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Genetic Parameters for Spiral Grain, Stem Form, Pilodyn and Growth in 13 Years Old Clones of Sitka Spruce (*Picea sitchensis* (BONG.) CARR.)

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(Received 20th November 1996)

Summary

Spiral grain measured at ring number 6 or 8 from the pith on 13-years old ramets coming from 191 Sitka spruce clones tested at 4 sites showed a broad sense heritability on single tree level from 0.36 to 0.54. Standard deviations were in the interval from 1.61 to 1.97 degrees and the mean was on all sites about 5 degrees to the left. Predicted genetic gains equal to about 2 degrees reduction of spiral grain in the juvenile wood seems realistic even with moderate selection intensities. Genetic correlations with height, diameter, stem form and pilodyn were small or absent, and almost no genotype-environment interaction was present. Individual broad sense heritabilities for heights and diameters were moderate to low ranging from 0.08 to 0.31 and with coefficients of variation about 0.30. Moderate genotype-environment interaction was present for the 2 traits with genetic correlations across sites ranging from 0.57 to 0.85. Pilodyn had a moderate heritability about 0.32 and a coefficient of variation about 8%. The genetic correlation with diameter was 0.53 and with height 0.22 so the density must be taken in consideration when selecting for growth in Sitka spruce. The broad sense heritability for stem form using a scale from 1 to 9 was 0.37 and the coefficient of variation 0.22. Positive, but moderate genetic correlations with diameter and height was present, 0.27 and 0.21 respectively. Pilodyn and stem form were only measured in one trial.

Key words: Clonal trials, heritability, genetic correlations, genotype-environment interaction, spiral grain.

FDC: 165.3; 165.411; 232.11; 174.7 *Picea sitchensis.*

Introduction

Sitka spruce (*Picea sitchensis* (BONG.) CARR.) is an important tree species in the western parts of Denmark influenced by the Atlantic, where the salt impact makes it impossible to grow Norway spruce. It further plays a role in the eastern parts of Denmark on more swampy soils. It has therefore been subject for breeding since 1970 and the importance of the species has been growing in the eighties (ROULUND, 1990). The main disadvantage of Sitka spruce wood is that the sawn timber and boards are twisting considerably, which causes a considerable amount of wastage.

The relationship between spiral grain and twist has theoretically and empirically been shown by STEVENS and JOHNSON (1960) and BALODIS (1972). Specifically for Sitka spruce, HARVALD (1988, 1989) and DANBORG (1994a) has shown significant correlations about 0.5 between twist and spiral grain with higher correlations in small dimensions and boards from the inner parts of the trees.

The spiral grain in the juvenile wood of Sitka spruce is of particular importance. Firstly because of the normally high level of spiral grain in the juvenile wood of Sitka spruce, (BRAZIER, 1967; PEDINI, 1990; JENSEN, 1994). Secondly because fast growth in the youth and a limited rotation length of about 50 to 60 years, means that the wood of the adult trees from Sitka spruce plantations in Denmark will normally have a considerable percentage of juvenile wood. Thirdly, because the boards from the inner parts of the stems, as mentioned before, are more susceptible to twist. Spiral grain in Sitka spruce has been found to be under considerably genetically control concerning the level of spiral grain, the radial pattern and the height pattern within same ring number (HANSEN and ROULUND, in preparation). However more broadly based genetic parameters such as heritability and genetic correlations with other traits still needs to be revealed. The high degree of genetic control is in agreement with findings in other tree species (see HARRIS, 1989, for a review).

Therefore spiral grain is being considered as an important selection criteria in the breeding programme (ROULUND, 1990). In the light of this, the objectives in this paper are primarily to describe the genetic variation of spiral grain in the juvenile wood and the correlations with other traits. The paper also looks at the genetic parameters for height, diameter, stem form and pilodyn 10 years after establishment. A comprehensive description of selection strategies in Sitka spruce will be discussed in a subsequent paper.

Material

The 4 trials designated A, B, C and D consist of 191 clones propagated in 1982 and planted in 1985. The clones were selected for height growth in a population of 4-years old seedlings, originating from a bulked seedlot of the provenance Havredal F. 379 of Washington origin. It was not possible to trace back the mother trees of the clones. The trials are

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designed as randomized complete blocks with eight blocks (replications) and single tree plots. Seedlings of Queen Charlotte Island origin are included in the trials as a reference. Each block is about 300 m^2 (*Table 1*).

Sampling and Methods

The spiral grain was measured on the outside of the trees in opposite directions (north and south) and the average of the opposite measurements was used to correct for non vertical stem axis (BRAZIER, 1965). A protractor with a level as described by HARRIS (1984) was used to measure the spiral grain on the outside of the trees. The spiral grain inside the bark was detected using a needle on a free pivot arm, with the needle going through the bark and scribing along the spiral grain. Inclinations to the left of the vertical axis were assigned positive and inclinations to the right negative. The spiral grain was measured between the 7th and the 8th branch whorl (SG8) in trial B and D and between the 5th and 6th branch whorl (SG6) in trial A and C. It was further possible to measure the spiral grain between the 7th and 8th branch whorl on 585 trees in trial A. The sampling levels were between 0.25 m and 2 m. Different growth patterns on the sites made it impossible to measure between the same branch whorl in all trials. The spiral grain was measured between the same branch whorls instead of a fixed level e.g. 1.3 m, to ensure that the spiral grain was measured on the same ring number counted from the pith on all clones.

Pilodyn was measured only on the 629 largest trees in trial B with one penetration per tree after removal of the bark. Heights (H95) measurements from 1994 and 1995 were available on all sites. Diameters at 1.3 m (D95) were measured in trial A and B in 1995 and trial D in 1994. Stem form was measured in 1995 in trial B using a score from 1 to 9, with 9 being the best.

Statistical Analyses within Sites

The following linear model was used to analyse the data within sites:

$$Y_{ij} = \mu + B_j + c_i + \varepsilon_{ij}$$

where Y_{ij} performance of ramet of ith clone within jth block. μ overall mean, b_j random effect of the jth block, c_i random effect of the ith clone, $E(c_i) = 0$ and $Var(c_i) = \sigma^2_c$, ε_{ij} random error, equal to the interaction between the ith clone and jth block, $E(\varepsilon_{ij}) = 0$ and $Var(\varepsilon_{ij}) = \sigma^2_e$.

The analysis of variance was performed using the procedure GLM with the option MANOVA in SAS® (SAS Institute Inc., 1990) to estimate covariances. Tests for normal distributions of single tree data, clone means data and residuals were done, using the SHAPIRO-WILK statistic, W, in the procedure Univariate in SAS®. Variance homogeneity was controlled graphically by plots of residuals as function of predicted values, RUDEMO and SKOVGÅRD (1984).

Pronounced skew distributions of height and diameter were present in F216D. Logarithmic and square transformations did not succeed in achieving a normal distribution. Nevertheless heritabilities and predicted gains for height and diameter on single tree level in F216D are reported.

The data was not fully balanced. This was especially the case for the measurements of spiral grain on ring no. 8 in trial A, the measurements of spiral grain in trial C and D, and further pilodyn measurements in B. The missing measurements in trial A and C were mainly due to small trees and small distances between the branch whorls, which made it impossible to measure the spiral grain, while several trees were missing in trial D. Broad sense heritabilities on single tree- and clone means levels were calculated. According to COTTERILL (1987) a distinction was made between different heritabilities depending on the purpose. The calculated broad sense heritability on single tree level is in this case used to calculate genetic gains by mass selection on sites similar to the trials, where the block effects can not be taken into account. The broad sense heritability on a clonal mean basis is appropriate for predicting genetic gains from selection among the clones in the trials. In this case, the effect of blocks can be accounted for prior to selection.

The individual broad sense heritability h^2_j was therefore calculated as:

$$h_i^2 = \frac{\sigma_c^2}{\sigma_c^2 + \sigma_b^2 + \sigma_e^2}$$

where σ_c^2 is the genetic variance or covariance components between clones, σ_b^2 is the block variance and σ_e^2 the error variance components.

The broad sense heritability on clone mean level h^2_m was calculated as:

$$h_m^2 = \frac{\sigma_c^2}{\sigma_c^2 + \frac{\sigma_e^2}{b}}$$

where b is the harmonic mean of ramets per clone in the trial (as given in the GLM procedure). Approximate standard deviations of heritabilities were found using the delta technique (BULMER, 1980). The genetic correlations r_g between trait x and y within sites were calculated according to FALCONER (1989) as:

$$r_g = \frac{Cov_{c_{xy}}}{\sqrt{\sigma_{c_x}^2 \sigma_{c_y}^2}}$$

The genetic covariance Cov_{cxy} was obtained by using mean cross products from the MANOVA option in the GLM procedure. Approximately standard deviations of the genetic correlation's within sites were calculated according to FALCONER (1989). The phenotypic correlations r_p between trait x and y was calculated as the PEARSON correlations using the procedure CORR in SAS. This could be done since the phenotypic correlations in this case included all elements of covariances/variances: The genetic – , the block – and the error covariance/variance. So according to FALCONER (1989):

$$r_p = \frac{Cov_{c_{xy}} + Cov_{b_{xy}} + Cov_{e_{xy}}}{\sqrt{(\sigma^2_{c_x} + \sigma^2_{b_x} + \sigma^2_{e_x})(\sigma^2_{c_y} + \sigma^2_{b_y} + \sigma^2_{e_y})}}$$

where Cov_{cxy} genetic covariance between trait x and y. Cov_{bxy} block covariance between trait x and y. Cov_{exy} error covariance between trait x and y. σ_c^2 genetic variance or variance components between clones. σ_b^2 block variance. σ_e^2 error variance components. Subscripts refer to trait x or y.

Statistic Analyses Across Sites

The linear model for the analysis of variance across sites had the following composition:

$$Y_{ijk}=\mu+E_i+B_{j(i)}+c_k+ce_{ik}+\varepsilon_{ijk}$$

where Y_{ijk} is the performance of the ramet of the kth clone in jth block within ith site, μ is the overall mean, E_i is the fixed effect of ith site, c_k is the random effect of kth clone with $E(c_k) = 0$ and $\mathrm{Var}(c_k) = \sigma^2_c$, ce_{ik} is the random effect of interaction between ith site and kth clone with $E(ce_{ik}) = 0$ and $\mathrm{Var}(ce_{ik}) = \sigma^2_{ce}$, $B_{i(i)}$ is the fixed effect of jth blocks within ith sites, and ε_{ijk} is the random error (or residual) due to clone by block interaction within the ith site with $E(\varepsilon_{ijk}) = 0$ and $\mathrm{Var}(\varepsilon_{ijk}) = \sigma^2_\varepsilon$.

The test of genotype-environment interaction in the model requires in order to be valid 1) homogeneous clonal variances across the different sites to avoid a generation of genotype-environment interaction due to scale effects 2) homogeneous residual variance among environments and 3) normal distribution of the residuals (BURDON, 1977). These conditions for the model was fulfilled, testing the genotype-environment interaction concerning spiral grain between the four trials. However, some transformation of data from trial D, was necessary in the analyses between trial A-D, B-D and C-D. The transformations implied a reduction of the values by a factor equal to the ratio of variance of residuals from the 2 sites in the analyses, to secure homogenous residual variances across sites. In those cases, it was necessary further to use logarithmic values to get normal distributions of the residuals. The conditions for testing the genotype-environment interaction in the model were not present concerning height and diameter.

Genetic correlations r_g across sites for all traits were calculated using type B covariances (BURDON, 1977) and the genetic variances of the traits within sites, considering the same trait measured on different sites as different traits. So the genetic correlation across sites according to the definition in FALCONER (1989) was found as:

$$r_g=\frac{Cov_{g_{xy}}}{\sqrt{\sigma^2_{g_x}\sigma^2_{g_y}}}$$

The method gave in some instances correlations above 1 for spiral grain due to sampling errors. Correlations across sites for spiral grain were therefore afterwards found as intra class correlations on basis of the variance components in the model used for the analyses across sites. The intra class correlations r_g is alternatively calculated as:

$$r_g=\frac{\sigma^2_c}{\sigma^2_c+\sigma^{2'}_{ce}}$$

where r_g correlation across sites. σ^2_c clone variance across 2 sites. $\sigma^{2'}_{ce}$ clone-environment interaction, adjusted for site differences in variance, estimated as:

$$\sigma^{2'}_{ce}=\sigma^2_{ce}-\frac{\left(\sqrt{\sigma^2_{c_x}}-\sqrt{\sigma^2_{c_y}}\right)^2}{2}$$

where σ^2_{cx} genetic- or clone variance on site x. σ^2_{cy} genetic- or clone variance on site y. From EISEN (1994) based on ROBERTSON (1959), DICKERSON (1962), YAMADA (1962), EISEN et al. (1963). FERNANDO et al. (1984) found the method to give biased estimates in case of unbalanced data, unless genetic variances and residual variances on different sites are equal to each other. Although data were not fully balanced, given that genetic variances and residual variances on at least 3 of the sites, A, B and C were similar. Formula 8 was considered appropriate to estimate the genetic correlations.

Differences between clone means on one site and clone means on another site were calculated in order to investigate differences between clones, concerning sensitivity to changes in the environment. The differences were found after adjustments due to differences in variances between 2 sites x and y. This was done by multiplying the clone mean on one of the sites with a regression coefficients b_{yx}. The difference between a clone mean on site x and y, dif_{xy}, was e.g. found as:

$$dif_{xy}=(b_{yx}\overline{m}_x)-\overline{m}_y$$

where b_{yx} regression coefficient to adjust for differences in variances between clone means on 2 sites x and y. In this case used to make means on site x comparable to means on site y. $\overline{m}_x$ clone mean on site x. $\overline{m}_y$ clone mean on site y.

The regression coefficient b can be found as:

$$b_{yx}=\frac{Cov_{xy}}{V_x}=\frac{r\sqrt{V_x}\sqrt{V_y}}{V_x}$$

where Cov_{xy} is the covariance between clone mean on site x and site y assuming zero genotype-environment interaction. r is the clonal means correlation across sites equal to 1 since the genotype-environment interaction is assumed to be zero, V_x is the clone mean variance on site x and V_y is the clone mean variance on site y.

Differences were calculated having one site that was both independent and dependent in relation to another site. An analysis of variance of the numeric differences between clone means on different sites was then carried out in order to examine if some clones in general reacts more sensitive to changes in the environment than others.

Results

In trial A the mean spiral grain on ring 6 was 4.99 degrees, the mean diameter 34.2 mm and the mean height 28.1 dm. In trial B the mean spiral grain on ring 8 was 4.69 degrees, the mean diameter 49.8 mm, the mean height 49.8 dm, the mean stem form score 5.69 and the mean pilodyn 12.8 mm. In trial C the mean spiral grain on ring 6 was 5.02 degrees and the mean height 24.9 dm. In trial D the mean spiral grain on ring 8 was 5.32 degrees, the mean diameter 44.3 mm and the mean height 36.6 dm.

Spiral grain

Differences between clones were highly significant in all trials and the individual broad sense heritability was about 0.50 in trials A, B and C and lower ($h^2 = 0.36$) in trial D, which probably can be attributed to a sampling error due to missing trees in the trial and variable growth conditions within the blocks (*Table 2*). The phenotypic standard deviations were between 1.7 and 2.0 degrees and the average of spiral grain in the trials were about 5 degrees. Compared to the other traits the heritabilities were high, but absolute values of the phenotypic standard deviations were low. A moderate selection intensity i = 1.40 equal to a selection of the 20% best clones will give a predicted genetic gain about 1.5 degrees, while a mass selection outside the trials will give a predicted gain about 2 degrees with a selection intensity i = 2.655 equal to a selected proportion about 1%.

Table 1. – Site characteristics.

Site:	Latitude	Longitude	Blocks	Number of trees	Soil	Precipitation mm
A	56° 16' N	8° 30' E	8	1399	Sand	700-750
B	56° 20' N	9° 17' E	8	1230	Sand	650-700
C	56° 49' N	8° 17' E	8	1044	Sand	650-700
D	53° 41' N	11° 50' E	8	1022	Clay/chalk	550-600

Table 2. – Variance components and individual broad sense heritabilities on the different sites. Furthermore predicted gains (G) by phenotypic selections with selection intensity i = 2.655 and by selection among the clones in the trial, using the clonal mean heritability and with a selection intensity of i = 1.400.

Traits/trails	Vb	Vc		Ve	Vp	h²	s.e.	G	G %	G	G %
								Phenotypic sel.		Selection in trial	
SG6											
A	0.02	1.32	***	1.42	2.77	0.48	*0.03*	2.1	43	1.5	30
C	0.03	1.09	***	1.47	2.59	0.42	*0.16*	1.8	36	1.2	25
SG8											
A	0.02	1.80	***	1.55	3.37	0.54	*0.04*	2.6	48	1.7	31
B	0.02	1.58	***	1.36	2.96	0.54	*0.03*	2.4	52	1.6	35
D	0.06	1.39	(***)	2.42	3.87	0.36	*0.04*	1.9	35	1.4	26
Height											
A	11.74	12.03	(***)	61.63	85.40	0.14	*0.03*	3.5	12	3.7	13
B	1.51	44.51	(***)	96.67	142.69	0.31	*0.03*	9.9	20	8.1	16
C	25.44	25.19	(***)	83.83	134.46	0.19	*0.13*	5.8	23	5.6	22
D	146.49	23.02	***	101.63	271.14	0.08	*0.03*	3.7	10	5.0	14
Diameter											
A	33.74	24.62	***	141.88	200.24	0.12	*0.03*	4.6	14	5.1	15
B	4.00	91.75	(***)	281.45	377.20	0.24	*0.03*	12.5	20	11.0	17
D	367.15	63.08	***	313.85	744.08	0.08	*0.03*	6.1	14	8.0	18
Stem form											
B	0.02	0.63	***	1.05	1.696	0.37	*0.03*	1.28	22	0.97	17
Pilodyn											
B	0.12	1.06	***	2.12	3.297	0.32	*0.04*	1.55	12	1.15	9

In the table. Non significant differences between clones = n.s., $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***. Brackets = lack of normal distributions for residuals.

The mean spiral grain of about 5 degrees on ring no. 6 and 8 in the trials is in agreement with former findings by Brazier (1967) and Pedini (1990).

Investigations of *Pinus radiata* has shown individual broad sense heritabilities of about 0.70 (Harris, 1989). So the heritabilities found in these investigations seems small compared to that. More precise measurements, e.g. on stem discs, would probably have led to smaller residual variances and hence higher broad sense heritabilities. The phenotypic standard deviations were similar to those reported by Pedini (1990) for rings 6 to 8.

Height, diameter, stem form, pilodyn

Clonal differences in height and diameter after 13 years, were highly significant on all sites (*Table 2*) with low to moderate individual broad sense heritabilities, ranging from 0.08 to 0.31 for height and from 0.08 to 0.24 for diameter at 13 years. Predicted genetic gain was 15% for a selection intensity of 20% based on clonal means. The predicted gain from a mass selection is about 10% to 20% for a selection intensity of 1% (i = 2.655). The heritabilities on clone mean levels and phenotypic standard deviations are close to those reported by Nielsen (1994) in the same and other 5 year old Sitka spruce trials. Heritabilities for heights and diameters on site D were lower compared to the other sites, probably due to very uneven growth conditions within the blocks and the relatively small number of trees.

Stem form had a moderate broad sense heritability on single tree level at 0.37 and a coefficient of variance at 0.23. Predicted gains are about 15% for a selection of the best 20% clones in the trials, and about 22% following mass selection of the 1% best individuals.

Pilodyn had a moderate individual broad sense heritability of 0.32 and a coefficient of variation of 0.14. The sampling on the largest trees in trial B may have lowered the heritability due to the strong correlation of this trait with pilodyn. Also the selection in the nursery may indirectly have reduced the genetic variation of pilodyn, although Nielsen (1994) did not report any effects of selections in the nursery at height 5 years after establishment in the trials. The clonal differences in trial B were highly significant. The relatively small coefficient of variation of about 14% for pilodyn, is in agreement with findings by Petty et al. (1990) in Sitka spruce, concerning basic density, where the coefficient of variation was 10%. Predicted gains are 9% in a selection among clones in the trials with 20% selected and 12% by a mass selection with 1% selected. The pilodyn measurements can give reasonable estimates of the basic density according to findings by Silva e Costa et al. (1994) in 7 23-years old Sitka spruce clones, where the phenotypic correlation for pilodyn with basic density was –0.84, based on clone means. The correlations in Silva e Costa et al. (1994) are however not fully comparable to the measurements in this investigation, because of differences in ages.

Correlations between traits within sites

Spiral grain in ring number 6 and 8, showed in general very small or null genetic- and phenotypic correlations with other traits (*Table 3*). This is in agreement with findings by Hansen and Roulund (in preparation) in 7 clones and Jensen (1994) in 24 Sitka spruces of different ages. Also Brazier (1967) found, in 116 Sitka spruce trees from 19 sites, no pronounced differences in spiral grain between fast growing- and slow growing trees in the innermost 10 rings. However, fast growing trees of Sitka spruce have a tendency to maintain a higher level of positive (to the left) spiral grain after ring number 10. Brazier (1967) found furthermore large standard deviations within the groups, which would suggest a strong genetic influence on spiral grain. Results from Pedini (1990) from an investigation of 24 and 16 Sitka spruces from different provenances in 2 stands showed that the fastest growing trees also had higher positive spiral grain in the inner ring numbers, compared to the medium and slow growing groups, however results should be interpreted with caution given the reduced number of trees in each group. The stands were further characterized by high site indices, which might explain why the correlation with growth for the trees in the most fast growing group was apparent in the inner rings. Like Brazier (1967), Pedini (1990) also found the fastest growing trees had a tendency to maintain a high level of positive spiral grain. Findings by Danborg (1994b) in Norway spruce, support that increased growth leads to a delay in the normal reorientation of the inclination from the left (positive) to the right (negative), at least on fertile soils, although the tendency was not significant on one fertile site. Furthermore differences were not evident in the rings 1 to 5 from the pith, which Danborg (1994) ascribes to less pronounced differences of ring width between fast growing and slow growing trees in the juvenile stage. The same delay of reorientation in fast growing Norway spruce on a fertile soil has been found by Jensen (1994) and Jørgensen et al. (1996).

Very high phenotypic and genetic correlations were found between height and diameter (*Table 3*). The high positive correlations found between growth and pilodyn in Sitka spruce in agreement with former findings concerning growth and basic density in Sitka spruce (e.g. Silva e Costa et al., 1994;

PETTY et al., 1990 and HARVALD and OLESEN, 1987). Moderate positive phenotypic and genetic correlation between stem form and height and diameter was also found in trial B (*Table 3*). Similar results have been found by NIELSEN (1994) in 2 half sib trials.

Table 3. – Phenotypic (below diagonal) – and genetic (above diagonal) correlations within sites. (PIN: Pilodyn).

F216A: Sandfær Plantage

	SG8	SG6	Height	Diameter
SG8		0.85	0.18	0.16
		0.02	*0.12*	*0.15*
SG6	0.53		0.02	-0.03
	***		*0.10*	*0.12*
Height	0.04	0.06		0.86
	n.s.	n.s.		*0.04*
Diameter	0.01	0.07	0.94	
	n.s.	*	***	

F216B: Havredal plantage

	SG8	Height	Diameter	Form	PIN
SG8		0.07	0.05	0.05	0.02
		0.07	*0.09*	*0.07*	*0.10*
Height	0.06		0.77	0.21	0.22
	*		*0.04*	*0.09*	*0.12*
Diameter	0.07	0.90		0.27	0.53
	*	***		*0.10*	*0.12*
Form	0.05	0.23	0.22		0.10
	n.s.	***	***		*0.13*
PIN	0.08	0.55	0.70	0.15	
	*	***	***	***	

F216C: Lodbjerg plantage

	SG6	Height
SG6		0.24
		0.14
Height	-0.03	
	n.s.	

F216D: Roden skov, Ålholm.

	SG8	Height	Diameter
SG8		0.20	0.10
		0.16	*0.18*
Height	-0.04		0.68
	n.s.		*0.13*
Diameter	-0.05	0.95	
	n.s.	***	

H_0: Correlations = 0. Non significant = n.s., $P < 0.05$ = *, $P < 0.01$ = **, $P < 0.001$ = ***.

Effects of sites and genotype-site interaction

Spiral grain

Although the differences of spiral grain between the sites were small, they were statistical significant different, except between trial A and C (*Table 4*).

Table 5. – Genetic correlations within and across sites.

	SG8A	SG6A	H95A	D95A	SG8B	H95B	D95B	FORM	PIN	SG6C	H95C
SG8B	0.90	0.69	-0.19	-0.17							
H95B	-0.10	0.11	0.62	0.43							
D95B	0.01	0.10	0.54	0.57							
FORM	0.07	0.00	0.00	0.03							
PIN	0.02	0.00	0.02	0.09							
SG6C	0.91	0.82	-0.09	-0.10	0.74	0.12	0.07	0.22	0.00		
H95C	-0.10	-0.12	0.68	0.51	-0.18	0.58	0.56	0.28	0.14		
SG8D	0.84	0.67	0.03	0.01	0.91	0.08	0.03	0.14	0.04	0.77	-0.06
H94D	-0.30	-0.13	0.85	0.75	-0.17	0.84	0.68	0.24	0.33	-0.05	0.60
D94D	-0.37	-0.18	0.78	0.81	-0.10	0.76	0.78	0.21	0.63	-0.10	0.58

Very high genetic correlations across sites showed that spiral grain in Sitka spruce exhibit very little genotype-environment interaction (*Table 5*). However, all hypothesis of genotype-environment interactions equal to zero between different environment were rejected in the analysis of variance across sites. The analysis of variance of the differences between clone means on different sites revealed significant differences among clones concerning sensitivity to changes in the environment (*Table 6*).

Table 6. – Results from the analyses of variance on differences between clone means on different sites. Spiral grain.

Source:	D.F.	MS	F-value	P > F
Clone	185	327	6.8	0.0001
Residual	1710			

Height and diameter

Significant differences between the sites were present, except between site A and site D (*Table 7*). Site B had the highest growth and site C the poorest growth.

Genotypic correlations for heights and diameters across sites are moderate to high, ranging from 0.43 to 0.85 (*Table 5*) and agree with previous estimates by NIELSEN (1994).

The analysis of variance of the differences between clone means of height on different sites showed here as well that some clones in general were more sensitive to changes in the environment (*Table 8*).

Correlations between different traits across sites

Genetic correlations between different traits across sites, using the type B – covariances between clone means as described by BURDON (1977) were in general smaller and of opposite signs compared with the correlations found within sites, although

Table 4. – Results from the analyses of variance across sites concerning spiral grain. Results from analyses using transformed (tr.) – and non transformed data from trial D shown.

Trials	A-B			A-C			A-D			A-D (tr.)		
Source:	D.F.	F	P>F	D.F.	F	P>F	D.F.	F	P>F	D.F.	F	P>F
Site	1	5.4	0.0256	1	0.1	0.7917	1	5.5	0.0252	1	32.4	0.0001
Block(site)	12	2.8	0.0008	13	2.5	0.0027	13	3.0	0.0002	13	2.8	0.0005
Clones	190	2.7	0.0001	186	4.3	0.0001	187	3.1	0.0001	187	3.0	0.0001
Clones x sites	181	2.8	0.0001	141	1.6	0.0001	169	2.1	0.0001	169	2.1	0.0001
Residual	1676			1183			1337			1337		

Trials	B-C			B-D			B-D (tr.)			C-D			C-D (tr.)		
Source:	D.F.	F	P>F	D.F.	F	P>F	D.F.	F	P>F	D.F.	F	P>F	D.F.	F	P>F
Site	1	5.1	0.0296	1	20.6	0.0001	1	7.1	0.0130	1	5.7	0.0234	1	37.4	0.0001
Block(site)	13	2.3	0.0050	13	2.9	0.0004	13	2.7	0.0008	14	2.3	0.0036	14	2.4	0.0033
Clones	187	3.9	0.0001	188	4.0	0.0001	188	4.5	0.0001	178	3.7	0.0001	178	3.5	0.0001
Clones x sites	143	1.7	0.0001	171	1.4	0.0011	171	1.5	0.0001	137	1.2	0.0561	137	1.4	0.0050
Residual	1223			1377			1377			884			884		

Table 7. – Results from the analyses of variance across sites concerning height growth.

Trial	A-B	Height		Diameter		A-C	Height		A-D	Height		Diameter	
Source:	D.F.	F	P > F	F	P > F	D.F.	F	P > F	D.F.	F	P > F	F	P > F
Site	1	217,0	0,0001	149,0	0,0001	1	6,1	0,0261	1	3,0	0,1056	1,2	0,3004
Block(site)	14	15,0	0,0001	14,8	0,0001	14	36,2	0,0001	14	122,0	0,0001	100,2	0,0001
Clones	190	2,1	0,0001	2,0	0,0001	187	1,7	0,0001	187	2,0	0,0001	1,6	0,0004
Clones x sites	185	2,4	0,0001	2,1	0,0001	179	2,0	0,0001	181	1,7	0,0001	1,8	0,0001
Residual	2238					2061			2037				

Trial	B-C	Height		B-D	Height		Diameter		C-D	Height	
Source:	D.F.	F	P > F	D.F.	F	P>F	F	P>F	D.F.	F	P>F
Site	1	204,0	0,0001	1	11,8	0,004	12,3	0,0033	1	7,1	0,0182
Block(site)	14	18,8	0,0001	14	87,9	0,000	66,1	0,0001	14	108,9	0,0001
Clones	189	2,1	0,0001	190	2,2	0,000	1,7	0,0002	185	1,7	0,0001
Clones x sites	178	1,9	0,0001	179	1,7	0,000	1,6	0,0001	175	1,8	0,0001
Residual	2273			1825					1690		

Table 8. – Results from the analyses of variance on differences between clone means on different sites. Height growth.

Source:	D.F.	MS	F-value	P > F
Clone	187	169	2.38	0.0001
Residual	1978			

differences were small (*Table 8*). Probably the differences can be ascribed to influence of sampling errors, genotype-environments interactions for the traits and by the fact that the environmental correlations are zero across sites, but negative within sites. The moderate genetic correlation between stem form and height in trial B disappear between stem form in trial B and height in trial A, as well as the strong correlation between pilodyn and diameter in trial B disappear between pilodyn in trial B and diameter in trial A. Possibly the change in correlations across trial A and B are caused by genotype-environment interaction for heights and diameters which eliminates the correlations between those traits and stem form and pilodyn seen within B.

Conclusion

Reducing spiral grain in Sitka spruce juvenile wood by 1 to 2 degrees seems achievable, without loosing substantial gains in growth as a result of low correlations between spiral grain and growth. Low correlations with the other traits (pilodyn and stem form) was also apparent. Measurements of spiral grain on one site seems to be sufficient given the very high genetic correlations across sites. Considerable gains in growth above 10% are possible even with moderate selection among the clones. The genetic correlations across the sites did not clearly indicate any significant advantages, using target environments. Pilodyn showed the expected positive high correlation with growth and the trait must definitely be taken into consideration, when selecting for growth. Heritability and standard deviation for pilodyn is moderate. The potential for improving the stem form of Sitka spruce is high with moderate heritability and positive correlations with height and diameter.

Clone-height interactions and clone-ring number interactions in spiral grain will not be revealed by the present measurements. However, the vertical pattern in the individual clones might be of minor importance as analyses in HANSEN and ROULUND (in preparation) suggest. So the measurements in one height can be used in a selection for low spiral grain in the juvenile wood and they can then be repeated after some years in the same height if it seems necessary to reduce the spiral grain in the mature wood.

Acknowledgement

A great thanks to JOAN TVESTED, The Arboretum for comments on the final manuscript.

Notes

This paper is a part of a Ph. D. project by JON K. HANSEN concerning the genetics of spiral grain in Sitka spruce and will be a part of a series of papers concerning the genetics of spiral grain in Sitka spruce.

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Altitudinal Variation in *Pinus brutia* Ten. and its Implication in Genetic Conservation and Seed Transfers in Southern Turkey

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(Received 27th December 1996)

Abstract

Seed collections along 2 elevational transects, 1 in the central part and the other on the western edge of the Antalya basin were made to study within- and between- population variation for growth characteristics of *Pinus brutia* Ten.. Four common garden experiments were established at different elevations along the western transect. In addition, seed samples from 4 populations along a third elevational transect on the far eastern edge of the basin were collected to perform isoenzyme analyses. Population parameters for 6-year height growth showed that middle elevation populations have better performance and better uniformity than lower- and higher-elevation populations within each of the 4 test sites. They also exhibit higher adaptational plasticity and higher stability under varying environmental conditions. Furthermore, isoenzyme analyses indicated that middle-elevation populations have a higher heterozygosity level and higher numbers of alleles per locus. Our results based on growth and isoenzyme analyses indicate that middle-elevation populations of *P. brutia* present higher genetic variability for *in situ* conservation, and they can serve much wider elevational zones for afforestation and reforestation purposes than the lower and higher elevation populations. Therefore, they should be given high priority in forest tree breeding and selection activities in the region.

Key words: Pinus brutia, altitudinal variation, genetic conservation, isozyme analysis, adaptation.

FDC: 165.52; 181.2; 165.3; 232.314; 174.7 *Pinus brutia;* (560).

Introduction

Pinus brutia Ten. is an important forest tree species in Turkey for various economic and ecological reasons. It occupies 3.1 million ha of forest land, which constitutes 15% of the total forest areas in the country (Neyisci, 1987). About 88% of *P. brutia* forests are located in southern and western Anatolia, mainly in the mountains facing the Mediterranean and Aegean Seas. It grows from sea level up to 1200 m, occasionally to 1400 m elevation in the Taurus Mountains along the Mediterranean. Within its altitudinal and horizontal distribution range, *P. brutia* exhibits considerable variation in various form and growth characteristics (Selik, 1958; Arbez, 1974; Isik, 1986; Isik *et al.,* 1987).

In Turkey, 296.000 ha. of forest land were planted with *P. brutia* between 1985 and 1991; yearly average plantations being near 42000 hectares. In terms of plantation areas established in Turkey, areas planted with *P. brutia* constitute about 37% of the total area planted annually (Gunay and Tacenur, 1993). A large proportion of the seeds used for these plantations are collected from 61 seed stands situated at different localities within the natural range of the species. A relatively small proportion of the seeds are obtained from 48 seed orchards, all of which are of first generation; many have not yet reached commercial stage in seed production. In the Antalya region alone there are 11 seed stands and 9 seed orchards (94.6 ha), as of 1995.

Because of this large planting programme and the high economic importance of the species it can be argued that *Pinus brutia* is the single forest tree species in Turkish forestry that deserves most attention for future selection, breeding and gene conservation purposes. Several questions remains to be answered on genetic architecture across the altitudinal and horizontal distribution range of the species in order to define seed transfer zones, and to determine genetically superior populations for future selection and breeding. Designation of appropriate and adequate areas of seed stands, establishment of seed orchards and determination of seed transfer zones all require additional information on the genetics and adaptability of the species. The purpose of the present study is to make a contribution along these lines. A specific purpose is to illustrate altitudinal variation of certain growth and isoenzyme characteristics of samples from natural populations grown around the Antalya basin in southern Turkey.