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Estimation of Clonal Variation in Seed Cone Production Over Time in a Scots pine (*Pinus sylvestris* L.) Seed Orchard

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(Received 17th December 2007)

Abstract

Possibilities for early selection of clones for future seed cone production were studied in a clonal seed orchard of Scots pine (*Pinus sylvestris* L.) in northern Sweden over the first 30 years following establishment. The annual data were modelled as series of bivariate analyses. The correlations between cone production of clones in any individual year and that of a previous year, and cumulative cone production over all years were studied. The corresponding multivariate analysis for a full data fit simultaneously was best estimated

with a genetic distance-based power model (AR). The genetic (variation among clones) and environmental variation were of the same magnitude. The genetic correlations were larger than the phenotypic correlations and both increased with orchard age. Basing selection of clones on a single observation at an early age to improve future cone production was not effective, but efficiency increased if cumulative cone count over many years was used. Year-to-year genetic correlations indicated that early forecasts by clone of cone production at mature ages are highly uncertain. Reliable predictions (moderate correlations) could be achieved only if based on rather mature grafts, 14 or more years after establishment.

Key words: *Pinus sylvestris*, fruitfulness, longitudinal data, reproductive competence, broad-sense heritability.

Introduction

Seed production is fundamental to the economy of seed orchards. One way to increase seed production is to select clones which are prolific seed producers. Seed production ability can then be weighed against breeding value when selecting clones (LINDGREN et al., 2004), provided a reliable forecast of future fertility is available.

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Often, the available material for predicting future fertility exists only as young grafts. Previous studies have reported considerable variation in fertility among clones and ramets in young Scots pine (*Pinus sylvestris* L.) seed orchards (e.g., JONSSON et al., 1976; PULKKINEN, 1994).

A review of fertility variation in seed orchards of different species and ages found, on average, a sibling coefficient close to 2, equivalent to a coefficient of variation of 100%, indicating that variability in fertility is typically large (KANG et al., 2003). Fertility variation was greater in young populations and during poor flowering years. PRESCHER et al. (2007) studied variation in cone production and seed set among grafted mature Scots pine clones and observed lower fertility variation with sibling coefficient of magnitude 1.3 and broad-sense heritability in the order of 0.6, supporting the earlier findings of KANG et al. (2003), who found that fertility variation is lower in mature operational seed orchards. Forecasts based on observations in a single year do not seem reliable (LINDGREN et al., 2007) and the progression of development of cone production over many years has not been reported previously in Scots pine. Only a few studies have followed orchard flowering abundance over a relatively long period in commercially important, north-temperate tree species (e.g., SCHMIDTLING, 1983, in *Pinus taeda* L.; EL-KASSABY et al., 1989, in *Pseudotsuga menziesii* (Mirbel) Franco; NIKKANEN and ROUTSALAINEN, 2000, in *Picea abies* (L.) Karst.).

Longitudinal data arise when measurements are repeated over time. These data allow studies of the pattern of inheritance for a given trait as a function of time. Multitrait mixed-model techniques have been applied extensively for evaluation of genetic components in forest trees; however, the quality of data can limit the possibility to fit all data simultaneously in an unstructured multitrait model. When observations have been repeated over time, several models can simultaneously examine fixed and random effects for all data through modeling of the variance-covariance patterns that exist among observations (APIOLAZA and GARRICK, 2001). An autoregressive correlation structure implies that two observations close to each other over time are more highly correlated than two observations spread further apart. The most flexible model is the random regression mixed model (RRM) methodology, which at every time (point) calculates (co)variances from the covariance function (CF) (KIRKPATRICK et al., 1994; VAN DER WERF et al., 1998). A longitudinal model with a structured (co)variance may be more informative and can be modelled with a reduced number of parameters than the traditional unstructured multitrait model, where observations at different times are treated as different traits. To-date, random regression techniques generally have not been applied to genetics studies with forest trees (see APIOLAZA et al., 2000).

The objectives of this study were: 1) to analyze how well seed cone production in young grafts corresponds to production in later years in the same population; and 2) to compare estimates from a traditional pair-wise mixed model with those from a longitudinal data model. We consider seed cone production in each year of observation, as well as cumulative data over all years.

Material and Methods

The experimental seed orchard

An experimental seed orchard (S23FP1605, Sävar) with Scots pine grafts was established in 1969 close to Umeå, Sweden, at latitude 63°54'N, longitude 20°34'E and altitude 10 m above sea level. The orchard's population was comprised of 42 clones from phenotypically selected "plus trees" and some controls from mature Swedish forests of an origin regarded as suitable for a seed orchard at latitude 64°N. The average latitude of the selected clones was 65°35'N and average altitude 406 m. The experiment was originally intended to investigate the effect of different cultural treatments on cone production. The experimental design was 16 square plots, each 50 x 50 m and representing a unique combination of treatments. The clones were not regarded as treatment effects at establishment and were completely randomized among plots. The treatments included herbicide, mowing, cultivation, soil fertilization, pruning and spacing, with a general spacing between trees of 5.5 x 5.5 m (in mowed or cultivated and fertilized plots (6 in total) additional spacing of 4 x 4 m and 8 x 8 m were also included). Two of the plots with the closest spacing were thinned in 1991. Two of the plots were planted with seedlings and are not considered in the present study. The 14 plots used in this study were originally planted with 947 grafts.

While the majority of assessed grafts (55%) were planted in the autumn of 1969 (orchard year zero), replacement of initial mortality resulted in 35% and 10% of the grafts being planted in years 4 and 7 after establishment, respectively. Replacements were made with surplus material from the original grafting operation held over in nursery beds, or were new grafts with scions collected from other orchard ramets. Seed cone yields have been measured repeatedly, starting at year 11 and thence periodically through to year 30. Data for cone and seed production as well as many other characters were collected over several years, but this study considered only cone count (number) per ramet (although some environmental characteristics were also used for correction of the data in the model). Cone maturation in pines is the growing season after pollination (OWENS and BLAKE, 1985), so that ripe cones counted in the autumn 1980 on the first planted graft are regarded as observed at year 11. The seed orchard was considered to be in full production at the end of the study period (i.e., 1999).

Statistical analysis

Cone production was examined both as single-year production (cone yield per ramet, CY) and as cumulative production (total cone yield per ramet, CCY). If Y_t is the total cone yield at year t , then $Y_t = X_1 + X_2 + X_3 + \dots + X_t$, where X_t is the single-season yield in year t . The statistical analyses were carried out with general linear mixed models using the ASReml software (GILMOUR et al., 2002). In general form, all model equations were fitted as

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}, \quad (1)$$

with $E(\mathbf{y}) = \mathbf{Xb}$ and $\text{Var}(\mathbf{y}) = \mathbf{V} = \mathbf{ZGZ}' + \mathbf{R}$,

wherein each single-year observation in a \mathbf{y} vector is assumed to be a linear function of fixed effects, with plot and planting year as factors and degrees latitude transfer (a negative value is a southward transfer, with a range of -2.6 to 1.3 degrees of latitudes) as a covariate, in a \mathbf{b} vector, and of random effects in a \mathbf{u} vector (with sub-vectors of clone and clone-by-plot interaction) with $\mathbf{u} \sim N(\mathbf{0}, \mathbf{G})$; \mathbf{X} and \mathbf{Z} are the design matrices relating observations to the fixed and random effects, respectively; and \mathbf{e} is the vector of residual errors with $\mathbf{e} \sim N(\mathbf{0}, \mathbf{R})$; \mathbf{R} is the (co)variance matrix of the residuals; and \mathbf{G} is the direct sum of the (co)variance matrices for each of the random effects. ASReml estimates components of variance and covariance by restricted maximum likelihood (REML; PATTERSON and THOMPSON, 1971) using an average-information algorithm.

Series of bivariate analyses (pair-wise) were obtained through the above model (1) with

$$\mathbf{y} = [\mathbf{y}'_i \mathbf{y}'_j]', \mathbf{b} = [\mathbf{b}'_i \mathbf{b}'_j]', \mathbf{u} = [\mathbf{u}'_i \mathbf{u}'_j]' \text{ and } \mathbf{e} = [\mathbf{e}'_i \mathbf{e}'_j]',$$

where we used the vector \mathbf{y} of phenotypic observations in years i and j (reduced to one trait in the preliminary univariate analyses); and \mathbf{u} includes sub-vectors of clone \mathbf{c} and clone-by-plot interaction \mathbf{pc} . All pair-wise combinations between years of observation were calculated which resulted in 14 estimates of variance parameters for a single year. The dependence of tree-stem diameter at year 16 and cone production was also modelled using a bivariate model for two distinct traits in a single year. For this analysis, records without a stem diameter could not be used and were removed. In the bivariate analyses, the structure of basic covariances (including variances) was defined by

$$\text{Var} \begin{bmatrix} \mathbf{c} \\ \mathbf{pc} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G}_c \otimes \mathbf{I}_c & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G}_{pc} \otimes \mathbf{I}_{pc} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \otimes \mathbf{I}_n \end{bmatrix},$$

where $\mathbf{0}$ is a null matrix; \mathbf{I}_c and \mathbf{I}_{pc} are the identity matrices of appropriate order relating to the sub-vectors of the clone effect (ramets from unrelated clones) and clone-by-plot effects; \mathbf{I}_n is the $n \times n$ identity matrix for n records; \mathbf{G}_c , \mathbf{G}_{pc} and \mathbf{R} are the (co)variance matrices between year i and j for clone ($\{\sigma_{c_{icj}}\}$) effects, clone-by-plot ($\{\sigma_{pc_{ipcj}}\}$) effects and of random residual ($\{\sigma_{e_{iej}}\}$) effects (denoting variance when $i=j$), respectively; and \otimes denotes the direct product operator.

For the complete analysis of all data simultaneously, various longitudinal models were considered following the structure of model (1). The best model included a third-order polynomial plot effect of the year trend, a second-order polynomial latitude transfer effect, and a second-order polynomial planting year effect of the year trend. The residual (co)variances (\mathbf{R}) were always modelled with an unstructured fit (i.e., not assuming any correlation pattern between observations), and the clone-by-plot interaction (co)variances (\mathbf{G}_{pc}) were assumed to be homogeneous within year. Attempts to fit the full unstructured genetic (\mathbf{G}_c) and residual (\mathbf{R}) (co)variance model did not converge. Different struc-

tures of the (co)variance matrix (\mathbf{G}_c) were tested, and finally modelled as: $\mathbf{G}_c = \mathbf{SCS}$, where \mathbf{S} is a diagonal matrix of the square roots of the genetic variance components for each year, and \mathbf{C} is the symmetric correlation matrix. The best fit to the data was obtained with an autoregressive correlation structure

$$\mathbf{C} = \begin{bmatrix} 1 & a^{|\ell_{12}-\ell_{11}|} & \dots & a^{|\ell_{30}-\ell_{11}|} \\ a^{|\ell_{12}-\ell_{11}|} & 1 & \ddots & \vdots \\ \vdots & \ddots & 1 & a^{|\ell_{30}-\ell_{25}|} \\ a^{|\ell_{30}-\ell_{11}|} & \dots & a^{|\ell_{30}-\ell_{25}|} & 1 \end{bmatrix},$$

where the correlation coefficient = $\hat{r}_{kj} = a^{|\ell_k-\ell_j|}$. The distance-based power model was fitted as an autoregressive model (AR), with heterogeneous variances fitted with a power function on the natural scale (the logarithmic and square-root scales were also tested, but without a better fit to the data) in order to allow for unequal time intervals. To identify the best models, fixed effects, covariates and interactions were tested using an approximate F -test calculated by ASReml, and random effects generally tested using a chi-square test (likelihood ratio test; $LRT = -2(\log L \text{ of full model} - \log L \text{ of reduced model})$), with effects regarded as significant at a threshold level of $p \leq 0.05$. Latitude transfer was often not significant, but was retained to maintain homogeneity among years. Also, for simplicity, the same model of random components was used over all years.

Genetic interpretation

The genetic interpretation of the statistical model was based on the equation $P = C + E$, where a phenotypic value (P) is the sum of a genetic effect (the clone value, C) and an independent environmental effect (E) with variance $\sigma^2_P = \sigma^2_C + \sigma^2_E$. The phenotypic covariance between two years i and j subdivides, correspondingly, into genetic and environmental covariances: $\sigma_{P_i P_j} = \sigma_{C_i C_j} + \sigma_{E_i E_j}$. Genetic correlation between age i and j was estimated as $\hat{r}_{C_{ij}} = \hat{r}_{C_i C_j} = \hat{\sigma}_{C_i C_j} / \hat{\sigma}_{C_i} \hat{\sigma}_{C_j}$, and the corresponding phenotypic correlations as $\hat{r}_{P_{ij}} = \hat{\sigma}_{P_i P_j} / \hat{\sigma}_{P_i} \hat{\sigma}_{P_j}$. Arithmetic averages for the estimated components of variance approximating genetic and environmental variances from all 14 pair-wise bivariate analyses gave the final variances for the genetic (clonal) coefficient of variation calculated as

$$CV_C = 100 \sqrt{\hat{\sigma}_C^2 / \bar{x}},$$

where \bar{x} is the phenotypic mean. Broad-sense heritabilities, calculated as

$$\hat{H}^2 = \hat{\sigma}_{C_y}^2 / \hat{\sigma}_{P_y}^2,$$

were also obtained as arithmetic means from 14 separate analyses. The standard errors were approximated by ASReml using a first-order Taylor series expansion.

Cone production forecasts were calculated as the arithmetic mean of all pair-wise correlations for a given number of years ahead.

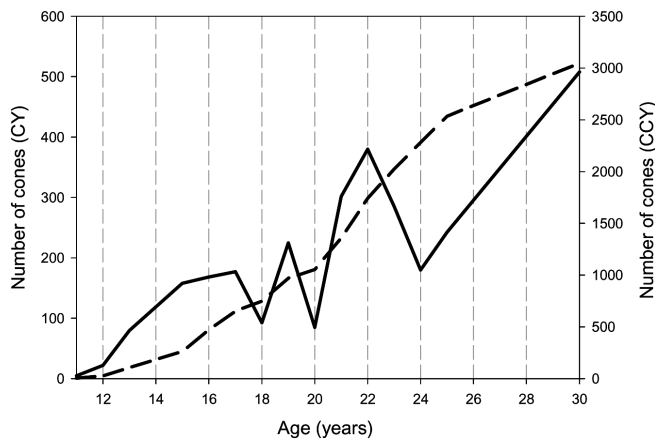


Figure 1. – Average single-year cone yield per graft (CY, solid line) and average cumulative cone yield per graft (CCY, dashed line).

Results

The cone yield per graft (CY) and the cumulative cone yield (CCY) increased over time (Figure 1). Up to year 11, cone production per graft was less than 5, but then generally increased, reaching a plateau around year 16; after this point, production was characterised by large annual fluctuations, between 200 to 500 per graft, but no general increase. The genetic coefficient of variation decreased over time as the reproductive competence of clones increased. For cumulative cone production, the genetic coefficient of variation stabilized at around 45% after the seed orchard entered the adult phase (Table 1).

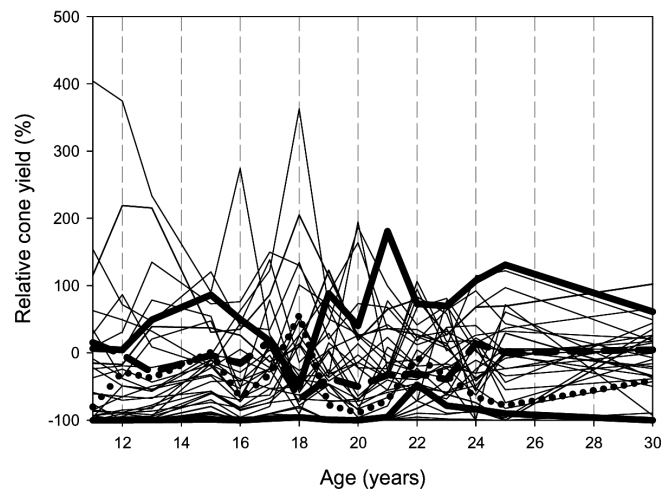


Figure 2. – Yearly arithmetic mean clone cone yield (CY) in percent of average cone yield per graft that year. Individual profiles, with four examples of clone performance highlighted in bold (two solid, a dotted and a dashed line).

There was considerable interaction among clones and years (Figure 2). While it seems possible to identify prolific seed producers at an early age, rankings after age 19 are more reliable.

The heritability of cone production was low at younger ages (Figure 3), indicating that the onset of production is mainly controlled by environmental factors. The heritability is low despite considerable variation in the genetic variance among years, as the environmental

Table 1. – Overview of number of grafts observed (n), mean values of cones per graft, genotypic standard deviations (σ_C), and genetic coefficient of variation (CV_C) in single year and for cumulative yield over 30 years.

Age	n	Single-year cone yield (CY)			Cumulative cone yield (CCY)		
		Mean	σ_C	CV_C	Mean	σ_C	CV_C
11	842	4.6	2.5	55%	4.6	2.6	57%
12	842	21.9	13.7	63%	26.5	16.6	63%
13	842	79.5	46.2	58%	106.0	64.3	61%
15	832	157.8	62.4	40%	263.6	121.5	46%
16	280	168.3	102.6	61%	471.2	235.0	50%
17	279	177.4	82.5	46%	651.3	303.7	47%
18	280	93.0	56.4	61%	748.5	341.3	46%
19	280	223.2	111.2	50%	969.4	449.3	46%
20	280	85.3	61.0	72%	1055.0	506.3	48%
21	280	298.4	171.8	58%	1357.0	654.2	48%
22	281	372.1	149.6	40%	1741.0	792.8	46%
23	280	281.0	111.2	40%	2024.0	895.1	44%
24	218	180.4	69.6	39%	2282.0	951.5	42%
25	277	235.9	97.7	41%	2536.0	1040.1	41%
30	276	488.7	151.5	31%	3047.0	1155.8	38%

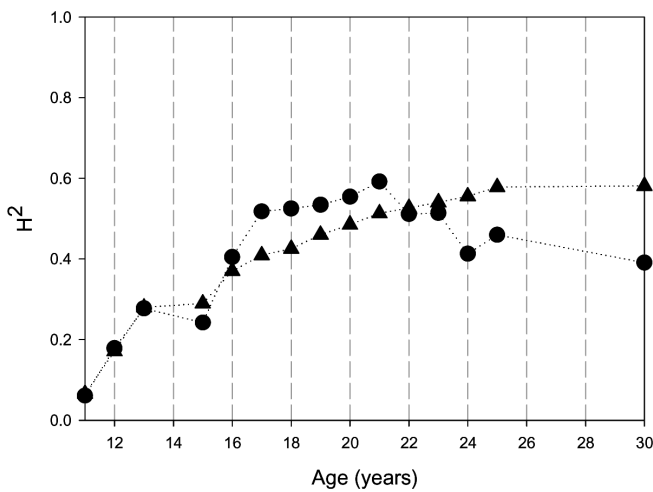


Figure 3. – Heritability for cumulative cone yield (triangle) and single-season cone yield (circles).

variance is large. As the seed orchard matured, the heritability seemed to fluctuate around 0.4. Heritability for cone production in individual years was around 0.5, suggesting that environmental (among grafts within clone) and genetic (among clones) components of variation are equally important. The heritability for cumulative cone production is similar to that for a single year up to year 20, but then it is higher, indicating that the fluctuation among years and among clones in a seed orchard is essentially random.

Correlations for all pairs of combinations of cone production between all 15 years of observations are summarised in Appendix A and Appendix B, for CY and CCY, respectively. The correlations of CY showed a somewhat cyclic pattern along rows in the matrix, with mainly high to moderate genetic correlations between years (excluding the 30-year data). Overall, the correlations decreased with increasing time intervals increases along a single row (towards the right in the matrix). This declining trend was weaker, but more evident, for correlations of CCY in Appendix B, where the genetic correlations were high between all years. CY showed high genetic correlations (>0.62) between the first five years of observation, the following ten years sub-matrix (years 17–30) had lower correlations between years. The correlation between cone count for a specific clone in a particular year and that at year 30 increased over time (last column in the matrix). The genetic correlation for cone production at “mature ages” (above 20 years) was about 0.5, about double that found at “juvenile ages” (below 13 years) (Appendix A). Cumulative cone yield showed a rather strong genetic correlation with the cumulative cone yield at the end of the 30-year observation period, even though the phenotypic correlation was substantial (Appendix B). That correlations become very strong at later ages is probably due, in part, to autocorrelation (the 30-year cumulative cone crop is the sum of earlier cumulative crop counts). At younger ages, this autocorrelation is rather weak. The strong correlations indicate that single-year cone production at year 30 could be unrepresentative, while the cumulative count averages out clone-by-year interactions and errors

resulting from observations made in poor flowering years. The phenotypic correlation was much lower than the genetic correlation, indicating that clonal averages of few clones are poor predictors of clonal genotypic values.

Forecasts of future cone production were made from an analysis of arithmetic averages from correlations of cone production over various intervals from the correlation matrices in Appendices A and B (which in most cases are evident from examination of the diagonal element in the matrices). The average correlations of CY and CCY for forecasts of years shown in *Figures 4* and *5* are thus based on an uneven number of values (with a range between 1 and 12, and declining with large time

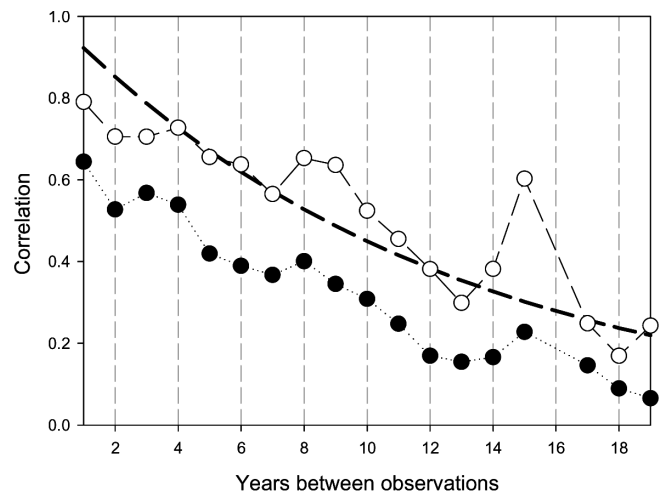


Figure 4. – Correlations between single-year cone yield (CY), averaged for different time-interval between observation and forecast for the clones. Open circles are the genetic correlations, and solid circles are the phenotypic correlations from the pair-wise analysis. The bold long dashed line tracks the genetic correlations from the full-fit analysis.

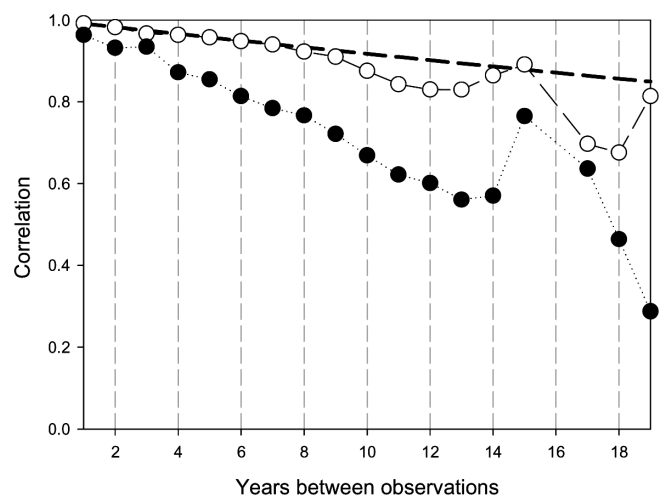


Figure 5. – Correlations between cumulative cone yield (CCY), averaged for different time-interval between observation and forecast for the clones. Open circles are the genetic correlations, and solid circles are the phenotypic correlations from the pair-wise analysis. The bold long dashed line tracks the genetic correlations from the full fit analysis.

intervals in the forecast). This illustrates that average correlations between different years, based on uneven number of values, lead to better forecasts over short time intervals than over longer intervals. This is also reflected in the fluctuating pattern of correlations for longer time intervals in *Figures 4* and *5*. Analyses through the AR model corresponded well with the pair-wise analyses in the overall pattern of the correlations. AR predicted lower correlation over larger time intervals, but higher over short intervals, compared to the pair-wise analysis (*Figure 4* and *5*).

Allowing for a heterogenous variance structure for the interaction between different combinations of treatments with genotypes (clone-by-plot interaction), specific years had a significant effect on the model fit; however, the results revealed large differences in the magni-

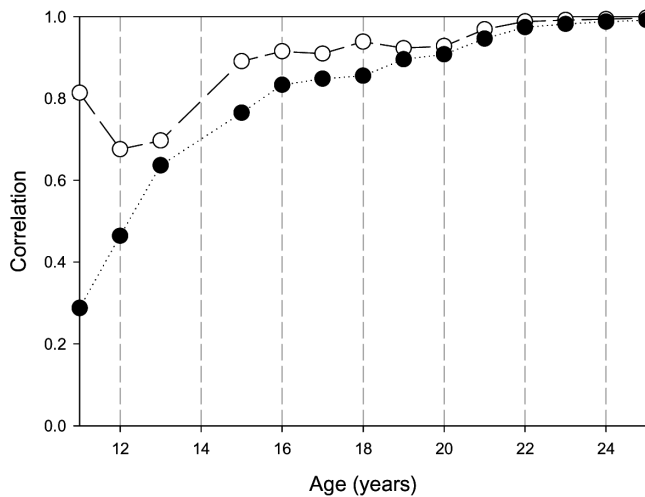


Figure 6. – Correlations between cumulative cone yield (CCY) in different years and single-year cone yield (CY) at age 30. Open circles are the genetic correlations between years within clones, and solid circles are the phenotypic correlations of clonal observations with cone yield at age 30 from the pair-wise analysis.

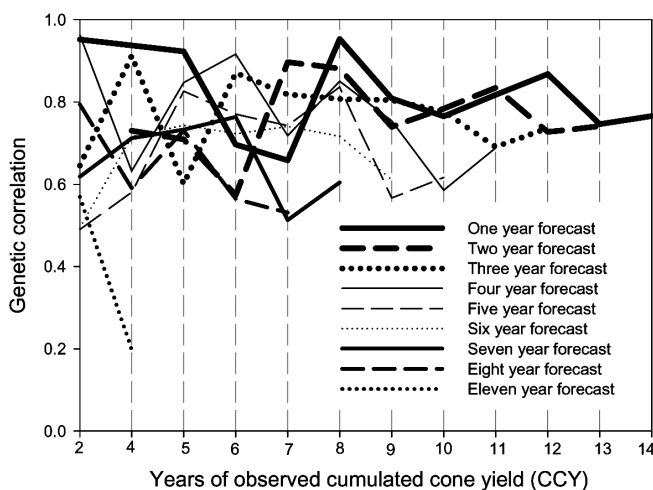


Figure 7. – Genetic correlations between cumulative cone production (CCY) and of following single-year cone yield (CY) at different time intervals from the pair-wise analysis. Only a few values were available for forecasts over long intervals.

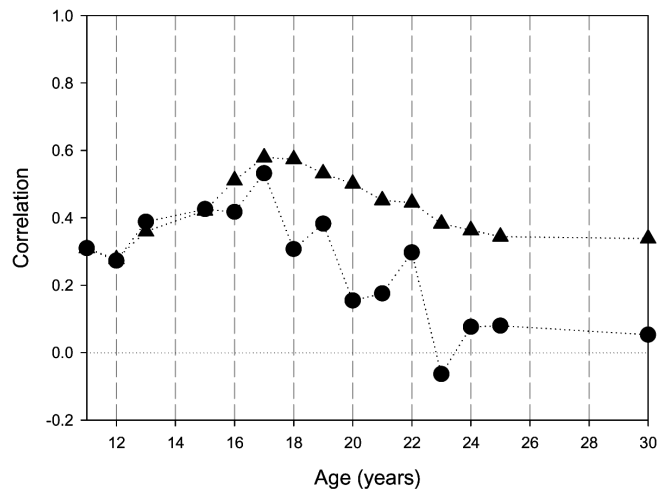


Figure 8. – Correlations between clone values for cone production and a diameter observation at age 16. Circles are the single-season cone yield per clone (CY), and triangles are the cumulative cone yield (CCY) from the pair-wise analysis.

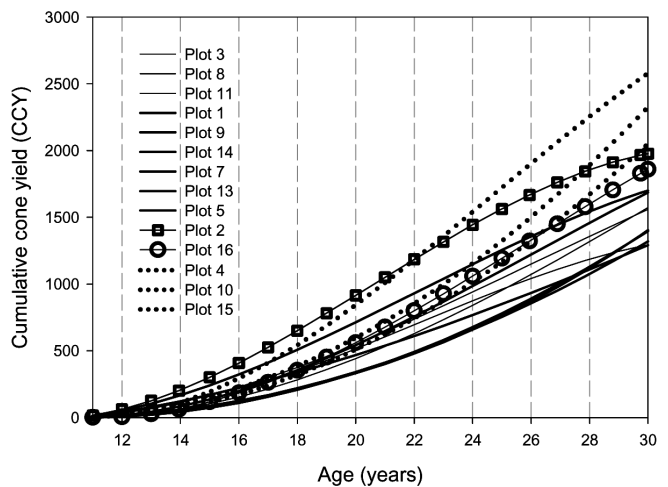


Figure 9. – Average plot effects of cumulative cone yield estimated from the full-fit AR model. Plots 3, 8 and 11 have a plant spacing of 4 x 4 m; plots 1, 9, 14, 7, 13, 5, 2 and 16 have a spacing of 5.5 x 5.5 m; plots 4, 10 and 15 have a spacing of 8 x 8 m; Plot 2 has a yearly herbicide treatment only; and plot 16 is an untreated control.

tude and level of significance for the interactions in different years. On average across years, half of the treatment plots showed no clone-by-plot interaction variation, where the other half, overall, revealed low to moderate variation components (with few exceptions).

The predictive power of cumulative cone yield as an indicator of future cone yield was rather strong (*Figure 6* and *7*). The genetic correlations were in the range 0.5 to 0.7, with the stronger correlations found when the time interval between observations was shorter.

Earlier studies have sometimes shown a negative genetic correlation between growth and reproductive fertility (e.g., ALMQVIST et al., 2001). *Figure 8* illustrates the correlation between diameter growth and cone production developing over time. The data have high standard errors, especially for single-year observations (data

not shown). Nevertheless, these data suggest that larger orchard trees have a larger capacity to produce cones.

Adjustment for differences in clone origin showed that northward transfer increased flowering (data not shown). The effects of different levels of the treatments were also adjusted in the mixed model. The development of plot means over time was shown in *Figure 9*, where it is clear that trees responded to greater spacing and herbicide treatment by producing greater numbers of cones, even at an early age and continuing throughout the period of the study.

Discussion

The annual variation in number of strobili has been well documented in seed orchards and has been shown to be highly variable between clones (e.g., SCHMIDTLING, 1983). Cone production in the present study increased to harvestable levels by year 11 or 12, and continued to increase to at least year 15 to 20, and beyond. Correspondingly, the genetic coefficient of variation (CV_C) decreased sharply at first and later stabilized as all clones reached reproductive competence, reflecting the greater imbalance of clones contributing to the cone crop in the earlier life of the seed orchard. The genetic variation among clones in this orchard was low compared to other Scots pine seed orchards (PRESCHER et al., 2007). In a seed orchard with greater variation among clones, the phenotypic correlations may have been stronger. At younger ages, there are two factors contributing to the variation among clones: variation in the onset of cone production, and cone producing ability of mature clones. Only the latter cause of variation is expressed as the orchard matures; therefore, a decrease over time in CV_C was expected. As a result, CV_C was smallest for the last year observed, a year with the greatest overall cone production, indicating that variation in fertility decreases as seed orchards mature and become more productive. The observed decrease was, however, lower than expected. In general, the imbalance of clones contributing to the cone crop tend to be high, where the rule-of-thumb states that less than 20% of orchard's clones contribute 80% of the cone crop (e.g., EL-KASSABY, 1985).

The pair-wise analyses revealed low phenotypic correlations, especially when single-year data were used. Phenotypic correlations reflect limitations on the number of observed ramets and that non-genetic influences on cone production may persist over years, i.e., the larger ramets produce more cones all the time. Genetic correlations reflect what might be possible with unlimited number of ramets and observations, no interactions and no imbalance. Logistical and practical reasons are likely to make it impossible to realise the potential indicated by the genetic correlations. The phenotypic correlations are probably more indicative of what might be possible if early data from the seed orchard are applied (such as when rouging the seed orchard).

Cumulative clonal values obtained in experiments are useful for ranking clones, but have not been seen as worthwhile to guide operational collections, at least not for Scots pine in Sweden. Even when harvesting is carried out by clone, the practical utility of clonal produc-

tion data is limited. On the other hand, cumulative cone yield data are considerably more reliable for ranking clones. As poor cone production is rather easy to assess, a practical procedure may be simply to record poor production, and then to consider removing some of the less well performing ramets of clones which consistently over several years produce few cones. It should be remembered, however, that in an open-pollinated seed orchard, even the poor cone producers can be useful as producers of pollen.

Correlation estimates using the pair-wise analysis and the AR model were comparable. Using all data simultaneously in a full-fit model ought to be better for fitting an overall trend across years, as more data are taken into account. The autoregressive (AR) genetic structure introduces restrictions in the analysis. The annual variability in cone production, where a heavy flowering year (mast year) is often followed by a light year, seems to influence the genetic correlations from the bivariate analysis. This result may be exaggerated, but some kind of periodicity also in the genetic correlations between years seems logical. This behaviour was not modelled in the simple genetic AR structure in the full-fit analysis. The AR model, however, corresponded well with the overall trend from the pair-wise analyses.

The results reported in the present study refer to a single orchard. The correlation between cone production in the studied orchard and the same clones observed a single year in a clonal archive just a few hundred meters away was remarkably poor ($r = -0.21$), indicating a large genotype-by-environment interaction. (TELLALOV, 2006). This suggests that inherent seed production ability of clones cannot be predicted reliably.

The low heritability for female fertility found at early ages was surprising. For young ortets, the expectation would be that the different genotypes would reach reproductive competence at different ages (ALMQVIST, 2001). This expectation is supported by the correlation between early cone production and diameter, suggesting that fast early growth will result in more cones in a larger crown. This should be reflected in a high heritability for cone production at young ages, which would later decline. However, environmental variation among small young grafts is likely to be greater than for large, mature trees that more fully occupy the site. It is also likely that the selected clones were already reproductively competent at time of grafting, so that cone production was then a matter of graft development, rather than onset of competency.

Extensive studies of genetic parameters for cone production in northern seed orchards are rare. Early empirical findings in *Picea abies* have also indicated that broad-sense heritability for cone production increased with age from 0.19 to 0.63 over a period of 11 years (NIKKANEN and ROUTSALAINEN, 2000). Moderately high broad-sense heritability (0.20–0.46) for number of female strobili were reported by CHOI et al. (2004b) in *Pinus koraiensis* Sieb. et Zucc over three years, with the highest value in a high flowering year. Similar heritabilities were found by MATZIRIS (1997) after a two-year study in *Pinus halepensis* Mill.

Our model “corrects” for plot effects, so that much of the environmental variation in a common seed orchard has been partitioned. The model also accounts for the slight age differences of replacement grafts, compared with the original orchard planting. Although replanting was done during the early years, those replacement grafts were only a half meter shorter in 1985 (average height about 4 meters). The model considers just the within-plot variation (thus variation over 50 x 50 m) while a typical seed orchard occupies over 10 hectares. Being an experimental research orchard, the management is likely better than that found in a typical operational seed orchard. Heritability estimates were based on phenotypic values not including clone-by-plot interaction which, if it had been included, would likely have been greater than in a real seed orchard receiving a single management regime. The development of the per-area seed production over time for Scots pine seed orchards in Sweden has been more fully considered in the works of PRESCHER et al. (2007) and EL-KASSABY et al. (2007), where the data from this seed orchard have been included.

Other studies of fertility over time have also shown “unstable” results in terms of coefficient of variation (CV) for individual years. CHOI et al. (2004a) observed female and male strobili production over an eight-year period in a Japanese red pine (*Pinus densiflora*) seed orchard, beginning at age 18, and reported that the CV for phenotypic data changed from year to year without any clear trend. In other *Pinus sylvestris* seed orchards with low numbers of observations at different ages, the CV among clones for number of cones per graft seemed to decrease with age by a factor of 2 (BILIR et al., 2008).

The correlations in the present study are valid for the observed seed orchard only, and if used for thinning among clones the correlations give correct estimates. If instead used for selections for a new seed orchard the correlations are expected to be much lower and the selection effect much less. In addition, even if the value of selecting good flowering and seed producing clones could be high, it will be decreased if cost of reproduction is essential. A low to moderate negative influence of seed-cone production on somatic growth was shown in EL-KASSABY and BARCLAY (1992).

In conclusion, selection of clones based on a single observation at an early age to improve future cone production in seed orchards was not effective, but efficiency increased if cumulative cone count over many years was used. Year-to-year genetic correlations observed in this study indicated that early forecasts by clone of cone production at mature ages are highly uncertain. Reliable predictions (moderate correlations) could be achieved only if based on rather mature grafts, 14 or more years after establishment.

Acknowledgements

Financial support was provided by the Research School in Forest Genetics and Breeding at SLU and from Föreningen Skogsträdsförädling, Sweden. Thanks to the staff at Skogforsk, who collected cones and measured the

trees during all years in the seed orchard. We also acknowledge the contribution from two anonymous referees.

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Appendix A. – Full correlation matrix of single-year cone yield (CY), with standard errors in parentheses from the pair-wise analysis. Genetic and phenotypic correlations are given in the upper and lower diagonals, respectively.

Age	11	12	13	15	16	17	18	19	20	21	22	23	24	25	30
11		1.04	0.98	0.77	0.99	0.51	0.43	0.73	1.03	0.70	0.60	0.78	0.35	0.36	0.24
		(0.04)	(0.09)	(0.14)	(0.00)	(0.21)	(0.22)	(0.06)	(0.07)	(0.16)	(0.20)	(0.16)	(0.25)	(0.24)	(0.26)
12	0.67		0.95	0.63	0.94	0.49	0.50	0.60	0.76	0.56	0.45	0.54	0.19	0.22	0.17
	(0.02)		(0.03)	(0.13)	(0.05)	(0.06)	(0.16)	(0.14)	(0.10)	(0.15)	(0.18)	(0.16)	(0.22)	(0.20)	(0.21)
13	0.36	0.75		0.76	0.89	0.67	0.60	0.74	0.67	0.58	0.55	0.50	0.20	0.33	0.25
	(0.04)	(0.02)		(0.09)	(0.05)	(0.12)	(0.14)	(0.10)	(0.11)	(0.13)	(0.06)	(0.16)	(0.21)	(0.18)	(0.20)
15	0.35	0.47	0.64		0.78	0.66	0.53	0.81	0.78	0.79	0.81	0.79	0.69	0.66	0.60
	(0.04)	(0.04)	(0.03)		(0.09)	(0.12)	(0.15)	(0.08)	(0.09)	(0.09)	(0.09)	(0.06)	(0.15)	(0.13)	(0.16)
16	0.37	0.60	0.73	0.70		0.58	0.42	0.80	0.92	0.77	0.64	0.77	0.51	0.46	0.40
	(0.04)	(0.04)	(0.04)	(0.04)		(0.14)	(0.18)	(0.08)	(0.05)	(0.09)	(0.13)	(0.10)	(0.09)	(0.18)	(0.19)
17	0.03	0.29	0.59	0.46	0.46		0.68	0.74	0.35	0.42	0.61	0.49	0.31	0.48	0.32
	(0.06)	(0.07)	(0.05)	(0.06)	(0.08)		(0.12)	(0.10)	(0.18)	(0.17)	(0.14)	(0.16)	(0.21)	(0.08)	(0.20)
18	0.13	0.30	0.43	0.53	0.39	0.53		0.74	0.61	0.57	0.63	0.54	0.43	0.33	0.23
	(0.06)	(0.07)	(0.07)	(0.06)	(0.09)	(0.53)		(0.13)	(0.17)	(0.17)	(0.17)	(0.19)	(0.23)	(0.21)	(0.08)
19	0.31	0.35	0.52	0.65	0.68	0.57	0.62		0.77	0.80	0.85	0.77	0.63	0.82	0.49
	(0.05)	(0.06)	(0.06)	(0.04)	(0.05)	(0.07)	(0.07)		(0.09)	(0.08)	(0.07)	(0.09)	(0.15)	(0.09)	(0.18)
20	0.35	0.44	0.48	0.47	0.69	0.31	0.38	0.70		0.78	0.55	0.79	0.56	0.52	0.31
	(0.05)	(0.06)	(0.06)	(0.06)	(0.05)	(0.10)	(0.10)	(0.06)		(0.08)	(0.15)	(0.09)	(0.16)	(0.16)	(0.20)
21	0.23	0.37	0.48	0.50	0.65	0.39	0.39	0.67	0.71		0.75	0.85	0.82	0.78	0.53
	(0.05)	(0.06)	(0.06)	(0.06)	(0.06)	(0.10)	(0.10)	(0.06)	(0.05)		(0.09)	(0.07)	(0.10)	(0.09)	(0.16)
22	0.18	0.30	0.43	0.57	0.56	0.49	0.45	0.71	0.52	0.67		0.87	0.71	0.83	0.72
	(0.06)	(0.07)	(0.07)	(0.05)	(0.07)	(0.09)	(0.09)	(0.05)	(0.08)	(0.06)		(0.06)	(0.13)	(0.08)	(0.13)
23	0.26	0.38	0.43	0.49	0.57	0.39	0.34	0.67	0.69	0.72	0.77		0.74	0.68	0.61
	(0.06)	(0.06)	(0.07)	(0.06)	(0.07)	(0.09)	(0.10)	(0.06)	(0.06)	(0.05)	(0.04)		(0.12)	(0.13)	(0.16)
24	0.11	0.06	0.10	0.31	0.27	0.19	0.20	0.46	0.41	0.51	0.52	0.57		0.82	0.81
	(0.06)	(0.08)	(0.09)	(0.08)	(0.10)	(0.11)	(0.11)	(0.09)	(0.09)	(0.08)	(0.08)	(0.07)		(0.10)	(0.12)
25	0.06	0.13	0.24	0.34	0.23	0.34	0.26	0.57	0.37	0.59	0.65	0.57	0.57		0.64
	(0.06)	(0.07)	(0.08)	(0.07)	(0.10)	(0.10)	(0.11)	(0.07)	(0.10)	(0.07)	(0.06)	(0.07)	(0.07)		(0.16)
30	0.07	0.09	0.15	0.23	0.27	0.22	0.12	0.33	0.24	0.37	0.49	0.39	0.44	0.32	
	(0.06)	(0.07)	(0.08)	(0.08)	(0.09)	(0.10)	(0.11)	(0.09)	(0.10)	(0.09)	(0.08)	(0.09)	(0.08)	(0.09)	

Appendix B. – Full correlation matrix of yearly cumulative cone yield (CCY), with standard errors in parentheses from the pair-wise analysis. Genetic and phenotypic correlations are given in the upper and lower diagonals, respectively.

Age	11	12	13	15	16	17	18	19	20	21	22	23	24	25	30
11	1.00	0.99	0.98	0.98	0.99	0.98	1.00	0.95	0.97	0.95	0.92	0.91	0.88	0.81	0.81
		(0.00)	(0.06)	(0.07)	(0.00)	(0.00)	(0.09)	(0.06)	(0.09)	(0.09)	(0.10)	(0.11)	(0.12)	(0.14)	(0.14)
12	0.80		0.98	0.90	0.93	0.89	0.87	0.84	0.86	0.83	0.79	0.77	0.74	0.70	0.68
			(0.01)	(0.02)	(0.05)	(0.05)	(0.04)	(0.07)	(0.08)	(0.07)	(0.08)	(0.10)	(0.10)	(0.11)	(0.12)
13	0.54	0.86		0.94	0.93	0.93	0.93	0.91	0.91	0.87	0.84	0.81	0.76	0.73	0.70
				(0.02)	(0.03)	(0.03)	(0.03)	(0.04)	(0.04)	(0.05)	(0.03)	(0.08)	(0.09)	(0.10)	(0.11)
15	0.50	0.74	0.91		0.98	0.99	0.98	0.98	0.99	0.96	0.96	0.94	0.93	0.90	0.89
					(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.02)	(0.03)	(0.02)	(0.04)	(0.05)	(0.05)
16	0.42	0.71	0.88	0.97		0.98	0.97	0.96	0.98	0.97	0.96	0.95	0.94	0.93	0.92
						(0.01)	(0.01)	(0.02)	(0.01)	(0.02)	(0.02)	(0.03)	(0.00)	(0.04)	(0.04)
17	0.35	0.65	0.88	0.96	0.98		0.99	0.99	0.99	0.97	0.96	0.95	0.94	0.92	0.91
							(0.00)	(0.01)	(0.01)	(0.02)	(0.02)	(0.03)	(0.03)	(0.02)	(0.04)
18	0.34	0.63	0.87	0.95	0.97	1.00		1.00	1.00	0.98	0.97	0.96	0.96	0.93	0.94
								(0.00)	(0.01)	(0.02)	(0.02)	(0.03)	(0.03)	(0.04)	(0.03)
19	0.35	0.60	0.83	0.93	0.95	0.98	0.99		1.00	0.98	0.98	0.96	0.95	0.94	0.92
									(0.00)	(0.01)	(0.01)	(0.02)	(0.02)	(0.03)	(0.03)
20	0.37	0.61	0.82	0.92	0.95	0.97	0.98	1.00		0.99	0.98	0.97	0.96	0.95	0.93
										(0.01)	(0.01)	(0.01)	(0.02)	(0.02)	(0.03)
21	0.36	0.58	0.79	0.88	0.93	0.95	0.96	0.98	0.99		0.99	0.99	0.99	0.98	0.97
											(0.00)	(0.01)	(0.01)	(0.01)	(0.02)
22	0.34	0.55	0.75	0.86	0.91	0.93	0.94	0.97	0.97	0.99		1.00	1.00	0.99	0.99
												(0.00)	(0.00)	(0.00)	(0.01)
23	0.34	0.55	0.73	0.83	0.90	0.91	0.95	0.95	0.96	0.98	1.00		1.00	1.00	0.99
													(0.00)	(0.00)	(0.00)
24	0.33	0.53	0.71	0.82	0.94	0.89	0.90	0.95	0.95	0.98	0.99	1.00		1.00	0.99
														(0.00)	(0.00)
25	0.31	0.51	0.68	0.80	0.86	0.87	0.88	0.92	0.93	0.96	0.98	0.99	1.00		1.00
															(0.00)
30	0.29	0.46	0.64	0.76	0.83	0.85	0.86	0.90	0.91	0.95	0.97	0.98	0.99	0.99	
															(0.00)

Responses of *Falcataria moluccana* seedlings of Different Seed Sources to Inoculation With *Uromykladium tepperianum*

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(Received 7th January 2008)

Abstract

Falcataria moluccana (batai) is one of the valuable multipurpose tree species for forest plantations, particularly in Malaysia and Indonesia. Gall rust disease caused by *Uromykladium tepperianum* (Sacc.) is one of the most destructive diseases in Batai plantations. The

disease causes severe damage at all developmental stages of the plant from the nursery stage to mature trees in the field and includes the development of chocolate brown, cauliflower-like or whip-like galls on the stem, branch, petiole, shoot and pod. Different seed sources may respond differently to gall rust fungus. Thus, the responses of *F. moluccana* seedlings from 6 selected seed sources to gall rust disease caused by *U. tepperianum*, were evaluated, at the Brumas Estate, Malaysia, in terms of gall rust disease severity, mortality, and disease infection rate of the seedlings. Based on disease severity, infection rate and cumulative mortality due to gall rust disease, the wamena was found to be the best seed source in relation to gall rust disease resistance.

Key words: *Falcataria moluccana*, seed sources, *Uromykladium tepperianum*, artificial inoculation, resistance.

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