traits at different ages in slash pine and some implications for breeding. Silvae Genetica **41**: 252–262 (1992). — HODGE, G. R., WHITE, T. L., POWELL, G. L. and DE SOUZA, S. M.: Predicting genetic gains from one generation of slash pine tree improvement. South. J. Appl. For. **13**: 51–56 (1989). — LA FARGE, T.: Realized genetic gains in volume, volume per acre, and straightness in unrogued orchards of three southern pine species. In: Proc. 22nd South. For. Tree Imp. Conf. June 14 to 17, Atlanta, GA, pp. 183–193 (1993). — LOWERTS, G. A.: Realized genetic gain from loblolly and slash pine first generation seed orchards. In: Proc. IUFRO Conference – A joint meeting of working parties on breeding theory, progeny testing, seed orchards. Williamsburg, VA. pp. 142–149 (1986). — LOWERTS, G. A.: Tests of realized genetic gain from a coastal Virginia loblolly pine first generation seed orchard. In: Proc. Nineteenth South. For. Tree. Imp. Conf. June 16 to 18, College Station, TX. pp 423–431 (1987). — PIENAAR, L. V., PAGE, H. H. and RHENEY, J. W.: Yield prediction for mechanically prepared slash pine plantations. South. J. Appl. For. **14**: 104–109 (1990). — PORTERFIELD, R. L.: Economic aspects of tree improvement programs. In: Forest Tree Improvement – Third Decade. B. A. THIELGES (Ed.). School of Forestry and Wildlife Management, Louisiana State Univ., Baton Rogue, LA. pp. 99–117 (1975). — ROCKWOOD, D. L.: Volume prediction for genetically improved slash pine trees. Agric. Expt. Stat., Bulletin 819 (Technical), Inst. Food & Agric. Sci., Univ. Florida, Gainesville, FL. 17 p. (1981). — ROW, C. and DUTROW, G.: Measuring genetic gain by projected increases in financial returns. In: Proc. 13th South. For. Tree. Impr. Conf., Raleigh, NC. pp 17–20 (1975). — SAS® Institute Inc.: SAS/STAT® User's Guide. Release 6.03 Edition. SAS® Institute Cary, NC. 1028 p. (1988). — TANKERSLEY, L., BONGARTEN, B., BRISTER, G. and ZOERB, M.: Operational plantations of improved slash pine: Age 15 results. In: Proc. 17th South. For. Tree. Imp. Conf. June 6 to 9, Athens, GA. pp. 271–280 (1983). — VANDERPLANK, J. E.: Genetic and Molecular Basis of Plant Pathogenesis. Springer-Verlag, Berlin, Germany. 167 p. (1978). — WEIR, R. J.: Realizing genetic gains through second-generation seed orchards. In: Proc. 12th South. For. Tree Imp. Conf. June 12 to 13, Baton Rouge, LA. pp. 14–23 (1973). — WRIGHT, J. W.: Introduction to Forest Genetics. John Wiley and Sons, Inc., New York. 463 p. (1975). — WHITE, T. L. and HODGE, G. R.: Best linear prediction of breeding values in forest tree improvement. Theor. Appl. Genetics. **76**: 717–719 (1988). — WHITE, T. L. and HODGE, G. R.: Predicting Breeding Values with Applications in Forest Tree Improvement. Forestry Sciences Series, Vol. 33. Kluwer Academic Publishers, Dordrecht, Netherlands. 367 p. (1989). — ZOBEL, B. and TALBERT, J.: Applied Forest Tree Improvement. John Wiley and Sons, Inc., New York. 505 p. (1984).

Genetic Variation in Characters of Importance for Stand Establishment in Sitka Spruce (*Picea sitchensis* (BONG.) CARR.)

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Summary

This paper summarizes the results of 2 series of clonal trials-F206 including 151 clones and F215 including 196 clones. The characters measured are: selection intensity for height growth in the nursery, height, autumn coloration, flushing, leader breaks, April-frost damage, and mortality, all characters of expected importance for stand establishment. Genotype-environment interaction and correlation between characters are studied as well.

Compared to the standard, a direct import from Queen Charlotte Islands, the clones, selected in a danish second generation material, have a superiority in height growth of 23% to 31%, fewer leader damage, 16% to 17%, and less damage due to April-frost, score 1.1 to 2.5, whereas there is hardly no differences in flushing time and only minor differences in mortality, 1 % to 5 % less dead trees.

There is considerable variance among clones for April-frost damage, but the results are only based on one year. If the frost hits later in the spring the differences between the clones will probably be less because they all are closer to the growing season and all will have an active cambium. Severe damage due to April-frost is a rather seldom event in Denmark and one may question the effort to avoid damage by selecting less sensitive clones, unless it is an indirect gain by selecting for late flushing clones to late spring frost exposed sites, where even small differences in time of flushing will make a difference.

There is only a very limited possibility to select for late flushing in spite of high heritability estimates.

Autumn coloration shows no reasonable correlations to field damage and may not be an appropriate measure of autumn hardening.

Selection based on 3 year old cuttings yield about 63% to 77% of the results obtained by direct selection 5 years later in the field. Concerning the ageing-problem of the hedges for cutting production 3 year nursery results seem to be a reasonable basis to start commercial production of selected clones.

Early selection of ortets among 3 or 4 year old seedlings for height growth seems not to be an appropriate way to increase height growth within the danish provenance.

General problems with ageing of propagation material restricts the practical use of the clonal material.

Clonal mean values of ecovalence as a stability measure is estimated for the characters showing genotype-environment interaction. Only a rather limited number, around 15%, of the clones acounts for more than 50 % of the genotype-environment interaction sums of square.

Key words: Sitka spruce, broad sense heritablility, genetic variation, height, flushing, April-frost damage, genotype-environment interaction.

FDC: 165.3; 165.5; 181.221.1; 181.6; 232.11; 422.12; 228.0; 174.7 *Picea sitchensis.*

Introduction

Sitka spruce (*Picea sitchensis* (BONG.) CARR.) is a common used exotic conifer in Denmark, actually, in the recent years the most planted. Traditionally, Sitka spruce is one of the most

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desired tree species for the windy and salt exposed coastal sites of Western Denmark, especially in the dune areas of Jutland. Here, Sitka spruce is preferred for Norway spruce, which have a poor adaptation to these oceanic growth conditions. The first forest plantings of sitka spruce took place in Denmark around the 1880s (POULSEN, 1883; FABRICIUS, 1926). First generation sitka spruce was often planted under a nurse stand or in mixture with other conifers. Today, establishment of 2nd generation causes problems for the growers and a part of the reason is todays practice, clear cutting or lack of stable nurse stands. Especially frost damage show to be even more serious now than in the first generation. Further, there is an increasing tendency to use sitka spruce on what previously was typical Norway spruce sites, i. e. more sandy soil types often on old heathland which typically is more frost exposed. Therefore, a selection for more adapted clones is very desirable.

In 1991 severe frost damage before budburst – "April-frost" were observed in newly established and young stands of sitka spruce. The general picture of the damage was normal developing shoots until the beginning of June, where shoots suddenly became hanging and later died. Similar damage have already been described in Denmark by LADEFOGED (1938), BORNEBUSCH and LADEFOGED (1940), and from Scotland by REDFERN (1982), LINES (1983), LINES and SAMUEL (1993). CANNEL and SHEPPARD (1982) show provenance variation in the succeptability to frost before budburst, but no correlation to flushing. The frost damage before budburst arises from frost injuries of the cambium and occurs when the temperature suddenly drops in late April after a warm period in March and early April.

In 1970, a breeding program was initiated in Denmark by BRANDT (1970) and ROULUND (1974a). The present program is outlined by ROULUND (1990). Clonal propagation was early recognized as a promising tool in sitka breeding. Encouraged by the first results (ROULUND, 1974b) several series of clonal material were established, comprizing approximately 850 clones. 23 years' results of the first clonal trial in Denmark, including 7 clones, have recently been published (COSTA E SILVA et al., 1994), showing the coefficient of variation for clones, for growth traits to vary between 5% to 18%, and 3% to 14% for quality traits.

CAHALAN (1981) provides estimates of genetic parameters for 5 year old sitka spruce clones in Scotland. Repeatabilities of clone means for phenology and growth traits ranging from 0.57 to 0.84 and estimated coefficients of variation for clones ranging from 19% to 22% for height, 8% to 35% for branch angle and number, 2% and 12% respectively for flushing and budset.

The objective of this study is to provide estimates of genetic parameters for traits influencing the establishment of sitka spruce stands based on two populations of clones, totally 347 clones. The objectiv includes: Gain estimates, broad sense heritabilities and genetic variation for height, flushing, autumn coloration and April-frost damage, clonal repeatabilities for leader damage and evaluation of genotype-environment interactions. Further to evaluate early selection for height growth in the nursery and provide estimates of correlations between characters.

Material and Methods

Plant material

The selected clones originate from a single seedlot harvested in the Danish stand Rønhede (Danish approval number F.405) located in the Northwestern part of Jutland. The stand originates from the Queen Charlotte Islands (QCI), B.C., Canada. The two experimental series F206 and F215 were started in 2 subsequent years. Selection for height growth were carried out in the nursery at age 3 and 4 from sowing (in the year 1978 and 1979 respectively). 151 and 196 ortets were selected in the first and second series respectively, cuttings rooted and planted in hedges for further propagation. After 3 years the ramets were planted in field experiments.

Test series and localities

Two series were established. Number F206 comprizing 151 clones were planted in 1984 and number F215 comprizing 196 clones were planted in 1985. The F206 experiments are located at 4 sites Frijsenborg, Sostrup, Lindet and Thy forest districts and the F215 experiments at other 4 sites Ulborg, Viborg, Thy and Ålholm forest districts. All experiments are unbalanced randomised block designs with single tree plots, 10 blocks, each clone represented by 3 to 12 ramets, spacing 1.5 m x 1.5 m. A direct import from the Queen Charlotte Islands is used as a standard.

Characters measured

Selection intensity: Visually the highest trees in the nursery bed were marked. Height was measured at each selected individual and the 22 neighbours. Sums of squares from each group of 23 trees were pooled to an overall estimate of the phenotypic variation and the selection differential for each ortet was estimated as the height difference between the marked tree and the mean of the 22 neighbours. The selection intensity "i" is the selection differential divided by the phenotypic standard deviation.

Height: Total height was measured at age 3 in the nursery (6 trees per clone) and after 5 growing seasons (i.e. 8 years from rooting of cuttings) in the field experiments, all trees were measured.

Autumn coloration: Autumn coloration is expected to be a measure of autumn hardening expressed as the percentage of the leader that have turned from green to brown. The character was measured at age 3 in the nursery on the same trees as used for height measurement (6 ramets per clone).

Flushing: Flushing were scored into classes using the method described by KRUTZSCH (1973). As examples score 0 is dormant, score 3 is burst of budscales and score 8: all needles more or less spread, new buds developing. The measurements are carried out at a time, where the majority of trees had passed phase 3 at the scale. Some ramets still have score 0 in late May. The frequency of score 0 ranges from 1.1% to 2.8%. Two experiments are showing a higher frequency of zeros respectively 32.3%, F206C, and 19.9%, F215C. The frequency of score 2 and 3s are in every experiment less than 0.6% indicating a very distinct group of zero-observations. If any at all, only a very few will flush later and these buds are in general considered dead. Date of scoring is shown in *table 1*.

Leader breaks: Trees with leader breaks were marked one others zero.

Mortality: Dead trees marked one others zero.

Frost damage before budburst – "April-frost": The damage were divided into 7 groups and scored in July 1991 in one experiment in each series. Score 1: dead, score 2: dying, only a few green needles, score 3: the last 2 years top growth and the 2 upper branch whorls are dead, score 4: leader dead, and also side branches could be damaged, score 5: damage developing, this year needles in the upper part are dying, the plant is generally green, score 6: few damages and only on side branches, 7: no frost damage.

Statistical analyses

All statistical analyses were carried out using the statistical program package SAS using Proc GLM for analysis of variance (SAS, 1990).

In the individual trials 5 year height, flushing and April-frost score are analysed in the model:

$Y = m + B + c + e$,

and an overall analysis of variance across trials is based on the model:

$Y = m + S + B(S) + c + c \cdot S + e$,

where Y : observed values, m: mean value, S: site, B: block, c: clone, c · S: clone x site interaction, and e: residual, e is assumed NIID and S and B assumed fixed other effects random.

The bivariate variables mortality and frequency of leader breaks were analysed after pooling block 1 to 5 and 6 to 10 respectively into 2 super-blocks and then using the same model as above, but caution in interpretation of the results is needed due to certain lack of randomisation within the super-blocks. The assumption for analysis of variance were highly violated for mortality due to severe skewed error distribution and data from the analyses are not presented. Different types of power-transformations did not solve the problem. As an alternative mortality was analysed by use of logistic regression using the SAS procedure Catmod (SAS, 1990). The Maximum Likelihood method was used for succesive iterations in the model $Y_{ij} = m + s_j + c_i$, where m: mean logit, s: site, c: clone and $Y_{ij} = In(p_{ij}/(1-p_{ij}))$, where p_{ij} is the probability of being dead at site j for clone i (ANDERSEN, 1989). Observations with zero mortality were added the value 0.001 and therefore regarding these observations as sampling zeros in order to secure estimates of all clones (SAS, 1990, p. 463).

Height in nursery and autumn coloration were analysed in a one-way analysis of variance, again caution is needed due to lack of replications.

Components of variance were estimated by using REML in the procedure Proc Varcomp.

Broad sense heritability across sites for clone means are estimated as

$$H^2_{BS} = \frac{V_c}{V_c + \frac{V_{cxs}}{r} + \frac{V_e}{r \cdot n}} \qquad [1]$$

where V: variance and subscripts, c: clone, c x s: clone-site interaction, e: error, r: number of sites, and n: number of replicates within site. Estimates of broad sense heritabilities for characters tested only on one site i.e. April-frost and nursery measurements of height and coloration are biased due to not estimated genotype environment interaction, and the nursery results are probably slightly biased due to some lack of randomisation.

Phenotypic correlations were calculated by using the procedure Proc Freq. Genetic correlations between measurements from 2 different sites, Type B correlations according to BURDON (1977), were estimated 2 by 2 as the phenotypic correlation among clonal mean values divided by the square root of the product of the clonal mean heritabilities from the 2 sites.

Ecovalence, the contribution of a genotype to the total genotype-environment interaction (GE), is calculated for the each clone according to WRICKE (1962, 1964) and interpreted as stability in an 'agronomic concept', i.e. small ecovalence values are preferred, as described by BECKER (1981).

In a similar way, calculations are carried out for the contribution of a single site to the sums of squares of the genotype-environment interaction. The expression gives an easy possibility to recognize deviating test-sites and their actual influence on the genotype-environment interaction sums of squares.

Efficiency of indirect selection in % (CR/R) is the gain by indirect selection on one site (X) for performance of the same trait on another site (Y) compared to direct selection on the site (Y) (FALCONER, 1981). Assuming equal selection intensity on both sites CR/R is estimated as the genetic correlation multiplied by the square root of ratio between clonal mean heritabilities of the site (X) over (Y).

Results and Discussion

Genotype-environment interaction

The 5 year measurements shows statistical significant interaction for height growth and flushing in both test series, see *table 1*. Analyses of variance using weigthed least square (wLS) estimates using reciprocal mean square error variances for each site gave nearly the same results (F-values for GE 1.63/1.70 and 1.33/1.35 respectively for series F206 and F215, where the denominator represents the wLS analysis), in spite of some differences in the error terms among sites (range 16.27 to 32.41 and 16.23 to 23.80 respectively in series F206 and F215).

For height the proportion of the variance components GE over G is 0.41 to 0.48 where as for flushing the proportion of GE over G is considerably lower 0.18 to 0.20 indicating a more stable ranking than for height, see *table 1*.

SHELBOURNE (1972) consider a GE over G coefficient less than 50% to have minor importance for selection purposes. The loss in potential gain by selection based on an omitted GE term is calculated for series F206 and F215. Percentage loss is respectively for the 2 series, 4.0% to 4.2% for height, 2.2% to 4,2% for flushing and 6.4% for leader breaks in series F206 (MATHESON and RAYMOND, 1986, p. 287), which generally seems to be of minor importance. Anyway, the numbers of clones contributing to the GE term also influence the decision how to rank and select clones. *Figures 1* and *2* show the accumulated ecovalence for height, flushing and leader breaks, the later only for series F206. The clones are sorted in descending order of GE contribution. Especially in series F206 only a few clones is responsible for half the sums of square of the GE term, i.e. 25 to 26 clones (out of 151 clones) for height and flushing respectively. In F215 the clones add more evenly to the GE for height growth, however, only a few are involved in the GE for flushing.

Further the ecovalence estimates for height growth (data not shown) for each clone is correlated to the characters shown in *table 4* and no significant correlations were detected. However, a weak (r = 0.18, p = 0.0250) correlation between ecovalence and mortality in series F206 and a weak negative correlation (r = 0.15, p = 0.0405) between ecovalence and autumn coloration (indicates higher ecovalence values for late colouring clones) was noticed in series F215.

For a proper evaluation of the GE term it is also necessary to evaluate the test sites. Height is further evaluated because it is the character showing the highest GE interaction. Correlation between sites for height based on clone mean values are shown in *table 2*, together with an estimate of the contribution of each site to the GE sums of squares. All correlations between sites

Table 1. – Site means, range and variance components, broad sense heritability (repetability) and potential gain estimates. Experiment F206, 5 year field measurements: height, leader breaks and mortality (status spring (1989), 6 year data flushing (24/5 to 28/5 1992), April-frost damage at one site (July 1991). Measurements in the nursery: height 3 years from cutting (autumn 1983) and autumn colouration (16/8 1983). Experiment F215, 5 year field measurements: height, leader breaks and mortality (status spring 1990), 6 year data flushing (21/5 to 27/5 1992), April-frost damage at one site (July 1991). Measurements in the nursery: height 3 years from cutting (autumn 1984) and autumn colouration (12/9 1984).

Experiment/ Character	Clones, Overall mean	Clones, Site mean range	Clones, mean range 1)	Standard, overall site mean	Standard, site mean range	Var.comp. clone	Var.comp. site x clone 2)		Var.comp. error	Var total	H^2 (B.S.)	Gain per selection unit		Grand clone mean rel. to std.overall, mean (range)
						%	%		%			units	%	
F206														
Height 5 year (cm)	180	105-220	26-332	149	67-207	14.5	6.0		79.5	3127.41	0.77	18.7	10	131 (102,159)
Flushing (score)	6.16	5.77-6.55	4.58-8.00	6.20	5.91-6.41	26.8	5.4		67.8	0.5432	0.87	0.36	6	100 (98,102)
Leader breaks (%)	41	32-53	0-100	58	38-86	8.6	10.8	**	80.6	904.59	0.39	5.5	13	-17 (-33,-4)
Mortality (%)	11	5-31	0-100	16	3-28	-	-		-	-	-	-	-	-5 (-21,3)
April-frost damage (score)	6.41	-	3.81-7.43	5.48	-	32.8	-		67.2	0.8925	0.74	0.47	7	1.10 score
Height nursery (cm)	50	-	25-87	-	-	44.0	-		56.0	259.6	0.83	9.7	20	-
Autumn colouration nursery (%)	68	-	45-95	-	-	38.0	-		62.0	230.9	0.79	8.3	12	-
F215														
Height 5 year (cm)	141	105-166	43-229	123	64-165	7.3	3.5		89.2	2224.48	0.68	10.5	7	123 (100,164)
Flushing (score) 3)	5.50	5.36-5.68	4.1-6.99	5.66	5.63-5.70	33.3	6.1		60.6	0.4869	0.88	0.38	7	97 (95,101)
Leader breaks (%)	38	13-60	0-100	54	31-84	10.0	3.2	ns	86.8	589.5	0.46	5.2	14	-16 (-6,-25)
Mortality (%)	12	3-20	0-100	12	3-24	-	-		-	-	-	-	-	-1 (-4,2)
April-frost damage (score)	5.39	-	2.24-7.06	2.89	-	30.4	-		69.6	3.4943	0.77	0.86	16	2.50 score
Height nursery (cm)	60	-	31-94	-	-	35.8	-		64.2	231.68	0.77	7.9	13	-
Autumn colouration nursery (%)	86	-	59-100	-	-	39.7	-		60.3	173.67	0.80	7.4	9	-

[1] Some lsmean values in % or scored value slightly exceeds the range of characters, character limits are used instead.

[2] All estimated effects are strongly significant $p < 0.001$ unless other notes are added, ns: non significant, *:$p < 0.05$ or **:$p < 0.01$.

[3] Only 3 sites.

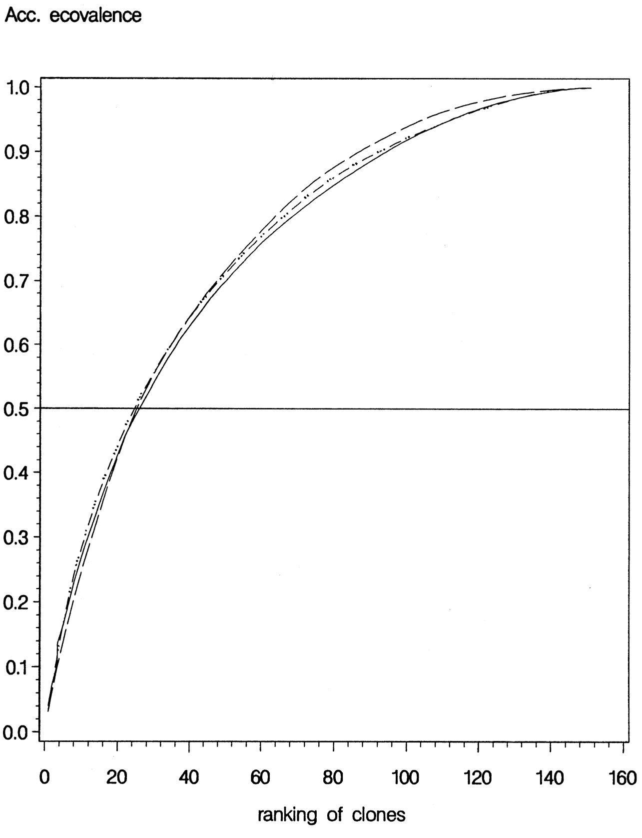

Figure 1. – Accumulated clonal ecovalence values sorted in descending order on absissa for the characters height (solid line), flushing (dashed line) and leader breaks (dot-dashed line). Results from experiment F206.

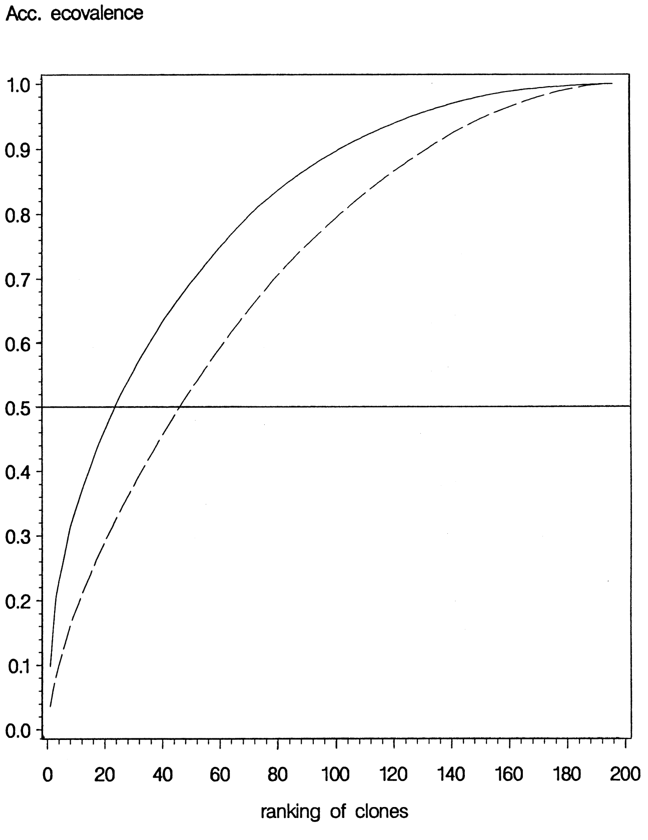

Figure 2. – Accumulated clonal ecovalence values sorted in descending order on absissa for the characters height (solid line) and flushing (dashed line). Results from experiment F215.

Table 2a. – Height growth. Correlations between sites based on clonal mean values, phenotypic under and genotypic above diagonal. Unless other is mentioned phenotypic correlations are significant at levels p < 0.001. The different sites contribution to the GE sums of squares in % is shown in the far right column.

Site	Heritability b.s.	Correlations genetic above and phenotypic under diagonal					Sums of squares GE (%)
F206		A	B	C	D	N	
A: Frijsenborg	0.70	1	0.64	0.71	0.78	0.71	28
B: Sostrup	0.67	0.44	1	0.57	0.75	0.59	23
C: Lindet	0.47	0.41	0.32	1	0.55	0.41	23
D: Thy	0.71	0.55	0.52	0.32	1	0.67	26
N: Nursery	0.79	0.53	0.42	0.25 (**)	0.42	1	-
F215		A	B	C	D	N	
A: Ulborg	0.51	1	0.65	0.71	0.50	0.50	23
B: Viborg	0.56	0.35	1	0.61	0.74	0.52	28
C: Thy	0.40	0.32	0.29	1	0.73	0.71	24
D: Ålholm	0.57	0.27	0.42	0.35	1	0.67	25
Nursery	0.80	0.32	0.35	0.40	0.45	1	-

Table 2b. – Efficiency of indirect selection in %. Direct selection on horisontal sites and indirect gain on sites indicated by vertical columns. Sites comprizing the nursery results (N) 3 years from cutting.

Site	Heritability b.s.	Efficiency of indirect selection (%)				
F206		A	B	C	D	Mean
A: Frijsenborg	0.70	100	66	87	77	77
B: Sostrup	0.67	63	100	68	73	68
C: Lindet	0.47	59	48	100	45	51
D: Thy	0.71	79	78	68	100	75
N: Nursery	0.79	76	63	53	59	63
F215		A	B	C	D	Mean
A: Ulborg	0.51	100	63	80	47	63
B: Viborg	0.56	69	100	73	74	72
C: Thy	0.40	63	52	100	61	59
D: Ålholm	0.57	53	75	88	100	72
Nursery	0.80	63	64	100	79	77

are positive, and the sites show in general an even contribution to the sums of square for GE.

Table 3 shows results from logistic regression analysis of mortality. Neither of the series show significant likelihood ratio test and therefore acceptance of the hypothesis of additivity between sites, i.e. no genotype-environment interaction. There are significant differences in mortality between sites, but only significant differences among clones in series F215.

As a conclusion, in spite of strong statistical significant GE interaction is present, it is considered of minor practical importance. Consequently, the following presentation on potential gains by selection is based on no subdividing of the test sites into zones. Therefore, also correlations between traits are based on clonal mean values across sites.

Gain by selection among clones for single traits

Table 1 shows genetic parameters and gain estimates based on overall analysis of the single traits.

Clonal mean broad sense heritabilities are very similar in the two series, showing highest values for flushing, slightly lower estimates for height, autumn coloration and April-frost, and a moderate clonal mean repeatability is seen for leader breaks. No estimates are made for mortality due to severely skewed mean and error distributions, and lack of homogeneity of variances. In general, there seems to be a slightly bigger variance in the F206 series compared to F215, see also *Selection for height in nursery.*

A present C-effect (LIBBY and JUND, 1967) or ”clone effect“ (ROULUND, 1981) will bias the estimates of heritabilities as well as variances. Anyway, CANNEL et al. (1988) shows that ”clone effects“ are neglectable after 5 years testing under field conditions.

Estimated gains for selection of the 30 best clones in each series are for height growth respectively 16% to 26%, flushing approximately 1/2 of a scoring unit, which corresponds to 3 to 4 days depending on weather conditions, April-frost is score 0.7

Table 3. – Logistic regression of mortality at year 5 from planting. Maximum-likelihood analysis of variance for the series F206 and F215.

Source	DF	Chi-square	Prob
Series F206			
Intercept	1	561.58	0.0000
Site	3	458.00	0.0000
Clone	150	144.47	0.6120
Likelihood ratio	448	435.69	0.6528
Series F215			
Intercept	1	605.23	0.0000
Site	3	285.13	0.0000
Clone	195	267.96	0.0004
Likelihood ratio	583	578.11	0.5494

to 1.3 which on both test sites is enough to avoid very severe damage. However, data on April-frost is only from one year and on one site in each series. Damage due to frost later in April or in the beginning of May will probably reduce the genetic differences, because more clones will have an active cambium the closer to the growing season the frost incident happens.

Autumn-coloration can be increased by 11%-points to 12% points, but the character seems to be a very poor predictor of mortality and number of leader damage, see *table 4*.

Number of leader breaks can roughly be reduced by 8%-point. In both series it is possible to select among a substantial number of clones with no or very little mortality, see *figure 3*. The higher mortality in experiment F206B is due to a severe flooding 2 years after planting.

Overall clonal deviation from the standard

The mean of the clonal populations is in each experiment compared to a standard provenance imported from Queen Charlotte Islands, see *table 1*. Height growth of the clones exceeds the standard by on average 23% to 31%. Especially on the poorer and probably more frost exposed sites are the mean of the clones considerably higher, maximum 59% to 64%, however on the milder sites no differences shows up, 0% to 2%. There is no practical differences in flushing and mortality between overall clone means and the standard, but the clones have in general fewer leader breaks, 16%-points to 17%-points.

The overall mean of clones shows remarkably fewer damages due to April-frost than the standard, scoring points 1.10 to 2.50. A part of the difference could be caused by the slower growth of the standard and therefore higher risk of being damaged.

Among direct imports, provenance studies shows that QCI provenances in general is among the very best adapted provenances under Danish conditions, NIELSEN (1994). Further, Danish second or later generation material is generally superior to direct imports from the same areas of origin concerning height growth, and in some experiments also for survival. The superiority is generally less expressed on milder conditions (NIELSEN, 1994).

Selection for height in the nursery

The estimated selection intensity for the individual ortets for height growth do not show significant correlation with the height growth at age 3 in the nursery nor with height growth after 5 years in the field, *table 4*. Unfortunately, a population sample of the stand from which the clones are selected is not included. Therefore, the ortet-ramet correlation is based on the ramets true heights from the nursery and the field tests and not on deviation from the population mean. This method could hide a general superiority of the selected clones compared to the population mean. Anyway, the selection intensities ranges from 1.54 to 5.96 (a single observation 8.02) and 0.83 to 4.59 respectively in the series F206 and F215 which should give a reasonable basis to estimate a possible linear relationship if a strong ortet-ramet relationship excists.

Indirect selection based on nursery measurements at age 3 yield about 63% to 77% of the estimated gain by direct selection at age 5, *table 2*. However, the correlation to older age could be quite different, as shown by LAMBETH (1980) for early measurements. Age 3 or 8 from cutting still is far before canopy closure and the results is expected to be more heavily influenced by environmental conditions such as frost damage etc.

Phenotypic correlations between characters

Table 4 shows the phenotypic correlations between characters based on clonal grand means over all four sites. Grand means are used in spite of the significant GE interaction for especially height growth, but correlations based on single sites shows in general the same picture, data not shown.

Table 4. – Phenotypic correlations between characters based on grand mean for each clone over all sites. April-frost score 0 = dead to 7 = no damage. Above diagonal experiment F215 under diagonal experiment F206. Correlation coefficients and probability level in brackets, unless other is mentioned correlations are non significant (o:p < 0.100, *:p < 0.05, **:p < 0.01, *** < 0.001).

F206\F215	Selection intensity	Height nursery	Height field 5 year	Flushing	Autumn colouration	Leader breaks	Mortality	April-frost score
Selection intensity	1	0.13 (o)	0.05	0.03	-0.06	0.01	0.01	-0.12 (o)
Height nursery	0.10	1	0.53 (***)	0.16 (*)	-0.52 (***)	-0.17 (*)	0.02	0.04
Height 5 year	0.04	0.57 (***)	1	0.07	-0.33 (***)	-0.49 (***)	-0.15 (**)	0.14 (*)
Flushing	-0.01	-0.01	-0.05	1	-0.14 (*)	0.09	0.17 (*)	-0.37 (***)
Autumn colouration	-0.07	-0.12	-0.21 (**)	0.02	1	0.19 (**)	0.03	0.09
Leader breaks	0.01	-0.06	-0.42 (***)	0.18 (*)	0.14 (o)	1	0.17 (*)	-0.14 (*)
Mortality	-0.03	-0.10	-0.31 (***)	0.01	0.04	0.21 (**)	1	-0.19 (**)
April-frost damage	-0.03	0.14 (o)	0.26 (**)	-0.33 (***)	-0.01	-0.31 (***)	-0.10	1

Between site correlations for height growth are shown in *table 2*.

The GE interaction for flushing is assumed to have minor importance for the overall mean values (GE interaction is only 18% to 20% of genetic variation between clones) and *figure 1* and *2* shows also a minor part of the clones are involved in the GE interaction.

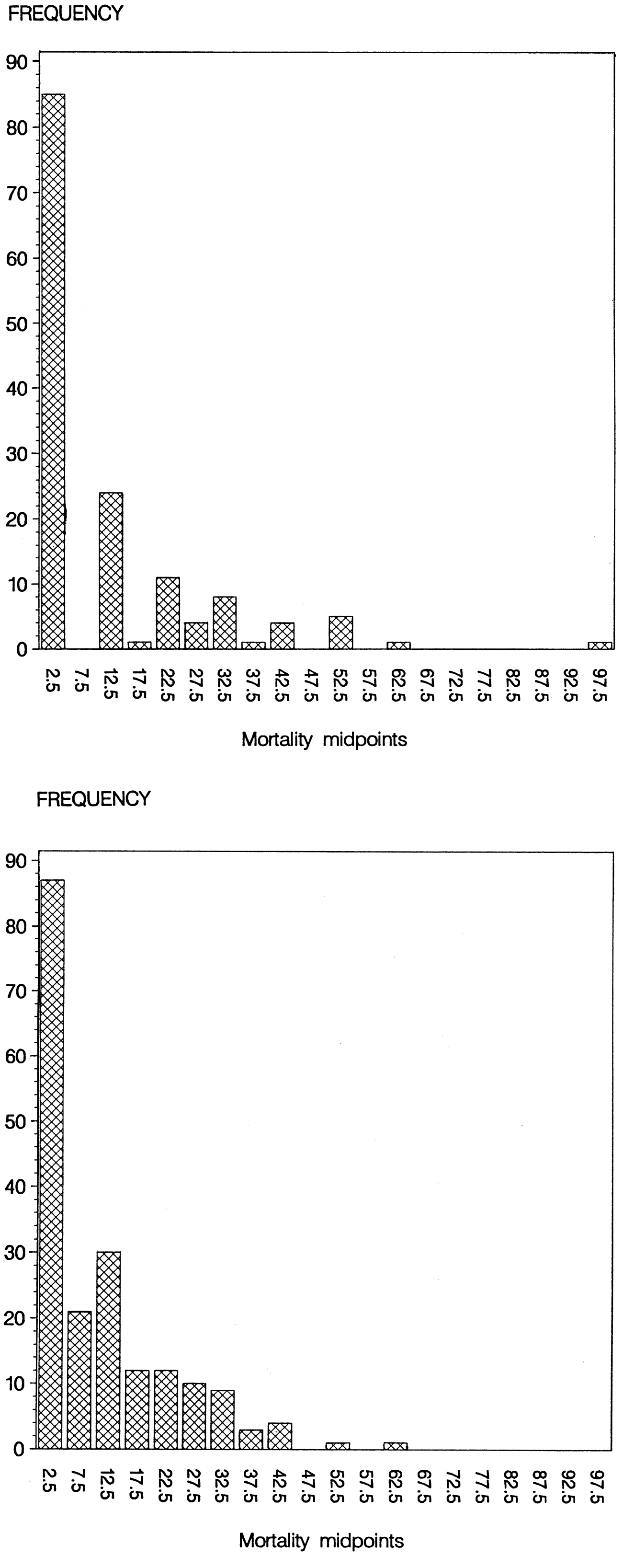

Figure 3a and *3b*. – Mortality. Frequency of clonal mean values for mortality calculated as grand means over sites. a) experiment F 206 and b) experiment F215.

Height at year 5 correlates negatively to leader damage and mortality at year 5. SHAW et al. (1988) found in a comparable study of Norway spruce clones, not surprising, that leader damaged ramets had a strong impact on the GE interaction for height growth evaluated only after 5 years. Lammas growth seems also to have some impact on genotype-environment interaction based on families (BIROT and CHRISTOPHE, 1983), but this trait is not measured in the experiments dealt with here. There is no detectable relationship between height growth and flushing, but a negative correlation between height and autumn coloration indicating a longer growing season for the tallest clones.

Two measures of phenology i.e. flushing and autumn coloration were carried out as indicators of frost sensitivity respectively in spring and autumn.

Early flushing seems to increase the numbers of dead trees and the numbers of trees with leader damage. An early autumn coloration indicating a short growing season are surprisingly (series F215) positive correlated with the numbers of leader damage, however early autumn coloration also have a strong negative relationship to height growth, which finally gives the slower growing clones i.e. clones with high value of coloration, a longer period in the risk zone for damage caused by frost and weed competition, which is far more severe close to the ground. Another possibility is that autumn coloration is a simple morphological trait and have no relationship with hardiness of the single clones. TOIVONEN et al. (1991) finds in Scots pine no correlation between coloration and hardening within provenances.

Flushing and autumn coloration is only weakly correlated and only in the series F215, indicating that early flushing gives an earlier autumn coloration.

April-frost damage seems to be more severe the earlier flushing of the clone. CANNEL and SHEPPARD (1982) shows strong differences between provenances in succeptability to April-frost, but no correlation to flushing evaluated on provenance mean values. April-frost damage are caused by freezing of the cambium weeks before flushing, but the flushing time seems fairly to match the ranking of frost damage of the cambium, and therefore probably also the start of cambium activity.

The better growth of the clones the fewer and less severe damage are seen due to April-frost, but this could partly be due to frost avoidance, because the damage is generally more severe on smaller trees.

Clones with many leader breaks seems also to have more severe damage due to April-frost, and this could partly be caused by the generally lower height of the leader damaged trees.

Utilization of the Results for Practical Purposes

The experimental series described in this paper is a part of a propagation programme as described for other species by a number of authors (KLEINSCHMIT et al. 1973; ROULUND, 1976). The problem here is the ageing of the clones, wether the method practised is propagation hedges or serial propagation (ST. CLAIR et al., 1985). Large scale propagation of Norway spruce and Sitka spruce is difficult after 10 years of hedging or 20 years of serial propagation. Therefore there is a limited number of years in which the results described in the previous part can be utilized. Unfortunately it is not possible directly from clonal trials to calculate breeding value or narrow sense heritability. In the literature there are only few examples dealing with the ratio of additive genetic variance and dominant genetic variance in the characters investigated here. Wellendorf (1983) found for height at 9 years in Norway spruce, that the ratio between additive and dominant variances was 2:1. Therefore although one may use the total genetic value of the clone as an estimate for its breeding value one has to admit that it is an overestimation. Further investigations on the ratio between additive and dominant variation in the most important traits in tree breeding are urgently needed.

Conclusions

The most important trait for stand establishment is survival. Essential is also resistance to various types of frosts and height growth in order to bring the tree up to a height, where climatic conditions and weed competition do not influence the survival.

The evaluated material of 347 clones gives us a possibility to draw conclusions about the genetic variation for some important traits, and how to utilize the results for practical purposes.

- There is a good possibility for selection of survival at age 5.
- There is a considerable variance among clones for April-frost damage.
- There is only a limited possibility to select for late flushing in spite of high clonal mean broad sense heritability estimates.
- Autumn coloration shows no reasonable correlation to field damage and may not be an appropriate measure of autumn hardening.
- Genotype-environment interaction exists, but are restricted to a limited number of clones.
- Early selection of ortets for height among 3 or 4 year old seedlings seem not to be an appropriate way to increase height growth at later stages.
- Compared to the direct imported standard the clones have a superiority in height and fewer damage, but there are hardly no differences in flushing time and mortality.

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References

Andersen, S.: Statistik analyse af tælledata. Matematisk Institut. Kgl. Veterinær- og Landbohøjskole. Duplicated (1989). — Becker, H. C.: Correlations among some statistical measures of phenotypic stability. Euphytica **30**: 835–840 (1981). — Birot, Y. and Cristophe, C.: Genetic Structures and Expected Genetic Gains from Multitrait Selection in Wild Populations of Douglas fir and Sitka spruce. Silvae Genetica **32** (5–6): 141–151 (1983). — Bornebusch, C. H. and Ladefoged, K.: Hvidgranens og Sitkagranens Dødelighed i Hede- og Klitplantager i 1938 og 1939. Forstl. Forsøgsv. Danm. **15**. 205–232 (1940). — Brandt, K.: Statusopgørelse for sitkagran. Dansk Skovf. Tidskr. **55**: 300–329 (1970). — Burdon, R. D.: Genetic Correlation as a Concept for Studying Genotype-Environment Interaction in Forest Tree Breeding. Silvae Genetica **26** (5–6): 168–175 (1977). — Cahalan, Ch. M.: Provenance and Clonal Variation in Growth, Branching and Phenology in *Picea sitchensis* and *Pinus contorta*. Silvae Genetica **30** (2–3): 40–46 (1981). — Cannel, M. G. R. and Sheppard, L. J.: Seasonal Changes in the Frost Hardiness of Provenances of *Picea sitchensis* in Scotland. Forestry **55** (2): 137–153 (1982). — Cannel, M. G. R., Sheppard, L. J. and Cahalan, C. M.: C Effects and Second Generation Clone Performance in *Picea sitchensis* and *Pinus contorta*. Silvae Genetica **37** (1): 15–19 (1988). — Costa et Silva, J., Nielsen, U. B. and Roulund, H.: Sitka Spruce Clonal Performance with Special Reference to Basic Density. Silvae Genetica **43**: 82–91 (1994). — Fabricius, O.: Douglas- og sitkagran. Dansk Skovf. Tidskr. **11**: 405–541 (1926). — Kleinschmit, J., Müller, W., Schmidt, J. and Racz, J.: Entwicklung der Stecklingevermehrung von Fichte (*Picea abies* Karst.) zur Praxisreife. Silvae Genetica **22**: 4—15 (1973). — Krutsch, P.: IUFRO S. 2.02.11. Norway spruce Development of buds. The Royal College of Forestry, Stockholm (1973). — Ladefoged, K.: Frostringsdannelser i Vårveddet hos unge Douglasgraner, Sitkagraner og Lærketræer. Forstl. Forsøgsv. Danm. **15**: 97–112 (1938). — Lambeth, C. C.: Juvenile-Mature Correlations in Pinaceae and Implications for Early Selection. Forest Science **26** (4): 571–580 (1980). — Libby, W. J. and Jund, E.: Variance associated with cloning. Heredity **17**: 533–540 (1967). — Lines, R.: Seed origin – sitka spruce. Rept. For. Res. For. Commn. 1983, London. p. 13 (1983). — Lines, R. and Samuel, C. J. A.: The main IUFRO Experiments with Sitka Spruce in Britain: Ten Year Results. *In:* Proceedings of the IUFRO International Sitka Spruce Provenance Experiment (Sitka Spruce Working Group S2.02.12) IUFRO 1984 Edinburgh, Scotland. Ed. Ying, C. C. and McKnight, L. A. pp. 21–36 (1993). — Matheson, A. C. and Raymond, C. A.: A Review of Provenance x Environment interaction: Its Practical Importance and Use with Particular Reference to the Tropics. Commonwealth Forestry Review **65** (4): 283–302 (1986). — Nielsen, U. B.: Genetisk variation i Sitkagran (*Picea sitchensis* (Bong.) Carr.) i højdevækst, stammeform og frosthærdighed – vurderet ud fra danske proveniens-, afkoms-, og klonforsøg. Forskingscentret for Skov & Landskab. Forskningsserien 9-94, x + 332 p. ill. (1994). — Poulsen, C. M.: Om nogle i vort Skovbrug anvendelige Nåletræer fra det vestlige Nordamerika. Tidsskrift for Skovbrug **6**: 47–104 (1883). — Redfern, D. B.: Spring Frost Damage on Sitka spruce. Forestry Commision Report on Forest Research – for the year ended March 1982. Her Majesty's Stationery Office, London (1982). — Roulund, H.: Forædling af sitkagran. Skoven **3**: 56–58 (1974a). — Roulund, H.: Klonskovbrug. Skoven **10**: 216–217 (1974b). — Roulund, H.: Stiklingeformering en hensigtsmæssig metode til skovbrugets forsyning med forædlede træsorter. Dansk Skovf. Tidsskr. **61**: 137–150 (1976). — Roulund, H.: A comparison of Seedlings and Clonal Cuttings of SItka Spruce (*Picea sitchensis* (Bong.) Carr.). Silvae Genetica **27**: 104–108 (1978). — Roulund, H.: Problems of Clonal Forestry in Spruce and their Influence on Breeding Strategies. Forestry Abstracts **42** (10): 457–471 (1981). — Roulund, H.: Outline to a Revision of the Sitka Spruce Breeding Plan in Denmark. Forest Tree Improvement **23**: 132–143 (1990). — Roulund, H. and Bergstedt, A.: Sammenligning mellem frøplanter og stiklingeformerede kloner af sitkagran (*Picea sitchensis* (Bong.) Carr.) 10 års resultater. Dansk Skovf. Tidsskr. **67**: 218–235 (1982). — SAS: SAS/STAT User's Guide. Vol. 1. ACECLUS-FREQ. Version 6, Fourth Edition. SAS Institute Inc., Cary, NC, USA (1990). — Shaw, D. V., Hellberg, A., Foster, G. S. and Bentzer, B.: The effect of Damage on Components of Variance for Fifth-Year Height in Norway Spruce. Silvae Genetica **37** (1): 19–22 (1988). — St. Clair, J. B., Kleinschmit, J. and Svolba, J.: Juvenility and Serial propagation of Norway Spruce Clones (*Picea abies* Karst.). Silvae Genetica **34**: 42–48 (1985). — Toivonen, A., Rikala, R., Repo, T. and Smolander, H.: Autumn Colouration of First Year *Pinus sylvestris* Seedlings during Frost Hardening. Scandinavian Journal of Forest Research **6** (2): 31–39 (1991). — Wellendorf, A. H.: Estimates of genetic parameters for 9-year Height in unbalanced disconnected factorial crosses in Norway spruce (*Picea abies* (L.) Karst). Forest Tree Improvement **16**: 1–11 (1983). — Wricke, G.: Über eine Methode zur Erfassung der Ökologischen Streubreite in Feldversuchen. Zeitschr. Pflanzenzüchtung **47**: 92–96 (1962). — Wricke, G.: Zur Berechnung der Ökovalenz bei Sommerweizen und Hafer. Zeitschr. Pflanzenzüchtung **52**: 127–138 (1964).