

Low Cost Improvement of Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) By Application of The Breeding Seed Orchard Approach in Denmark

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(Received 20th May 2005)

Abstract

An evaluation of a seedling seed orchard in Denmark of Coastal Douglas-fir showed variation between open pollinated families in their susceptibility to windthrow, height and diameter growth, stem straightness, number of forks at age 10 and bud burst at age 9. Individual narrow-sense heritability was 0.63 for bud burst, 0.40 for height and diameter, respectively, 0.48 for stem straightness, 0.20 for number of forks and 0.17 for windthrow susceptibility. Fast growing families were characterised by late bud burst, and poorer stem straightness. The approach of using seedling seed orchards in Denmark is discussed in relation to genetic gains, genetic diversity and risk of inbreeding. Predicted gains concerning a reduction of windthrow susceptibility were poor due to low genetic variability. In multi-trait selection scenarios aiming to improve growth, stem straightness and reducing windthrow susceptibility, the approach of using seedling seed orchards demonstrated that it might be possible to obtain gains in height above 5% combined with significant improvements of stem straightness while retaining an effective population size above 50.

Key words: heritability estimates, genetic correlation, growth, stem straightness, forking, windthrow, bud burst, genetic diversity, genetic gain.

Introduction

In Danish forestry, Coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) has generally shown better growth, health and storm stability in older stands compared with other introduced conifers such as Norway spruce (*Picea Abies* L.) and Sitka spruce (*Picea sitchensis* Bong Carr.) (HENRIKSEN, 1988). The higher storm stability was also revealed after a severe storm in France in 1982 (DE CHAMPS *et al.*, 1982). However, major drawbacks for a wider use of the species, are a comparably higher sensitivity to frost, poor stem form, especially stem straightness, and a higher risk of damages from browsing and fraying of bark with antlers by roe deer (e.g. HENRIKSEN, 1988). Paradoxically, Coastal Douglas-fir seems also to be highly susceptible to windthrow compared to Norway spruce and Sitka spruce in the first years after planting until they become 30 to 40 years (HENRIKSEN, 1988; JØRGENSEN, 2001). This is likely due to a poor root-shoot ratio, compared with Sitka spruce

and Norway spruce that gradually improves with age (NIELSEN and HANSEN, 1999).

This poor stability stresses the need to investigate the possibility of improving juvenile stability in breeding programs for Coastal Douglas-fir. Genetic variation in the susceptibility to windthrow is found for other coniferous species (e.g. LIEGEL, 1984; TELEWSKI and JAFFE, 1986; WOOLASTON *et al.*, 1990; GWAZE *et al.*, 2000; JOHNSTON *et al.*, 2003) and in 6-7-year-old Coastal Douglas-fir (SILEN *et al.*, 1993).

From a breeding point of view, Douglas-fir represents a dilemma when allocating priorities to species. The species is on the one hand sparsely used in Danish forestry mainly due to the problems mentioned above, which point toward low priority compared to more widely planted species. On the other hand, tree improvement may reduce some of the weaknesses of the species, and thereby lead to increased planting of the species in the Danish Forestry. As a compromise, it was decided by the Danish Tree Improvement Station, the managing authority for a majority of Forest Seed Orchards in Denmark, to establish a low cost breeding programme based on a breeding seed orchard (BSO) concept (BARNES, 1995), i.e. a seedling seed orchard (SSO) that combines progeny testing, , and commercial seed production. This approach was chosen in order to avoid establishment of separate progeny trials, and in order to avoid grafting, which is difficult in Douglas fir due to incompatibility.

In this study, we wanted to examine the suitability of the BSO approach for Douglas fir in Denmark by estimating (i) the genetic variation for in particular windthrow susceptibility, but also growth, stem straightness, forking, and bud burst in young Coastal Douglas-fir, (ii) predict the possible gains that we can achieve from multi-trait selections in a seedling seed orchard with Coastal Douglas-fir.

Material and Methods

A seedling seed orchard (SSO) FP.262 with Coastal Douglas fir was in 1994 established by the Danish State Forest Tree Improvement Station on farm land at the farm Sønder Skovgård (55°14'N, 10°10' E) with 4-year-old seedlings based on 97 open pollinated families. These originated from 54 plus-trees selected in five selected stands, and from 43 plus-tree clones represented in four older clonal seed orchards (*Table 1*). All trees in the five stands, and trees represented as clones in the

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clonal seed orchards (CSO), originate from Danish commercial plantations, mainly classified as approved seed stands.

The origin of the open pollinated families in the SSO

Plus-trees selected for CSO FP.210 were primarily selected for superior stem straightness and for low frequency of second flushing in their original stands. Plus trees selected for CSO FP.228 and CSO FP.229 were among the dominant trees with the straightest stems. CSO FP.228 consists of 17 clones and CSO FP.229 consists of 15 clones. 13 of the clones are common in the two clonal seed orchards. Thus, the two clonal seed orchards are almost identical and they are located close to each other. Consequently, they were considered as one population. Seed was harvested from different clones in the two clonal seed orchards with one exception.

The CSO FP.232 – located in France – consists of grafts from dominant trees selected for late flushing, stem straightness and for low contrast between early and late wood determined by X-ray densiometry. The trees were selected in a Danish stand, Department 295, Kompedal Plantage (56°15'N, 9°15'E) originating from Darrington, USA (KJÆR *et al.*, 1996). All trees from one of the families from the CSO FP. 232 were dead when the seedling seed orchard was measured last time in 1999.

Stem straightness and above average growth was the selection criterion when selecting plus-trees in the five stands F.398, F.488, F.580, F.581 and F. 582.

Three of the populations, the approved stands F.580, F.581 and F.582 are of the same origin. This is also the case for the two clonal seed orchards CSO FP.228, CSO FP. 229 and the approved stand F.488 (*Table 1*).

None of the clones from the clonal seed orchards had previously been progeny tested, but seedlots from the clonal seed orchards FP 210, FP228 and FP229 has been included in a provenance test in Denmark, where they exhibit superior stem form suggesting that the simple plus tree selection has provided some gain in this trait (KJÆR *et al.*, 1996).

Experimental design

The seedling seed orchard was established with 22 blocks. Each of the 22 blocks consisted of 99-101 plots made up of three plants in a row from one family. Some unbalance was present, thus some families were not represented in all blocks and some families were represented twice in some of the blocks. Blocks were placed consecutively after each other from west to east and family plots were distributed randomly in the blocks. Each block consisted of approximately three rows. The distance between rows was 3 metres and the distance between trees in the rows 1 metre.

Assessments

The developmental stage of the lateral bud was scored in spring 1999 using the KRUTZSCH (1973) scale with scores from 0-7, where 7 denotes a fully developed shoot.

In November 1999, a severe westerly storm caused many trees to lean over. The degree of inclination was recorded in the spring 2000, i.e. 6 years after establishment (10 years old trees) using a score from 0 to 6 for the inclination deviation from vertical of 0–10° (score 0), 11–20° (score 1), 21–30° (score 2), 31–40° (score 3), 41–50° (score 4), 51–60° (score 5) and > 60° (score 6), respectively. A protractor was used to record the inclination. A line with a weight was used to find the vertical line for the protractor. Height and diameter at breast height was also measured, the number of forks were recorded and stem straightness was scored using a scale from 1 to 9 where trees with a perfect straight stem received the score of 9 (*Table 2*).

Statistical analysis

The following linear mixed model was applied to estimate genetic parameters and breeding values

$$Y_{ijkl} = \mu + P_j + b_i + \delta_{ij} + f_{k(j)} + \rho_{ik(j)} + e_{ijkl} \quad [1]$$

where Y_{ijkl} is the measurement on a single tree l of family k of population j in block i , μ is the general mean, P_j is the fixed effect of population j , b_i is the random effect of block i , δ_{ij} is the random interaction between block i

Table 1. – Base populations and number of families within populations represented in the seedling seed orchard.

Populations	Number of OP Origin families in SSO	
Clonal seed orchards:		
CSO. FP.210	17	Ortets selected in nine stands.
CSO. FP.228/229	18	F.280, Hvidkilde Forest District, which again possibly origin from stand F.58, Langesø.
CSO. FP.232	8	Kompedal plantage. Origin Darrington, USA.
Approved seed stands:		
F.398	7	Silkeborg State Forest District
F.488	22	F.280, Hvidkilde Forest District.
F.580	6	F.41b, Linå Vesterskov.
F.581	8	F.41 and F.41b, Linå Vesterskov.
F.582	11	F.41 and F.41b, Linå Vesterskov.

CSO: Clonal seed orchard; SSO: Seedling seed orchard; F: Approved seed stand.

Table 2. – Principles for the score of stem straightness.

Stem straightness score	Description
1	Uncertain leader direction and several very serious leader losses.
2	Uncertain leader direction and several serious leader losses.
3	Uncertain leader direction and several leader losses.
4	Curved stems, up to 1-2 leader losses.
5-6	In principle almost straight stem, up to 1-2 leader losses.
7	Straight stems that may have weak curves at the base.
8	Straight stems, accepted with small leader losses at the top.
9	Fully straight stems.

and populaton j , $f_{k(j)}$ is the random effect of family k within population j with $\text{Var}(f_{k(j)}) = \sigma^2$, $\rho_{ik(j)}$ is the random effect of plots with $\text{Var}(\rho_{ik(j)}) = \sigma_\rho^2$, and e_{ijkl} is the residual error (within plot error) with $\text{Var}(e_{ijkl}) = \sigma_e^2$ assumed to have a normal distribution.

The linear mixed model equation in matrix notation was

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{u} + \mathbf{e} \quad [2]$$

where \mathbf{y} is the $n \times 1$ vector of observations, \mathbf{X} is the $n \times p$ design matrix associating the observations with fixed effects in vector \mathbf{b} , \mathbf{Z} is the $n \times q$ design matrix associating the observations with the random effects in vector \mathbf{u} (block, family- and plot effects) and \mathbf{e} is the $n \times 1$ vector of residual effects. Estimates of fixed and prediction of random effect were obtained solving the mixed model equation (HENDERSON, 1984)

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{u}} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix} \quad [3]$$

where \mathbf{R} is the variance-covariance matrix of residuals and \mathbf{G} is the direct sum of the variance-covariance matrices of each of the random effects. Residuals are normally considered independent giving $\mathbf{R} = \sigma_\eta^2 \mathbf{I}$ where σ_η^2 is the independent residual variance and \mathbf{I} is an identity matrix. However, spatial analysis was examined at individual tree level in rows and columns of the SSO (according to GILMOUR *et al.*, 1997; GILMOUR *et al.*, 1999; DUTKOWSKI *et al.*, 2002). Thus, (according to GILMOUR *et al.*, 1997; GILMOUR *et al.*, 1999; GILMOUR *et al.*, 2002; DUTKOWSKI *et al.*, 2002), \mathbf{R} was expanded to

$$\mathbf{R} = \sigma_\xi^2 [\text{AR1}(\rho_{\text{col}}) \otimes \text{AR1}(\rho_{\text{row}})] + \sigma_\eta^2 \mathbf{I} \quad [4]$$

where σ_ξ^2 is the spatial residual variance, σ_η^2 is the independent residual variance, \mathbf{I} is an identity matrix, and $\text{AR1}(\rho)$ is a first-order autoregressive correlation matrix for ordered spatial coordinates of size n (rows or columns)

$$\text{AR1}(\rho) = \begin{bmatrix} 1 & \rho & \rho^2 & \dots & \rho^n \\ \rho & 1 & \rho & \dots & \dots \\ \rho^2 & \rho & 1 & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots \\ \rho^n & \dots & \dots & \dots & 1 \end{bmatrix} \quad [5]$$

where ρ is the autocorrelation parameter (GILMOUR *et al.*, 1999; GILMOUR *et al.*, 2002; DUTKOWSKI *et al.*, 2002).

Only significant ($P < 0.05$) autoregressive correlation parameters were used. The significance of a parameter

was tested using a one-tailed likelihood ratio test (GILMOUR *et al.*, 1999); for model A with the parameter included and sub-model B without the parameter included. The test statistic computed was

$$G_{A \rightarrow B} = 2[\text{Log}L_B - \text{Log}L_A]$$

where $\text{Log}L_B$ is the log likelihood value for the sub-model B and $\text{Log}L_A$ is the log likelihood value for the model A and where $G_{A \rightarrow B}$ follows a χ^2_1 - distribution (GILMOUR *et al.*, 1999). Additionally, the criterion AIC of Akaike was used to select between models (AKAIKE, 1973; WADA and KASHIWAGI, 1990).

$$\text{AIC} = -\text{Log}L + 2p$$

where $\text{Log}L$ is the log likelihood and p the number of independent fitted parameters included in the model and where the model with lowest value was chosen.

Breeding values across populations were estimated by adding the predicted population deviation from the overall mean (WHITE and HODGE, 1989). The estimation of genetic parameters, prediction of breeding values, examination of heteroscedasticity and distribution of residuals was made in the software program ASReml (GILMOUR *et al.*, 1999; COSTA E SILVA *et al.*, 2001; DUTKOWSKI *et al.*, 2002; GILMOUR *et al.*, 2002).

Phenotypic correlation coefficients between traits x and y were estimated as

$$\hat{r}_p = (\hat{\sigma}_{fxy} + \hat{\sigma}_{pxy} + \hat{\sigma}_{exy}) / \sqrt{\hat{\sigma}_{fxy}^2 + \hat{\sigma}_{pxy}^2 + \hat{\sigma}_{exy}^2}$$

where $\hat{\sigma}_{fxy}$ is the estimated family covariance between trait x and y , $\hat{\sigma}_{pxy}$ is the estimated plot covariance between trait x and y , and $\hat{\sigma}_{exy}$ is the estimated within plot covariance between trait x and y . Genetic additive correlation coefficients between trait x and y were estimated as:

$$\hat{r}_a = \hat{\sigma}_{fxy} / \sqrt{\hat{\sigma}_{fx}^2 \hat{\sigma}_{fy}^2}$$

(e.g. BECKER, 1984; FALCONER, 1989). The individual tree narrow-sense heritability in the SSO was estimated as

$$\hat{h}_{ns}^2 = 4\hat{\sigma}_f^2 / (\hat{\sigma}_f^2 + \hat{\sigma}_p^2 + \hat{\sigma}_e^2)$$

where $\hat{\sigma}_f^2$ is the estimated family variance, $\hat{\sigma}_p^2$ is the estimated plot error variance and $\hat{\sigma}_e^2$ is the residual variance. Thus, we considered the open pollinated families as half-sib families (FALCONER, 1989), i.e. the narrow-sense heritability estimates are possibly exaggerated since some of the trees in the families possibly are

full sibs (CAMPBELL, 1979; CAMPBELL, 1986). Standard errors for the genetic parameters were estimated from Taylor series approximations (GILMOUR *et al.*, 1999).

Prediction of genetic gains and genetic diversity as consequence of a thinning in the SSO

Based on the predicted breeding values for the trees in the seedling seed orchard, it was possible to predict the genetic gains assuming first a selection of one of the three trees in each plot (i.e. two of three trees in each plot were assumed removed), and then making selections among the remaining trees in the seedling seed orchard. Multi-trait selection among these trees was based on index values calculated by multiplying the predicted breeding values of the trees for the different traits with certain weights. Different multi-trait scenarios were examined with three sets of weights for the traits (Table 5). The number of individuals selected from each family was restricted to obtain different status number, but the restriction was less for families with trees of high breeding or index values to obtain higher genetic gains at the same genetic diversity (as found by LINDGREN and MATHESON, 1986; LINDGREN *et al.*, 1989; RODRIGUEZ, 2000).

The following exponential function (SIT and POULIN-COSTELLO, 1994) was found sufficient variable (by varying the parameters in the function) to vary the maximum number of trees selected from each family $i = 1, 2, \dots, 96$ where family $i = 1$ is the family with the highest average breeding value and family $i = 96$ is the family with the lowest average breeding value.

$$\max_i = \text{Integer}((e^{a-bi}) + c) \quad [6]$$

where \max_i is the maximum number of trees that can be selected from family i , and a , b , and c are parameters. Trees with the best breeding values among these remaining trees were then selected. The average coancestry and status number (LINDGREN *et al.*, 1996; LINDGREN *et al.*, 1997) was estimated for these final selected trees using the relationship matrix. The relationship matrix was estimated by use of the procedure INBREED in SAS® (SAS Inst. Inc, 1999). The relationship coefficient is twice the coancestry (FALCONER, 1989). Thus, by summing up the coancestry coefficients (half the relationship coefficients) and dividing by the number of crosses between the trees it was possible to obtain the average coancestry assuming random mating. The status number was then estimated according to LINDGREN *et al.* (1996) and LINDGREN *et al.* (1997) as

$$N_s = \frac{1}{2\Theta} \quad [7]$$

where N_s is the status number and Θ is the average coancestry. A variety of selection scenarios were examined with different parameter values for the different sets of weights. Thus, for different sets of weights on the traits, combinations of parameters (a , b , c in function 6) were found to maximise the average index value at different levels of relatedness expressed by the status number N_s .

Tree to tree variation in flowering and seed production has proved highly variable in a Coastal Douglas fir clon-

al seed orchard in Denmark and might reduce the expected effective size by 50% (KJÆR and WELLENDORF, 1998; HANSEN, 1999). Thus, we estimated a possibly more realistic effective population size from the status number $N_e = 0.5N_s$.

The number of potential crosses between half sibs was estimated from the average coancestry as

$$(0.5N + 0.125N_{SC})/N^2 = \Theta \Leftrightarrow (\Theta N^2 - 0.5N)/0.125 = N_{SC} \quad [8]$$

where N is the number of selected trees, N_{SC} is number of potential crosses between sibs (all assumed to half sibs in this case) and Θ is the average coancestry. From the number of potential crosses between half sibs it was possible to estimate an average coancestry assuming that half of the sibs actually are full sibs using equation 8, i.e.

$$(0.5N + (0.125N_{HSC} + 0.250N_{FSC})/N^2 = \Theta \quad [9]$$

where N_{HSC} is the number of crosses between half sibs and N_{FSC} is the number of crosses between full sibs and where $N_{HSC} = 0.5N_{SC}$ and $N_{FSC} = 0.5N_{SC}$.

A possible influence of inbreeding on the results for height growth was investigated by reducing the predicted gains for height from potential selfings and crosses between half sibs, while considering that a large proportion of seedlings from these crosses are purged already at the nursery (WOODS *et al.*, 2002; WANG *et al.*, 2004). Thus, it was assumed that the height in offspring from mating between half-sibs was reduced by 12.6% of the mean height and that the height in offspring from self-fertilisations was reduced by 47% of the mean height according to figures in table 2 in WANG *et al.* (2004). According to figures from WOODS *et al.* (2002), it was assumed that the probability of producing acceptable seedlings was 3% and 55% from self-fertilisations and mating between half sibs, respectively.

To obtain an indication of the importance of reducing the average inclinations score, we estimated the regression between the mean inclination score of a population and the mean percentage of trees with no inclination of the population in the seedling seed orchard. Thus, the percentage of trees with an inclination score of 1 to 6 was estimated for each population within each block, as well as the mean inclination score for each provenance in each block. Afterwards least square means were estimated for the populations from the following mixed model

$$Y_{ij} = \mu + P_j + b_i + e_{ij} \quad [10]$$

where Y_{ij} is mean inclination score of population j in block i , or the percentage of trees with an inclination score above 0 of population j in block i , μ is the general mean, b_i is the random effect of block i , P_j is the fixed effect of population j , and e_{ij} is the residual error. A linear regression between percentage of trees with an inclination score above 0 for a population and the inclination score for the population proved highly significant with a regression coefficient of 55% ($P < 0.0001$) per unit score (R^2 of 0.95), i.e. a reduction of the inclination score with one unit corresponded to a reduction of the percentage of trees with an inclination score of 1 to 6 by 55%.

Results

At age 10 years, the mean height and diameter at breast height was 3.5 metres and 4.2 cm, respectively. The mean stem straightness score was 5.4. The mean number of forks was 1. The mean inclination score was 0.78. Mean bud burst score was 2.8. Inclination scores above 2 were seldom (*Fig. 1*). The frequency of trees with an inclination was 60%, mainly distributed to the score 1 and 2 (*Fig. 1*). The frequency of trees with forks was 74%. In comparison with other studies dealing with Coastal Douglas fir of approximately same age this seems high. In a 9-year-old progeny test SCHERMANN *et al.* (1997) found a frequency of trees with at least one fork or ramicorn of 26% and 46%, respectively. The total proportion of trees in a progeny tests series at three sites with forks, or forks and ramicorns, was 7.5% at age 12 in a study by TEMEL and ADAMS (2000).

The narrow sense heritability estimate was $h^2 = 0.40$ for both height and diameter when considering the families as half-sib families (*Table 3*). Both traits showed significant autocorrelation in the row and column direction (*Table 3*). The narrow sense heritability estimate was $h^2 = 0.17$ and $h^2 = 0.20$ for inclination score and number of forks, respectively. There was significant autocorrelation in the column direction for the inclina-

tion score and in the row and column direction for number of forks (*Table 3*). Stem straightness score showed a narrow sense heritability of $h^2 = 0.48$ and significant autocorrelation in both the row and column direction. The narrow sense heritability estimate for bud burst score was $h^2 = 0.63$.

Height and diameter was highly correlated with an additive genetic correlation of $r_g = 0.93$ (*Table 4*). Otherwise, genetic correlation coefficients were low to moderate. The additive genetic correlation of stem straightness with height and diameter was $r_g = -0.17$ and $r_g = -0.30$, respectively. Thus, fast growing families had a tendency to have fewer trees with straight stems. The additive genetic correlation was $r_g = -0.30$ between number of forks and inclination score; indicating that families with an inclination avoided leader breaks. Families with high bud burst scores, i.e. early bud burst tended towards a comparable lower height as indicated by the additive genetic correlation of $r_g = -0.22$ between burst of buds and height. The genetic correlation between stem straightness and inclination score was $r_g = -0.34$, i.e. trees with high stem straightness scores had lower inclinations (*Table 4*). This could indicate an earlier influence of a poor stability on the stem straightness.

Predicted genetic gains

The genetic gain in inclination score by removing 2 of 3 trees with the worst inclination in each plot in the seedling seed orchard was predicted to $R = -0.08$ (not shown). This corresponded to a 4% decrease of the frequency of trees with an inclination above 10° in a population. The status number was 246 among the selected 2017 half sibs (not shown).

Predicted gain in inclination score from selections within family plots followed by selection among the remaining 2017 half sibs, i.e. a combined within and between family selection, varied between $R = -0.18$ and

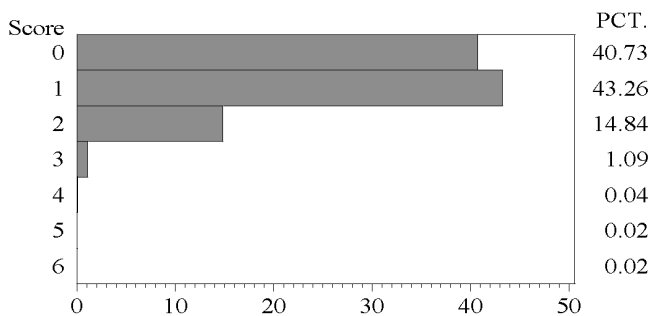


Figure 1. – Distribution of inclination scores in 1999.

Table 3. – Variance components and individual narrow sense heritability for height, diameter at breast height, stem straightness, bud burst, inclination score and number of forks. Non-significant parameters are excluded (n.s.).

	Height	Dia- meter	Stem straight- ness	Bud burst	Inclina- tion	N-forks
Unit	dm	mm	score 1-9	score 1-9	score 0-6	
Mean	35	42	5.41	2.8	0.78	1.00
Source of variation						
Provanance x replication interaction	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Replication	n.s.	n.s.	n.s.	0.042	n.s.	n.s.
Family within population	3.2	12	0.072	0.060	0.023	0.040
Plot variance	1.8	2	0.019	0.033	n.s.	0.030
Residual	26.9	101	0.512	0.289	0.532	0.716
Phenotypic variance	31.9	114.3	0.603	0.381	0.555	0.786
Phenotypic standard deviation	5.6	10.7	0.78	0.617	0.745	0.887
CV %#	16	26				
h^2_{ns}	0.40	0.40	0.48	0.63	0.17	0.20
StdErr(h^2_{ns})	0.07	0.07	0.11	0.09	0.04	0.04
Autocorrelation parameter rows	0.94	0.95	0.97	n.s.	n.s.	0.88
Autocorrelation parameter columns	0.95	0.95	0.94	n.s.	0.97	0.96

Coefficient of variation (%): 100 x phenotypic standard deviation divided by the mean.

Table 4. – Phenotypic (r_p) and genetic (r_a) correlation coefficients with standard errors (italic).

Trait	Trait	r_p		r_a	
Height	Diameter	0.84	0.00	0.93	0.02
	Inclination	-0.04	0.02	0.05	0.16
	Number of forks	0.08	0.02	-0.09	0.15
	Stem straightness	-0.15	0.02	-0.17	0.14
	Bud burst	-0.06	0.02	-0.22	0.13
Diameter	Inclination	0.07	0.02	0.13	0.15
	Number of forks	0.02	0.02	-0.12	0.15
	Stem straightness	-0.29	0.02	-0.30	0.13
	Bud burst	-0.06	0.02	-0.22	0.13
Inclination	Number of forks	-0.14	0.02	-0.30	0.15
	Stem straightness	-0.31	0.01	-0.34	0.13
	Bud burst	0.05	0.02	0.22	0.14
Number of forks	Stem straightness	0.06	0.02	0.00	0.00
	Bud burst	-0.03	0.02	0.00	0.00
Stem straightness	Bud burst	0.00	0.02	0.17	0.64

Table 5. – Results from different selection scenarios with combined between family and within family selections and with different weights for different traits – height (H), diameter at breast height (DBH), stem straightness (STR), inclination (INCL), change in % trees with inclination (INCL%), number of forks (FORK) and bud burst (BUD). Selection scenario A1-A3 has only a weight on inclination, B1-B6 have a second, and C1-C6 a third set of economic weights. To prevent frost damages due to early bud burst, this trait was given a negative weight. The parameters a, b, c refer to the function [6], i.e. the function determining the maximum number of individuals selected in each family, depending on the average breeding value of the family.

SSO spacing after thinning																											
Parameters in function [6]				Economic weights							Predicted change (genetic gains) in traits								Genetic diversity								
				H	DBH	STR	INCL	FORK	BUD	H	H	DBH	STR	INCL	INCL%	FORK	BUD	Ave- coan- cestry		Status number	N matings between sibs		N ma-tings be-tween sibs of total matings (%)		Status number	Ave- rage m ² per tree	
Sce- nario	a	b	c	N selec- ted								%	%*	%	score	score	%	N	score	N _e	N _e		N _e	N _e			
A1	3.0	2.0	1	650	0	0	0	-1	0	0	0.2	0.1	-1	0.17	-0.18	-10	0.0	0.1	0.00261	191	96	6225	1.5	142	71	30	5.5
A2	3.0	3.0	3	500	0	0	0	-1	0	0	0.4	0.3	0	0.18	-0.20	-11	0.1	0.1	0.00313	160	80	4268	1.7	119	60	39	6.3
A3	3.0	4.0	1	300	0	0	0	-1	0	0	0.2	-0.1	-1	0.23	-0.25	-14	0.1	0.1	0.00597	84	42	3098	3.4	62	31	66	8.1
B1	2.5	1.0	1	597	1	0	4	-1	0	-1	7.5	7.4	9	0.22	-0.05	-3	0.0	-0.1	0.00215	232	116	3756	1.1	178	89	33	5.7
B2	2.5	1.5	3	492	1	0	4	-1	0	-1	8.4	8.3	10	0.23	-0.05	-3	0.0	-0.1	0.00241	208	104	2698	1.1	161	80	40	6.3
B3	2.0	1.0	1	350	1	0	4	-1	0	-1	9.1	9.0	11	0.23	-0.05	-3	0.0	-0.1	0.00267	187	94	1214	1.0	152	76	56	7.5
B4	2.5	3.0	3	350	1	0	4	-1	0	-1	9.8	9.7	12	0.24	-0.06	-3	0.0	-0.1	0.00303	165	82	1572	1.3	130	65	56	7.5
B5	2.0	2.5	1	200	1	0	4	-1	0	-1	11.3	11.2	14	0.26	-0.06	-3	0.0	-0.2	0.00414	121	60	526	1.3	101	50	98	9.9
B6	2.5	2.5	1	200	1	0	4	-1	0	-1	12.1	11.8	15	0.27	-0.09	-5	0.1	-0.1	0.00681	73	37	1378	3.4	56	28	98	9.9
C1	2.5	1.0	1	600	1	0	8	-1	0	-1	4.9	4.8	5	0.39	-0.07	-4	0.0	-0.1	0.00217	231	115	3836	1.1	177	88	33	5.7
C2	2.5	1.5	4	500	1	0	8	-1	0	-1	5.5	5.4	6	0.41	-0.07	-4	0.0	-0.1	0.00243	206	103	2858	1.1	159	80	39	6.3
C3	2.5	2.5	2	350	1	0	8	-1	0	-1	6.5	6.4	7	0.47	-0.09	-5	0.0	-0.1	0.00322	155	78	1756	1.4	121	61	56	7.5
C4	2.0	3.5	2	200	1	0	8	-1	0	-1	7.0	6.9	8	0.50	-0.08	-5	0.0	-0.1	0.00396	126	63	466	1.2	107	53	98	9.9
C5	2.0	1.5	1	200	1	0	8	-1	0	-1	8.1	7.9	9	0.50	-0.09	-5	0.0	-0.1	0.00496	101	50	786	2.0	81	40	98	9.9
C6	2.5	2.0	1	200	1	0	8	-1	0	-1	8.5	8.2	10	0.52	-0.11	-6	0.0	0.0	0.00741	68	34	1570	3.9	51	25	98	9.9

* Considers inbreeding depression due to matings between half sibs and self-fertilisation.

assumes that half of the matings between sibs are between full sibs.

$R = -0.25$ depending on the number of selected trees and the restrictions on the average coancestry in the seedling seed orchard (Table 5, scenarios A1–A3). A selection of more individual trees in families with good overall performance concerning the index value was superior compared to a selection with equal selection in each family as expected from RODRIGUEZ (2000), (Fig. 2).

More balanced selection scenarios were examined, aiming to increase growth and improve stem straightness as well. Again, the first approach was to make within plot selections based on index values (selection of one of three trees), followed by combined between family and within family selections. In these scenarios the

genetic gains in height varied between 5 and 12 percent-age, genetic gains in stem straightness score varied between $R = 0.22$ to 0.52, while the wind susceptibility score was reduced by $R = 0.05$ to 0.11 depending on selection intensity, weights for the traits and restrictions on the number of trees selected from families with the best average index values (Table 5, fig. 3, scenarios B1–B6 and C1–C6).

The predicted gains in height were only slightly reduced when considering the influence of inbreeding, reflecting that the proportion of crosses between half-sibs was below 4% in all scenarios B1-B6 and C1-C6 (Table 5).

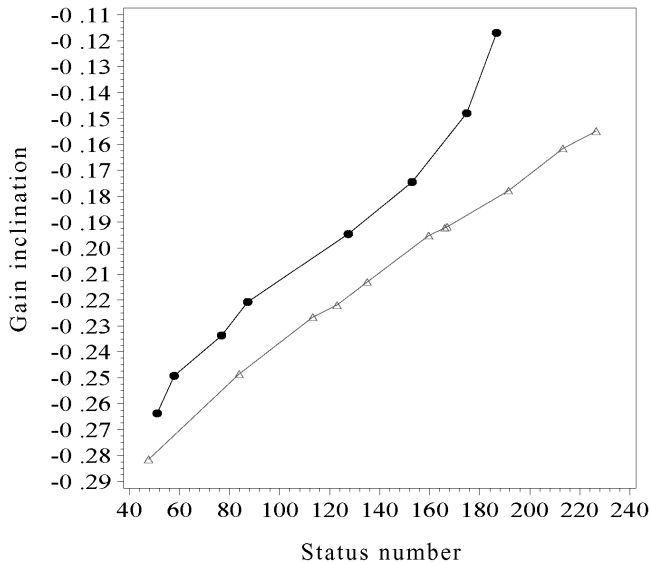


Figure 2. – Comparison of predicted genetic gains (reduction of inclination) selecting the same number of trees from each family (dots), or selecting more individual trees from the best performing families (triangle). Notice that a large negative value in the gain, i.e. a reduction in the score, is preferable.

Discussion

In this study, the opportunity to reduce windthrow susceptibility in Coastal Douglas-fir was low and the missing effect of height on the inclination in the seedling seed orchard was a surprise, but is possibly explained by a comparative low frequency of severe inclinations (*Fig. 1*). A genetic variation in the susceptibility to windthrow in Coastal Douglas-fir was also found in a 6-year-old and a 7-year-old genetic field test with families from controlled crosses of 9 and 13 parents, respectively. The mean height was 1.6 and 2.1 metres in the two tests, respectively (SILEN *et al.*, 1993). General combining ability (GCA) and specific combining ability (SCA) accounted for 18.6% and 22.5% of the total variance for susceptibility in the two genetic field tests, respectively – after adjustments due to height, and the variation from SCA was near equal to GCA (SILEN *et al.*, 1993). Height as covariant proved significant and explained approximately a third of the variation in susceptibility. Therefore, only seven out of 138 crosses in the two sets exceeded 10% superiority in both mean height and windthrow susceptibility (SILEN *et al.*, 1993). As noticed by SILEN *et al.* (1993), it seems difficult to

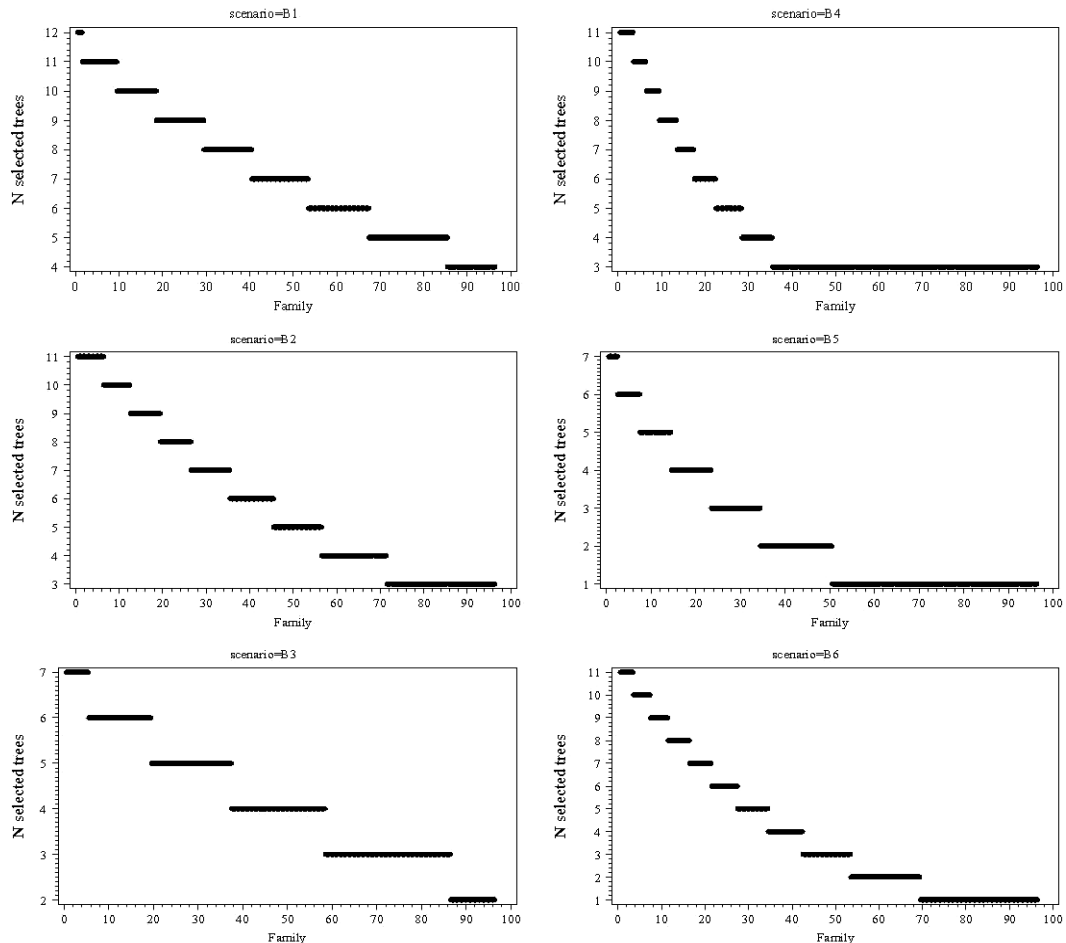


Figure 3. – Maximum number of trees allowed selected from the families 1-96 in the selection scenarios B1-B6 determined by the parameters in function [6], see table 5. The families are sorted according to their average index value, i.e. family 1 is characterised by the best average index value and family 96 by the poorest average index value. The final number of selected trees are the same in scenario B3-B4 (see table 5), but the gains are slightly higher in scenario B4 compared with B3, since families with the highest average index value were allowed to contribute with more trees. The situation is similar for scenario B5 versus B6.

include wind susceptibility in breeding programs if these rely on natural, and thus occasional and random events. Nevertheless, the significant genetic variation encourages further investigations on the genetic variation of stability in young Coastal Douglas-fir trees.

This study showed a favourable, though moderate additive genetic correlation between late bud burst and height as found in previous studies (e.g. BIROT and CHRISTOPHE, 1983; LI and ADAMS, 1993; STEVENSON *et al.*, 1999). The importance of late bud burst is stressed by a high genetic correlation with spring frost susceptibility (O'NEILL *et al.*, 2000). Unfortunately, late bud burst is moderately genetically correlated with autumn frost susceptibility (STEVENSON *et al.*, 1999; O'NEILL *et al.*, 2000) making it necessary to include early autumn frost susceptibility in the breeding programs of Coastal Douglas-fir.

Weak to moderate individual tree and family heritability estimates for stem sinuosity was also found in other investigations of young Coastal Douglas-fir (BIROT and CHRISTOPHE, 1983; ADAMS and BASTIEN, 1994; SCHERMANN *et al.*, 1997; TEMEL and ADAMS, 2000; VARGAS-HERNANDEZ *et al.*, 2003). The indication of a weak unfavourable genetic correlation between stem straightness and growth in this study corresponds to the findings concerning growth and stem sinuosity in other investigations with material of corresponding age (BIROT and CHRISTOPHE, 1983; SCHERMANN *et al.*, 1997; TEMEL and ADAMS, 2000; VARGAS-HERNANDEZ *et al.*, 2003). In material of age 9-12 years there was a connection between stem sinuosity and the development of forks and ramiforms in contrast to this study, whereas there was only a weak to moderate genetic correlation between second flushing frequency and stem sinuosity (ADAMS and BASTIEN, 1994; SCHERMANN *et al.*, 1997). Second flushing frequency is positively correlated with growth in the first 10 years (ADAMS and BASTIEN, 1994; SCHERMANN *et al.*, 1997). The negative correlation between stem straightness and inclination score is favourable, but the finding needs verification from other studies.

TEMEL and ADAMS (2000) found a genetic correlation of 0.36 between stem sinuosity at age 12 and stem sinuosity at the outer bole in the lowest 5 metres from the ground after 24 years. In another study with Coastal Douglas-fir, 11-15% of the log volume was affected by grain defects because of stem sinuosity in logs from trees with an average diameter at breast height of 23.9 to 26.2 cm (SPICER *et al.*, 2000). These results suggest at first sight that the importance of reducing early stem sinuosity is small. However, inner boards cut from logs with a sinuous centre are downgraded.

In the seedling seed orchard only 6% of the trees scored 7 and 8 in stem straightness and none scored 9. Therefore, it seems reasonable to improve stem straightness at least moderately at age 10 years to obtain sufficient trees with satisfactory stem straightness at the time where the most valuable timber production starts.

A moderate family heritability concerning forking has also been found in previous investigations (ADAMS and BASTIEN, 1994; SCHERMANN *et al.*, 1997), or steep angled

branches-ramiforms (TEMEL and ADAMS, 2000; VARGAS-HERNANDEZ, 2003). However, a positive and unfavourable genetic correlation with growth was not seen in this study. This contrasts findings in other studies of Coastal Douglas-fir showing a moderate positive genetic correlation between growth and frequency of forking/ramiforms, but the height and diameter at ages from 9-13 were also twice as large as observed in this study (ADAMS and BASTIEN, 1994; SCHERMANN *et al.*, 1997; TEMEL and ADAMS, 2000; VARGAS-HERNANDEZ, 2003).

The heritability estimates for height and diameter were high, compared with heritability estimates from other field trials with Coastal Douglas-fir (e.g. JOHNSON *et al.*, 1997). This reflects possibly that the seedling seed orchard is established on farmland with small climatic variations and heterogeneity in soil fertility. Some concern might rise if the selections based on a farm-field trial are reliable for forest conditions, but WOODS *et al.* (1995) found in a study of Coastal Douglas-fir that farm field test breeding values correlated well with field test breeding values.

The evaluation of the seedling seed orchard suggest that it is possible to obtain significant gains in growth, stem straightness and to some extent reduce wind susceptibility, while retaining an effective population size above 50. Thus, the establishment of the seedling seed orchard was favourable with respect to genetic gains and retaining diversity.

Predicted gains in the SSO are possibly overestimated since the offspring of the plus trees are considered to be half sibs and since future realised gains from the selections naturally depend on genotype-environmental interactions and age-age correlations (FALCONER, 1989). Different flowering and seed production of the trees will also reduce the genetic diversity (e.g. KANG *et al.*, 2003a; KANG *et al.*, 2003b), and emphasise the importance of delaying the final selections in the seedling seed orchard as long as possible, to have the chance to include flowering and seed production in the selections. Selections in the seedling orchard are targeting the specific environment of the seedling seed orchard stressing the need for several seedling seed orchards in case genotype-environment interactions are high for the traits of interest.

The risk that inbreeding depressions will decrease the predicted gains from the seedling seed orchard is substantially low, due to small proportions of crosses between related trees. In particular, when it is considered that trees showing inbreeding depressions are purged from the forest populations and thus will contribute little to the final revenue from a stand (WANG *et al.*, 2004). Thus, WANG *et al.* (2004) simulated that the final yield of marketable timber at age 90 was decreased by $100 \times (0.120P_{F=0.125} + 0.200P_{F=0.25})\%$ where $P_{F=0.125}$ and $P_{F=0.25}$ was the proportion of seedlings with inbreeding coefficients of 0.125 and 0.25, i.e. with proportions of half sib, or even full sib crosses, of less than 4% in this study, the effect of inbreeding depression seems small. The effect of inbreeding will probably be even smaller for stem form, because this trait is less fitness related and therefore likely to be less subject to inbreeding depression.

The predicted gains from the seedling seed orchard were not compared with genetic gains from a selection in a hypothetical clonal seed orchard with grafted parent plus trees. Thus, it was not possible to estimate comparable genetic gains from such a seed orchard and the SSO that account for the genetic gains from the plus tree selections in the original populations/stands. Only half of these genetic gains are transferred to the offspring in the seedling seed orchard, while genetic gains from the plus tree selections in the original populations are fully retained in the parent trees. This means that the gains from the original plus tree selections are fully reachable in a clonal seed orchard. The possibility that the gains from the plus tree selections outweigh the differences depends naturally on the selection intensity, narrow sense heritability and the phenotypic variance when selecting the plus trees (e.g. RUOTSALAINEN and LINDGREN, 1998; BURDON and KUMAR, 2004). It also depends on the degree of genotype-environment interaction between the sites where the plus trees are standing and the site with the SSO. An advantage using the clonal seed orchard approach is that the plus tree selections are based on mature trees making it more certain that gains are achieved and not reduced significantly due to a poor genetic age-age correlation.

BURDON and KUMAR (2004) did not find the approach of selecting among half sib offspring in progeny tests for the formation of a production population superior to the selection in clonal seed orchards with progeny tested plus trees unless the heritability was above 0.60. RUTSALAINEN and LINDGREN (1998) compared backward and forward selections for a range of different selection intensities and found also that a forward selection approach was mainly superior to a backward selection approach for a narrow sense heritability > 0.50 and when plus tree selection intensities were low and/or when the number of offspring in the families was high (100 and mostly 500). Forward selections were contrary to this in general favourable if it was assumed that the whole genetic gain from the plus tree selection was transferred to the progeny, assuming that the progeny was made by pollinating the plus trees with a pollen mix from the selected plus trees (RUTSALAINEN and LINDGREN, 1998).

So far, we have mainly discussed the results in the context of seed production from improved material, but the SSO approach in Coastal Douglas fir in Denmark is also an attempt to combine seed production from improved material while the SSO along with other seedling seed orchards, also serves as a breeding population for the next generation in the breeding program. This, along with an expected wide use of natural regeneration in Denmark in plantations of Coastal Douglas fir, stresses the need for maintaining a reasonably high genetic diversity in the SSO. This study showed good opportunities to combine genetic gains while at the same time retaining a genetic diversity – corresponding to a status number above 50.

Acknowledgement

We wish to thank the Danish State Forest Tree Improvement Station and Forest Engineer JENS ERIK GALBY who collected part of the data for this study.

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