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Genetic Correlations Among Field Trials of Norway Spruce Clones Representing Different Propagation Cycles

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Abstract

Serial cutting propagation means that clones are produced in consecutive propagation cycles, where a new round of cuttings are taken from the previously rooted cuttings, etc. The objective of this study was to judge the importance of propagation cycle on height growth in field trials. In a field trial series with Norway spruce clones, comprising nine trials in four cutting propagation cycles, propagation cycle only had a minor effect on height growth compared to the site effect. For inter-site

correlation models where all trials were included, the best fit was obtained by an unstructured model, while the most parsimonious model included constraints on the correlations depending on cycle structure. Model constraints based on grouping of the trials by site productivity did not improve the fit. Testing for generally good performers over a range of different site conditions appears to be a good approach, unless drivers of genotype by environment interaction can be identified.

Key words: cuttings, field performance, genotype x environment interaction, Norway spruce, propagation effects.

Introduction

An important purpose of vegetative propagation is to identify and clonally propagate superior genotypes in order to increase the genetic gain compared to a sexual-

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ly propagated material. Another attractive feature is the possibility to test a genotype itself rather than by its offspring, which for many forest tree species enables a considerable time gain and higher selection intensity in the breeding programme. However, vegetative propagation can give rise to effects that are not purely genetic, but rather related to particular propagation events. Such non-genetic effects that can be confounded with genetic effects are called C (“common”) effects (LERNER, 1958; LIBBY and JUND, 1962; LIBBY, 1976). A typical situation when such effects can appear and may cause bias in the genetic interpretation is propagation in sequential cycles of Norway spruce (*Picea abies* (L.) Karst.) in a serial propagation programme (KLEINSCHMIT *et al.*, 1973). Propagation events in different cycles are separated in time, and normally also propagation conditions differ among cycles. If these factors influence different clones differently, C effects are created. That time itself may be important for the appearance of C effects is suggested by the ageing phenomena that have been observed in the serial propagation of Norway spruce, where rooting success decreases and the frequency of plagiotropic growth and branch asymmetry of rooted cuttings increases with cycle number (ST CLAIR *et al.*, 1985; DEKKER-ROBERTSON and KLEINSCHMIT, 1991).

More environmental influence is introduced when establishing field trials with the vegetatively propagated plants. Also in field trial series, the time factor (i.e. effects of planting year) may contribute to genotype × environment (G×E) interaction.

In this study, field trials belonging to four vegetative cycles of serial propagation by rooted cuttings of Norway spruce clones were studied. The trials provided data for studying the effects of both cycle and site, and thus enable us to judge the importance of possible effects associated with the propagation cycle.

Materials and Methods

Norway spruce clones were propagated by rooted cuttings in six consecutive vegetative propagation cycles. The first propagation cycle was in 1976, when 1595 three to four-year old clones were selected as seedlings from north-east European and Swedish provenances grown in 10 different nurseries in southern Sweden. Cuttings collected from the selected seedlings were rooted in early spring in a greenhouse at the Ekebo research station in southern Sweden (55°58'N, 13°45'E). The rooted cuttings were moved outdoors in late summer and developed dormancy and winter hardening in natural conditions. During winter, the rooted cuttings were lifted and moved to a –3°C storage facility where they remained until spring when they were transplanted as bare-root plants to the Kolleberga nursery (56°12'N, 13°54'E). When the plants were four years old, a second cycle of cuttings was collected, rooted and grown as described earlier. For a subset of 178 clones, this procedure was repeated at three to four year intervals, except that the cuttings in cycle 5 and cycle 6 were transplanted to large containers and remained at the Ekebo station during growth instead of going to bare-root beds. Thus, rooted cuttings were produced and subsequently

planted, three or four years after rooting, in nine field trials, representing four different vegetative cycles (cycles 3, 4, 5 and 6) (Table 1, Fig. 1). The field trials were randomised incomplete block experiments with single-tree plots within blocks and 4–7 replications per clone.

Individual tree height was measured at different ages in the different trial series, ranging from 9 to 18 years in the field (c.f. comments in the legend of Table 1).

Univariate analysis on each site was performed according to the model:

$$y_{ijk} = b_i + c_j + e_{ijk} \quad (i)$$

where y_{ijk} = observed individual value, b_i = fixed effect of block i , c_j = random effect of clone j and e_{ijk} = random error term.

Broad-sense heritabilities (H^2) were calculated as $\sigma_G^2/(\sigma_G^2 + \sigma_E^2)$, where σ_G^2 was estimated by σ_c^2 and σ_E^2 by σ_e^2 .

Table 1. – Trials, site index, Number of clones (n_c), establishment year (Year), years in the field at the time of height measurement (Yfield) and distribution of trials on vegetative propagation cycles.

Cycle	Trial no.	Site index*	n_c	Year	Yfield
3	F1011	G28	178	1985	9
3	F1012	G32	178	1985	9
3	F1013	G26	178	1985	9
4	F1106	G30	169	1988	18
4	F1107	G28	169	1988	18
5	F1185	G34	168	1991	15
5	F1186	G24	168	1991	15
6	F1243	G34	110	1995	11
6	F1244	G28	110	1995	11

* a high value indicates high production

Figure 1. – Map showing geographic location of the trials. Trials F1011, F1012, F1013 represent vegetative cycle 3, F1106, F1107 cycle 4, F1185, F1186 cycle 5 and F1243, F1244 cycle 6, respectively.

Inter-site clonal correlations were estimated with all observations from all trials according to the model:

$$\mathbf{y} = \mathbf{X}\mathbf{b} + \mathbf{Z}\mathbf{c} + \mathbf{e} \quad (\text{ii})$$

where $\mathbf{y}$ = vector of observed values across all sites, $\mathbf{X}$ = incidence matrix of site and block effects within sites, $\mathbf{b}$ = vector of fixed site and block effects within sites, $\mathbf{Z}$ = incidence matrix relating observations to interaction effects between site and clone, $\mathbf{c}$ = vector of random interaction effects between site and clone, and $\mathbf{e}$ = vector of random error terms.

The vector $\mathbf{y}$ was partitioned as $\mathbf{y}_I - \mathbf{y}_g$, representing each site. The random effect variance-covariance matrix ($\mathbf{G}$) comprised the inter-site covariance matrix structured as the direct product of a 9 x 9 genetic variance-covariance matrix ($\mathbf{G}_0$) and an identity matrix of the order of the number of clones tested ($\mathbf{I}_{n_c}$) and the residual ($\mathbf{R}$) variance-covariance matrix as the direct sum of the product of individual site error variances ($\sigma^2_{e_i}$) and identity matrices of the order of the number of observations on each site (n_i):

$$\text{Var} \begin{bmatrix} \mathbf{c} \\ \mathbf{e} \end{bmatrix} = [\mathbf{G} \ \mathbf{R}] = \begin{bmatrix} \mathbf{G}_0 \otimes \mathbf{I}_{n_c} & \mathbf{0} \\ \mathbf{0} & \sum_{i=1}^{n_i} \oplus \sigma^2_{e_i} \mathbf{I}_{n_i} \end{bmatrix} \quad (\text{iii})$$

where $\mathbf{c}$ corresponds to the vector of clonal effects for each site, $\mathbf{e}$ the residuals, with sub-vectors $\mathbf{e}_i$ for each site, $\otimes$ denotes the direct (or Kronecker) product and $\oplus$ denotes the direct sum. The $\mathbf{G}_0$ matrix was further decomposed into a correlation matrix and a variance vector to enable constraints to be applied to the correlations to test hypotheses about correlation patterns.

Initial testing showed that there was significant heterogeneity of genetic variance between sites, the values being related to the variation in site means due to different growth rates and ages of measurement. Hypotheses about the effects of site and propagation cycle on the inter-site genetic correlations were investigated by applying different constraints to $\mathbf{G}_0$. Vegetative propagation cycle and site index groups were tried as explanatory factors for the correlation structure. Four site index groups were created, corresponding to the classes G24-26, G27-29, G30-32, G33+ (Hägglund and Lundmark, 1981) (Table 1).

The following constraints were applied to $\mathbf{G}_0$ to test hypotheses about the patterns of genetic correlations between sites and each model was given a code:

- U: Uniform site-site correlations. Basic model, correlations among all trials set to be equal.
- X: All site-site correlations constrained to be 1. To test whether there is any GxE interaction, and thus whether investigating the pattern is necessary.
- C: Correlations structured to be equal among trials within each cycle and equal among trials within each pair of cycles. To test if the correlation patterns are related to propagation cycle.
- I: As C, but with “site index groups” instead of “cycles”. To test if the correlation patterns are related to site index.

- IB: Correlations structured to be equal among trials within cycles and equal among trials within pairs of cycles with the same difference in cycle number. To test if the correlation patterns are related to how far apart in time the propagation cycles are.
- C1: correlations set to 1 among trials within cycle and equal among trials within each pair of cycles. To test if there is GxE interaction within propagation cycles.
- G: All correlations unconstrained. The full correlation model, to see if there are other patterns in the correlations not modelled by the constraints above.

The actual pattern of constraints applied is shown for five models in the Appendix (Tables A1–A5).

The models were compared using the Akaike Information Criteria (AIC) (AKAIKE, 1974), calculated as:

$$\text{AIC} = -2 (\log L_j) + 2 p_j \quad (\text{iv})$$

where $\log L_j$ = logarithmic residual maximum likelihood for model j, and p_j = number of estimated variance parameters in model j.

The $\mathbf{G}$ and $\mathbf{R}$ matrices were incorporated into the mixed-model equations of HENDERSON (1984) for Restricted Maximum Likelihood (REML) estimation of variance components.

$$\begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{X}'\mathbf{R}^{-1}\mathbf{Z} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{X} & \mathbf{Z}'\mathbf{R}^{-1}\mathbf{Z} + \mathbf{G}^{-1} \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{c} \end{bmatrix} = \begin{bmatrix} \mathbf{X}'\mathbf{R}^{-1}\mathbf{y} \\ \mathbf{Z}'\mathbf{R}^{-1}\mathbf{y} \end{bmatrix} \quad (\text{v})$$

Estimates of clonal and residual variances obtained in the univariate analyses were used as starting values, while site-site clonal correlation starting values were arbitrarily set to 0.75. Estimates were performed using the ASReml software (GILMOUR *et al.*, 2006).

The resulting predictions of each clone in each trial, using model G, were used for calculations of contribution of each clone to the total genotype x environment interaction, denoted ecovalence, and suggested to be a measure of phenotypic plasticity (WRICKE, 1962). To investigate the relationship between ecovalence and site productivity, mean height growth per year (height divided by years in the field), was used as the site productivity measure. Trials F1011-13 were measured at a relatively young age, where the establishment phase represents a greater portion of total height, and the mean height growth per year will be thus biased downward. Therefore, a correction of the site productivity measure was performed for these trials by multiplying with the

Table 2. – Mean values (mean), estimated broad sense heritabilities (H^2), clonal coefficients of variation (c.v.) and number of observations (n), for height in the different trials.

Trial	Height (dm)			
	mean	H^2	c.v.	n
F1011	23.1	0.225	0.149	693
F1012	36.0	0.267	0.106	1324
F1013	24.6	0.139	0.129	1301
F1106	73.4	0.163	0.099	1043
F1107	102.4	0.427	0.138	1090
F1185	97.3	0.432	0.088	742
F1186	84.7	0.226	0.080	765
F1243	76.0	0.214	0.069	433
F1244	66.9	0.089	0.084	202

Table 3. – Comparison of the different correlation models tried. For model descriptions, see Materials and Methods. p = number of parameters estimated in the model. The smallest AIC value indicated the best model.

Model	LogL	p	AIC
U	-1402.57	10	2825.14
X	-1498.42	9	3014.84
C	-1387.74	19	2813.48
CB	-1402.24	13	2830.48
C1	-1427.93	16	2887.86
I	-1395.04	19	2828.08
IB	-1401.84	13	2829.68
G	-1370.49	45	2830.98

ratio between mean height growth per year for trials F1106-07, F1185-86, F1243-44 and the mean height growth per year for trials F1011-1013.

Results

Trial mean height values reflected site productivity and age at measurement as expected. In general, broad sense heritabilities were moderate, exceeding 0.1 in all but one trial (*Table 2*).

Based on AIC values (*Table 3*), Model X (no GxE interaction) was much worse than model U (uniform correlations), indicating that there was GxE interaction among the trials. Model C (correlations based on cycle) performed slightly better than model U which demonstrated that propagation cycle explained some of the GxE interaction. Structuring correlations to consider differences in cycle number (model CB) did not improve the AIC value (see *Tables 4* and *5*), indicating that propagation cycles closer together in time were not better correlated. Thus, GxE interaction effects associated with ageing of the clones could not be shown. Model C1 (further restricting all inter-site correlations within a cycle to be

1) did not improve the AIC value (*Table 3*), so there was still substantial GxE interaction within a propagation cycle. The model with unconstrained correlations (model G) gave the highest maximum logarithmic likelihood value but a higher AIC value than model C (*Table 3*). Models I and IB, attempting to explain the correlation pattern by site productivity, did not improve the model fit.

Ecovalence related to mean clone performance over sites showed that there were few clones with high ecovalence values and that these were located in the centre of the distribution. There were several clones with low ecovalence values and these were spread over the whole distribution (*Fig. 2*). For example, the three best, worst and medium performing clones showed different responses to site productivity, but no clear linear relationship for any of them (*Fig. 3*).

Discussion

Broad-sense heritabilities were in two cases above 0.4, quite high values indicating that some unusual events affecting the genetic expression of height growth have occurred (cf. HÖGBERG and DANELL, 1989; KARLSSON and HÖGBERG, 1998; KARLSSON *et al.*, 1998).

Even though no such event can be traced in the trial history, a trial neighbouring F1107, planted at the same time, has documentation of early summer frost damage and this is suspected to be the cause of the high heritability in that trial. Increased heritability due to frost damage has been reported by KARLSSON *et al.* (2001). No information of a frost event in F1185 is available. The early summer frost risk is a well known negative factor for spruce establishment and early growth, and the strategy for minimizing damage on frost prone sites is to select late flushing clones (SHAW *et al.*, 1988; KLEIN-SCHMIT, 1992; KARLSSON *et al.*, 2001).

Table 4. – Inter-site clonal correlations for height from the model with heterogeneous variances and correlations set to be equal within cycle and equal among pairs of cycles (C).

	F1011	F1012	F1013	F1106	F1107	F1185	F1186	F1243	F1244
F1011	-	0.746	0.746	0.541	0.541	0.686	0.686	0.691	0.691
F1012		-	0.746	0.541	0.541	0.686	0.686	0.691	0.691
F1013			-	0.541	0.541	0.686	0.686	0.691	0.691
F1106				-	0.348	0.529	0.529	0.369	0.369
F1107					-	0.529	0.529	0.369	0.369
F1185						-	0.744	0.791	0.791
F1186							-	0.791	0.791
F1243								-	0.760

Table 5. – Inter-site clonal correlations for height from the model with heterogeneous variances and correlations set to be equal within cycle and equal among pairs of cycles with the same difference in cycle number (CB).

	F1011	F1012	F1013	F1106	F1107	F1185	F1186	F1243	F1244
F1011	-	0.640	0.640	0.601	0.601	0.569	0.569	0.651	0.651
F1012		-	0.640	0.601	0.601	0.569	0.569	0.651	0.651
F1013			-	0.601	0.601	0.569	0.569	0.651	0.651
F1106				-	0.640	0.601	0.601	0.569	0.569
F1107					-	0.601	0.601	0.569	0.569
F1185						-	0.640	0.601	0.601
F1186							-	0.601	0.601
F1243								-	0.640

Figure 2. – Ecovalence values in relation to clone performance, expressed by average predictor value over sites in standard deviation units (sd).

Figure 3. – Response curves in height for three top-performing clones, three median-performing clones and three weak-performing. Clone performance is expressed by predicted clone values in standard deviation units (sd). Site productivity corresponds to mean annual height growth (dm/year).

Although other available studies deal with data from field trials younger than those in the present study, the magnitude of inter-site correlations at the clonal level corresponded well with other published studies on Norway spruce (BENTZER *et al.*, 1988; KARLSSON and HÖGBERG, 1998; KARLSSON *et al.*, 2001).

Although the unconstrained model (G) gave the best fit on LogL, model C (constrained by cycle) was more parsimonious on AIC. The propagation cycle thus appears to be a component of G×E interaction, but not a strong component. The model where distance in time between cycles (model CB) was taken into account did not improve the AIC value. Hence, there was no evidence that ageing effects have influenced relative clone

performance in any substantial way. However, it should be remembered that the number of clones in the trials decreased in the later cycles, and that this reduction was partially due to poor rooting which itself could indicate that ageing occurred.

Height measurements spanned between 9 and 18 years of field growth in different cycles. Establishment effects influenced particularly the earlier measurements and were confounded with propagation cycle. This complicates the interpretation. There is a risk that some of the cycle effects were reflections of different age at measurement. However, as the analyses did not show stronger correlations within than among cycles, and thus within and among ages, possible age effects have

not caused any detectable bias. The attempt to use site productivity for describing the correlation pattern did not improve the explanation of the observed variation.

The most variable clones were found in the mid-section of the performance distribution and there were no indications that top-ranked clones in height growth should be more variable than medium or low-ranked ones (Fig. 2). Selection from the top seemed to be quite reliable over a wide range of sites (Fig. 3). This contrasted somewhat to results from a Norway spruce clone trial series in Germany, where 10-year data suggested that some of the best growing clones were unstable over sites, as judged by their ecovalence (ST CLAIR and KLEINSCHMIT, 1986). The same series was revisited at age 17 years by ISIK and KLEINSCHMIT (2003) with essentially the same result. However, the range of ecovalence values was considerably lower than in the present study. Furthermore, the number of clones was lower: 40 compared with more than 100 in the present study. Clonal correlations among sites in the study by ST CLAIR and KLEINSCHMIT (1986) reached approximately the same average as the clonal correlations among sites after simultaneous analysis in a correlation model in the present study, but the range of correlations was narrower in the first case. Experimental conditions differ too much between the trial series to determine whether top-performing clones will introduce more stability or not.

Many sources of variation can contribute to Norway spruce GxE interaction, which can leave the breeder or plant producer in a difficult selection situation. The present findings suggest that selection of clones for good field growth in southern Sweden should be made after field tests in a range of environmental conditions, accepting the fact that inter-site correlations normally average 0.5–0.7 and that site definitions at present are too imprecise for identifying clones suitable for different sites. Serial cutting propagation in cycles does not change this conclusion in any decisive way.

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Table A1. – Correlation matrix, model U, Uniform clonal site-site correlations. The same letter indicates that the correlations were constrained to be equal in the model.

	F1011	F1012	F1013	F1106	F1107	F1185	F1186	F1243	F1244
F1011		A	A	A	A	A	A	A	A
F1012			A	A	A	A	A	A	A
F1013				A	A	A	A	A	A
F1106					A	A	A	A	A
F1107						A	A	A	A
F1185							A	A	A
F1186								A	A
F1243									A
F1244									

Table A2. – Correlation matrix, model X, clonal site-site correlations constrained to 1.

	F1011	F1012	F1013	F1106	F1107	F1185	F1186	F1243	F1244
F1011		1	1	1	1	1	1	1	1
F1012			1	1	1	1	1	1	1
F1013				1	1	1	1	1	1
F1106					1	1	1	1	1
F1107						1	1	1	1
F1185							1	1	1
F1186								1	1
F1243									1
F1244									

Table A3. – Correlation matrix, model C, clonal site-site correlations structured to be equal among trials within each cycle and equal among trials within each pair of cycles. The same letter indicates that the correlations were constrained to be equal in the model.

	F1011	F1012	F1013	F1106	F1107	F1185	F1186	F1243	F1244
F1011		A	A	B	B	C	C	D	D
F1012			A	B	B	C	C	D	D
F1013				B	B	C	C	D	D
F1106					E	F	F	G	G
F1107						F	F	G	G
F1185							H	I	I
F1186								I	I
F1243									J
F1244									

Table A4. – Correlation matrix, model CB, clonal site-site correlations were structured to be equal among trials within cycles and equal among trials within pairs of cycles with the same difference in cycle number. The same letter indicates that the correlations were constrained to be equal in the model.

	F1011	F1012	F1013	F1106	F1107	F1185	F1186	F1243	F1244
F1011		A	A	B	B	C	C	D	D
F1012			A	B	B	C	C	D	D
F1013				B	B	C	C	D	D
F1106					E	B	B	C	C
F1107						B	B	C	C
F1185							F	B	B
F1186								B	B
F1243									G
F1244									

Table A5. – Correlation matrix, model C1, clonal site-site correlations were structured to be equal among trials within cycles and equal among trials within pairs of cycles with the same difference in cycle number. The same letter indicates that the correlations were constrained to be equal in the model.

	F1011	F1012	F1013	F1106	F1107	F1185	F1186	F1243	F1244
F1011		1	1	A	A	B	B	C	C
F1012			1	A	A	B	B	C	C
F1013				A	A	B	B	C	C
F1106					1	D	D	E	E
F1107						D	D	E	E
F1185							1	F	F
F1186								F	F
F1243									1
F1244									

Provenance Productivity of High and Low Elevation *Pinus tecunumanii* in Zimbabwe

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Abstract

The productivity potential of provenances and families of *Pinus tecunumanii* were determined across a range of environments in four orthogonal field trials in Zimbabwe. Provenances of *P. tecunumanii* from altitudes above 1500 m (High Elevation) in natural stands in Mexico and Central America were significantly superior ($P < 0.05$) to provenances from altitudes below 1500 m (Low Elevation) when planted in Zimbabwe in eight-year mean individual tree volume (1729.2 versus 1588.6 dm³) at 1760 m a.s.l.; were not significantly different (1163.1 versus 1143.9 dm³) at 1450 m a.s.l.; but the latter was significantly superior (1756.4 versus 1468.6 dm³) at 1050 m a.s.l., and (720.7 versus 531.5 dm³) at 780 m a.s.l. The most productive provenances were Juquila (26.1 m³ha⁻¹yr⁻¹) at 1760 m, Yucul (17.3 m³ha⁻¹yr⁻¹) at 1450 m, San Francisco (24.9 m³ha⁻¹yr⁻¹) at 1050 m and Villa Santa (11.1 m³ha⁻¹yr⁻¹) at 780 m a.s.l. Improved *P. patula* was

significantly superior to *P. tecunumanii* at 1760 m a.s.l. but the differences were nonsignificant at 1450 m a.s.l. In the warm lower altitude sites, *P. tecunumanii* was not significantly different from improved *P. oocarpa*, the commonly planted species, although some provenances of *P. tecunumanii* were significantly superior by as much as 31%. The top 10 ranked families of the high elevation *P. tecunumanii* had an eight-year volume advantage of 1% and 23% over *P. patula* at Stapleford and Cashel, and 40% and 34% over *P. oocarpa* at Gungunya and Maswera respectively. Genotype-environment interaction was significant by elevation group, provenance and family level. The interaction at the family level was however largely contributed by families from the high elevation *P. tecunumanii*. Opportunities exist for immediate deployment of seed of selected provenances of *P. tecunumanii* in medium and low altitude areas to improve plantation productivity. There is however, no immediate yield advantage of using *P. tecunumanii* seed in high potential environments currently planted to *P. patula*. Breeding and selection could also bring about the planting of *P. tecunumanii* in the higher altitudes in the near future.

Key words: Low and High Elevation *P. tecunumanii*, provenance, productivity.

Introduction

The Tecun Umán pine, *Pinus tecunumanii* Eguluz & J. P. Perry is a closed-cone pine that occurs from southern Mexico to central Nicaragua in a series of disjunct populations (STYLES and McCARTER, 1988; DVORAK *et al.*,

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