris* (Johnsson 1965, Ehrenberg 1966), the greater branch angles of the inland trees in section P/52 suggest genetic differences between the parent provenances in this trait. In section P/53, where other seed sources had been used, no differences between provenances in branch angle size were established, but

differences as regards branch length in whorl 6 and branch diameter in whorl 3 ( $I > K$ ) were shown. In both sections the number of branches in the lowermost whorl was smaller in the inland trees.

An effect of different *spacing* on branch development appeared in 1967. Irrespective of provenance, the trees in the plots with wide spacing had significantly larger branches in whorls 3 and 6, and a significantly higher number of branches, as well as larger branch angles in the lower whorl. The relatively small number of branches in whorl 6 of trees in the dense plots is probably due to natural pruning in these plots at this stage.

#### *Inland plantation (Eh 87)*

In contrast to the results obtained in the plantation at the coast, those obtained inland revealed no differences between provenances in any of the branch characteristics studied in any year (App. 11.3). Trees with narrow or broad crowns were included among the selected trees in both provenances, and the crown form was on the average similar in both.

The effect of different *spacing* on branch development was demonstrated for branch length in 1959 and 1967, and for branch diameter in 1967. The higher mean values refer to the wide spacing ( $2 \times 2$  m). As in the case of tree height and stem diameter, the differences increased with increasing age, when competition between trees became greater in the dense plots. The branch angle size and the number of branches varied irregularly from year to year, and the latter trait also from whorl to whorl. In 1967 no effect of increasing density on self-pruning was registered for either spacing, the number of branches in whorl 7 being equal to that in the upper whorls.

The difference in tree height between *methods of establishment* mentioned above (p. 14), was significant when all trees were measured. The difference was not significant when only the 20 selected trees per plot were compared in the two sections, but the trees in the planted section were still superior in height in all years. Owing to the usually strong correlation found between stem and branch growth, the mean values of branch length and diameter obtained in the planted section were consistently greater, too, than those in the sown blocks.

Significant differences in branch angle size were demonstrated in whorl 7, the smaller trees in the sown section having the largest angles.

The number of branches in whorls 2—7 varied independently of provenance, spacing and establishment method. No correlation was demonstrated between branch number and tree height or any other characteristic studied in the present material (cf. p. 18). The climate of the year when the buds in the leading shoot are set and the branches in the uppermost whorl develop, appears to be the decisive factor for bud and branch number.

**Table 5.**  $\chi^2$  test of differences between provenances, between spacings and between methods of establishment in frequency of straight and crooked trees.

Test plantation	Established method/year	Provenance	Spacing	$\chi^2$	Stem form (mean)
Eh 86 Coastal	P/52	I	2.0+1.3	2.66	1.31
		K			1.36
		I+K	2.0	1.26	1.32
			1.3		1.34
	P/53	I	2.0+1.3	24.52***	1.26
		K			1.42
		I+K	2.0	25.10***	1.38
			1.3		1.31
	S/50	I	2.0+1.3	19.89***	1.16
		K			1.35
	P/52	I	2.0+1.3	16.29***	1.01
		K			1.14
Eh 87 Inland	S/50+P/52	I+K	2.0	13.79**	1.13
			1.3		1.19
	S/50	I+K	2.0+1.3	54.92***	1.26
	P/52				1.07

### 3.7. Stem form

The classification of trees by stem straightness, carried out in 1967, revealed significant differences between *provenances* within plantations (Table 5). It also revealed a different reaction of the two provenances on the climatic and site conditions prevailing inland and at the coast.

When all plots are considered, the inland provenances exhibited a higher frequency of straight or nearly straight stems than did the coastal provenances in both plantations.

On the average, the inland trees in the coastal plantation had the better stem form at the close *spacing* in P/52, but not in P/53. Within the coastal provenances, trees in P/52 were superior at the wide spacing, but in P/53 at the close spacing. This might indicate that genetic differences exist in this trait between the provenances used in 1950 and 1951 respectively.



In the inland plantation the frequency of straight stems was significantly greater at the wide *spacing*, when all plots were taken together. As regards the *sown and planted sections*, taken separately, the frequency of straight stems in the sown blocks was significantly higher at the wide spacing; in the planted blocks it was the reverse. Very crooked trees were rare in this material, and occurred to less than 5 per cent in the inland provenances.

The stem form is strongly genetically controlled, as shown by Nikles (1965) and Stonecypher (1966) for American pine species. According to Shelbourne (1966), sweeps are less strongly controlled than irregular small crooks. A strong parent-progeny-relationship is also demonstrated for this trait (for review of literature see Ehrenberg 1969). Evidently, the significant differences between the provenances in the frequency of straight stems shown in the present material are conditioned by genetic differences between the original seed stands. More or less crooked stems are common among the pines growing along the coast, and were probably frequent also in the coastal stands used as seed sources in this case. The inland stands were classified as "above normal" as regards stem straightness and crown form and the present results indicate that a relatively high frequency of straight stems occurred in these stands.

### 3.8. Comparison between test localities

The main differences between the two localities are in climate and soil conditions, day length being about the same in both. In the conditions prevailing *inland*, both provenances were on the average taller, had significantly smaller stem diameter, shorter and more slender branches with a slightly smaller branch angle and finally, a smaller number of branches in the upper whorls, while the number in the basal whorls was higher, as compared with the coastal plantation (App. III). At both localities the provenances reacted similarly to different spacing, growth being slower in the dense plots.

In the *coastal plantation* increased density, irrespective of provenance and spacing, initiated self-pruning at an earlier age, and the mean number of branches was relatively low at crown base.

As regards the growth characteristics, no major interactions between spacing and locality or between spacing and provenance were recorded. There was some indication that different spacing affected the number of branches in whorls 2 and 7 to a different degree at the two localities.

The frequency of straight stems was significantly higher in the inland plantation in both provenances (Table 6), with the exception of the coastal trees at the wide spacing. Here the mean stem form was 1.30 and 1.31 on the

**Table 6.**  $\chi^2$  test of differences between test plantations Eh 86 and Eh 87 (P/52) in frequency of straight and crooked trees.

Provenance	Spacing	$\chi^2$	Mean stem form	
			Eh 86, coastal	Eh 87, inland
I	2.0 $\times$ 2.0	59.18***	1.33	0.96
	1.3 $\times$ 1.3	22.90***	1.26	1.05
K	2.0 $\times$ 2.0	0.25	1.31	1.30
	1.3 $\times$ 1.3	91.66***	1.41	0.99

inland and coastal plantations respectively. In general the inland conditions had a favourable influence on stem development. The stem form of the coastal trees was improved by the transfer to the inland environment. The inland trees, on the other hand, developed more crooks and bends when transferred to the coast.

### 3.9. Relationships between characteristics

The values obtained from measurements in 1967 were used for calculating the relationships between the various characteristics. The results obtained are exemplified by data from the two planted blocks (P/52) at each locality and based on two individual branches per whorl and 20 trees per plot (App. IV).

Tree height and stem diameter were strongly correlated with one another and usually also with length and diameter of the branches. Strong correlations between traits referring to size are generally demonstrated in forest trees and will not be discussed here. The branch angles, however, varied irregularly with height and diameter of the tree but were usually negatively correlated with the size of the branches in the same whorl. A strong positive correlation was established between the branch angles of the two whorls. A tree with comparatively small branch angles in whorl 3 also had relatively acute angles in the lower whorl.

No correlation was established between the development of the stem form and any of the other characteristics, except with the number of branches in the lower whorl. The branch number in this whorl may bear some relation to stem development, but the relationship is weak. In all other cases the number of branches of the two whorls studied varied independently of other characteristics, and there was no relationship between the whorls themselves, probably due to the fact that the number of buds set each year is influenced mostly by the weather of the year and the nutritional conditions during the growing season.

The independent variation of branch angles and stem straightness confirms earlier results obtained in pine and other tree species as to the stronger

genetical control of these characteristics than of, for instance, characters related to size. Nanson (1969) established a strong relation between branch angle size on the one hand and tree height and stem diameter on the other hand, in Scots pine. No such relationship was apparent in the present material.

#### 4. Summary and conclusions

In the present material differences between *provenances* were established as regards germination, survival, occurrence of prolepsis, and some stem and branching characteristics. A strong effect of differences in *spacing* was demonstrated as well as an influence of different *methods of establishment* and of different *sites* on the development of the trees.

1. A detailed comparison between *provenances* revealed the following:

A difference in seed quality existed as shown by the lower germination percentage of the coastal seed and the higher number of blank sown patches in the coastal plots.

The inland provenances were inferior to the coastal as regards survival when transferred to the coast. They are less well adapted to site and climate at the coast than is the coastal provenance to inland conditions.

Differences in the frequency of trees with proleptic shoots were demonstrated in the coastal plantation. The inland trees reacted on the conditions prevailing at the coast with a higher percentage of proleptic trees than the coastal ones.

No significant differences were established in height or diameter growth in either test plantation in 1961 and 1967. The inland provenance was inferior in height in 1959 but not later, which indicates slower growth only at the younger stages in this provenance. The development of the trees from nine and up to eighteen growing seasons suggests that no genetically controlled differences between provenances exist in height growth up to this age.

Differences in branch size and branch number were established only in the coastal plantation, the coastal provenances having a more pointed crown and a relatively dense crown base.

The branch angles in the lower whorls were consistently larger in the inland than in the coastal provenance (used as seed sources in 1950), but significantly so only in the planted section at the coast in 1959.

The results obtained indicate that the branch angles varied within a great range also in the original seed stands. A slightly higher frequency of trees with open angles in one of the inland stands is probable, but is not conclusively demonstrated.

The stem form of the inland provenances was on the average superior to that of the coastal one in 1967. The differences demonstrated were highly significant. Evidently the superior stem form of the inland trees is due to genetic differences between the provenances.

## 2. Comparison between *spacings*.

A positive effect of wide spacing on growth was demonstrated, and increased with increasing density and age. The branch angle size, on the other hand, varied irrespective of spacing, as did also the number of branches in most of the whorls. The effect on stem straightness varied with provenance and site.

## 3. Comparison between *methods of establishment*.

Differences were recorded for survival, height and diameter growth, and stem straightness. The trees grown in the nursery had fewer losses and superior growth as well as straighter stem form in the dense plots than had the trees sown directly in the field.

## 4. Comparison between *test localities*.

In both provenances the mean height of the trees was superior in the inland plantation as compared with the coastal. The difference was, however, not significant in any year. The leading shoot length as well as the stem diameter were inferior in the inland plantation (significant differences in 1967) and thus both provenances exhibited a relatively more slender stem under inland than under coastal conditions.

The stands used as seed sources differed widely in crown form. The broad crowns characteristic of the coastal stand did not reappear in the young trees of this provenance grown inland, *i.e.* they did not differ conspicuously from the young inland trees at the same site. On the other hand, the two provenances displayed a slightly different crown form when grown near the coast. This indicates that inherent differences in branching exist between the seed sources, which are manifested in young trees only in the coastal environment.

The frequency of straight stems was significantly higher in both provenances in the inland plantation. The coastal pines had on the average a better stem form when grown inland. The inland pines displayed a poorer stem form when moved to the coast.

## 5. *Relationships* between characteristics.

A strong relationship between the various growth characteristics within the individual trees was established for 1967. The branch angle size varied irregularly with height and diameter of the tree but was usually

negatively correlated with the size of the branch. There was a positive correlation between the branch angles within the same tree. The variation in number of branches as well as in stem form was independent of the variation in other traits.

The morphological differences existing between the pines growing along the coast in southern Sweden and the pines growing further inland have been attributed partly to natural selection, acting in a different way in different environments, and partly to continuous felling of the best trees for timber. In both cases some special kinds of phenotypes are reduced in number or disappear altogether from the populations. The pines growing along the coast were described by Hemberg (1904) as "a degenerescent biological race" which genotypically differs widely from the inland pines in a negative direction. According to Lindquist (1935), "the coastal pines have for thousands of years been exposed to selection, felling and to some extent to wind-blasting". In 1946 he also refers to "the degenerate pines in the archipelago and along the coast" and "pines degenerated by felling practices". In his opinion "the direct importance of exposure and climate to the development of stem and crown form of the pines along the southeastern Swedish coast is exaggerated". Wretling (1936), in his studies of the variation in crown form of Scots pine in Sweden, points out the strong influence of environment on height growth and branching characteristics. He also emphasizes that "there is no reason to assume that the poor crown form of the 'wolf pines' is due to genotypes different from and inferior to those existing in the well developed trees". Thus he ascribes to the environment a dominating influence on the phenotype. In a report on the quality classification of the pine forests in southern Sweden, Johnsson *et al.* (1956) discusses the historical background of the forests in these regions. In their opinion the generally poor quality of the pines may be explained by the silvicultural measures or rather, lack of measures, applied in earlier times.

In the present provenance test, differences between coastal and inland pines due to genetical differences between the parent stands have been established as regards crown form and especially stem straightness. However, the experiment contained only few provenances and, therefore, general conclusions cannot be drawn with regard to the race differentiation of coastal and inland pine populations. A high frequency of trees having poor stem form and broad crowns is characteristic of the coastal pine stands. This may be due to inbreeding, to natural or to artificial selection.

## 5. References

- EHRENBERG, C. 1966. Parent-progeny relationship in Scots pine (*Pinus silvestris* L.). — Stud. For. Suec. 10: 1—135.
- 1969. Breeding for high yielding characters. Stem quality. — FO-FTB-69-3/1, pp. 19.
- EICHE, V. 1966. Cold damage and plant mortality in experimental provenance plantations with Scots pine in northern Sweden. (Köldskador och plantdöd i proveniensförsök med tall i Norrland.) — Stud. For. Suec. 36: 1—219.
- EKLUND, B. 1956. Ett förbandsförsök i tallskog. Några erfarenheter från ett 50-årigt skogsodlingsförsök på kronoparken Granvik. (An experiment in sowing and planting pine with different spacings.) — Medd. Statens Skogsforskningsinst. 46: 10: 1—98.
- HEMBERG, E. 1904. Tallens degenerationszoner i södra och västra Sverige. — Skogsvårdsför. Tidskr. 2: 121—136, 169—194, Stockholm.
- JOHNSON, H., PERSSON, A. & ERIKSSON, G. 1956. Tallens rastyper i Sydsverige. — Fören. växtförädling skogsträd, årsberättelse 1955: 19—32.
- JOHNSON, H. 1965. Miljöns och genotypens inflytande på tallens växtform i experimentell belysning. — Fören. skogsträdförädling, årsbok 1964: 115—125.
- LANGLET, O. 1936. Studier över tallens fysiologiska variabilitet och dess samband med klimatet. Ett bidrag till kännedomen om tallens ekotyper. (Studien über die physiologische Variabilität der Kiefer und deren Zusammenhang mit dem Klima.) — Medd. Statens Skogsförsöksanst. 29: 4: 219—470.
- 1937. Om miljö och ärftlighet samt om förutsättningarna för växtförädling av skogsträd. (Über Umwelt und Vererbung, sowie über die Voraussetzungen für Züchtung der Waldbäume.) — Norrl. Skogsvårdsförb. Tidskr. 1: 49—99.
- 1938. Proveniensförsök med olika trädslag. (Provenienzversuche mit verschiedenen Holzarten.) — Svenska skogsvårdsför. Tidskr. I-II: 55—278.
- 1943. Photoperiodismus und Provenienz bei der gemeinen Kiefer (*Pinus silvestris* L.). (Fotoperiodism och proveniens hos tallen.) Medd. Statens Skogsförsöksanst. 33: 5: 295—330.
- 1945. Om möjligheterna att skogsodla med gran- och tallfrö av ortsfrämmande proveniens. — Svenska skogsvårdsför. Tidskr. 43: 68—78.
- LINDQUIST, B. 1935. Studier över skogligt betydelsefulla svenska tallraser. (Studies of the races of Swedish pine and their importance to forestry.) — Norrl. Skogsvårdsförb. Tidskr. 1, pp. 86.
- 1946. Den skogliga rasforskningen och praktiken. — Svenska skogsvårdsför. förlag, Stockholm, pp. 176.
- MAASS, A. 1910. Redogörelse över Skogsförsöksanstaltens verksamhet. I. Berättelse rörande skogsafdelningens verksamhet åren 1902—1908. — Medd. Statens Skogsförsöksanst. 6.
- NANSON, A. 1969. Tests de descendance de Pin Sylvestre. — Station de Recherches des Eaux et Forêts, Groenendaal-Hoeilaart, Travaux — Serie E, No. 3, pp. 49.
- NIKLES, D. G. 1965. Progeny tests in slash pine (*Pinus elliottii* Engelm.) in Queensland, Australia. — Proc. 8th South. Conf. Forest Tree Improvement, Sponsored publ. 24, Macon, Georgia, pp. 112—121.
- NORDSTRÖM, L. 1954. Om den inom vissa delar av vårt land dåliga talltypen — dess uppkomstätt samt praktiska konsekvenser därav. — Norrl. Skogsvårdsförb. Tidskr. 1954: 435—487.
- NÄSLUND, M. 1944. Diskussionsinlägg vid Svenska skogsvårdsföreningens årsmöte 1944. — Svenska Skogsvårdsfören. tidskr. 2: 1—9.
- SHELBORNE, C. J. A. 1966. Studies on the inheritance and relationships of bole straightness and compression wood in southern pines. — N. C. State Univ., Dept. Forest Management, Raleigh. (Thesis), pp. 275. Diss. Abstr. in Agriculture 1967, 27 B (12), 1 p.
- STONECYPHER, R. W. 1966. Estimates of genetic and environmental variances and covariances in a natural population of loblolly pine (*Pinus taeda* L.). — Techn. Bull. No. 5, Southlands Expt. Forest, Bainbridge, Georgia, pp. 128. (Thesis)
- WÄSTERBERG, T. Personal communication.
- WRETTLIND, J. E. 1936. Om orsakerna till krontypsväxlingen hos den svenska tallen. (Über die Ursachen der Variation des Kronentyps bei der schwedischen Kiefer.) — Norrl. Skogsvårdsförb. Tidskr., pp. 241.

## 6. Sammanfattning

### Proveniensförsök med kust- och inlandstall

Karaktéristiskt för den utmed svenska Östersjökusten förekommande tallen är det stora inslaget i bestånden av grovgreniga fenotyper med breda, flacka kronor och relativt dålig stamform. Dess kvalitet är i allmänhet sämre än den längre inåt landet förekommande rakstammiga och relativt smalkroniga tallens. Genom en mer eller mindre stark naturlig selektion anses dessa kustpopulationer (Lindquist 1946) ha utbildat sin speciella typ och anpassat sig till klimat och ståndort i kustbandet. Avverkning av de ur virkessynpunkt bästa träden i närheten av bebyggelse skulle därvid vara en bidragande orsak till kustbeståndens sämre kvalitet. Den stora variationen inom bestånden liksom det starka inslaget av avvikande trädtyper förklaras av att tallen trängt ut till kustbandet och skärgården relativt sent allteftersom landhöjningen fortgått (Nordström 1954). En hög grad av inavel bör enligt denna förklaring ha förekommit och verksamt bidragit till att öka den fenotypiska variationen.

Kusttall och inlandstall har säkerligen under tidernas lopp utsatts för olika urvalsprocesser och torde i genetiskt hänseende vara väl skilda. För att experimentellt söka klarlägga något av dessa skillnaders karaktär och omfattning anlades åren 1950—1952 ett jämförande försök med material från kusttallbestånd och normalbestånd av inlandstyp. I försöksplanen ingick prövning av materialet på två försöksytor, i två förband och med två kulturmetoder (sådd respektive plantering). Försöket planerades och anlades i samarbete med skogsårdsstyrelsen i Kalmar län.

Kott insamlades vintern 1949/50 från fällda träd. Vid kusten skedde insamlingen i samband med ljushuggning, varför ett visst negativt urval torde ha skett; i inlandet i samband med slutavverkning. Försöken anlades på två lokaler, ett vid kusten, Eh 86, "Horn", ett i inlandet, Eh 87, "Fågelhem". Fröet från vardera ursprungsbestånden uppdelades i två partier för sådd våren 1950: 1. marksådd (S/50) direkt på försöksytan. 2. sådd i plantskola (P/52). Det senare materialet utplanterades som 2/0 våren 1952. Marksådden på Horn misslyckades och nytt frömaterial insamlades vintern 1950/51, såddes i plantskola och utplanterades som 2/0 våren 1953 (P/53, Horn). Endast delytorna P/52 på respektive lokaler är således direkt jämförbara.

I såddrutor med mer än en planta friställdes 1958 den högsta i varje ruta. Mätningar utfördes 1959, 1961 och 1967. Höjd, toppskottslängd och diameter mättes på samtliga träd. För mätning av grenkaraktärer utvaldes de 20 högsta oskadade träden i varje parcell, tre grenar i två-tre grenvarv per träd inmättes och medeltalet för de tre grenarna i respektive varv användes för beräkning av parcellmedelvärden. Grenvarven numrerades från topp mot bas. En klassificering av träden efter rakvuxenhet (stamtyp) utfördes 1967. Bedömningen skedde okulärt. Klass 0 betecknar raka och klass 3 starkt krökta stammar. Plantavgång, insekts- och svampangrepp samt abnormiteter registrerades kontinuerligt. Vid den statistiska bearbetningen av insamlade data har parcellmedeltalet använts med undantag för beräkningen av sambandet mellan olika stam- och grenegenskaper vilken baserats på enskilda grenvärden.

I försöken har skillnader mellan provenienser fastställts liksom en effekt

av olika förband, kulturmetoder och ståndort i fråga om frögroning, plantavgång, förekomst av prolepsis samt trädens senare tillväxt och utveckling.

### 1. Jämförelse mellan *provenienser*.

Olikheter i frökvalitet förelåg. Frö av kustproveniensen hade sämre grobarhet än inlandsfröet och antalet tomma såddrutor efter marksådd (S/50, Eh 87) var större i kust- än i inlandsparcellerna.

Inlandstallens överlevelseförmåga var underlägsen kusttallens efter förflyttning till lokal med annan jordmån och klimat. Plantavgången var större hos inlandsprovenienser på kustytan upp till 18 års ålder. Inlandstallen i detta försök är sämre anpassade till miljön vid kusten än kusttallen är till inlandsmiljön.

Olikheter i frekvensen träd med prolepsis konstaterades på kustytan. Inlandstallen reagerade för förhållandena vid kusten med en högre procent proleptiska träd än kusttallen.

Inga signifikanta skillnader mellan provenienser i höjd- eller diameter-tillväxt konstaterades på någondera försöksytan vid mätningar 1961 och 1967. Inlandsproveniensen hade lägre höjdmåttal 1959, vilket tyder på en något svagare tillväxt hos denna proveniens under det tidigaste ungdomssta-diet. Den senare utvecklingen av träden visade emellertid att genetiskt kontrollerade skillnader mellan provenienser i fråga om tillväxt upp till 18 års ålder inte förelåg.

Skillnader i grenlängd, grendiameter och antalet grenar registrerades endast på försöksytan vid kusten (Eh 86). Inlandstallen på delyta P/52 hade något längre grenar och ett signifikant större antal grenar i de övre grenvarven. På delyta P/53, där två andra provenienser prövades, förelåg proveniesskillnader i grenlängd i varv 6 och grendiameter i varv 3 ( $I > K$ ). På båda delytorna var antalet grenar i varv 7 lägre hos inlandstallen.

Grenvinklarna i de nedre grenvarven var genomgående större hos inlands- än hos kustproveniensen (1950 års material), men signifikant större endast på delytan P/52 1959. Grenvinkelstorleken hos tall är relativt starkt genetiskt kontrollerad. De i detta försök erhållna resultaten tyder på att grenvinkelstorleken var i hög grad varierande inom ursprungspopulationerna. En något högre frekvens fröträd med relativt stora grenvinklar i ett av inlandsbestånden är trolig men icke säker.

Frekvensen rakvuxna stammar var 1967 signifikant högre hos inlandstallen än hos kusttallen på båda försöksytorna oberoende av förband och kulturmetod. Stamtypen är liksom grenvinkeln i hög grad ärftligt betingad och ett starkt samband mellan föräldraträd och avkomma har konstaterats för denna egenskap (tidigare undersökningar). Inlandstallens överlägsna stamtyp i detta försök tyder på att genotypiska skillnader mellan ursprungspopulationerna förelåg i denna karaktär.

### 2. Jämförelse mellan *förband*.

Förbandsskillnader har fastställts beträffande höjdtillväxt, diameter, grenlängd och grendiameter samt på kustytan i fråga om antalet grenar i varv 2 och 7. Grenvinkelstorleken varierade oberoende av förbandet liksom antalet grenar i övriga grenvarv. Stamtypen varierade med prove-



niens och ståndort. Det större förbandet hade positiv effekt på samtliga tillväxtegenskaper och förbandskillnaderna ökade med ökad slutenhet i parcellerna. Likaså registrerades ett större antal grenar i de lägre grenvarven inom detta förband. Kust- och inlandstill reagerade lika för ökat förband, dvs. ingen signifikans för samspel proveniens—förband kunde konstateras.

### 3. Jämförelse mellan *kulturmeter*.

Svagt signifikanta skillnader mellan sådd- och planteringsytorna förelåg i fråga om plantavgång, höjd- och diameterstillväxt, grenvinkeln i varv 7 samt stamtyp. De i plantskolan uppdragna plantorna hade större överlevelseförmåga, snabbare tillväxt, spetsigare grenvinkel samt högre frekvens rakvuxna stammar än plantorna i såddrutorna.

### 4. Jämförelse mellan *försökslokaler*.

Hos båda provenienserna var medelhöjden på inlandsytan överlägsen den på kustområdet, men skillnaden var icke signifikant något år. Toppskottslängden 1967 var signifikant mindre på inlandsytan liksom diametern. En genomsnittligt smalare stam var utmärkande för båda provenienserna under de förhållanden som råder på inlandsytan.

De inlands- och kustpopulationer, som valts för frötäkt, var fenotypiskt vitt skilda beträffande kronformen. Signifikanta skillnader i kronform mellan avkommorna från respektive bestånd kunde icke fastställas på försöksytan i inlandet. På kustområdet konstaterades en svagt signifikant skillnad mellan provenienserna i utvecklingen av kronan. Genotypiska skillnader mellan proveniensavkommorna i grenkaraktärer föreligger troligen men har framkommit hos de unga träden endast i kustmiljön.

Frekvensen raka stammar var signifikant större hos båda provenienserna på inlandsytan. Kusttallen hade en genomsnittligt bättre stamtyp efter förflyttning till ståndorten i inlandet. Inlandstill reagerade för förflyttning till kusten med försämrade stamtyp.

### 5. *Sambandet mellan egenskaper.*

Ett starkt samband konstaterades 1967 mellan olika tillväxtegenskaper inom de enskilda träden. Grenvinklarna i de båda mätta varven inom samma träd var starkt positivt korrelerade men hade i genomsnitt ett negativt samband med den egna grenens längd och diameter. Inga samband förelåg med övriga egenskaper. Variationen i antalet grenar per varv och i stamtyp var oberoende av variationen i andra egenskaper.

Orsakerna till att tallen utmed kusten i Sydsverige i morfologiskt hänseende skiljer sig från tallen längre inåt landet skulle som inledningsvis nämnts ligga dels i miljöskillnader och olika urvalsprocesser, dels i den selektion som betingas av kontinuerligt uttag av de bästa träden i en population.

I båda fallen skulle vissa fenotyper minska i antal eller försvinna helt ur populationerna med åtföljande förändringar i dessas gensammansättning. Kusttallen beskrevs av Hemberg (1904) som "en degenerescent biologisk ras-

form" med en genotyp som väsentligt skiljer sig från inlandstallens i negativ riktning. Enligt Lindquist (1935) skulle "kusttallen under årtusenden utsatts för selektion genom virkesfångst och i någon mån vindpining". Samme författare (1945) talar om "skärgårdens och kusttrakternas degenererade tallformer" och "kulturdegenererad" tall, och anser att "expositionens och klimatets *direkt* formgivande betydelse för tallskogarna inom det sydsvenska kustområdet är överdriven". I motsats härtill har Wretling (1936) i sin undersökning av krontypsväxlingen hos svensk tall betonat miljöns starka inflytande på gren- och höjdtutveckling, och att "skäl saknas för antagandet att vargtallarnas dåliga krontyp skulle bero på andra och sämre anlag än som förefinnes hos de välformade träden". Han tillskriver alltså miljön en dominerande effekt på fenotypens utformning. I samband med en översikt av frötäktsklassificering av tallbestånd i Sydsverige diskuterar Johnsson et al. (1956) den historiska bakgrunden till den sydsvenska tallens ofta dåliga kvalitet. Denna kan förklaras bl. a. av de skogsskötselåtgärder, eller snarare brist på åtgärder, som vidtagits under gångna tidsperioder.

De i föreliggande proveniensförsök konstaterade skillnaderna mellan kust- och inlandstall hänför sig till frökvalitet, överlevelseförmåga, proleptisförekomst, vissa grenkaraktärer samt stamtyp. Dessa egenskaper är mer eller mindre starkt ärftligt betingade. De signifikanta skillnaderna mellan proveniensavkommorna i försöket styrker antagandet att ursprungsbestånden var i genetiskt hänseende väl skilda populationer. Försöket omfattar endast få provenienser och prövning av ytterligare ett flertal är nödvändigt för att klarlägga om skillnader av samma natur och omfattning föreligger mellan andra populationer av kust- resp. inlandstyp.

**Appendix I. 1. Test plantation Eh 86. Mean squares and means of characteristics measured in 1967. All trees.**

Source of variation	D.F.	Estab- lished method/ year (block)	Height	Leading shoot length	Diameter	Stem form	Estab- lished method/ year (block)	Height	Leading shoot length	Diameter	Stem form
<i>Mean squares</i>											
Block	1	P/52 (III+IV)	392.00	0.98	0.50	0.00	P/53 (V+VI)	2 244.50*	1.44	84.50	0.00
Spacing	1		544.50	9.24	612.50***	0.00		200.00	27.38*	392.00*	0.01
Provenance	1		84.50	4.80	2.00	0.01		40.50	0.12	0.50	0.06
Spacing x provenance	1		84.50	1.44	0.50	0.01		2 178.00	8.40	50.00	0.02
Error	3		446.00	1.38	2.17	0.002		218.83	1.20	12.83	0.02
<i>Means</i>											
Spacing      2.0 × 2.0			472.50	52.95	79.75	1.32		411.25	50.50	70.75	1.37
1.3 × 1.3			456.00	50.80	62.25	1.34		401.25	46.80	56.75	1.31
Provenance    I			461.00	52.65	70.50	1.30		408.50	48.50	64.00	1.25
K			467.50	51.10	71.50	1.36		404.00	48.78	63.50	1.43

**Appendix I. 2 .Test plantation Eh 87. Mean squares and means of characteristics measured in 1967. All trees.**

Source of variation	D.F.	Height	Leading shoot length	Diameter	Stem form
<i>Mean squares</i>					
Method of establishment	1	30 189.06*	261.63	495.00*	0.14
Block error	2	1 377.31	19.45	24.31	0.03
Spacing	1	5 148.06*	78.76**	945.50***	0.02
Provenance	1	45.56	38.13*	0.50	0.10*
Method x spacing	1	2 280.06	25.25*	3.12	0.10*
Method x provenance	1	76.56	0.86	18.12	0.00
Spacing x provenance	1	264.06	7.70	5.12	0.06
Method x spacing x provenance	1	637.56	15.40	52.50	0.02
Plot error	6	645.81	4.20	23.81	0.015
<i>Means</i>					
Method of establishment					
S		387.4	41.0	53.1	1.26
P		474.2	49.1	64.2	1.08
Spacing	2.0 × 2.0	448.8	47.2	66.4	1.14
	1.3 × 1.3	412.9	42.8	51.0	1.20
Provenance	I	432.5	46.6	58.5	1.09
	K	429.1	43.5	58.9	1.25

Appendix II. 1. Test plantation Eh 86, P/52 (blocks III + IV). Mean squares and means of characteristics measured in 1967. 20 trees per plot.

Source of variation	D.F.	Height	Lea- ding shoot length	Diameter	Branch length whorl		Branch angle whorl		Branch dia- meter whorl		Number of branches whorl					
					3	6	3	6	3	6	2	3	4	5	6	7
<i>Mean squares</i>																
Block	1	1953.12	22.78	2.00	136.12*	188.50	12.50	15.12*	4.50	0.50	0.60**	0.01	0.06	0.36*	0.12	0.04
Spacing	1	2628.12	2.31	112.50	78.12*	1104.50*	2.00	21.12*	4.50	98.0***	0.12*	0.21	0.001	0.06	0.24	6.12**
Provenance	1	406.12	0.15	1404.50*	10.12	98.00	2.00	1.12	0.50	0.00	0.24**	0.001	0.001	0.15*	0.00	0.60
Provenance x spacing	1	10.12	1.36	32.00	28.12	8.00	0.00	10.12	0.50	0.50	0.04	0.001	0.10	0.28*	0.04	0.24
Error	3	560.12	4.12	48.33	7.46	48.17	1.83	1.46	0.50	0.17	0.005	0.02	0.19	0.015	0.06	0.16
<i>Means</i>																
Spacing 2.0 × 2.0		605.50	57.82	114.75	119.0	211.0	51.5	59.0	21.0	32.2	6.2	6.3	6.6	6.4	5.2	5.4
1.3 × 1.3		591.25	58.10	88.25	112.8	187.5	52.5	55.8	19.5	25.2	6.4	6.6	6.6	6.2	4.8	3.6
Provenance I		580.25	57.42	97.75	117.0	195.8	52.5	57.8	20.5	28.8	6.5	6.5	6.5	6.5	5.0	4.2
K		616.50	58.50	105.25	114.8	202.8	51.5	57.0	20.0	28.8	6.2	6.4	6.6	6.2	5.0	4.8

**Appendix II. 2. Test plantation Eh 86, P/53 (blocks V+VI). Mean squares and means of characteristics measured in 1967. 20 trees per plot.**

Source of variation	D.F.	Height	Lea- ding shoot length	Diameter	Branch length whorl		Branch angle whorl		Branch diameter whorl		Number of branches whorl					
					3	6	3	6	3	6	2	3	4	5	6	7
Mean squares																
Block	1	2738.00*	5.00	91.12	55.12	144.50	1.12	1.12	0.50	0.12	2.00	0.12	0.04	0.01	0.01	0.28
Spacing	1	128.00	18.60	276.12**	136.12*	612.50**	1.12	10.12	18.00**	66.12*	8.00	10.12	0.12	0.10	0.10	4.06**
Provenance	1	4.50	2.44	1.12	45.12	364.50**	1.12	1.12	2.00*	3.12	8.00	36.12	0.12	0.001	0.03	1.53**
Provenance x spacing	1	648.00	0.72	36.12	28.12	2.00	1.12	0.12	0.50	0.12	8.00	6.12	0.08	0.03	0.03	0.66*
Error	3	155.67	4.30	12.46	7.46	87.50	3.12	4.46	0.17	3.12	2.00	5.46	0.17	0.04	0.04	0.04
Means																
Spacing 2.0×2.0		514.25	56.82	94.25	117.0	194.8	53.0	58.8	21.8	30.8	6.5	6.7	6.6	6.0	4.7	4.7
1.3×1.3		506.25	53.78	82.50	108.8	177.2	51.2	56.5	18.8	25.0	6.3	6.5	6.3	6.2	4.5	3.3
Provenance I		511.00	54.72	88.75	115.2	192.8	52.0	57.2	20.8	28.5	6.3	6.4	6.3	6.2	4.5	3.6
K		509.50	55.88	88.00	110.5	179.2	51.2	58.0	19.8	27.2	6.5	6.8	6.6	6.1	4.6	4.5

Appendix II. 3. Test plantation Eh 87. Mean squares and means of characteristics measured in 1967. 20 trees per plot.

Source of variation	D.F.	Height	Lea- ding shoot length	Diameter	Branch length whorl		Branch angle whorl		Branch diameter whorl		Number of branches whorl					
					3	7	3	7	3	7	2	3	4	5	6	7
<i>Mean squares</i>																
Method of establishment	1	10660.56	67.24	64.00	272.25	885.06	12.25	56.25	1.00	4.00	0.56	0.03	0.10	0.09	0.00	0.68
Block error	2	4469.06	20.29	81.62	126.25	353.81	4.25	8.50	2.00	4.00	0.10	0.14	0.21	0.53*	0.05	0.35
Spacing	1	2678.06	0.02	729.00***	462.25**	1463.06*	12.25	2.25	12.25**	56.25**	0.20	0.60	0.02	0.00	0.04	0.39
Provenance	1	203.06	4.20	12.25	4.00	27.56	16.00	30.25	0.00	0.25	0.01	0.18	0.46	0.04	0.09	0.10
Method x spacing	1	715.54	2.40	30.25	0.25	27.56	2.25	6.25	0.25	0.25	0.09	0.02	0.00	0.04	0.06	0.60
Method x provenance	1	22.54	1.82	16.00	9.00	3.06	0.00	2.25	0.00	0.25	0.56**	0.23	0.60	0.25	0.02	0.00
Spacing x provenance	1	689.04	9.00	36.00	64.00	217.56	9.00	6.25	0.25	1.00	0.12	0.05	0.00	0.01	0.04	0.03
Method x spacing x provenance	1	370.64	0.36	90.25	49.00	217.56	0.00	0.25	2.25	4.00	0.04	0.01	0.33	0.00	0.06	0.22
Plot error	6	629.56	1.76	18.79	31.42	113.31	5.25	8.50	0.67	2.17	0.04	0.12	0.19	0.05	0.20	0.29
<i>Means</i>																
Method of establishment	S	558.12	52.10	84.12	92.2	138.6	47.0	58.5	16.2	20.2	5.6	6.1	6.2	6.0	5.5	6.2
Spacing	P	609.75	56.20	88.12	100.5	153.5	45.2	54.5	16.8	21.2	6.0	6.2	6.4	6.2	5.5	5.8
Spacing 2.0 x 2.0		596.88	54.11	92.88	101.8	155.6	45.2	56.2	17.4	22.6	5.9	6.4	6.4	6.1	5.5	6.1
Spacing 1.3 x 1.3		571.00	54.19	79.38	91.0	136.5	47.0	57.0	15.6	18.9	5.7	6.0	6.3	6.1	5.4	5.8
Provenance	I	587.50	54.66	87.00	96.9	144.8	47.1	58.0	16.5	20.6	5.8	6.3	6.5	6.2	5.6	6.0
	K	580.38	53.64	85.25	95.9	147.4	45.1	55.2	16.5	20.9	5.8	6.1	6.1	6.1	5.4	5.9

Appendix III. Test plantations Eh 86 and Eh 87 (P/52 blocks III + IV). Mean squares and means of characteristics measured in 1967. Comparison between sites. All trees: Height, leading shoot length, diameter, 20 trees per plot: branch characteristics.

Source of variation	D.F.	Height	Leading shoot length	Diameter	Branch length whorl	Branch angle whorl	Branch diameter whorl	Number of branches whorl						
								2	3	4	5	6	7	
<i>Mean squares</i>														
Site	1	400.00	31.64*	182.25*	945.56	182.25	49.00	0.46	0.23	0.12	0.07	0.95	6.00	
Blocks within site	2	658.25	1.02	6.50	104.06	10.25	3.25	0.40	0.06	0.04	0.67	0.06	0.33	
Spacing	1	812.25	16.60	1024.00***	297.56**	4.00	12.25**	0.02	0.02	0.01	0.07*	0.33	6.00**	
Provenance	1	56.25	17.43	12.25	22.56	9.00	0.25	0.46**	0.23	0.42	0.39**	0.05	0.16	
<i>First order interactions</i>														
Site x provenance	1	30.25	1.15	2.25	0.07	1.00	0.25	—0.01	0.17	0.65	0.01	0.05	0.50	
Site x spacing	1	20.25	0.05	9.00	22.57	0.00	0.25	0.38*	0.59	0.00	0.01	0.02	1.11*	
Provenance x spacing	1	4.00	0.08	9.00	18.07	2.25	0.00	0.04	0.02	0.30	0.11*	0.14	0.26	
<i>Second order interactions</i>														
Site x provenance x spacing	1	121.00	2.04	4.00	10.55	2.25	1.00	0.02	0.04	0.01	0.18**	0.01	0.02	
Plot error	6	842.75	3.72	22.00	20.90	5.08	0.75	0.03	0.11	0.19	0.01	0.13	0.17	
<i>Means</i>														
Eh 86	1	461.0	52.6	70.5	117.0	52.5	20.5	6.5	6.5	6.5	6.5	5.0	4.2	
Eh 87	1	473.8	50.4	63.0	101.8	46.2	16.8	6.1	6.4	6.8	6.4	5.6	5.8	
K		467.5	51.1	71.5	114.8	51.5	20.0	6.2	6.4	6.6	6.2	5.0	4.8	
Eh 87	1	474.8	47.8	65.5	99.2	44.2	16.8	5.8	6.0	6.0	6.0	5.4	5.7	
2.0 × 2.0		472.5	53.0	79.8	119.0	51.5	21.0	6.2	6.3	6.6	6.4	5.2	5.4	
Eh 86	1	480.2	49.5	71.5	106.0	44.8	17.8	6.2	6.4	6.4	6.2	5.6	6.1	
Eh 87	1	456.0	50.8	62.2	112.8	52.5	19.5	6.4	6.6	6.6	6.2	4.8	3.6	
1.3 × 1.3		468.2	48.1	57.0	95.0	45.8	15.8	5.8	6.0	6.4	6.2	5.4	5.4	



**Appendix IV. 1. Test plantation Eh 86, P/52. Correlation coefficients of characteristics measured in 1967. Provenance: I No. of trees: 73.**

Characteristics	Height	Diameter	Stem form	Branches						Number of branches	
				whorl 3			whorl 6			whorl	
				length	diameter	angle	length	diameter	angle	3	6
Height	—	0.30**	0.00	0.34**	0.21	—0.06	0.34**	0.27*	0.01	0.11	0.25*
Diameter		—	0.06	0.35**	0.51***	—0.09	0.61***	0.79***	0.28*	—0.06	0.16
Stem form			—	—0.12	—0.07	0.07	—0.07	0.02	0.12	—0.18	0.04
<i>Branches</i>											
whorl 3											
length				—	0.66***	—0.36**	0.51***	0.33**	0.08	0.10	0.08
diameter					—	—0.20	0.44***	0.58***	0.32**	0.15	0.24*
angle						—	—0.11	—0.06	0.23*	0.10	0.03
whorl 6											
length							—	0.70***	—0.08	0.00	0.19
diameter								—	0.18	0.03	0.19
angle									—	0.08	0.03
<i>Number of branches</i>											
whorl 3										—	0.05
whorl 6											—



Appendix IV. 3. Test plantation Eh 87, P/52. Correlation coefficients of characteristics measured in 1967. Provenance: I No. of trees: 77.

Characteristics	Height	Diameter	Stem form	Branches					Number of branches		
				whorl 3			whorl 7			whorl	
				length	diameter	angle	length	diameter	angle	3	7
Height	—	0.54*** —	0.04 —0.08 —	0.40***	0.26*	0.19	0.31*	0.33**	0.22*	—	0.14
Diameter				0.48**	0.48***	0.02	0.54***	0.67***	0.12	0.20	0.24*
Stem form				0.05	0.02	0.08	—0.07	—0.00	—0.09	—0.13	—0.25*
Branches											
whorl 3				—	0.74***	—0.21	0.58***	0.44***	0.21	—	0.11
length					—	0.15	0.46***	0.42***	0.24*	0.19	0.14
diameter						—	—0.06	0.06	0.36***	0.00	—0.11
angle											
whorl 6											
length							—	0.77***	0.04	0.12	0.15
diameter								—	—0.16	0.17	0.11
angle									—	—0.07	0.05
Number of branches											
whorl 3										—	0.07
whorl 6											—

Appendix IV. 4. Test plantation Eh 87, P/52. Correlation coefficients of characteristics measured in 1967. Provenance: K No. of trees: 78.

Characteristics	Height	Diameter	Stem form	Branches						Number of branches	
				whorl 3			whorl 7			whorl	
				length	diameter	angle	length	diameter	angle	3	7
Height	—	0.39***	0.19	0.24*	0.18	0.06	0.09	0.18	0.07	—0.06	0.05
Diameter		—	0.33**	0.39***	0.48***	—0.06	0.44***	0.76***	0.08	0.10	0.11
Stem form			—	0.17	0.22	—0.13	0.15	0.20	0.08	—0.06	—0.10
Branches											
whorl 3				—	0.80***	—0.37***	0.27*	0.29**	—0.17	0.08	0.22**
length					—	—0.13	0.30**	0.34**	0.02	0.16	—0.08
diameter						—	—0.24*	—0.14	0.48***	0.06	0.23
angle											
whorl 6							—	0.62***	—0.22*	0.08	—0.03
length								—	—0.12	0.01	0.06
diameter									—	0.01	0.03
angle											
Number of branches											
whorl 3											0.06
whorl 6											—