Results of a Progeny Test with Pinus sylvestris and Estimation of Genetic Gains from different Selection Methods

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Summary

The progenies of 10 open-pollinated clones of a seed orchard with *P. sylvestris* (provenance Trappönen, formerly East Prussia) were tested with respect to several growth characters until age 11 on 3 locations in Northern Germany. The information from this progeny test is used for predicting the genetic gains from this seed orchard and from other possible selection methods. For seed from the seed orchard there is an expected genetic gain of 5.1% for height(11) and of 5.9% for dbh(11) under suitable conditions. Further reselection of the best 50% clones will double the gain, i.e. 10% for height(11) and 13% for dbh(11). A new clonal seed orchard with increased selection intensity (1 out of 100) would reveal 10% gain for height(11) and 11% for dbh(11). Further reselection of the best 20% clones would increase the gain at values of about 19% and 24% resp., but a parallel progeny test would be necessary.

As a further result of the progeny test a decrease of heritability of the height growth with the age was observed.

Key words: Scots pine, progeny test, seed orchard, selection methods, genetic gain.

Zusammenfassung

Die Nachkommen von 10 frei abgeblühten Klonen einer Samenplantage mit *P. sylvestris* (Herkunft Trappönen, früher Ostpreußen) wurden hinsichtlich ihrer Wuchsmerkmale bis zum Alter 11 auf 3 Standorten in Norddeutschland geprüft. Die Information aus diesen Prüfungen ermöglicht, den genetischen Gewinn aus dieser Samenplantage und aus anderen Selektionsmethoden einzuschätzen. Für die Höhe im Alter 11 ergibt sich unter günstigen Bedingungen für Saatgut aus der Samenplantage ein berechneter genetischer Gewinn von etwa 5,1%, für den BHD im Alter 11 ein solcher von etwa 5,9% gegenüber der Ausgangspopulation. Nach weiterer Selektion der 50% besten Klone betrüge der zu erwartende genetische Gewinn etwa das Doppelte, nämlich 10% für die Höhe(11) bzw. 13% für den BHD(11). Bei Anlage einer neuen Klonsamenplantage mit erhöhter Selektionsintensität (1 aus 100) würde der zu erwartende Gewinn 10% für die Höhe(11) und 11% für den BHD(11) betragen. Eine weitere Selektion der 20% besten Klone würde den Gewinn auf 19% bzw. 24% anwachsen lassen. Allerdings wäre hierfür eine Nachkommenschaftsprüfung erforderlich.

Als weiteres Ergebnis der Nachkommenschaftsprüfung war eine Abnahme der Heritabilität für das Höhenwachstum mit dem Alter festzustellen.

Introduction

Pinus sylvestris L., a tree species of great commercial value, has a very wide natural range in Europe and Asia and is also extensively cultivated outside its natural occurrence. The improvement of this species is under study in many provenance trials, selective breeding projects and seed orchards (WRIGHT, 1976).

In Central Europe, Polish provenances are reputed to be of outstanding character, with provenances from East Prussia particularly suited to this region. Therefore the Institute of Forest Genetics and Forest Tree Breeding in cooperation with the Forestry Department of the State of Schleswig-Holstein (Northern Germany) established in 1952 a seed orchard with clones of selected plus trees from an East Prussian provenance. In 1967 and 1968 a progeny trial was initiated to assess the breeding value of the parental clones and other genetic parameters. The paper is divided into two parts, namely (A) the results of the progeny test and (B) the estimation of genetic gains for several selection methods.

A. Evaluation of the progeny test

Materials and Methods

Provenance trial. A provenance trial was established in 1911 in the forestry district of Rendsburg (Schleswig-Holstein) in Northern Germany with 5 provenances from Saxony, East Prussia, South Sweden, Central Sweden and West Norway. Initially about 2000 plants from each provenance were planted.

Plus tree selection and propagation. In the year 1950 it was set up a commercial clonal seed orchard out of the Trappönen provenance (formerly East Prussia), which was considered phenotypically the best. Ten plus trees were selected out of about 170 trees in this provenance. These plus trees were propagated vegetatively by grafting on *Pinus mugo* TURRA in the nursery at Schmalenbeck.

Seed orchard establishment. The seed orchard was established in 1952 near Rendsburg. The plant spacing was 4 m in a triangular design. Members of the same clone were not adjacent to each other. The mean number was 12 ramets per clone.

Progeny test. During 1965/66 open-pollinated cones were harvested from each clone, kept separately, and the seed sown in nursery beds at Schmalenbeck in spring 1966.

Using one year old seedlings one progeny trial was initiated in the nursery beds at Schmalenbeck (Ki 27) *(Table 1)* in May 1967. The design adopted was a completely randomized blocks design with four replications of 8 tree row plots. The distance between and within rows was 15 cm.

Field trials were established at two locations, Uetze (Ki 28) in Northern Germany, and Geldern (Ki 29) in Western Germany *(Table 1)*, in the spring of 1968 with two year old seedlings (1/1), according to a completely randomized blocks design with four replications of 16 plants in square plots. Spacing was 1 × 1 m.

Measured traits. In the nursery trial height measurements were recorded at age 2,3 and 4 years after sowing.

In the field trial height measurements and survival percentage were recorded at the age of 3, 6 and 11 years (1976). Diameter measurement was recorded at age 11 (1976). Assessment of the stem form of the progenies was made in the field trial at Uetze (Ki 28) in summer 1979 when the trees were 14 years old. 3 categories for stem form were used: straight, slightly malformed, heavily malformed. Forking was also assessed.

Statistical methods. Height, diameter and form were analyzed according to a linear variance component

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Table 1. — Test locations for the *Pinus sylvestris* progeny trial

location	Schmalenbeck	Uetze	Geldern
exp. no.	Ki 27	Ki 28	Ki 29
state	Schleswig-Holstein	Niedersachsen	Nordrhein-Westfalen
latitude	53°40' N	52°26' N	51°30' N
longitude	10°15' E	10°06' E	6°15' E
elevation	45 m	60 m	30 m
soil	loamy sand	sand	sand, podsol
mean ann. prec.	780 mm	650 mm	747 mm
mean ann. temp.	8.0°C	8.4°C	9.4°C

Figure 1. — Height growth development of 10 *Pinus sylvestris* progenies on two locations.

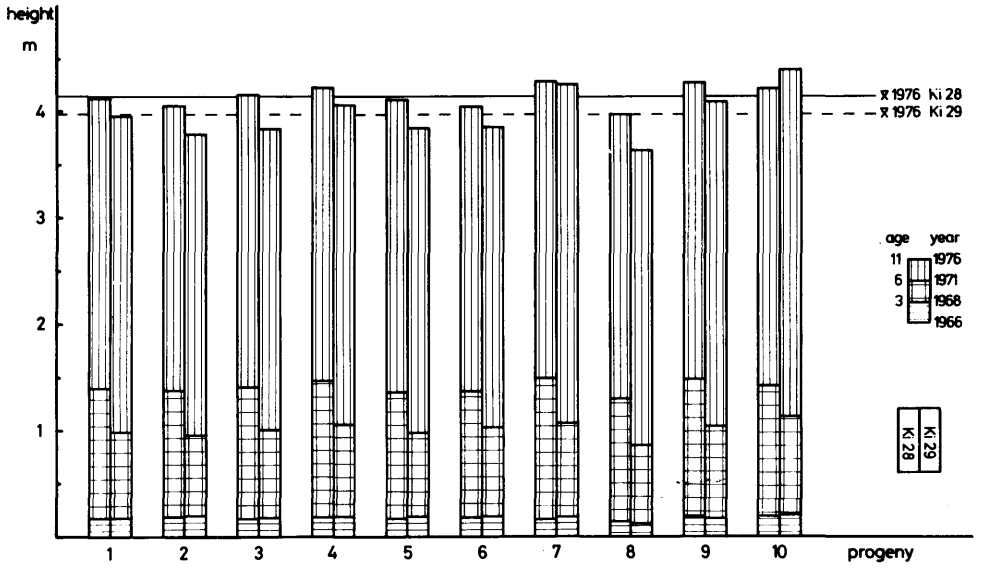
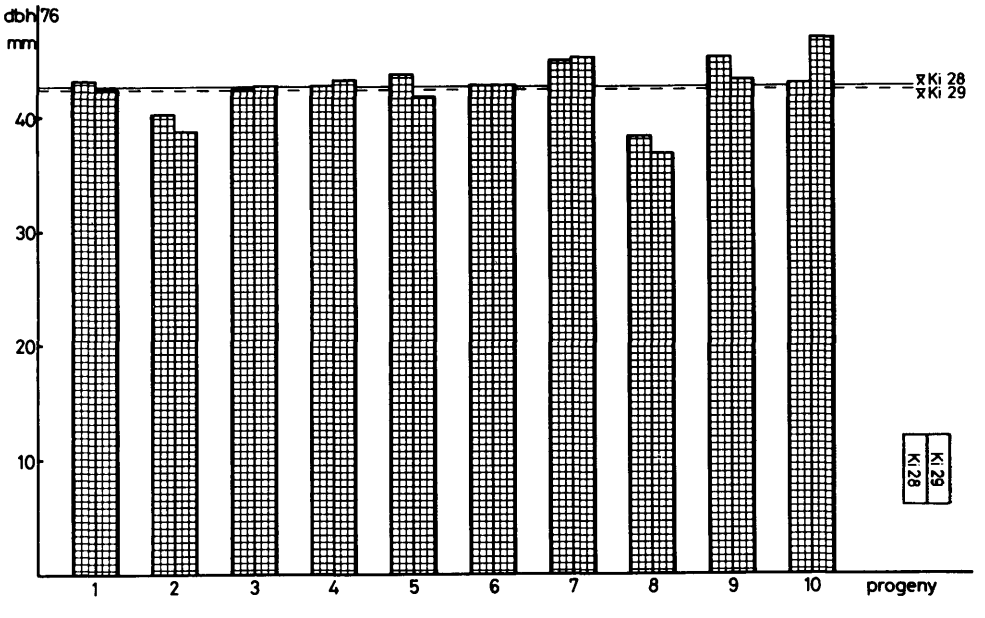


Figure 2. — Dbh of 10 *Pinus sylvestris* progenies on two locations at the age of 11 years (1976).



model. The number of forked trees within plots was transformed by taking square roots before analysis. The harmonic mean of the numbers of trees per plot was 15.

Results

a) *Survival.*

The survival of the plants was observed at the time of each measurement. At the last measurement in 1976 the survival percentage was between 83 and 97 at Geldern (Ki 29) and between 88 and 99 at Uetze (Ki 28). There were no significant differences between the individual progenies.

b) *Height growth and diameter.*

The performance of the progenies on the locations at Uetze and Geldern is given in the *figures 1* and *2*.

In examining the above figures it may be seen that progeny no. 8 is the slowest growing offspring, while progeny no. 10 is comparatively the fastest growing offspring followed by progeny no. 7 and 9. The difference between the fastest and the slowest growing progeny is 13% for height(11) and 18% for diameter(11).

c) *Form assessment and forking.*

Differences between the 10 progenies with respect to these traits were non significant, and are not further investigated.

d) *Correlation between height and diameter between and within locations.*

Results are given in *table 2*. The height correlation from the nursery trial with the field trial for the first measurements is quite high as is expected one year after the establishment of the individual trials. The correlation of the progenies between the locations was quite good with values of approximately 0.8 for both height and diameter. This fact is also corroborated by the low interaction between progenies and locations in the ANOVA *(Table 5)*. The correlations for height growth and diameter(11) on both locations are very high *(Table 2)*.

B. Calculation of genetic gains for the existing seed orchard and of gains from possible alternate selection methods

The information from the progeny test will be used a) for estimation of genetic parameters, b) for the existing seed orchard (method A1) and for reselection of best clones of the existing seed orchard (method A2) and c) for calculating estimated genetic gains for alternate selection methods within possible future breeding programmes (methods S1—S4). The calculations of the genetic gains are based on papers of Namkoong *et al.* (1966) and Shelbourne (1969).

Estimation of genetic parameters

Methods and assumptions

The evaluation is done for single locations separately and for the combined locations according to a variance component model. In *table 3* the expected mean squares are given together with degrees of freedom and approximate

Table 2. — Correlation coefficients, based on progeny means

	Ki 28				Ki 29			
	height(3)	height(6)	height(11)	dbh(11)	height(3)	height(6)	height(11)	dbh(11)
Ki 28 height(3)	--	.45 -	.34 -	.50 -	.78 ++	.66 +	.52 -	.54 -
" (6)	.45 -	--	.95 +++	.77 ++	.45 -	.77 ++	.78 ++	.73 ++
" (11)	.34 -	.95 +++	--	.82 ++	.39 -	.79 ++	.84 +++	.79 ++
dbh (11)	.50 -	.77 ++	.82 ++	--	.49 -	.73 ++	.68 +	.79 ++
Ki 29 height(3)	.78 ++	.45 -	.39 -	.49 -	--	.68 +	.47 -	.58 -
" (6)	.66 +	.77 ++	.79 ++	.73 ++	.68 +	--	.91 +++	.96 +++
" (11)	.52 -	.78 ++	.84 +++	.68 +	.47 -	.91 +++	--	.91 +++
dbh (11)	.54 -	.73 ++	.79 ++	.79 ++	.58 -	.96 +++	.91 +++	--
Ki 27 height(2)	.90 +++	.55 -	.52 -	.57 -	.65 +	.76 ++	.66 +	.65 +
" (3)	.57 -	.72 ++	.58 +	.50 -	.51 -	.58 +	.53 -	.42 -
" (4)	.63 +	.66 +	.57 -	.53 -	.66 +	.63 +	.52 -	.50 -

significance level: - = not significant; + = 5 %; ++ = 1 %; +++ = .1 %

Table 3. — The ANOVA table for single and combined locations

combined locations				single location			
source of variation		d.f.	E(MS)	source of variation		d.f.	E(MS)
locations	(l)	1	$\sigma_p^2+\sigma_t^2/15+4\sigma_{fl}^2+40\sigma_l^2$	replic.	(r)	3	$\sigma_t^2+15\sigma_p^2+150\sigma_r^2$
families	(f)	9	$\sigma_p^2+\sigma_t^2/15+4\sigma_{fl}^2+8\sigma_f^2$	families	(f)	9	$\sigma_t^2+15\sigma_p^2+60\sigma_f^2$
fam x loc	(fl)	9	$\sigma_p^2+\sigma_t^2/15+4\sigma_{fl}^2$	fam x repl	(p)	27	$\sigma_t^2+15\sigma_p^2$
fam x repl	(p)	60	$\sigma_p^2+\sigma_t^2/15$	within plot	(t)	572 (Ki 28) 568 (Ki 29)	σ_t^2
within plot	(t)	1140	σ_t^2				
$\hat{V}(\hat{\sigma}_f^2)=2/64(MS_f^2/11+MS_{fl}^2/11)$				$\hat{V}(\hat{\sigma}_f^2)=2/3600(MS_f^2/11+MS_p^2/29)$			

Table 4. — Formulas for estimating genetic gains for methods A1, A2 and S1—S4

$n = 15$ - harmonic mean of the number of trees in plots

$r = 4$ - number of replications in locations

$l = 2$ - number of locations

$\hat{\sigma}^2_{A'} = 4\hat{\sigma}^2_f$ - estimate of reduced additive genetic variance

$\hat{\sigma}^2_{A'} = \hat{\sigma}^2_A(1 - \frac{\sigma^2_A}{\hat{\sigma}^2_1}\gamma)$ - estimation formula for additive genetic variance. $\gamma = 0.7813$ (from Finney 1956) is a parameter related to a proportion selected of 20 %. This equation is solved by an iteration process for $\hat{\sigma}^2_A$.

$\hat{\sigma}^2_1 = \hat{\sigma}^2_w + \hat{\sigma}^2_p + \hat{\sigma}^2_{fl} + \hat{\sigma}^2_A + \hat{\sigma}^2_D$ - phenotypic variance of the base population, estimated from the progeny test data

$\hat{\sigma}^2_t$ - within plot variance inclusive genetic variance

$\hat{\sigma}^2_w = \hat{\sigma}^2_t - 3/4\hat{\sigma}^2_A - d\hat{\sigma}^2_A$ - within plot variance due to purely environmental effects

$\hat{\sigma}^2_p$ - interaction fam x plot (microsite)

$\hat{\sigma}^2_{fl}$ - interaction fam x location (macrosite)

$\hat{h}^2 = \hat{\sigma}^2_A/\hat{\sigma}^2_1$ - estimated heritability (narrow sense)

$S.E.(\hat{h}^2) = 4\hat{\sigma}^2_A/\hat{\sigma}^2_{A'} \cdot S.E.(\hat{\sigma}^2_f)$ - estimated standard error of h^2 (approximately)

$\bar{x}$ - grand mean in progeny test

i_1 - selection intensity for mass selection

i_2 - selection intensity between families

i_4 - selection intensity of phenotypes in seedling seed orchard

$\hat{\sigma}^2_{A'''} = 3/4\hat{\sigma}^2_A + 1/4\hat{\sigma}^2_{A'}$

$\hat{\sigma}^2_2 = MS_f/rl$; $\hat{\sigma}^2_2 = MS_f/nr$ - variance of family means estimated from the combined locations ANOVA and single locations ANOVA resp.

$\hat{\sigma}^2_4 = \hat{\sigma}^2_w + \hat{\sigma}^2_p + \hat{\sigma}^2_{A'''}$ - variance of phenotypes in seedling seed orchard

(A1) $\Delta G(\%) = i_1 \frac{\hat{\sigma}^2_A}{\hat{\sigma}_1 \bar{x}}$

(A2) $\Delta G(\%) = (i_1 \frac{\hat{\sigma}^2_A}{\hat{\sigma}_1} + 2i_2 \frac{1/4\hat{\sigma}^2_{A'}}{\hat{\sigma}_2}) / \bar{x}$

(S1) $\Delta G(\%) = i_1 \frac{1/2\hat{\sigma}^2_A}{\hat{\sigma}_1 \bar{x}}$

(S2) $\Delta G(\%) = i_1 \frac{\hat{\sigma}^2_A}{\hat{\sigma}_1 \bar{x}}$

(S3) $\Delta G(\%) = (i_1 \frac{1/2\hat{\sigma}^2_A}{\hat{\sigma}_1} + i_4 \frac{\hat{\sigma}^2_{A'''}}{\hat{\sigma}_4}) / \bar{x}$

(S4) $\Delta G(\%) = i_1 \frac{\hat{\sigma}^2_A}{\hat{\sigma}_1 \bar{x}}$

variance of the family component. In the case of the combined locations the evaluation is based on plot means, and the within plot component is pooled from the separate locations. For the following calculations we have to make several assumptions which we will state below.

Base population. We assume that the individuals in the provenance trial from 1911, which serve as the base population, can be regarded as a representative sample of the original population.

Plus tree selection. Ten trees out of 170 were selected from the base population, the East Prussian provenance Trappönen. It was reported that the "plus trees" were selected with respect to several characters as height, diameter, crown habit and branching characteristics. Therefore we assume that the plus trees are not only the best 10 out of 170, but are only within the best 20% for height and diameter, i.e. the intensity of selection is $i_1 = 1.40$ from tables of the standardized selection differential.

Additive and dominance genetic variance. The additive genetic variance is estimated as four times the family variance component, $\hat{\sigma}^2_A = 4\ \hat{\sigma}^2_f$. This implies that the families are true half-sibs. But in practice this condition may be not completely fulfilled due to the restricted number of male parents, unequal amount of pollen from each clone, differential fertility and inbreeding. Therefore the additive genetic variance might be overestimated, but will be an upper bound for the true value.

The progeny are derived from a restricted (selected) population with decreased genetic variance. According to Finney (1956) we correct for this bias and estimate σ^2_A according to *table 4*. The dominance variance cannot be estimated, because no fullsib families or clones are included in the progeny test. We consider two cases: with dominance ($\sigma^2_A = \sigma^2_D$, d = 1) and without dominance ($\sigma^2_D = 0$, d = 0) (Shelbourne, 1969). Epistatic and linkage effects are assumed to be zero.

Single and combined locations. The heritability and genetic gains are calculated for the two locations separately and for the combined locations. In the case that the progeny × macrosite (family × location) variance component and the progeny × microsite (family × replication) component from the combined locations analysis is significant, it will be included in the phenotypic variances, in order to account for this additional source of error.

Results

Table 5 lists the results of the ANOVA according to the models in *table 3*. In all cases the family × macrosite interaction was non significant and is therefore not included in the phenotypic variance. The size of the unbiased additive variance component according to Finney (1956) is influenced very little by the actual size of ν, i.e. from the selection intensity of the plus tree selection. This stems

Table 5. — Results of ANOVA, variance components with significance levels from F-test[a], parameters calculated from formulas of *table 4*.

variance component	height(3)(cm) (nursery)	height(3)(cm) Ki 28	height(3)(cm) Ki 29	height(3)(cm) combined	height(6)(cm) Ki 28	height(6)(cm) Ki 29	height(6)(cm) combined	height(11)(cm) Ki 28	height(11)(cm) Ki 29	height(11)(cm) combined	dbh(11)(cm) Ki 28	dbh(11)(cm) Ki 29	dbh(11)(cm) combined
$\hat{\sigma}^2_r$	0^-	0^-	$.75^+$	--	10.6^-	0^-	--	121^{++}	2.1^-	--	0^-	0^-	--
$\hat{\sigma}^2_{fl}$	--	--	--	$.37^-$	--	--	0^-	--	--	11.8^-	--	--	0^-
$\hat{\sigma}^2_f$	3.75^+	1.92^{++}	4.87^{++}	3.17^{++}	17.9^+	41.62^{++}	34.12^{++}	93.5^-	380.7^{++}	203^{++}	$.02^-$	$.055^{++}$	$.049^{++}$
$\hat{\sigma}^2_D$	1.13^-	1.41^{++}	1.1^{++}	1.5^{++}	31.3^{++}	5.7^-	23.25^{++}	0^-	151^-	191^{++}	0^-	0^-	0^-
$\hat{\sigma}^2_t$	46.56	24.22	23.32	23.77	608.2	468.3	538.3	2609	4709	3660	1.24	1.59	1.42
grand mean $\bar{x}$	33.2	17.5	18.1	17.8	141	101	121	416	399	406	4.27	4.24	4.25
$\hat{\sigma}^2_p$ b)	0	1.5	1.5	1.5	23.3	23.3	23.3	191	191	191	0	0	0
$\hat{\sigma}^2_A$	14.98	7.68	19.48	12.7	71.6	166	136	--[c]	1522	812	--[c]	.22	.196
$\hat{\sigma}^2_w$ d = 1	20.33	10.78	--[d]	--[d]	483	177	299	--	2045	2239	--	1.2	1.07
d = 0	35.32	18.5	8.71	14.26	554	343	436	--	3567	3051	--	1.425	1.27
$\hat{\sigma}^2_A$ d = 1	20.25	10.15	--	--	79	229	171	--	2036	984	--	.25	.22
d = 0	21.2	10.5	57.9	24	79	241	174	--	2120	994	--	.25	.22
$\hat{\sigma}^2_I$ d = 1	60.8	32.6	--	--	664	657	664	--	6308	4398	--	1.7	1.52
d = 0	56.5	30.5	68.1	39.8	657	608	633	--	5877	4236	--	1.67	1.49
$\hat{h}^2$ d = 1	.33	.31	--	--	.12	.34	.25	--	.32	.22	--	.15	.15
d = 0	.38	.35	.85	.60	.12	.40	.27	--	.36	.24	--	.15	.15
S.E.(h^2)[e] d = 1	.21	.19	--	--	.1	.18	.13	--	.17	.13	--	.08	.07
d = 0	.24	.21	.41	.30	.1	.2	.14	--	.19	.13	--	.09	.07
ratio family variance to within plot variance	.08	.08	.21	.13	.03	.09	.06	0	.08	.06	0	.03	.03

a) significance levels: — = not significant; + $\leqq$ 5%; ++ $\leqq$ 1%
b) fam × repl interaction used for calculating variances
c) non significant $\hat{\sigma}^2_f$, all further calculations omitted
d) the assumption d = 1 ($\sigma^2_A = \sigma^2_D$) results in negative σ^2_w, only the case d = 0 is resumed
e) the S. E. of h^2 is a rough approximation only in order to demonstrate the order of magnitude

Table 6. — Relative genetic gains (%) predicted for the seed orchard (methods A1, A2) and for different growth traits. The gain is based on the assumption d = 1, but for method A1 the gain for d = is given in parentheses.

	height(3) (nursery)	height(3) Uetze (Ki 28)	height(6) combined loc	height(11) combined loc	dbh(11) combined loc
A1: selection of 20 % best trees ($i_1 \hat{=} 1/5$). Open pollinated seed collected from clonal seed orchard					
$i_1 \hat{=} 1/5$	11(12)	14(15)	7.7(8)	5.1(5.3)	5.9(6)

A2: as in A1, but reselect best clones (intensity i_2) on the basis of progeny test

	gain	test gain	gain	test gain	gain	test gain	gain	test gain	gain	test gain
$i_1 \hat{=} 1/5$ $i_2 \hat{=} 1/2$	20	9	26	12	14	6	10	5	13	7
1/5	26	15	34	20	20	12	14	9	19	13
1/10	30	19	39	25	23	14	16	11	22	16
1/20	34	23	44	30	26	18	18	13	25	20

from the low heritabilities in the growth traits under study. Further, the assumption on the size of the dominance variance component has a very low influence on the size of the parameters, especially when low heritabilities ($h^2 < 0.2$) are recognized. This is due to the relatively large non genetic variation in traits with low heritability. Therefore the predicted gains for the selection methods S1—S4 will be based on the assumption, that dominance variance exists (d = 1).

Gains from the existing seed orchard (methods A1, A2)

Methods

A1: No selection, all clones used (simple recurrent selection). This scheme is equivalent to a clonal seed orchard without progeny testing, and also to a seed stand or seed production area. Both parents are selected, interpollinate randomly, and the seed produced is used commercially. The gain is given in formula A1, *table 4*. The results are in *table 6*.

A2: Reselection of best clones (recurrent selection for GCA). The GCA of each clone is estimated by the performance of the open pollinated progenies of the clones in the seed orchard. The progenies are tested and the clones corresponding to the best progenies are left for further seed production. The gain is according to formula A2, *table 4*. The additional gain, using the information of the progeny test, is separately shown in *table 6*.

Results

For the case $i_2 \hat{=} 1/2$ the total gain for height(11) is composed of 5.1% gain from simple recurrent selection and of 5% gain from additional progeny testing *(Table 6)*. For dbh(11) the figures are 5.9% and 7% respectively which gives a total of 13%. This clearly shows that the test gain for the low heritability trait dbh(11) ($\hat{h}^2 = .15$) is relatively higher than for the higher heritability trait height(11) ($\hat{h}^2 = .22$).

Gains for other selection methods (S1—S4)

Methods

The genetic parameters estimated from the progeny test are used for predicting genetic gains with other selection methods, not currently in use. We will not study all possible selection methods, but only those which are practical with *P. sylvestris*. Methods are not investigated which depend on a precise estimate of the dominance variance, as are the utilization of specific combining ability (biclonal orchard) and mass vegetative propagation, because production of rooted cuttings of *P. sylvestris* is not yet possible in large scale. The below mentioned methods are different with respect to the time of first improved planting stock and to the labor and skill required in establishment and maintenance of seed orchards. The precision of the estimates of genetic parameters is not very high as can be seen from the approximate standard error of the heritabilities *(Tab. 5)*. The impression of what can be expected together with the particular situation of the breeder may lead to a "suboptimal" decision.

S1: Mass selection. This method simply involves the selection of best trees in natural stands and the collection of their open-pollinated seed. The gain is given by formula S1, *table 4*. The selection intensity can be made very high, but is limited by the great variation in natural stands, due to non genetic influence.

S2: Seed production area or seed stand. This is simple recurrent selection without progeny testing. An existing stand is thinned to leave only a neighbourhood of selected trees. The selection intensity is seldom greater than one tree out of twenty, because otherwise the average distance between trees would be too large. The gain is twice what is expected for mass selection differential (formula S2, *table 4*).

S3: Mass selection and progeny testing. Open pollinated seed from plus trees (only female trees selected) may be bulked and the offspring are planted at close spacing. Later on, the individuals in this seedling seed orchard are selected on the basis of their own performance. The seedlings left are used for seed production. The gain by this method may be considerable, when the juvenile-mature correlation of the traits used for selection is sufficiently high. As the parentage of the individuals selected is not recorded, there may be a risk of inbreeding due to selection of predominantly outstanding families. The expected gain is from formula S3, *table 4*. The second term of this expected gain formula is only valid for infinite number of progenies and offspring within progenies*).

S4: Establishment of a new clonal seed orchard. This is only advisable when the individual heritability is sufficiently high. Low heritabilities may require a parallel progeny test with subsequent reselection of best GCA clones, but at the expense of a certain time delay.

*) We acknowledge that one of the referees has made the corresponding calculation for the finite case. A numerical comparison for the present material revealed only minor differences less than 1 ‰.

Results

The expected gains (relative to the best means) are presented in *table 7* for the methods S1—S4. The gain for the growth traits height(11) and dbh(11) in the case of simple mass selection (method S1, one parent selected) is up to 5% depending on the selection intensity. With additional phenotypic selection (method S3) the gain is increased to about 14%, but at the expense of 20 years delay. In the case of simple recurrent selection (method S2, both parents selected) the gain is somewhat higher than that for mass selection, about 7.5%.

A new clonal seed orchard (method S4) with a selection intensity 1 out of 100 would reveal 10% gain for height(11) and 11% for dbh(11). A tenfold increase of selection intensity will give a gain of only 12% and 14% resp., which clearly shows that the cost for a stronger selection must

Table 7. — Expected relative genetic gains (%) and time (years) to first improved seed according to the time scale for different selection schemes (S1—S4) in *Pinus sylvestris* **a)**. It is assumed throughout that $\sigma^2_A = \sigma^2_D$ (d = 1) but for d = 0 (no dominance) the gains for methods S1, S2 are given in parentheses. i_1 refers to the selection intensity of initial selection and i_4 to phenotypic selection within seedling seed orchards. The intensity is given in proportion selected.

	height(3) (nursery)	height(3) (Ki 28)	height(6) (combined)	height(11) (combined)	dbh(11) (combined)	time to first improved seed (years)	rel. gain[b] height(11)	rel. gain[b] dbh(11)	rel. gain/year[b] height(11)	rel. gain/year[b] dbh(11)
S1: mass selection, female trees only										
i_1=1/5	5.5(5.9)	7.1(7.6)	3.8(4)	2.5(2.6)	2.9(3)	(a) = 1	7.4	8.4	7.4	8.4
1/10	6.9(7.4)	8.9(10)	4.5(5)	3.2(3.3)	3.7(3.7)					
1/20	8.1(8.7)	10.5(11)	5.6(5.9)	3.8(3.9)	4.3(4.4)					
1/100	10.5(11.3)	13.5(15)	7.3(7.6)	4.9(5)	5.6(5.7)					
1/10000	15.8(17)	20.3(22.5)	10.9(11.4)	7.4(7.5)	8.4(8.6)					
S2: seed production area or seed stand, both parents selected										
i_1=1/10	14(15)	18(19)	9.6(10)	6.4(6.6)	7.4(7.5)	(a+e) = 3	15	17	4.9	5.6
1/20	16(17)	21(22)	11(12)	7.5(7.8)	8.7(8.8)					
S3: open pollinated seed from select females bulked and plantation established.										
i_1=1/1000 Later thinned to best phenotypes										
i_4=1/5	26	33	18	12	13	(a+d) = 21	13	15	0.62	0.72
1/10 c)	29	37	20	13	15					
1/20	32	41	22	14	16					
S4: new clonal seed orchard without progeny testing										
i_1=1/100	21	27	15	10	11	(a+b+c) = 18	14	17	0.77	0.94
1/1000	26	34	18	12	14					
1/10000	31	40	22	14	17					

a) time scale for *Pinus sylvestris* (approx.)

	years	
selection in wild stands	1	(a)
grafting	2	(b)
seed from clonal seed orchard	15	(c)
seed from seedling seed orchard	20	(d)
time from pollination to seed	2	(e)
controlled crossings	4	(f)
age of progeny test for main assessment	15	(g)

b) for a total selection intensity of 1/10000 and dominance assumed, $i_1 \leqq 1/1000$, $i_4 \leqq 1/10$

c) These selection proportions do not apply to the seed orchard described in this paper and are made for comparison purposes only

be balanced against the relatively low increase of the genetic gain.

Discussion

Additive genetic variance and heritability

The indirect estimate of additive genetic variance from the reduced population of progenies of selected plus trees is not influenced very much by the proportion assumed to be selected. If we had taken this proportion as 1 out of 20 instead of 1 out of 5 as we did, the estimate of σ^2_A is only altered a negligible amount. The reason is that the heritability entering the correction formula of FINNEY (1956) is low for the characters presently studied. The precision of the heritability estimate *(table 5)* is not very high. This is due to the low degrees of freedom for families, as can be seen from the general formula for the approximate standard error of $\hat{\sigma}^2_f$ *(table 4)*.

Variation of heritability

The difference of the heritabilities depends only little on the assumption of the size of dominance variance *(table 5)*, especially for characters with low heritability as are height and diameter for age 11. This fact may be due to the relatively large phenotypic variance, which enters the denominator of $\hat{h}^2$, and is not affected very much by variations of the total genetic contribution. Another phenomenon is the decrease in heritability of height with increasing age of the test material *(table 5)*. This is mainly due to the decrease of the family variance relative to within plot variance. It can be argued that the average height increment in the younger stage is more genetically controlled than the average height increment at age 11, where competition effects are present. This result could be important for the establishment of new plantations where weed competition can be reduced by selection for early height growth.

The heritability estimates are very different on the two locations due to different variation between family means *(table 5)*. For height(11) no significant progeny variance could be observed on location Ki 28 whereas on location Ki 29 highly significant differences were found. Our results are in line with EHRENBERG (1963), who found heritability estimates between 0.16 and 0.65 for height growth in a trial with 10-year old progenies of *P. sylvestris* on different macrosites. These differences clearly demonstrate that a reliable estimate of heritability should be based on tests conducted on more macrosites, desirably on the whole range of planned use of East Prussian provenances of *P. sylvestris*.

Gains from other methods (table 7)

The numerical comparison of the different methods with respect to predicted gain is only of limited value. The costs and time required for different stages of the methods are quite different and strongly dependent on the local realities and skill of personnel. A rough comparison can be made, however, on the basis of the time period to the first improved seed, when it is assumed that the total selection intensity is 1 plant out of 10 000 for each method, and the maintenance costs per hectar of seed orchard are approximately linear in time and the initial cost for selection and establishment of the orchard are within the same magnitude. The gain per year is given for height(11) and dbh(11) for each method in *table 7*. Method S1 (mass selection) reveals the highest gain for both traits. A rapid gain within some years is expected from method S2 (seed stand, seed production area) but cannot be recommended. The neighbouring individuals may be related and inbreeding depression in the resulting plants may be present. Another disadvantage is repeated bark injury from harvesting of cones. The cheapest method is probably method S3, but 21 years are necessary for first improved seed. Approximately the same gain as method S2 is attained with method S4 (new clonal orchard), within 18 years.

All methods assume that information for additive genetic variance is available in advance. In spite of this shortcoming method S4 should be studied seriously given that clonal propagation is possible.

Additionally as shown with method A2, the clonal seed orchard should be progeny tested, and the best clones reselected. For *P. sylvestris* the first improved seed is expected at 18 years from initial selection, and the age of the parallel progeny test for the main assessment for judging the clones, is 15 years, i.e. there is no time delay from testing. The gain may be considerable and compensate for the cost of progeny testing, especially when the test plantation can be converted into a seedling seed orchard.

The genetic base of the existing seed orchard composed of ten clones only is very restricted. Therefore this orchard should be used at most for seed production and not as a breeding population for second generation selection, because the risk of inbreeding depression in advanced generations will speed up considerably.

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