mentary treatments, such as supplemental mass pollination or artificial controlled pollination.

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# Genetic Parameters for Spiral Grain in Scots Pine and Norway Spruce

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## Abstract

Genetic parameters were estimated for grain angle, growth and exterior quality traits in two 18-year-old Scots pine (*Pinus sylvestris* L.) progeny trials and for grain angle and growth traits in two 12-year-old clonal trials of Norway spruce (*Picea abies* L. Karst.). Mean grain angles under bark ranged from 1.4 to 2.0 degrees and from 2.1 to 2.6 degrees in the Scots pine and Norway spruce trials, respectively. Heritabilities for grain angle were high in Scots pine ($h^2 > 0.40$) and moderate in Norway spruce ($H^2 > 0.30$). The genetic standard deviations were approximately, or slightly less than one degree. In general, grain angle was genetically and phenotypically uncorrelated with the growth and exterior quality traits. All traits showed low levels of genotype by environment interaction, and there was no tendency for grain angle to be more stable than the other traits studied.

A recently developed device for measuring grain angle was tested and found to be suitable for measurements in genetic tests. The device pushes a wedge through the bark and into the wood, following (and thus revealing) the inclination of the tracheids.

*Key words: Pinus sylvestris* L., *Picea abies* L. Karst., grain angle, heritability, genetic correlations.

## Introduction

Spiral grain, i.e. the helical orientation of the tracheids in a tree stem, is a wood property that has attracted much research interest in recent years, because it has proven to be closely associated with the shape stability (NORTHCOTT, 1965; BALODIS, 1972) and strength of lumber (DINWOODIE, 2000), which are key properties for the quality of sawn products (PERSTORPER et al., 1995). Forestry-oriented research has focused on studies of the silvicultural effects on grain angle (PAPE, 1999), and the patterns of variation within and between trees (COWN et al., 1991; SÄLL, 2002) as well as between stands (DANBORG, 1994). Technically-oriented research has focused on studies of the relationship between grain angle and end-use properties, particularly twist (see for instance, ORMARSSON, 1999; FORSBERG and WARENSJÖ, 2001), as well as measurement techniques. Recently, NYSTRÖM (2003) presented a method for automatically measuring grain angle on logs that will enable logs to be sorted with respect to grain angle, and thus the propensity of the lumber to twist.

In breeding-related research various genetic parameters have been estimated, particularly in radiata pine (*Pinus radiata* D. Don) and Sitka spruce (*Picea sitchensis* Bong. Carr.) In

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both species, studies report a moderate to high heritability for grain angle, a low genotype by environment interaction for the trait and a weak adverse genetic correlation with growth traits (SORENSSON et al., 1997; HANSEN, 1999). The few available studies in Norway spruce (*Picea abies* L. Karst.) have noted the same trends i.e. spiral grain is a moderately to highly heritable trait that is stable across sites and is subjected to only a mildly disadvantageous genetic correlation with growth traits (COSTA E SILVA et al., 2000; HANNRUP et al., 2002). In Scots pine (*Pinus sylvestris* L.) there have been, to our knowledge, no reports on genetic parameters of grain angle.

Efficient breeding for optimizing grain angle requires, apart from appropriate genetic parameters, the use of reasonably rapid, non-destructive, measurement techniques. Several approaches have been used for this, such as measurements on increment cores (NOSKOWIAK, 1968) and measurements on standing trees using radioactive tracers (ARBEZ et al., 1978). The most commonly used method in recent years has been the bark window method described by HARRIS (1984), in which a small piece of bark is removed, the exposed wood is scribed with a freely pivoted needle and grain angle is measured with a protractor and a spirit-level. Measurements are always taken on two opposite radii and averaged to obtain a measure of the grain angle relative to the stem axis. In this study we tested a recently developed device that is based on the principles of the bark window method but the grain angle is revealed by a wedge that is pushed through the bark into the wood and follows the inclination of the tracheids.

The aims of this study were to estimate genetic parameters for grain angle in Scots pine and Norway spruce, and to test a device that may have practical value for measuring grain angles in genetic tests.

## Materials and Methods

### *Plant material and experimental design*

Two Scots pine progeny trials and two Norway spruce clonal trials, all situated in central Sweden, were used in the study.

The progeny trials, Råda (lat. 60°01'N, long. 13°34'E, 140 m elevation) and Brunsberg (lat. 59°37'N, 12°58'E, elevation 80 m), were established in 1984 and included half-sib progenies of 29 parents that were polycrossed. The parents were plus trees, originally phenotypically selected in natural stands for vigour, height, diameter, straightness, and branches with low diameter and straight angle within the geographic range of 60°37'–61°65'N lat. and 270–550 m elevation. In each trial, the progenies were randomised in single-tree plots in 10 blocks with each parent represented by four progenies per block. The spacing was 2 x 2 m.

The clonal trials, Dunderbo (lat. 59°71'N, long. 15°34'E, elevation 140 m) and Salungen (lat. 59°84'N, long. 12°73'E, elevation 225 m), were planted in 1990 with three-year old rooted cuttings that were randomised in single-tree plots in six replications with one ramet per clone and replication. The number of clones represented in each trial was 483, and the spacing was 2.0 x 1.5 m. All clones originated from a Belorussian seedlot from the Vitebsk region. The clones were phenotypically selected in the nursery for late bud burst and intermediate autumn growth cessation.

### *Sampling and measurements*

In the progeny trials, a sample representing 25 of the parents was used. A larger family sample size was used at Råda and in total, 790 and 476 trees were sampled at Råda and Brunsberg, respectively. In the clonal trials, tree height data collected in 1998 were used to ensure that the sample of clones reflected the distribution of mean clonal heights. Forty-nine clones were sampled, for which all surviving ramets were used, resulting in a total sample of 237 and 235 trees at Dunderbo and Salungen, respectively.

*Figure 1.* – Measurement device for measuring grain angle of standing trees. On the measurement scale "H" and "V" indicate right-handed and left-handed spiral grain, respectively.

Measurements were made during the winter 2001/2002. For all the sample trees, breast height diameter and grain angle were measured. The grain angle was measured in the upper part of the internode closest to 1.3 m above ground using a mechanical device, recently developed at Chalmers Technical University in Sweden. This device pushes a wedge with an attached arm into the wood (*Fig. 1*). The wedge is shaped like an arrow with blunt edges and it follows the inclination of the tracheids. The edges are blunt in order to avoid cutting the tracheids when the wedge penetrates into the wood of the first annual rings closest to the bark. A measurement scale, that also acts as a weight, is freely pivoted on the wedge and is brought into a vertical position by the force of gravity. Spiral grain is recorded on the measurement scale by the arm that is attached to the wedge. For each tree, measurements were made at two opposite radii. Averaged measurements were then used to compensate for leaning stems and to obtain a measure of the grain angle relative to the axis of the stem (BRAZIER, 1965). Positive and negative angles were used to designate left-handed and right-handed spirality, respectively.

The grain angle is strongly dependent on the number of annual rings from the pith, particularly in the annual rings close to the pith. For comparative purposes, in order to measure clones at the same position with respect to annual ring number, the number of internodes was counted from the top of the tree to the internode where grain angle was measured, providing an indirect measure of the number of annual rings at this internode. This trait was only recorded in the clonal trials. Because the trees were tall and had dense crowns it was not possible to record this trait in the Scots pine progeny trials.

In order to test the relationship between the grain angle measurements on the standing trees and grain angle measurements on discs using laboratory procedures, a sample of 18 trees was taken from the Brunsberg progeny trial. Available height data from field age 11 years were used to make the sample consistent with the total height distribution. From each sample tree a disc was cut at the same height that the grain angle had been measured on the standing trees. Diametrical strips were sawn from the discs. The grain angle was then marked on the tangential surface with a scribe and measured relative to the stem with a calibrated inclinometer as described in SÄLL (2002). Measurements were taken at every second annual ring from the bark to the pith by sequentially removing ring layers with a wood chisel. Two opposite radii were measured and averaged values for each annual ring were used in the analysis.

### *Previous assessments*

In the progeny trials, data related to tree height (HT), branchiness (BR), branch angle (BA) and straightness (STR) were available from measurements taken after 11 growing seasons in the field. For classified traits, scales with nine classes were defined in such a way that high values denote favourable characteristics. Thus for branchiness, 9 denotes a low degree and 1 a high degree of branchiness; for branch angle 9 denotes a straight angle and 1 an acute angle, while for straightness 9 denotes a straight stem and 1 a crooked stem.

For the clonal trials, height data from measurements taken after nine growing seasons in the field were available and included in the study.

### *Statistical analysis*

Linear regression was used to explore the relationships between the grain angle measurements on discs using laboratory procedures and the grain angle measurements on standing trees.

Estimation of variance components involved a two-step statistical analysis: univariate analysis, where variance components for each trait within each trial were estimated; followed by multivariate analysis, where variances and covariances between pairs of traits within trials were estimated. Estimates of genotype by environment interaction (GxE), expressed as genetic correlations, were obtained from the multivariate analysis by considering variables measured in the two trials as different traits, e.g. grain angle measurements in the two progeny or clonal trials were considered as measurements of two different traits. The following mixed linear model was used in the analysis of the progeny trials and clonal trials:

$$y_{ijk} = \mu + b_i + u_j + e_{ijk} \qquad [1]$$

where $y_{ijk}$ is an observation of each trait of the ijk$^{\text{th}}$ tree, $\mu$ is the overall mean, $b$ is the fixed effect of block, $u$ is the random parent or clonal effect and $e$ is the random residual. For the trait grain angle, an additional fixed effect of number of internodes was included in the clonal model. The random effects were assumed to be normally distributed, with expectation zero and, furthermore, to be independent of each other.

The following model, expressed in matrix notation, was used in the multivariate analysis of the progeny trials and clonal trials:

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

where $i$ pertains to traits 1 and 2, **b** is the vector of the fixed block effects, **u** is the vector of random parent or clonal effects and **e** is the vector of random residuals. As in the univariate model, the fixed effect of the number of internodes was also included for the grain angle trait in the clonal model. **X** and **Z** are the design matrices connecting the observations to the model effects. The random effects are assumed to have a multivariate normal distribution with expectation zero and may be summarized as $\mathbf{u}' = (\mathbf{u}_1', \mathbf{u}_2')$ and $\mathbf{e}' = (\mathbf{e}_1', \mathbf{e}_2')$. The variance-covariance matrix is assumed to be

$$Var\begin{bmatrix}\mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{G}\otimes\mathbf{I} & \mathbf{0}\\ \mathbf{0} & \mathbf{R}\otimes\mathbf{I}\end{bmatrix} \qquad [3]$$

where **G** is the matrix with the parental or clonal variances and covariances, **R** is the matrix with the residual variances and covariances and **I** is an identity matrix. Finally, $\otimes$ symbolises the direct product.

Variances and covariances were estimated with the Average Information algorithm (GILMOUR et al., 1995) for restricted maximum likelihood (PATTERSON and THOMPSON, 1971; SCHAEFFER et al., 1978) estimates, as implemented in the ASReml software (GILMOUR et al., 1999).

### *Genetic parameters*

In the progeny trials, the additive genetic variance ($\hat{\sigma}^2_{\mathrm{A}}$) and the additive genetic covariance ($\hat{\sigma}_{\mathrm{A_1A_2}}$) were obtained as four times the parental variance and parental covariance, respectively. The phenotypic variance ($\hat{\sigma}^2_{\mathrm{P}}$) is the sum of the parental variance and residual variance. Narrow sense heritability ($\hat{h}^2$) and additive genetic correlations, $\hat{r}_{\mathrm{A}}$, between traits within sites and between the same trait measured in the two trials were estimated as $\hat{h}^2 = \hat{\sigma}^2_{\mathrm{A}} / \hat{\sigma}^2_{\mathrm{P}}$ and $\hat{r}_{\mathrm{A}} = \hat{\sigma}_{\mathrm{A_1A_2}} / \hat{\sigma}_{\mathrm{A_1}}\hat{\sigma}_{\mathrm{A_2}}$.

In the clonal trials, the genotypic $\hat{\sigma}^2_{\mathrm{G}}$, environmental $\hat{\sigma}^2_{\mathrm{E}}$ and phenotypic $\hat{\sigma}^2_{\mathrm{P}}$ variance components were estimated as $\hat{\sigma}^2_{\mathrm{G}} = \hat{\sigma}^2_{\mathrm{c}}$, $\hat{\sigma}^2_{\mathrm{E}} = \hat{\sigma}^2_{\mathrm{e}}$ and $\hat{\sigma}^2_{\mathrm{P}} = \hat{\sigma}^2_{\mathrm{G}} + \hat{\sigma}^2_{\mathrm{E}}$ where $\hat{\sigma}^2_{\mathrm{c}}$ and $\hat{\sigma}^2_{\mathrm{e}}$ are the estimated clonal and residual variances, respectively. The estimates of broad-sense heritability ($\hat{H}^2$) were obtained from $\hat{H}^2 = \hat{\sigma}^2_{\mathrm{G}} / \hat{\sigma}^2_{\mathrm{P}}$. Genotypic correlation ($\hat{r}_{\mathrm{g}}$) between traits within sites and genotypic correlations between the same trait measured in the two trials were estimated as $\hat{r}_{\mathrm{g}} = \hat{\sigma}_{\mathrm{G_1G_2}} / \hat{\sigma}_{\mathrm{G_1}}\hat{\sigma}_{\mathrm{G_2}}$ where $\hat{\sigma}_{\mathrm{G_1G_2}}$ is the genotypic covariance between two traits.

Estimates of the standard errors of the genetic parameters were calculated from a Taylor series approximation as performed in the ASReml software (GILMOUR et al., 1999).

## Results

The regression of the mean grain angle from annual ring one to annual ring three from the bark measured in discs on grain angle measured on standing trees was significantly different from zero ($p < 0.0001$) (*Fig. 2*). The grain angle of individual annual rings and mean grain angles of successive annual rings from the bark were also regressed on the grain angles measured on the standing trees, and the strengths of these relationships were very similar.

The mean grain angle was positive in all trials (*Tables 1* and *2*), indicating that the juvenile wood has left-handed spirality. In the progeny trials, the additive genetic standard deviation for grain angle was approximately one degree, slightly higher than the genotypic standard deviation of the same trait in the clonal trials. Heritabilities of grain angle were moderate to high and significantly higher than the values for growth traits, diameter and height.

No genetic relationship was observed between the grain angle of the juvenile wood and growth traits in any of the trials studied (*Tables 3* and *4*). At the phenotypic level, some of the corresponding relationships were significant, but all correla-

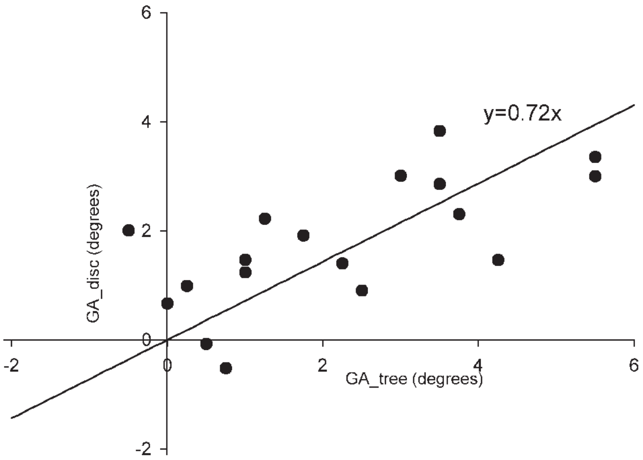

*Figure 2.* – The relationship between grain angle measured on standing trees (GA_tree) and mean grain angle of annual rings one to three from the bark measured on discs (GA_disc).

*Table 1.* – Units of measurement, number of observations (n), arithmetic mean values, additive genetic standard deviations ($\sigma_A$) and narrow-sense heritabilites ($h^2$) with standard errors in parentheses for the measured traits in the Scots pine progeny trials at Råda and Brunsberg (B-berg).

| | Unit | n | | Mean | | $\sigma_A$ | | $h^2$ (S.E.) | |
|---|---|---|---|---|---|---|---|---|---|
| Trait | | Råda | B-berg | Råda | B-berg | Råda | B-berg | Råda | B-berg |
| GA18 | ° | 790 | 476 | 1.38 | 1.96 | 0.94 | 1.08 | 0.40 (0.14) | 0.49 (0.18) |
| DBH18 | mm | 790 | 476 | 104.9 | 96.0 | 7.6 | 11.1 | 0.12 (0.07) | 0.23 (0.12) |
| HT11 | mm | 871 | 523 | 433.2 | 284.2 | 31.8 | 34.1 | 0.21 (0.09) | 0.26 (0.12) |
| BR11 | - | 843 | 494 | 5.3 | 6.3 | 0.42 | 0.38 | 0.27 (0.10) | 0.32 (0.14) |
| BA11 | - | 842 | 494 | 5.2 | 6.4 | 0.74 | 0.50 | 0.38 (0.13) | 0.38 (0.15) |
| STR11 | - | 833 | 492 | 6.6 | 6.4 | 0.34 | 0.32 | 0.18 (0.08) | 0.16 (0.10) |

GA18, DBH18 – grain angle and breast height diameter at age 18, respectively; HT11, BR11, BA11, STR11 – tree height, branchiness, branch angle and straightness at age 11, respectively.

*Table 2.* – Units of measurement, number of observations (n), arithmetic mean values, genotypic standard deviations ($\sigma_G$) and broad-sense heritabilites ($H^2$) with standard errors in parentheses for the measured traits in the Norway spruce clonal trials at Dunderbo (D-bo) and Salungen (S-gen).

| Trait | Unit | n | | Mean | | $\sigma_G$ | | $H^2$ (S.E.) | |
|---|---|---|---|---|---|---|---|---|---|
| | | D-bo | S-gen | D-bo | S-gen | D-bo | S-gen | D-bo | S-gen |
| GA12 | ° | 237 | 235 | 2.57 | 2.14 | 0.58 | 0.72 | 0.30 (0.07) | 0.38 (0.07) |
| DBH12 | mm | 237 | 235 | 41.8 | 54.9 | 2.86 | 5.43 | 0.04 (0.05) | 0.13 (0.06) |
| HT9 | mm | 237 | 235 | 271.4 | 321.5 | 20.3 | 25.3 | 0.07 (0.05) | 0.11 (0.06) |

GA12, DBH12 – grain angle and breast height diameter at age 12, respectively; HT9 – tree height at age 9.

*Table 3.* – Additive genetic correlations (above the diagonal) and phenotypic correlations between the measured traits in the Scots pine progeny trials at **a**) Råda and **b**) Brunsberg. Estimates shown in bold are statistically significant ($p < 0.05$).

**a**) Råda

| | GA18 | DBH18 | HT11 | BR11 | BA11 | STR11 |
|---|---|---|---|---|---|---|
| GA18 | x | 0.10 | 0.04 | 0.13 | 0.23 | -0.04 |
| DBH18 | **0.13** | x | **0.66** | -0.46 | -0.04 | -0.22 |
| HT11 | **0.12** | **0.78** | x | 0.24 | 0.17 | 0.21 |
| BR11 | 0.01 | **-0.46** | **-0.23** | x | **0.63** | 0.21 |
| BA11 | 0.03 | -0.06 | -0.02 | **0.29** | x | -0.07 |
| STR11 | -0.05 | **-0.13** | -0.02 | **0.11** | 0.00 | x |

**b**) Brunsberg

| | GA18 | DBH18 | HT11 | BR11 | BA11 | STR11 |
|---|---|---|---|---|---|---|
| GA18 | x | -0.19 | -0.25 | 0.48 | **0.59** | 0.42 |
| DBH18 | 0.03 | x | **0.83** | -0.42 | -0.06 | -0.36 |
| HT11 | -0.03 | **0.77** | x | -0.37 | -0.38 | 0.02 |
| BR11 | 0.07 | **-0.33** | **-0.18** | x | 0.47 | **0.79** |
| BA11 | 0.09 | **-0.18** | **-0.21** | **0.36** | x | 0.16 |
| STR11 | 0.04 | 0.05 | **0.16** | **0.14** | 0.09 | x |

GA18, DBH18 – grain angle and breast height diameter at age 18, respectively; HT11, BR11, BA11, STR11 – tree height, branchiness, branch angle and straightness at age 11, respectively.

*Table 4.* – Genotypic correlations (above the diagonal) and phenotypic correlations between the measured traits in the Norway spruce clonal trials at **a**) Dunderbo and **b**) Salungen. Estimates shown in bold are statistically significant ($p < 0.05$).

**a**) Dunderbo

| | GA12 | DBH12 | HT9 |
|---|---|---|---|
| GA12 | X | 0.18 | -0.10 |
| DBH12 | -0.09 | x | 0.63 |
| HT9 | **-0.17** | **0.92** | x |

**b**) Salungen

| | GA12 | DBH12 | HT9 |
|---|---|---|---|
| GA12 | X | 0.05 | 0.02 |
| DBH12 | -0.03 | x | **0.91** |
| HT9 | **-0.15** | **0.90** | x |

GA12, DBH12 – grain angle and breast height diameter at age 12, respectively; HT9 – tree height at age 9.

tions were close to zero. Grain angle also tended to be genetically and phenotypically uncorrelated with the branch and stem quality traits, measured in the progeny trials. The only exception was an unfavourable positive genetic correlation with branch angle at Brunsberg, indicating that clones with low grain angle tended to have an acute branch angle.

All traits showed low genotype by environment interaction, as indicated by high additive genetic ($r_A > 0.73$) and genotypic ($r_G > 0.87$) correlations across sites. There was no obvious tendency for grain angle to be more stable as compared to growth traits.

## Discussion

There was a good agreement between the rapid measurements of grain angle on standing trees and the accurate measurements on discs (*Fig. 2*). The latter are here considered reference measurements. The strongest correlation was observed for the mean grain angle of annual rings 1 to 3, reflecting the fact that the wedge of the instrument penetrates some distance into the wood. The slope of the regression line was lower than one. We do not consider this to reflect a bias in the method of measuring grain angle on standing trees, but rather that the lower precision of this method causes higher variation. Repeated measurements on the standing trees would be an alternative way to decrease the random measurement errors and thus increase the precision in the measurements. However, for genetic testing it is not usually necessary to have very high measurement precision for individual trees for parental (backward) or clonal selection. The purpose of the testing is basically to rank selection candidates, and many observations per candidate can be obtained by measuring their progeny or ramets, which gives the predicted candidate values sufficient precision. Altogether, the results indicate that the method of measuring grain angle on standing trees can be successfully used to measure grain angle in genetic tests of Scots pine and Norway spruce.

The left-handed spirality observed at all sites (*Tables 1* and *2*) reflects the general pattern in conifers, in which left-handed spirality tends to occur in the juvenile wood, followed by straightness or right-handed spirality at greater ages. The results do not indicate any apparent difference in mean grain angle between Scots pine and Norway spruce. Grain angle in the Scots pine trials was on average measured in the 11th annual ring from pith, and the mean values of these measurements correspond well with the mean grain angle of similar annual ring number in Norway spruce clonal trials (Hannrup et al., 2002).

Of the two clonal trials, Salungen showed a lower arithmetic mean grain angle than Dunderbo (*Table 2*). The mean number of internodes, which equals the mean number of annual rings, at the point of grain angle measurements, was 5.8 and 6.8 at Dunderbo and Salungen, respectively (data not shown). This difference could have affected the results, but in the comparison at the same number of internodes, a significantly lower grain angle was again found at Salungen. Thus, as the genotypes are the same at the two sites, the difference in grain angle appears to be a true site effect. It may be speculated that the more fertile site at Salungen promotes greater diameter growth, and thus a higher number of cambial anticlinal cell divisions in the trees at this site. Also, among the progeny trials, the faster growing trial at Råda showed a lower mean grain angle (*Table 1*). However, as no data on the number of internodes were available for the progeny trials, this difference may be an age effect i.e. the trees at Råda may have on average more annual rings, and (if so) probably a lower grain angle value.

Clonal mean values ranged from 1.0 to 4.2 degrees at Dunderbo and from 0.08 to 4.4 degrees at Salungen. The mean values of the five clones with lowest grain angles were 1.3 and 0.8 degrees, respectively, at the two sites. Such low grain angles are normally found at annual ring numbers 20 to 40 from the pith in Norway spruce (Säll, 2002). These findings indicate that it is possible to select clones in which the wood close to the pith has similar grain angle characteristics to mature wood. In addition, among the tested Scots pine parents there are parents that give rise to progenies in which the wood formed close to the pith has mature grain angle characterstics. Mean parental values ranged from 0.4 to 3.2 degrees and from 0.9 to 3.8 degrees at Brunsberg and Råda, respectively.

The estimates of additive genetic and genotypic standard deviations for grain angle were between 0.57 and 1.08 degrees (*Tables 1* and *2*). Previous estimates from Norway spruce progeny and clonal trials fall within this range (Costa e Silva et al., 2000; Hannrup et al., 2002) and several estimates are close to one degree. Grain angle showed medium to high heritabilities in all trials (*Tables 1* and *2*). The tendency of this trait to be strongly genetically controlled has been confirmed in several other conifer species (see Hansen, 1999 for review). The derived heritabilities further support the conclusion that the measurement device tested here is suitable for measuring grain angle in breeding operations.

Grain angle was genetically uncorrelated with the growth traits in the progeny trials (*Table 3*). The correlations estimated in these trials may be downwardly biased by the fact that fast growing trees have more growth rings at the assessed internode, and consequently lower grain angles than slow growing trees. In the clonal trials, the unequal number of growth rings is taken into account in the analysis, and in these trials the grain angle was found to be genetically uncorrelated with the growth traits (*Table 4*). These latter correlations should be interpreted with caution as the growth traits did not show significant clonal variation in the univariate analysis (data not shown). However, overall, the genetic correlations indicate that different sets of genes control grain angle and growth traits in Scots pine and Norway spruce, which is encouraging from a breeding perspective, implying there are good opportunities to identify and select parents or clones that combine high growth with desirable grain angles.

In both the progeny trials and clonal trials, low or negligible genotype by environment interaction was found for all the traits studied, as indicated by the strong genetic correlations across trials. Extensive earlier studies in the two species reported lower genetic correlations for height growth than those found in the present study. Haapanen (1996) reported an average type-B correlation across trials of 0.54 for Scots pine and the corresponding correlations were found to be 0.61 by Karlsson et al. (2001) in Norway spruce.

## Conclusions

There is high genetic variation and moderate to high heritability for juvenile wood grain angle in Scots pine and Norway spruce. Hence, there are good opportunities to change the trait by selection.

The low genetic correlations between grain angle and growth traits in the two species imply that selection for grain angle will have negligible effects on growth traits and vice versa.

The tested measurement device has sufficient precision to rank selection candidates in progeny or clonal trials and can therefore be used in breeding operations.

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# Genetic Gain and Diversity Caused by Genetic Thinning in a Clonal Seed Orchard of *Pinus densiflora*

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## Abstract

Estimates of genetic gain (in volume growth) and diversity (expressed as status number, $N_s$) were determined after the application of genetic thinning in a *Pinus densiflora* clonal seed orchard. The genetic thinning was based on: 1) clonal breeding values (represented by general combining ability, *GCA*) obtained from progeny tests, 2) clonal fertility estimated by strobilus production, and 3) clonal size variation determined by the ramet numbers per clone. Genetic gain and diversity estimates were determined under assumptions of 30% pollen contamination and inferior genetic value of contaminating pollen. Thinning 45% of seed orchard (from 67.5 to 41.9 ramets/clone) raised genetic gain to 6.3% in volume growth and reduced the status number to 28.1% of the census number. Further volume growth gain of 11.6% and diversity reduction ($N_s$ = 29.2%) were attained after 70% thinning (from 41.9 to 24.8 ramets/clone). The orchard clones were grouped into 10 *GCA* groups to allow for the linear deployment of clones (i.e., clones were deployed in proportions that reflect their gain estimated), which was implemented for the six top groups. Some ramets from lower groups were intentionally left or removed to avoid the creation of wide gaps or clumps. The effect of pollen contamination on the genetic gain and the consequence of genetic thinning for seed production in the clonal seed orchard were also discussed.

*Key words:* genetic gain, status number, roguing, *Pinus densiflora,* pollen contamination.

## Introduction

Genetic improvement is defined as a process that enhances the genetic value while giving deliberate consideration to the genetic diversity of deployed materials (Kang *et al.,* 2001a). The calculations of genetic gain and diversity in seed orchard populations are of great theoretical and of practical importance. Knowledge of such genetic parameters is essential in the determination of the genetic composition and design of seed orchards as well as the ability to assess the factors influencing genetic quality of orchards' seed. Additionally, it should be realized that clonal genetic value, relatedness among orchard clones, clonal fertility, and pollen contamination, all strongly affect the genetic gain and diversity of orchard seed crops (Lindgren and Mullin, 1998).

Seed orchards represent the seed production populations in which the genetic gain attained from tree improvement programs is packaged and delivered to the field foresters in the form of genetically improved seed. Genetic gain of seed orchard crops is realized from the general combining ability (*GCA*) of the selected trees, which comes from the additive variance in the reference/breeding population (Kang, 2001). Seed orchard evolution/advancement overtime (i.e., from first to second and/or advanced generations) is expected to deliver higher gains. These gains parallel the advancement of selection-breeding-testing cycles. Due to the long time required for seed orchards to reach their optimum seed production and the high cost associated with their establishment, the rate of seed orchards generation turnover is often lagging behind that of breeding generations and different strategies were proposed to overcome this limitation (Williams and Askew, 1993).

Genetic gain in the first-generation seed orchard, on the other hand, is unpredictable due to the untested nature of the orchard clones/families. These clones/families were included in the production populations mainly based on their phenotypes. As breeding and testing information becomes available, the necessity of genetic upgrading in the seed orchard population becomes important. The most common practice applied for this genetic upgrading is the implementation of genetic thinning (i.e., roguing). In most cases, genetic thinning is implemented after several years of seed orchard establishment. Thus, the available information on the orchard clones/families such as genetic value, fertility, and reproductive phenology as well as

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