Prediction of Breeding Values and Expected Genetic Gains in Diameter Growth, Wood Density and Spiral Grain from Parental Selection in Picea abies (L.) Karst.

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(Received 20th September 1999)

Abstract

Parental breeding values were predicted for diameter growth, pilodyn penetration, basic density and spiral grain in Norway spruce (Picea abies (L.) Karst.). Cross- and open-pollinated progenies, tested across a range of sites, were evaluated under univariate and multivariate individual tree mixed models. Best Linear Unbiased Predictions (BLUP) of breeding values were obtained by linking data from different mating designs, in order to evaluate parents present as both females (open-pollinated progenies) and males (controlled crosses). The BLUP analysis of diameter followed a multivariate approach that combined correlated information across two different planting environments in Denmark. For selection targeting one of the planting zones, the analysis took simultaneously into account the data available on different characters, and the BLUP solutions of the parent effects were then applied to construct an index for genetic improvement of multiple traits. In this context, the evaluations used pilodyn as a selection criterion, basic density as a goal trait, and spiral grain and diameter as both selection criteria and goal traits. The single and multiple trait evaluations served as a basis to discuss strategies and associated genetic gains from parental selection.

Key words: Picea abies, open-pollination, controlled crosses, REML, BLUP, heritability, genetic correlation, genotype by environment interaction, genetic gain, sawn timber production.

Introduction

The breeding programme of Norway spruce (Picea abies (L.) Karst.) in Denmark is structured in one multiple purpose central population and a number of small elite populations with alternative selection goals: growth rate, wood quality, health or a multi-trait breeding objective (Wellendorf et al., 1994). In the early 1980s, two clonal seed orchards were established with the same set of 100 plus trees, from 1st generation selections in mature Danish stands of German origin. These orchards are expected to be culled based on progeny testing results and supply improved seed for two planting environments, the eastern and western regions of Denmark, contrasting in silvicultural treatments and in some edaphic and climatic factors.

Short-rotation forestry has been common in the eastern region, where sites are in general more productive and the mean annual increment reaches its maximum early, being then followed by a rapid decline. Marketable timber dimensions under short rotations have been obtained by enhancing diameter growth rate, through intense early thinnings. This has also been practised to promote root development which, in combination with lower thinning intensities at later stages, is expected to reduce the risk of windthrow (Nielsen, 1990). However, the increase in diameter growth rate, associated with high site fertility and more intense silvicultural practices, has decreased key quality properties (stability, visual grading outcome, strength) for sawn timber (Danborg, 1996). Wider annual rings in early years and short rotations result in a larger amount of juvenile wood present in the harvested log, which also contributes to a drop in quality of the sawn timber: juvenile wood in itself has poorer properties when compared with the mature wood (Brazier, 1985; Senft, 1986; Danborg, 1996). Therefore, while the intended use of Norway spruce plantations in both regions is structural timber, a much greater emphasis on wood quality is required in the eastern zone, in order to improve the end-product value. In the western region, sites are generally less fertile, and resistance to needle cast and increasing growth rate could be targeted without affecting significantly wood quality.

Wood density and spiral grain are two important basic properties influencing the quality of structural timber. Strength properties of spruce boards are reduced by decreasing wood density and increasing knot size (Danborg, 1996), with other factors such as spiral grain and microfibrillar angle being also involved (Brazier, 1985). Among the stability properties studied in Norway spruce boards, twist was found to be the most serious downgrading parameter, and it is induced by higher incidence of spiral grain (Danborg, 1996).

As with other conifers, in Norway spruce, large annual rings will contribute to lower wood density in both juvenile and mature wood (Olesen, 1976, 1977; Danborg, 1994; Rozenberg and Cahalan, 1997). Moreover, faster diameter growth in young wood will increase the average grain angle in the tree, because the incidence of spiral grain is higher in the juvenile wood (Brazier, 1985; Senft, 1986; Harris, 1989; Danborg, 1996). Thus, particularly for spruce plantations growing in productive environments, attempts to decrease the amount of juvenile wood in the stem and/or improve its quality (as by selecting material with higher wood density and reduced grain angle) may improve the value of timber for structural purposes.

The aim of this study was to predict parental breeding values and associated genetic gains for diameter growth, wood density and spiral grain. Additive genetic (co)variance estimates were pooled across sites and then used to derive Best Linear Unbiased Predictions (BLUP) of breeding values (Henderson, 1984; White and Hodge, 1989; Borralho, 1995), under univariate and multivariate analyses. Results concerning site estimates of (co)variance components and genetic parameters have been reported previously for the cross- and open-pollinated progenies used in the evaluations (Costa e Silva et al., 2000). The BLUP analysis allowed for heterogeneous residual variances across sites and used pedigree information to link data from different mating designs. The evaluations served as a basis to develop strategies and related genetic gains from parental selection.

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Material and Methods

Details about the plant material, mating schemes, field experimental design and characters used in this study have been described previously (COSTA E SILVA et al., 2000). Briefly, the data are from three groups of 15 to 18-year-old progeny tests, comprising cross- and open-pollinated families (for summary information, see Table 1 of COSTA E SILVA et al., 2000). The progeny test data refer to 90 out of 100 parents represented in the seed orchards, plus a parent that belongs to the general breeding population. The remaining 10 parents will be evaluated in the near future, following collection of data in other progeny tests.

BLUPs of breeding values (and their standard errors) were obtained for male parents used in the controlled crosses (group I) and female parents of open-pollinated families (groups II and III), under the following general mixed linear model:

\[ y = Xb + Z_a a + Z_s s + W_1 m + W_2 p + e \]

where \( y \) is the vector of individual tree observations; \( b \) is the vector of fixed effects; \( a \) is the vector of random additive genetic effects of individual trees; \( s \) is the vector of random non-additive genetic effects due to the specific combinations of males with females; \( m \) is the vector of random main plot effects; \( p \) is the vector of random subplot effects; \( e \) is the vector of random residual deviations of individual trees; \( X, Z_a, Z_s, W_1, \) and \( W_2 \) are incidence matrices relating the observations to the model effects. It is assumed that the random terms are jointly normal with zero mean and (co)variance matrix:

\[
\begin{align*}
\text{VAR} & = \begin{bmatrix} a \\ s \\ m \\ p \\ e \end{bmatrix} \\
& = \begin{bmatrix} G \otimes A & 0 & 0 & 0 & 0 \\ 0 & S \otimes I & 0 & 0 & 0 \\ 0 & 0 & M \otimes I & 0 & 0 \\ 0 & 0 & 0 & P \otimes I & 0 \\ 0 & 0 & 0 & 0 & R \otimes I \end{bmatrix}
\end{align*}
\]

where \( G \) is the additive genetic (co)variance matrix, \( S \) is the (co)variance matrix due to the specific combinations of males with females, \( M \) is the (co)variance matrix with main plot effects, \( P \) is the (co)variance matrix with subplot effects, \( R \) is the residual (co)variance matrix, \( A \) is the additive genetic relationship matrix between trees, \( I \) is an identity matrix and \( \otimes \) denotes the Kronecker product.

The progeny groups I and II were combined in the BLUP analysis, as there were eleven common parents between them. Data of group III were analysed separately because, apart from a common reference population, the group has no connections with series I and II. As in previous analyses (COSTA E SILVA et al., 2000), the bulked stand seedlots in groups II and III and the common reference seedlot were not used in the evaluations.

Single trait evaluations were first carried out to identify superior parents for the allocation to elite breeding populations, aiming to improve growth rate or wood quality. A multivariate BLUP analysis was also applied to construct indices for genetic improvement of multiple traits, and an important objective here was parental selection for roguing the seed
orchard (known locally as FP241) which targets the eastern region.

Table 1 shows the additive genetic (co)variance estimates applied in single and multiple trait BLUP analyses. REML (Restricted Maximum Likelihood) estimates of (co)variance components have been reported previously (Costa e Silva et al., 2000) for diameter growth (DM), pilodyn penetration (PL) and spiral grain (SG). For these traits, the additive genetic (co)variances were pooled across trials (Table 1), assuming that true genotype by environment interactions were not serious for the wood properties, as well as for DM within defined planting zones in Denmark (Costa e Silva et al., 2000). Basic density (usually termed here as wood density) determinations were absent in the studied progeny trials. Therefore, external information (see Discussion) was used to get estimates for the genetic variance of wood density (WD) and its genetic covariance with DM, PL and SG. For these traits, the additive genetic (co)variances were estimated (Table 1) with raw measures and with values adjusted for differences in radial growth by means of covariance analysis, using ring width and DM as covariates (respectively).

The pooled estimates of additive genetic (co)variances used in the evaluations (Table 1) were constrained to remain fixed at their initial values when iterating to obtain solutions for the model effects. Heterogeneous (co)variances across sites were allowed for non-additive genetic (i.e. the s effects in group I only), main plot, subplot and residual terms. Previous analyses provided starting values for these (co)variances, and indicated significant main plot and subplot effects to be fitted.

The ASREML programme (Gilvar et al., 1999) was used in the BLUP evaluations. Details concerning the analysis are described below.

Single trait evaluations

To reduce the risk of genotype by environment interactions for DM, the field trials across the three groups were allocated to the eastern and western regions (Costa e Silva et al., 2000). This allocation of sites refers to an adjusted version of a previous proposal for environmental zonation of the breeding programme (Wellendorf et al., 1999). No division in different planting zones was made for the wood quality traits. Given the heterogeneous additive genetic variances between sites for all traits (Costa e Silva et al., 2000), the data was adjusted to a common estimate within a region for DM, or overall for PL and SG, as follows:

\[
y_{j(adj)} = \frac{\hat{\sigma}_a}{\hat{\sigma}_{a_j}} y_j
\]

where \(y_{j(adj)}\) and \(y_j\) are the adjusted and original records (respectively) in site \(j\); \(\hat{\sigma}_a\) is the additive genetic standard deviation for the trait, estimated in site \(j\); \(\hat{\sigma}_{a_j}\) is a prior estimate for the additive genetic standard deviation of the population at the specified environment and age (i.e. in the range from 15 to 18 years). The \(\hat{\sigma}_a\) was obtained as the average of individual site estimates, but excluding trials F245 and F246 (as the variances here were estimated from a small set of male parents) and F242 (because the heritability was too low here for DM).

For DM, and using correlation estimates involving pairs of representative trials from the two regions, a weighted genetic correlation was calculated as:

\[
\hat{r}_{a_j} = \sum_{j=1}^{s} \frac{1}{w_j} \frac{\hat{r}_{a_j}}{\text{VAR}(\hat{r}_{a_j})}
\]

with

\[
w_j = \frac{1}{\sum_{j=1}^{s} \frac{1}{\text{VAR}(\hat{r}_{a_j})}}
\]

where \(w_j\) is a weighting factor and \(\text{VAR}(\hat{r}_{a_j})\) is the variance of the correlation estimate \(\hat{r}_{a_j}\) for the \(j\)th site pair. A common additive genetic covariance across the two regions was calculated by multiplying \(\hat{r}_a\) by the product of the within-region \(\hat{\sigma}_a\) estimates.

The BLUP analysis of DM followed a multivariate approach that considered the performance of the same trait in the two regions as two different traits, and took into account the additive genetic covariance (estimated as described above) across regions. The analysis combining groups I and II included four trials in the eastern region and one trial in the western region (see Table 1 of Costa e Silva et al., 2000). The estimators and predictors of model terms were obtained by solving the mixed model equations (MME) which, for the full model, are represented in the form of partitioned matrices as:

\[
\begin{bmatrix}
D_{11} & D_{12} \\
D_{21} & D_{22}
\end{bmatrix}
\begin{bmatrix}
E_{11} \\
E_{12}
\end{bmatrix}
= \begin{bmatrix}
F_{11} \\
F_{12}
\end{bmatrix}
\]

where the submatrix \(D_{11}\) referring to data adjusted to a common genetic scale in the eastern region (denoted as \(k\)), is defined as

\[
\begin{bmatrix}
X;R;X, & X;R;Z, & X;R;W_0, & X;R;W_1, \\
Z;R;X, & Z;R;Z, & Z;R;W_0, & Z;R;W_1
\end{bmatrix}
\]

\(D_{22}\) pertaining to data adjusted to a common genetic scale in the western region (denoted as \(l\), is defined as

\[
\begin{bmatrix}
X;R;X, & X;R;Z, & X;R;W_0, & X;R;W_1, \\
Z;R;X, & Z;R;Z, & Z;R;W_0, & Z;R;W_1
\end{bmatrix}
\]

\(D_{22}\) concerning correlated information between the two regions, is defined as

\[
\begin{bmatrix}
W_1;R;X, & W_1;R;Z, & W_1;R;W_0, & W_1;R;W_1, \\
W_2;R;X, & W_2;R;Z, & W_2;R;W_0, & W_2;R;W_1
\end{bmatrix}
\]

\(D_{21} = D'_{12}\) (with ' denoting transpose), and
where $y_k$ and $y_l$ are the observations in regions $k$ and $l$ (respectively); $g_k^k$, $g_k^l$, and $g_l^l$ are the elements of

$$
\begin{bmatrix}
g_k^k & g_k^l \\
g_l^k & g_l^l
\end{bmatrix} = G^{-1} \otimes A^{-1} = 
\begin{bmatrix}
\hat{\sigma}_{kk}^2 & \hat{\sigma}_{kl}^2 \\
\hat{\sigma}_{lk}^2 & \hat{\sigma}_{ll}^2
\end{bmatrix}^{-1} \otimes A^{-1}
$$

where $G$ is the additive genetic variance-covariance matrix with elements $\sigma_{kk}$, $\sigma_{kl}$, and $\sigma_{ll}$ pertaining to the common estimates for variances within $k$ and $l$ and the covariance between $k$ and $l$ (respectively); $S_k^k$ is the inverse of $S_k \otimes I$, where $S_k$ is the variance-covariance matrix due to the specific combinations of males with females (for the two sites from group I within $k$); $M_k^i$ is the inverse of the block diagonal matrix $M_k = \oplus_{i=1}^s M_i$, where $M_i$ is the inverse of the block diagonal matrix $P_i = \oplus_{j=1}^s P_j$, where $P_j$ is the inverse of the block diagonal matrix $R_j = \oplus_{l=1}^t R_l$ where $R_l$ is the identity matrix of an appropriate order (i.e. equal to the number of main plots, subplot and residual effects (respectively) in site $j$ within region $k$, and $\otimes$ denotes the direct sum; $M_i^j = \frac{1}{\sigma_{kk}^j}$, $P_j^l = \frac{1}{\sigma_{ll}^l}$ and $R_l^j$ are defined as:

- $M^j = \frac{1}{\sigma_{kk}^j}$
- $P^l = \frac{1}{\sigma_{ll}^l}$
- $R_l^j = \frac{1}{\sigma_{ll}^l}$

$I$ refers to main plot, subplot and residual effects in the site from region $l$; the matrix $A$ is as defined before; $I$ is an identity matrix of an appropriate order (i.e. equal to the number of full-sib families to fit the $s$ term, or equal to the number of main plots, subplots or trees for the given site in the $M$, $P$ and $R$ matrices); $X$, $Z$, $Z_1$, $Z_2$, $W_1$, $W_2$ are design matrices. The estimators of fixed effects (regions, sites within regions, blocks within regions and sites ) are given in $B$. The vector $a$ has predictions of breeding values for parents, as well as for individual trees in each region. Correlated information across regions makes it possible to obtain predictions for all parents in $k$ and $l$, even if parents are only represented at one region.

As zonation was not taken into account for SG and PL, the BLUP analysis followed a univariate approach combining the trials F246 (group I) and F228 (group II). The set-up of the MME was simplified to $D_{ij}E_{ij} = F_{ij}$, where the submatrix elements (without a subscript denoting the region) were defined in a similar form and $g_{i}^i$ was replaced by $\frac{1}{\hat{\sigma}_{ii}^2}$ with $\hat{\sigma}_{ii}^2$ is the pooled additive genetic variance for the character.

The progeny group III refers to open-pollinated data only, and thus the $s$ term was not fitted. In the BLUP analysis, the MME were set up as in the other series, accommodating the correlated information across the two regions for DM and accounting for differences of heritability amongst sites in all cases. The evaluations used one trial in region $k$ and three trials in region $l$ for DM, and two trials were combined in the analysis of SG and PL.

For WD, the predictions of breeding values were obtained by (after Falconer and Mackay, 1996):

$\hat{a}_{wd} = \frac{\hat{\sigma}_{pl}G_{wd}(pl)G^{-1} \otimes A^{-1} \otimes A^{-1} \otimes A^{-1}}{\sigma_{pl}^2} \hat{a}_{pl}$

where $\hat{a}_{wd}$ and $\hat{a}_{pl}$ are breeding values for WD and PL, predicted for the $i$th parent; $\sigma_{pl}^2$ and $\sigma_{wd,pl}$ are genetic estimates for the variance of PL and covariance between WD and PL (respectively).

Multiple trait evaluations

A multiple trait BLUP analysis was applied to take simultaneously into account the information available on different characters. The BLUP solutions of parent effects were then used to construct an index for genetic improvement of multiple traits.

To predict parental breeding values for roguing the seed orchard FP241, the evaluations used the DM records from the target (i.e. eastern) region only and all data for SG and raw PL measures (as no zonation was made for the wood properties).

The analysis combined groups I and II as previously, including DM records from three tests (F246, F228, F229) and observations from two tests (F246, F228) for SG and PL. Trial F245 was excluded from this analysis: the heritability was low for DM and data was missing for the wood properties, which suggested that the penalty from discarding this information would have a marginal effect on gain in accuracy. The analysis of group III involved measures of SG and PL from two trials (F241, F243) and DM observations from the eastern site only (F241).

In the multivariate BLUP analysis, the data vector $y$ contained adjusted (to a common genetic scale) records on up to three characters per individual. The analysis combining groups I and II used a structure $S \otimes I$, where $S$ is a variance-covariance matrix for relationships between traits that are due to the combinations of males with females (for F246 in group I only). In all cases, the structure $G \otimes A$ was applied to fit the additive genetic effects, with $G$ defining the corresponding variance-covariance matrix of traits. A common estimate for the additive genetic covariance between SG and PL at age 18 was obtained by multiplying a weighted genetic correlation (using individual estimates from F228, F241 and F243) by the product of the pooled genetic standard deviations. The genetic covariances between DM and the wood properties at age 18 were derived in a similar form, but using individual correlations (from F228) and a similar form, but using individual correlations (from F228) multiplied by a weighted genetic correlation (using individual estimates from F228, F241 and F243) by the product of the pooled genetic standard deviations. The genetic covariances between DM and the wood properties at age 18 were derived in a similar form, but using individual correlations (from F228) and a similar form, but using individual correlations (from F228) and a similar form, but using individual correlations (from F228) multiplied by a weighted genetic correlation (using individual estimates from F228, F241 and F243) by the product of the pooled genetic standard deviations.

A general aggregate objective for genetic improvement was defined as:

$H = v_{sg} \hat{a}_{sg} + v_{wd} \hat{a}_{wd} + v_{dm} \hat{a}_{dm}$

where $\hat{H}$ is the aggregate breeding objective predicted for the $i$th parent; $\hat{a}_{sg}$, $\hat{a}_{wd}$ and $\hat{a}_{dm}$ are breeding values for the target traits – SG, WD and DM (respectively) – predicted for the $i$th parent; $v_{sg}$, $v_{wd}$ and $v_{dm}$ are the relative economic values of the target traits. For WD, the breeding values were predicted by (after Schneeberger et al., 1992):

$\hat{a}_{wd} = \hat{e} G^{-1} a$

where $\hat{e}$ is a (1x3) vector of estimated additive genetic covariances between WD and SG, PL and DM; $G$ is a (3x3) variance-covariance matrix with additive genetic estimates for SG, PL and DM; $a$ is a (3x1) vector of breeding values for SG, PL and DM, predicted for the $i$th parent.
Expected genetic gains from parental selection

The top 20 parents (i.e., about the top 22% of all parents) were selected following ranks of breeding values or index scores, and genetic responses (expected at an age within the range from 15 to 18 years for DM, or at 17 to 18 years for the wood properties) were estimated for each trait by averaging the breeding value predictions of the selected individuals.

Under multiple trait selection, the index scores were calculated with arbitrary "economic" weights set to the target traits. Estimates of expected genetic responses based on the index were used to evaluate alternative options, produced by modifying iteratively the arbitrary weights (COTTERILL and DEAN, 1990). To overcome scale effects due to different measurement units, the searching procedure applied weighting coefficients that were pre-multiplied by the reciprocal of the additive genetic standard deviation of the traits. This amounts to specify the relative importance of different traits on the basis of changes in genetic standard deviation units. Ultimately, the aim was to use biological and end-product information (as outlined in Introduction) for choosing combinations of trait responses which may contribute to increase (or, at least, not degrade) the value of Norway spruce young wood for structural timber.

Results

The expected genetic responses in goal traits (SG, WD and DM) are presented in tables 2 and 3 for single and multiple trait selections, respectively, using SG, PL and DM as selection criteria. The overall trait means are also shown in table 2; for SG and DM, they were estimated by averaging the individual means of representative sites (i.e., trials used for pooling the additive genetic variances); for WD, the estimate is based on 17-year-old basic density determinations at breast-height (see Discussion), and is taken as an approximate average value for the density of young Norway spruce wood produced under fast growing conditions. The multiple trait selection options in table 3 refer to indices constructed to select parents for the elite population aiming to improve wood quality (option 1) or for roguing the seed orchard FP241 targeting the eastern region (options 2).

Table 2. – Expected genetic responses in spiral grain (SG), wood density (WD) and diameter (DM) from single trait selections. For DM, the responses are given for the eastern (E) and western (W) regions.

<table>
<thead>
<tr>
<th>trait</th>
<th>mean</th>
<th>expected genetic response</th>
</tr>
</thead>
<tbody>
<tr>
<td>SG (°)</td>
<td>2.2</td>
<td>-1.0</td>
</tr>
<tr>
<td>WD (kg/m³)</td>
<td>325</td>
<td>14.5</td>
</tr>
<tr>
<td>DMₑ (mm)</td>
<td>104</td>
<td>11.4</td>
</tr>
<tr>
<td>DMₐ (mm)</td>
<td>76</td>
<td>7.1</td>
</tr>
</tbody>
</table>

The expected genetic gains from single trait selection (Table 2) were 11.5 mm and 7.1 mm for DM in the eastern and western regions, respectively. This difference in predicted responses reflects partly a scale effect associated with larger stem diameters (and thus larger additive genetic variances) in the eastern zone. Expressing the results in percentage of the overall trait means, the predicted relative gains were 11.1% and 9.3% in the eastern and western regions, respectively. For wood properties, the expected gains in SG and WD were -10° and 14.5 kg/m³, respectively.

An index combining wood properties only (Table 3, option 1), resulted in improvements of -0.8° and 9.3 kg/m³ for SG and WD, by giving equal weighting per genetic standard deviation change in each trait. For an aggregate breeding objective combining all traits (Table 3, options 2), improvements of -0.7° and 7.1 kg/m³ and a slight loss of -0.8 mm were predicted for SG, WD and DM, following selection on an index giving equal importance to each trait (option 2a). Decreasing only the weight placed on SG led to predicted responses ranging from -0.5° to -0.6° for SG and from 7.3 kg/m³ to 8.3 kg/m³ for WD, while the expected changes were close to zero for DM (options 2b and 2c). Optimizing selection for growth rate over wood quality, but keeping the responses in SG and WD near by zero, gave a gain of 7.9 mm in DM (option 2d). For a selection option approaching maximum simultaneous improvements (KING et al., 1988; MAGNUSSEN, 1990), the predicted responses were modest for all traits (i.e., -0.3°, 5.2 kg/m³ and 3.7 mm for SG, WD and DM, option 2e).

The correlation between the true and predicted breeding value (rₑw) was calculated for each parent and trait, and table 4 lists mean estimates for the analysed groups of progeny trials. The correlation rₑw is an indicator of the precision of the predicted breeding values for a given trait, and may be affected by several factors as the number of parents and progeny per parent, the relationships in the data, the heritability of the observations and the importance of correlated information. As shown in table 4, for DM evaluations, rₑw was lower in the western region for parents of the set 1 (rₑw = 0.70), as well as in the eastern region for parents of the set 2 (rₑw = 0.68). These results probably reflect predictions of breeding values that are based on direct observations from one trial only: F226 in set 1 and F241 in set 2. Although the heritability was lower for DM in F226 when compared with F241, the accuracy of the estimate was higher in F226 (COSTA E SILVA et al., 2000). The larger number of parents and trees per parent in F226 contributed to this result, and also influenced the accuracy of the predicted breeding values for DM (i.e., 0.70 versus 0.68).
Within each set of parents, the amount of information available for evaluation was similar for PL and SG, and the trends in $r_{av}$ values (Table 4) are comparable to the heritability estimates (Costa et al., 2000).

**Discussion**

**Genetic variances and covariances**

Estimates for the genetic variance of WD and its genetic covariance with SG, PL, and DM (Table 1) were based on heritability and genetic correlation estimates taken from external data.

Basic density, PL and DM were measured in the same trees of a 17-year-old clonal trial (F168), established on a fertile soil in the eastern part of Denmark. If it can be assumed that the total genetic variation in WD reflects mainly additive effects, then the additive genetic variance may be approximated by clonal variance estimates. The same applies to clonal correlation estimates for WD and the other traits. A random sample of 21 clones from trial F168 provided individual heritabilities for WD, being 0.62 (s.e = 0.12) and 0.76 (s.e = 0.08) for raw measures and for values adjusted for differences in ring width, respectively (data not shown). Heritabilities based on clone means were reported previously for adjusted WD measures (Larsen et al., 1997). The genetic correlations were –0.52 (s.e = 0.21) and –0.87 (s.e = 0.07) for raw WD observations with DM and raw PL measures (respectively), and –0.88 (s.e = 0.07) between WD adjusted for ring width and PL adjusted for DM (data not shown).

The (co)variance estimates based on adjusted values were used only for selection aiming to improve WD alone (Table 2) or combining WD and SG in an index (Table 3, option 1). As reported by Costa et al. (2000), adjusting raw PL readings to a common DM, reduced substantially the variance due to residual deviations of individual trees; this usually increased the magnitude and accuracy of the heritability estimates of the indirect measure of WD. Moreover, the adjustment by covariance analysis always improved the accuracy of the predicted breeding values for PL (Table 4). Therefore, if selection is targeting wood quality only, DM may be applied as a covariate to increase the precision of the PL measure used as a selection criterion. A similar adjustment may be applied to WD, the goal trait. In this context, methods to adjust basic density variation for differences in ring width have been described elsewhere (Olesen, 1976, 1977; Costa et al., 1994; Danborg, 1994; Larsen et al., 1997). However, for the aggregate breeding objective targeting both growth rate and wood quality (Table 3, options 2), the multiple trait BLUP analysis used parameter estimates based on raw measures of PL and WD, in order to take simultaneously into account genetic and residual relationships between DM and the wood properties.

In a previous study, raw and adjusted PL measures showed similar favourable genetic correlations with SG, and the estimates tended to be low (Costa et al., 2000). Reports on the relationship between WD and SG are scarce in the literature: in young pine wood, an additive genetic correlation of –0.07 was found by Allen (1977) and a phenotypic correlation of –0.05 was reported by Burdon and Low (1992). In the current work, a correlation of –0.15 was found between the basic density of 90 mature parents and their breeding value predictions for SG based on the performance of the offspring (data not shown). All of these estimates are low in magnitude and negative in sign and, from this information, a value of –0.1 was assumed for the genetic correlation between WD and SG.

**Prediction of breeding values**

The methodology followed here to predict breeding values for DM assumed no serious genotype by environment interactions within the defined planting regions, which amounts to assume unit genetic correlations across the respective sites. From the data analysis, there was no indication of important violations of this assumption for trials in the eastern region only although, for the western zone, the results from group III pointed out that the examined sites were equally correlated with a common estimate of 0.55 (Costa et al., 2000). To verify possible bias in the BLUP analysis applied in this study, that assumed unit genetic correlations, a second evaluation was also carried out for parents in group III, following a multivariate approach that used a common additive genetic correlation of 0.55 across the trials within the western region. Apart from this, both of the analyses used the same estimates for the other parameters (i.e. the genetic variance within each region and the genetic covariance across the two regions).

The predictors of parent effects from the second evaluation were averaged for the western sites, and then the predictions obtained from the two BLUP analysis were compared within each region. Spearman rank correlations between predictions from the two analysis were close to 0.99 in both regions and, when comparing breeding value ranks, both of the approaches identified the same top 7 parents (i.e. nearly the top 20% of 37 parents). However, as expected, the predicted breeding values in the western region were more regressed toward their mean of zero after the second evaluation: when comparing mean values of $r_{av}$, the estimate for the western region was 0.83 under the analysis applied here (Table 4) but only 0.72 following the second evaluation. For the eastern region, the $r_{av}$ values were similar under both approaches. Moreover, when averaging the predicted breeding values of the top 7 parents, the difference between the two analysis was 1.0 mm in the western region, but only 0.1 mm in the eastern region. These results indicate that the BLUP analysis applied here may overestimate the parents in group III for selections targeting the western region, thus overestimating expected genetic gains. Yet, when all parents (from all groups) were ranked on the basis of predicted breeding values in the western region, the two analysis led to marginal differences in expected genetic responses (around 0.4 mm, by selecting either the 10 or 20 best parents).

In summary, compared with the applied analysis assuming unit correlations, the parental evaluations were not substantially affected by using across-site genetic correlations of 0.55, albeit the lack of sufficient precision in trial F242 (Costa et al., 2000) limits possible inferences concerning the homogeneity of correlations for the sites in the western region.

**Expected genetic gains from parental selection**

The poor correlations between wood properties result in some genetic progress in both spiral grain and basic density

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Table 4. - Average accuracy of breeding value estimates, given as the correlation between the true and predicted breeding value. The results refer to single trait evaluations of parents in the two sets.

<table>
<thead>
<tr>
<th>sets of parents</th>
<th>diameter</th>
<th>plubdyon</th>
<th>spiral grain</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>east region</td>
<td>west region</td>
<td>raw</td>
</tr>
<tr>
<td>set 1</td>
<td>0.81</td>
<td>0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>(parents in groups I and II)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>set 2</td>
<td>0.68</td>
<td>0.83</td>
<td>0.77</td>
</tr>
<tr>
<td>(parents in group III)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In summary, compared with the applied analysis assuming unit correlations, the parental evaluations were not substantially affected by using across-site genetic correlations of 0.55, albeit the lack of sufficient precision in trial F242 (Costa et al., 2000) limits possible inferences concerning the homogeneity of correlations for the sites in the western region. **Expected genetic gains from parental selection**

The poor correlations between wood properties result in some genetic progress in both spiral grain and basic density
judged to be worthy. Therefore, optimizing selection for diameter growth over wood quality (option 2d) is not currently considered to be appropriate for structural timber, and selection options 2b or 2c are more desirable than a lower risk solution (option 2e) that compromises the gains in all traits (Table 3).

Diameter growth was generally the most weighted character under multiple trait selection (Table 3, options 2). This result reflects the structure of the relationships between traits, but does not necessarily bear a useful interpretation in economic terms. In fact, diameter may be the trait with less relative economic importance, as the FP241 orchard is intended to supply improved seed for the production of structural timber from Norway spruce plantations in fast growing conditions and under shorter rotations. Studying stability, visual grading outcome and strength properties of structural boards from spruce, DANBORG (1996) concluded that diameter growth rate has a direct negative impact on twist, longitudinal shrinkage, knot density (i.e. size and frequency of knots), stiffness and bending strength. Faster diameter growth will also increase the size of the juvenile wood. This contributes further to lower structural performance, particularly because inner boards tend to twist more than outer boards (DANBORG, 1996).

These results suggest that some control of growth rate is required to produce acceptable timber for structural use. Selections based on either 2b or 2c (Table 3) are reasonable options for the specified end use and growth environment, because they are expected to increase the quality of the juvenile wood and reduce its amount in the harvested log. Lower left-handed grain angles in spruce juvenile wood contribute to reduce twist in sawn wood, and thus may improve the grading outcome (BRAZIER, 1985; DANBORG, 1996; HANSEN, 1999). Particularly for small and medium inner boards from fast-grown Norway spruce plantations, the grading outcome can be poor even for a low incidence of spiral grain (DANBORG, 1996). Recently, HANSEN (1999) reported that reducing the grain angle (measured in ring numbers 6 and 8 from the pith) by 1° may increase the proportion of the best quality grade by 8% for inner boards from Sitka spruce. As also noted by BRAZIER et al. (1985), for sawn timber from fast-grown spruce plantations, the reduction of the proportion of the best quality grades is likely to be not compensated for by an increase in yield associated with a larger stem diameter. In Norway spruce, the basic density level of the juvenile wood may be higher than that of the mature wood (DANBORG, 1994). However, the low value of 325 kg/m³ (Table 2), estimated for a mean ring width of 4.7 mm, may be below the limit of acceptance for structural use (i.e. the strength properties of the sawn timber may be poor), and thus a further improvement of 7 kg/m³ or 8 kg/m³ in basic density is judged to be worthy. Therefore, optimizing selection for diameter growth over wood quality (option 2d) is not currently considered to be appropriate for structural timber, and selection options 2b or 2c are more desirable than a lower risk solution (option 2e) that compromises the gains in all traits (Table 3). Finally, although it may be reasonable to emphasize selection on wood properties in relation to diameter growth in spruce, the same strategy may not apply to other conifers with other patterns of variation (within the annual ring, as well as within the tree) for anatomical and physical properties.

Conclusion
The results obtained in this work give strength to the actual breeding strategy of Norway spruce in Denmark, which uses a structure based on a large central population and a number of smaller specialized units or elite populations (WELLENDORF et al., 1994). The presence of a reasonably strong genotype by environment interaction for diameter (WELLENDORF et al., 1999; COSTA E SILVA et al., 2000) gave some support for an environmental zonation, and thus for a definition of distinct breeding populations for improving growth rate. In this context, growth rate may be combined with health (i.e. resistance to needle cast) to achieve simultaneous gains targeting the wind-exposed sites of the western part of the country. On the moderate to low site indices of this region, wood quality is considered to be satisfactory. For the more productive sites of the eastern region, the simultaneous gains in growth rate and wood quality are limited because the genetic relationships are adverse. Thus, improvements in growth and wood quality traits may be faster accomplished through separate elite populations.

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Although current short-term objectives for the deployment population placed more emphasis on wood properties relatively to growth rate for improving the quality of sawn timber, the structure of the breeding population is flexible in the sense that it can accommodate other end-use goals or future changes in market conditions. Furthermore, the structure of small elite breeding populations combined with a good environmental zonation will be an advantage for a strategy applying marker-aided selection (MAS). The breeding value predictions enabled the identification of superior parents for individual traits, and then the aim is to map a restricted number of quantitative trait loci (QTL) for the target trait in the outstanding parents and their progeny. This entails the screening of molecular markers for co-segregation with the individual characters in the progeny from the best parents (as described by O’MALLEY and McKEAN, 1994; WELLENDORF and SKOV, 1997; SKOV and WELLENDORF, 1999). The objective is then to employ MAS in the offspring of crosses between mapped parents from different elite populations, for selecting and mass-propagating individuals that have favourable trait combinations. If feasible, this strategy will be particularly useful for achieving simultaneous genetic gains in adversely correlated characters, as the growth and wood quality traits studied here. Finally, MAS can be also be applied for accelerating recurrent selection within each of the elite breeding populations.

Acknowledgements
We are grateful to Fundação para a Ciência e Tecnologia (Lisboa, Portugal) for financial support. Thanks to Dr. ARTHUR GILMOUR for helpful discussions during this work. The technical support in the field given by VIGO JENSEN is gratefully acknowledged.

References

(Table 3, option 1). On the other hand, the adverse relationship between diameter and the wood properties (COSTA E SILVA et al., 2000) restricts simultaneous genetic gains in growth rate and wood quality. Thus, an aggregate breeding objective combining spiral grain, wood density and diameter growth may either emphasize selection on a trait (or a combination of traits) or compromise the gains in all characters (Table 3, options 2).

Der Autor zeigt, (1.) dass im Bereich der Zuwachskunde eine Neuorientierung notwendig wird; (2.) dass zusätzliche Parameter erhoben werden müssen, um den anthropogen bedingten Teil am ursachenursprünglichen erhobenen Nadelverlust spezifizieren zu können; (3.) welche von den gemessenen bzw. abgeleiteten Parametern die größte Aussagekraft hinsichtlich des Potentials, anthropogen bedingte Waldschäden zu klären, besitzen; und nennt (4.) geeignete Methoden zur Verknüpfung dieser Parameter mit den okular geschätzten Nadelverlusten.


M. LIESEBACH (Großhansdorf)


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Bei der vorliegenden Arbeit handelt es sich um eine Disser
tation, die im Rahmen des Sonderforschungsprogramms „Nachwachsende Rohstoffe“ des Landes Baden-Württemberg erstellt wurde. Neben Pappeln und Weiden wurden 16 weitere Laubbäumearten auf ihre Eignung für den Kurzumtrieb geprüft. Auf 4 ehemaligen Ackerstandorten in Baden-Württemberg und einem Waldstandort in Rheinland-Pfalz wurden wachstumskundliche und bodenökologische Fragestellungen untersucht. Im wachstumskundlichen Teil wurden Anwuchs-
erfolg, Biomasseproduktion und vegetative Regenerations-
masseproduktion wurde nach einer Produktionszeit von 5 Jahren ermittelt, als der Bestandeszuwachs bei den meisten Baumarten kulminiert hatte. Abhängig von Baumart und Standort wurden bis 20 t Trockenmasse je Hektar und Jahr (Grauerle auf ehemaligem Niedermoorstandort) produziert. Die bodenökologischen Untersuchungen beinhalten Durchwurzelungsvermögen, Lagerungsdichte, chemische Bodenanalysen des Bodenwassers und der Festsubstanz, Nährstoffanaly-
sen der Biomasse, Nährstoffein- und -austräge sowie Unter-
suchungen zum Wasserhaushalt. Einige der bodenökologischen Untersuchungen erfolgten beispielhaft und bedürfen daher vor

genetische Vielfalt der als Arten betrachteten Sippen, die Anzahl handelt, ist ihre eindeutige Bestimmung in vielen Obwohl es sich hierbei um eine relativ kleine, überschaubare derum für das Gebiet der Flora 33 Arten beschrieben werden. Hiervon liegt als erste Lieferung die Neubearbei-
tung der Wildrosen-Arten vor. Von den weltweit bekannten 100 (S. 30). Hinzu kommt, dass die nomenklatorische Situation der

kurzumtriebsbewirtschaftung auf landwirtschaftlichen Grenzertragssätzen. Biomasseproduktion und bodenökologi-

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Teil I: Dokumentation der Sturmschäden vom 29. 6. 1997 in Niedersachsens Wäldern verursacht durch „schwere lokale Stürme“. Von M. HUBRIG.


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