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HARVEST INDEX IN A PROGENY TEST OF SCOTS PINE WITH REFERENCE TO THE MODEL OF SELECTION

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Seloste

SATOINDEKSIN SOVELTAMISESTA VALINTAJALOSTUKSEEN MÄNNYN JÄLKELÄISKOKEEN TULOSTEN PERUSTEELLA

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A 16-year-old Scots pine progeny test, based on full-sib families was measured for harvest index and for a number of other yield components. It was found, that harvest index is a highly heritable trait and that a number of yield components are positively correlated with it.

It is suggested, that harvest index and tree ideotypes should be the basis of selection in cultivated trees. It is emphasized, that an integrated approach to tree improvement including silviculture, soil science, industrial and economic constraints and tree breeding is a prerequisite for maximal response.

1. INTRODUCTION

Partitioning of the phytomass to different parts or organs of the plant has been shown to be a major cause for yield increases in agricultural and horticultural plants. It can be shown, that plant breeding has in many cases caused a change in the allometric growth of the plant. Often this effect has been unintentional, it has been an effect following selection for yield in a plant stand. However, since the early sixties there has also been deliberate selection for high harvest index (Donald 1962).

The total phytomass synthesized per unit area and time is fairly constant for a wide range of plants. The inherent rate of photosynthesis appears to be difficult to improve genetically once the photosynthesizing canopy has reached complete coverage, i.e. the leaf-area-index (LAI) has reached a critical upper level. This level is reached at different LAI-values by different plant species due to conditions of light extinction within the stands.

Many conifers reach LAI-values that are far above saturation, in which case environmental factors become limiting to phytomass yield. Increased respiratory load or direct decrease of available carbondioxide within the stand at times of highest photosynthesis, water stress, temperature stress and lack of essential nutrients may all interact in causing limitations to phytomass yields. Cannell (1978) notes, that LAI-values of above about 10 give very little increases in gross photosynthesis of the most efficiently architectured grass swards at temperate latitudes. He argues, that LAI-values of 12–14 may be about optimal in conifer canopies.

Under conditions prevailing in south-central Finland, a dry matter yield of maximally 15 tonnes per hectare and year, corresponding to a fresh weight of about 37 tonnes seems possible in forest stands. This is an estimation done on the basis of the IPB project "Photosynthesis and productivity in different environments" (Wassink 1975). Of this mass, approximately 40 % can be partitioned as useful wood. Converted to volume of wood it corresponds to about 18 m^3. We believe that this figure is close to a maximum under our conditions. Clearly such values can be reached only under very favourable conditions and only during a short period (10–20 years) of the rotation age.

However, let us look closer at the figure of 40 % of useful wood. Can that value be changed upwards? Can we change the harvest index (HI) of our trees? By genetic means? By silvicultural means? It has been shown, that yield increases of many important agricultural crops have been achieved through the rebuilding of the whole plant so that a larger part of the phytomass is translocated from the source of synthesis in the green parts to the sink constituting the useful part of the plant; the stem, the grain or the tuber. The change in harvest index during this century has been drastic in many cases. Thus wheat has gone from a harvest index of 0,32 to 0,49 in green revolution ideotypes. Beans have changed from 0,55 to 0,67 and potato from 0,50 to as much as 0,84. The change has resulted in plant ideotypes that produce a maximum yield in dense cultivated stands. Characteristic of such ideotypes is their lack of competitive ability in many cases. The spreading "competitive" type is favoured by natural selection, thus non-competitive types are usually succumbing at an early stage of development.

A plant that best meets human needs is one that produces a maximum amount of useful material. Generally speaking it is a non-competitive phenotype that can be grown at a high density and yet produce a maximum yield. A minimum amount of phytomass should be lost in wasteful competition by a spreading, highly branched phenotype.

The concept of harvest index (HI) was first introduced by Donald in 1962. Since then it has become a widely used concept in agricultural crops. The harvest index refers to the proportion of the total dry matter produced that is harvested:

$$HI = \frac{\text{Harvested Dry Matter}}{\text{Total Dry Matter}}$$

In trees, where dry matter evaluations are cumbersome to undertake, a useful approximation is either harvested volume to total volume, which is also difficult to assess, or harvested fresh weight to total weight. The concept is not novel to forest scientists. In German forest research litterature the concept of "Schaftholz" has been used in forest biology (Burger 1941). We believe that it may become as important in tree breeding as it has been in many common agricultural crops due to the fact, that the useful part of a tree is easily defined and measured.

In assessing harvest index in trees the roots have usually to be excluded due to practical measurement problems. Naturally this introduces an error to harvest index measurements which may be of considerable importance. We have almost no information available at the moment about the genetic control of root shape in trees. Of particular interest would be the information whether or not the shape of root systems are covariant with crown ideotypes or branching characteristics. We expect root systems to be highly influenced by the environment, i.e. edaphic conditions, perhaps even more so than some branch characteristics like thickness. However, just as branch angle has been shown to be rather highly heritable so we believe is also root branching angle or general root-system "habitus".

It should be mentioned that phenotypic selection has all the time favoured trees with a high harvest index, even though this special term has not been applied. This report on harvest index in a Scots pine progeny test is an attempt to quantify the selection of qualitatively superior trees. We have in addition measured a number of tree quality characteristics which we hope will further explain the complexity of harvest index.

In fact Raulo measured and calculated bole-branch ratios for birch plus tree progenies in 1979. In addition, several Finnish and foreign studies, concerning whole-tree utilization, stand structure and biomass production, have dealt with the distribution of the produced biomass into stem wood, branches and leaves (needles) in such a way that the results can be used for calculation of harvest index estimates (e.g. Ovington 1957, Hakkila 1971, Kanninen et al. 1979, Albrektson 1980).

2. MATERIAL AND METHODS

The Scots pine progeny test No. 346 from which all information in this study is retrieved is located in Hausjärvi, South Finland (lat. 60°45′, long. 25°02′, alt. 90 m a.s.l.) (Fig. 1). The progeny trial is owned by the Finnish Central Forestry Board Tapio. Controlled crosses between plus tree clones in seed orchard No. 17 (planned in 1954 by Max. Hagman) were done in 1965 and 1966 by P. M. A. Tigerstedt. The mating design and the field layout was done by Tigerstedt.

The field trial was planted in 1969 on former fieldland using 2 + 0 bare-rooted plants. A preliminary study on height growth heritability has been published in 1969 on two year old seedlings (Tigerstedt 1969). Totally the trial includes 68 full-sib families from a factorial mating design of 4 pollinators and 22 maternal clones. Thus 20 combinations are missing due to the fact that flowering was almost nil in some clones.

The total area of the trial is 2,45 hectares. Plants are spaced 2,5 × 2,5 meters, plots include 9 plants. There are 7 replications and the total amount of plants in the trial is 3 924. Measurements in the trial have been done on 5 occasions. In 1982 individuals were sacrificed in order to make measurements on harvest index. Simultaneously a number of quality traits were also measured. The report given here is based exclusively on 1982 measurements when the trees were 16 years old from seed. We observed in 1982 that 80 % of the original planting was alive, some plots had been lost due to construction of an electrical powerline. In spite of minor rust contaminations trees looked exceptionally healthy and the trial was classified as being in excellent condition with very little natural damage occurring.

The aim of the investigation was to make reliable computations on harvest indices and related characters. In order to accomplish highest possible exactedness an orthogonal 10 × 3 complete factorial was delimited in the trial. Also it was necessary to delimit the amount of harvest index measurements due to the excessive amount of work involved and due to the fact, that we wish to save the trial for future measurements; exact measurements on harvest index means that trees must be cut.

Harvest index was measured from only one systematically selected tree per plot, i.e. the center tree in a 3 × 3 plot. This was done in 5 of the 7 replications. Thus 30 × 5 = 150 trees were sacrificed, 5 full-sibs per family. Characters related to harvest index were measured in the same plots by selecting systematically 3 trees diagonally across the plot. Thus this part of the material comprises 450 individuals, 15 per full-sib family. The two replications that were left out were incomplete due to powerline constructions. Characters related to harvest index were measured for growth and quality parameters. Prior to numerical measurements a visual estimate of the general quality of the tree was made. The purpose of this estimate was to find out, if a fast visual classification can eliminate some of the more elaborate measurements of quality. In this context however, no effort was done to compare the different modes of measurement. By visual inspection tree injuries and other unpredictable external factors affecting measured characters were also eliminated.

Harvest index (HI) was determined by weighing separately the stems and the total fresh weight of branches including needles:

$$HI = \frac{(SWFW)}{(BFW) + (SWFW)}$$

SWFW = stem wood fresh weight
BFW = branch fresh weight including needles

However, we introduce here an error. The complete stem should actually be partitioned so that only merchantable wood is included in the numerator while the rest of the stem is included in the total phytomass denominator. The problem here is obvious; at the age of 16 years, practically no individual in the progeny test has yet reached merchantable size. We believe however, that quality measurements, including tapering and branching characteristics may be correctly assessed at this age.

It was obvious, that harvest index is no indicator for total phytomass yield. Thus in addition a relative yield was computed on the basis of family means (5 stems per full-sib family). These means were compared to the trial grand mean given a mean stem value of

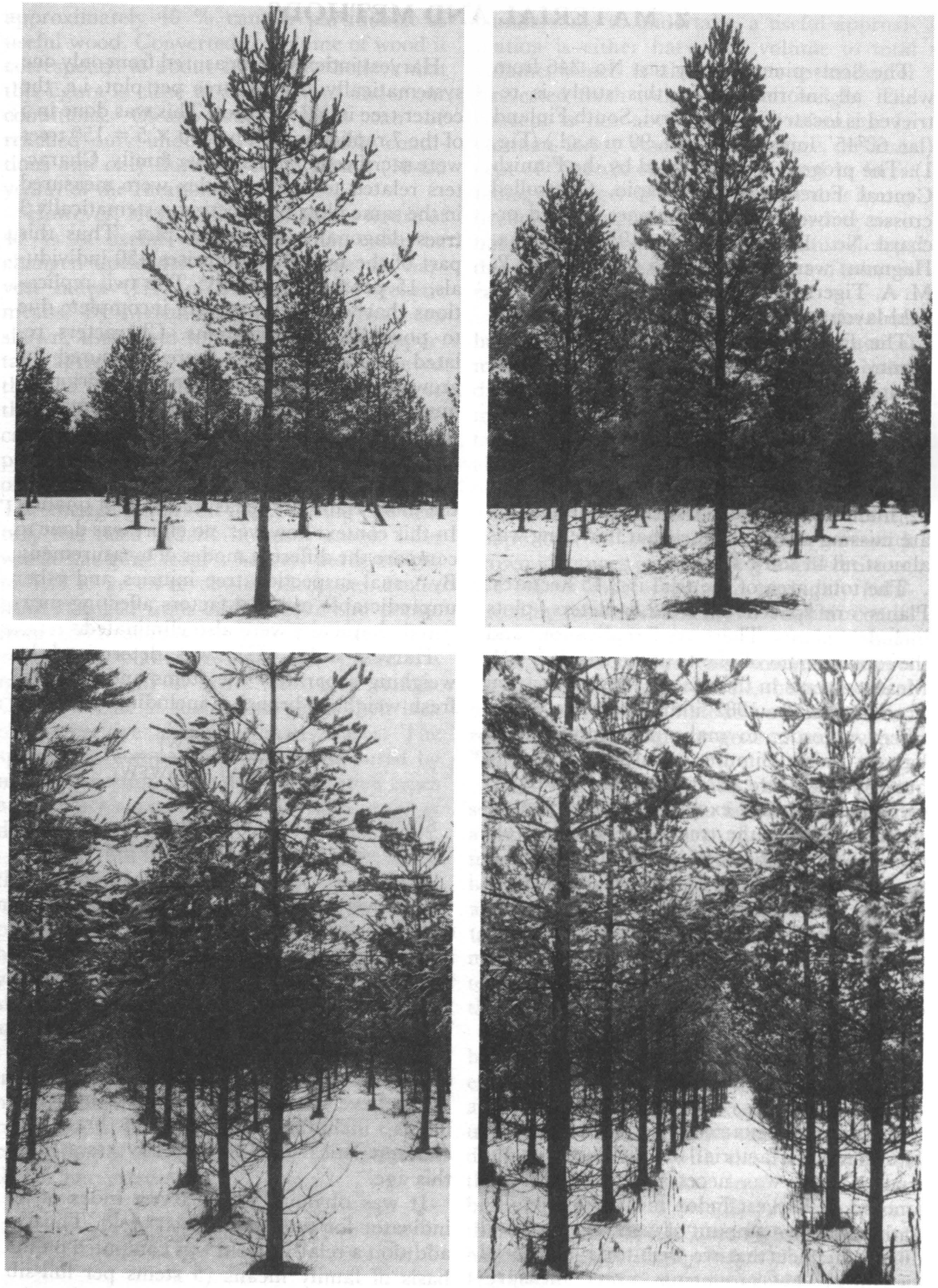

Fig. 1. Examples of clones in seed orchard No. 17 and their progenies in test No. 346. Upper left: Clone E 468. Upper right: Clone E 79. Lower left: Progeny E 468×E 80. Lower right: Progeny E 79×E 80. Photo T. Nikkanen.

100. Thus an answer was sought to the question whether high yield is correlated positively to high harvest index or whether high yield means strong branch growth and possibly even a low harvest index.

3. RESULTS AND DISCUSSION

31. Harvest index and fresh weight of the stem

The harvest indices of 30 full-sib families evaluated on the basis of 5 trees per family showed a very large variation compared as family means (Table 1). The mean of all families was 0,51 and families ranged from 0,43 to 0,57. Corresponding values for stemwood fresh weight (SWFW) were grand total mean 23,3 and range 18,0–32,2. Thus relative SWFW values ranged from 77 to 138 %. The family having the highest harvest index ranked third in stem wood yield. Generally high harvest index was an indication of high stemwood yield but a few clear exceptions to the rule were also recorded. Thus the correlation computed on family means was positive (r = 0,297) but not significant.

Special attention should be given to the selfed family, E 702 × E 702 (Fig. 2). Not only is it an excellent example what an enormous effect inbreeding has in pine trees, but it also shows, that a high harvest index may not always be correlated to high relative yields. The selfed family is specially marked in Table 1. Due to its very much depressed growth characteristics it is not included in the computations of grand total means given at the bottom of the table. The inbred trees have a fine branching habit as seen in the figure, but the relative yield is only about 1/5:th of the grand total mean. This definitely shows, that extra care should always be taken to avoid inbred seed in collections made from seed orchards. It should be mentioned, that the selfed family is not involved in any of the following statistical computations.

Principally fresh weight is a somewhat inexact measure because possible differences between individuals and families in dry weights may be masked by differences in wood water retention. Thus we set out to undertake a second measurement of harvest index in July 1983 after a long continuous period of warm and dry weather. At this time the material must be considered to have been completely air-dry and in equilibrium with

Table 1. Harvest index and relative yield of 30 full-sib families and one selfing.

Full-sib families		Harvest index		Stem weight kilogram		Family means Relative yield	
Maternal	Paternal	Fresh	Dry	Fresh	Dry	Fresh	Dry
E 636C	× E 80	0,57	0,74	29,8	22,3	128	140
E 468D	× E 80	0,56		32,2		138	
E 636C	× E 702	0,56	0,75	19,4	13,5	83	85
E 636C	× E 736	0,55	0,72	18,2	12,1	78	76
E 731	× E 80	0,55		27,2		117	
E 724	× E 702	0,54	0,75	24,2	17,1	104	108
E 727	× E 702	0,53	0,72	30,2	20,0	130	126
E 731	× E 736	0,53		19,0		83	
E 701	× E 80	0,52	0,73	28,2	18,9	121	119
E 468	× E 702	0,52		21,2		91	
E 727	× E 80	0,52		20,4		88	
E 731	× E 702	0,52		22,0		94	
E 724	× E 80	0,52		29,8		128	
E 727	× E 736	0,51	0,69	25,0	16,8	107	106
E 724	× E 736	0,51		21,0		90	
E 726A	× E 80	0,51		26,6		114	
E 701	× E 702	0,50	0,73	19,6	13,6	84	86
E 468D	× E 702	0,50		19,4		83	
E 361	× E 702	0,50		26,8		115	
E 708	× E 702	0,50		18,8		81	
E 468D	× E 736	0,49	0,64	18,0	11,1	77	70
E 361	× E 736	0,49		18,8		81	
E 708	× E 80	0,49		29,4		126	
E 468	× E 80	0,48	0,68	21,2	14,3	91	90
E 468	× E 736	0,47	0,64	23,0	15,9	99	100
E 361	× E 80	0,47		20,6		88	
E 726A	× E 702	0,47		22,0		94	
E 701	× E 736	0,45	0,65	19,0	13,1	82	82
E 726A	× E 736	0,44	0,69	25,2	18,4	108	116
E 708	× E 736	0,43	0,62	22,8	16,1	98	101
Grand Total Mean $\bar{X}$		0,51	0,70	23,3	15,9	100	100
E 702 × E 702 (self)		0,55	0,78	5,4	3,2	23	20

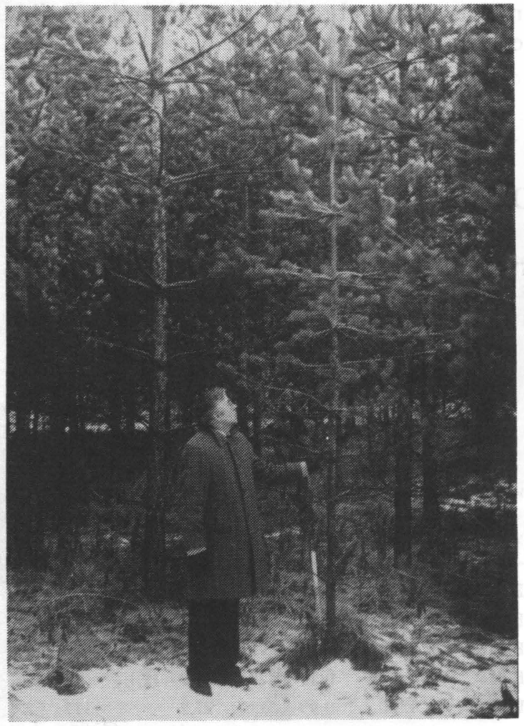

Fig. 2. Example of the effect of inbreeding on progeny growth. The selfed progeny E 702×E 702 on this picture yields roughly ⅓:th of cross-pollinated family means.

the relative humidity of the air. We recon that the water content of the phytomass must have been about 10–13 %.

We note a considerable increase in harvest index, on the average from 0,51 based on fresh weight to 0,70 based on air-dry weight (Table 1). This reflects strikingly the differences in water retention in needles and branches against stemwood. However, the overall correlation between the two different values indicates very little change in ranking, the correlation being r = 0,834***.

A parameter reflecting general combining ability (GCA) of the plus trees involved in the crosses can be obtained by inspecting harvest indices and relative SWFW yields in female and male groups (Table 2). In ten measured maternal groups there is no apparent correlation of HI and relative SWFW yields. Also the range of SWFW-values is much compressed when compared to single crosses (94–108 % vs. 77–138 %). This may indicate a considerable specific combining ability (SCA) for stemwood fresh weight yield. However, it may also be due to the fact, that the material is too small for accurate statistical analysis, each mother is tested in only 3 male combinations and each combination is represented by only 5 sacrificed and measured individuals. However, as can be seen from Table 4, differences in harvest index are highly significant in the analysis of variance. In the three measured paternal groups HI and SWFW appeared to be well correlated. Here the estimates are done on large materials, each father being tested in 10 mother combinations, 5 individuals sacrificed per combination. It is regrettable that we could not measure more than 3 paternals but the excessive work involved plus the fact that the initial mating design is a factorial with only four fathers set the limits.

Table 2. Harvest index (HI) and relative stem wood fresh weight (SWFW) yield in female- and male-groups.

Maternal	Harvest index	Relative SWFW
E 636C	0.56	96
E 731	0,53	98
E 468D	0,52	99
E 724	0,52	107
E 727	0,52	108
E 361	0,49	95
E 468	0,49	94
E 701	0,49	96
E 708	0,47	102
E 726A	0,47	105
Paternal		
E 80	0,52	114
E 702	0,51	96
E 736	0,49	90

Inspecting the summaries given in Table 4 reveal some interesting facts. Harvest index appears to be a highly heritable trait. On the other hand SWFW-values showed significant variation between replications which must be anticipated to indicate low heritability of this growth character. Also a weak but significant interaction mother × father was here detectable substantiating specific combining ability of the stemwood fresh weight character.

Table 3. Statistical parameters of characters, their heritability estimates and standard errors.

Character	Mean $\bar{X}$	Var. δ^2	Range	$h^2_{ns}6$	S.E
Tree height (H), m	6,37	0,56	5,84– 7,04	0,14	0,08
Current annual height increment (CAHI), m	0,69	0,04	0,60– 0,75	0,07	0,04
Diameter b.h. (D), cm	9,30	1,10	7,80–10,70	0,37	0,23
Slenderness (H/D)	0,70	0,06	0,64– 0,79	0,26	0,13
Crown width (CW), m	2,63	0,36	2,29– 3,03	0,26	0,18
Relative crown width (CW/H)	0,41	0,05	0,35– 0,48	0,31	0,20
Branch diam. (BD), cm	1,80	0,30	1,60– 2,00	0,05	0,01
Rel. branch diam. (BD/D)	0,19	0,03	0,15– 0,24	0,17	0,14
Branch angle (BA)°	76,70	5,00	69,20–83,30	0,22	0,09
Nr branches/whorl (NB)	5,70	0,60	5,10– 6,50	0,18	0,08
Pilodyn value (Pi), mm	23,80	2,20	20,40–26,10	0,81	0,50
Harvest index (HI)	0,51	0,04	0,43– 0,57	0,52	0,23
Stemwood fresh weight (SWFW), kg	23,30	8,00	18,00–32,20	0,07	0,07

Table 4. Summaries of the analysis of variance of a 10×3 factorial mating design. For abbreviations see Table 3.

Source of variation	d.f.	F-values of 13 characters 1)H	2)CAHI	3)D	4)H/D	5)CW	6)CW/H	7)BD	8)BD/D	9)BA	10)NB	11)Pi	12)HI	13)SWFW
Between mothers	9	1,55	0,99	2,69**	5,13**	0,47	1,50	1,64	2,72**	4,54***	3,13**	7,16***	4,42***	0,46
Between fathers	2	10,59***	8,13***	23,86***	13,56***	19,06***	15,46***	0,40	10,41***	9,56***	7,11**	60,33***	5,28**	8,08***
Between rep:s	4	6,38***	2,87*	3,10*	1,09	3,27*	0,28	10,63***	5,75***	9,05***	4,13**	9,20***	0,90	4,82**
Mother × father	18	1,84*	1,45	1,23	1,50	1,17	1,01	0,73	1,72	2,15**	1,37	0,88	0,78	1,73*
Error	116													

Heritabilities estimated on the basis of this small experiment (Table 3) must be judged with appropriate scepticism, particularly as there is no replication in time or locations and due to the fact that the material is so restricted. As can be seen from Table 3, the standard errors of the heritability estimates of all the characters studied are large and so the confidence limits wide, because of the small sample size. However, we do not intend to use heritabilities for gain estimations in selection but rather to compare the magnitude of heritability of various traits in one trial. In this chapter the narrow sense heritability of harvest index and stemwood fresh weight are scrutinized, in the next chapter related traits are compared to these principal objects of the investigation.

For harvest index we obtained a narrow sense heritability of 0,52 ± 0,23 (Table 3). This high value must of course be accepted with due considerations. This is, according to our knowledge, the first time that this important yield component has been genetically analysed. Its surprisingly high heritability is somewhat perplexing considering the complexity of the character. We consider the high heritability of harvest index as of great importance in the breeding of Scots pine.

For stemwood fresh weight we obtained a very low heritability. In addition we noticed a relatively high between replication (block) variation (Table 4). We suggest that this variation depends on the small sample size and the rather high individual random variation which also affects other variance components. Obviously stemwood fresh weight is composed of a number of yield components of which volume growth, as we shall see later, is of crucial importance. Also wood density and wood water content appear to be of significance. The heritabilities for traits affecting volume growth; height, height growth and diameter increment exhibited relatively low heritability values. This is also known from many earlier studies. However, wood density, which was measured indirectly by the Pilodyn value (Pi),[1] showed high heritability as was expected.

We have not computed heritability for wood water content but expect this trait to be low in heritability judging from the results recorded on air-dry phytomass in July 1983.

32. Traits related to harvest index

A number of growth and quality characters were measured in conjunction with harvest index (Table 3). Statistically significant differences between maternal trees (half-sib families) could be registered for d.b.h., slenderness, relative branch diameter, branch angle, number of branches per whorl and in Pilodyn value (wood density). The results are given in Table 4. Paternal trees differed in all characters except in branch diameter. Replications (blocks) differed statistically in almost all traits except for relative crown width and slenderness. Weak interaction in the variance component mother x father was found for tree height, relative branch diameter and branch angle. High heritability (narrow sense) of over 0,40 was recorded for wood density. Intermediate h^2_{ns}-values of between 0,20–0,40 were recorded for crown width, d.b.h., slenderness and branch angle. Low values of under 0,20 were recorded for current annual height increment, branch diameter and number of branches per whorl. Results are in good agreement with a number of previously reported studies on heritability.

33. Relationships between harvest index and related traits

Correlations based on individual values and on progeny (family) means are given in Table 5. We conclude that the correlations based on individual values are phenotypic, including both genetic and environmental effects and thus of minor value for the tree breeder. Correlations based on family means on the other hand reflect in a crude way genetic effects that are of great importance for the tree breeder. However, they are not genetic correlations *sensu stricto* but only approximations. A more careful analysis based on genetic components of variance has not been done at this time mainly due to the rather limited sample size.

Generally individual and family mean correlations, here crudely called "phenotypic" and "genetic", are consistent. In no case have we found statistically significant but opposite correlations on the two levels. Many correlations are significant on the individual level, but not on family mean level. This depends on the large differences in the degrees of freedom, 446 on individual and 28 on family mean level. Nevertheless "genetic" correlations appear significant between a number of important yield components (traits). In most cases the correlations are favourable from a tree breeder's point of view, although a few harmful correlations can be found.

Harvest index and d.b.h. are positively correlated on family level. In other words stem volume or increment appers to be an important component in harvest index, possibly even more important than tree height, the latter being positively correlated but statistical significance appears only on phenotypic level. Crown width (CW) and branch diameter (BD) correlate negatively with harvest index but only on phenotypic level. However corresponding relative values (CW/H and BD/D) are significant also on the genetic level which is encouraging for the tree breeder. There is an indication of a slight positive correlation between the Pilodyn value and harvest index, the relationship being highly significant on the phenotypic level. As the Pilodyn value is an inverse measure of wood density, it indicates a somewhat less dense wood at higher harvest index.

There is also an indication of a positive correlation between stemwood fresh weight (SWFW) and harvest index. We consider this to be an excellent proof of good progress achieved in the breeding of Scots pine. The correlation indicates, that the progenies of selected plus trees produce valuable stem-

[1] The Pilodyn wood tester measures the penetration of a spring-loaded steel striker pin into the wood. The measured value in mm. is inversely proportional to wood density (see for example Cown 1978).

Table 5. Correlation matrix for yield components. Upper: individual values × 1000. Lower: family means × 1000. For abbreviations see Table 3.

	1)H	2)CAHI	3)D	4)H/D	5)CW	6)CW/H	7)BD	8)BD/D	9)BA	10)NB	11)Pi	12)HI	13)SWFW
1)H													
2)CAHI	553***												
	717***												
3)D	722***	163***											
	721***	411*											
4)H/D	–131**	235***	–737***										
	–205	– 1	–807***										
5)CW	457***	209***	428***	–186***									
	427*	449*	276	– 40									
6)CW/H	–177***	–143***	– 29	–107*	787***								
	–246	– 25	–210	96	770***								
7)BD	339***	– 6	505***	–368***	459***	292							
	– 7	–152	268	–352***	71	114							
8)BD/D	–349***	–185***	–432***	400***	64	342***	504***						
	–698***	–535**	–774***	565**	–179	316	366*						
9)BA	– 32	90	–110*	155**	18	39	–338***	–216***					
	205	346	26	158	429*	300	–189	–108					
10)NB	294***	87	373***	–241***	110*	– 74	232***	–103*	–103*				
	349	322	613***	–498**	22	–208	323	–328	15				
11)Pi	396***	159**	447***	–266***	227***	– 2	360***	– 54	–133**	282***			
	302	99	726***	–731***	–159	–384*	283	–496**	–138	510**			
12)HI	286***	210***	113*	146**	–258***	–505***	–252***	–417***	94	– 77	169***		
	168	291	393*	– 53	– 88	–493**	– 51	–365*	149	168	279		
13)SWFW	860***	219***	912***	–527***	551***	– 10	589***	–211***	–134*	320***	478***	180***	
	634***	476**	757***	–467**	302	–148	–148	–581***	113	634***	427*	298	

wood without wasting phytomass on large branches. The fact that number of branches per whorl correlates strongly positively with stemwood fresh weight is of minor harmful influence due to the fact that very significant negative correlation can be found between relative branch diameter and stemwood fresh weight or harvest index. We consider the relative branch diameter to be of great importance in the determination of wood quality.

Generally, the strong influence of yield components on harvest index and stemwood fresh weight must by-and-large outweigh the harmful effect of a negative correlation between stemwood weight and wood density (here recorded as a positive Pilodyn correlation).

An encouraging feature for the tree breeder is the fact that relative crown width decreases with increasing yield, i.e. narrow-crowned trees are good woodproducers. The negative correlation (significant only on phenotypic level however) between branch diameter and branch angle is of definite value for breeding. The likewise negative correlation between number of branches per whorl and relative branch diameter should be further investigated on the basis of technological wood properties.

From a tree breeder's point of view, the most harmful correlations are those between growth components and wood density. The rather strong positive correlation which can here be found between d.b.h. and Pilodyn value actually means a strong negative correlation to wood density. The same tendency can be found in correlations of wood density (inverse of Pi) and height or current annual height increment. Correlations of this kind have been recorded in many earlier studies. On the other hand, in this study high wood density appears to be positively correlated to stem slenderness, the correlation being particularly strong when measured on a family mean basis. This must again be considered to be favourable for the tree breeder.

We may conclude, that many of the correlations measured here in conjunction with harvest index and stemwood fresh weight have been favourable for efficient tree breeding. However, our measurements are only preliminary and often the material used has been too incomplete. In future years, much more exact estimates should be made on the genetic correlations of various yield components.

4. APPLICATIONS

In recent years it has particularly been stressed that selection on an individual basis may sometimes render response to selection almost noneffective (Griffing 1967 and later). This theoretical finding has also been verified, but ambiguously, in field experiments. The reason for ineffectiveness of individual selection, and also the variable results obtained in practical experiments, depend first of all on competition in relation to stand density. From an agronomic or silvicultural point of view it has source-sink relationship, i.e. how much of the synthesized biomass goes to the spreading of the leaves, branches and roots and how much to the economically interesting parts; kernels, tubers and stems.

Are we to select for fast growing competitive types that show pronounced spreading and competitive ability? Or are we better off by selecting noncompetitive genotypes that may show slower growth on the seedling stage but which can endure higher final density? Or should we combine different types in mixed culture to make maximal use of ecological resources: light interception, nutrition etc.?

Predictions of response to selection have all been developed assuming that interactions between genotypes are unimportant. However Gallais (1976) has suggested that the whole theory of response to selection ought to be reformulated to take account of plant interaction. Particularly strong emphasis on this point has recently been given by forest ecologists and tree breeders as trees have to compete in forests and stands during most of their productive life, some 50–100 years (Cannell 1978). Can individual selection here give any indication of yield under competitive stress? Do superior "competitive" individuals show yield superiority when grown as dense stands? What are the crop physiological repercussions of strong competition? Does a strong competitor fill its sink differently than a weak competitor.

Griffing (1967) began by considering groups of size 2. He showed that response to selection is now

$$R = \frac{i(V_A\delta + Cov_A\delta\alpha)}{\sqrt{V_p}}$$

Here $Cov_A\delta\alpha'$ is the covariance between direct (δ) and associate (α) additive effects. Since $Cov_A\delta\alpha$ *can be negative,* R may be positive, zero or negative. i is the intensity of selection.

If selection is made on the basis of group means, the response will be

$$R = \frac{(\tfrac{1}{2})i(V_A\delta + 2Cov_A\delta\alpha + V_A\alpha)}{\sqrt{V_p\ (group)}}$$

It can be shown that

$$V_A\delta + 2Cov_A\delta\alpha + V_A\alpha \geq 0$$

Griffing showed later (1968), that group selection can in some cases be ineffective. However it precludes a negative response to selection which may be the case after individual selection. Griffing showed (1969) how a selection index based on direct and associative additive effects could be constructed corresponding to an index on individual and within family values used in animal breeding.

The progeny test of pine that we have been investigating is now 16 years old. It was initially planted at spacings of 2,5×2,5 meters. As can be seen from figure 1 it is just now that the tree canopy is getting fully closed and competition between individuals for crown space becomes severe and recognizable even visually. We ask ourselves, whether progenies that we have ranked superior at this time shall keep their positions through the coming period of high competition up to the point of the first economic thinning at the age of about 25 years? We have been keen to open the discussion with some theoretical considerations that have been elaborated by specialists on the population biology of agricultural crops. Forest trees are of course different because the crop is removed in shorter or longer intervals thereby alleviating competitive stress. However, the remark by Gallais that the whole theory of response to selection ought to be reformulated to take account of plant interaction must be carefully considered also in the selection process in forest tree progenies. Gallais has mainly worked with the maize plant, but in many ways stands of maize resemble stands of trees, with competition increasing rapidly as the stand develops.

Also we must recognize, that observations made on plots consisting of full-sibs is a rather unnatural situation in a cultivated tree stand. In a 3×3 plot it is however only the center tree which competes with close relatives of equal structure. This was the tree now sacrificed for harvest index measurements and this may to some extent bias our estimates, even if competition is rather mild at this age and spacing.

We would like to put special emphasis in this discussion on the fact, that the most favourable tree type for cultivation is probably a lot different in allometry from its wild progenitor, that has to endure very high competitive stress during most of its development. We would likewise like to emphasize, that the ideal tree for cultivation is very much dependent on the silvicultural regime that is applied. Are we aiming at none, one or several thinnings during the development of the stand? What are the economic conditions of different approaches in the silvicultural regimes? What is the rotation?

We ask the questions above, because we think that they are imperative for the tree breeder. By breeding, as we have shown, the tree form can be changed quite readily as many of the traits involved are highly heritable. Thus in trees, it is apparently easy to breed for ideotypes, probably even easier than in agricultural crops where this approach has proven so successful. In searching for yield the tree breeder must look at stand development and not so much at the development of the individual tree. The only correct way to search for higher yields is to make an integrated effort towards yield increase, considering silvicultural regimes, soil and water conditioning and industrial constraints, all at one time. Under such integrated conditions we may visualize an ideal crop-tree ideotype.

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SELOSTE

SATOINDEKSIN SOVELTAMISESTA VALINTAJALOSTUKSEEN MÄNNYN JÄLKELÄISKOKEEN TULOSTEN PERUSTEELLA

Satoindeksi (rungon massan osuus puun maanpäällisen osan kokonaisbiomassasta) ja eräitä siihen liittyviä ominaisuuksia mitattiin 16-vuotiaasta, täyssisarjälkeläistöjä sisältävästä männyn jälkeläiskokeesta. Todettiin, että satoindeksi periytyi voimakkaasti ja korreloitui tuotosominaisuuksien kanssa positiivisesti. Saatujen tulosten perusteella esitetään satoindeksiä ja ns. ideotyyppejä, ihannemalleja, viljelypuiden valintaperusteiksi. Samalla korostetaan sitä, että parhaan mahdollisen viljelytuloksen saavuttamiseksi tarvitaan jalostuksen ja muiden metsäntutkimuksen sektorien yhteistyötä sekä teollisten ja taloudellisten näkökohtien huomioon ottamista.