the reports mentioned above. In any case, until the reason for the inferiority of the Colombian seed orchard material is clarified, it would be imprudent to use this seed source for reforestation in Costa Rica.

The values of heritability and AGCV are within the ranges typically found for these traits in progeny tests of forest trees (CORNELIUS, 1994), and confirm the potential for improvement of the local base population.

The results do not permit firm conclusions to be drawn on possible variation in growth rate at later stages. However, unless age-to-age correlations are negative, then the selection of seed sources based on juvenile growth should produce a reduction in rotation length concomitant with the increased early growth. If, as LAMBETH's (1980) results suggest, age-to-age correlations tend to be positive, then this effect will be further enhanced by more rapid growth at later stages. However, it should be stressed that early growth rate is in itself a trait of key economic importance, as improvements in early growth rate can reduce early cleaning costs and their associated high interest charges.

Conclusions

1. The Cipresal, Bosque de la Hoja, Monte de la Cruz (all north of Heredia) and La Lucha provenance – all represented by plus-trees selected for form and girth – have faster juvenile growth rate than the 3 commercial controls included. It is recommended that commercial seed collections be made from well-formed trees of better than average diameter in these stands. Seed collections from the Santa María Dota source should be avoided, as should use of seed from the La Arcadia clonal seed orchard.

2. The estimated values of the genetic parameters suggest that worthwhile gains in growth traits may be made.

3. These conclusions apply principally to the breeding zone in question, i.e. the Cordillera Central of Costa Rica, at altitudes between 1900 m and 2300 m a.s.l..

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A Progeny Trial with Domesticated *Picea sitchensis* (BONG.) in Denmark

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Summary

In 1972 a progeny trial with *Picea sitchensis* (BONG.) were established on 3 harsh locations in Denmark. Growth and qualitative parameters have been measured several times. Growth, stem form, wood density (pilodyne), frost resistence and resistence to aphids were found to be partly under genetic control, and the characters are mostly interrelated. The age-age correlations for growth are high, and selection could be carried out with advantage before 10 years of age.

High variation in growth within site, high plant departure and aphid attacks were found in one of the trials. Substantial genotype by environment interaction for growth parameters was revealed between this trial and the 2 trials with lower mortality.

Key words: Progeny trial, genetic correlation, *Picea sitchensis,* heritability, genotype by environment.

FDC: 232.11; 165.3; 165.4; 174.7 *Picea sitchensis;* (489).

Introduction

Sitka spruce (*Picea sitchensis* (BONG.)) is a major exotic species in Danish forestry grown on semi-fertile soils for timber and pulpwood production. It was introduced to Denmark approximately 100 years ago. Provenance research in the intermediate period has revealed that seedsources of Washington origin are suited to Danish conditions except for wind and frost exposed sites, where seedsources of British Columbian origin (Queen Charlotte Island) are better adapted. Some adaptational problems remain even for these provenances, especially due to frost, wind and to some extend aphids. These damages do, beside of reducing general adaptability, decrease the general stemform and thereby the commercial value of the trees.

Breeding of sitka spruce in large scale was initiated in Denmark in the late 1960'ties and the breeding activities are now entering advanced generations (ROULUND, 1990). The oldest sitka progeny trial in Denmark was established in 1972 as offspring of 15 clones selected in a Danish stand of Washington origin (Seed orchard FP 611).

This article reports the genetic parameters of economical and adaptational important traits from this trial based on a 24 years old (from seed) progenies in Denmark. Special focus is put on age-age correlation, because reliable juvenile-mature correlations are important for the analysis of trade offs for early selection (see BENZER et al., 1989 for references). Indirect selection is important in breeding, especially if time of testing can be reduced.

Material

The first clonal seed orchard of sitka spruce was established in Denmark in 1958 based on 15 trees selected in a 51 year old sitka spruce stand in Vroegum, in the western part of Denmark, who survived a major attack by the green spruce aphid (*Elatobium abietinum* WALK.). The origin of this stand is assumed to be Washington.

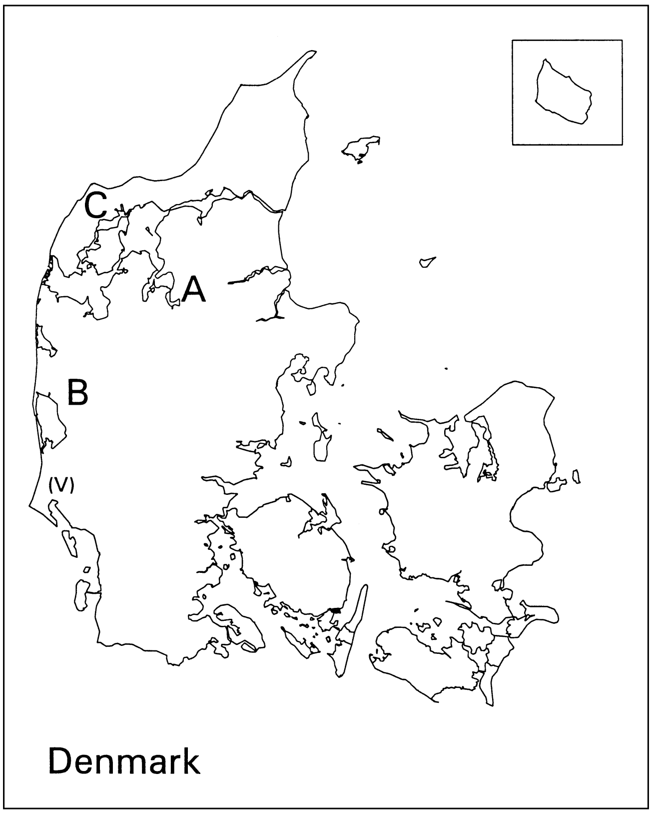

Figure 1. – The distribution of the 3 trials (A), (B), and (C) in Denmark. All trials are placed on rather harsh locations. (V) is indicating the origin of the parents (Vroegum).

In 1968 seeds were harvested in the seed orchard for the progeny test. The test thus include 15 half-sib progenies (5 cones per single tree). A few percent of the trees within the progenies are unquestionably hybrids of *Picea glauca* x *Picea sitchensis* due to background pollination, but no differentation have been made in the analysis. The progenies were tested along with a commercial seedlot from the seed orchard and a reference provenance (F 235, Frijsenborg).

The progeny trials series F154 was established in 1972 on 3 sites in Jutland near Ringkoebing (A), Viborg (B) and Thisted (C) (*Figure 1*). All trials are placed on relative poor soil conditions with location (C) only 6 km from the North-sea. Each trial were established with 6 blocks each containing 17 plots with each 16 3 year old seedlings. F154A and F154B are placed on quite homogenous surface, whereas F154C is placed on small sand dunes.

A number of traits of economical importance have been assessed in one or more of the trials: Height, diameter, straightness (form), pilodyn score, broken leaders and attack of aphids (*Table 1*).

Table 1. – Measurements made in trial F154. Measurements of height, diameter, stem form, pilodyne, broken leaders and aphid-attack.

Trial	Age	Height	DBH	Stem-form	Pilodyne	Forks	Broken Leader	Aphid-attack
	2	X						
F154	5	X						
A	9	X						
	14	X	X	X		X	X	
	21		X			X	X	
F154	2	X						
B	5	X						
	9	X	X			X		
	14	X	X	X	X	X	X	
	21		X			X	X	
F154	2	X						
C	9	X				X		
	14	X	X	X	X	X	X	X
	21		X			X	X	X

Pilodyne score is the penetration into the stem of a needle. It is a simple, non-destructive, but also indirect measure of wood density (YANCHUK and KISS, 1993).

The frequency of trees with broken leaders is a indirect measure of frost- and wind damage.

The stem form is scored into 9 classes: Class 9 being absolutely straight and class 1 being very crooked. The aphid attack were estimated as the percentage needles damaged or lost due to insects. In 1989 an attack was only found at one location (trial (C)).

Mortality and frequency of trees with forks was also recorded.

At age 21 (from establishment), only diameter have been recorded as a growth character.

Statistical Analysis

For each trial progeny differences in height, diameter, straightness (form), pilodyn score, broken leader, forks and aphid-attack were analysed by simple ANOVA subject to standard test of independence, normality and variance homogeneity. All analysises were based on family plot means.

$$Y_{ij} = \mu + A_i + B_j + x1(B_j) + x2(B_j) + \epsilon_{ijk} \qquad (1)$$

Y_{ij} is the plot mean response variable (trait), A; is the random effect of family (i = 1..15), B_j the random effect of blocks (j = 1..6), x1 and x2 are geographical cordinates within blocks used as covariates, and ϵ_{ijk} the residual. Due to high influence

Table 2. – Estimates for mean values for different traits measured in the F154 trials. The F values and probabilities (in %) are noted as well as the family heritabilities. The calculations for frostresistance are based on data from both F154A and F154B.

	F154 A			F154 B			F154 C		
	Mean	F/P	h^2_f	Mean	F/P	h^2_f	Mean	F/P	h^2_f
Frost 1972 (A and B)	43.1 %	4.35 0.2	0.77						
Height 1974 (H2)	.51 m	4.46 0.01	0.78	.65 m	4.68 0.01	0.79	0.51 m	2.12 4.3	0.53
Height 1986 (H14)	4.9 m	6.35 0.01	0.84	5.6 m	9.81 0.01	0.90	3.5 m	3.01 0.59	0.67
Diameter 1993 (D21)	102 mm	3.86 0.01	0.74	114 mm	7.78 0.01	0.87	110 mm	2.82 8.9	0.65
Basal area 1993	0.15 m^2	3.62 0.02	0.72	0.18 m^2	7.16 0.01	0.86	0.12 m^2	3.12 0.47	0.68
Pilodyne 1986				17.2 mm	5.38 0.01	0.81	14.8 mm	3.89 0.09	0.74
Stem form 1986	4.66	2.07 0.28	0.52	5.81	3.26 0.01	0.67	4.90	1.84 7.5	0.45
Leader damage	12 %	2.00 1.5	0.50	25 %	3.03 0.2	0.67	23 %	NS.	
Departure anno 1986	2 %	NS.		3 %	NS.		24 %	2.17 2.3	0.54
Aphid 1989 needle loss							15 %	2.49 0.2	0.60

from statistical outliers (WEISBERG, 1985), the analysis for trial (C) were rather unstable. Four plots had to be eliminated in this experiment to improve the analysis.

Diameter age 14 was included as covariates in the analysis of pilodyne penetration. This was done in order compare the *level of wood density* rather than the actual value. Fastgrowing trees generally has low wood density in coniferous species, and the diameter was included in the model in order to purge this variation (COSTA E SILVA et al., 1994).

For some traits (*Table 4* and *5*), a joint analysis across sites have been applied – using the model:

$$Y_{ik} = \mu + A_i + L_k + B_j(L_k) + \epsilon_{ijk} \quad (2)$$

Where L_k is the fixed effect of trials (k = 1..3), and $B_j(L_k)$ the effects of blocks nested within the trials.

Genetic Interpretation

Family heritabilities (h_f^2) were calculated according to NAMKOONG (1979) from interpretation of the variations components estimated from model (1) above. Phenotypic correlations between trials were estimated as PEARSON correlation coefficient between average family performance (least square estimates corrected for any unbalance in the trials).

Genetic correlations (r_A) between different traits within trials (and age-age correlations) were estimated based on analysis of co-variance according to BECKER (1984). Expected response from selection for trait (ΔG) was calculated as a product of the estimates for phenotypic variance (V_p), family heritability (h_f^2) and a standard selection intensity of (i). Correlated response at the latest stage – from selection at a younger stage – was calculated after FALCONER (1989). Genetic correlation between performance in different traits were calculated according to BURDON (1977).

Results

Differences between progenies

Significant variance between progenies were found for nearly all traits (*Table 2*). The heritabilities for growth traits are high for trial (A) and (B), but more modest for (C). However, there were no large differences in mean growth rate at age 21 (diameter 1993) between the trials.

Table 3. – Measurements of mean height and diameter (trial A and B), mean corrected pilodyne (trial B and C) and height from trial C (differs from A and B due to genotype x environment interaction). All measurements from 1986. Averages are given along with values from the commercial seedlot and the reference provenance.

Families	H14 AB dm	D14 AB mm	Pilo 14 BC mm	H14 C dm
8052	46.2	59.2	14.4	24.9
8053	51.1	65.8	13.8	36.1
8054	50.4	65.4	13.7	37.6
8055	58.6	73.8	15.0	36.5
8056	48.6	62.4	14.3	32.0
8057	50.0	63.9	14.5	32.9
8058	42.9	56.3	14.3	40.1
8059	57.0	74.6	14.8	32.8
8060	47.1	59.6	14.9	35.7
8061	56.9	72.8	14.0	30.1
8062	54.7	73.8	14.7	45.4
8063	52.2	70.4	14.1	
8064	56.7	74.2	15.8	40.8
8065	53.5	68.2	14.2	34.1
8066	59.8	79.2	15.5	39.5
Average	52.4	68.0	14.5	35.6
Commercial	49.8	65.1	14.3	36.9
Reference	54.7	73.3	14.1	39.4

Substantial environmental variance was observed in (C), and high plant departure has been recorded. The trial has been target for heavy aphid damage as well. Both departure and aphid attack showed high heritability.

There seems to be a site effect of pilodyne, as the diameter in both (B) and (C) are much alike.

Mean family values for height, diameter and corrected pilodyne are presented in *table 3*. Due to genotype by environment interaction for height and diameter (not pilodyne), means for trial (C) height are presented separately.

Interaction between trials

Correlations between traits in different trials (Type B correlations according to BURDON (1977)) are presented in *table 4* in order to examine any presence of progeny by trial interaction. Early height (2 year) and height, stemform and pilodyne are analysed.

Generally the correlations between trial (A) and (B) are high indicating only modest interaction (H2, H14). The correlations between trial (A) and (B) on the one hand -and trial (C) on the other – is not significant – except corrected pilodyne. Trial (C) can therefore be said to belong to a different site-type, as long as GxE interaction is used for classification of environments.

There is no relation between aphid attack and growth within trial (C). It can be seen from *table 2* that aphid damage in trial (C) correlates *negatively* with growth in trial (A) and (B) (slow growing families are generally more damaged by aphids than fast growing families). The actual genotypic values within (C) are highly biased by the aphid attack. Pilodyne is another character having high correlation between trials.

Correlation between traits within each trial

A sample of the correlations within each trial is presented in *table 3* as well. The correlations should be seen in combination with the estimated heritabilities (*Table 2*).

High correlations were generally found between growth characters: Colliniarity is present between diameter and basal areas, especially in the (A) and (B) trials with low mortality.

Stem straightness measured in 1986 is found to be correlated with height, most clearly in trial (B) and a little less in (A).

Some results are not presented in *table 3:* No correlation was found between stem form and height in (C). In all trials, stem form was highly correlated with shoot deformation and fork formation, but not with frost damage and mortality. It was not possible to find any connection between the estimations of frost damage at age 0 (nursery assessment) and later registrations of mortality.

A correlation between the number of non-frost-damaged plants at the age of 2 years and growth measurements at age 21 are positive, but not large.

Age-age correlation and response of early selection

Age-age correlations are estimated for all combinations of earlier and late assessments of height. Phenotypic correlations based on family averages of all three trials are presented in *table 5*. It should be noted, that the correlation between the height at age 0 (nursery stage) remains around 0.60 with significance level about 1%. There does not seem to be any trends in the size of correlation with age, which is unexpected.

The relation between the first height measurements at age 2 in 1974 shows high phenotypic correlation with later growth character measurements. Within each trial the correlations are even higher (*Table 4*).

LAMBETH (1980) showed with empirically data (height) for different coniferous species a simple relation between phenotypic correlation and the so called LAR (logarithmic age relation = $\log(age_{young}/age_{old})$). This formula was used to predict the loss of correlation, and expected correlated response from early selection. In *figure 2*, the height correlations from the 3 trials are plotted against their corresponding LAR (plot basal

Table 4. – Phenotypic correlations within and between trials F 154A, B and C. The probability in percent is noted under the correlation H = height, pilo = pilodyne. Measurements made at age 2 and 14 (aphid 17 years).

		Trial F154 A			Trial F154 B				Trial F154 C			
		H2	H14	F14	H2	H14	F14	Pilo	H2	H14	Pilo	Aphid
		1.0	.85	.28	.80	.62	.04	.09	.34	.26	.34	-.42
	H2		.01*	32	.01*	1.2*	89	74	22	36	21	13
Trial			1.0	.51	.73	.81	.32	.14	.12	.28	.31	-.53
F154 A	H14			5.0*	.19	.02*	24	62	67	32	26	5.3*
				1.0	.22	.51	.55	.14	-.06	-.26	.31	-.47
	F14				43	5.4*	3.5*	62	84	37	26	.09*
					1.0	.80	.00	.12	.45	.28	.20	-.38
	H2					.04*	98	66	11	33	47	17
Trial						1.0	.58	.37	.67	.26	.40	-.61
F154 B	H14						3.1*	20	20	38	14	.02*
							1.0	.03	.02	-.05	.41	-.38
	F14							91	95	85	13	18
								1.0	.56	.49	.81	-.25
	Pilo								3.6*	7.7*	.03*	37
									1.0	.53	.40	-.03
	H2									5.4*	16	91
Trial										1.0	.31	.26
F154 C	H14										27	40
											1.0	-.49
	Pilo											6.0*

*) more than 10% probability for correlation hypothesis rejection

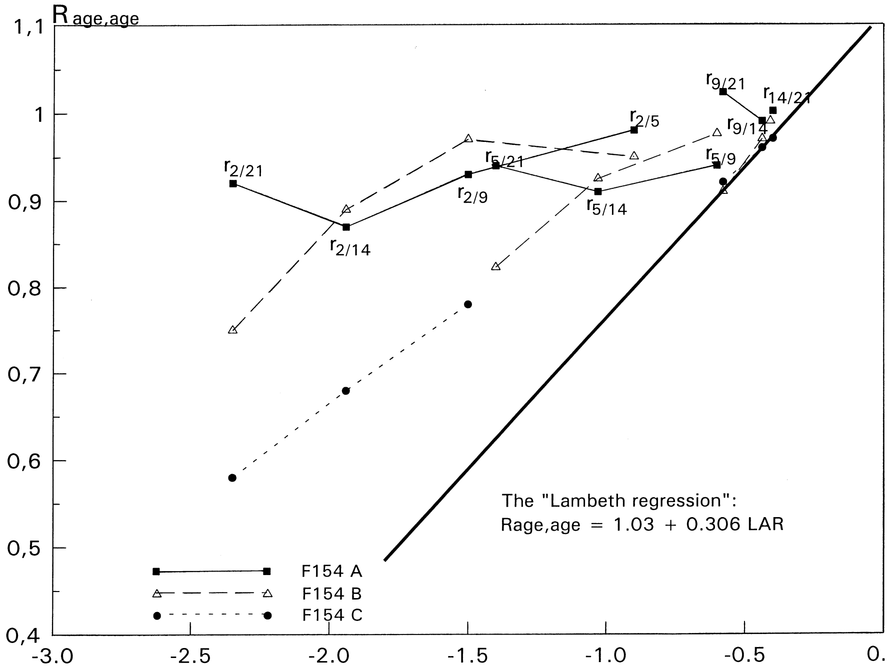

Figure 2. – The relation between LAR (log age_{young}/age_{old}) and genotypic correlations on height growth from age 2 to 21 (plot basal area). Due to LAMBETH (1980), this regression should be fairly constant. There are a set of curves (r2,.), (r5,.), (r9,.) and (r14,.) for each trial (except (r5,.) for trial (C). All correlations starting from age 2, 5, 9 are connected with lines (r14, 21 are points). Only the points for trial (A) are marked with a label. The label should also reflect all other points in trial (B) and trial (C) with same LAR. The material from this Danish trial provides a better possibility for early selection.

area is used at age 21). Genetic correlations are used instead of phenotypic correlations, because it is the genetic correlations that determine the expected correlated response.

The age-age correlations in the present analysis are above the LAMBETH regression at all 3 trials. This is partly because the LAMBETH regression is based on phenotypic correlations, which tend to be lower than genetic correlation. The slopes of the curves are *not* independent of the younger age. Correlations from 9 years and forward seem, however, to match the slope of the LAMBETH regression.

The gain from early selection in terms of correlated response at age 21 is estimated in *table 5*. About 80% to 90% of the possible gain is achieved by selection at age 9 (trial (B)).

Table 5. – Phenotypic correlations for growth traits within trials F154A, B and C. The probability in % is noted under the correlation.

	H2	H5	H9	H14	Basal area 14	D14	Basal area 21	Frost
H0	.61 3.1*	.66 2.1*	.61 2.1*	.57 3.4*	.56 3.6*	.57 3.5*	.57 3.2*	.04 90
H2		.79 .07*	.82 .04*	.67 .84*	.63 .17*	.56 3.9*	.64 1.4*	.42 13
H5			.90 .01*	.86 .01*	.75 .20*	.73 .03*	.76 .18*	.43 11
H9				.96 .01*	.92 .01*	.88 .01*	.92 .01*	.60 2.3*
H14					96.1 .01*	.94 .01*	.96 .01*	.61 2.1*
Basar 14						.92 .01*	.92 .01*	.60 2.5*
D14							.95 .01*	.47 8.8*
Basar 21								.58 3.0*

*) more than 10% probability for correlation hypothesis rejection

Discussion

Progenies in this series show some differences in performance between trial (C) and (A)+(B). The difference may be due to a combination of exposure towards the North Sea and low fertility of the soils. This results is in concordance with the general experience, that some GxE interaction exists between the wind-exposed costal sites (i.e. trial (C)) and the interior frost exposed sites ((A), and to some extend (B)). It has a practical implication on the Danish breeding plan for sitka spruce. The GxE-interaction must be considered in future decisions concerning geographical stratification of trial sites and genetic composition of breeding populations and seed orchards. Some of the problems come into view by the attack by aphids, which could appear by chance. Generally more test-sites should be applied if breeding zones should be defined properly.

The size of genetic variance, correlation between different trials, traits and ages are important for prediction of genetic gain practical purposes. Additive genetic variance was found for aphid resistance. An option for including aphid resistance in the breeding objective is thus present. Fortunately it correlates positively to growth.

Age-age correlations were found to be higher than predicted by standard LAMBETH regression. A tendency to increased drop in correlation after approximately age 12 was found. After this age a linear relation with stepper slope may give an acceptable description of the relation between age-age correlation and

Table 6. – Correlated response for basal area at age 21 (from establishment), when selecting for height in a sitka spruce progeny test at ages 2, 5, 9 and 14 years. The correlated response is measured in relation to the mean basal area in 1993 (0.165 m^2 (trial (A) and (B)) and 0.15 m^2 (trial (B)).

Trial (A+B)	Selection intensity	Family heritability trait B	Family heritability trait A	Standard deviation family means	Genetic correlation trait (A,B)	Gain in trait B %	Correlated response CR_A	Relative effiency	Effiency per year %
H2	1.3	0.88	0.87	0.0244	0.85	2.4	14.3	84.8	7.1
H5	1.3	0.87	0.87	0.0244	0.90	2.5	15.0	89.4	0.3
H9	1.3	0.91	0.87	0.0244	0.98	2.8	16.9	100.2	0.5
H14	1.3	0.92	0.87	0.0244	0.98	2.8	16.8	100.1	0.0
BAS21	1.3	0.87	0.87	0.0244	1.00	2.8	16.8	100.0	0.0
Trial (B)									
H2	1.3	0.79	0.86	0.0257	0.70	1.9	10.7	63.5	5.3
H5	1.3	0.80	0.86	0.0257	0.83	2.3	12.7	75.4	0.7
H9	1.3	0.88	0.86	0.0257	0.91	2.7	14.7	87.6	0.5
H14	1.3	0.90	0.86	0.0257	0.97	2.8	15.8	93.8	0.2
BAS21	1.3	0.86	0.86	0.0257	1.00	2.9	16.0	100.0	0.0

LAR. The result support the present praxis in Denmark of making the first selection decisions based on assessments after only 5 years in field trial (age 8 to 9). Assessment of growth after 5 years is expected to correlated relative well with evaluations after 10 years. Ten years (13 years to 14 years of growth) is an important time span, because at this age the seed orchards produce seed in commercial scale, and genetic gain can therefore be realized. After this period the correlation may decrease more rapidly, because of new factors becoming limiting.

The number of progenies within the trials are quite low, and the results should be interpreted with care. However the low number of progenies is weighed up by many replications and very low environmental influence in trial (A) and (B).

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