STUDIA FORESTALIA SUECICA

Nr 148 · 1978

Variation among Clones and Ortet-Ramet Relationship in Grafted Scots Pine (Pinus sylvestris L.)

Variationen mellan kloner och sambandet ursprungsträd — klon för olika egenskaper hos tall

ENAR ANDERSSON and HANS H. HATTEMER
Department of Forest Genetics, College of Forestry, Stockholm, Sweden

THE SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES
COLLEGE OF FORESTRY
UPPSALA SWEDEN

Abstract

ODC 165.3: 181.51—174.7 Pinus

In order to study the relationship between ortets and ramets (grafts) growing in the same environment or at widely different localities, clone trials were established with 20 and 45 clones, respectively, at two localities in central Sweden. The ortets selected were plus trees or trees with poor to normal growth and quality, and of considerably varying age. The characteristics studied in 1—3 years were stem dimensions; number of branches; branch length, diameter and angle; stem straightness; and cone yield. The variation among clones was studied and the components of variance estimated. The main source of variation were the site differences within each locality. The variation between clones was pronounced in most traits, particularly in cone yield, and increased with age. The repeatability in each clone was good in one test field but poor in the other. Correlations among various clone characteristics, e.g. cone production and graft habitus, have an impact on the gain to be obtained in a seed orchard. The relationships beween ortets and ramets varied but were not as close as those reported from other similar investigations with the exception of those concerning branch angles.

Ms received 1977-04-27

LiberFörlag/Allmänna Förlaget
ISBN 91-38-04626-1, ISSN 0039-3150
Berlings, Lund 1979

Contents

1 Introduction

In 1957 two experimental plantations were established in central Sweden to compare characteristics of ortet trees with the respective grafted clones. The experimental material was produced by the Coordination Committee for Forest Tree Breeding and Genetics (Samarbetsnämnden för skoglig växtförädling och genetik).

Two different approaches to studying the relationships between ortets and ramets were taken. In one experiment, located near Sya, the ramets were planted directly beside the stand where the ortets were growing. In the other experiment, located near Uddeholm, trees from a given area in central Sweden were classified into several phenotypic classes; the field trial containing the ramets should show whether these classes were detectable there. This experiment was designed and established in co-operation with the late Sven G. Ekman, formerly in charge of forest operations with the Uddeholm concern.

A preliminary analysis of part of the data at Sya was published by Wellendorf (1970). The present paper reports on the relations between ortets and ramets in various measurements of tree dimension, stem form, branch habit and cone onset.

Financial support for the project was given by the Swedish Council for Forestry and Agricultural Research.

2 Description of experiments and analysis

2.1 The Sya experiment

The 20 ortets represented in this experiment were, with one exception, taken from one stand aged 119 to 148 years (counted at breast height); this stand was planted using material of indigenous local origin. The northern latitude is 58° and the elevation 100 m above sea level. Among the ortets, various phenotypic classes were represented. Some were plus trees in the sense of Andersson (1966), others had rather poor dimensions and/or growth habits which made them ineligible for use in clonal seed orchards. The ortets thus represented the variation within the respective natural stand. Since the history of stand development could not be traced in detail, a sample of three to four neighbouring trees was taken as a comparison. In these comparison trees, the same traits were measured as in the ortets themselves. In the present context it was hoped that correlations among ortets and ramets would be closer after correction for the comparison trees, i.e. by expressing character manifestation in the ortets as the difference between ortets and the mean of their neighbours.

The adjacent clonal test involved the planting of 5 grafts per plot at a 3 m×3 m spacing. Originally there were 6 complete randomized blocks, two of which were cut during subsequent road construction activities. In order to provide comparable averages, the analyses were run on the data from the remaining four replicates.

2.2 The Uddeholm experiment

The 45 ortets represented in this experiment were taken from various stands in central Sweden, 20 ortets growing at each of the two planted stands (Vågbacken, Uddeholm and Bybergsåsen, Hagfors) located close to each other at latitude 60° N and 160 to 180 m above sea level. Some of the ortets, however, are from natural regeneration. The ages of the trees range between 14 and 31 years (determined at breast height). The other 5 ortets are older plus trees aged 86 to 157 years (determined at breast height) from natural stands located within 15 miles north or south of the 60th degree of latitude.

In each of the two stands named above, four groups each containing 5 trees were formed: Z-trees normally had to be rogued since they could not possibly yield anything better than pulpwood, having very crooked stems and coarse branches. Y-trees have better forms, so that at the end of the rotation period they could be expected to yield very poor quality sawlogs; this is the type of tree that was allowed to grow until the end of the rotation period when there was no better tree around. X-trees in turn have a better form than Y-trees, so that low-quality sawlogs could be expected from them. The fourth group or N-trees (normal trees) would be expected to yield average-quality sawlogs. Ortets in the latter group originated from natural regeneration of the previous pine stands.

This is a total of eight groups; the ninth group consists of the older plus trees mentioned above.

Five grafts per plot of these 45 clones were outplanted, also at a 3 m×3 m spacing. Within the 5 replications, the randomization was restricted, in that incomplete blocks containing 9 plots were formed. Each of the above 9 groups was represented at random in every incomplete block by one clone. However, this condition of the lay-out was neglected in the statistical analyses to avoid further complication of the model; instead, the design was treated as complete randomized blocks.

3 Statistical analysis of the data

In contrast to a field experiment with seedlings, there was much initial mortality, but once the grafts actually grew in the field, there were only minor subsequent losses. Since the various measurements in the Sya experiment were taken on three different occasions, i.e. in 1966, 1967 and 1970, it appeared to be desirable to have the averages independent of the mortality occurring in between: the few trees that were still alive in 1966 and 1967, but that had died before 1970, were rejected from the very beginning, so that all analyses were based on identical samples of trees.

In the Uddeholm experiment, the measurements were taken on two occasions: in 1967 and 1970; the few trees that died between 1967 and 1970 were also rejected. In this experiment partial replanting was performed using material grafted one year later. Moreover, one plot was missing in this test.

The general mortality rate in the 400 ramets at Sya was 18 per cent, while, in the 1125 ramets at Uddeholm, it was as high as 42 per cent. The number of grafts that died no doubt differed from clone to clone in both of the field tests. At Sya the minimum number of ramets surviving in a clone was 8. At Uddeholm the clone with the most severe mortality was represented by only 5 grafts. This wide variation in early mortality among the plots had to be accounted for in the analysis.

In the Sya experiment the following model was assumed:

$$y_{jkl} = \mu + \beta_j + \gamma_k + (\beta\gamma)_{jk} + \varepsilon_{jkl},$$

where β_j refers to the effect of the j-th clone; γ_k to the effect of the k-th block, and ε_{jkl} to the l-th tree within the jk-th plot. $(\beta\gamma)_{jk}$ is formally the interaction between clones and blocks but measures the experimental error.

The model adopted for the Uddeholm experiment was augmented by the effect of the groups as defined in the foregoing paragraph:

$$y_{ijkl} = \mu + \alpha_i + \beta_{ij} + \gamma_k + (\alpha\gamma)_{ik} + (\beta\gamma)_{ijk} + \varepsilon_{ijkl}.$$

The effect of the i-th group is denoted by α_i, and one additional term of the model is $(\alpha\gamma)_{ik}$, the interaction between groups of clones and blocks.

A least-squares fit of these models was adopted after trying various short-cuts, such as an unweighted analysis of means, and method 1 of Henderson (1953). A careful study of those results made it clear that only a complete least-squares analysis was appropriate. Such analyses were run by programs written according to algorithms published by Harvey (1960). The phenomena to be studied in the field tests were generally the variation among clones and, in the Uddeholm experiment, the variation among groups of clones. The significance of differences among clones in the traits measured was of no interest, since such significances were found in many other instances. The significance of differences between the groups formed in the Uddeholm material could not be tested in the present analysis; but this was regarded as minor, since the size of the variance component among groups relative to the one between clones of the same groups was considered to be more important.

In the correlation analyses all data were weighted, because of the wide variation in the number of surviving grafts per clone. In estimating correlations between ortets and the averages of ramets, the assigning of weights according to the number of grafts in clones was doubtful. In this case the quality of measurements in the ortets was the same regardless of the number of observations that entered a clonal mean. The correlations were, however, generally closer after weighting had been applied.

4 Results and discussion

4.1 Mean values in the field trials

4.1.1 *The Sya experiment*

A description of the traits measured in this experiment is given in Table 1. Stem dimensions were assessed repeatedly by tree height and diameter. Additional measurements were the length of the leader and the upper diameter. This latter diameter is not measured at breast height but rather 65 cm above half of the tree height. For example, in a graft that is 4 m tall, the upper diameter is taken 2.65 m above the ground. It gives some indication of stem taper when the trees compared are not too different in height. In the experimental average, the ratio of the two diameter measurements is 0.55 at the ages of 11, 12 and 15 years, regardless of the considerable increase in tree height during this period. A look at the averages of the two extreme clonal means reveals moderate differentiation among the 20 clones as far as dimensions of the stem are concerned.

The number of branches on trees is an important indicator of stem quality. The counts made in six whorls are reported in a sequence to show the development from small numbers at the age of 5 years to larger numbers that do not change very much from year to year. The range of variation among clonal means increases also with age and amounts on the average to two or three branches. The branch count of trait no. 17 was subsequently subdivided into normal (no. 19) and small branches (no. 20). These small branches occurring regularly in pine do not grow very much and die off long before the others. Their numbers show little variation among clones and apparently are not responsible for the variation in total branch number. The same is true of trait no. 18, which was subdivided into traits nos. 21 and 22. Note that the extreme means do not add up as the overall averages do, since different clones are involved in the extreme means.

The nine traits in group c) refer to whorls formed in three successive years. Since they were assessed at different whorl ages, there are naturally some differences in the mean values. Branch length in the 8th whorl from the top at age 15 (trait no. 24) is such that the branch tips may almost touch the stems of neighbouring trees. This contact was even more pronounced in the lower branches, suggesting that heavy competition must have been present. The branch length was measured in a typical branch of a given whorl, and the measurements show a wide range among the clones. The same is true of branch thickness (traits nos. 26 through 28), which was measured close to the stem by means of a special protractor. Branch angle was assessed at a distance of 10 cm from the stem. It shows much variation even in the 8-year-old whorl, where the weight of the branch had already changed the branch angle toward a horizontal position.

Stem straightness was assessed by visual inspection in the following way: 0 = absolutely straight; 1 = slightly crooked; 2 = moderately crooked; and 3 = heavily crooked. The range of variation, though small, denotes rather pronounced variation among the clones, as will be seen later.

For economic reasons, the cones were not counted directly. As in the Uddeholm test, they were roughly estimated and only later transformed to actual data:

Table 1. Traits measured in the Sya experiment.

Description	Age	Experimental mean	Extreme	means
a) *Stem dimensions*				
1 tree height	11	389 cm	307	479
2 tree height	12	448 cm	366	541
3 tree height	14	563 cm	472	651
4 tree height	15	620 cm	511	723
5 leader growth	11	37 cm	25	51
6 leader growth	12	60 cm	44	70
7 tree diameter (d.b.h.)	11	67 mm	51	91
8 tree diameter (d.b.h.)	12	80 mm	62	106
9 tree diameter (d.b.h.)	15	107 mm	81	129
10 upper diameter	11	36 mm	26	51
11 upper diameter	12	44 mm	32	59
12 upper diameter	15	58 mm	42	75
b) *Number of branches*				
13 number of branches in top whorl	5	3.3	2.0	4.5
14 number of branches in top whorl	7	5.3	4.2	6.9
15 number of branches in top whorl	9	6.0	4.1	7.7
16 number of branches in top whorl	11	5.1	4.1	6.7
17 number of branches in top whorl	13	5.9	4.1	7.4
18 number of branches in top whorl	15	5.8	4.3	7.5
19 no. normal branches (top whorl)	13	5.3	4.0	6.6
20 no. small branches (top whorl)	13	0.6	0.1	1.4
21 no. normal branches (top whorl)	15	5.5	4.3	7.4
22 no. small branches (top whorl)	15	0.4	0.0	0.8
c) *Branch morphology*[1]				
23 branch length in whorl 5	11	170 cm	127	208
24 branch length in whorl 8	15	237 cm	190	280
25 branch length in whorl 3	11	112 cm	77	137
26 branch thickness in whorl 5	11	27 mm	20	33
27 branch thickness in whorl 8	15	30 mm	24	34
28 branch thickness in whorl 3	11	22 mm	17	27
29 branch angle in whorl 5	11	63 degrees	52	74
30 branch angle in whorl 8	15	71 degrees	62	84
31 branch angle in whorl 3	11	55 degrees	44	70
d) *Stem straightness*				
32 stem straightness	11	2.2	1.8	2.8
e) *Cone counts*				
33 1-year-old cones[2]	11	17	0.3	53
34 2-year-old cones[2]	12	22	0.5	52
35 1-year-old cones	12	137	19	300
36 1-year-old cones	15	91	13	203

[1] The three whorls sampled were formed in three successive vegetation periods, i.e. from the age of 7 to 9 years.
[2] The cones formed in 1966, i.e. 11 years after grafting, were recounted one year later employing another method (see text).

Table 2. Traits measured in the Uddeholm experiment.

Description	Age	Experimental mean	Extreme	means
a) *Stem dimensions*				
1 tree height	12	352 cm	254	435
2 tree height	14	451 cm	333	552
3 tree height	15	504 cm	374	612
4 leader growth	12	58 cm	44	71
5 tree diameter (d.b.h.)	12	51 mm	25	64
6 tree diameter (d.b.h.)	15	75 mm	46	88
7 upper diameter	12	27 mm	15	34
8 upper diameter	15	39 mm	24	47
b) *Number of branches*				
9 number of branches in top whorl	6	3.1	2.1	3.9
10 number of branches in top whorl	8	4.9	3.5	6.7
11 number of branches in top whorl	10	5.9	4.2	7.9
12 number of branches in top whorl	12	6.5	5.2	8.4
13 number of branches in top whorl	13	5.8	4.2	7.3
14 number of branches in top whorl	15	5.7	4.4	7.9
15 sum of traits, 9 through 12		20.3	15.2	25.9
c) *Branch morphology*[1]				
16 branch length in whorl 5	12	114 cm	67	142
17 branch length in whorl 7	15	153 cm	94	189
18 branch length in whorl 3	12	94 cm	74	112
19 branch thickness in whorl 5	12	19 mm	12	23
20 branch thickness in whorl 7	15	20 mm	13	25
21 branch thickness in whorl 3	12	17 mm	13	19
22 branch angle in whorl 5	12	68 degrees	58	81
23 branch angle in whorl 7	15	70 degrees	57	90
24 branch angle in whorl 3	12	53 degrees	42	71
d) *Stem straightness*				
25 stem straightness	12	2.1	1.6	2.5
e) *Cone counts*				
26 2-year-old cones	12	11	0	88
27 1-year-old cones	12	18	0	116
28 1-year-old cones	15	31	0	90

[1] The three whorls sampled were formed in three successive vegetation periods, i.e. from an age of 7 to 9 years.

Score	Condition of tree	Transformed score
0	no cones	0
1	between 1 and 10 cones	5.5
2	between 11 and 30 cones	20.5
3	between 31 and 100 cones	65.5
4	between 101 and 300 cones	200.5
5	more than 300 cones	300.0

There was one exception in this procedure, namely, in the counting of the 2-year-old cones in 1967 (trait no. 34). The counts were then made more precisely: 0 = no cones; 1 = between 1 and 14; 2 = between 15 and 24; 3 = between 25 and 34; etc. These scores were subsequently transformed to class means. The one-year-old cones in 1966 (trait no. 33) were recounted one year later (trait no. 34). This time the average was slightly larger, which, besides errors in counting, must be due to the difference between the two methods of counting. It is common in the case of pine to find that the number of cones after the second vegetation period is

Table 3. Variance components among clones in the Sya experiment.

Trait no.	Component	Trait no.	Component
1	1,451.80	19	0.08
2	1,591.05	20	0.30
3	2,725.99	21	0.04
4	3,423.85	22	0.54
5	34.89	23	321.19
6	31.69	24	70.19
		25	165.80
7	81.85		
8	97.11	26	8.61
9	119.38	27	5.87
		28	5.52
10	32.24		
11	36.09	29	32.75
12	53.36	30	34.06
		31	29.79
13	0.22		
14	0.46	32	0.05
15	0.92		
16	0.57	33	0.32
17	0.34	34	1.21
18	0.63	35	35.73
		36	0.47

considerably smaller than after the first summer. Brown (1970, 1971) has studied various factors responsible for this premature abscission of conelets. As can be seen from table 1, there was no clone that had no cones at all. Also, there was one clone averaging 300 1-year-old cones per tree. All 20 surviving grafts of this clone were classified as bearing more than 300 cones.

4.1.2 *The Uddeholm experiment*

The means of the growth data in Table 2 show that the general conditions in the Uddeholm experiment were not as favourable as in Sya. The ratio between upper diameter and breast height diameter was slightly reduced. In most of the traits, however, the spread of the 45 clonal means was not smaller.

The data on branch counts are much the same as in the Sya test. In addition to counting the number of branches in single whorls, the sum computed from four of the whorls is also reported. There is a range among clonal means of almost 10 branches in these four whorls (the extreme values do not add up since different clones are involved in the various traits); this is a considerable difference and must be due to a certain consistency of clones to produce more or less side buds in successive years.

Branch lengths were much shorter in this test, but the ranges among extreme clones were about as wide as in the foregoing experiment; a similar situation is true of branch thickness.

The development of the average branch angle with increasing age of the whorl was the same as in the Sya test. However, due to the larger number of clones, the range of variation was more than 30 degrees. Regardless of the average number of cones per tree, there were always a couple of clones that did not bear any cones at all.

4.2 **Variation among clones**

4.2.1 *The Sya experiment*

The estimates of the variance components due to clones presented in Table 3 are all positive. In tree height (traits nos. 1 through 4), the estimates naturally increase with age since various correlated increments are all incorporated in total height up to a given age. The components for leader lengths (traits nos. 5 and 6) are much smaller. In common with tree height, the diameter measurements show greater components at later ages. Also, closer to the top of the trees there are less pronounced clonal differences in diameter than at breast height. Among the branch counts (traits nos. 13 through 18) the estimates are variable; the smallest component was estimated at age 5, but from then on the variation among the estimates cannot be explained by the increase in branch numbers in the various whorls. At ages of 13 and 15 years, the clones apparently vary much more in the number of small branches than in the number of branches that were classified as normal (traits nos. 19 through 22). There was also a clear differentiation between clones

Table 4. Variance components estimated in the Sya experiment, expressed as percentages of their sums.

Trait no.	Clones	Blocks	Clones × blocks	Trees
a) *Stem dimensions*				
1	29.7	9.6	0	60.7
2	28.3	9.9	0	61.8
3	32.6	7.1	0	60.3
4	33.7	6.4	0	59.9
5	15.7	3.9	11.4	69.1
6	28.8	2.1	1.8	67.2
7	28.4	7.1	0	64.5
8	29.3	6.4	0	64.3
9	32.4	2.0	0	65.6
10	31.8	5.3	0	62.9
11	30.4	5.0	0	64.5
12	31.4	5.6	0	63.1
b) *Number of branches*				
13	19.3	2.9	9.0	68.9
14	24.0	4.7	4.7	66.6
15	35.6	0	0	64.4
16	19.0	10.0	5.3	65.6
17	30.3	1.9	2.2	65.5
18	34.8	1.3	0	63.9
19	12.1	15.8	6.1	66.1
20	16.2	14.5	5.2	64.1
21	8.3	25.0	3.8	62.9
22	22.9	12.6	1.5	63.0
c) *Branch morphology*				
23	31.2	1.0	1.4	66.5
24	26.3	1.1	5.0	67.8
25	33.2	0.9	0	66.0
26	27.1	2.5	3.3	67.2
27	18.4	3.6	9.0	69.0
28	29.7	3.6	0.5	66.2
29	30.2	6.9	0	63.0
30	23.2	7.5	3.5	65.8
31	26.6	10.4	0	63.0
d) *Stem straightness*				
32	24.7	1.6	6.0	67.7
e) *Cone counts*				
33	26.5	6.4	1.4	65.7
34	18.9	1.7	9.4	70.0
35	29.5	0.8	2.1	67.6
36	33.2	2.0	0	64.8

in branch size in a given whorl, but there was more variation in the number of small branches.

Branch length (traits nos. 23 through 25) did not show greater clonal variance with increasing age. But even the estimate for 3-year-old branches exceeded that for leader elongation. The variance components for branch thickness (traits nos. 26 through 28) are remarkable, since they all amount to small fractions of those for upper diameter (traits nos. 10 through 12), yet have only slightly smaller means. The differences in branch morphology may give the individual clones a typical appearance, as Hadders and Åhgren (1958) reported in detail.

Stem form (trait no. 32) has a fairly small component, but keeping in mind the way this trait was assessed, this implies pronounced variation (the standard deviation is around 0.2). It is, however, uncertain whether or not this assessment of early stem straightness allows forecasts to be made of the quality of stems at a much later date. Last, but not least, the cone counts vary considerably among clones.

Besides the direct influence of the weather conditions, two other factors may be responsible for this change in clonal variance of cone number, which was also observed in other experiments by Andersson and Hattemer (1975). The amount of pollen from both the clone itself and other clones, and from trees outside the experiment reaching the receptive female flowers of a ramet of a given clone, may vary strongly from year to year. Also, the group of pollinators of a given clone may vary in different years with a different weather regime. The incompatibility system may then contribute to this year-to-year variation. Finally, the trees in the present experiments are grafts; the mutual influence among scion and seedling root stock (of local origin) in these is only little understood today.

The estimates of all variance components for the 36 traits are presented in Table 4. The components are expressed as proportions of their respective sums in order to facilitate comparison of their relative orders of magnitude. Almost the same picture

Table 5. Variance components estimated in the Uddeholm experiment. The components (omitting blocks and trees within plots) are expressed as percentages of their sums.

Trait no.	Groups	Clones	Groups ×blocks	Clones ×blocks
a) *Tree dimensions*				
1	3.7	11.8	0	84.5
2	8.5	13.0	0	78.4
3	9.5	15.0	0	75.5
4	11.0	33.5	0	55.5
5	9.6	0	0	90.4
6	7.9	22.5	0	69.6
7	1.7	18.6	0	79.7
8	8.2	19.8	0	72.0
b) *Number of branches*				
9	0	27.4	0	72.7
10	0.5	24.7	0	74.8
11	0	95.1	4.9	0
12	11.7	54.2	0	34.2
13	0	55.5	1.6	42.9
14	2.3	67.8	0	30.0
15	2.5	70.5	1.0	26.1
c) *Branch morphology*				
16	0	17.8	0	82.2
17	0	26.0	0	74.0
18	0	32.3	0	67.7
19	0	18.3	0	81.7
20	0	29.1	0.2	70.7
21	0	27.0	0	73.0
22	0	37.8	0	62.2
23	10.3	41.8	0	48.0
24	0	54.4	0	45.5
d) *Stem straightness*				
25	11.6	37.5	0	50.9
e) *Cone counts*				
26	18.1	33.6	2.0	46.3
27	10.4	52.7	3.5	33.3
28	1.1	47.5	0	51.4

evolves in all groups of measurements, though these refer to biologically very different characteristics. The variation among grafts within plots always amounts to 60—70 per cent of the total variance, the component among clones ranging from about 10 to about 35 per cent. In leader growth there is slightly less relative clonal variance than in total height; leader growth is also the only growth trait where the clones× blocks component has a positive estimate. The diameter measurements yielded much the same relative estimates as tree height. There is some variation among the estimates of variance components in the branch counts. As can be seen from traits nos. 19 through 22, there is also relatively more clonal variation involved in the number of small branches. It is striking that the groups of characters as such do not reveal any pattern of the percentage of variance due to the differences among clones.

4.2.2 *Variation between and within groups of clones in the Uddeholm experiment*

Unlike the Sya experiment, the analysis of the Uddeholm field test does already contain some information about the relationship between the ortets and their vegetative offspring. This time, only the estimates of variance at the plot level (all relative to their sums) are reported. The variance of trees in the same plots amounted to 60—70 per cent in all traits referring to tree dimensions, number and morphology of branches. In stem straightness it amounted to as much as 80 per cent. For the cone counts, the within-plot variance was lowest, being responsible for only 40 per cent in the average of the three traits in this group.

This has to be kept in mind when looking at the results presented in Table 5. In height and diameter growth, the component for groups is always estimated to be greater than zero. However, the component for clones within the groups is usually larger. Most genetic variance occurs in leader growth (trait no. 4). The number of branches shows variance predominantly due to experimental error. Only in later years is there a stronger genetic component. As in the Sya experiment the variation among clones increases with age. The total number of branches from four whorls (trait no. 15) may have yielded the most reliable estimate; but also in this instance, the variance among groups is exceeded by far by the variance of clones within these groups.

Length and thickness of branches (traits nos. 16 through 21) do not vary among groups and, on the average, show large experimental error variances. The highest proportion of genetic variance occurs in branch angle (traits nos. 22 through 24); but only the assessment in the 7-year-old whorls shows at least a slight variation among the groups. One-half of the small part of the variance in stem straightness that pertains to differences among plots is due to genetic sources. This trait is among the few that possess a variance due to groups that was worth mentioning.

Similar conditions are found in the cone counts, where both the variance of ramets in plots and experimental error are only moderate. But again it does not seem reliable to study the sources of variation of a trait like this by assessing its manifestation in only one year.

Besides limited time overlap of the flowering periods of clones in seed orchards (Schmidt 1970), their differential fertility has recently caused some concern. This differential fertility is probably met in most stands (Andersson 1965, Schmidt 1970) but, with its environmental component, it is most conveniently observed in grafted clones. The implication is a reduced chance of offsprings from all matings being uniformly represented in the seed crop. This prevents an estimated genetic gain from being realized in a production population and gives rise to other implications. Arnborg and Hadders (1957) and Hadders and Åhgren (1958) reported very pronounced differences in cone production between clones. Eriksson et al. (1973) have described differential fertility and its consequences for breeding in a clone trial in Norway spruce. Recently Jonsson et al. (1976) reported on a similar study in a Scots pine seed orchard.

In all, the variance component among groups is always much smaller than the component for clones within the groups. This indicates the inadequacy of classifying phenotypes in stands as fine or poor candidate trees. The basis of this classification was mainly a combination of stem form, branch habit, and growth. These characteristics were the ones that should have shown some variance among the groups of clones in the field tests.

4.3 **Heritabilities**

The estimates of variance components were finally entered into expressions for estimating broad-sense heritabilities of the characteristics measured. These operational heritabilities could be used as part of the prediction formula of the genetic gain to be expected from selection of clones in the field tests. They are based on 4 replicates with 4 ramets each (Sya) and 5 replicates with 3 ramets each (Uddeholm). In the Uddeholm experiment the variance components for clones within groups were taken as appropriate estimates of the genetic variances of the traits.

These estimates from the two field tests were combined in Table 6 in order to find some common features in the differences among the various groups of characteristics. But in the Sya test the estimates range from 0.7 to 0.9 (with only a single exception) and in the Uddeholm test these groups differ only slightly.

It should be noted that these estimates may incorporate large error variances. For instance, tree diameter measured at an age of 12 years yielded a component of variance less than zero, though only three years later it was estimated to be well above zero. The resulting heritability estimates then amount to 0 and 0.55. The growth traits have the lowest average heritability. The number of branches and branch angle possess rather high heritabilities, while in the other traits related to branch habit the estimates are markedly smaller. Stem straightness in both tests yielded relatively large estimates. The number of cones does not have the largest heritabilities in either of the two tests. But with reference to clonal seed orchards, it is clear that decisions on retention or removal of certain clones have genetic implications.

The fundamental difference between the results of the two experiments is due to the

Table 6. Broad-sense heritabilities (clonal repeatabilities) of the traits measured in the two field experiments. Corresponding traits are entered in the same lines of the table.

Sya		Uddeholm	
Trait no.	Heritability	Trait no.	Heritability
a) *Stem dimensions*			
1	0.89		
2	0.88	1	0.36
3	0.90	2	0.39
4	0.90	3	0.44
5	0.60		
6	0.86	4	0.68
7	0.88		
8	0.88	5	0
9	0.89	6	0.55
10	0.89		
11	0.88	7	0.48
12	0.89	8	0.84
b) *Number of branches*			
13	0.82	9	0.59
14	0.85	10	0.56
15	0.90	11	0.96
16	0.82	12	0.83
17	0.88	13	0.81
18	0.90	14	0.87
19	0.75		
20	0.80		
21	0.68		
22	0.85		
		15	0.88
c) *Branch morphology*			
23	0.88	16	0.46
24	0.86	17	0.58
25	0.89	18	0.64
26	0.87	19	0.47
27	0.81	20	0.61
28	0.88	21	0.59
29	0.88	22	0.69
30	0.85	23	0.75
31	0.87	24	0.80
d) *Stem straightness*			
32	0.85	25	0.72
e) *Cone counts*			
33	0.87		
34	0.81	26	0.71
35	0.87	27	0.83
36	0.89	28	0.76

fact that both the material and the site conditions differ. But the site conditions alone may have some noticeable though unknown influence on the size of such quantities, as Burdon (1971) found in a series of clone experiments.

4.4 **Correlations of clonal means**

4.4.1 *Sya*

The various assessments of tree dimensions are closely and positively inter-correlated. The same is true of the various branch counts. However only the numbers of branches formed at ages of 5 to 9 years (traits nos. 13 through 15) are positively correlated to tree height, leader growth and diameter (r ranging from 0.4 to 0.7); the branch counts in later years (traits nos. 16 through 22) are only weakly correlated with tree dimensions. This change may be explained by the presumable onset of competition in the plantation, although it may just as well be purely coincidental. Clones with more rapid height and diameter growth not only had more numerous branches; their branches were longer and thicker, as was stated for seedling progenies by von Wedel et al. (1968). More interest should be paid to the relationship between tree height and bole straightness. In many instances taller trees are poorly rated for straightness, while short and stunted trees leave the observer with a better impression. In the Sya test this was all but confirmed by $r = -0.51^{*}$ (see Figure 1). Clones with fine branches unfortunately had less straight stems (Figure 2). It cannot be decided whether the correlation coefficient of $r = -0.70^{***}$ has some importance for breeding, or whether, even in the absence of topophysis, these early observations reflect the conditions in trees approaching harvesting age.

The correlations among average cone numbers produced by the clones in different years support the hypothesis of their differential fertility. With two exceptions the coefficients combined in Table 7 are all significant. It may be noted that they are largest when the number of mature cones

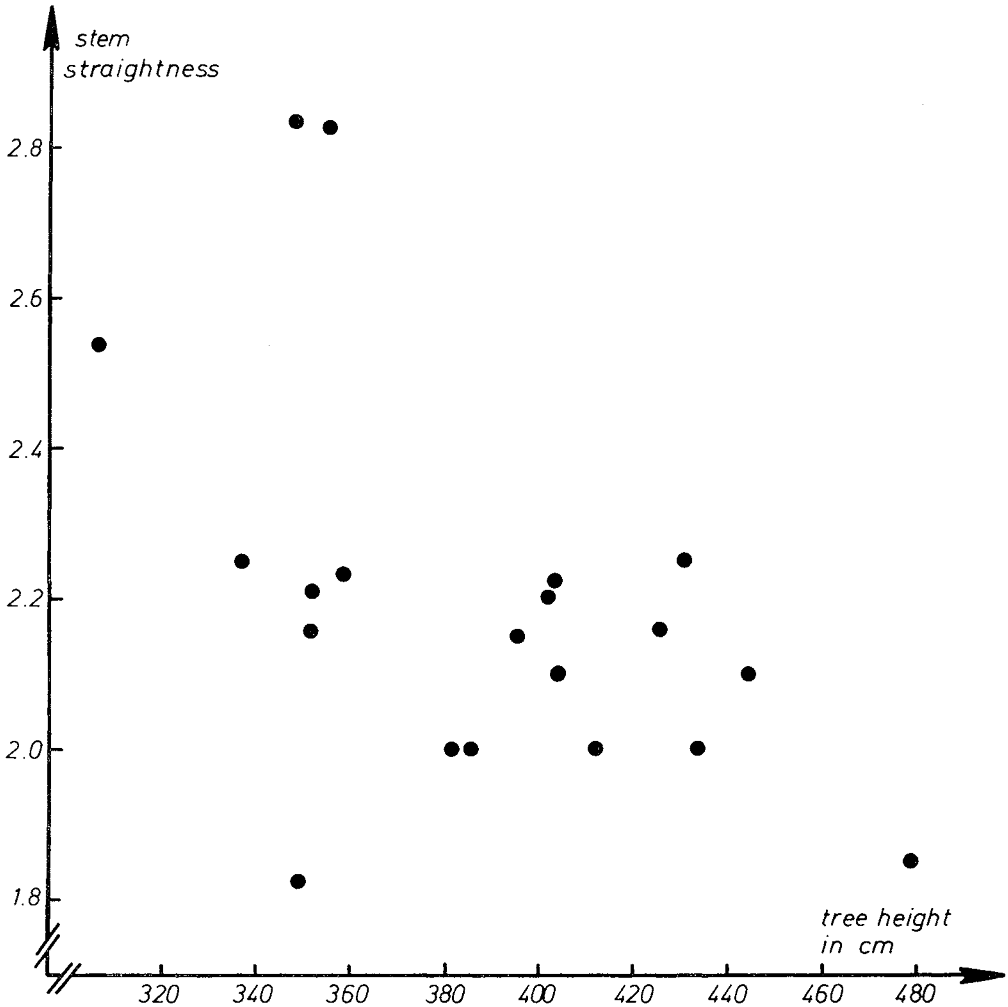

Figure 1. Stem straightness plotted against tree height at the age of 11 years in the Sya experiment.

Table 7. Correlations between four cone counts made in the Sya experiment in different years.

		Cone age	2	1	1
		Tree age	12	12	15
		Trait no.	34	35	36
Cone age	Tree age	Trait no.			
1	11	33	(0.62**)	0.35	0.49*
2	12	34		0.63**	0.73***
1	12	35			0.44

The estimates in parentheses refer to inventories of one and the same cone crop made at the age of 1 and 2 years.

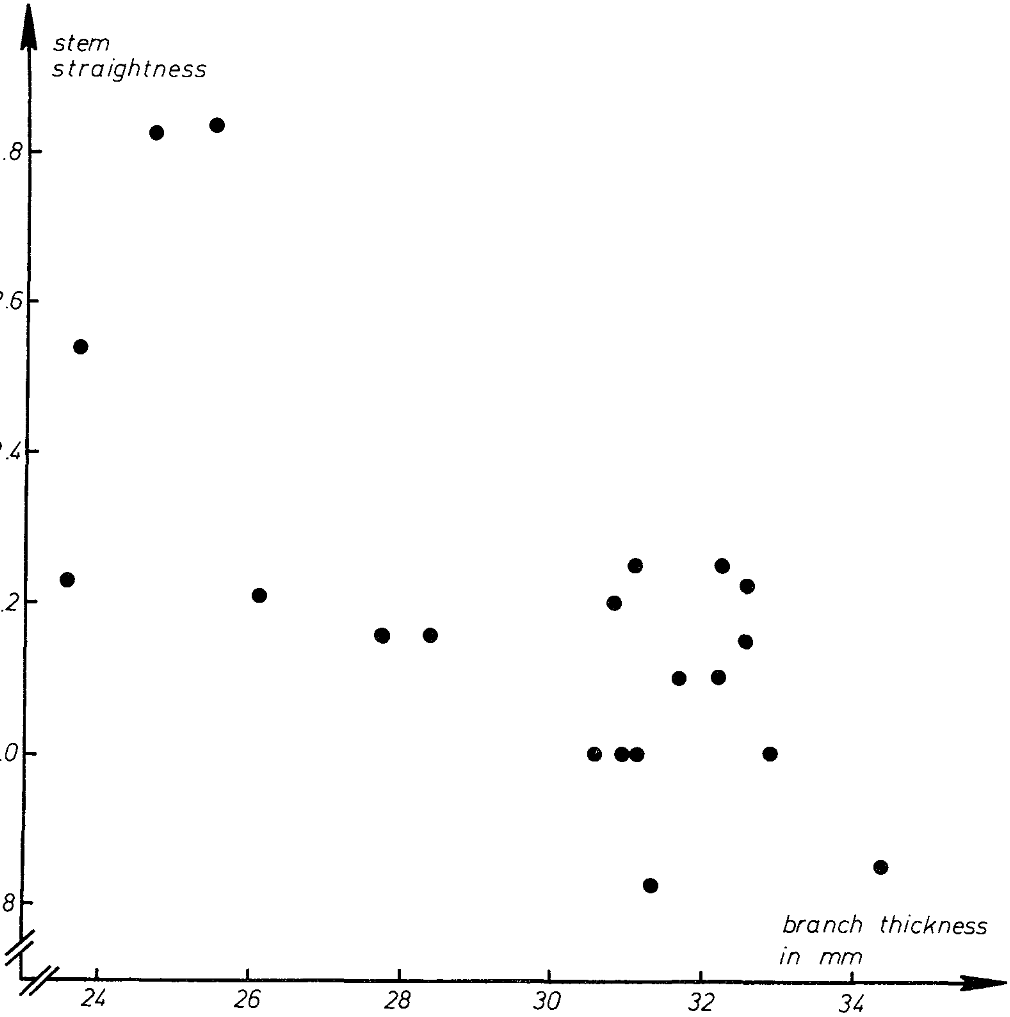

Figure 2. Stem straightness (rated at the age of 11 years) plotted against branch thickness (measured in the 8th whorl from the top at the age of 15 years) in the Sya experiment.

Table 8. Correlations between tree height and the average number of cones produced per tree.

Cone age	Tree age	Clonal means (18 d.f.)	Trees within plots (262 d.f.)
1	11	−0.20	0.28***
1	12	0.38	0.39***
2	12	0.12	0.13*
1	15	0.19	0.44***

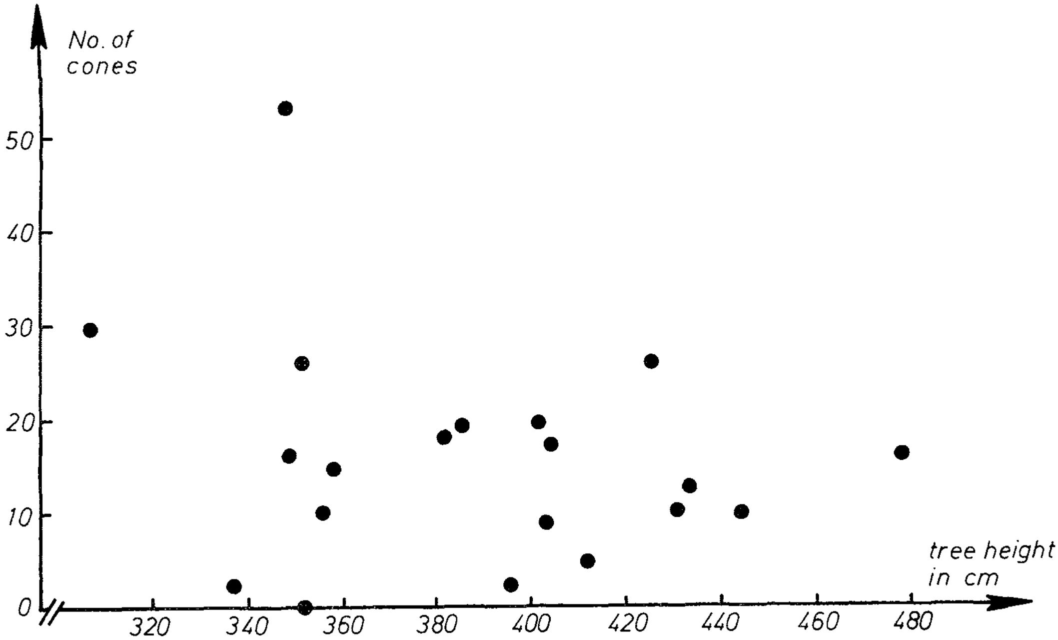

Figure 3. Average number of 1-year-old cones per graft plotted against tree height at the age of 11 years in the Sya experiment.

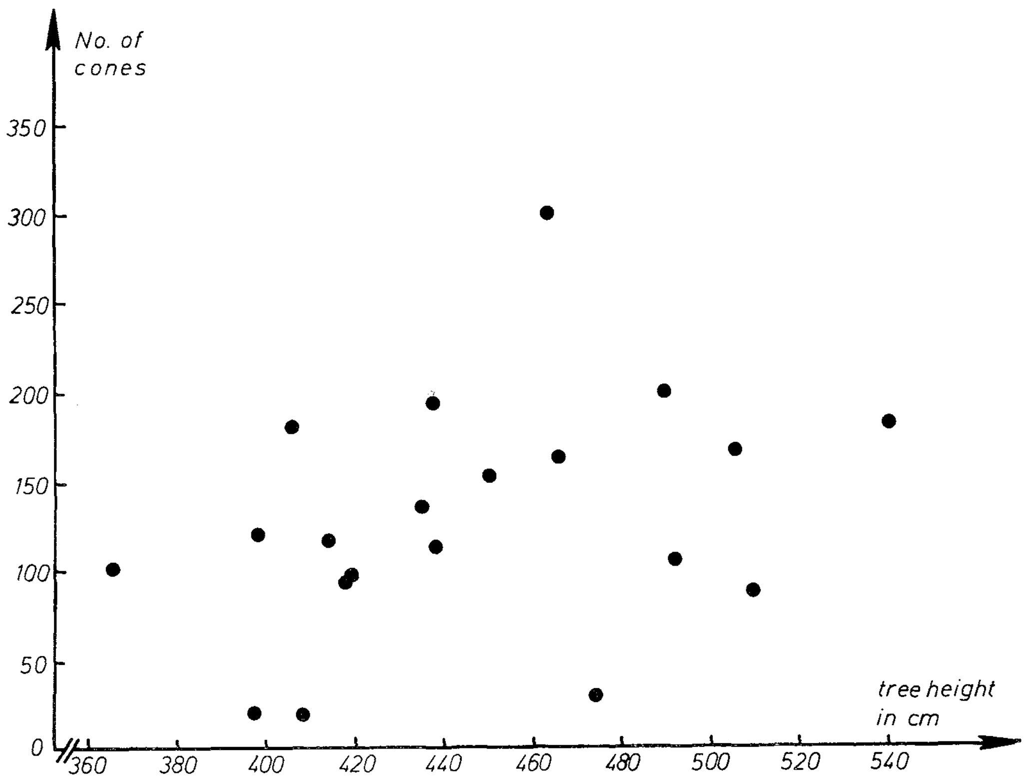

Figure 4. Average number of 1-year-old cones per graft plotted against tree height at the age of 12 years in the Sya experiment.

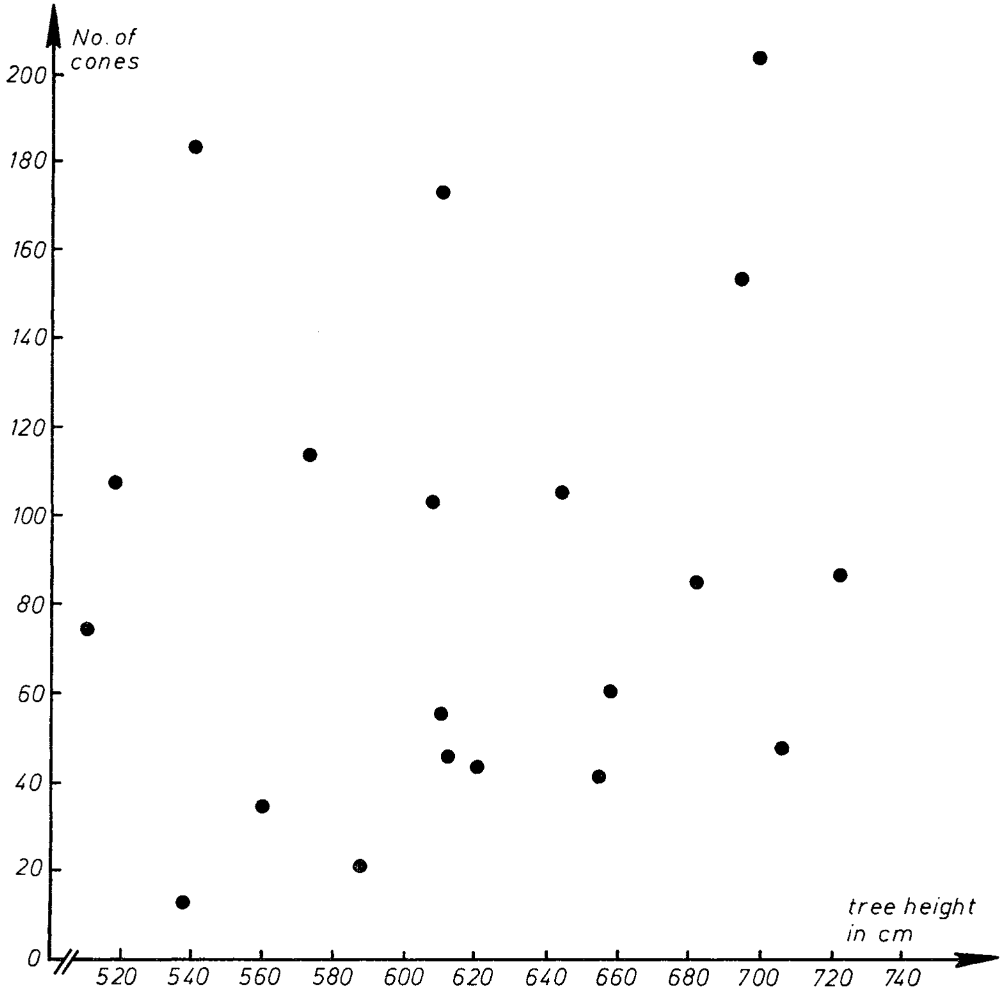

Figure 5. Average number of 1-year-old cones per graft plotted against tree height at the age of 15 years in the Sya experiment.

at the age of 12 years is involved—possibly because of the more precise method of estimation used in this trait. These roughly estimated cone numbers may be poor predictors of the number of viable seeds produced by a ramet of a certain clone (cf. Alfjorden 1972 and Hadders 1972). In addition, a very different pattern of variation may be observed in different years (cf. table 3). But the sole causal explanation for these correlations is the inherent tendency of genotypes to reproduce more or less abundantly.

The correlation of clonal means of the 1-year-old and mature cones at the age of 12 years is 0.63**, for instance. But the respective environmental correlation among

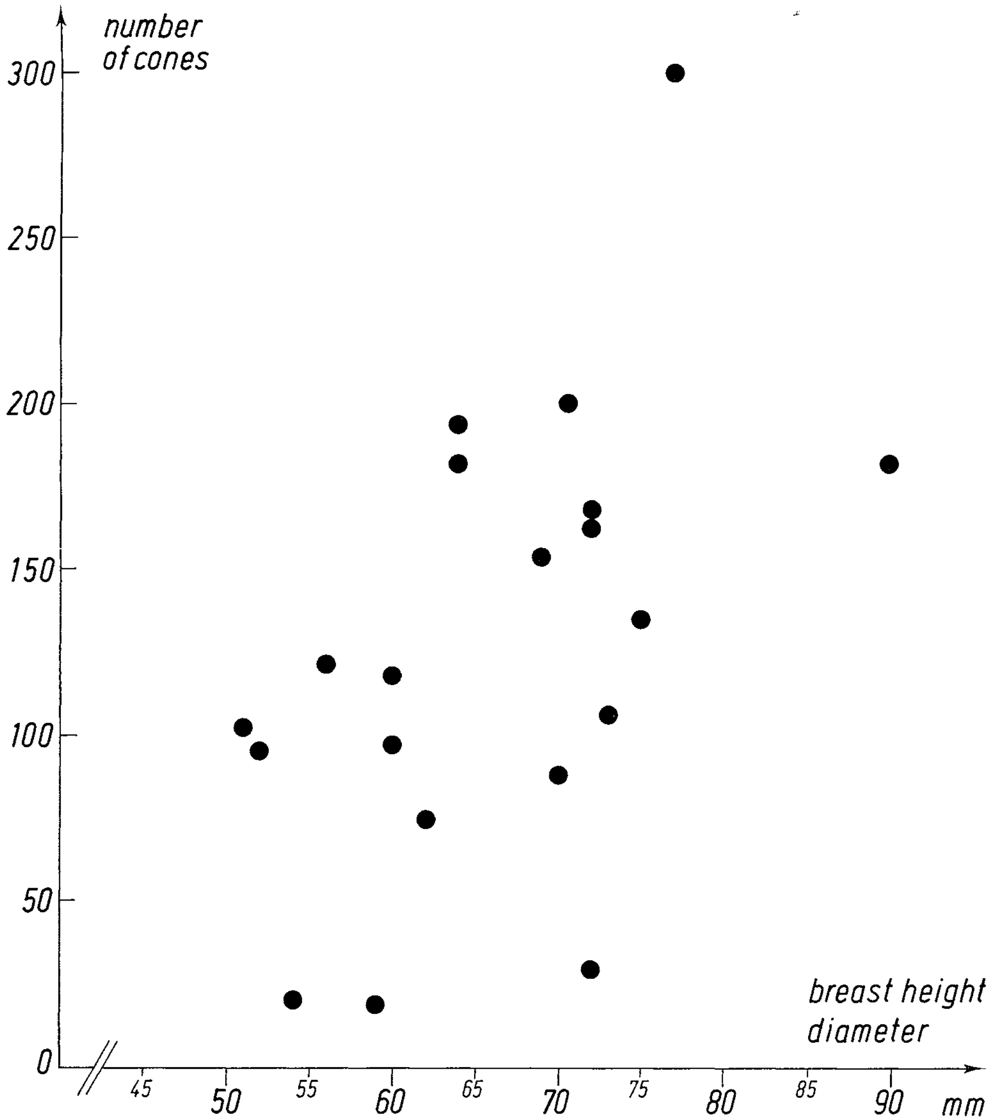

Figure 6. Average number of 1-year-old cones per graft at the age of 12 years plotted against stem diameter at breast height the year before in the Sya experiment.

ramets within plots is only 0.20*** (with 262 d.f.), which is within the range of estimates of the environmental correlation at the plot level obtained by Andersson and Hattemer (1975). Furthermore, the correlations among clonal means of cone numbers are not caused by any variation in the average size of the trees among clones. It is true that more cones are borne by the taller trees of a clone, but, as shown in Table 8, this does not mean that clones with faster growth produce more cones. The absence of the latter correlation is also demonstrated by the graphs in Figures 3 through 5. These graphs also indicate the varying magnitude of the variation among clones.

	Vågbacken		Bybergsåsen	
Z-trees	group 1	○	group 5	□
Y-trees	group 2	⊕	group 6	⊞
X-trees	group 3	◐	group 7	⧅
N-trees	group 4	●	group 8	■
plus-trees	group 9	▲		

Legend to figures 7 through 13.

One may question whether the size of a tree is best measured by its height. Breast height diameter is an equally suitable yardstick. As shown in Figure 6, there is a moderately high correlation between this variable and the cone number. However it is not clear whether diameter, crown size or the number of shoots that may carry flowers is causal at all; the dimensions of a tree of a given genotype do not necessarily govern its ability to flower.

4.4.2 *Uddeholm*

In this test, the trait tree dimension is also strongly correlated with the trait branch

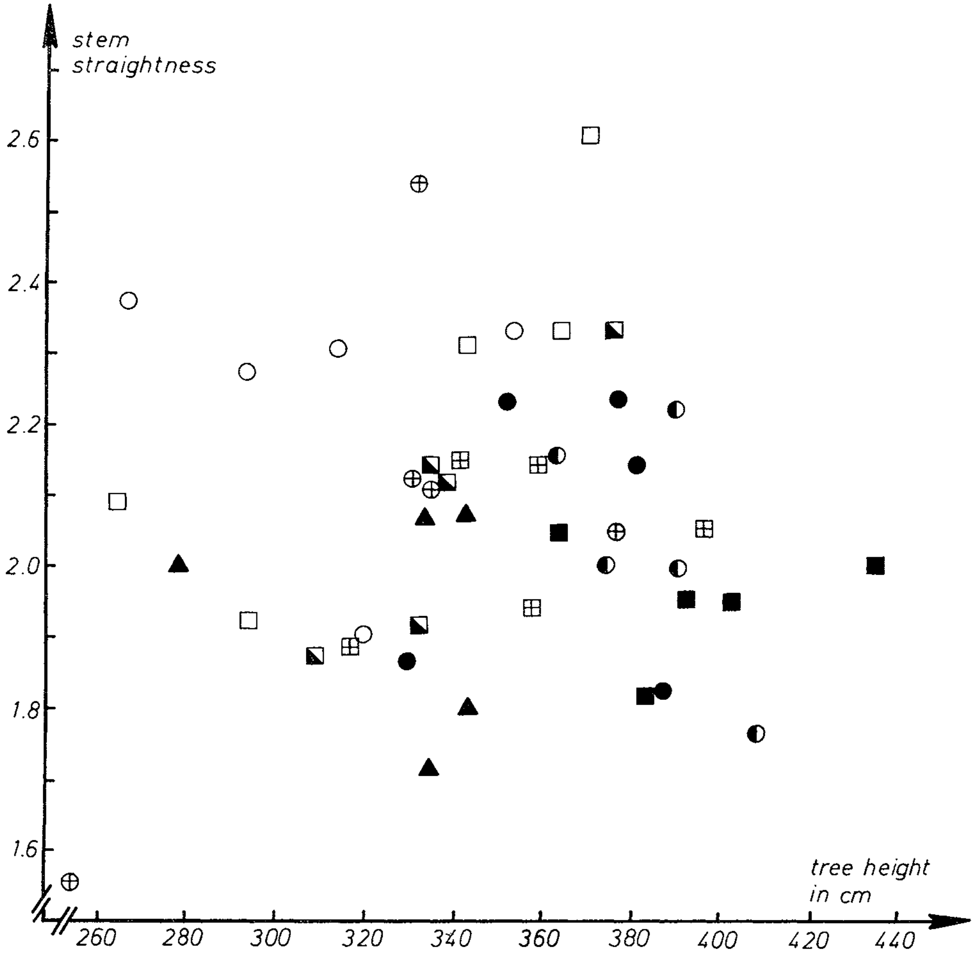

Figure 7. Stem straightness plotted against tree height at the age of 12 years in the Uddeholm experiment.

count. As in the Sya test, the early branch counts (traits nos. 9 and 10) and the sum of four whorls (trait no. 15) are the only ones in this group that are correlated with tree dimensions.

But unlike the Sya test, other conditions were found for straightness.

Figure 7 does not indicate any correlation between the average tree height of the clones and their straightness. The sign of the relationship between straightness and branch thickness is even reversed (Figure 8), the pertinent correlation coefficient being r = 0.31*.

The average cone numbers counted on three occasions are very closely correlated.

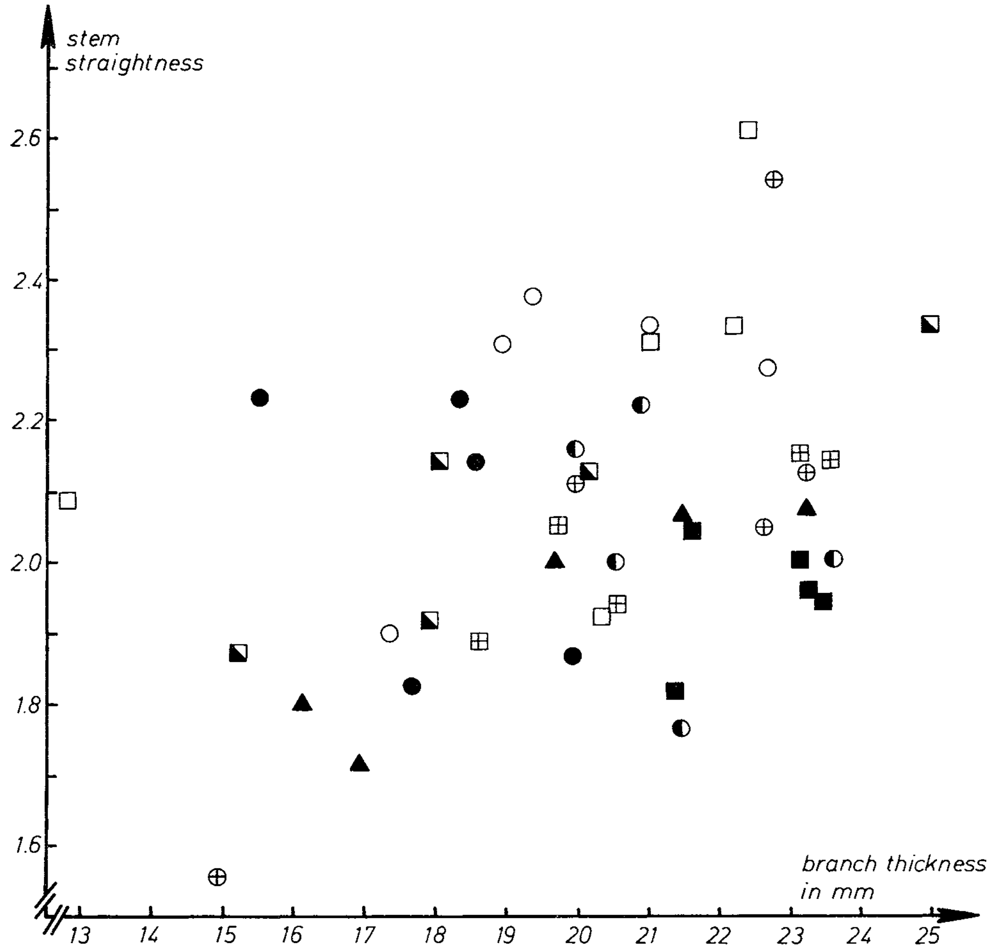

Figure 8. Stem straightness rated at the age of 12 years plotted against branch thickness (measured in the 7th whorl from the top at the age of 15 years) in the Uddeholm experiment.

Because of the skewed distributions, the rank correlations are used as estimates; these are between 0.7 and 0.9 and are highly significant.

As in the Sya test, this lasting tendency of the clones to produce small or large numbers of cones cannot be explained by their height growth (Figure 9). But nor in this case can it be explained by the diameters (Figure 10). The pertinent correlation coefficient of 0.23 is not significant.

An attempt to relate the abundance of the cone crop to the measure of branchiness, i.e. trait no. 15, revealed no such dependence of the number of cones, the correlation coefficients all being smaller than 0.2.

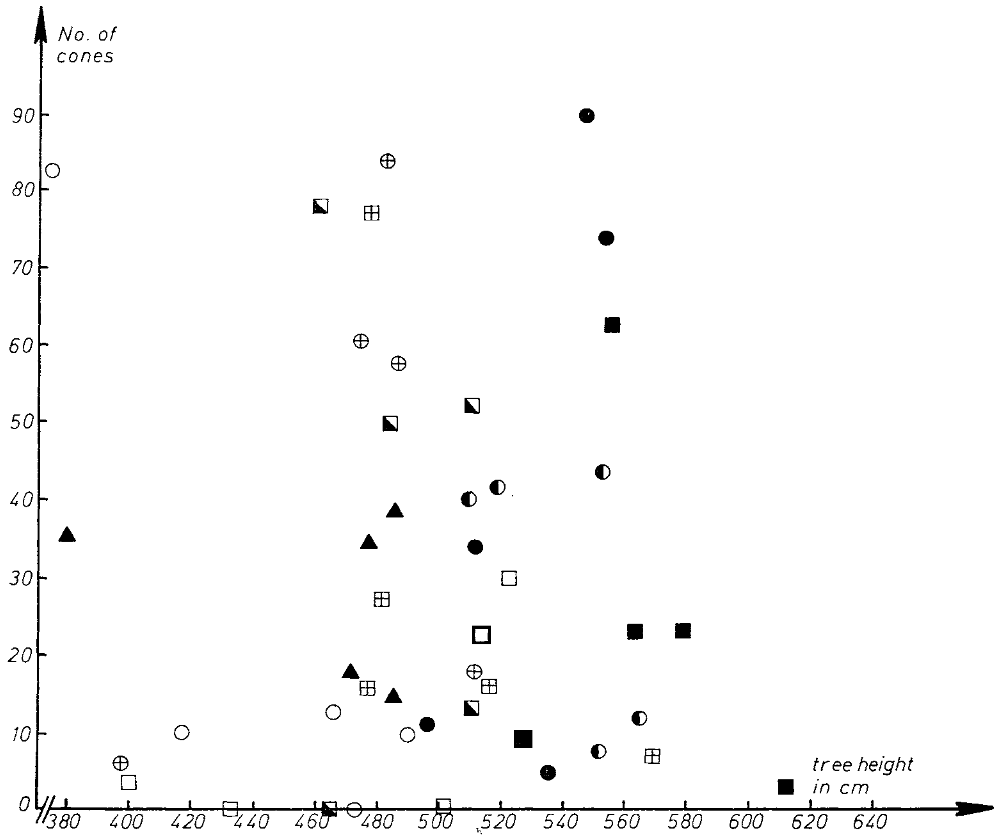

Figure 9. Average number of 1-year-old cones per graft plotted against tree height at the age of 15 years in the Uddeholm experiment.

The graphs in Figures 11 through 13 are presented here to illustrate this and also the markedly different variation pattern among the clonal means.

4.5 **Correlations between ortets and ramets**

4.5.1 *Sya*

If variables measured in the ortet trees reveal a linear dependence upon age, they have to be corrected for this. This condition normally has to be expected in such tree dimensions as height and diameter (pro-

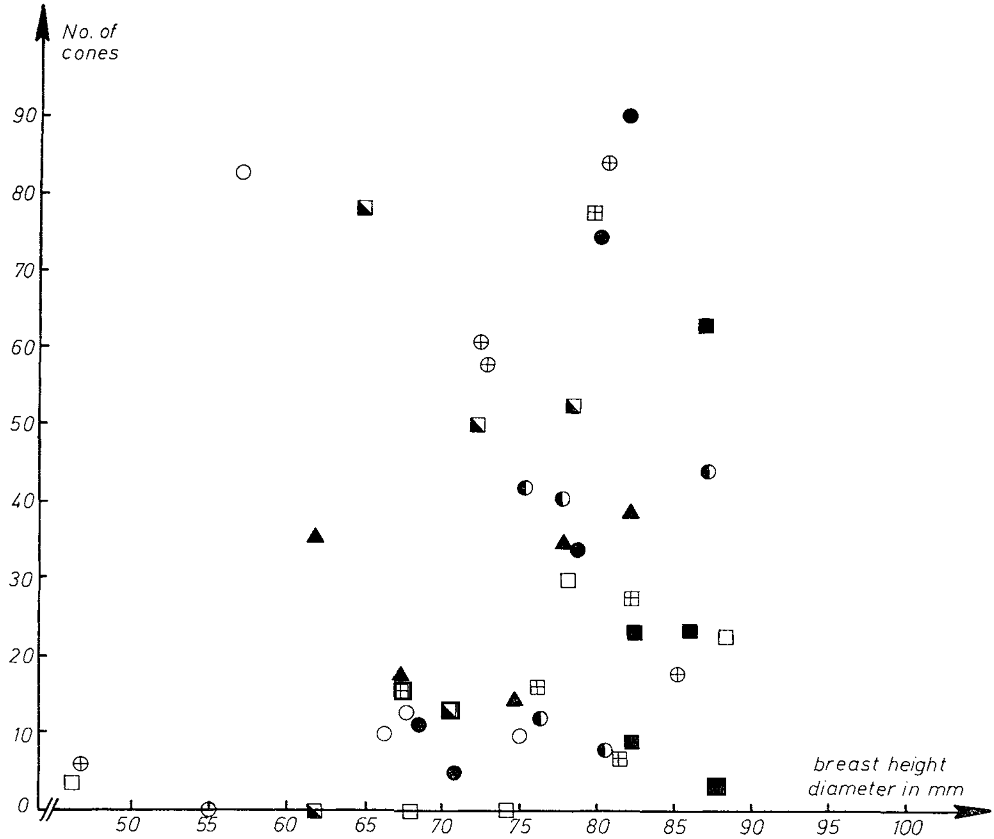

Figure 10. Average number of 1-year-old cones per graft plotted against breast height diameter at the age of 15 years in the Uddeholm experiment.

vided that the range of variation of age is not too wide). However, in the trees sampled, height was uncorrelated with age (r = 0.08). Neither was diameter closely correlated with age (r = 0.37). Therefore no corrections for ortet age were made in estimating the correlations between ortets and clonal means. These correlations were then rather loose (r being about 0.3) and could not be improved (for prediction purposes) by expressing the measurements in the ortet relative to the mean of the nearest three neighbours.

The numbers of branches were uncorrelated between ortets and ramets. In branch length, correlation coefficients ranged between 0 and 0.3. In branch thickness they reached 0.6 and were closest in branch angle

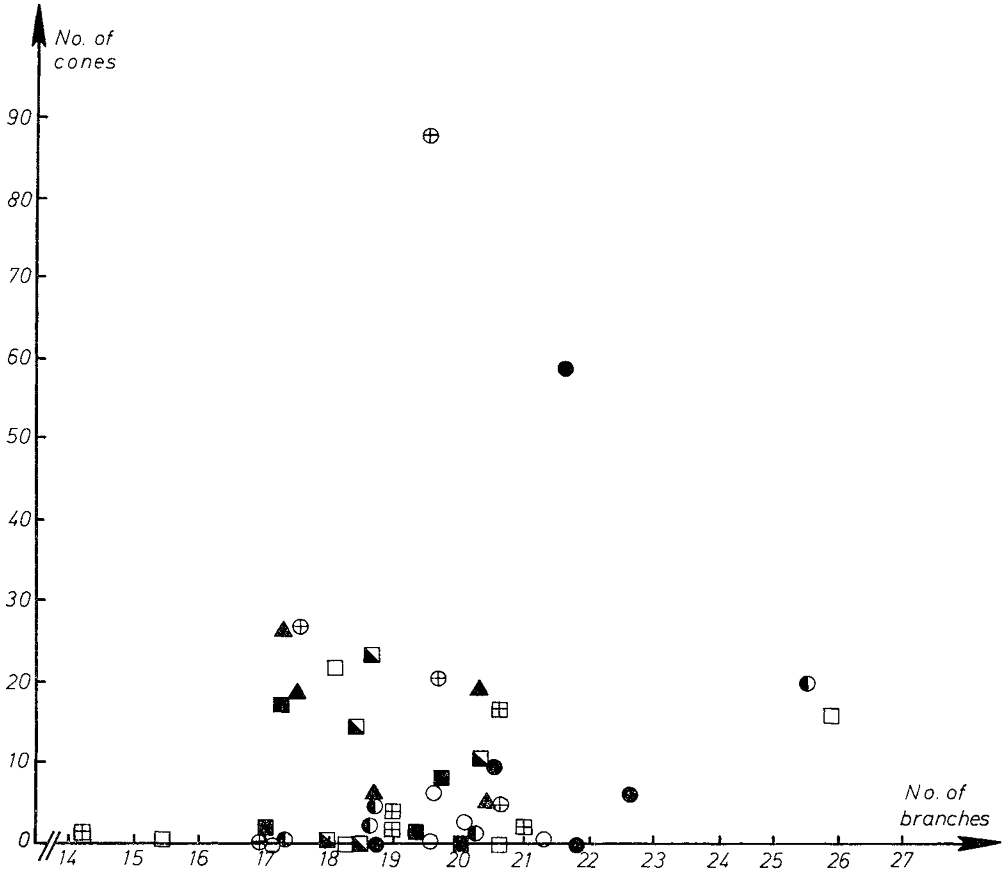

Figure 11. Average number of 1-year-old cones per graft (at the age of 12 years) plotted against the number of branches (summed over four whorls) in the Uddeholm experiment.

(r ranging from 0.4 to 0.6). It appears that only in the latter trait can the conditions in the ramets be inferred from the ortet. Similar results were reported by Nilsson (1956), who obtained correlations of r = 0.4 for both branch thickness and branch angle. In a more recent study, Blomqvist (1975) reported much closer correlations in a clone trial 10 years older than the present one.

4.5.2 *Uddeholm*

As stated above, the absence of a variance component between groups provides some information on the relationships of tree quality in ortets and ramets. Besides this, the correlations among ramets and ortets were also computed irrespective of their group membership. The five trees of group

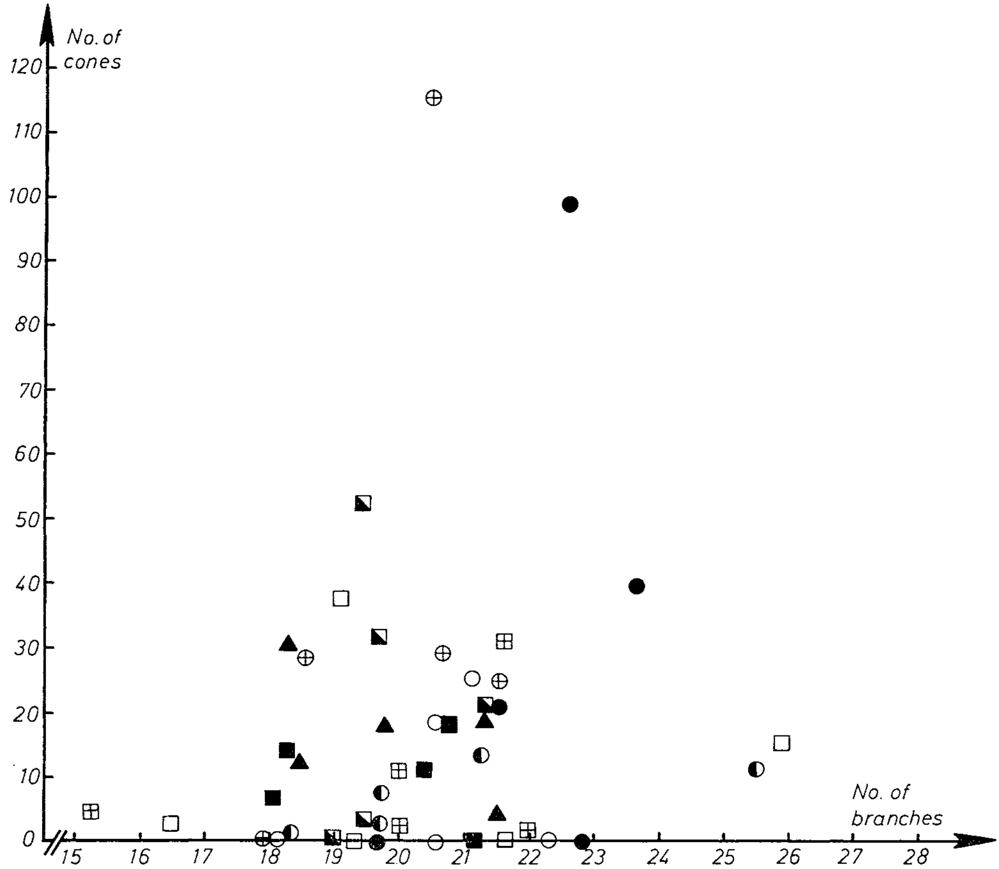

Figure 12. Average number of mature cones per graft (at the age of 12 years) plotted against the number of branches (summed over four whorls) in the Uddeholm experiment.

9 had to be excluded from the material because of their much greater age. Between 39 of the ortets and the means of their clonal offspring, the correlation in height and diameter was about 0.4. This estimate was a little higher after correction for the obviously linear covariation of age, the partial correlation coefficients being about 0.5.

Unlike in the Sya experiment, the numbers of branches showed some correlation (r ranging from 0.1 to 0.6) between ortets and ramets. This increase may easily be explained by the lower age of the ortets and

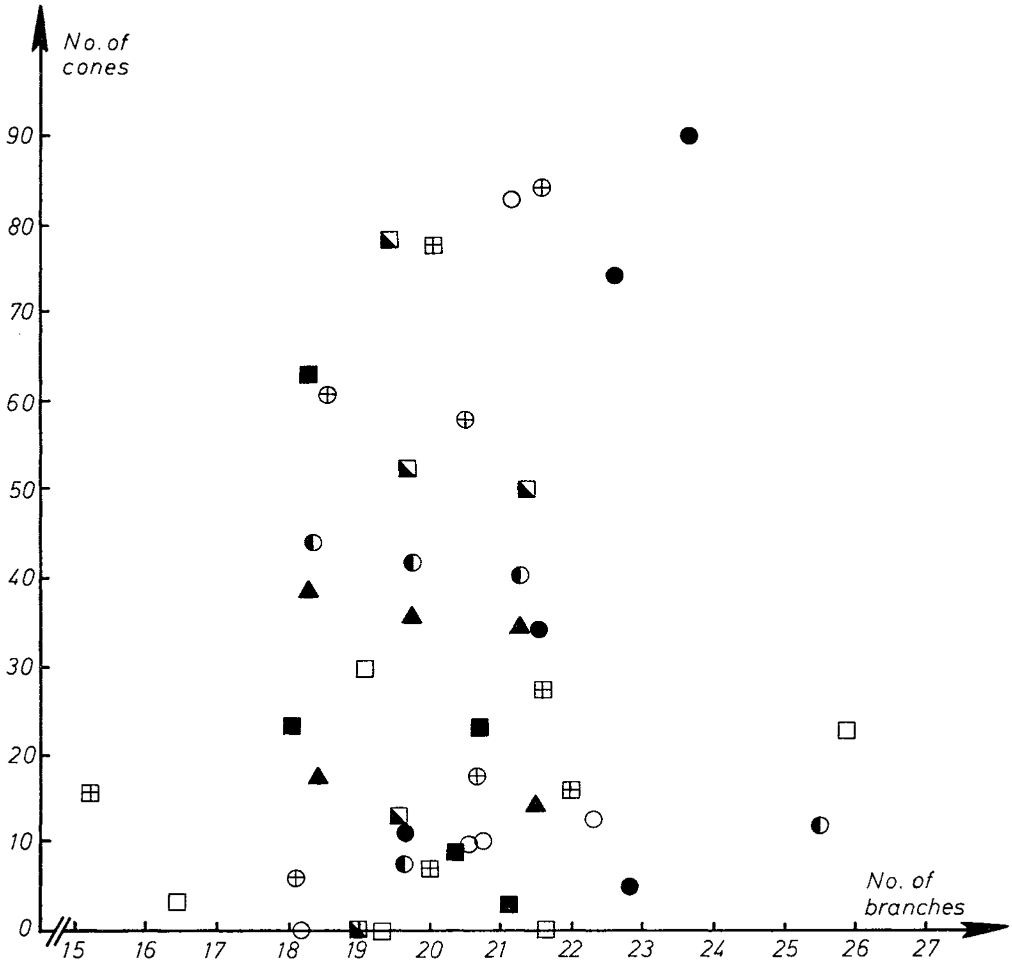

Figure 13. Average number of 1-year-old cones per graft (at the age of 15 years) plotted against the number of branches (summed over four whorls) in the Uddeholm experiment.

the greater precision in assessing this trait. Branch thickness in the clones was uncorrelated with that of the ortets; branch length had coefficients of 0.3 and less. However, branch angle in the ramets and ortets possessed rather close correlations between 0.5 and 0.8.

Though a quantitative-genetic theory was worked out by Touchberry (1960), the study of these relationships was not further pursued, since the genetic and environmental causes of variation in the stand are unknown and the nature of this interplay is not yet fully understood.

Sammanfattning

Syftet med två klonförsök med tall har varit studiet av utveckling, blomning och samband mellan klonernas och ursprungsträdens kvalitets- och tillväxtegenskaper.

Försöket vid Sya i Östergötland omfattar 20 kloner om 20 ympar per klon, försöket på Rävtallheden vid Uddeholm 45 kloner om 25 ympar per klon. Ursprungsträden till klonerna i sistnämnda försök indelades i fem fenotypklasser.

Resultaten visar att miljövariationen inom försökslokalen i båda fallen är den största variationskällan. Dessutom föreligger utpräglad variation mellan kloner i ekonomiskt betydelsefulla egenskaper, dvs. ymparnas dimension, kronmorfologi och kottantal. Upprepningsförmågan vid observationer i en och samma klon är i regel hög i Syaförsöket, däremot skattades betydligt lägre värden vid Uddeholm. Sambandet mellan klon och ursprungsträd undersöktes i Sya med hjälp av korrelationsanalys, i Uddeholm genom variansanalys och uppskattning av varianskomponenten mellan fenotypklasserna. Sambandets styrka varierar från egenskap till egenskap men är i allmänhet inte så stark som angivits i jämförbara undersökningar. Endast grenvinkeln hos ymparna kan förutsägas med måttligt stor noggrannhet med ledning av ursprungsträdets värde. Skillnader mellan klonernas kottproduktion och dess samband med ymparnas växtegenskaper påverkar den vinst som kan uppnås i fröplantager.

References

Alfjorden, G. 1972. Pollineringsförsök på tall. — Föreningen Skogsträdsförädling — Institutet för Skogsförbättring, Årsbok, Uppsala, pp. 81—86.

Andersson, E. 1965. Cone and seed studies in Norway spruce (Picea abies (L.) Karst.). — Stud. For. Suec. 23, 214+XLI pp.

— 1966. The selection of plus trees in Sweden. — Sumarski list: 21—40.

Andersson, E. & Hattemer, H. H. 1975. Growth and flowering of 'primary' and 'secondary' grafts of Scots pine. — Silvae Genetica 24: 49—54.

Arnborg, T. & Hadders, G. 1957. Studies of some forestry qualities in clones of Pinus silvestris. — Acta Horti Gotoburgensis 21: 125—157.

Blomqvist, S. 1975. Samband plusträd—kloner—avkommor hos tall. — Institutet för Skogsförbättring, Årsbok, Uppsala, pp. 171—194.

Brown, I. R. 1970. Premature cone loss in grafted clones of Scots pine. — IUFRO Section 22, Sexual reproduction of forest trees, Proc. Meeting in Varparanta, 15 pp.

— 1971. Flowering and seed production in grafted clones of Scots pine. — Silvae Genetica 20: 121—132.

Burdon, R. D. 1971. Clonal repeatabilities and clone-site interactions in Pinus radiata. — Silvae Genetica 20: 33—39.

Eriksson, G., Jonsson, A. & Lindgren, D. 1973. Flowering in a clone trial of Picea abies Karst. — Stud. For. Suec. 110, 45 pp.

Hadders, G. & Åhgren, A. 1958. Kott- och fröproduktion samt frökvalitet hos 12-åriga ympträd av tall. — Svenska Skogsvårdsföreningens Tidskrift 56: 455—468.

Hadders, G. 1972. Kontroll av inkorsningen i en tallplantage. — Föreningen Skogsträdsförädling — Institutet för Skogsförbättring, Årsbok, Uppsala, pp. 120—139.

Harvey, W. R. 1960. Least squares analysis of data with unequal subclass numbers. — USDA, Agric. Res. Serv. ARS-20-8, 158 pp.

Henderson, C. R. 1953. Estimation of variance and covariance components. — Biometrics 9: 226—252.

Jonsson, A., Ekberg, I. & Eriksson, G. 1976. Flowering in a seed orchard of Pinus sylvestris L. — Stud. For. Suec. 135, 38 pp.

Nilsson, B. 1956. Kvalitets- och produktionsförhållanden i ett klonförsök av tall. — Svenska Skogsvårdsföreningens Tidskrift 54: 61—74.

Schmidt, H. 1970. Versuche über die Pollenverteilung in einem Kiefernbestand. — Diss. Göttingen, 60 Seiten.

Touchberry, R. W. 1960. Forest trees as a population of genotypes. — Proc. 2nd Central States For. Tree Impr. Conf., Franklin Park, Ill., 14 pp.

von Wedel, K., Zobel, B. J. & Shelbourne, C. J. A. 1968. Prevalence and effects of knots in young loblolly pine. — For. Prod. Jour. 18: 97—103.

Wellendorf, H. 1970. Resemblance in height growth between original trees and clones of Scots pine. — Forest Tree Improvement 1: 25—45.